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DISCUSSION

Polar and K/Pg nonavian dinosaurs were low-metabolic rate reptiles vulnerable to cold-induced extinction, rather than more survivable tachyenergetic bird relatives: comment on an obsolete hypothesis

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Abstract The great majority of researchers concur that the presence of dinosaurs near the poles of their time are part of a large body of evidence that all Cretaceous dinosaurs had elevated metabolic rates more like their avian sub-branch and mammals than low-energy reptiles. Yet a few still propose that nonavian dinosaurs were bradyenergetic ectothermic reptiles, and migrated away from the polar winters. The latter is not biologically possible because land animals cannot and never undertake very long seasonal migrations because the cost of ground locomotion is too high even for long limbed, tachyenergetic mammals to do so, much less low-energy reptiles. Nor was it geographically possible because marine barriers barred some polar dinosaurs from moving towards the winter sun. The presence of external insulation on some dinosaurs both strongly supports their being tachyenergetic endotherms and helps explain their ability to survive polar winters that included extended dark, chilling rains, sharp frosts, and blizzards so antagonistic to reptiles that the latter are absent from some locations that preserve dinosaurs including birds and mammals. The hypothesis that nonavian dinosaurs failed to survive the K/Pg crisis because they had reptilian energetics is illogical not only because they did not have such metabolisms, but because many low-energy reptiles did survive the crisis. The global super chill that apparently plagued K/Pg dinosaurs should have seriously impacted dinosaurs at all latitudes, but does not entirely readily explain their loss because some avian dinosaurs and other land tetrapods did survive. High- as well as low-latitude dinosaurs add to the growing evidence that high-energy endothermy has been a common adaptation in a wide variety of vertebrates and flying insects since the late Paleozoic.

Keywords Dinosaurs · Alaskan · Australian · Polar · Winters · Energetics · Physiology · Migration · Cretaceous

Introduction

In an attempt to ease the vexing but probably not critical problem of why nonavian dinosaurs failed to get through the severe cold snap of the K/Pg event that their avian winged relatives survived, Lewy (2015, 2016) works to revive the long ago widely held, but never rigorously examined, presumption that the group was warm climate "reptiles" with no close-living relatives other than crocodilians that possessed correspondingly similarly low metabolic rates and, therefore, depended primarily on environmental heat to boost body temperatures. More in depth analyses began to lead to the hypothesis that dinosaurs were instead more energetic in the manner of their avian descendants as well as mammals in the late 1960s going into the 1970s (Bakker 1968, 1971, 1972, 1975; Ostrom 1970; Desmond 1976; Ricqles 1976). The result of the scientific revolution is a broad strong current majority opinion that most or more probably all nonavian latest Cretaceous dinosaurs, including those dwelling near the poles, acquired most body heat by generating it internally via resting and maximal aerobic metabolic rates significantly above observed reptilian maximums and, therefore, at least in the lower avian–mammalian ranges (such as Paul 1988, 1994, 2002, 2012, 2013; Barrick et al. 1997; Erickson and Brochu 1999; Carrier and Farmer 2000; Fricke and Rogers 2000; Seymour and Lillywhite 2000a, b; Seymour et al. 2012; Erickson et al.

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2001, 2009a, b; Padian et al. 2001; Rich and Vickers-Rich 2001; Schweitzer and Marshall 2001; Fiorillo 2004; Horner and Padian 2004; Pontzer et al. 2009; Amiot et al. 2006, 2011; Organ et al. 2007; Perry et al. 2009; Eagle et al. 2011; Sander et al. 2011; Erickson and Druckenmiller 2011; Kohler et al. 2012; Reid 2012; Seymour 2013, 2016; Grady et al. 2014; Bakker et al. 2016; Huttenlocker and Farmer 2017). Modern dissenters (McNab 2009; Ruben et al. 2012; Clarke 2013; Lewy 2015, 2016) are comparatively few. The impression given by Lewy (2016) that the thermoenergetics of dinosaurs remains a highly contentious debate is correspondingly spurious, as is his implication that entertainment media portrayals of dinosaurs as highly energetic have had anything to do with the development of the current state of the science (it is the film industry that has followed the majority scientific lead as seen in the acknowledgments in Crichton 1990). More critically, the data and arguments Lewy uses are insufficient and selective to the degree that they produced errant results.

