Polar dinosaurs on parade: a review of dinosaur migration

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Cretaceous polar dinosaur faunas were taxonomically diverse, which suggests varied strategies for coping with the climatic stress of high latitudes. Some polar dinosaurs, particularly larger taxa such as the duckbill *Edmontosaurus* Lambe, 1917, were biomechanically and energetically capable of migrating over long distances, up to 2600 km. However, current evidence strongly suggests many polar dinosaurs (including sauropods, large and small theropods, and ankylosaurs of New Zealand) overwintered in preference to migration. Certain groups also appear more predisposed to overwintering based on their physical inability (related to biomechanics, natural history, or absolute size) to migrate, such as ankylosaurs and many small taxa, including hypsilophodontids and troodontids. Low-nutrient subsistence is found to be the best overwintering method overall, although the likelihood that other taxa employed alternative means remains plausible. Despite wide distribution of some genera, species-level identification is required to assess the applicability of such distributions to migration distances. Presently, such resolution is not available or contradicts the migration hypothesis.

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MIGRATION in the Dinosauria was first proposed in 1928 by von Huene for the prosauropod *Plateosaurus* von Meyer, 1837, after consideration of its distribution across Europe (von Huene 1928). The idea was later popularized by D.A. Russell, who envisioned great herds of hadrosaurs travelling south from the Arctic with the sun, followed by similarly inclined tyrannosaurs in pursuit of the weak and the old (Russell 1973). The attractiveness of this scenario has sparked considerable discussion over the past 30 years, drawing on many contentious themes such as thermoregulation, energetics, and even extinction. While far from resolved, the topic warrants a summary and review of the key papers and ideas to this date.

Attempts to differentiate migration from other forms of movement have been proble-matic. Baker (1980) even proposed that all forms of movement were synonymous with migration. Under this hypothesis, even plants can be shown to be migratory, as they have the ability, over successive generations, to move great distances, even across the globe. This is more commonly regarded as dispersal. In an attempt to operationally separate migration from localized movements and dispersal, an adaptation of Berger's (2004) definition is used. Here, migration may be defined as a deliberate or instinctive seasonal round-trip movement completed by a single individual between discrete habitats not used at other times of the year, and completed at least once annually. This definition covers the double migrations seen in some modern mammals (Stewart & De Long 1995, Thouless 1995) and makes a clear division between organisms such as plants and butterflies, which 'migrate' over several

generations. It also discounts others, including most invertebrates that disperse stochastically over one or more seasons, ensuring that some individuals exploit adequate resources and increasing their (and their population's) chance of survival (Baker 1980).

Extant terrestrial animals migrate to take advantage of seasonal resources and longer daylight hours or to avoid climatic extremes. Migration distances can range from several thousand to just a few kilometres (Table 1); however, in order to move between climatic regimes (as proposed for polar dinosaurs), animals are required to cover distances at the higher end of the scale. Hotton (1980) suggested that dinosaurs living at the poles would have to pass through 30° of latitude, or 3200 km, in order to avoid the total darkness of a polar winter. In the discussion that follows, only terrestrial vertebrates are considered analogous to dinosaurs. Aquatic and aerial migrations are subject to different pressures than those of terrestrial vertebrates and are,

therefore, much less useful for comparisons when considering dinosaur migration.

Extremes in weather and resources at the poles force animals living at these latitudes either to move on when conditions become deleterious (migration) or to endure environmental privations (overwinter). Naturally, an animal's biology substantially dictates which path to take. As a consequence, and under the definition used here, modern terrestrial reptiles are incapable of long-distance migration. Ectotherms in cold climates are susceptible to tissue damage and, therefore, must brumate (hibernate) or burrow instead (Powell & Russell 1985, Russell & Bauer 2001, Diller & Wallace 2002). Endotherms are less prone to tissue damage; however, they are limited by their ability to find forage in order to maintain homoeothermy. Provided that food is abundant, it is less crucial for an endotherm to migrate, although they will frequently hibernate or burrow also. Migration and overwintering will be dealt with independently, and evidence for and against these hypotheses will be critically examined.

