

Dinosaur demise in light of their alleged perennial polar residency

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Abstract The end-Cretaceous biological crisis is represented by the demise of the non-avian dinosaurs. However, most crucial biologically was the elimination of the photosynthesizing marine phyto- and zooplankton forming the base of the marine food chain. Their abrupt demise attests to sunlight screening darkening the atmosphere for a few years. Alvarez et al. (Science 208:1095–1108, 1980. doi:10.1126/science.208.44) noticed in deep marine end-Cretaceous sediments an anomalous rise in the chemical element iridium (Ir), which is rare on planet Earth and thus suggests an extraterrestrial origin through an impact of a large asteroid. This impact would have ejected enormous quantities of particles and aerosols, shading the solar illumination as attested to by the elimination of the marine photosynthesizing plankton. Such a dark period must have affected life on land. The apparent cold-blooded non-avian dinosaurs, which were used to living in open terrains to absorb the solar illumination, became inactive during the dark period and were incapable of withstanding predators. This was in contrast to cold-blooded crocodilians, turtles and lizards that could hide in refuge sites on land and in the water. Dinosaur relics discovered in Cretaceous Polar Regions were attributed to perennial residents, surviving the nearly half-year-long dark winter despite their ability to leave. The polar concentrations of disarticulated dinosaur bones were suggested as having resulted from a catastrophic burial of a population by floods. However, this should have fossilized complete skeletons. Alternatively, herds of dinosaurs living in high latitudes might have been

sexually driven to spend the half year of continuously illuminated polar summer for mating rather than for nourishment, in which the lower latitudes provided as well. The aggressive mating competitions would have left victims among the rivals and of young ones incidentally trampled over, all being consumed and their skeletons disarticulated. Accordingly, the alleged ‘polar dinosaurs’ do not challenge the logical conclusion that the non-avian dinosaurs were cold-blooded, as a result of which they became inactive and subjected to predation during the end-Cretaceous dark period.

Keywords Polar dinosaurs · End-Cretaceous biological crisis · Cold-blooded dinosaurs · Annual migration for mating

Introduction

The latest publication of a new Arctic hardrosaurid dinosaur from the lower Maastrichtian Prince Creek Formation of Northern Alaska (USA; Mori et al. 2016) adds to the growing evidence that dinosaurs might have been perennial polar residents during the Cretaceous period. Palaeoclimate analyses indicate a rise in temperature during the Cretaceous in a fluctuating pattern since the lower Aptian reaching higher levels than today with poles free of ice (Hay 2011). The biostratigraphic ages of many of the polar bone sites coincide with deduced palaeotemperature maxima. The main ecological hazard in the polar regions in cases of dinosaurs that were cold-blooded reptiles would have been the half year of darkness during the winter. The end-Cretaceous biological crisis is represented by the demise of the non-avian dinosaurs. However, most crucial biologically was the elimination of the photosynthesizing

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marine phyto- and zooplankton at the base of the marine food chain. Alvarez et al. (1980) noticed in exposed end-Cretaceous deep marine sediments an anomalous rise in the chemical element iridium (Ir), which is rare on planet Earth and thus suggests an extraterrestrial origin through an impact of a large asteroid. Such an impact would have ejected large quantities of particles and aerosols, shading the solar illumination as attested to by the elimination of the marine photosynthesizing microplankton and the collapse of the marine food chain (Alvarez et al. 1980). Such a dark period must have affected life on land and was probably critical in the elimination of the non-avian dinosaurs. Therefore, the physiology of the dinosaurs was intensively analysed by advanced techniques (e.g. bone histology: Chinsamy et al. 2012; Woodward et al. 2011) to clarify their puzzling end-Cretaceous disappearance. However, this research was complicated by the many discoveries of dinosaur relics in Cretaceous Polar Regions, which were attributed to perennial polar residents that must have stayed there throughout the nearly half-year-long polar dark winter.

