THE DIET OF OSTRICH DINOSAURS (THEROPODA: ORNITHOMIMOSAURIA)

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Abstract: The diets of ornithomimosaurian dinosaurs (Theropoda: Ornithomimosauria) have proved to be contentious owing to a dearth of unambiguous evidence in support of carnivory, omnivory or herbivory. Re-assessment of anatomical, taphonomical and palaeoecological evidence, and estimates of daily minimal energy budgets for two derived ornithomimosaurian genera, indicate that suspension-feeding and carnivory were unlikely. The combined presence of a keratinized rhamphotheca and gastric mill is strongly indicative of a herbivorous habitus for these dinosaurs. Herbivorous and omnivorous forms are rare among the non-avian Theropoda, but are more common than previously suspected. Rejection of carnivorous habits for derived ornithomimosaurs redresses apparent discrepancies in the relative abundances of the herbivore and carnivore guilds of several Late Cretaceous faunas.

**Key words:** Ornithomimosauria, suspension-feeding, herbivory, energetics, palaeoecology.

ORNITHOMIMOSAURIA is a monophyletic clade of derived coelurosaurian theropod dinosaurs (e.g. Barsbold and Osmólska 1990; Osmólska 1997). As the name suggests, members of this clade bear a strong superficial resemblance to large ground-dwelling birds such as extant ratites, and have slender necks, relatively small heads and elongate, powerful hindlimbs. The arms are long and strongly muscled, with specialized hands, and there is a long tail that acts as a counterbalance to the rest of the body (Russell 1972; Nicholls and Russell 1985; Paul 1988; Barsbold and Osmólska 1990; Osmólska 1997; Kobayashi and Lu 2003). Ornithomimosaurs are thought to be among the most cursorially adapted of all dinosaurs, with estimated running speeds of up to 60 km h^{-1} (Thulborn 1990). The earliest known representative of the group, *Pelecanimimus*, is known from Early Cretaceous (Barremian) deposits in Spain (Pérez-Moreno *et al.* 1994), but the majority of ornithomimosaurs are found in the Late Cretaceous strata of East Asia and North America (Barsbold and Osmólska 1990; Weishampel 1990).

The composition of ornithomimosaur diets has provoked much debate among vertebrate palaeontologists: were they predominantly carnivorous, omnivorous or herbivorous (Osmólska *et al.* 1972; Russell 1972; Osmólska 1980; Nicholls and Russell 1985; Paul 1988; Barsbold and Osmólska 1990; Kobayashi *et al.* 1999)? The principal reason for this lack of agreement is that the edentulous jaws characteristic of the majority of, though not all, ornithomimosaurs confound the use of the dental comparisons that usually provide the foundations for dietary inference in extinct vertebrate taxa (cf. Barrett 2000; Text-fig. 1A). Moreover, other morphological features that have been cited in support of these competing hypotheses, such as the inferred presence of a keratinous beak (rhamphotheca), have proved to be ambiguous as they have a wide distribution among extant analogues (birds, turtles) that exhibit a variety of dietary attributes. The most recent contribution to this debate has been the suggestion that these dinosaurs were suspension feeders that used a rhamphotheca to strain food-bearing sediments in aqueous environments, in a manner analogous to that employed by extant anseriform birds (Norell *et al.* 2001). This recalls earlier suggestions that ornithomimosaurians lived in close proximity to rivers and lakes, preying upon a range of aquatic animals (Osmólska 1980).

The objectives of this paper are to: (1) assess critically the functional anatomical, palaeoenvironmental and taphonomic evidence that has been used to support the various dietary hypotheses that have been proposed for ornithomimosaurians; (2) investigate the energetic viability of suspension feeding, carnivory and herbivory in these animals utilizing calculations for minimum daily energy budgets; and (3) use a combination of these lines of evidence to evaluate the composition of ornithomimosaurian diets in general terms.

Institutional abbreviations. BMNH, The Natural History Museum, London; IGM, Institute of Geology, Ulaan Baatar, Mongolia; RTMP, Royal Tyrell Museum of Palaeontology,
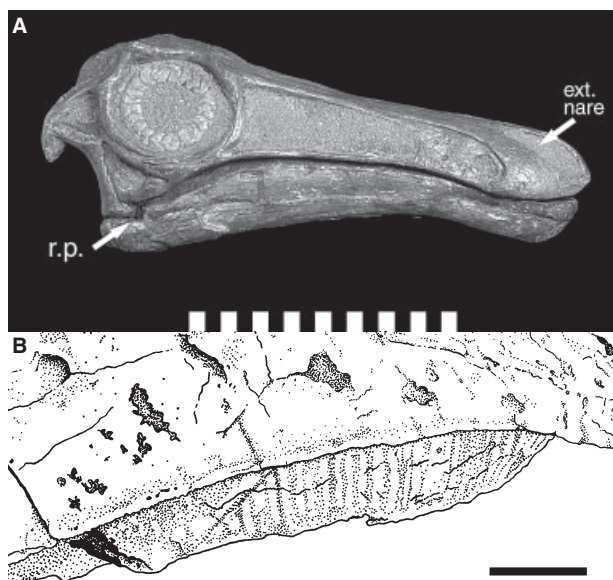
TEXT-FIG. 1. Skull and rhamphotheca of the ornithomimosaurian theropod dinosaur *Gallimimus bullatus*. A, BMNH R9284, model of skull based on specimens IGM DPS 100/11 and Z.Pal. Mg.D-I/1; scale bar represents 10 cm. Abbreviations: ext. nare, external naris; r.p., retroarticular process. B, drawing of the preserved right upper rhamphotheca of IGM 100/1133, in lateral view, based on Norell *et al.* (2001). Anterior is to the right of the drawing. Scale bar represents 3 mm.