Most of the evidentiary and analytical reasons for the modern paradigm are detailed by Paul (2002, 2012 who defines the terminology used herein), and include: avian–mammalian rather than reptilian skeletal form including erect limb posture, frequent obligatory bipedalism and large attachments for aerobic leg muscles rather than the smaller anaerobic muscles of reptiles; normally long-stride trackways indicating high aerobically sustained cruising walking speeds rather than the short-stride trackways and low cruising speeds characteristic of bradyaerobic reptiles; avian style, high oxygen intake air-sac respiration in theropods and sauropods; a high differential between the height of the brain and the heart in many medium-sized and gigantic dinosaurs that is observed only in birds and land mammals that have the high metabolic rates needed to generate high blood pressures up to 0.5 m or more against the gravity well; the dinosaurs' common tendency to exceed one tonne, a mass often achieved by tachyenergetic land mammals but by no clearly bradyenergetic nonaquatic reptile; the presence of external fibrous insulation in a growing array of small and moderately large dinosaurs similar to that of endothermic birds and mammals that is never present on ectothermic dinosaurs; preavian brooding of partially exposed eggs by some small theropods that would have required high internal heat production; rapid growth in many dinosaurs that is only achieved by birds and mammals among land animals; complex dental batteries in some herbivorous dinosaurs indicating rapid consumption of large amounts of calories; evidence for reduced genome and blood cell size; bone isotopes; the presence of dinosaurs in high-latitude habitats that lacked both adequate solar radiation for much or all the year and

populations of bradyenergetic reptiles. It is the last set of evidence that shall be considered herein.

The severity of dinosaur dominated polar habitat climates, to flee or not to flee

Lewy (2016) tries to give the impression that bradyenergetic reptiles were able to dwell near the north pole during the Late Cretaceous by citing the example of crocodilian like arctic champsosaurs in the early Late Cretaceous. What Lewy (2016) does not note is the crucial data that the late Late Cretaceous Alaskan Prince Creek Formation that has produced an abundance of dinosaurs as well as some pterosaurs, both of which are known to have been insulated in many cases, plus tachyenergetic feathered birds and furry mammals, has after decades of prospecting failed to produce a single example of a unambiguously bradyenergetic continental tetrapod in the form of an amphibian, turtle, lizard, snake, or crocodilian that are abundant in more southerly contemporary paleohabitats (Brouwers et al. 1987; Paul 1988; Clemens and Nelms 1993; Fiorillo 2004; Spicer and Herman 2010). This remarkable disparity of presence strongly indicates that while tachyenergetic tetrapods could thrive in the arctic paleoclimes, bradyenergetic examples could not when winter conditions were at the more severe Mesozoic levels. The same absence of reptiles appears to be true of the slightly later Siberian high-latitudes sites (Godefroit et al. 2008).

This differential in survivability is not surprising. Lewy (2016) attempts to portray the Prince Creek habitat as fairly benign for bradyenergetic forms, especially in the summer, and denies that the paleohabitat experienced freezing winter conditions. This is very incorrect because a large body of work that Lewy (2016) neglects indicates that the North Slope climate was too severe for the survival of ectotherms at any time of the year (Spicer and Herman 2010; Spicer et al. 2016). A north Pacific cold gyre contributed to deep winter temperatures on the Alaskan North Slope averaging just at or below freezing, which during cold snaps down to −10 °C would have resulted in periodic, sometimes extended, strong frosts, and coastal winter snow storms (Fig. 1), especially in particularly cold winters. Near-freezing winter rain storms would have resulted in strong skin cooling via the chilly and evaporating water, worsened by the accompanying wind chill factor. In the summer, temperatures averaged only ~14 °C, probably rarely exceeded 20 °C, and the sky was almost perpetually cloudy. The last item contradicts the sunnier summer Prince Creek scene portrayed by Lewy (2016), and would have deprived ectothermic land animals of the abundant direct solar radiation they must have to attain and maintain operational body temperatures when ambient air temperatures are too low

