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## UPPER CRETACEOUS AMNIOTIC EGGS FROM THE GOBI DESERT

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There are described several types of Upper Cretaceous fossil amniote eggs, clutches and eggshells, collected during the Polish-Mongolian Paleontological Expeditions (1963—1971) in several localities of the Gobi Desert. Isotopic ratios of C and O are reported and discussed. The eggs may be attributed to saurischian and ornithischian dinosaurs, and palaeognathous birds. Four types of problematica are also described. Taphonomy and restoration of eggshells' diffusive properties as compared with modern hard-shelled eggs suggest paleoecological interpretation of the nesting conditions as rather dry for smooth-shelled eggs, humid for ornamented eggs, and very humid for the thickest-shelled eggs. Different nest types are postulated for ornamented and smooth eggs, based on taphonomy and shell parameters.

**Key words:** Eggshells, Dinosauria, Aves, paleobiology, taphonomy, stable isotopes, Upper Cretaceous, Gobi.

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## INTRODUCTION

The first fossil dinosaur eggs and nests were discovered by the Central-Asiatic Expeditions of the American Museum of Natural History in the Gobi Desert in the 1920s (Andrews 1932). Since then new sites yielded numerous fossil amniote eggs, ranging from the Permian (Hirsch 1979) to Recent (for review of geographical, stratigraphical data and bibliography, see e.g.: Penner 1983, Hirsch and Packard 1987, Hirsch 1989, Chure and McIntosh 1989), but the Gobi Desert still remains the classic site for search of Late Cretaceous dinosaurian and avian eggs. Northern part of the Gobi Desert has been explored by Soviet (since 1940s), Soviet-Mongolian (since 1969), Polish-Mongolian (1963—1971) and Mongolian expeditions. The southern part of the desert has been visited by Soviet-Chinese, and recently, Chinese-Canadian ones. Many of these expeditions were successful in finding the fossil eggs.