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ANATOMICAL EVIDENCE

Rhamphotheca

Discovery of two ornithomimosaur specimens with soft-tissue preservation has demonstrated that a keratinous rhamphotheca covered the rostral part of the snout and mandible in these animals (Norell *et al.* 2001), confirming predictions made on the basis of osteological evidence (Russell 1972; Barsbold and Osmólska 1990). One of these specimens (RTMP 95.110.1), from the Dinosaur Park Formation (late Campanian) of Alberta, Canada, is referable to *Ornithomimus edmontonicus*, while the other (IGM 100/1133), from the Nemegt Formation (middle Maastrichtian) of Mongolia, has been identified as *Gallimimus bullatus* (Norell *et al.* 2001). The surface of the preserved *Gallimimus* rhamphotheca bears a large number of small, regularly spaced columnar structures that are orientated perpendicular to the jaw margins and which would have formed part of the lingual surface of the beak in life (Text-fig. 1B). Norell *et al.* (2001)

interpreted these columnar features as a series of keratinous maxillary lamellae, similar to those of extant anseriform birds (Norell *et al.* 2001). In phoenicopterid and anseriform birds, the marginal laminae are distinct, bristle-like structures that are arranged in a comb- or sieve-like fashion to form an integral part of a sophisticated suspension-feeding apparatus, acting as a filter to remove small planktonic or infaunal prey items (such as diatoms, copepods and gammarid shrimps) from mouthfuls of water and/or sediment (Jenkin 1957; Zweers *et al.* 1977, 1995; Crome 1985; Kooloos *et al.* 1989; Sanderson and Wassersug 1993; Pl. 1, figs 1–2). Norell *et al.* (2001) suggested that the apparent similarities between the columnar structures seen in *Gallimimus* and the marginal lamellae on the beaks of filter-feeding birds indicated a suspension-feeding habitus for at least some ornithomimosaurs.

However, observations on the rhamphothecae of extant and extinct birds and reptiles suggest that there are alternative functional explanations for the structures seen on the preserved ornithomimosaurian beaks. The marginal lamellae in suspension-feeding birds are durable but flexible, as they are only fixed in position basally and are not conjoined along their lengths (Jenkin 1957; Zweers *et al.* 1977, 1995; Crome 1985; Kooloos *et al.* 1989). Consequently, individual lamellae are susceptible to bending and can move out of alignment with the beak margin and/or overlap each other to a certain extent. In addition, these delicate structures would be expected to exhibit postmortem collapse, at least partially obscuring the regular arrangement of the lamellae along the beak. In contrast, IGM 100/1133 appears to display no indication of any overlap between the columnar features preserved on the beak or of any apparently collapsed structures (Norell *et al.* 2001, fig. 1c). The maintenance of such a regular series suggests that these ornithomimosaurian 'lamellae' were either exceptionally rigid (which seems unlikely if they were constructed in the same way as bird lamellae) or that they were conjoined in some way, helping to preserve the integrity of the series. However, if the 'lamellae' were conjoined, this would severely compromise their efficacy as a filtration device. An alternative explanation is that the ornithomimosaur 'lamellae' were not distinct, separate structures at all, but that these columnar structures are merely an integral feature of rhamphotheca architecture.

The preserved pattern of serially arranged, regularly spaced, thin vertical structures on the beak of *Gallimimus* is strongly reminiscent of rhamphotheca morphology in some chelonians and hadrosaurid dinosaurs. Chelonians do not possess beaks with marginal rows of bristle-like lamellae, but many genera (including testudinids, some emydids and some cheloniids) do exhibit a large number of prominent, vertically orientated ridges that are situated on the internal surface of the beak (Bramble 1974;

Pritchard 1979; E. S. Gaffney, pers. comm. 2003; Pl. 1, fig. 3). In many cases, these ridges support small tubercles, or denticles, that line the oral margins of the rhamphothecae. Ridges and denticles are found in herbivorous, omnivorous and carnivorous genera (E. S. Gaffney, pers. comm. 2003), but there is a partial correlation between possession of the ridges and an exclusively herbivorous diet among terrestrial chelonians, for which it has been demonstrated that both ridges and denticles are involved in the trituration and prehension of plant material (Bramble 1974; Pritchard 1979). Indeed, the coarser the vegetation in the diet, the more prominent the ridges appear to be (Bramble 1974). Similar ridges are present on a rhamphotheca of the hadrosaurid dinosaur *Edmontosaurus*, which give the inner surface of the beak a fluted appearance (Morris 1970; Pl. 1, fig. 4). Although it was initially suggested that the hadrosaurid beak served as a filter for feeding on aquatic plants and invertebrates (a proposal founded on the notion, prevalent at the time, that these animals were largely aquatic: Morris 1970), studies on the jaw mechanics, locomotory capabilities and gut contents of these dinosaurs have demonstrated that they were obligate terrestrial herbivores and that the beak was used for cropping tough vegetation (Weishampel 1984; Forster 1997). 'Filing ridges' on the lingual surface of the rhamphotheca in psittaciform birds are used in grinding and shelling seeds, although in this case the ridges are orientated parallel to the beak margin, rather than perpendicular to it (Homberger 1989; J. Cooper, pers. comm. 2003).

The high level of similarity between the internal beak surfaces of hadrosaurids, herbivorous chelonians and *Gallimimus* suggests that rather than representing a series of separate anseriform-like lamellae, the serially arranged vertical structures preserved in IGM 100/1133 may represent a natural cast of the internal surface of a chelonian- or hadrosaurid-like beak. If this alternative interpretation is accepted, the preserved rhamphothecae would provide circumstantial evidence for high-fibre herbivory in *Gallimimus* and *Ornithomimus*.