Fig. 1 The Alaskan North Slope Prince Creek dwarf *Tyrannosaurus* (*Nanuqsaurus*) *hoglundi*, breaking through thin river ice to get a drink during the snowy polar winter night. The ~500 kg dinosaur is insulated, as is known for another tyrannosauroid of greater mass. The legs are restored as short for a tyrannosauroid of this size as a speculative adaptation for minimizing heat loss in a specialized polar taxon. Modified from Paul (1988)

to infuse and sustain adequate body heat. Cool and windy summer rain storms would have actually depleted the body heat of low-metabolism resident tetrapods. With month-long winter nights featuring near-freezing rains and outright blizzards, and chilly summers sporting sun-clouded skies and cooling rains, it is obvious why fossils of ecto-therms are missing from an arctic formation that includes known tachyenergetic endotherms and other tetrapods that probably were the same.

That even the summer climate was unsuitable for low-energy reptiles of any type in the Prince Creek paleohabitat means that there was no point for bradyenergetic tetrapods to try to migrate to the North Slope during that season, and move south for the winter. In any case, the concept of migrating polar dinosaurs has always been critically defec-tive. The point of migrating polar dinosaurs would be to always be in habitats warm enough to remain active rather than hibernate—doing the latter means there is no need to migrate. The improvement in winter conditions progress-ing towards lower latitudes was very gradual, so the dis-tances that would have needed to have been covered to enjoy a reasonably warm sunny winter were immense. The absence of the remains of gigantic phobosuchid crocodil-ians north of much over paleo 55N confirms the unsuitabil-ity of higher latitudes for big continental bradyenergetic reptiles, and these aquatic reptiles may have hibernated and/or swum further south in the winter (Paul 1988). At paleolatitude 55N, the winter solstice sun is up just 5 h a day and rises no higher than 11° above the horizon, per-haps marginally able to heat low-metabolic rate large land animals enough to remain active. That paleolatitude was at about the Montana–Wyoming border at that time (Fig. 2). Migrating to there from northern Alaska and then return-ing along the coastal plain, including probable modest diversions around terrain obstacles, would have meant a 9000-km round trip every year, matching an epic walk from New York to Los Angeles and back (Paul 1988, 1994; Gan-gloff 2012). No extant land mammal migrates more than ~1600 km straightline per year (Fancy et al. 1989; Paul 1994, 2012, 2013; Fiorillo and Gangloff 2001; Gangloff 2012; Teitelbaum et al. 2015). Even modern polar ungu-lates such as long, gracile limbed caribou and reindeer do not attempt to actually escape the polar winter. Land migra-tions are extremely dangerous, arduous and energy expen-sive expeditions, the cost of locomotion on the ground over long distances being very high. Only swimming and flying organisms can achieve super migrations because the cost of locomotion at a given size is three to a dozen times less than is walking the same distance (Paul 1988, 1994, 2002, 2012; Gangloff 2012). Eggshells indicate the polar dinosaurs were reproducing locally (Spicer et al. 2016), and the apparently long incubation periods of nonavian dinosaur eggs (Erickson et al. 2017), plus the small size of dinosaurs in their first years or two of life, would have hin-dered their achieving super migrations (Fiorillo 2004; Paul 2012, 2013; Gangloff 2012). That the bone microstructure
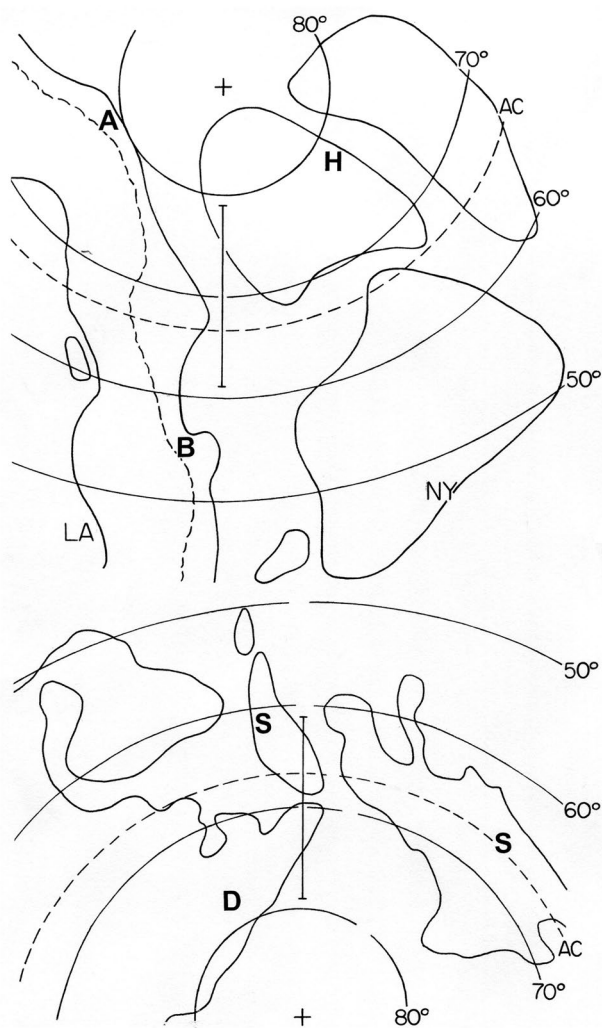
Fig. 2 *Top* North America in the late Late Cretaceous: highlands bordering coastal plain of Laramidia along interior seaway indicated by *irregular dotted line*; *A*, Prince Creek Formation; *B*, farthest north that nonaquatic bradyenergetic ectothermic dinosaurs could probably remain active in the winter, now the Montana-Wyoming border; *H*, hadrosaur from Franklinia; distance from future New York City and Los Angeles indicated. *Bottom* Australia–Antarctica in the late Early Cretaceous on left, and Zealandia in the late Late Cretaceous on right: *D* and *S* dinosaur sites, latter two including sauropods. Positions of the paleospin poles indicated by *crosses*, with paleolatitudes correspondingly plotted. *Top and bottom* AC Ant/Arctic circles; maps to same scale, bars equal 2000 km; paleo seaways included. In part updated from Paul (1988)