Migration

Long-distance migration in modern ecosystems occurs in only three terrestrial habitats: tundra, desert, and grassland (Baker 1980). Migratory mammals use a variety of adaptations not seen in other groups to facilitate these movements, including endothermy (a prerequisite for long-distance migration; Pough *et al.* 2005) and energy-efficient limb mechanics. In accordance with demands obligated by endothermy and migration, migrating mammals possess several adaptations that minimize the amount of energy required during the step cycle and can also manipulate the performance of those adaptations to optimize various modes of locomotion, e.g. running vs walking (Alexander 1991).
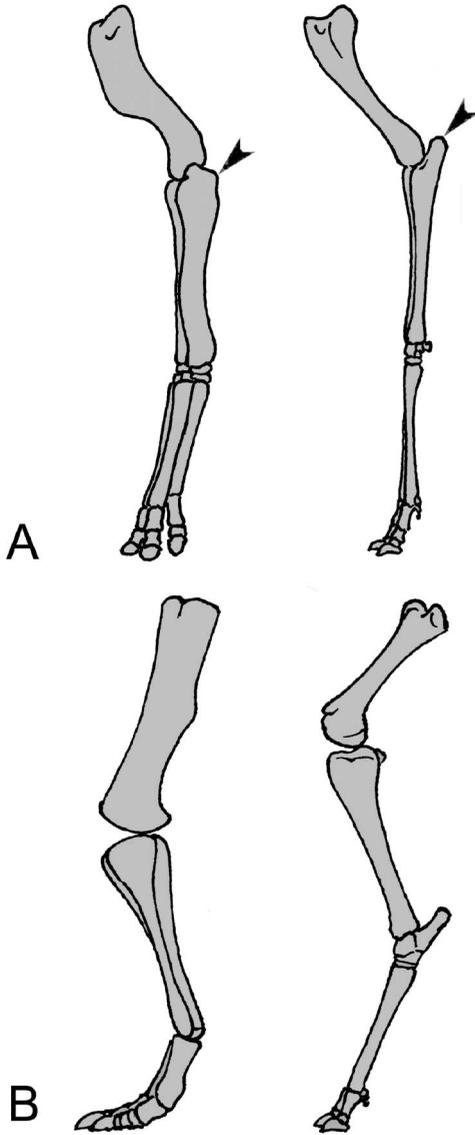
Common name	Roundtrip migration distance (km)	Reference
Caribou	5505	Fancy *et al.* (1989)
Chiru	600	Berger (2004)
Elephant	560	Thouless (1995)
Giraffe	80	Berger (2004)
Kob	700	Berger (2004)
Moose	120	Berger (2004)
Mule deer	285	Berger (2004)
Reindeer	2000	Baker (1980)
Wildebeest	700	Berger (2004)
Wolf	720	Berger (2004)
Saiga	600	Baker (1980)
Bison	500	Baker (1980)
Mongolian gazelle	1100	Ito *et al.* (2005)

Table 1. Selected roundtrip migrational distance of modern terrestrial mammals. Where possible, maximum recorded distances have been included.

For example, the olecranon process on the ulna and a prominent calcaneal heal both provide sites for the attachment of strong elastic ligaments and tendons. These projections have sufficient translational excursion for tendons to stretch and rebound accordingly. The elastic potential of these structures and other limb connective elements (Alexander 1988, Dowling & Dart 2005) allow the limb to straighten upon takeoff, thereby minimizing the total energy requirement (Alexander 1991). Other muscles also provide elastic recoil (e.g. *m. femorococcygeus* in kangaroos, Alexander 1991), although both of these springs are ineffective at walking speed. By using these springs, humans and kangaroos can save as much as 50% of their metabolic demand by moving at higher speeds (Alexander 1984). In tammar wallabies, pennate foot extensor muscles achieve spectacular efficiency, contracting with great force and economy as they extend and enabling elastic energy storage and return by attached tendons (Biewener 1998). Two dinosaur groups that were potential candidates for migration, the frilled ceratopsian dinosaurs like *Pachyrhinosaurus* Sternberg, 1950, and some giant sauropods, have the moderately long olecranons expected in migrators. However, these moment arms most likely assisted with moving and supporting the animals' large head and/or great body weight (Fig. 1).

However, large dinosaurs had locomotor energetic advantages over smaller ones and nearly all terrestrial mammals. Elastic energy savings are potentially greater in larger animals (Pollock & Shadwick 1994a). Body mass increases more quickly than tendon and ligament cross-sectional area, applying greater stress and more effective elasticity to the connective elements. Also, in larger animals, muscle force production is higher relative to tendon cross-section than in smaller ones (Pollock & Shadwick 1994a), whereas tendon stiffness/area does not increase (Pollock & Shadwick 1994b).