Kobayashi and Lü (2003) noted that the upper rhamphotheca of *Ornithomimus* and *Struthiomimus* may have been more extensive than that of *Sinornithomimus* and *Gallimimus* on the basis of the distribution of vascular foramina on the lateral surface of the upper jaws. In *Ornithomimus* and *Struthiomimus* foramina are present on both premaxillae and maxillae, whereas in *Gallimimus* and *Sinornithomimus* maxillary vascular foramina are absent. Moreover, these authors (ibid.) also noted that the anterior margins of the beaks are different shapes in dorsal view (acute in *Ornithomimus* and *Struthiomimus*; rounded in *Gallimimus* and *Sinornithomimus*). Such morphological differences may imply some ecological/dietary divergence between these taxa.

Cranial morphology

Several features present in the skulls of suspension-feeding birds are not present in ornithomimosaurs. For example, both phoenicopterid and anseriform birds have elongate retroarticular processes for the insertion of M. depressor mandibulae that are enlarged relative to those of birds with other feeding mechanisms (Pl. 1, fig. 1). The large jaw depressors are necessary to overcome the resistance of the water surrounding the beak during jaw opening (Sanderson and Wassersug 1993). In contrast, the retroarticular process of ornithomimosaurs is small and similar in size to that of many other non-avian theropod dinosaurs (Barsbold and Osmólska 1990; Text-fig. 1A). In addition, all suspension-feeding birds have a reduced oral gape which functions to exclude large, indigestible items from the mouth (Sanderson and Wassersug 1993). Conversely, the structure of the ornithomimosaur craniomandibular joint and the lines of action of the principal jaw adductor muscles suggest that these dinosaurs had a wide gape, which might have allowed the ingestion of relatively large prey items (Barsbold and Osmólska 1990). Finally, extant phoenicopterids and anseriforms have strongly retracted external nares (as do most other extant birds), which allow them to feed without inhaling large quantities of water (Pl. 1, fig. 1). The external nares of ornithomimosaurs are placed at the rostral tip of the snout (Osmólska *et al.* 1972; Russell 1972; Text-fig. 1A), however, suggesting that they would have been subject to water inhalation unless the nares could be closed by soft-tissue structures (a problem that would have been exacerbated by the anterior positioning of the fleshy nostril within the external narial opening; Witmer 2001). The lack of these cranial specializations argues against a suspension-feeding habitus for ornithomimosaurs, but does not exclude herbivory, omnivory or carnivory.

The jaws of ornithomimosaurs are often characterized as weak, due to the small size of the postorbital adductor chamber and of the adductor musculature housed within this region, and this has formed the basis for the suggestion that they were limited to soft food items, such as insects, eggs, fruits and small vertebrates (Barsbold and Osmólska 1990). Nevertheless, several apparent similarities between the skulls of ornithomimosaurs and diornithid birds, in the bracing of the quadrate and suspensorium for example, may indicate that the jaws of the former were stronger than usually supposed (Paul 1988), though this hypothesis remains to be tested. In summary, the various cranial features of ornithomimosaurs suggest that they were potentially capable of eating relatively resistant foodstuffs, including animal material and high-fibre vegetation, and of using the rhamphotheca as a cutting/shearing device.

Postcranial evidence

Functional morphological analysis of the manus suggests that the hands of derived ornithomimosaurians were not raptorial, therefore differing from those of other non-avian theropods, and did not have extensive manipulative abilities (Ostrom 1969; Nicholls and Russell 1985). Instead, the ornithomimosaur manus combined special-ized 'hooking' and 'grasping' functions analogous to those of extant chameleons and tree sloths (Nicholls and Russell 1985). As ornithomimosaurs were obviously not arboreal animals, one possible use for this specialized manus was suggested to be pulling branches towards the mouth dur-ing feeding (Nicholls and Russell 1985). However, it still remains possible that this specialized mechanism may have played some role in procuring prey (e.g. Barsbold and Osmólska 1990), though the lack of extant or extinct faunivorous, non-arboreal analogues makes assessment of this latter hypothesis difficult. Moreover, it has been sug-gested that the manus of basal ornithomimosaurs, such as *Harpymimus* and *Sinornithomimus*, had more raptorial grasping capabilities than their derived relatives (Kobayashi and Lü 2003).

Finally, the abdominal regions of 12 well-preserved *Sinornithomimus* specimens from the Upper Cretaceous of China were found to contain a large number of gastro-liths, demonstrating unequivocally the presence of a gastric mill in at least one member of this clade (Kobayashi et al. 1999; Kobayashi and Lü 2003). Among terrestrial animals, gastric mills are most frequently encountered in herbivores, usually (but not exclusively) occurring in those taxa that lack sophisticated oral processing mecha-nisms, such as chelonians, sauropodomorphs and birds (Farlow 1987; Moskovits and Bjorndal 1990; Christiansen 1996; Gionfriddo and Best 1996). Gastric mills have been reported in several non-avian theropods, where they are either associated with other features indicative of herbivory (as in the oviraptorosaurian *Caudipteryx*: Ji et al. 1998) or occur in taxa for which dietary preferences cannot be deduced accurately owing to missing craniodental evi-dence (e.g. *Lourinhanosaurus*: Mateus 1998; *Nqwebasau-rus*: de Klerk et al. 2000). On the basis of current evidence, therefore, ornithomimosaurian gastric mills are most strongly indicative of an herbivorous diet (see also Kobayashi et al. 1999).