End-Cretaceous dinosaur demise

The disappearance of the non-avian dinosaurs symbolizes the catastrophic biological crisis ending the Mesozoic Era. This end-Cretaceous major extinction event in Earth's history puzzled scientists of various disciplines. The latest comprehensive evaluation of the possible causes for the extinction of the non-avian dinosaurs by eleven scientists (Brusatte et al. 2015) did not solve the enigma. The intensive professional research was associated with the increase in dinosaur interest especially among the youth. It was inflamed by commercial companies and the media, which built up the image of the dinosaur as energetic, furious, frightening predators reaching gigantic sizes. These exaggerated affinities of highly active predators suggested that they might have been warm-blooded reptiles comparable to their present-day related warm-blooded birds, making their nearly instantaneous global elimination some 66 million years (My) ago puzzling. The anomalous increase in iridium content was further detected in many other countries exactly at the Cretaceous–Palaeogene boundary (K/Pg) separating between different Cretaceous and Tertiary faunal compositions. The Ir anomaly at the K/Pg suggests that the profound end-Cretaceous biological crisis was caused by an impact of a large asteroid. The ejected particles and aerosols would have risen high into the stratosphere and screen the solar radiation, considerably reducing photosynthesis. This would have led to the collapse of the food chain in the marine and terrestrial environments. The resulting food shortage would drastically have increased predation

of the temporary vulnerable organisms that could not hide, whereby many taxonomic groups were thus totally eliminated (Alvarez et al. 1980). This innovative explanation was challenged by studies in favour of terrestrial causes such as intensive volcanism during the Cretaceous–Tertiary transition recorded from the Indian Deccan Province. Accordingly, the emitted volatiles would have led to chemical and physical ecological perturbations, though the associated dust would not decrease much solar radiation (Officer et al. 1987). The asteroid impact theory was later supported by subsurface analyses at the Yucatan Peninsula (Mexico) after discovering a huge impact crater about 180 km in diameter situated on top of upper Cretaceous sediments. Further studies in the region yielded impact melt spherules and shocked quartz grains in the post-impact pelagic sediments and evidence of tsunami mobilized sandstone in areas to the north (Kring 2007). These sedimentary sequences with impact components were suggested to have started to accumulate 300 ky before the Cretaceous–Tertiary boundary (Keller et al. 2007; or 100–150 ky, Keller 2014) and that this impact did not cause any extinctions in foraminifera species (Keller et al. 2009), lending support to the suggested end-Cretaceous devastating ecological effect of the Deccan volcanism (Keller 2014). Volcaniclasts and aerosols of the Deccan eruptions of phase 2 supposedly created a greenhouse warming effect that was isotopically detected on latest Cretaceous (Cretaceous Foraminifera zones = CF2 Zone and lower CF1 Zone) calcareous skeletons of planktonic (surface water) and benthonic (deep water) foraminifera in the Indian province (Keller et al. 2011). This was associated with a profound increase in the abundance of dwarfed foraminifera attesting to the ecological changes as the result of the Deccan eruptions. However, during the upper part of the CF1 Zone about 100 thousand years before the K/Pg the sea water temperature and ratio of dwarfed foraminifera returned to their previous setting (Keller et al. 2011). The latest Cretaceous sea water temperature rise was detected earlier on deep sea cores in the south Atlantic (Li and Keller 1998; Abramovich and Keller 2003). Like in the Indian province, the elevated palaeotemperatures returned to their previous levels some 100 thousand years (upper CF1 Zone) before the K/Pg. The ecological change occurring simultaneously in two remote regions corroborates the suspected global greenhouse warming effect of the Deccan volcanism. Nevertheless, the analytical data contradict the assumption that the Deccan volcanism resulted in the end-Cretaceous 'mass extinction'. The Ir anomaly detected worldwide at the Cretaceous–Tertiary biostratigraphic boundary (Schulte et al. 2010) was observed within marine sediments in northeast India (Meghalaya) about 800–1000 km east of the Deccan volcanic province precisely at the K/Pg and nowhere else (Keller et al. 2011), attesting to its non-volcanic origin.

Thus, the biological and chemical isotopic data from the Indian province lend unequivocal support to the end-Cretaceous asteroid impact theory (Alvarez et al. 1980) while questioning the exclusive devastating effect of the Deccan volcanism on the global ecosystems.