Fig. 1. Size-independent anatomy of migration. **A**, Forelimb of a hadrosaur (left) and a caribou (right). Note the enlarged olecranon process (indicated by an arrow) of the caribou compared to the hadrosaur. **B**, Hindlimb of the caribou (right) shows an enlarged calcaneal heal, which is lacking in hadrosaurs (left) and other dinosaurs. These processes are the sites of attachment for highly efficient elastic tendons that reduce the total energy required to take a step, crucial for terrestrial migration. The different morphologies of the caribou and hadrosaur necessitate separate evaluations of elastic mechanisms and locomotor energetics. Images are not to scale but are modelled so that the limbs are of equal length.

Fig. 2. Distribution of the hadrosaur, *Edmontosaurus regalis*. Actual localities are indicated by stars. The shaded area is the inferable range based on locality data.

Therefore, tendons are able to stretch and rebound over larger excursions than in geometrically similar smaller animals, enabling energy savings based on size without additional adaptations. Large animals typically travel faster and require less energy per unit body mass than smaller animals (Alexander 2002), in part by adopting an upright posture that minimizes muscle energy requirements (Biewener 1991). In very large animals, this deviation from geometric similarity probably diminishes advantages of tendon elasticity (Pollock & Shadwick 1994a), by minimizing angular deflection of muscle insertions relative to those in smaller animals. Efficiency trade-offs of elasticity vs posture must be tested experimentally and by modelling approaches, to incorporate them into migratory energetics.

Metabolic scaling (Engelmann *et al.* 2004) conferred energetic advantages to the largest dinosaurs found at high lati- tudes, including a New Zealand sauropod (Molnar & Wiffen 1994), over extant migratory mammals. With low mass-specific resting metabolic rates (Engelmann *et al.* 2004), giant sauropods of the Morrison Formation are envisioned as subsisting on low-quality fodder during drought-induced migration (Turner & Peterson 2004). The distances of travel would have been lower than proposed for polar migrators, how- ever. These must be circumscribed when considering the upper bounds of dinosaur- ian migratory capability.

Alexander (2002) demonstrated that annual land migrations over 5000 km are unlikely to benefit most animals because of the energy demand. Large dinosaurs could take advantage of their size and concomi- tant locomotor efficiency, but other con- siderations are also necessary for evaluating how far they could and did travel, and which dinosaurs were especially suited for migration. The duckbilled *Edmontosaurus* Lambe, 1917 typifies the type of dinosaur hypothesized to have migrated. We, there- fore, use *Edmontosaurus* as a test case for assessing evidence surrounding migratory activity.

While even the longest extant migrators travel at a leisurely pace of 24 km/day (Fancy *et al.* 1989), energy requirements for migration are enormous, making it a rare phenomenon in modern terrestrial verte- brates (Paul 1997). Nevertheless, polar dinosaurs were extraordinarily diverse and include hadrosaurs, ceratopsians, tyranno- saurids, troodontids, hypsilophodontids, ankylosaurs, prosauropods, sauropods (probably titanosaurs), ornithomimids and oviraptorosaurs. At least some were testably capable of long-distance travel. The longest round-trip migration of a terrestrial verte- brate is that of the caribou, *Rangifer tarandus granti* Allen, 1902 at 5055 km (Fancy *et al.* 1989), whereas aquatic mam- mals are capable of over four times that, e.g. the elephant seal at 21 000 km (Stewart &