In Mongolia, the Central-Asiatic Expeditions have found dinosaur

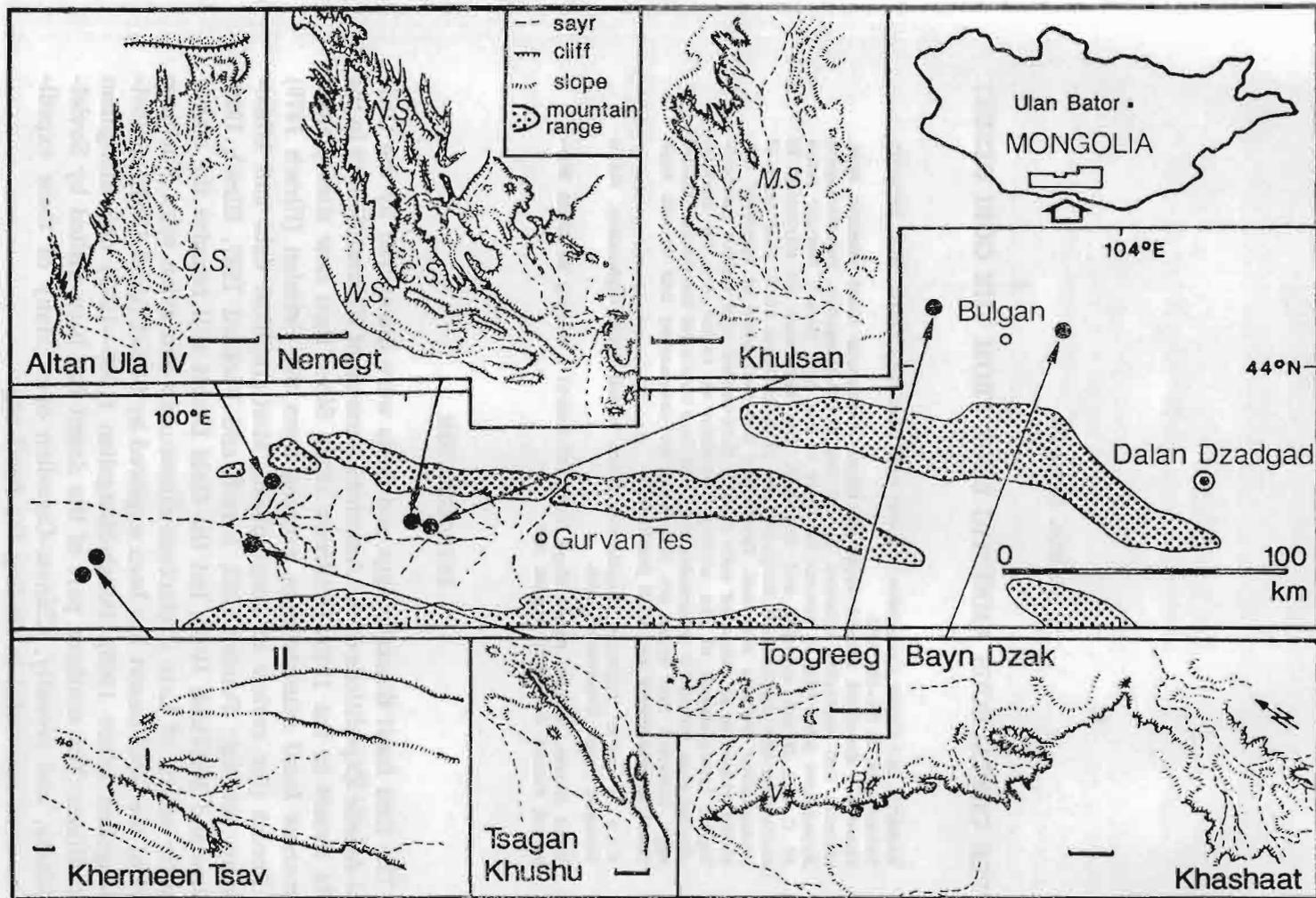


Fig. 1. Egg-bearing sites visited by the Polish-Mongolian Paleontological Expeditions (1963—1971), modified after Gradziński *et al.* (1969) and Gradziński and Jerzykiewicz (1972). Scale bars in insets equal 1 km. Abbreviations: C.S. — Central Sayr; M.S. — Main Sayr; E.S. — Eastern Sayr; W.S. — Western Sayr; R. — “Ruins”; V. — “Volcano” (= “Pyramid”).

nests and eggs at a locality named Shabarakh Usu (= Bayn Dzak; Andrews 1932: 162—163, 207—214). The eggs found there were attributed to a ceratopsian dinosaur *Protoceratops andrewsi*, since its bones were common in the same fossil-bearing strata. Claims regarding direct identification of taxonomic position of the egg-laying animal via recognition of the dinosaur embryos inside the eggs (Andrews 1932: 210) though long persisting in the literature (e. g. Kitching 1979) proved to be unfounded (Elżanowski 1981). Only hatched juveniles of Mongolian protoceratopsid dinosaurs are known (Coombs 1980). "*Protoceratops*" eggs' morphology was described shortly after their discovery (Van Straelen 1925), later their microstructure was revealed (Schwartz *et al.* 1961, 1962) as well as their ultrastructure (SEM study by Erben 1970, who studied, in fact, mostly elongatoolithid and not protoceratopsid eggshells; see Mikhailov 1991). Another type of eggs — smaller and smooth-shelled — was also mentioned by Andrews (1932) as common in Shabarakh Usu.

The Soviet Paleontological Expeditions working in Mongolia from 1946 till 1949 and subsequent Joint Soviet-Mongolian Paleontological and Geological Expeditions also have found eggs and eggshells, described later by Sochava (1969, 1970, 1971, 1972), who distinguished in the Mongolian Cretaceous material at least three types of eggshells: angusticanaliculate, prolatocanaliculate and multicanaliculate. Paleobiochemical studies on these eggs (Kolesnikov and Sochava 1972) revealed that some shell scleropeptides were preserved. Other bio- and geochemical analyses on the Mongolian and other Cretaceous eggshells were also done by Krampitz *et al.* 1977, Schwartz *et al.* 1961, verzilin and Rogozina 1981, Verzilin *et al.* 1985 and Dauphin and Jaeger 1990). The main Soviet fossil egg collection (housed in the Paleontological Institute, U.S.S.R. Academy of Sciences, Moscow) was restudied by Mikhailov (1988, 1991).

The rich Mongolian collection of fossil eggs (including part of the fossil material found by the Polish-Mongolian expeditions) has not been described yet.

The Chinese part of the Gobi Desert yielded recently five types of Cretaceous eggs, but only preliminary information was published (Zhiming *et al.* 1989). For bibliography of numerous earlier fossil egg finds in China see Zhen *et al.* 1985.

Polish collection of Upper Cretaceous fossil eggs from Gobi desert, gathered since 1963 to 1971, is remarkably abundant. It comprises about 300 specimens of eggs and egg fragments as well as abundant shell debris, belonging to as much as 10 different groups. Being, at least at the time of completing, one of the world's most diverse single set of Mesozoic eggs, it has been only preliminarily mentioned so far (Małeckı 1977, Mierzejewska 1977, 1981).

The aim of the present paper is to describe the collection, housed at

the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (ZPAL), and to present some paleobiological speculations concerning adaptation aspects of fossil eggs.