of North American polar dinosaurs is distinctive from those found in more temperate latitudes relatives that would be expected to have migrated to the poles by the migration hypothesis is compelling paleozoological evidence that the populations did not migrate and mix (Erickson and Druckenmiller 2011; Chinsamy et al. 2012). This is in line with the evidence that the Prince Creek dinosaurs were taxonomically and adaptatively distinct from those further to the south, including the typically big tyrannosauroids being

dwarfed (Fig. 1), and small troodonts larger, than those found closer to the equator (Fiorillo 2004; Fiorillo and Tykoski 2012, 2014).

Especially poorly suited for long continental migrations are bradyaerobic land animals. The aerobic capacity of reptiles is so low relative to the cost of ground locomotion that they can sustain cruising walking speeds of a mere 1–2 km/h, too low to cover long distances in a reasonable time period, especially while feeding to sustain the long journey (Paul 1994, 2002, 2012; Thompson 1995). Because low-energy budgets result in slow walking speeds and limited activity periods, land reptiles are short-range animals with small home territories, and even large examples move only hundreds of kilometers total in a given year. Migrating 9000 km per annum would have forced a yearly energy budget well above the reptilian maximum, and into at least the lower mammalian range (Paul 1988, 1994). The possibility that dinosaurs could have combined high-energy budgets driven by high levels of exercise, or heat production in response to cold environmental temperatures, with low reptilian metabolic rates is biologically impossible, because the tightly co-linked respirocirculatory system of vertebrates prevents them from having the high maximal/minimal aerobic metabolic levels achievable by trachea respiring insects (see Paul 2002, 2012).

