

ULTRASTRUCTURAL AND FUNCTIONAL MORPHOLOGY OF EGGSHELLS SUPPORTS THE IDEA THAT DINOSAUR EGGS WERE INCUBATED BURIED IN A SUBSTRATE

by D. C. DEEMING

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Abstract: The reproductive biology of dinosaurs is of great interest, particularly in light of the many fossil eggs assigned to this group. The ultrastructural characteristics of dinosaur eggshells are examined in order to calculate water vapour conductance, which indicates the nesting environment. Data were mainly derived from the literature but new values are also presented. Allometric analyses were carried out on a variety of shell parameters against predicted egg mass, and comparison was made with allometric equations for bird eggs. Shell thickness was generally larger than seen for extant birds. Total pore number and pores per unit area were similar to values predicted from bird eggs. Total pore area showed an isometric increase with egg mass, parallel to the relationship for birds, but the constant value was an order to magnitude higher than the bird values. Pore radius was unaffected by egg mass. Water vapour conductance showed an allometric increase with egg mass, parallel to the bird val-

ues, but for any given egg mass values for dinosaurs were an order of magnitude higher. Mass-specific water vapour conductance was unaffected by egg mass but was an order of magnitude higher than the bird values. Water vapour conductance per pore showed an allometric decrease with egg mass but again the predicted values were an order of magnitude higher than for bird eggs. The ultrastructural characteristics of dinosaur eggshells indicate that the nesting environment had to be saturated with water vapour and that dinosaur eggs had to be fully buried in a substrate. In this sense, therefore, dinosaur eggs resemble more those of modern reptiles than those of birds. As a consequence, maintenance of incubation conditions would have depended on the prevailing environment.

Key words: dinosaur, eggshells, ultrastructure, water vapour conductance, pore, nesting environment.

INTEREST in the reproductive biology of dinosaurs over the past 25 years has been fuelled by numerous discoveries of fossil eggshells, nests and nesting grounds (see Carpenter *et al.* 1994; Bravo and Reyes 2000). Additionally, recent fortuitous discoveries of embryos in eggs and adults on top of their clutches have provided correlations between egg types and egg-layers (reviewed by Zelenitsky and Hirsch 1997). The direct association of adults and eggs has led to various inferences on dinosaur behaviour, including habitual sitting on nests, protection of eggs and egg incubation similar to that of birds (Norell *et al.* 1995; Dong and Currie 1996; Varricchio *et al.* 1997; Clark *et al.* 1999), although the last interpretation has been challenged (Geist and Jones 1996; Deeming 2002a; Ruben *et al.* 2003).

Fossil eggshells have received considerable attention and their ultrastructure is well described (see for example Mikhailov 1997a). The functional aspects of eggs, how-

ever, have been largely ignored despite their potential for providing palaeobiological inferences. For example, water vapour conductance calculated from eggshell porosity is a valuable tool for inferring the nesting conditions of an egg (Seymour 1979; Deeming 2002a). However, only a few studies on supposed dinosaur eggs have reported such values (Seymour 1979; Williams *et al.* 1984; Sabath 1991; Grigorescu *et al.* 1994; Mikhailov *et al.* 1994; Sahni *et al.* 1994). Deeming (2002a) showed that in general water vapour conductance was high, relative to that predicted for bird eggs, and supported the idea, first proposed by Seymour (1979), that these dinosaur eggs were buried during incubation. This idea may be accepted by some palaeontologists (e.g. Carpenter 1999) but the idea that eggs may be only partially buried is well established in the interpretation of dinosaur reproductive biology (e.g. Horner 2000; Varricchio and Jackson 2004).

The shell conductance value of an egg corresponds closely to its nesting environment and therefore nest conditions can be inferred from these values. For example, most bird eggshells are relatively exposed during incubation, being surrounded by the nest and the adult (Deeming 2002a), and hence experience humidity conditions only modified slightly from the prevailing ambient humidity conditions (Rahn 1991). As a result, the shells have relatively low values for water vapour conductance and lose water during incubation (Ar and Rahn 1985; Ar and Sidis 2002). Megapode birds (Megapodiidae) are exceptional in that they bury their eggs in mounds or holes, and that relative to other birds, their eggshells have high conductance values that actually increase during incubation (see reviews by Booth and Thompson 1991; Booth and Jones 2002). Similarly, grebes (Podicipediformes) lay eggs in wet nests and have eggshells with high conductance values to ensure that they can lose sufficient weight during incubation (Carey 2002). By contrast, reptiles generally bury their eggs in a substrate and the eggs experience humidities at or close to saturation. Reptile eggs have high values for water vapour conductance but under normal conditions do not lose weight during incubation (Deeming and Thompson 1991). However, many gecko (Gekkonidae) eggs are incubated in the open air and have conductance values that are less than those exhibited by equivalent-sized bird eggs (Deeming and Thompson 1991). The preceding examples illustrate that high conductance values correspond to enclosed humid nesting conditions, whereas low conductance values indicate a more open nesting environment. Therefore, contrary to the impression given by Carpenter (1999, pp. 166–170), in modern species knowledge of the water vapour conductance of an eggshell provides a superb insight into the nesting environment.

The increasingly extensive fossil record of eggshells from the Mesozoic permits a re-assessment of the water vapour conductance, a measure of the porosity of dinosaur eggshells. I present an investigation of the relationships between eggshell characteristics and egg mass in these extinct taxa. A review of the functional aspects of eggshells in several dinosaur clades allows a better comparison with extant species and a clearer interpretation of the nesting environment experienced by dinosaur eggs.

Although there is little doubt that most of the eggs analysed for this study belong to dinosaurs, few specimens studied had associated skeletal remains and therefore the taxonomic affinity of most of these eggs remains somewhat questionable. Currently, the identity of eggs (without associated skeletons) is based on the comparison of their egg characteristics with those of eggs that are intimately associated with embryonic or adult remains. It is

only during the past decade, however, that there has been a notable increase in the discovery of such associated specimens. These occurrences are still relatively rare and therefore only a few 'egg types' have assigned taxonomic affinities. Currently, good associations between egg and skeletal taxa exist for allosauroids (preprismatoolithids, embryos; Mateus *et al.* 1997), hadrosaurs (spheroolithids, embryos; Hirsch and Quinn 1990), troodontids (prismatoolithids, embryos and adult; Zelenitsky 2000; Varricchio *et al.* 2002), titanosaurs (megaloolithids, embryos; Chiappe *et al.* 1998) and oviraptorids (elongatoolithids, embryos and adults; Norell *et al.* 1995; Dong and Currie 1996; Clark *et al.* 1999). References in the literature to eggs belonging to other taxa remain unsubstantiated because egg-skeletal associations are unknown. Many references prior to the 1990s may be incorrect in this respect due to a distinct lack of known egg-skeletal associations at that time. In this paper, where possible, I correct the previous assignments of eggs to skeletal taxa based on the egg characteristics.

METHODS

Data on water vapour conductance (G_{H_2O}) and the eggshell characteristics of dinosaur eggshells were collected directly from new fossil specimens (see below) and from a variety of literature and internet sources together with some unpublished data. Published data were re-calculated in order to standardize the techniques employed to determine G_{H_2O} (assuming Fick's law of diffusion). Two types of records are available. The first type provided sufficient data for the calculation of unreported shell parameters, whereas the data reported in the second type were limited to values of water vapour conductance. These are reported for completeness but were not included in the analyses.