ECOLOGICAL ENERGETICS

Although the calorific values of freshwater plants and invertebrates fall within the same broad range as those for terrestrial forms (values for most taxa range between 3·5 and 5·5 kcal g^{-1}; Cummins and Wuycheck 1971), the density, biomass and production of animal and plant material in freshwater lakes, rivers and streams are extre-mely low (Wetzel 2001). For example, average zooplank-ton productivity in freshwater lakes ranges between 0·00009 and 0·57 g m^{-3} day^{-1} depending upon the taxon under investigation, levels of available primary productivity and numerous abiotic variables (e.g. temperature, nutrient concentrations), among other factors (Wetzel 2001, table 16.20). Here, calculations of ornithomimosaurian daily energy budgets have been compared with those of another suspension-feeder (the Lesser Flamingo) to provide some constraints on whether these animals could have sub-sisted on such a 'patchy' food resource.

There is a well-documented relationship between body mass (*m*, in kg) and minimal metabolic rate (*R*$_{min}$, in watts), which can be expressed in the following simple equation (Alexander 1999): $R_{min} = am^b$. Factor *a* and exponent *b* are constants that are known to vary with such variables as body temperature (for an ectotherm) and taxonomic affiliation (Table 1).

Mass estimates for adult ornithomimosaurs range from 85 to 440 kg (Paul 1988). As dinosaur metabolism is the subject of intense debate (e.g. Farlow 1990; Farlow and Brett-Surman 1997), a range of *R*$_{min}$ was calculated for ornithomimosaurs with estimated masses of 165 kg (*Ornithomimus edmontonicus*) and 440 kg (*Gallimimus bullatus*), using the various combinations of exponents listed in Table 1. These values were converted to daily minimal energy budgets for *Ornithomimus* and *Gallimi-mus* as endotherms, 'hot' ectotherms (i.e. with a body temperature of 37°C due to high ambient temperature,

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EXPLANATION OF PLATE 1

Rhamphothecae of various dinosaurs (including birds) and chelonians.

Fig. 1. Skull of the Shoveller Duck [*Spatula* (*Anas*) *clypeata*; BMNH unnumbered], complete with rhamphothecae, in lateral view. Note the many fine keratinous laminae lining upper and lower jaws. Scale bar represents 50 mm.

Fig. 2. Upper rhamphotheca of the Pacific Black Duck (*Anas superciliosa*; BMNH S/1964.1.8) in ventral view. Scale bar represents 50 mm.

Fig. 3. Upper rhamphotheca of the Green Turtle (*Chelonia mydas*; BMNH 1971.1731) in ventral view, showing the many ridges that line the lingual surface of the beak. Scale bar represents 50 mm.

Fig. 4. Skull of the hadrosaurian ornithopod dinosaur *Edmontosaurus* in ventrolateral view, showing the internal ridging of the pre-served rhamphotheca (from Morris 1970). Not to scale.
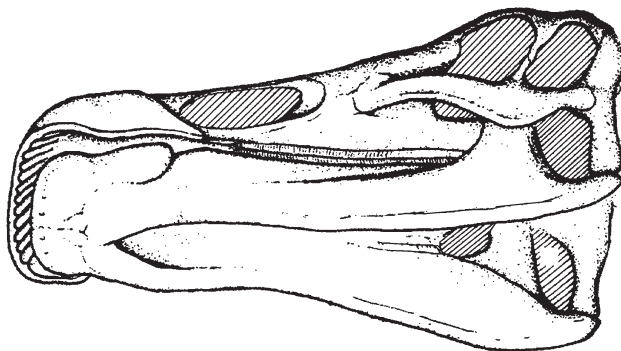
PLATE 1

BARRETT, rhamphothecae

TABLE 1. Minimal daily energy requirements for two ornitho-mimosaurian dinosaurs of differing body mass (m), under various metabolic regimes (body masses taken from Paul 1988). Minimal metabolic rate was calculated (in watts) using the equation $R_{min} = am^b$ (after Alexander 1999) and this was converted to a daily requirement in MJ. The various exponents fitted to the equation for the different model organisms were: mammals [body temperature (T_b) normal], $a = 3 \cdot 3$, $b = 0 \cdot 76$; passerine birds (T_b normal), $a = 6 \cdot 3$, $b = 0 \cdot 72$; non-passerine birds (T_b normal), $a = 3 \cdot 6$, $b = 0 \cdot 72$; 'hot' lizard ($T_b = 37°C$), $a = 0 \cdot 68$, $b = 0 \cdot 82$; 'cold' lizard ($T_b = 20°C$), $a = 0 \cdot 13$, $b = 0 \cdot 80$ (all from Alexander 1999).

Model organism	Daily energy requirement (MJ day^{-1})	
	Ornithomimus ($m = 165$ kg)	*Gallimimus* ($m = 440$ kg)
Mammalian metabolism	13·81	29·11
Passerine bird metabolism	21·50	43·57
Non-passerine bird metabolism	12·29	24·89
'Hot' lizard (37°C) metabolism	3·87	8·64
'Cold' lizard (20°C) metabolism	0·67	1·46

TABLE 2. Mean energy values for a variety of prey animals and plants that are common in extant freshwater ecosystems, converted from the calorific values given in Cummins and Wuycheck (1971). Means are taken across a wide range of taxa, but energy values are remarkably consistent within major clades and are generally subject to only minor variation.