The thousands of kilometers tachyaerobes can indefinitely sustain at walking speeds of 3-8 km/h is typical of dinosaur trackways (Paul 1994, 2002, 2012), but as already noted even tachyaerobic terrestrial tetrapods are not known to migrate more than a few hundred kilometers straightline in a given year. Ergo, even if polar dinosaurs were tachyenergetic then it is almost certain that they did not attempt to flee approaching winter conditions in the fall and return poleward in the spring, but if polar dinosaurs did engage in such unrealistically long migrations they would have had to have been tachyenergetic to do so.

Any dinosaurs that inhabited late Late Cretaceous northernmost Asia (Godefroit et al. 2008), Greenland, and Appalachia would have faced similar migratory limitations. Of special importance to this issue are how the dinosaurs dwelling on arctic Franklinia (Russell 1990; Vavrek et al. 2014) when it was separated from the rest of Appalachia were outright blocked from migrating below the paleo arctic circle by the Hudson Seaway (Fig. 2), a factor that essentially disproves the hypothesis of long-ranging polar dinosaurs that is ignored by Lewy (2015, 2016).

Enjoying less of a coastal marine moderating effect, the southern Australian Wanthaggi Formation winter climate may have been even more severe than that at Prince Creek (Rich et al. 1988; Constantine et al. 1998; Rich and Vickers-Rich 2001). Large amphibians were present, but they were able to hibernate in bottom muds. Otherwise bradyenergetic tetrapods are again absent in

polar sediments that produce dinosaurs including birds. Although not discovered in the most southerly sites, high-latitude dinosaurs included gigantic sauropods in Australia and Zealandia that would have been vulnerable to low core temperatures and superficial frostbite when exposed to persistent local winter conditions if not tachy-energetic enough to generate adequate heat, and lacked a geographic migration route to paleolatitude 55S (Fig. 2; Molnar and Wiffen 1994; Bell and Snively 2008; Paul 2012). Distinctive anatomical adaptations further suggest the southern polar dinosaurs were adapted to the winter dark (Rich and Vickers-Rich 2001).

If dinosaurs migrated the thousands of kilometers postulated by some workers as a means of removing dinosaurs from polar winters, then the dinosaurs were achieving extraordinary annual land voyages not close to being matched by even large, long-legged mammals. This possibility is so low that it must be rated extremely speculative and very probably impractical. If the dinosaurs had to move away from polar dark and cold because they had low-energy, reptilian energetics, then the viability of the hypothesis becomes all the more implausible if not impossible in view of the failure of high-power land mammals to achieve such super journeys. Combined with the reality that some dinosaurs lived on polar islands, and the failure to demonstrate the conspecific status of dinosaurs between the Alaskan North Slope down to the lower 48 states, the hypothesis that dinosaurs regardless of their metabolic performance migrated south or north to get away from the dark season is so defective that it should not be repeated in the scientific literature unless compelling, logical bioenergetic and geographic evidence, and analysis in support of the extremely implausible notion can be produced.

More strong evidence that Cretaceous polar dinosaurs were tachyenergetic endotherms that Lewy (2015, 2016) neglected to pay attention to is provided by the existence of external insulation, probably protofeathers, in examples up to at least one tonne (Xu et al. 2012) that lived at high-temperate latitudes that experienced cold winters (Amiot et al. 2011). Because keratin fibers covered some large temperate latitude dinosaurs, the same very probably was present on examples closer to the poles (Fig. 1). No bradyenergetic ectothermic tetrapods have external insulation because that would only serve to hinder absorption of any solar radiation (as noted by Paul 2002, 2012). Such a critical thermal limitation would be a particular problem for low-metabolic rate animals living in polar regions, in which the little heat from the always low summer sun shone from between the chronic clouds only occasionally. While the presence of insulation on large high-latitude dinosaurs is entirely incompatible with their having reptilian energetics, it is entirely in accord with and strongly supports their having an avian–mammalian physiology.