Determination of shell characteristics from fossil material

A considerable amount of new data were provided by Darla Zelenitsky (pers. comm. 2002) using the following methodology. Depending on the specimen, 2–10 shell fragments per egg were analysed by her for porosity. Tangential thin sections of fragments were photographed using a Nikon Coolpix 990 digital camera mounted on a petrographic microscope. The area examined ranged from approximately 1 to 8 cm². The cross-sectional area of each pore was highlighted in Adobe Photoshop 5.5, and then each image was analysed using the Image Processing Toolkit 4.0. The software counted and measured the area of each pore, allowing complete pore size and distribution statistics to be determined.

Calculation of eggshell characteristics

The variables (with units) and equations employed in this study are summarized in Tables 1 and 2, respectively. Using linear dimensions (maximum length, L , and maximum breadth, B) egg mass (M) was calculated on the basis of the equation established for elongate symmetrical crocodilian eggs (Eq. 1, Table 2). Using the constant derived from bird eggs [5.28×10^{-4} g mm $^{-3}$; (Eq. 2) Hoyt 1987] produced an M value only 2 per cent larger than that from crocodilian eggs. Although most sources reported surface area for the dinosaur eggs together with shell thickness (L_s), in order to standardize values for further analysis, surface area of the eggs (A_s) was recalculated using the calculated value of M (Eq. 3).

Pore density (D), total number of pores (N) and A_s are related by Eq. 4. Total pore area (A_p), mean individual pore area (A) and total number of pores (N) are related by Eq. 5. Provided enough parameters were reported, these equations were used to calculate unreported variables, e.g. pore number. Although it may not be applicable to all species, for simplicity pore canals were assumed to be circular in cross-section for the calculation of the mean effective pore radius (r ; Eq. 6).

Values for G_{H_2O} were calculated on the basis of A_p and L_s using the equation of Ar and Rahn (1985) (Eq. 7), whereas the equivalent G_{H_2O} for a bird egg of the same mass was calculated using M (Eq. 8; again Ar and Rahn 1985). These equations reported by Ar and Rahn (1985) were employed in preference to those of Ar *et al.* (1974), which had been used by previous authors (e.g. Williams *et al.* 1984), because they were derived from a much

TABLE 1. Variables used in calculations for egg characteristics.

Variable	Definition	Units
L	Maximum egg length	mm
B	Maximum egg breadth	mm
M	Egg mass	g
L_s	Shell thickness	mm
A_s	Surface area	mm 2
N	Total number of pores	per egg
D	Pore density	Nmm $^{-2}$
r	Pore radius	μ m
A_p	Total pore area	mm 2
A	Mean individual pore area	mm 2
G_{H_2O}	Water vapour conductance	mgH $_2$ O day $^{-1}$ Torr $^{-1}$
spG_{H_2O}	Mass-specific water vapour conductance	mgH $_2$ O day $^{-1}$ Torr $^{-1}$ g $^{-1}$
pG_{H_2O}	Water vapour conductance per pore	μ gH $_2$ O day $^{-1}$ Torr $^{-1}$ pore $^{-1}$

TABLE 2. Formulae used for calculations of egg characteristics.

Equation no.	Formula	Reference
(1)	$M = 5.60 \cdot 10^{-4} LB^2$	Calculated for crocodilian eggs (Deeming and Ferguson 1990)
(2)	$M = 5.48 \cdot 10^{-4} LB^2$	Calculated for bird eggs (Hoyt 1987)
(3)	$A_s = 4.835M^{0.662}$	Paganelli <i>et al.</i> (1974)
(4)	$N = D \cdot A$	
(5)	$A_p = N \cdot A_s$	
(6)	$r = \sqrt{A\pi^{-1}}$	Standard formula for radius of a circle of area A
(7)	$G_{H_2O} = A_p(0.477L_s)^{-1}$	Ar and Rahn (1985)
(8)	$G_{H_2O} = 0.384M^{0.814}$	Ar and Rahn (1985)
(9)	$spG_{H_2O} = G_{H_2O} \cdot M^{-1}$	
(10)	$pG_{H_2O} = G_{H_2O} \cdot N^{-1}$	

larger number of species. Mass-specific water vapour conductance (spG_{H_2O}) was determined by dividing G_{H_2O} by M (Eq. 9) and water vapour conductance per pore (pG_{H_2O}) was calculated by dividing G_{H_2O} by N (Eq. 10).

Table 3 shows the morphological characteristics of eggs and eggshells for various dinosaur or egg taxa. Based on the characteristics of eggs with associated embryonic remains, it was assumed that ornithopods laid prolatospherulitic-type (prolatocanalliculate pores) eggshells ($N = 4$), whereas titanosaur sauropods laid tubospherulitic (tubocanalliculate pores) eggshells ($N = 24$). Dendroolithid eggs were considered to belong to ornithopods due to the morphological characteristics they share with known ornithopod eggs. Those eggs ($N = 11$) with angusticanalliculate pores and two structural zones, an inner mammillary layer and an outer continuous (ratite ornithoid-type) or prismatic (prismatic-type) layer, were considered to belong to non-avian theropods (subsequently herein referred to just theropods). Based on its morphological characteristics, an egg described by Kolesnikov and Sochava (1972) I assigned to the Faveoololithidae. Faveoololithid eggs ($N = 4$) could belong to either sauropods or ornithischians, so I considered the egg-laying taxon as indeterminate. There were three reports (see Table 3) of eggshells as yet unassigned to either dinosaur taxa or ootaxa.

Only reports with complete sets of values (i.e. complete rows in Table 3) were employed in the allometric analysis. There were several instances where different eggshell specimens were assigned to the same type of dinosaur (e.g. indeterminate theropods, originally assigned by Sabath 1991 to 'Protoceratopsidae') or even to the same oogenus (e.g. *Megaloolithus* spp.). For the data analysis,

these individual records were considered separately. This approach was adopted because: (1) within individual oögenera there was considerable variation in egg size and shell characteristics, and (2) the taxonomic identity of most of these specimens is not confirmed by the association with fossil embryonic remains.

All statistical analyses were carried out using Minitab (release 12.21). Allometric relationships between various eggshell variables and M were investigated by least-squares regression analysis carried out on Log_e -transformed data in order to generate power function equations (Reiss 1991) for all dinosaur eggshells combined. The relatively large number of values for Theropoda and Sauropoda eggshells meant that regression analysis could also be performed on these subsets of data but sample size was considered to be too small for the ornithipod and unknown dinosaur type data. The morphological characteristics of the eggs and eggshells described in Table 3 were used to assign these eggs to taxonomic groups that were compared using one-way analysis of variance that employed Tukey's comparison set at a family error rate of $P < 0.05$.

RESULTS

My calculated values for $G_{\text{H}_2\text{O}}$ of 24 eggs were, on average, 82.7 per cent lower than previously reported values for $G_{\text{H}_2\text{O}}$ (Table 3). However, my calculated values for shells reported by Williams *et al.* (1984) were between 51 and 81 per cent of the published values. Given the possibility that this discrepancy reflected the constant in the equation supposedly used by the various authors to calculate $G_{\text{H}_2\text{O}}$ (0.427; Ar *et al.* 1974), the constant value was calculated for each reported value by rearranging Eq. 8 (Ar and Rahn 1985). The resulting values were variable, with a mean value of 0.370 (SD = 0.069) and a range of 0.227–0.427.

Here new data are provided for allosauroid and oviraptorosaur eggs, which have predicted $G_{\text{H}_2\text{O}}$ values 7.0 and 2.1 times greater than that of equivalent-sized bird eggs, respectively. The lowest conductance was for a troodontid egg, which showed a value consistent with that of an equivalent-sized avian egg. New values for titanosaur, hadrosaur and faveoololithid eggs were similar to my corrected values of previous reports for these eggs.