De Long 1995). *Edmontosaurus* is often regarded as the 'poster-boy' of migrating dinosaurs with perhaps the greatest distribution, spanning North America from Alaska to Mexico, of any single dinosaur genus. Often omitted from such records is that species-level identification is required to validate any connection between distribution and migration. As it is, several respective species of *Edmontosaurus* span that distance, and the often-cited northernmost occurrence in Alaska (Nelms 1989, Clemens & Nelms 1993, Fiorillo & Gangloff 2003) is in doubt (Gangloff pers. comm.). Of the three recognized species of *Edmontosaurus*, *E. regalis* Lambe, 1917 has the greatest distribution spanning some 1300 km between central Alberta, south to Colorado (Fig. 2). Although wide distribution is not direct evidence of migration, if we assume this value to be its maximum migratory distance, then a seasonal round trip of twice that is necessary. In his vigorous argument in support of migration, Hotton (1980) recognized polar animals would have followed the 'sun-line', the latitudinal cutoff point where the sun ceases to rise for part of the year. This sun-line migrates across 30° of latitude representing the maximum limit of photosysnthesis (and presumably, herbivorous dinosaurs), hence his suggestion that 'no animal would have had to cover more than 30° of latitude, about 2000 miles [3200 km]' (Hotton 1980, p. 348); in other words, a seasonal migration of 6400 km. No terrestrial animal achieves such distances today. Unfortunately, many of Hotton's claims were based on the lack of insulative integument in dinosaurs, which he felt must have forced them from the poles to lower latitudes during the winter months; however, feathers and filamentous integuments are well known on a wide variety of small dinosaurs (e.g. Chen *et al*. 1998, Xu *et al*. 1999, 2004), although they are unknown for large taxa, including hadrosaurs, ceratopsians, and tyrannosaurids. If

dinosaurs really did undertake such journeys, then they were truly the greatest migrators in history. Even the caribou with its locomotor efficiencies falls short by nearly 1400 km. For an animal to cover this distance in the 3 months it takes for the sun to pass over 30° of latitude, it would have to travel at ∼6 km/h, assuming it spent 18 h of each day eating and resting. In contrast, for *Edmontosaurus regalis* to achieve a seasonal migration of 2600 km (based on its known distribution) in 6 months, assuming adherence to the sun-line, then it would have had to travel at a leisurely 2.4 km/h, a slow walking pace for the average human. This speed falls within the observed speed range of dinosaurs as deduced from fossil trackways, which indicate dinosaurs typically travelled at speeds between 2 and 10 km/h (Paul 1997). Modern migrators travel at similar speeds of between 2 and 3 km/h (Paul 1997) and can travel up to 24 km in a single day (Fancy *et al*. 1989), although distances of up to 50 km have been recorded (Baker 1980). These values all seem plausible in the case of a migrating dinosaur, and certainly large animals (i.e. dinosaurs) would have had an advantage in stride length and perhaps postural efficiency (although not stride frequency, or necessarily in elastic efficiency) over smaller, extant mammalian counterparts (Alexander 2002; Fig. 3).

One problem we are still faced with, however, are the distances required for polar migration. Are these distances simply too much to ask of a dinosaur? Using a simplified equation, Alexander (1998) demonstrated that roundtrip migrations over 10 000 km are unsustainable by 3-tonne terrestrial animals. At this rate, they would be required to accumulate and store energy (fat) at the enormous rate of 6.41 times standard metabolic rate (birds have the highest rate of energy storage of up to 2.5 times normal metabolic rate). Based on his numbers, a three tonne hadrosaur travelling 6400 km in the winter would still require a
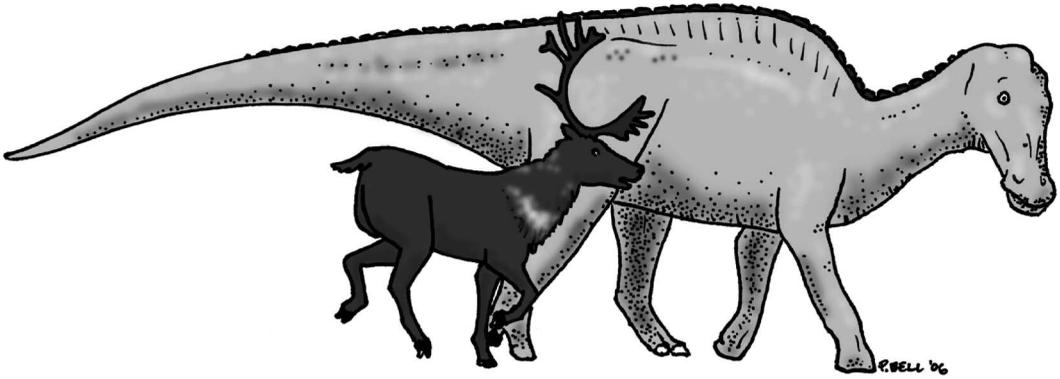
Fig. 3. Size-dependent anatomy of migration. Although dinosaurs lacked the specific efficient mechanisms in the mammalian limb, they may have benefited energetically by simply being larger. A longer stride length and more upright limb posture in a 13-m-long *Edmontosaurus*, in comparison with the caribou, meant it could cover the same distance while potentially using less energy relative to body mass.

ratio of fat deposition vs metabolic rates similar to or exceeding that of a bird. A 2600-km journey (based on the known distribution of *E. regalis*) on the other hand was probably achievable. Several taxa including *Troodon* Leidy, 1856, *Edmontonia* Sternberg, 1928*, Pachyrhinosaurus* and *Albertosaurus* Osborn, 1905-like large theropods, which are found from Alaska to Alberta, demonstrate distributions applicable to Hotton's 30° sun-line. In all cases, except *Troodon*, species-level diagnosis is not available at this time, therefore preventing unequivocal correlation between regions and hence migration.