In addition to insulation small, high-energy polar dinosaurs could utilize burrows to cope with winter climates (Martin 2009). In principle so could low-energy reptiles, but the failure of the latter to inhabit some Mesozoic polar habitats indicates that underground refuges were not adequate for them to do so. Whether it was the cold winters or cloudy cool summers, or the combination, that excluded the bradyenergetic ectotherms is not certain. Interestingly, the critical factor was not likely to have been the ground being too chilly in the cool summers to incubate buried eggs, because most of the polar dinosaurs could not brood their eggs. Indeed, how dinosaurs incubated eggs in polar soils is a perplexing mystery. In geologically active locations, they may have taken advantage of geothermal ground warmth (see Grellet-Tinner and Fiorelli 2010). The long walking range associated with being tachyaerobic would have facilitated the ability of dinosaurs to exploit such rare site-specific heat sources for reproduction and then roam far across the landscape in search of forage the rest of the year compared to being bradyaerobic reptiles. But most polar regions would have lacked geothermally warm soils, including geologically static high-latitude Franklinia. Another possibility is longer egg retention, perhaps up to essentially live birth.

By far, the most logical reason that a diverse array of dinosaur species, at least some of them insulated, were inhabiting polar habitats that were hostile to reptiles, while being tolerable for birds and mammals, is that all the dinosaurs were tachyenergetic in the manner of the latter two groups. This extremely parsimonious hypothesis is in accord with the large body of evidence that dinosaurs were closer to their avian descendants and mammals in their energetics than to their bradyenergetic reptilian ancestors, and that polar dinosaurs had no choice but to put up with the winter due to the inability of land animals to move very long distances on a seasonal basis, and the isolation of some populations at high latitudes by ocean barriers. Dinosaurs were not identical in their energetics, some may have been mesoenergetic like some modest-energy mammals and kiwis, others supraenergetic like most mammals and birds (Paul 2002, 2012).

The big K/Pg chill problem

As for why dinosaurs did not survive the K/Pg cooling event, the latter would have put the thermoregulatory abilities of even tachyenergetic dinosaurs in all climate regimes to a severe test. Chronic temperatures would have been lowered far below normal levels at any given latitude (Brugger et al. 2017). Ergo, conditions in the tropics would have become semi-polar, while polar circumstances would have become even more and extremely, late Cenozoic like,

frigid than they had been during the Mesozoic. Consider that high-latitude zoos are deleting elephants from their collections and sending them to lower latitude institutions because the two extant species, although fully tachyenergetic, homeothermic mammals probably broadly thermoregulatorily similar to nonpolar sauropods, are sub/tropical species unable to fully cope with cold winters (while keeping them indoors over the winter is psychologically adverse). If a K/Pg scale superchill occurred 20 kyr ago, then the proboscideans of the period would have been highly vulnerable to extinction—those inhabiting low and middle latitudes being unable to cope with the sudden onset of polar class weather, while wooly mammoths would have been overstressed by a degree of cold not normal even for polar glacial maximums. Severe post-impact cooling would have killed off a very large portion of a population of tachyenergetic dinosaurs and archaic birds, including their eggs, that managed to survive the other intensely adverse after effects of the impact.