Regression estimates for the power relationships between different eggshell variables and egg mass for 35 examples are shown in Table 4 and Text-figure 1. The regression estimates for bird eggs (taken or derived from Ar and Rahn 1985) in this figure are shown as a solid line for eggs up to the egg mass of the largest living species, i.e. 1500 g for an average-sized ostrich egg (Deeming and Ar 1999), and then a dotted line shows the values

extrapolated to egg masses equivalent to those calculated for dinosaur species.

For all dinosaur eggs in the sample, shell thickness increased slowly with increasing mass (Text-fig. 1A). Regardless of the M value, regression estimates of theropod eggshells were consistently 1.5 times thicker than for equivalent-sized bird eggs (Text-fig. 1A). However, as M increases the regression estimates for titanosaur and bird eggs converge, and thus shell thickness was similar among eggs with an M greater than 2000 g. Although regression estimates could not be provided for ornithopods, their shells were at least twice as thick as that of avian eggs of an equivalent mass.

For pore number and pores per mm^2 dinosaur eggs were similar to those of extant birds (Text-fig. 1B–C). Values for theropod eggs lay below the regression estimates for bird eggs (Ar and Rahn 1985), whereas titanosaur and, in particular, faveoololithid eggs were above the line.

The increase in A_p with M was nearly isometric for dinosaur eggshells (Table 4). Values derived from the regression estimate for all dinosaur eggs were an order of magnitude higher than those predicted for birds of an equivalent mass. Values for theropod eggs derived from the regression estimate were approximately four times that derived from the equation for bird eggs (Text-fig. 1D).

Pore radius was not significantly affected by M in dinosaur eggshells overall or in titanosaur or theropod eggshells alone (Text-fig. 1E; Table 4). By contrast, in bird eggs pore radius increases with increasing M (Text-fig. 1E). In general, for small ornithopod and theropod eggs pore radius was 6–8 times greater than for bird eggs of an equivalent mass and 1.5–2.5 times larger for dinosaur eggs greater than 1000 g.

$G_{\text{H}_2\text{O}}$ increased with a power of 0.827 in dinosaur shells, which was almost identical to the exponent exhibited by bird eggs (0.825; Ar and Rahn 1985). However, values derived from the regression estimate in the former were around an order of magnitude higher than the values derived from the regression estimate for the latter (Text-fig. 1F; Table 4). Values from the regression estimate for theropod eggs were three times greater than that of birds, whereas values derived from the equation for titanosaur eggs were an order of magnitude greater than that of birds. $G_{\text{H}_2\text{O}}$ values for faveoololithid eggs were over two orders of magnitude higher than bird eggs of an equivalent mass (Text-fig. 1F).

$spG_{\text{H}_2\text{O}}$ was not significantly affected by M but values for dinosaur eggs overall were an order of magnitude higher than that predicted for bird eggs (Table 4; Text-fig. 1G), with theropods having a regression estimate value mid-way between all dinosaurs and birds. Faveoololithid eggs had $spG_{\text{H}_2\text{O}}$ values an order of magnitude higher than other dinosaurs and two orders of magnitude

TABLE 3. Data on the shell characteristics of dinosaur eggs. Values in bold are calculated from the reported values indicated in plain text. Dashes indicate that data were unavailable.

Species	Location	Eggshell morphotype	Pore type	L	B	M	A _s	L _s	D	N	A _p	A	r	Calculated G _{H₂O}	Reported pG _{H₂O}	Predicted avian G _{H₂O}	G _{H₂O} Ratio ¹	Source(s) ²		
Ornithischia																				
Ornithopoda																				
Spheroolithidae	1	3	2	90	70	247	18549	1.5	2.16	40000	1280	0.03200	100.9	1909	7.73	47.73	734, 2000	35	55.1	1, 7
<i>Spheroolithus albertensis</i>	7	3	2,5	80	80	287	20475	1.0	1.61	32986	308	0.00933	54.5	675	2.35	20.46	-	39	17.2	12
<i>Spheroolithus</i> sp.	9	3	2	80	80	287	20475	2.1	1.94	39743	417	0.01050	57.8	444	1.55	11.18	-	39	11.3	12
Dendroolithidae	1	4	2	115	108	751	38738	2.3	0.83	32000	1450	0.04531	120.1	1410	1.88	44.07	540.3, 1500	87	16.3	1, 7
Saurischia																				
Theropoda																				
Elongatoolithidae	1	5	1	160	60	323	22136	1.3	0.79	17500	130	0.00743	48.6	224	0.69	12.78	91, 250	43	5.2	1, 7
<i>Macroolithus yaotunensis</i>	10	5	1	-	-	911	47400	1.45	0.29	13500	139	0.01030	57.3	-	-	231	102	-	-	14
<i>Macroolithus rugustus</i>	10	5	1	-	-	592	35400	1.42	0.36	12700	71	0.00559	42.2	-	-	120	71	-	-	14
<i>Elongatoolithus andrewsi</i>	10	5	1	-	-	384	27400	0.98	0.31	8500	55	0.00647	45.5	-	-	136	50	-	-	14
<i>Lourinhanosaurus antunesi</i>	3	?	6	130	94	643	34958	0.9	0.25	8750	223	0.02545	90.0	541	0.84	61.88	-	76	7.1	10
<i>Macroelongatoolithus xixianensis</i>	10	5	1	390	120	3145	99958	2.1	0.99	98459	549	0.00558	42.1	600	0.19	6.09	-	283	2.1	12
<i>Prismatoolithus levis</i> (troodontid)	7	1	1	140	65	331	22528	1.0	0.34	7750	17	0.00221	26.5	39	0.12	5.06	-	44	0.9	12
Indeterminate theropod [Protoceratopsidae]*	1	1	1	120	50	168	14373	0.3	0.18	2600	10	0.00385	35.0	75	0.44	28.68	29, 80	25	3.0	1, 7
Indeterminate theropod [Protoceratopsidae]*	1	1	1	145	52.5	224	17379	1.3	0.53	9200	50	0.00544	41.6	89	0.40	9.73	32, 90	32	2.8	1, 7
Indeterminate theropod [Protoceratopsidae]*	1	1	1	150	50	210	16661	1.2	0.42	7000	35	0.00500	39.9	65	0.31	9.32	25, 70	30	2.2	1, 7
Indeterminate theropod [Protoceratopsidae]*	1	1	1	153	56.5	273	19803	1.3	0.35	7000	100	0.01429	67.4	176	0.65	25.16	189	38	4.7	2
<i>Sauropoda Titanosaurus [Hypselosaurus priscus]*</i>	4	?	?	154	154	2045	75182	2.3	3.20	240000	947	0.00395	35.4	921	0.45	3.84	1203	200	4.6	2
Titanosaur I	6	2	4	160	160	2294	8111	-	-	-	-	-	-	-	-	-	2650	218	12.2	4
Titanosaur II	6	2	4	160	160	2294	8111	-	-	-	-	-	-	-	-	-	3490	218	16.0	4
Titanosaur Type 2	4	2	?	160	140	1756	67967	1.4	1.75	118825	1723	0.01450	67.9	2753	1.57	23.17	3551	175	15.7	5
<i>Cairatoolithus roussetensis</i>	4	2	4	170	170	2751	91489	1.7	1.63	149127	1004	0.00673	46.3	1305	0.47	8.75	-	253	5.2	13

TABLE 3. Continued.