Prey organism	Energy value (MJ kg^{-1} dry weight)
Annelida: mean for all freshwater families	22·43
Mollusca: Viviparidae	19·52
Mollusca: mean for all freshwater families	13·04
Crustacea: Amphipoda	16·83
Crustacea: microcrustaceans	23·07
Insecta: mean for all freshwater families	20·16
Algae: mean for all freshwater families	13·69
Angiospermae: mean for all freshwater families	16·98

basking or some other behavioural mechanism) and 'cold' ectotherms (i.e. with a body temperature of 20°C, reflecting a lower ambient temperature) (Table 1). The amount of food needed to fuel these minimum daily energy budgets was then calculated using the energy values (dry weight) of a variety of prey species that are common in extant freshwater ecosystems (from Cummins and Wuycheck 1971; see Tables 2–3).

A 440-kg *Gallimimus*, with daily minimal metabolic requirements of between 1·46 and 43·57 MJ (depending on whether it was ecto- or endothermic), would require between 0·07 and 3·34 kg of food per day (Table 3): equivalent requirements for a 165-kg *Ornithomimus* are 0·67–21·5 MJ and 0·03–1·65 kg, respectively (Table 3). These quantities do not seem unreasonable when compared with feeding data from Lesser Flamingos (*Phoenic-onaias minor*). Experimental and field observations indicate that adult individuals of *P. minor* can filter 72 ± 6·5 g (dry weight) of the cyanobacterium *Spirulina platensis* per day (Vareschi 1978), which is within the 'cold' ectotherm range calculated for both ornithomimo-saurian taxa. However, filtration rates in *P. minor* are exceptionally high, with a clearance rate of water through the mouth of 31·8 ± 1·3 L h^{-1}. As Lesser Flamingos spend approximately 12·5 h a day feeding, this represents a total filtrate of almost 400 L per bird per day to support a total field energy budget (including R_{min} and corrections for food-gathering, locomotion, etc.) of approximately 1·3 MJ day^{-1} (Pennycuick and Bartholomew 1973;

Vareschi 1978). Consequently, it appears that an ornitho-mimosaur could have maintained R_{min} if it: (1) were equipped with a flamingo-like filtering apparatus; (2) was capable of processing a minimum of 400 L of water per day; and (3) conformed to a 'cold' ectothermic physiological model.

However, although the maintenance of R_{min} might be possible under the above-mentioned conditions, several lines of evidence indicate that suspension feeding was unlikely to be a viable habitus for a terrestrial animal as large as an ornithomimosaur. The results of the energetic calculations presented in Tables 1 and 3 reflect minimal (basal) metabolic rates, assume a digestive efficiency of 100 per cent and presuppose that all of the ingested food can be digested. In contrast, field metabolic rates are three to six times higher than minimal metabolic rates (Alexander 1999), digestive efficiencies of extant reptiles, birds and mammals range between 45 and 84 per cent (depending upon diet and thermal physiology; Brafield and Llewellyn 1982), and many components of animal diets (e.g. bone, shell, cellulose) cannot be completely digested. Moreover, all of these calculations are based on energy values per unit of dry weight and thus underestimate the actual biomass that an ornithomimosaur would need to collect in order to fulfil its energy requirements. The energetic costs of suspension feeding would therefore require daily food intakes that are at least three to four (and potentially many more) times greater than those given here, which would almost certainly preclude this behaviour in a large, terrestrial animal. Not only does the absolute food requirement increase, but the amount of water that would need to be filtered in order to obtain it also increases at the same rate, suggesting that an active ornithomimosaur would have to filter many thousands of litres of water to satisfy its daily requirements, an amount

TABLE 3. Amounts of each prey species (in kg day^{-1}) necessary to maintain R_{min} (assuming 100% digestive efficiency) for two orni-thomimosaur species under different metabolic regimes utilising different prey species. See text for further details.

Prey organism	Model organism				
	Mammal	Passerine	Non-passerine	Lizard (37°C)	Lizard (20°C)
Ornithomimus edmontonicus (*m* = 165 kg)					
Annelida	0·62	0·94	0·55	0·17	0·03
Mollusca (Viviparidae)	0·71	1·10	0·63	0·20	0·03
Mollusca	1·06	1·65	0·94	0·30	0·05
Crustacea (Amphipoda)	0·82	1·28	0·73	0·23	0·04
Crustacea (microcrustaceans)	0·60	0·93	0·53	0·17	0·03
Insecta	0·69	1·07	0·61	0·19	0·03
Algae	1·01	1·57	0·90	0·28	0·05
Angiospermae	0·81	1·26	0·72	0·23	0·04
Gallimimus bullatus (*m* = 440 kg)					
Annelida	1·30	1·94	1·11	0·39	0·07
Mollusca (Viviparidae)	1·49	2·23	1·28	0·44	0·07
Mollusca	2·23	3·34	1·91	0·66	0·11
Crustacea (Amphipoda)	1·73	2·59	1·48	0·51	0·09
Crustacea (microcrustaceans)	1·26	1·89	1·08	0·37	0·07
Insecta	1·44	2·16	1·23	0·43	0·07
Algae	2·13	3·18	1·82	0·63	0·11
Angiospermae	1·71	2·57	1·47	0·51	0·09

that does not seem feasible. Furthermore, availability of freshwater plants and invertebrates is heavily dependent on seasonal and other abiotic factors, and productivity in freshwater ecosystems is very low (Wetzel 2001), so it seems unlikely that ornithomimosaurs would have been able to depend on such an ephemeral food source. Flamingos are able to survive in these environments due to their low body mass (and hence low R_{min}; Pennycuick and Bartholomew 1973; Vareschi 1978), the unusually high concentration of planktonic organisms in the saline lakes they inhabit (Vareschi 1978), a lack of competition with other suspension-feeders (principally fishes; Hurlbert *et al.* 1986) and the low costs of transport that they incur when flying between patchily distributed food resources (as flying is energetically cheaper than walking: Schmidt-Nielsen 1997): the first and last of these caveats were certainly not true of ornithomimosaurs.