Although it is tempting and even intuitive to think of theropods following their food supply as herds of hadrosaurs and pachyrhinosaurs migrate (e.g. Currie 1997), modern carnivores are not known to do so. Instead, they prefer to remain in their home-ranges, preying on animals as they pass through and consequently possess large home ranges. Only the spotted hyena (*Crocuta crocuta*), has been observed to follow migratory prey (Trinkel *et al.* 2004).

The distribution of polar dinosaurs is widespread and taxonomically variegated (Rich *et al.* 1988, Nelms 1989, Hammer &

Hickerson 1993, 1994, Molnar & Wiffen 1994, Slaughter *et al.* 1994, Gangloff 1995, Case *et al.* 2000, Fiorillo & Gangloff 2003, Gangloff & Fiorillo 2003, Fiorillo & Parrish 2004, Gangloff *et al.* 2005; see Rich *et al.* 1997 for a review). Considerable taxonomic overlap is observable, at least at the generic level, between polar and more temperate latitudes. A wide distribution, however, is not a symptom of migration and can be equally interpreted as dispersal over time. For example, the saltwater crocodile (*Crocodylus porosus* Schneider 1801) is well known for its remarkable dispersal across open water and is found from Australia to India; however, this does not constitute migration.

Perhaps the best evidence for dinosaur migration are the enormous bonebeds of hadrosaurs and ceratopsians across western North America (e.g. Currie & Dodson 1984, Fiorillo & Gangloff 1999). These bonebeds can number in the hundreds to thousands of individuals. Herds of many thousands of individuals would represent serious energy (food) drains on the environment. A standing herd of such numbers would not be ecologically sustainable if those animals did not move from place to place (Baker 1980).

Modern ungulates such as caribou, wildebeest, and reindeer, which form herds of up to 100 000 individuals, do so only during their seasonal migrations and occasionally form similar-sized bonebeds to those of their dinosaurian counterparts following mass kills, often as a result of flooding (Capaldo & Peters 1995).

Fossil trackways have also been interpreted as evidence of migration. Megatracksites are track-bearing beds consisting of only one or a few layers in which tracks can be traced for hundreds to thousands of square kilometres (Lockley 1997). The Dakota megatracksite, nicknamed the Dinosaur Freeway, itself covers 80 000 km^2 and represents the Early Cretaceous palaeocoastline along the Western Interior Seaway. Iguanodont tracks dominate the ichnofauna. Since trackways are frequently found parallel to the shoreline, it has been suggested that these animals may have used the open coastal plains as a 'freeway' during migration. While the open environment certainly would have lent itself to long-distance travel, there is no evidence to confirm that it was actually a migration route (Lockley 1991).

Overwintering

Overwintering methods are employed by both modern endotherms and ectotherms. These strategies include burrowing, hibernation, and low-nutrient subsistence. Both burrowing and hibernation (*sensu stricto*) provide a means of escaping winter conditions by providing shelter and thus preventing tissue damage during subzero temperatures. However, burrowing is difficult to reconcile in large and/or herding animals like hadrosaurs and ceratopsians. Indeed, few dinosaurs possess potentially fossorial adaptations. Varricchio *et al.* (2007) recently described a hypsilophodont-grade dinosaur, *Oryctodromeus cubicularis* Varricchio, Martin & Katsura, 2007 that exhibited both fossoriality and

denning behaviour from the mid-Cretaceous of Montana. Senter (2005) described the unique range of motion in the alvarezsaurid, *Mononykus* Perle, Norell, Chiappe & Clark, 1993 as conducive to scratch-digging and the hook-and-pull motion seen in modern anteaters. The elongate claws of therizinosaurs and ornithomimids may have been capable of a similar function, although their morphology suggests some were better adapted for hook-like grasping (Nicholls & Russell 1985). Aside from hysilophodonts, burrowing is not a convincing mode of dinosaur overwintering. Similarly, hibernation (*sensu stricto*) requires shelter, but again it is unreasonable to assume that a herd of ceratopsians would find caves big enough or hollow logs plentiful enough to accommodate them. This hypothesis works better for small animals such as hypsilophodonts and troodontids; however, these animals are also thought to be the best adapted to surviving polar conditions (see below).