The nature of the end-Cretaceous biological crisis

Alvarez et al. (1980) suggested that the ejected aerosol and particles of a large asteroid impact may have screened the solar illumination and ceased photosynthesis as evidenced by the elimination of the marine phyto- and zooplankton. This led to the collapse of the marine food chain and affected the terrestrial environments as well. However, sunlight screening as the result of a single huge asteroid impact, or intensive volcanic eruption could clear up within weeks or a year depending on various factors (Kring 2007). This limited sun-screening effect raises doubts whether the asteroid impact exclusively caused the end-Cretaceous biological crisis, although it probably played a major role in the process. The end-Cretaceous elimination of marine photosynthesizing microorganisms indicates that planet Earth was shaded from solar radiation for a period that caused the total demise of the late Cretaceous dominating planktonic foraminifera and coccolithophorids (Kring 2007). The demise of the marine photosynthesizing phyto- and zooplankton within a few months eliminated the base of the marine food chain. However, to shake up the terrestrial food chain requires a dark period of a few years that does not only affect the vegetation, but would drastically disturb animal life including prey–predator relationships. Sunlight screening blurs seasonality, which controls mating, breeding, plant blooming and flower pollination. A couple of years without photosynthetic activity on land would kill the annual plants and cause even non-deciduous trees to shed their leaves, gradually reducing the food of small and large herbivores. These would gradually weaken and starve to death forming easy prey to carnivores and omnivores. About 2–3 years of lack of seasonality might be sufficient to cause the worldwide selective elimination of certain organisms that could not cope with the sudden ecological crisis. Those that succeeded hiding in refuge sites and adapted to the new ecosystems and the available food survived (Lewy 2015). Accordingly, the long puzzling, selective extinction–survival pattern was controlled by the elimination of the temporary vulnerable taxa and ‘the preservation of favoured races in the struggle for life’ (Darwin 1859). This geologically instantaneous ecological catastrophe caused by the incidental asteroid impact was superimposed on longer prevailing ecological instability during the latest Cretaceous (Maastrichtian) as reflected by the global fluctuations of the sea water temperature and foraminifera

dwarfing (Abramovich and Keller 2003; Keller et al. 2011). The associated rise in marine predatory pressure is attested by ammonites strengthening their conch (Machalski 2005), by the change in the breeding strategy of burrowing crustaceans (Lewy et al. 2011), and the gradual elimination of vulnerable taxa (Lewy 2015).

The combined devastating effect of the asteroid impact and the Deccan volcanism

The 2- to 3-year minimal duration of the end-Cretaceous dark period (Lewy 2015) was evaluated based on the combined sunlight screening effect of the incidental asteroid impact during the long-operating Deccan volcanism, which straddled the K/Pg. The impact shock waves might have intensified the ongoing volcanic eruptions and the ejection of hot gases and volcaniclasts, whose rising currents considerably slowed the settling down of the impact ejecta, especially the fine fraction containing iridium. The combined ejected components would have shaded the solar radiation for at least 2–3 years. During this period, the particles within the cloud zone (troposphere) might have enhanced rain fall, which together with the greenhouse warming effect should have resulted in the decomposition of the shed leaves and other dead plant material. This disruption of the terrestrial plant ecosystem was detected in New Zealand in the form of a 4-mm-thick fungal layer within 1 cm of continental coal and mud sequence just on top of the K/Pg identified by palynomorphs and a rise in iridium content along a centimetre. This fungal spike at the base of the iridium enriched interval attests to the ‘wholesale dieback of photosynthetic vegetation’ during a short period, being followed by the reappearance of ferns within the upper range of the Ir anomaly (Vajda and McLoughlin 2004). Thus, the duration of photosynthesis decline due to atmospheric darkening was shorter than the settling of the Ir-containing particles throughout the atmosphere and their lateral mobilization. A similar fungal spike was detected at the K/Pg in the Western Interior (USA) sediments attesting to the wide extent of this botanical and biological crisis (Tschudy et al. 1984) as the result of the global screening of the solar radiation for 2–3 years.