The minimum daily food requirements shown in Table 3 apply to ornithomimosaurs regardless of whether they were suspension-feeders, herbivores, omnivores or carnivores, as do the above mentioned corrections relating to field metabolic rates, digestive efficiencies, etc. However, it is feasible that an omnivorous, herbivorous or carnivorous ornithomimosaur could have collected the requisite amount of prey/fodder per day, even if a sus-pension-feeder could not. Taking the calculated daily minimum food requirements of *Gallimimus* as baseline data (Table 3), and assuming that field metabolic rates were six times higher than R_{min} (see above), a total food intake of approximately 20 kg (equivalent to around 95–110 MJ day^{-1}, depending on dietary preference:

calorific values taken for a range of animal and plant taxa from Cummins and Wuycheck 1971) is obtained to support the metabolic needs of a free-living ornithomimo-saur subject to the most energy-dependent physiological regime (based on a passerine bird model). As living mammals of similar body mass (100–500 kg) have equivalent, or higher, daily food intake rates (see Farlow 1976; Peters 1983), all three alternative dietary options (herbivory, omnivory and carnivory) appear to remain viable on the basis of ecological energetic calculations.

PALAEOENVIRONMENTAL AND TAPHONOMIC EVIDENCE

If ornithomimosaurs were obligate suspension-feeders, they would depend on a continuous supply of freshwater plants and invertebrates. This suggests that they would be confined to environments that were either not strongly seasonal (at least with respect to water availability) or which included substantial permanent freshwater bodies (cf. Norell *et al.* 2001). The Dinosaur Park Formation, which has yielded the remains of several ornithomimo-saurian genera (*Ornithomimus*, *Struthiomimus* and *Dromiceiomimus*), consists of a series of fine- to medium-grained sandstones that were deposited in a high-sinuos-ity fluvial/estuarine system on the western margin of the Western Interior Seaway (Eberth and Hamblin 1993). Various palaeoenvironments are represented, including fluvial channels, estuarine channels, floodplains, marshes, swamps and small lakes (Eberth and Hamblin 1993), all

of which indicate that the climate was probably humid for much of the year. Consequently, if these animals were suspension-feeders, then it is likely that suitable food sources were continuously available.

Norell *et al.* (2001) also categorized two other ornithomimosaur-bearing units as 'mesic', namely the Iren Dabasu (?Campanian) and Nemegt formations of Inner Mongolia (People's Republic of China) and Mongolia. However, the Iren Dabasu Formation represents a fluvial system that developed in a semi-arid climatic regime. The fluvial channels were broad, shallow and braided and the surrounding floodplain was the site of caliche formation and the development of ephemeral lakes, ponds and playa (Currie and Eberth 1993): all of these features are typical of modern semi-arid and arid environments. The lithological characteristics of the Nemegt Formation indicate the presence of meandering rivers on a broad alluvial floodplain, but variation in the composition of the channel deposits indicates that there were marked wet and dry seasons (Gradzinski 1970). Although it is probable that permanent watercourses were present in both Iren Dabasu and Nemegt palaeoenvironments throughout the year (Gradzinski 1970; Currie and Eberth 1993), the reduction in the extent and number of ephemeral water bodies and the presumed decrease in flow of major rivers during the dry season is likely to have had a deleterious effect on large populations of suspension-feeding animals, and ornithomimosaurians might therefore be expected to be rare components of the faunas recovered from these units. However, this is not the case as ornithomimosaur remains are abundant in both formations: over 1000 specimens have been recovered from the Iren Dabasu Formation alone (Currie and Eberth 1993). Furthermore, circumstantial evidence for flocking behaviour in ornithomimosaurians is provided by the discovery of a bonebed containing the remains of at least 14 *Sinornithomimus*, from the Ulansuhai Formation (Upper Cretaceous) of Inner Mongolia (Kobayashi *et al.* 1999; Kobayashi and Lü 2003). The abundance of these animals in semi-arid environments suggests that suspension-feeding would not have been a viable trophic adaptation. Moreover, as the volumes of water that would need to be filtered by each individual would have been in the range of 400 L or more per day (see above), it is unlikely that ephemeral ponds and streams could have provided sustenance to even transitory populations of suspension-feeding ornithomimosaurians.

DISCUSSION AND CONCLUSIONS

Consideration of ornithomimosaurian anatomy, physiological ecology and palaeoecology indicates that a suspension-feeding habitus is extremely unlikely for these large, active dinosaurs. However, herbivory, omnivory and carnivory are all equally viable under the various energetic and palaeoenvironmental regimes discussed above. Taken individually, no one anatomical characteristic can be used to argue rigorously for either carnivory, omnivory or herbivory in these animals; however, the combined presence of a keratinous rhamphotheca and gastric mill is most consistent with high-fibre herbivory in derived ornithomimosaurians, as this amalgam of features is otherwise found only in extant herbivorous turtles (Farlow 1987), herbivorous non-avian dinosaurs (e.g. stegosaurs, psittacosaurids and therizinosaurs: Paul 1984; Weishampel and Norman 1989; Norman and Weishampel 1991; Ji *et al.* 1998) and extant herbivorous birds (e.g. Gionfriddo and Best 1996). Recognition of herbivory in this clade of non-avian theropods demonstrates that dietary strategies within Theropoda were more varied than is usually supposed.