Species	Location	Eggshell morphotype	Pore	L	B	EM	A _s	L _s	D	N	A _p	A	r	Calculated G _{H₂O}	spG _{H₂O}	Reported pG _{H₂O}	Predicted avian G _{H₂O}	G _{H₂O} Ratio ¹	Source(s) ²	
<i>Cairanolithus dughii</i>	4	2	4	175	175	3001	96910	2.1	3.83	371167	679	0.00183	24.1	724	0.24	1.95	—	272	2.7	13
<i>Cairanolithus dughii</i> (Titanosaur Type 1)	4	2	4	175	175	3001	96910	1.9	3.02	297168	1412	0.00475	38.9	1662	0.55	5.59	1825	272	6.1	5
<i>Megaloolithus</i> sp. (<i>Telmatosaurus</i> <i>transsylvanicus</i>)	2	2	?	175	158	2446	84647	2.3	1.70	143899	2216	0.01540	70.0	2155	0.88	14.98	2782	230	9.4	3
<i>Megaloolithus</i> sp. (recrystallized)	4	2	4	150	150	1890	71353	1.6	2.21	157540	573	0.003634	34.0	787	0.42	5.00	—	186	4.2	12
<i>Megaloolithus</i> sp. (non-recrystallized)	4	2	4	170	170	2751	91489	2.4	6.25	571806	2989	0.005227	40.8	2786	1.01	4.87	—	253	11.0	12
<i>Megaloolithus mamillare</i> (Titanosaur Type 3.1)	4	2	4	210	210	5186	139195	1.6	1.78	252048	1661	0.00659	45.8	2322	0.44	9.21	4500	427	5.4	5
<i>Megaloolithus mamillare</i> (Titanosaur Type 3.2)	4	2	4	215	215	5565	145854	1.3	0.88	130504	1051	0.00805	50.6	1808	0.32	13.85	2893	453	4.0	5
<i>Megaloolithus mamillare</i>	4	2	4	—	—	—	—	0.9	—	—	1610	—	—	4002	—	—	4636.6	—	—	8
<i>Megaloolithus siruguei</i> (Titanosaur Type 4)	4	2	4	210	210	5186	139195	1.8	3.43	477440	1876	0.00393	35.4	2395	0.46	5.00	—	427	5.6	13
<i>Megaloolithus siruguei</i> (Titanosaur Type 4)	4	2	4	185	185	3546	108218	2.2	4.33	475434	2496	0.00525	40.9	2539	0.71	5.35	3144	312	8.1	5
<i>Megaloolithus siruguei</i> (Titanosaur Type 4)	4	2	4	215	185	4121	119538	2.2	3.89	464077	3439	0.00741	48.6	3497	0.85	7.54	4864	353	9.9	5
<i>Megaloolithus siruguei</i>	5	2	4	250	180	4536	127384	3.0	1.50	191076	1816	0.03801	55.0	1354	0.30	7.09	—	382	3.5	6,11
<i>Megaloolithus siruguei</i>	4	2	4	—	—	—	—	1.8	—	—	3280	—	—	4077	—	—	4244	—	—	8
<i>Megaloolithus siruguei</i>	4	2	4	195	195	4152	120145	2.2	2.99	359234	1487	0.00414	36.3	1512	0.36	4.21	—	356	4.3	13
<i>Megaloolithus aureliensis</i>	4	2	4	—	—	—	—	0.9	—	—	2040	—	—	5071	—	—	5137.2	—	—	8
<i>Megaloolithus aureliensis</i>	4	2	4	210	210	5186	139195	1.1	2.23	310405	2337	0.00753	49.0	4797	0.93	15.45	—	427	11.2	13
<i>Megaloolithus pseudomamillare</i>	4	2	4	200	180	3629	109890	1.6	2.72	298902	1187	0.00397	35.6	1629	0.45	5.45	—	318	5.1	13
<i>Megaloolithus petralta</i>	4	2	4	200	155	2691	90153	1.8	2.83	255132	1135	0.00445	37.6	1388	0.52	5.44	—	249	5.6	13
<i>Megaloolithus microtuberculata</i>	4	2	4	160	160	2294	81111	2.2	4.40	356888	899	0.00252	28.3	906	0.40	2.54	—	218	4.2	13

Unknown type	1	?	3	148	134	1488	60911	2.5	22:70	1382684	16440	0.01189	61:52	14712	9:89	10:64	153	96.5	9
?Faveooloolid	1	?	3	148	134	1488	60911	2.5	22:70	1382684	16440	0.01189	61:52	14712	9:89	10:64	153	96.5	9
Faveooloolithidae	1	6	3	150	135	1531	62063	2.3	1374:50	646000	20300	0.03142	100:0	19745	12:90	30:57	156	126.5	1, 7
Faveoolithis sp.	9	6	3	130	130	1230	53702	1.6	40:68	2179217	15261	0.00700	47:2	21338	17:34	9:79	130	163.7	12
?Faveooloolid	1	6	3	148	148	1815	69476	2.5	7:90	560000	17700	0.03161	100:3	15839	8:72	28:28	182	86.9	2
(Gobi Sauripod)																			
Ootype 1	4	?	?	-	-	-	-	1.0	-	-	7910	-	-	17696	-	-	-	-	8
Ootype 2	4	?	?	-	-	-	-	0.7	-	-	981	-	-	3135	-	-	-	-	8
Ootype 3	4	?	?	-	-	-	-	1.4	-	-	5320	-	-	8501	-	-	-	-	8

* Indicates published taxonomic designation that may no longer be valid. ¹Ratio = calculated G_{H_2O}/G_{H_2O} predicted from avian eggs of equivalent mass. ²References: 1, Sabath 1991; 2, Seymour 1979; 3, Grigorescu *et al.* 1994; 4, Sahni *et al.* 1994; 5, Williams *et al.* 1984; 6, López-Martínez *et al.* 2000; 7, Mikhailov *et al.* 1994; 8, Kérourio 2001; 9, Kolesnikov and Sochava 1972; 10, Mateus, pers. comm. 2002; 11, López-Martínez, pers. comm. 2002; 12, Zelenitsky, pers. comm. 2002; 13, Garcia and Vianey-Liaud 2001; 14, Mou 1992. Location: 1, Gobi Desert; 2, Romania; 3, Portugal; 4, France; 5, Spain; 6, India; 7, Canada; 8, USA; 9, Korea; 10, China. Eggshell morphology: 1, prismatic; 2, tubospherulithic; 3, prolatospherulithic; 4, dendrospherulithic; 5, ratite ornithoid; 6, filispherulithic. Pore type: 1, angusticanalliculate; 2, multicanalliculate; 3, tubocanalliculate; 4, tubocanalliculate; 5, obliquicanalliculate; 6, rimocanalliculate.

higher than values predicted for bird eggs of an equivalent mass.

In dinosaur eggs, pG_{H_2O} showed a significant decline as M increased and values derived from the regression equation were about an order of magnitude higher than predicted for bird eggs (Table 4; Text-fig. 1H). In bird, theropod and titanosaur eggs, pG_{H_2O} did not scale with M (Text-fig. 1H). pG_{H_2O} in faveooloolithid eggs was similar to that for other dinosaur taxa.

Correlation analysis on fully independent variables showed that L_s was significantly ($P < 0.001$) correlated with N , D and A_p . Neither L_s , N nor D were significantly correlated with r ($P > 0.05$ in all cases).