Dinosaur mode of life and distribution

Non-avian dinosaur nests were found at the sea shore (Sanz et al. 1995), on tidal flats (López-Martínez et al. 2000) and on sandy Aeolian dune fields (Fastovsky et al. 2011), where the parents could detect potential predators from far distance. Sunrise over these flat terrains provided these reptiles the vital warmth in case they were cold-blooded. Dinosaur

track sites containing thousands of exceptionally preserved footprints of hadrosaurids of different growth stages were discovered in central Alaska in Upper Cretaceous sediments of alluvial fans, braided and meandering streams and lacustrine environments, corroborating that these herbivorous dinosaurs lived in multigenerational herds (Fiorillo and Gangloff 2001), which migrated over open flatland up to the polar regions at that time in present-day northern Alaska (Fiorillo et al. 2014). Carnivorous dinosaurs may have formed small groups, whereas the large ones might have hunted individually like extant mammals.

The physiology of these non-avian dinosaurs puzzled vertebrate palaeontologists because of the gigantic dimensions reached by both herbivores and carnivores, and the large teeth and claws of many carnivores suggesting intensive predatory activity, which should have pointed to high metabolic rates. Analyses of dinosaur mode of life, anatomy, bone histology and isotopic data yielded controversial results (Endotherms: Bakker 1972; Eagle et al. 2011; Mesotherms: Grady et al. 2014). The total elimination of the non-avian dinosaurs during the end-Cretaceous short dark period hinted at their possible cold-blooded physiology (Lewy 2015). This logical deduction was inconclusive in the light of dinosaur relics discovered in the Cretaceous Arctic and Antarctic regions, which were related to polar perennial residents that survived the nearly six months of the dark polar winter (Chinsamy et al. 2012; Rich et al. 1988). The possible adaptation of dinosaurs to polar climates was corroborated by the increase in Cretaceous sites with dinosaur bones that were in the polar region. These comprise the Barremian sediments of northern Norway (Svalbard; Hurum et al. 2006), the early Aptian Strzelecki Group and early Albian Otway Group in south eastern Australia (Rich et al. 1988, 2002), the late Campanian of New Zealand (Molnar and Wiffen 1994), early Maastrichtian of northern Alaska (North America; Brouwers et al. 1987; Fiorillo et al. 2014) and late Maastrichtian of north eastern Russia (Godefroit et al. 2009). Analyses of Cretaceous climate yielded a fluctuating rise in the temperature in sea water and on land since the late Aptian, reaching higher levels than today with poles free of ice (Hay 2011). Accordingly, only the Barremian dinosaurs of Norway and the early Aptian dinosaurs in south eastern Australia might have been subjected to winter freezing temperatures, which were corroborated for Australia on the basis of sedimentological criteria and by $\delta^{18}\text{O}$ analyses on calcite concretions in sandstones that might have formed predominately during early diagenesis (Rich et al. 1988, 2002). Cretaceous terrestrial temperature maxima were observed in the Cenomanian–Turonian transition, Turonian–Coniacian, Campanian and late Maastrichtian (Hay 2011, fig. 2A). The pronounced temperature rise in the oceans during the latest Campanian–earliest Maastrichtian (Hay 2011, fig. 2B) might have

influenced the terrestrial regions as hinted by the early Maastrichtian Prince Creek Formation bone bed of Alaska (Mori et al. 2016). Most of the polar reptile assemblages accumulated during these temperature highs. The assumption that the dinosaurs stayed in the polar regions during the dark winter is challenged by their mobility, whereby they could have migrated to lower latitudes before the winter (Hotton 1980). All the sites of Arctic and Antarctic dinosaur relics could be reached by foot from lower latitudes. Only the late Campanian ‘polar dinosaurs’ of New Zealand raise some doubt. Present-day New Zealand was tectonically detached from Antarctica since the late Santonian–early Campanian (before 85–82 My). It maintained part of the terrestrial organisms inhabiting the high latitudes adapted to dim light under the Campanian temperate climate (Hay 2011, fig. 2A). The palaeolatitude of the late Campanian relics in New Zealand reconstructed to at least 66°S (Molnar and Wiffen 1994) was later emended to below the Palaeo-Antarctic Circle (ca 59°S; Bell and Snively 2008, fig. 4) outside the annually darkened winter period. The reconstructed large island of Zealandia (Bell and Snively 2008, fig. 4) suggests that dinosaurs could have wandered to lower latitudes outside the polar circle, although they were referred to as polar perennial residents (Molnar and Wiffen 1994).