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## GENERAL REMARKS ON EGGSHELL STRUCTURE AND TERMINOLOGY

### Methods

The shell portions to be analyzed in SEM were either non treated internal, external and radial fracture surfaces or treated surfaces of fractures or radial sections embedded in epoxy. Etching has been performed with 1% HCl, 10% EDTA,  $\text{Cr}_2(\text{SO})_4$  or by boiling in KOH. The specimens were then glued to brass specimen holder with colloidal silver and subsequently coated with gold *in vacuo*. The SEM micrographs were taken using JEOL (Japan Electronic Optical Laboratories) SM-1 scanning microscope at the Nencki Institute of Experimental Biology of the Polish Academy of Sciences, Warsaw.

The radial and tangential thin sections of eggshells embedded in epoxy were also viewed and photographed in normal and polarized light using Olympus SZH stereomicroscope.

The paleophysiological estimates were made by solving allometric equations for extant birds, since they are the closest living relatives of dinosaurs and their eggshell structure seems to correspond better to the dinosaur eggshells studied than less mineralized crocodylian or chelonian eggshells do (Table 1).

The eggshell sample material for isotope analysis was treated by pure phosphoric acid (McCrea 1950) and the resulting carbon dioxide studied by mass spectrometry at the Institute of Physics, Maria Curie-Skłodowska University, Lublin, Poland. The standard error of single measurements is less than 0.08 per mille (Hałas and Skórzyński 1982). The results are expressed in delta notation relative to the PDB standard, using the NBS-19 reference sample.

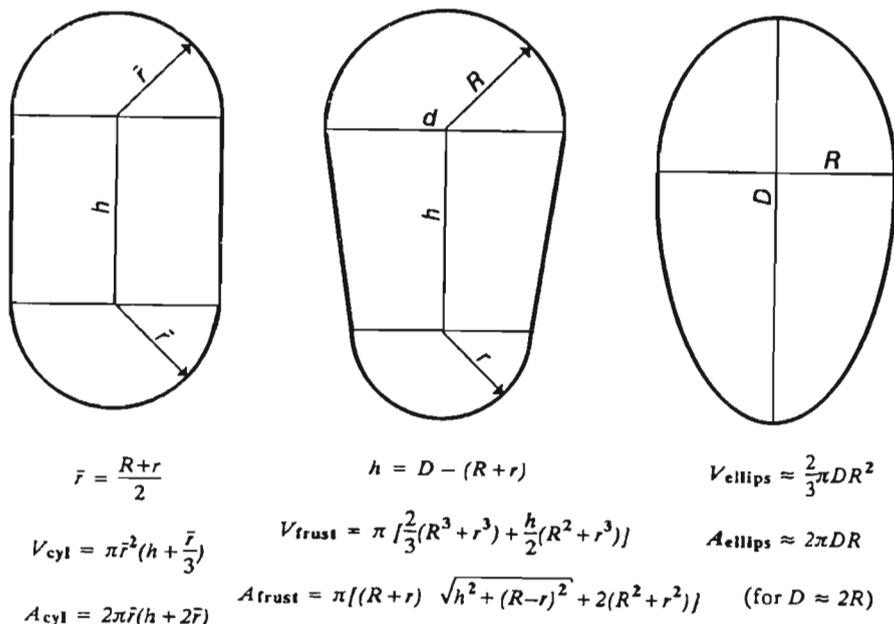


Fig. 2. Different geometrical approximations of the egg shape. R = greater radius; r = lesser radius; d = long axis of an egg, h = height of cylinder or frustum.

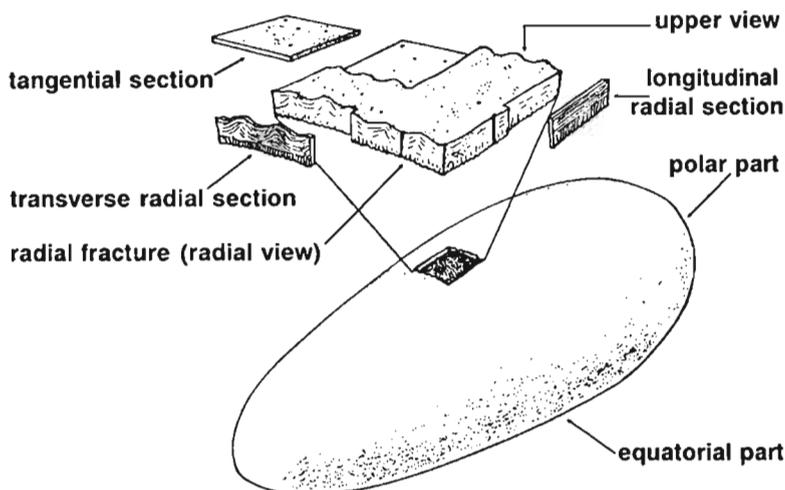


Fig. 3. The principal topological terms concerning the egg and eggshell preparations.