On average, titanosaurs laid significantly bigger eggs than the other dinosaurs (Table 5). Compared with titanosaurs and unknown dinosaur taxa (faveooloolithid eggs), shell thickness was significantly thinner in theropod eggshells. Faveooloolithid eggs had significantly higher values for most variables with the exception of pG_{H_2O} . Ornithopod eggs had significantly higher values for spG_{H_2O} compared with saurischians, whereas titanosaur eggshells had significantly lower values for pG_{H_2O} (Table 5).

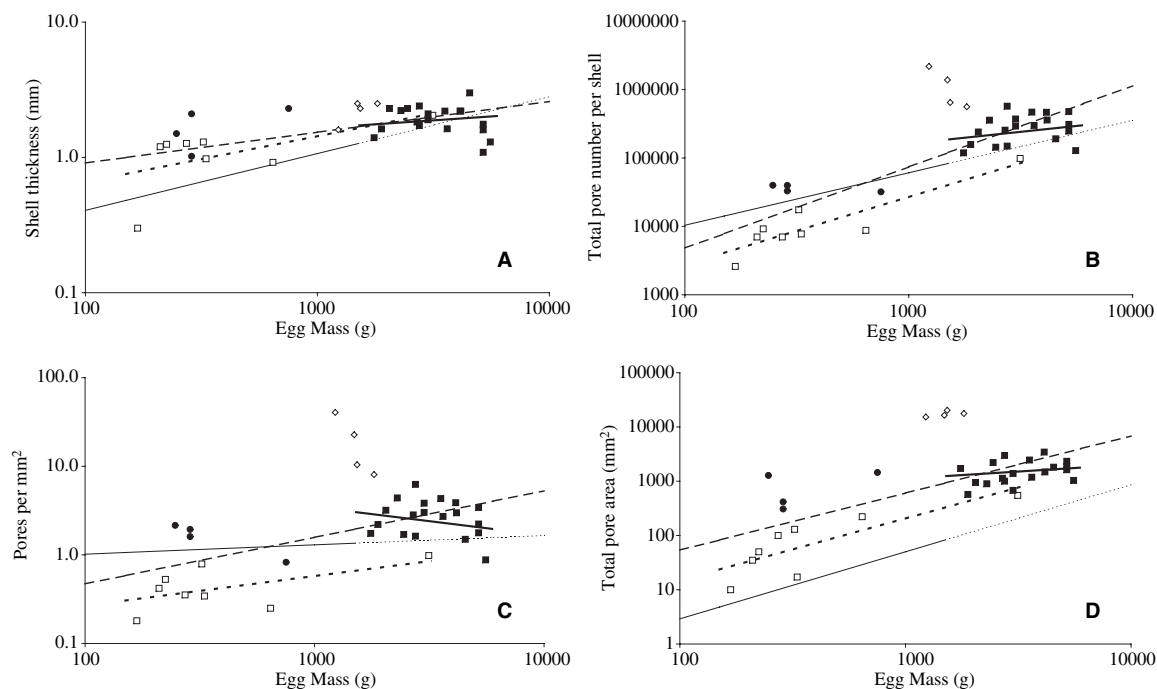
DISCUSSION

Reports of water vapour conductance in fossil eggshells

Reports by Sahni *et al.* (1994) and Kérourio (2001) could not be thoroughly analysed in this study due to the lack of complete descriptions of their material. Only egg dimensions and G_{H_2O} values were published by Sahni *et al.*, so a reassessment of water vapour conductance in their titanosaur eggs was not possible. Kérourio did not report egg dimensions or pore numbers in his six reports of eggshells, which precluded calculation of pore radius and other potentially useful values.

Most reports of dinosaur eggshells show high conductance values relative to birds, although both previous and current reports are, at best, estimates of values *in vivo*. Nonetheless, a notable result of my analysis of previous reports was the variability in the standard of accuracy of the calculations for determining water vapour conductance in dinosaur eggshells. Although some of the differences in calculation are explained by authors (e.g. Seymour 1979; Williams *et al.* 1984) there are other studies where the errors have detracted from a meaningful assessment of G_{H_2O} in dinosaur eggshells.

Morphometric characteristics and gas conductance values were provided for eggshells from Romania by Grigorescu *et al.* (1994), which they assumed to belong to the hadrosaur *Telmatosaurus transsylvanicus*. These eggs, however, share several characteristics (shape, size, ornamentation, ultrastructure) with those of known titanosaur eggs



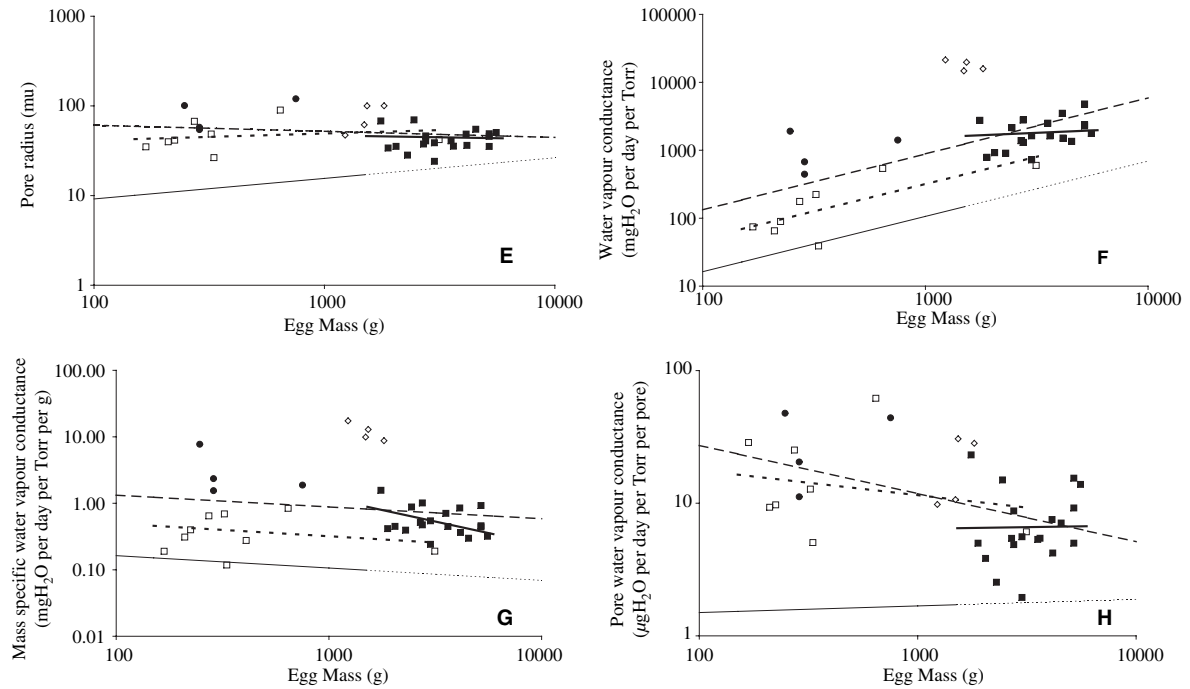
TEXT-FIG. 1. Relationship between various eggshell parameters and egg mass (g) for dinosaur eggshells. In each graph eggshells from saurischians are represented by square symbols (\square , Theropoda; \blacksquare , Sauropoda), from ornithomimiformes are represented by solid circles (\bullet) and from unknown types are indicated by diamonds (\diamond). - - - represents the regression line described in Table 4 for all dinosaur eggs; . . . is the regression estimate for theropod eggs; the bold solid line is for titanosaur eggs (Table 4). The regression estimate for avian eggs is shown by the thin solid line and extrapolated beyond 1500 g by the dotted line. A, shell thickness (L_s , mm); the regression estimate for avian eggs is $L_s = 0.05869M^{0.420}$ (Ar and Rahn 1985). B, total pores per eggshell (N); the regression estimate for avian eggs is $N = 304M^{0.767}$ (Ar and Rahn 1985). C, pores per mm^2 of eggshell (D); the regression estimate for avian eggs is $D = 0.629M^{0.105}$ (calculated using data from Ar and Rahn 1985). D, total pore area of the eggshell (A_p , mm^2); the regression estimate for avian eggs is $A_p = 0.0098M^{1.236}$ (Ar and Rahn 1985). E, pore radius (r , μm); the regression estimate for avian eggs is $r = 3.177M^{0.230}$ (Ar and Rahn 1985). F, water vapour conductance of the eggshell ($G_{\text{H}_2\text{O}}$, $\text{mgH}_2\text{O d}^{-1} \text{Torr}^{-1}$); the regression estimate for avian eggs is $G_{\text{H}_2\text{O}} = 0.368M^{0.825}$ (Ar and Rahn 1985). G, mass-specific water vapour conductance of the eggshell ($spG_{\text{H}_2\text{O}}$, $\text{mgH}_2\text{O d}^{-1} \text{Torr}^{-1} \text{g}^{-1}$). The regression estimate for avian eggs is $spG_{\text{H}_2\text{O}} = 0.384 M^{-0.186}$ (calculated using data from Ar and Rahn 1985). H, water vapour conductance per pore ($pG_{\text{H}_2\text{O}}$, $\text{mgH}_2\text{O d}^{-1} \text{Torr}^{-1}$); the regression estimate for avian eggs is $pG_{\text{H}_2\text{O}} = 1.190M^{0.050}$ (Ar and Rahn 1985).