Dinosaur relics suggested characterizing indigenous polar residents

The discovery of fossil terrestrial vertebrates anywhere is incidentally and thus a rare and exciting event for palaeontologists and the public. Such surprising findings usually consist of isolated bones, teeth, claws and rarely of a nearly complete skeleton. The rare discovery of a few articulated skeletons in a limited area may attest to a catastrophic killing event such as drowning by flood or sinking into unstable ground. The first discovery of dinosaur bones in Cretaceous Polar Regions of south eastern Australia and North America were exciting because of the unusual ecosystem which they might have inhabited. Further survey extended these bone sites into extensive bone beds, which yielded thousands of bones comprising hundreds of skulls of young and adult dinosaurs (Australia: Benson et al. 2012; North America: Mori et al. 2016). New genera and species were distinguished among the rather well-preserved skulls, being presented as an indigenous dinosaur community adapted to the polar cold and dark winter. The rise of the terrestrial temperatures since the lower Albian to above present-day levels (Hay 2011) left the long dark winter as the main ecological hazard to dinosaur perennial polar residents.

An Australian hypsilophodontid (*Leaellynasaura*) brain endocast has prominent optic lobes. The large brain and

large eyes suggest that it may have been adapted ‘for coping with the long periods of darkness or dusk associated with polar habitats’ (Rich et al. 1988, p. 1405), characterizing an indigenous species anatomically adapted to the dark polar winter. However, bone microstructure analyses of ‘polar’ Australian ornithomimid and theropod hypsilophodontid dinosaurs revealed that their growth trajectories were similar to those of their lower-latitude relatives, without any osteohistological evidence supporting seasonal hibernation during the polar winter, whereas they might have exploited the polar regions, during which some died there (Woodward et al. 2011). ‘Most tetrapod fossils have been recovered from channel lag deposits, fluviatile sandstone beds 5–10 m wide and 0–30 cm thick containing abundant intraclasts’ (Rich et al. 1988, p. 1403). This means that disarticulated, isolated skeletal elements were transported by the floods and deposited with minor damage in stream beds, overlooking the required preceding dinosaur killing, disintegration of their skin and flesh, and the dismembering of the skeletons into individual bones before their minor transportation by water streams and burial under fluvial sediments.

The early Maastrichtian (before 69 My) Prince Creek Formation of northern Alaska yielded disarticulated parts of a skull of a diminutive, adult, new kind of tyrannosaur (*Nanuqsaurus hoglundi*), which probably reflects its adaptation to a northern high-latitude harsh climate by rapidly reaching maturity (Fiorillo and Tykoski 2014). In this formation parts were found of the skull and horn of a new centrosaurine ceratopsid *Pachyrhinosaurus* distinguishing the ‘polar’ dinosaurs from those of the lower latitudes (Fiorillo and Tykoski 2012). A skull of a new hadrosaurid dinosaur discovered in the formation was recently attributed to the new genus and species *Ugrunaaluk kuukpikensis*, increasing the number of species of Palaeo-Arctic distinct and endemic polar dinosaurs (Mori et al. 2016). Another new genus distinguished in the formation is *Alaskacephale* based on a squamosal (skull part). The histological affinities of the ‘polar’ bones of the Prince Creek Formation were compared to the same genus *Edmontosaurus* discovered in lower latitudes of North America, which were at that time under a temperate climate (Chinsamy et al. 2012). The polar bones exhibit periodical textural shifts in growth layers between reticular fibrolamellar bone (R) suggesting fast deposition, to slower forming circumferential fibrolamellar bone (C), which suggested ‘periodically increased energy demands potentially associated with migration’ (Chinsamy et al. 2012, p. 612), although the authors present alternative interpretations. These alternating textures were less consistent in bone of *Edmontosaurus* from the temperate regions. Bone microstructures from both regions lack lines of arrested growth. Chinsamy et al. (2012, p. 613) concluded that ‘bone histology alone is inconclusive

regarding overwintering or migration in polar *Edmontosaurus*’ in contrast to the title of the article which firmly states that ‘hadrosaurs were perennial polar residents’.