Tundra, grassland, and deserts, areas in which long-distance migration takes place presently, are characterized by extensive open land ideal for large animals (and large herds of animals) to pass through unhindered by thick vegetation. Palaeobotanical reconstructions of the habitats of polar dinosaurs invariably suggest mixed-growth forests consisting of a dense understorey and canopy layers. Despite being close to its current latitude (Amiot *et al.* 2004), the flora on the North Slope of Alaska during the Late Cretaceous was typified by taxodiaceous conifers, and ginkgoes with an understorey comprising horsetails, ferns, and aquatic plants, with a low-diversity angiosperm groundcover consistent with a cold-month mean of 0–11°C (Parrish *et al.* 1987, Spicer & Parrish 1990, Gangloff & Fiorillo 2003) and supported by $\delta^{18}O$ values (Amiot *et al.* 2004). A similar climate persists today in some parts of Tasmania and South Island, New Zealand. The absence of evergreen conifers and marked seasonality in fossil wood growth reflects a light regime

similar to the modern conditions at those latitudes, i.e. long, dark winters and short, light summers. Similar conditions persisted in Australia at this time. Rich *et al*. (1988) described a flora dominated by ginkgoes, podocarps, and araucarian conifers. Isotopic (δ^{18}O) records indicate that mean annual palaeotemperatures were around 5°C (Rich *et al*. 1988, Gregory *et al*. 1989), with seasonal freezing as evidenced by cryoturbation structures (Constantine *et al*. 1998), although Morath & White (2004) have suggested that a marine influence may have had an ameliorating affect on the climate. As such, temperatures were markedly warmer at the poles then than they are today, allowing a flourishing dense polar vegetation that was not conducive to freedom of movement (i.e. migration).

These floral and seasonal regimes suggest hypotheses of potential fodder for endemic polar dinosaurs. Although seasonal and partly deciduous, the diverse flora and even detrital wood (Chin 2007) would have also provided forage for overwintering herbivorous dinosaurs, which in turn could have supported the resident theropod population. Although the lack of new growth may have posed a problem, the exceptional chewing apparatus in hadrosaurian dinosaurs was well suited to masticate such fibrous, low-quality foods (Weishampel & Horner 1990). Even at lower latitudes where growing conditions were more equitable, coniferous and other woody plants, including detritus, formed at least part of their diet, as evidenced from preserved stomach contents and coprolites (Murphy *et al*. 2002, Chin 2007).

The odd gait of ankylosaurs has been cited as a condition exclusive of migration (e.g. Hotton 1980, Paul 1997). Limited range of motion and stocky leg design contribute to the inefficient mechanics of the leg; however, ankylosaurs are known from several polar fossil localities (Molnar & Wiffen 1994, Gangloff 1995, Rich & Vickers-Rich 2001). If such a design precluded migration, then ankylosaurs, despite their relatively large size (up to 6.25 m, Carpenter 2004), must have over-wintered in Australia, Antarctica, and Alaska as they did in New Zealand during the Campanian.

The Late Cretaceous polar fauna of the New Zealand microcontinent is perhaps the biggest thorn in the foot of the migration theory. Molnar & Wiffen (1994) described the fragmentary remains of an ankylosaur, a sauropod, a large theropod and a small theropod or ornithischian from the Maungataniwha Member of the Tahora Formation on North Island. Theropod remains have also been described from reworked Tertiary-age Takatika Grit on the Chatham Islands (Stilwell *et al*. 2006). The Maungataniwha Fauna represents an isolated and unique fauna based on the large size of some of the species (the large theropod and the sauropod) and coexistence of the ankylosaur with a sauropod. New Zealand during the Campanian lay within the Antarctic Circle (Fig. 4), and seafloor spreading as
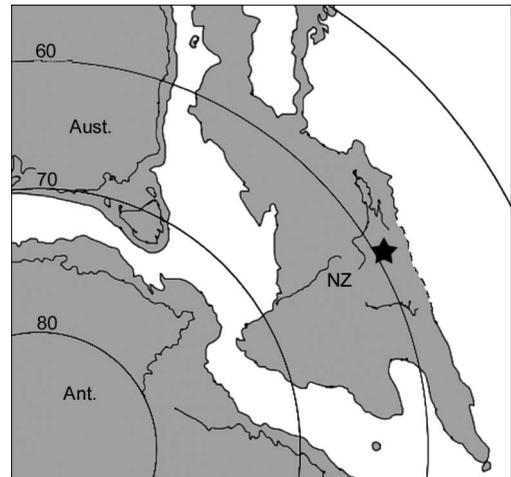