A census of the vertebrate specimens collected from the Nemegt Formation demonstrated that ornithomimosaurs were numerous in this fauna: only hadrosaurid and tyrannosaurid remains were more abundant (Osmólska 1980). Similar results were obtained from the Iren Dabasu Formation, where ornithomimosaurians were second only to hadrosaurids in terms of the amounts of material recovered (Currie and Eberth 1993). If these ornithomimosaurians are considered to be members of the carnivore guild in each of these faunas, which also contained numerous tyrannosaurids and rarer small theropods, the ratio of carnivores to herbivores would have been unusually high (Osmólska 1980). However, if the ornithomimosaurians are re-assigned to the herbivore guild, this apparent discrepancy is removed.

The majority of non-avian theropods were exclusively carnivorous and instances of herbivory or omnivory within this group are rare and sometimes controversial (Paul 1984; Barrett 2000; Holtz *et al.* 2000). Most authors agree that therizinosauroids ('segnosaurs') were either herbivorous or omnivorous, owing to their possession of leaf-shaped cheek teeth, probable presence of a rhamphotheca and small fleshy cheeks, and an opisthopubic pelvis (Paul 1984; Barsbold and Maryańska 1990; Clark *et al.* 1994). Tooth morphology and wear in the basal oviraptorosaurian *Incisivosaurus* suggests herbivorous habits for this taxon (Xu *et al.* 2002a), and the presence of a gastric mill in *Caudipteryx* (Ji *et al.* 1998), another basal oviraptorosaurian, suggests that herbivory may have been primitive for this clade as a whole. However, dietary inference in other purported theropod omnivores/herbivores has proved more problematic. For example, the teeth of *Troodon* share some morphometric characteristics with those of herbivorous amniotes (Holtz *et al.* 2000), whereas those of other troodontids (notably *Sinovenator*) are more 'typically' carnivorous, with small denticles that are more similar to those of faunivores, such as dromaeo-

saurids (Xu *et al.* 2002*b*). In addition, the absence of teeth and conflicting functional morphological interpretations for other anatomical characters continue to confound dietary interpretations in some non-avian theropods, such as derived oviraptorosaurians (Sues 1997; Barrett 2000).
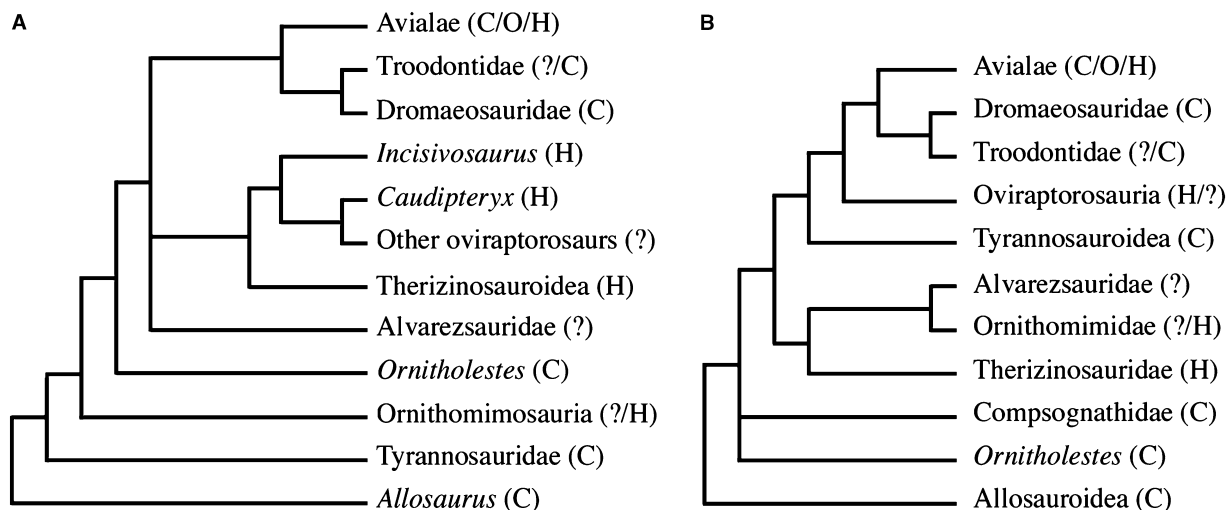
Ornithomimosaurian monophyly is uncontroversial and many systematists treat them as a single operational taxonomic unit in analyses of theropod phylogeny (e.g. Sereno 1999; Holtz 2000; Rauhut 2003). Until recently, however, existing schemes of ingroup relationships were not well established as they were either not based on explicit numerical cladistic analyses (Barsbold and Osmólska 1990; Osmólska 1997) or did not contain more than three taxa (Pérez-Moreno *et al.* 1994). Nevertheless, there was general agreement that the basalmost member of the clade is either *Pelecanimimus* (Early Cretaceous, Barremian, Spain: Pérez-Moreno *et al.* 1994) or *Harpymimus* (Early Cretaceous, Aptian–Albian, Mongolia: Barsbold and Perle 1984), a conclusion strengthened by the first comprehensive numerical cladistic analysis of ornithomimosaurian interrelationships (Kobayashi and Lü 2003). Both *Pelecanimimus* and *Harpymimus* retain teeth at the anterior tips of the jaws, whereas the dentition is lost in all more derived ornithomimosaurs (Barsbold and Perle 1984; Pérez-Moreno *et al.* 1994). The dentition of *Harpymimus* is strongly reduced and consists of 10–11 small, subcylindrical teeth that are confined to the front end of the dentary (Barsbold and Perle 1984); in contrast, *Pelecanimimus* possesses over 200 teeth, which are located in both upper and lower jaws (Pérez-Moreno *et al.* 1994). It has been suggested that the closely packed teeth of *Pelecanimimus* could have acted as the functional equivalent of a single cutting edge, analogous to the rhamphotheca of chelonians, which could have been used for the procurement and slicing of either flesh or vegetation (Pérez-Moreno *et al.* 1994; Barrett 2000). If so, this condition may have been a direct functional precursor of the edentulous, beaked snout of more derived ornithomimosaurs, and might represent an early adaptation to herbivory or omnivory. Moreover, the teeth of *Pelecanimimus* lack the small, closely packed serrations that are characteristic of many carnivorous animals (Pérez-Moreno *et al.* 1994), adding further support to the hypothesis that the diet of this animal differed somewhat from that of the majority of other non-avian theropods. Interestingly, although areas of soft tissue are preserved in the holotype specimen of *Pelecanimimus* (including a small, fleshy occipital crest and a gular pouch) there is no trace of a rhamphotheca in this animal (Pérez-Moreno *et al.* 1994). The basal position of *Pelecanimimus* in ornithomimosaur phylogeny may indicate that the beak appeared in derived ornithomimosaurians concomitant with the loss of teeth, though further material of these taxa is necessary to