The fossils of the Prince Creek Formation derive from a single layer known as the Liscomb Bone Bed (LBB), described and discussed in detail by Mori et al. (2016). More than 6000 hadrosaurid bones have been collected comprising about 400 cranial and post-cranial elements dominated by those of juveniles, individual adult hadrosaurid elements, and shed thescelosaurid, tyrannosaurid and troodontid teeth. The hadrosaurid remains are almost entirely disarticulated, show little evidence of weathering, predation, or trampling, and typically uncrushed and unpermineralized reflecting a mass mortality event associated with overbank flood deposits that might have suddenly buried hundreds of the dinosaur population (Fiorillo et al. 2010; Gangloff and Fiorillo 2010). However, this taphonomic reconstruction does not explain how the incidentally buried creatures turned into concentrations of individual bones. The buried corpses must have been exhumed and their rather tough skin and flesh had to be disintegrated. The exposed complete skeletons had to be disarticulated in situ or during minor transportation with little damage and dispersal, being covered again under fluvial sediments. Accordingly, the suggested taphonomic process for the origin of the polar bone beds was misinterpreted and thus erroneous.

Crocodile-like, freshwater fish eating, endotherm champsosaur reptiles were discovered in Turonian–Coniacian sediments in the Canadian Arctic archipelago, which in Late Cretaceous times was in the polar zone (Huber 1998; Tarduno et al. 1998) during temperature rise on land (Hay 2011; Tarduno et al. 1998). Their survival during the long dark winter period may be comparable to extant adult crocodylians that can slow their metabolic rate and survive without feeding for several months, even over a year if no other active predator would have killed them.

Dinosaurs annually migrated to the polar regions for mating

The anatomical and physiological features enabling certain dinosaur taxa to cope with dim light and harsh ecological conditions could have evolved among those living in high latitudes below the Polar Circle, where many winter days were cloudy and rainy for several months as suggested by the alternating two bone microstructures in *Edmontosaurus* of the temperate climate (Chinsamy et al. 2012). These populations wandered in herds within their wide ranges (Fiorillo et al. 2014), whereby they might have crossed into the polar zone early in their mating season beginning in spring. There they might have witnessed the continuous

solar illumination under a temperate climate and extensive blooming, providing an ideal setting for a prolific mating period. This suggested sex-driven annual migration is comparable to the migration of extant humpback whales some 2500 km from their Antarctic summer feeding ground to the subtropical coastal waters of western and eastern Australia and Fiji for their winter mating season (www.discoverherveybay.com). Once high-latitude dinosaur populations discovered the long-illuminated polar summer, they probably migrated to this region annually in early spring, driven by a rising sexual instinct. There they might have performed sexually triggered aggressive fights for mating as observed in extant mammals and some reptiles (Clutton-Brock and Huchard 2013). These fierce competitions must have resulted in serious or fatal injuries among the rivals and incidental trampling over young ones. The severely injured or killed dinosaurs were consumed by carnivores, whereby the disarticulated bones accumulated from season to season. Latest Cretaceous (68–66 My) Arctic diverse dinosaur relics from north eastern Russia comprise eggshell fragments suggesting that some polar dinosaurs ‘could have reproduced in polar regions and were probably year-round residents of high latitudes’ and actually stayed there throughout the year being adapted to survive prolonged darkness (Godefroit et al. 2009, p. 495). However, these eggshell fragments might have originated from eggs laid by early mated females at the beginning of the polar summer. Some may have hatched late in summer, whereby the young would have been unable to walk to the lower latitudes and thus the broken eggshells mixed with the other dinosaur bones, giving a false impression of dead, perennial polar residents (Godefroit et al. 2009).