from South America (Chiappe *et al.* 1998) and, therefore, also probably belong to titanosaurs (Carpenter 1999). Grigorescu *et al.* (1994) provided a range of values for $G_{\text{H}_2\text{O}}$, although a miscalculation in mean pore area resulted in an area almost twice that of the actual value (0.0258 mm^2 vs. 0.0154 mm^2). My corrected calculation for $G_{\text{H}_2\text{O}}$ is comparable to other values for known titanosaur eggs.

Sabath (1991) and Mikhailov *et al.* (1994) reported data for gas conductance on the same seven types of eggshell, although there are discrepancies in N and L_s values between these two papers. A miscalculation by Sabath resulted in reported $G_{\text{H}_2\text{O}}$ values that were approximately one-third of that subsequently reported in a revision by Mikhailov *et al.* (1994). The seven revised values reported by Mikhailov *et al.* were not all calculated using the same constant value, and thus a mean of 0.421 (with a range of 0.400–0.427) was used instead of 0.427. K  ourio (2001)

also reported values for $G_{\text{H}_2\text{O}}$ that appear to be derived using different values for the constant. The present study corrected these aforementioned discrepancies. In general, there was an acceptable degree of similarity between the reported surface area and values predicted from calculated egg mass for most eggshell types except for the data reported by Sabath (1991) and Mikhailov *et al.* (1994). In these publications A_s was overestimated by 50–90 per cent with the exception of a faveoolithid egg (Sabath 1991) that was underestimated by 32 per cent.

It is interesting to note that Sabath (1991) provided data on the morphology of eggshells attributed to the enantiornithine bird *Gobipteryx minuta* of the Upper Cretaceous of Mongolia (Elzanowski 1981). Deeming (2002a) showed that water vapour conductance of this eggshell was much higher than would be predicted on the basis of its egg mass. A new calculation of the values based on a new value for M derived from the technique



TEXT-FIG. 1. Continued

TABLE 4. Regression estimates for measured and derived variables from Table 1 as a function of egg mass. The equations have the form: variable = constant $\times M^{\text{exponent}}$. SE is the standard error of power. Significance values (P) are derived from one-way analysis of variance.

Unit	All Dinosaurs ($N = 35$)					Theropods ($N = 8$)					Titanosaurs ($N = 19$)				
	Constant	Exponent	SE	r^2 (%)	P	Constant	Exponent	SE	r^2 (%)	P	Constant	Exponent	SE	r^2 (%)	P
L_s	0.361	0.209	0.009	31.3	0.001	0.137	0.340	0.070	33.1	NS	5.387	-0.130	0.037	3.8	NS
N	22.18	1.182	0.026	63.3	0.001	27.58	0.997	0.072	80.1	0.003	11719	0.386	0.071	8.5	NS
D	0.046	0.521	0.027	25.1	0.002	0.056	0.338	0.072	31.4	NS	24.24	-0.276	0.071	4.5	NS
A_p	0.479	1.036	0.036	42.4	0.001	0.074	1.149	0.120	65.6	0.015	23.34	0.511	0.069	14.4	NS
r	83.02	-0.073	0.010	4.4	NS	29.14	0.076	0.057	3.5	NS	25.18	0.063	0.041	0.7	NS
G_{H_2O}	2.965	0.827	0.031	37.5	0.001	1.194	0.809	0.100	57.8	0.029	9.71	0.640	0.070	20.6	NS
spG_{H_2O}	2.971	-0.173	0.031	2.6	NS	1.202	-0.192	0.099	7.3	NS	9.92	-0.362	0.075	7.6	NS
pG_{H_2O}	134	-0.355	0.019	23.0	0.004	42.43	-0.189	0.128	4.3	NS	0.83	0.254	0.094	2.2	NS

employed here showed that G_{H_2O} was even higher than that shown by Deeming (2002a). Although L_s in *G. minuta* was close to that predicted from M for a modern bird, values for N , D , A_p and r in *G. minuta* were much higher than predicted for a modern bird egg (Table 6). The high value of G_{H_2O} was due to a high number of large pores.

Calculation of water vapour conductance

The method for determining the value for the parameter pore length was perhaps the most variable among reports, and herein it was assumed that shell thickness was equal

to pore length. In Williams *et al.* (1984), for example, pore length was calculated as the distance between the top of the mammillary layer and the pore orifice on the shell surface, and thus excluded the height of the surface ornamentation. Therefore, their effective pore length was considerably shorter, so their G_{H_2O} values were much higher than those calculated in the present study. Seymour (1979) also used this method but only for shells of the French titanosaur (*Hypselosaurus priscus*) and not for the two other types of shell he described. For the same reason Vianey-Liaud and Garcia (2000) also provided measurements for pore length that were 57–80 per cent of the maximum shell thickness. I think that because

TABLE 5. Mean (\pm SE) values for eggshell variables (Table 1) based on dinosaur type. Within rows, values with different superscripts are significantly different at $P < 0.05$.