**Egg and eggshell general morphology (fig. 2, 6)**

The eggs studied are of spherical, ovate, elongate ovate or elongate ellipsoidal shape (fig. 6). The blunt end of asymmetric eggs (possibly containing the air chamber *in vivo*) was presumably directed upwards, as in extant species and in the North American ornithopod nests (Horner 1984, 1987, Coombs (1989)). The outer (external) surface of eggshell may

appear smooth to the naked eye or shows different patterns of sculptured ornament. I follow Mikhailov's (1991) nomenclature of such patterns and pore systems.

### Shell micro- and ultrastructure

Since the 19th century it has been known that avian eggshell consists principally of two layers, of which the one adhering to the egg membrane forms small cusps, and the other one is more uniform. Nevertheless, several synonymical terms have been introduced to point at different properties (morphological or crystallographical) of shell unit and subunits as visible under ULM, PLM, and SEM, thus somewhat obscuring the understanding of eggshell structure. Because descriptions of various authors differ in terminology, I present a scheme, illustrating the relationships of certain terms (pl. 14, fig. 3, 4). Since Mikhailov (1991) presents his exhaustive analysis of shell ultrastructure, resulting from his studies on rich material, including analogous Cretaceous Gobi eggshells, I omit

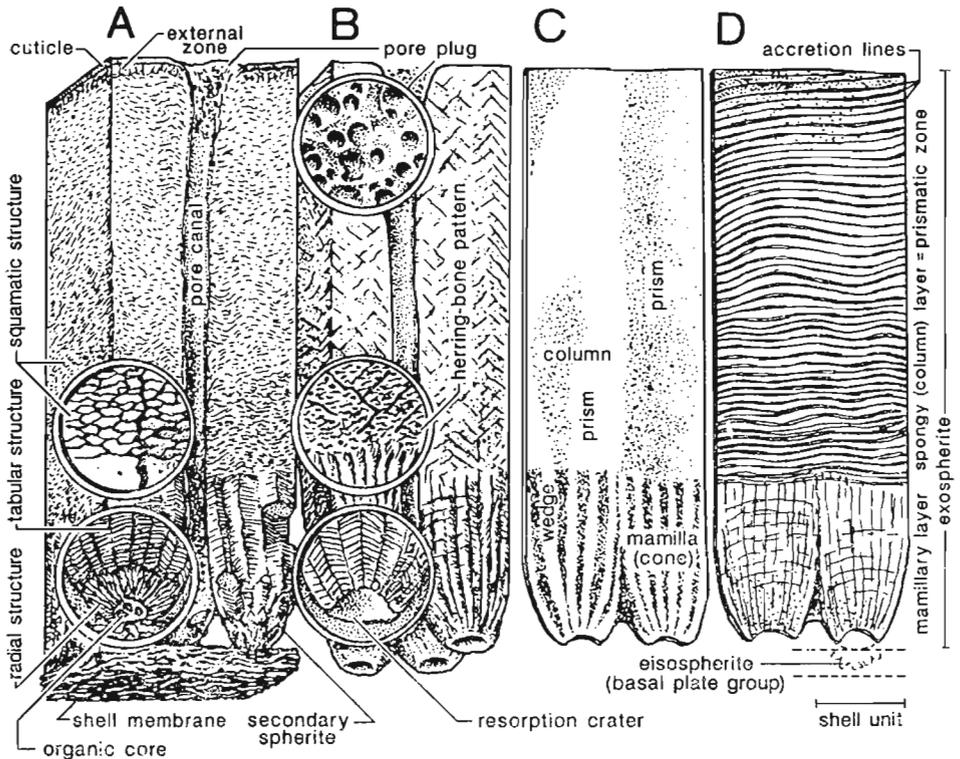


Fig. 4. Different aspects of the structure and nomenclature of ornithoid eggshell. A. Freshly laid egg (based on Recent ratite eggshells). B. Fossil incubated egg (note resorption craters and the herring-bone pattern). A and B as seen in SEM. C. Radial thin section of an incubated eggshell, polarized light. D. Radial thin section, transmitted light. Another features can be visualised after chemical staining of the Recent eggshells (Tyler and Simkiss 1959).

here a detailed discussion on the meaning of particular structures visible in the micrographs. For a comparative presentation of microstructure of the eggs from the collection described here see fig. 8.

The herring-bone pattern (fig. 4B) ("fish-bone pattern") described by Erben (1970) as an important structural feature of the outer layer of dinosaurian eggshells proved to be a typical result of diagenesis. This particular pattern of cracks is visible on fossil eggshell fractures and not in the fresh material (Hirsch 1984: fig. 5), and results from cleavage of calcite after decay of organic matrix (Mikhailov 1991).