Fig. 4. Palaeolatitude of New Zealand (NZ) during the Campanian. Note its location within the Palaeo-Antarctic Circle. The location of the Maungataniwha Fauna is indicated by a star. Ant., Antarctica; Aust., Australia (based on Stilwell 1997 and Sutherland 1999, 2001).

early as 85 Ma (Davy 2006) had begun to push the former from the Antarctic mainland. Despite the high latitude, the influence of relatively warm marine currents (annual average temperature $\sim 14^{\circ}$C) significantly warmed the climate. Molnar & Wiffen (1994) envisage a cool, humid climate with extensive winter frost and snow. Palaeogeographic reconstructions variably recognize New Zealand as insular by the Campanian (Sutherland 1999, Stock & Cande 2002). If this interpretation is correct, then both small and large dinosaurs must have overwintered. Where other authors have suggested large animals (e.g. hadrosaurs) were perhaps more predisposed to travel long distances to escape harsh winters (e.g. Rich *et al*. 1988, Clemens & Nelms 1993), New Zealand's dinosaurs may simply have been precluded from undertaking such journeys. Such a taxonomically diverse fauna implicates the adaptive ability of dinosaurs as a whole, and obviates a universal explanation for dinosaur migration. The presence of an ankylosaur in the Maungataniwha Fauna has implications for other polar ankylosaurids. As previously mentioned, the stockiness of ankylosaurs probably prevented them from undertaking long migrations. As the Maungataniwha ankylosaur likely overwintered, it was certainly within their physiological limits to do so in other parts of the world.

The thought-provoking biogeographical provinces of Lehman (2001) stand in opposition to the migration hypothesis. Lehman proposed that during the Late Cretaceous, a strict ecological partitioning of dinosaurs occurred along the west coast of the Western Interior Seaway. He divided these provinces based on the dominant taxon (or taxa) represented within contemporaneous dinosaurian faunas over a latitudinal gradient. Unsurprisingly, the dominant taxa turned out to be hadrosaurs and ceratopsians to the exclusion of all other taxa. A similar conclusion was fol-

lowed by Horner *et al*. (2004) in regards to the lowland preference exhibited by *Maiasaura peeblesorum* Horner & Makela, 1979. These authors suggested that hadrosaurs were far from ubiquitous and maintained a limited ecological niche. These results stand in stark contrast to the idea of vast wandering herds traversing the coastal plains on seasonal roundtrips. In such a scenario, one would expect to find a more even distribution of migrating animals between their northern and southern limits (a distance of thousands of kilometres in some instances). However, this is not the case. As tantalizing as these results seem, however, the provinciality theory is also being challenged based on insufficient datasets (Vavrek & Larsson 2006).

Polar assemblages tend to have unusual faunal compositions. Hysilophodonts are a group of small ornithischians that, while rare in the Northern Hemisphere, tend to dominate Austral polar communities (Rich *et al*. 1988). The enlarged optic lobes and expanded orbits found in the Australian hypsilophodont, *Leallynosaura amicagraphica* Rich & Vickers-Rich, 1989, suggest this animal had acute vision compared with its northern, low-latitude counterparts (Rich *et al*. 1988). Those authors argued this to be a possible adaptation to counter the long, dark polar winters. Although this hypothesis remains untestable, small taxa are often thought to be incapable of long-distance migration (Clemens & Nelms 1993), and an adaptation to polar endemism makes sense. Similarly, on the North Slope of Alaska, the large-brained, large-eyed troodontid *Troodon* dominates microfaunal assemblages (Gangloff & Fiorillo 2003) but is comparatively rare in the southern part of its range (Brinkman 1990). While the possibility exists that large eyes played a part in a nocturnal habit, both represent small species. Small species and juveniles of larger taxa typically possess enlarged orbits and big brains in comparison with other

cranial features, often associated with the 'cuteness' of a small animal. Possession of these characters, therefore, does not necessarily mean vision was exceptional. An analysis of maniraptoran theropod brains suggests allometry is not entirely responsible for this trend, and visual acuity was certainly a feature of at least some taxa (Burnham & Martin 2002).