	Ornithopods	Theropods	Titanosaurs	Unknown type (faveololithid eggs)
Number	4	8	19	4
M	393 ^a \pm 120	665 ^a \pm 358	3460 ^b \pm 282	1516 ^a \pm 120
L_s	1.73 ^a \pm 0.29	1.16 ^{a,b} \pm 0.17	1.94 ^{a,c} \pm 0.10	2.23 ^{a,c} \pm 0.22
N	36182 ^a \pm 2140	19781 ^{a,b} \pm 11336	294944 ^{a,c} \pm 30702	1191975 ^d \pm 377326
D	1.64 ^a \pm 0.29	0.48 ^a \pm 0.10	2.87 ^a \pm 0.30	20.44 ^b \pm 7.44
A_p	864 ^a \pm 293	139 ^a \pm 64	1623 ^a \pm 180	17425 ^b \pm 1080
r	83.34 ^a \pm 16.19	48.90 ^{a,b} \pm 7.21	43.18 ^{a,b} \pm 2.74	77.26 ^{a,c} \pm 13.54
G_{H_2O}	1110 ^a \pm 337	226 ^a \pm 78	1953 ^{a,b} \pm 236	17909 ^b \pm 1572
spG_{H_2O}	3.38 ^a \pm 1.46	0.46 ^b \pm 0.09	0.60 ^b \pm 0.07	12.21 ^c \pm 1.92
pG_{H_2O}	30.86 ^a \pm 8.91	19.84 ^a \pm 6.74	7.86 ^b \pm 1.24	19.82 ^a \pm 5.57

water vapour still has to diffuse through the outer surface of the shell membrane, to the void between the mammillae, to the inner pore orifice, and finally through any region delimited by surface ornamentation, these measurements of effective pore length are questionable. The inner and outer surface regions present their own resistance to gas diffusion and, although perhaps small (Seymour 1979), should be factored into the analyses until much needed work on such resistances in fossil eggshells is conducted. However, it has to be noted that if effective pore length does not correspond to actual pore length (Seymour 1979; Vianey-Liaud and Garcia 2000) then the values for G_{H_2O} all increase. This could be significant for eggs of theropods, which have a recognized cone layer. If the distance across which water vapour has to diffuse starts at the top of the cone layer then pore length will be reduced and G_{H_2O} will increase.

On the other hand, Grigorescu *et al.* (1994) concluded that pore length could be twice as long as shell thickness because some of the pores were oblique. The relative importance of these pores to an overall value of G_{H_2O} would depend on the proportion of these pores in the shell and the angle of the pore to the interior surface. Hence, the actual contribution of oblique pores to gas

conductance could not be determined. In light of these difficulties I assumed that pore length was equal to shell thickness, so any conductance values average out the total resistance network across the shell from the outer shell membrane.

The calculations in previous reports and this paper assume that gas diffusion through pores in dinosaur eggshells followed Fick's law (Ar *et al.* 1974). This assumes that the area of the pore is the same along the length of the pore canal and gas conductance is a function of A_p and the effective pore length (assumed here to equal L_s). However, if pore shape departs from this simple tubular structure to adopt a broader, more funnel-shaped structure then what effect does this have on conductance? Compared with a simple tubular pore canal, the broader parts of funnel-shaped pores have a lower resistance to gas diffusion and so overall gas conductance of an individual pore is increased (Tøien *et al.* 1988). Should further study reveal that funnel-shaped pores constitute a high proportion of the total number of pores in a dinosaur eggshell then the eggshell gas conductance will also increase.

In conclusion, the values for G_{H_2O} presented here almost certainly underestimate the actual values of the shells *in vivo*. To what extent pore length, shape and ori-

TABLE 6. Shell characteristics of the enantiornithine bird *Gobipteryx minuta* from the Upper Cretaceous of Mongolia, re-calculated from Sabath (1991) on the basis of $L = 42.5$ mm, $B = 20.5$ mm, $M = 10$ g and $A_s = 2189$ mm². Values in bold are calculated from reported values in plain text.

Symbol	Name	Units	Value	Predicted from bird relationships
L_s	Shell thickness	mm	0.14	0.15
N	Total pore number	per egg	5900	1778
D	Pores per mm ²	mm ⁻²	2.4	0.8
A_p	Total pore area	mm ²	4.00	0.17
r	Pore radius	μ m	14.7	5.4
G_{H_2O}	Water vapour conductance	mgH ₂ O (d Torr) ⁻¹	63.9	2.5

entation will contribute to the conductance values will require further investigation to determine the proportions of different pore types in the overall population of pores in an eggshell.

Intra-egg species variation

Despite the limitations of the available information it was possible to collect 35 complete sets of data, which is sufficient for an analysis of the effects of the interrelationships of egg characteristics. Often shell morphology was available for only a single example of one dinosaur species or one oospecies. However, for eggshells of the oospecies *Megaloolithus mamillare* and *M. siruguei* there were several examples of their morphological characteristics (Table 3). It was difficult to draw any conclusions about the results of these individual egg taxa because of the variability that they each exhibited in their morphological characteristics. For example, in *M. siruguei* egg shape was either spherical or ovoid, calculated M varied by 1000 g, L_s varied from 1.8 to 3.0 mm and D varied from 1.50 to 4.33 pores per mm^2 . It is not clear whether these differences reflect natural variation within a clutch or population of eggshells (Garcia and Vianey-Liaud 2001), or whether the eggshells actually represent different egg taxa. Although similar in microstructure, it is apparent that there are differences in other eggshell characteristics among eggs assigned to the same oospecies and further research is required to clarify variation among these specimens.

The allometric analyses showed that there was a similarity in eggshell characteristics within each dinosaur clade. Ornithopod, titanosaur and faveoololithid eggshells each showed relatively little variation and form clusters on the graphs (see Text-fig. 1), largely because of comparable values for M . Theropod eggshells were an exception because they exhibited a large range in M , from 168 to 3188 g.

Allometric relationships

An adequate number of values allowed for regression analyses not only on dinosaurs as a whole but also on theropod and titanosaur eggshells separately. The relationship between water vapour conductance values and egg mass was similar among eggshells of dinosaurs and birds, although the values were an order of magnitude higher in dinosaurs overall. These values for titanosaur eggs were high, although they showed no correlation between these two variables. Theropods showed a correlation comparable to that of birds and other dinosaurs with a regression estimate mid-way between the two. A similar correlation was found between A_p and egg mass.

High values for $G_{\text{H}_2\text{O}}$ in dinosaur eggs were associated with large values of A_p , which were a function of the large pore radius and a higher total pore number per shell. The similarities between values for avian and dinosaur eggs in terms of N and D suggest that the physiological importance of these shell characteristics is common among all, but that the influence of N on $G_{\text{H}_2\text{O}}$ was more apparent in large eggs. Hence, the high values for $G_{\text{H}_2\text{O}}$ exhibited by titanosaur eggshells were a function of the large pore radius and the high N , which together increased A_p . In small ornithopod and theropod eggs pores were relatively fewer in number and so the larger pore area had more effect on A_p .

Physiological consequences of the physical characteristics of eggshells

In bird eggs the relationship between M and $G_{\text{H}_2\text{O}}$ is attributed to the respiratory requirements of the embryos in the cleidoic eggs (Rahn and Paganelli 1990). The similarities in how $G_{\text{H}_2\text{O}}$ scales with M in bird and dinosaur eggs strongly imply that this same relationship applies in dinosaurs. Furthermore, the present data indicate that values of $G_{\text{H}_2\text{O}}$ higher than that of bird eggs of an equivalent mass were characteristic of titanosaur, hadrosaur, allosauroid, oviraptorosaur and some indeterminate, small theropod eggs. Given that eggshell conductance values of all gases are interrelated, the higher values for $G_{\text{H}_2\text{O}}$ in dinosaur eggshells indicate higher values for conductance to oxygen and carbon dioxide. This indicates that the gaseous conditions in these dinosaur nests were probably characterised by low levels of oxygen and high levels of carbon dioxide comparable to underground nests of reptiles and megapode birds (Seymour 1979; Seymour and Ackerman 1980; Booth and Thompson 1991; Booth and Jones 2002).