### Abbreviations used

- As — eggshell surface area [cm<sup>2</sup>]  
 A — single pore section area (average) [cm<sup>2</sup>]  
 Ap — total functional pore area [cm<sup>2</sup>]  
 D — egg length [mm]  
 d — egg equatorial diameter [mm]  
 D<sub>H2O</sub> — diffusion coefficient for water vapor in air [cm<sup>2</sup>·sec<sup>-1</sup>]  
 G<sub>H2O</sub> — water vapor conductance of the eggshell [mg·(day·Torr)<sup>-1</sup>]  
 I — incubation period [days]  
 L — length of pores (shell thickness) [mm]  
 M<sub>H2O</sub> — water loss rate [mg·day<sup>-1</sup>]  
 N — number of pores  
 T — absolute incubation temperature [K]  
 V — egg volume [cm<sup>3</sup>]  
 W — egg fresh weight [G]  
 ZPAL MgOv — Institute of Paleobiology, Polish Academy of Sciences, collection of Mongolian eggs.  
 ZPAL zpOv — comparative collection of eggshells.

### STRATIGRAPHIC AND GEOGRAPHIC SETTING

The fossil egg collection studied here comes from the following localities visited by the Polish-Mongolian Paleontological Expeditions (Kielan-Jaworowska and Dovchin 1969, Kielan-Jaworowska and Barsbold 1972):

1. Bayn Dzak (= Shabarakh Usu; Andrews, 1932: 162—163, 207—214; Gradziński *et al.* 1969: 69—72). The eggs found in that locality by the AMNH Central Asiatic Expeditions in 1923 and 1925 (Andrews 1932: 208—211, 256—257) were described by Van Straelen (1925), Schwartz *et al.* (1961) and Erben (1970). They represented mainly two types: a larger one, attributed to *Protoceratops*, and a medium size one, regarded by Andrews as laid by another dinosaur. Andrews called Shabarakh Usu "a dinosaur nesting place", where properties of sand suited the incubation requirements best. The amount and diversity of eggs found in Bayn Dzak

by members of the Polish-Mongolian Paleontological Expeditions support Andrews' statement.

All the Bayn Dzak material comes from the deposits of the Djadokhta Fm. (?late Santonian or early Campanian; Gradziński *et al.* 1977).

2. Toogreeg (Tugruk, Tugrikin-Shire) is ca 30 km WNW of Bayn Dzak (Gradziński and Jerzykiewicz 1972: 29—30) and the Toogreeg beds are biostratigraphic equivalent of the Djadokhta Fm. (Gradziński *et al.* 1977: 302). Fossil eggs found there by the 1971 expedition (Kielan-Jaworowska and Barsbold 1972: 11) were left in Ulan Bator (Osmólska, pers. comm. 1989). Only a few large broken eggs and shell debris (ZPAL MgOv-II/14a, b), collected there in 1968 are housed in Warsaw.

3. Altan Ula IV (Gradziński *et al.* 1969: 42—46). The deposits of the Nemegt Fm. (?late Campanian or early Maastrichtian) yielded remains of medium-sized, thin-shelled eggs (ZPAL MgOv-I/1) in 1964.

4. Tsagan Khushu (Gradziński *et al.* 1969: 49—53). The field work of the 1964 expedition at Tsagan Khushu resulted in gathering multiple pieces of well preserved eggshells ca 1.2—1.4 mm thick (ZPAL MgOv-I/2) from Nemegt Fm sediments.

5. Nemegt (Gradziński *et al.* 1969: 38—42, Gradziński and Jerzykiewicz 1972: 18—23). A medium size egg (ZPAL MgOv-I/3) was found in the Western Sayr (dry river-bed) in 1964. Several parts of larger eggs (ZPAL MgOv-I/4) embedded in weathered light sandstone ("Passage Series", Gradziński *et al.* 1969) were also found in the Western Sayr by the 1970 expedition. The Western Sayr deposits belong to the Nemegt Fm. Next year numerous eggshell fragments with different ornamentation (ZPAL MgOv-I/27a, b, 29) were collected at the SE Nemegt in Southern and Red Monadnocks, representing so called "barren series" ("nemaya tolshcha" of Soviet authors, see Gradziński 1970, Kielan-Jaworowska and Barsbold 1972: 9), in deposits of the Barun Goyot Fm (Gradziński *et al.* 1977) of ?middle Campanian age.

6. Khulsan (= East Nemegt; Gradziński and Jerzykiewicz 1972: 23—25) was surveyed by the 1970 and 1971 expedition. The eggs were very commonly found in deposits of the Barun Goyot Fm (Kielan-Jaworowska and Barsbold 1972: 10).

7. Khermeen Tsav (Gradziński and Jerzykiewicz 1972: 26—30) consists of two localities that were visited by the 1971 expedition (Kielan-Jaworowska and Barsbold 1972: 11).