The logical assumption that the mobile dinosaurs would avoid spending the half-year-long dark polar winter and migrate to lower latitudes despite the long distance of crossing about 30° (Hotton 1980) was further elaborated on in relation to additional discoveries of ‘polar dinosaurs’, without ruling out, however, that some may have wintered in the polar region (Bell and Snively 2008). The present analysis has shown that the taphonomic reconstruction of the polar bone beds as victims of a sudden cover by flood-transported fluvial sediments would bury these creatures and fossilize them into complete skeletons and not as individual bones. The polar concentrations of articulated bones suggest gradual accumulation of disarticulated bones of consumed dead creatures, probably of temporary visitors. The anatomical adaptation of some taxa to dim light could have evolved among populations living below the Polar Circle where the winters would have been cloudy and rainy. Early in spring they might have migrated to spend the nearly half-year-long illuminated summer for mating in the same site, well known to the elder generations. The fierce mating competitions (Clutton-Brock and Huchard

2013) fatally injured some of the rivals and also uninvolved young ones which were incidentally trampled over, all being consumed while disarticulating their bones, which accumulated in the same site from year to year. This sexually triggered annual migration is in contrast to recorded seasonal migration of mammals for food and water, which the summer in high latitudes provided to the dinosaurs rendering low dinosaur migration to the polar regions for these reasons.

Non-avian dinosaurs versus birds like ammonites versus octopods

Birds (avian dinosaurs) probably originated during the early Jurassic living and diversifying beside the non-avian dinosaurs and the pterosaurs for about 100 million years. Their innovative warm-blooded physiology turned highly advantageous during the darkening of the atmosphere for 2–3 years as the result of the incidental impact of the large asteroid, whereas the cold-blooded non-avian dinosaurs became inactive and subjected to predation up to their total elimination (Lewy 2015). A similar scenario was reconstructed for two cephalopod groups. Octopods were suggested to be ammonoids, which lost their external conch in early Jurassic times. Both groups proliferated for about 100 million years towards the KTB, when the external conch limited the manoeuvrability of the ammonites in coping with the high predatory pressure compared to the conch-less octopods (Lewy 1996). Both genetically allied groups lived side by side and diversified in the same environments for millions of years. This harmony was shaken up by an incidental severe ecological perturbation under which the veteran group could not cope with and was eliminated, while the innovative properties of the allied group turned advantageous, enabling conch-less ammonoids and warm-blooded avian dinosaurs to survive into the Cenozoic.

Summary and conclusions

Cretaceous Arctic and Antarctic dinosaur bones, eggshells and numerous footprints were interpreted to indicate that dinosaurs might have been perennial polar residents, surviving the half-year winter total darkness. These discoveries challenged the assumption that their demise resulted from being cold-blooded, inactive and exposed to predators during the end-Cretaceous dark period (Alvarez et al. 1980; Lewy 2015). Therefore, the question whether dinosaurs were perennial polar residents is of major significance. The dinosaur bones in south eastern Australia and North America are concentrated within alluvial sediments, interpreted as resulting from mass mortality by floods, and

burial under fluvial sediments. This taphonomic reconstruction could not have resulted in the concentrations of thousands of rather well preserved, disarticulated bones comprising hundreds of skulls. Catastrophic floods of fluvial sediment would have buried complete creatures, which would have been required to be exhumed, the skin and flesh to have deteriorated, and the skeletons disarticulated into isolated bones prior to their minor transport and final burial. The vast material collected yielded a few new taxa, some with anatomical features reflecting adaptation to darkness and harsh weather, which were presented as evidence for an indigenous polar population. However, the mobile dinosaur would not have stayed in the polar regions while the environmental conditions gradually deteriorated, and the anatomical features might reflect adaptation to dim light during the cloudy, rainy winter below the Polar Circle. Accordingly, the dinosaur relics in Cretaceous Arctic and Antarctic regions might have accumulated during a sexually driven annual migration from the moderate and high latitudes in order to spend the long-illuminated polar summer for mating. During the fierce mating competitions (Clutton-Brock and Huchard 2013), some rivals were most likely killed and young ones incidentally trampled over and killed. All these victims were consumed and their skeletons disarticulated, accumulating from year to year in the same site into a bone bed. The definition of dinosaurs as polar residents surviving the winter dark period is therefore misleading and should be abandoned. Hence, the cold-blooded physiology of the dinosaurs is herein substantiated, which is the reason why they did not survive the end-Cretaceous dark period (Alvarez et al. 1980; Lewy 2015).

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