explore this hypothesis. For the time being, the dietary preferences of basal ornithomimosaurians remain ambiguous: discrimination between carnivory, herbivory and omnivory is not possible on the basis of available anatomical evidence (Barrett 2000).

Interrelationships between the major clades within Theropoda, particularly within Coelurosauria, are controversial and currently in a state of flux (e.g. Gauthier 1986; Russell and Dong 1993; Makovicky and Sues 1998; Sereno 1999; Holtz 2000; Xu *et al.* 2002*a*; Rauhut 2003). Nevertheless, it is interesting to note that all theropods that are likely to have been herbivorous or omnivorous (therizinosauroids, ornithomimosaurians, troodontids?, oviraptorosaurians and many avian lineages) are coelurosaurs (Barrett 2000; Text-fig. 2), whereas all basal theropods were apparently faunivorous. However, the reasons why herbivory should be confined to Coelurosauria are currently unknown.

Unfortunately, the varied topologies of available coelurosaurian phylogenies and uncertainties in the dietary inferences for various theropod taxa obfuscate the evolutionary pattern of theropod herbivory (Barrett 2000; Holtz *et al.* 2000). For example, in some theropod phylogenies, therizinosauroids and oviraptorosaurians form a clade, but the relationship of this clade to Ornithomimosauria is either distant or unclear (Makovicky and Sues 1998; Holtz 2000; Xu *et al.* 2002*a*; Rauhut 2003; Text-fig. 2); other authors have suggested that ornithomimosaurians and therizinosauroids are sister-taxa and not closely related to oviraptorosaurians (Sereno 1999); and an alternative hypothesis suggests that all three of these groups comprise a monophyletic clade (together with troodontids: Russell and Dong 1993). Moreover, the diets of troodontids, basal ornithomimosaurs and derived oviraptorosaurians remain unclear (see above), further complicating the pattern of dietary evolution that can be inferred from combining theropod tree topology with existing dietary information. Consequently, it is not currently possible to determine the number of times that herbivory evolved within non-avian theropods. It may have appeared just once, at the base of an oviraptorosaur + troodontid + therizinosauroid + ornithomimosaurian clade (*sensu* Russell and Dong 1993), if basal ornithomimosaurians and troodontids were herbivorous. Conversely, herbivory may have originated on multiple separate occasions within these four theropod clades, with the exact number of origins dependent upon (1) the relationships of these groups to each other and (2) the assumptions made regarding dietary inference in clade members whose diets are currently ambiguous or unknown (Text-fig. 2).

Theropod herbivory remains poorly known: additional work on the functional anatomy, phylogeny and palaeoecology of candidate herbivores and omnivores is needed,

A

- Avialae (C/O/H)
- Troodontidae (?/C)
- Dromaeosauridae (C)
- *Incisivosaurus* (H)
- *Caudipteryx* (H)
- Other oviraptorosaurs (?)
- Therizinosauroidea (H)
- Alvarezsauridae (?)
- *Ornitholestes* (C)
- Ornithomimosauria (?/H)
- Tyrannosauridae (C)
- *Allosaurus* (C)

B

- Avialae (C/O/H)
- Dromaeosauridae (C)
- Troodontidae (?/C)
- Oviraptorosauria (H/?)
- Tyrannosauroidea (C)
- Alvarezsauridae (?)
- Ornithomimidae (?/H)
- Therizinosauridae (H)
- Compsognathidae (C)
- *Ornitholestes* (C)
- Allosauroidea (C)

TEXT-FIG. 2. Phylogeny of coelurosaurian theropod dinosaurs with the distribution of probable dietary habits shown in parentheses. Abbreviations: C, carnivory; H, herbivory; O, omnivory; ?, diet is currently uncertain in some or all members of a particular clade. Dietary determinations follow those given in the text. Where more than one dietary habitus is known for a clade, all possible diets are given. A, phylogeny after Xu *et al.* (2002*a*). B, phylogeny after Sereno (1999).

as is direct evidence of diet in these animals (coprolites and enterolites). Nevertheless, a fuller understanding of this rare phenomenon will provide insights into the assembly of herbivorous character complexes in amniotes generally. Moreover, some of the principal morphological features associated with non-avian theropod herbivory (toothlessness, rhamphothecae, gastric mills) also characterize herbivorous birds: consequently, more information on the evolution of these character complexes in non-avian dinosaurs has the potential to shed some light on the origins of avian herbivory.

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