At Khermeen Tsav I, in "Protoceratops horizon" (red beds of Khermeen Tsav) a voluminous set of different kinds of medium and smaller eggs has been found, sometimes in groups of ca 20 eggs, totaling more than 120 specimens (ZPAL MgOv-III/10a-b, 11a-c, 12—16, 21).

Khermeen Tsav II outcrops (red beds of Khermeen Tsav, probably

Barun Goyot Fm.) yielded mostly large eggs (ZPAL MgOv-III/1—8, 18a-c, 20).

For more information on the sites and their stratigraphy see Graziński *et al.* (1977).

#### TAPHONOMICAL AND PALEOECOLOGICAL ASPECTS

##### BURIAL CONDITIONS SUGGESTED BY SEDIMENTOLOGICAL FEATURES OF EGG-BEARING STRATA

The Upper Cretaceous deposits in the egg-bearing localities in southern Mongolia are regarded as originating from aeolian and water-accumulated sands. The description of the sedimentology of the Djadokhta Formation at Bayn Dzak and Khashaat given by Lefeld (1971) includes remarks on the preservation of the eggs and nests in the strata. Lefeld (1971: 122, fig. 14) concludes that they were buried by wind-blown sand, but in some cases the cementation of sediment in the lower end of eggshell was due to filling it with water. Such interpretation is in good concordance with the presumed lacustrine palaeoenvironment (Martinson 1972).

Some differences in the mode of preservation may be observed. The ornamented protoceratopsid eggs are found usually as horizontally oriented flattened whole eggs (both ends preserved), but the shell is excessively broken. The other ornamented eggs, with ornithoid basic structure (Elongatoolithidae), also happen to be preserved this way, but as a rule their shells are found scattered as loose debris of a centimeter size range. The smooth shelled elongated eggs are not flattened, and the eggshell, though thinner and cracked at places, retains regular shape. These eggs usually lack their blunt ends. The possible explanations of these taphonomical differences are given in the next chapter.

Lefeld (1971) gives also the list of horizons within the Djadokhta Fm. in which the eggshells of different types (and other vertebrate fossils) were found:

horizon 2, 3, 4 — smooth protoceratopsid, large ?bird eggs.

horizon 4 — small ellipsoid and ovate ?egg casts.

horizon 5 — smooth protoceratopsid eggs.

horizon 7, 9 — smooth and ornamented protoceratopsid, elongatoolithid eggs.

Potential egg-laying sauropsids from that site have been listed by Osmólska (1980). They include dermatemydid turtles, several lizard species, goniopholid and gobiosuchid crocodiles, protoceratopses, ankylosaurs, hadrosaurs, sauropods, and dromaeosaurid, troodontid and oviraptorid theropods.

In other localities eggs and shells were mostly collected from the surface of pediment, so their exact stratigraphic position in profile is