If it is accepted that morphology and the water vapour conductance value of an eggshell indicate the nesting environment experienced by the egg then the present study serves to reinforce the conclusion that dinosaur eggs were buried in some form of substrate (Seymour 1979). The rigid-shelled eggs of extant crocodylians and turtles may be smaller than the eggs described here but their eggshells are still 2–7 times more porous than avian eggs (with the exception of those laid by megapodes) of an equivalent mass (Deeming and Thompson 1991) and would lie close to the regression estimate for theropod eggshells. A high-conductance eggshell precludes incubation in an environment that is much less than 100 per cent saturated with water vapour. It is simply not possible for dinosaur eggs to lie partially exposed to the elements. Apart from considerations of exposure to predation, the physical evidence of water vapour conductance shows that

dehydration of the egg contents would be rapid. Even under humidity conditions of over 99 per cent relative humidity in a laboratory incubator, eggs of *Alligator mississippiensis* still lose water (up to 15 per cent of the initial egg mass) if they are not surrounded by a substrate (Deeming, unpubl. obs.). A dinosaur egg only half buried in a substrate would lose water rapidly to the air and because water is absorbed by reptile eggs in the gaseous phase (Ackerman *et al.* 1985), it could not be rapidly replaced from the substrate.

Many reptile eggs will gain weight if incubated under conditions of high water potential but lose weight under lower water potentials (Ackerman 1991; Packard 1991). Any weight loss from the egg affects embryonic metabolism and growth and impacts on the fitness of the hatching (Packard 1991). Seymour (1979) suggested that dinosaur eggs could tolerate a loss of weight during incubation of up to 20 per cent of the initial egg mass. Whereas megapode bird eggs lose water during buried incubation (Seymour *et al.* 1987) most reptile eggs do not lose water during incubation (Belinsky *et al.* 2004). There is no reason to presume that dinosaur eggs would normally lose water vapour during incubation. Indeed the G_{H_2O} values for faveoolithid eggs would mean that at a humidity other than saturation weight loss would be extremely rapid.

Such physical conditions mean that most of the eggs described here could not have been left exposed or even incubated by an adult. The latter possibility is further precluded by spatial relationships of eggs within the substrate as well as considerations of how a large dinosaur could actually sit on a mound of eggs (see Deeming 2002a). Therefore, this physical evidence, which contrary to the view of Carpenter (1999) is not ambiguous, strongly supports the idea that the dinosaur eggs examined in this study were incubated fully buried in a mound or in an underground chamber (Seymour 1979; Williams *et al.* 1984; Mikhailov *et al.* 1994). The implications of reinforcing this conclusion are wide-ranging.

Incubation environment of dinosaur eggs

The physics of gas diffusion are irrefutable and so the morphology of eggshells provides a valuable insight into part of the reproductive biology of dinosaurs. High-porosity eggshells indicate that the incubation environment is low in oxygen and high in carbon dioxide and that these shells need to be incubated in an environment saturated with humidity. This is supported unambiguously by our comprehensive understanding of the diverse nesting environments of both modern birds and reptiles (see Deeming 2002b, 2004). Most of the dinosaur eggshells studied here have conductance values higher than those calculated

for modern birds (with the exception of a few avian species that incubate their eggs in an atypical manner). Hence, most of the dinosaur eggshells studied here resemble more closely those of rigid-shelled eggs of living crocodylians and turtles and so it is inferred that their incubation conditions would have been similar. Faveoolithid eggs are more similar to soft-shelled eggs of squamate reptiles (Deeming and Thompson 1991). Reptile eggs are reliant on the environment for their incubation conditions, and the temperature and humidity experienced by the eggs during incubation are driven by the prevailing climate. The temperature of incubation will fluctuate on a daily basis (Ackerman and Lott 2004; Birchard 2004) and would average out at a lower level than that experienced by contact-incubated bird eggs, which are maintained at a near constant temperature close to the body temperature of the incubating adult.

Many fossil eggshells from the Mesozoic are assumed to be derived from dinosaur species even though few are directly associated with skeletal fossil remains. There have been no previous reports that describe the water vapour conductance of eggshells associated with dinosaur embryos despite the fact that such specimens exist (Horner and Weishampel 1988; Horner and Currie 1994; Chiappe *et al.* 1998; Norell *et al.* 2001). However, in this paper I provide data on two types of theropod (allosauroid, oviraptorosaur) eggs associated with embryonic remains. I also provide values for eggs in which their egg characteristics are similar to those associated with embryos of hadrosaurs, titanosaurs, troodontids and oviraptorids.

Embryos of the Jurassic allosauroid theropod *Lourinhanosaurus antunesi* are associated with eggshell (Mateus *et al.* 1997) and my data (with the grateful assistance of Octavio Mateus) show that the G_{H_2O} is seven times higher than that predicted for an avian egg of a similar mass (643 g). The emu (*Dromaius novahollandiae*) lays an egg of similar mass and has an eggshell G_{H_2O} value of 52 mgH₂O d⁻¹ Torr⁻¹ (Ar and Rahn 1978), which is a tenth of the value for the *L. antunesi* egg. Similarly, large elongatoolithid (*Macroelongatoolithus xixianensis*) eggs associated with embryos of a giant oviraptorosaur (D. K. Zelenitsky, pers. obs. 2002) have G_{H_2O} values 2.1 times that of an equivalent bird egg. Values for both of these large theropods are suggestive of egg incubation in a unexposed, humid environment.

Brooding-type incubation (with contact between the eggs and adults), akin to that of birds, has recently been attributed to *Oviraptor philoceratops* (Norell *et al.* 1995; Dong and Currie 1996; Clark *et al.* 1999) and *Troodon formosus* (Horner 2000; Varricchio *et al.* 1997). However, the theropod eggs including the elongatoolithid eggs studied, which are identical to those known to belong to oviraptorids, have an eggshell porosity over five times higher than the shell of bird eggs of an equivalent mass. Although

it is apparent that some theropods sat on their nests in a brood-like manner, the evidence presented here indicates a humid nesting environment that would have required the eggs to be completely covered by a substrate. Using additional factors such as egg orientation, nest morphology and adult position, elsewhere I reconcile this conflict by suggesting that the *Oviraptor* specimen was sitting on top of a nest mound rather than contact-incubating the eggs and so more resembled the nesting behaviour of some modern crocodylians (Deeming 2002a).

It is interesting that the morphological characteristics of the eggshell of the enantiornithine bird *Gobiteryx minuta* resemble those of dinosaurs. This prompted me to suggest previously that non-neornithine birds of the Cretaceous did not have eggshells typical of modern birds and incubated their eggs in a reptilian-like environment (Deeming 2002a). The recalculated values presented in Table 6 reinforce this idea. Perhaps contact incubation and relatively impermeable eggshells were distinguishing characteristics of neornithine birds? This idea is supported by observations of Mikhailov (1997b). For avian eggshells from the Cretaceous, ultrastructural shell morphology of eggs of the Laevisoolithidae, which are assigned to enantiornithine birds, most closely resemble theropod-like eggshell. By contrast, eggshells of the Gobioolithidae, assigned to ?palaeognathe birds, more closely resemble ratite and gallo-anserine eggshells. Perhaps, behavioural control of the incubation environment, which made the rate of embryonic development independent of the prevailing climatic conditions, was a factor in the survival of neornithine birds across the Cretaceous/Tertiary boundary?

In conclusion, this paper provides new information on the reproductive biology of several types of dinosaurs. Due to the nature of the fossil record, however, there are obvious gaps in the eggshell data for dinosaurs. Eggs are currently non-existent for numerous taxa, so data for the majority of dinosaur types are missing. I hope that this work will stimulate further research on the gas conductance of dinosaur eggs, especially those with associated embryonic or skeletal remains. There is also a need for more investigations of the true affinities of eggs assigned to the same oospecies but which show considerable variation in eggshell characteristics and egg mass.

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