Lewy (2015, 2016) fails to consider that it was not just nonavian dinosaurs that failed to make it into the Cenozoic, but also nonneornithine dinosaurs including nonneornithine birds that presumably were tachyenergetic. Note that shorter incubation periods of bird eggs may have contributed to the clade's survival into the Cenozoic. There is a possible difference in the thermoenergetics of nonneornithine dinosaurs relative to that of neornithine birds that may help explain the survival of the latter dinosaur group (Varricchio and Jackson 2016). Nonneornithine dinosaurs incubated their eggs either wholly or partly via ground heat, making their reproduction critically dependent on climatic conditions. Most neornithines incubate their eggs entirely with body heat. Decoupling egg incubation from ground heat may have allowed enough neornithines to reproduce, perhaps in the tropical zone, to sustain a sufficiently large population to squeak throughout the Mesozoic/Cenozoic cold boundary. However, the role played by these factors are not provably critical, because a number of reptiles that reproduced via slow incubating, ground-deposited eggs made it from the Mesozoic into the Cenozoic, perhaps largely by simply living long enough through the cold snap to enjoy egg survival after the planet warmed up again. Bradyenergetic animals may have an advantage in this respect in that low-energy animals tend to live longer than higher energy forms of similar size, although large tachyenergetic animals often have long lifespans.

The last item brings us to the important point, another that Lewy (2015, 2016) neglects, that nonavian dinosaurs being "cold blooded" would not readily explain their total liquidation in part by a post-impact global winter, simply because a number of bradyenergetic reptile groups did survive this crisis. There simply is no consistent correlation between the energetic status of adult terrestrial tetrapods that did and did not survive the K/Pg boundary; therefore, the paradox is false, and any need to make terminal Mesozoic nonavian dinosaurs energetically reptilian is at the least exaggerated. The extinction of nearly all dinosaurs was presumably due to a variety of intense stress factors of which the cold snap was probably important but not solely definitive.

Conclusion

In his analyses Lewy (2015, 2016) ignores much of the available data on the subject of polar dinosaurs including the absence of reptiles from some sediments that contain dinosaurs including birds as well as mammals, paleoclimatogical evidence of freezing, snowy winters and cool, cloudy summers in those habitats, presence of external insulation on small and large dinosaurs, the many lines of evidence that all terminal Mesozoic dinosaurs had elevated metabolisms, the absence of truly long-range land migrations even among large living mammals and the extreme difficulties of such epic journeys, and the impossibility of some polar dinosaurs including giants to move away from polar winters because of marine barriers. Lewy's (2015, 2016) conclusion that dinosaurs aside from birds are low-power ectotherms is not based on proper evidence and analysis.

Nor should conclusion derived from trying to explain why the bulk of the Dinosauria failed to survive an event that only some birds did live through be used to restore the metabolics of nonavian dinosaurs. The one-time event is too complicated in its possible modes of destruction, and sufficiently uncertain in the scale of the effects, to be definitive. Instead, the broad body of available evidence found across the span of the Mesozoic should be used to restore the energetics of nonavian dinosaurs, and the results used to better understand the probable causes of their extinction. Far from in anyway supporting the hypothesis that terminal Mesozoic dinosaurs were low-energy ectotherms, the increasing realization approaching and going into the current century that nonavian dinosaurs inhabited harsh climate polar regions has added another powerful argument to an overwhelming body of analysis that the very soon-to-be extinct archosaurs were high-energy endotherms. Indeed, the data are growing that rather than elevated aerobic capacity endothermy being a relatively recent, novel adaptation restricted to a few, very advanced crown groups, such tachyenergy may be a very common animal adaptation for increasing sustained activity levels, and in some cases for coping with environments lacking high heat levels that extends back into the late Paleozoic, arising in early synapsids and basal archosaurs and later lost in derived crocodilians, and also appeared in a variety of oceanic

vertebrates aside from marine mammals and birds, as well as large flying insects (Priede 1985; Heinrich 1993; Carrier and Farmer 2000; Brill and Bushnell 2001; Schweitzer and Marshall 2001; Paul 2002, 2012; Graham and Dickson 2004; Seymour et al. 2004; Bernal et al. 2005; Ricqles et al. 2008; Bernard et al. 2010; Farmer and Sander 2010; Wegner et al. 2015; Bakker et al. 2016; Harrell et al. 2016; Seymour 2016; Shelton and Sander 2017). In this case, polar dinosaurs are just another example of animals using self-heating to do things low-energy creatures cannot, in this case to dwell on lands where the sun never rises high in the cloudy sky and the dark winters are bitter cold.

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