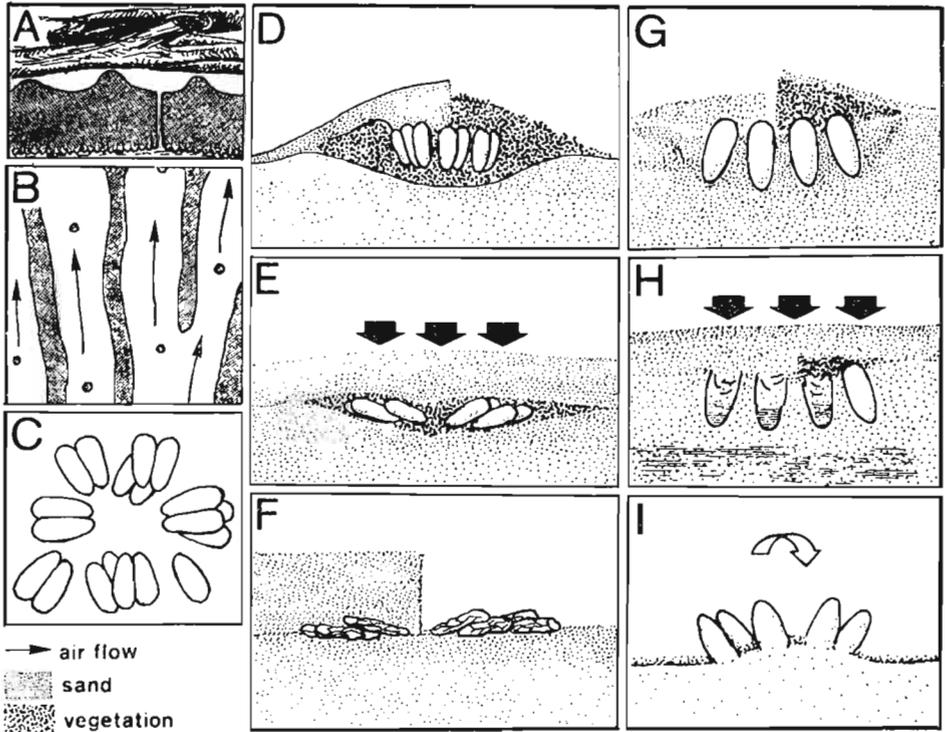


Fig. 5. The smooth and the ornamented elongate eggs: nesting differences. The ornamented eggs (A—F) are interpreted as adapted to incubation in nests made of decaying vegetation. The ridges and hillocks on the outer shell surface protected the pore openings situated in the grooves from obstruction (radial view, A.). The parallel vertical grooves formed a convection-driven ventilation system (B). The eggs were placed in decaying plant matter subvertically, to improve aeration, and possibly covered with sand (D). After burial and vegetation decay (E), the eggs fell apart, to form a spiral fan. The eggs pairs were still glued together (C, upper view, based on ZPAL MgOv-II/23). The pressure of the overlaying sediment crushed the shell when the shell membrane was still pliable (F). The smooth-shelled eggs (G—J) were placed in humid sand separately (no pairs preserved), with blunt ends up, and possibly covered with additional layer of vegetation and/or sand (G). After burial only the upper ends were pressed into the eggs and the interior of the shell was filled with the sediment. The lower part of the eggshell was not deformed, so that they were still water-tight (H based on ZPAL MgOv-II/3, Lefeld 1971). The fossil nests are often covered with plaster of Paris in the field and subsequently prepared from below, resulting in upside-down display position (I based on ZPAL MgOv-II/2), see also comments in Cousin *et al.* 1989, Horner 1987).

hardly known. They come, however, from sandstone beds, and since they were often found in pairs or clutches, we may assume that they were buried within the nesting area.

#### NESTING CONDITIONS INFERRED FROM EGGSHELLS' DIFFUSIVE PROPERTIES

The egg volume, mass and area were calculated using the following formulas, assuming different geometrical approximations of egg shapes: as a cylinder ended with two equal hemispheres, as a frustum capped

with two different hemispheres or as an ellipsoid and compared to allometric equations for extant birds (see fig. 2).

All the formulas for area and volume gave, expectedly, satisfactorily coherent results. Since the initial dimensional data were not exact, due to the imperfect state of preservation of the eggs and individual variation, and the formulas were describing only approximations of actual shapes of the eggs, the results are given rounded to the second digit.

The calculated values of egg area, volume and mass were also used, together with porosity data, to estimate shell diffusive resistance, and thus permit speculations about some paleophysiological parameters, like relative humidity of the incubation environment and incubation time. This calculations were possible only for the large eggs, which have relatively unaltered shell structure and well visible pores. Several pieces of eggshell from different part of the eggs were used to count the pores. In the smaller eggs their eggshells are eroded and recrystallized. The pore pattern is thus obscured, making any calculations unreliable.

The formulas used for calculations were taken from Hoyt 1976, Seymour 1979, Tullett 1978 (predicted surface area), Tullett and Board 1977 (expected pore number), Ar *et al.* 1974 (predicted shell thickness), Ar and Rahn 1978 (incubation to egg weight relation), Seymour 1979 and Ar and Rahn 1985 (water loss and water vapor conductance).

The estimated paleophysiological values for the fossil eggs were then compared with expectations based on regression curves for the eggs of extant birds (Ar and Rahn 1985, Rahn and Ar 1980), being the closest functional analogues for the large, hard-shelled Upper Cretaceous eggs (the eggs of extant reptiles have less calcified eggshells or are parchment-shelled and thus even absorb water from humid environment; Packard *et al.* 1982). It should be, however, remembered that the calculated pore conductances are — at least in extant birds — about two to three times higher than the actual ones (Tøien *et al.* 1987, 1988), due to organic plugging. If a similar bias is taken into account in interpreting fossil eggshell conductances, then the results would point to drier incubating conditions and longer incubation. Actually, the formula and data in Seymour (1979) yield values of  $G_{H_2O}$  almost three times lower than presented in his paper (the lower values may be closer to the actual *in vivo* conductances, as they resemble Recent Megapodidae eggs in this respect; Seymour and Rahn 1978). The conductances reported by Seymour (1979 and cited in Seymour and Ackerman 1980) are however correct if one uses the original formula of Ar *et al.* (1974).