The preponderance of hypsilophodonts in the Early Cretaceous, southern polar faunas has been suggested to be a function of niche specialization, surviving where most dinosaurs could not (Rich *et al.* 1997). Under this hypothesis, north polar faunas might also be expected to exhibit this skew in composition; however, hypsilophodonts remain exceptionally rare where hadrosaurs and ceratopsians dominate. Hadrosaurs dominate Campanian–Maastrichtian Northern Hemisphere polar and low latitude assemblages, yet hadrosaurs are virtually non-existent in southern latitudes at this time. Only two species are known from the Southern Hemisphere, both from Patagonia. A single hadrosaur tooth and an isolated limb bone are known from Antarctica (Case *et al.* 2000, P. Rich pers. comm.). Naturally, one cannot assume relative species abundance to remain stable across both time and space, and presumably this skew is a broad evolutionary artefact rather than a biogeographical preference for the Northern Hemisphere or for polar climates in either hadrosaurs or hypsilophodonts. It does, however, raise some interesting questions regarding the composition of polar faunas in relation to contemporaneous faunas. Although conditions were far more equable at the poles during the Cretaceous than they are today, the long polar night would have played a significant selective role, favouring animals that were apted to these conditions.

What is certain from this is that some dinosaurs were remarkably cold-tolerant (see also Buffetaut 2004), and that large

and small dinosaurs would have adapted differently to winter conditions at high latitudes. If palaeogeographic reconstructions are correct, the Maungataniwha Fauna demontrates that at least some dinosaurs were capable of overwintering through the dark Austral winter. Sauropods, theropods, and ankylosaurs all endured 3 months of winter darkness, and it is almost certain that the larger species must have survived on low-nutrient forage rather than hibernate or burrow. Metabolic efficiencies of large body size (Engelmann *et al.* 2004), although potentially useful for migrators (Turner & Peterson 2004), would have been advantageous for large endemic dinosaurs enduring truncation of the high-latitude growing season. Considerations that may contradict winter endemism of large polar dinosaurs include their apparent lack of insulation, and the low-latitude restriction of North American sauropods during the Late Cretaceous.

Hypotheses of dinosaurian migration or endemism will be testable through sensitivity analyses of metabolic, climatic, and biogeographic parameters. By varying estimates of metabolic rate, biomechanical efficiency, local temperatures, and nutrient availability, the ability of dinosaurs to migrate or overwinter can be assessed through holistic integration of such variables. This approach will avoid the attraction of quantum judgements about dinosaurian migratory or overwintering ability, and encompass their diversity of likely metabolic and natural history strategies.

Conclusions

The habits of polar dinosaurs can be divided into two categories: migration or overwintering. The Cretaceous ornithischian bonebeds found throughout western North America provide the best evidence for migration as large numbers of

mega-herbivores would be ecologically unsustainable if they did not move from place to place exploiting resources. Physiological equations provided by Alexander (1998) suggest that hadrosaurs and ceratopsians were incapable of the long-distance migrations advocated by Hotton (1980). However, *Edmontosaurus regalis* was probably capable of a 2600-km roundtrip migration, a distance extrapolated from its known distribution, although the corresponding climate was far from polar. Other evidence for migration may be found from trackways, although conclusions are highly equivocal. Hotton's (1980) arguments in favour of migration, primarily those invoking a lack of insulation, are not substantiated for all polar dinosaurs.

While many authors agree that dinosaurs were probably capable of migration and/or overwintering, only conclusive evidence for the latter is found. The New Zealand fauna described by Molnar & Wiffen (1994), if insular, illustrates the necessity for overwintering in at least one taxonomically diverse population. Because large dinosaurs lack fossorial adaptations and were likely incapable of finding sufficient shelter (therefore negating burrowing and hibernation), subsistence overwintering is found to be the most acceptable means of overwintering. Smaller animals were more likely to find shelter, and insulative integument on small theropods, and perhaps even small ornithopods, likely contributed to their survival in polar regions.

Acknowledgements

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