The extent to which the real conductances differed from the calculated ones may be roughly estimated by comparing e.g. eggshell conductances calculated as total pore conductance with estimates relying on conductance/weight correlation (Ar and Rahn 1978). Also incubation periods,

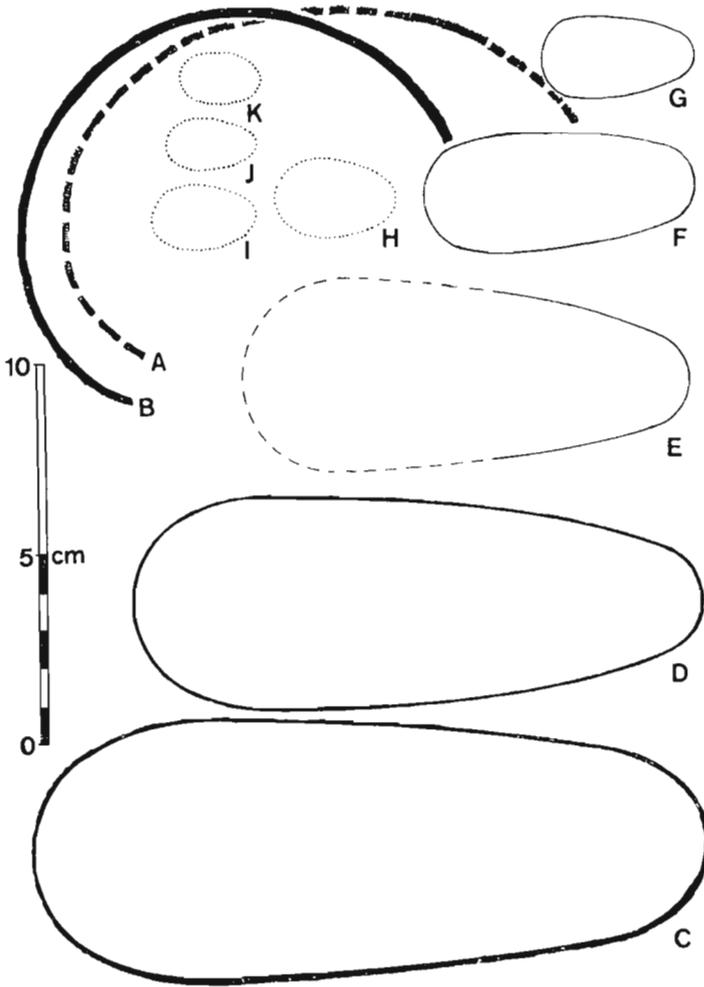


Fig. 6. Comparison of sizes and shapes of the eggs described. The shell thickness is roughly proportional to scale. A Faveoololithidae. B Dendroolithidae. C Elongatoolithidae. D Protoceratopsid eggs, ornamented and smooth. E Thin shelled protoceratopsid egg. F Larger ?avian eggs. G *Gobipteryx minuta* eggs. H—K ?egg casts or concretions: H ellipsoidal, I ovate, J asymmetrical ellipsoidal, K ?unfertilized ovate.

calculated both on the basis of lethal dehydration level given the eggshell permeability and in relation to weight, can be compared for this reason. The results of such comparisons suggest very humid incubation conditions (low  $\Delta P_{H_2O}$  in Table 1) and, probably, pore plugging reducing water loss with less effect on respiratory gases' exchange.

Moreover, it should be remembered that uncertainty of our estimates of the incubation conditions is due not only to possible errors in estimating porosity and conductance of eggshells, but also to such factors as the temperature of incubation and atmospheric gas composition. The tem-

Representative estimates of selected egg parameters. The error range is about 10% for most paleophysiological estimates, so that only relative proportions are relevant

Parameters	Faveoololithidae		Dendroolithidae		Spherolithidae		Elongatoolithidae		Protoceratopsidae		Laevisoolithidae		Problematica			
									smooth-shelled	thin-shelled	Larger avian	*Gobipteryx minuta*	ellipsoid	asymmetrical ovate	unfertilized	
R [cm]	5.5 <sup>a)</sup>	5.5	4.3 <sup>b)</sup>	3.4	2.8	2.7	2.3	1.7	1.6	1			0.85	1	0.7	0.65
r [cm]	5 <sup>a)</sup>	5	4 <sup>b)</sup>	2.5	1.5	2	1.2	1.2	1.2	0.7			0.8	0.8	0.6	0.6
D [cm]	14 <sup>a)</sup>	12	9 <sup>b)</sup>	17	15	15	11	7.5	7	4			2.8	3	2.1	1.8
D/2R = D/d	1.25	1.1	1.1	2.5	2.65	2.7	2.4	2.2	2.2	2			1.6	1.5	1.5	1.4
A <sub>cyt</sub> [cm <sup>2</sup> ]	461	415	235	315	203	221	121	68	61	21.4			14.5	16.9	8.6	7
A <sub>frust</sub> [cm <sup>2</sup> ]	464	400	237	318	209	223	125	69	62.2	21.7			14.5	17.2	8.6	7
A <sub>ellips</sub> [cm <sup>2</sup> ]	484	395	243	363	264	255	159	80	70.3	25.1			15	18.8	9.2	7.3
A <sub>s</sub> [cm <sup>2</sup> ]	470	400	240	320	230	230	130	70	65	25			15	17.5	9	7
A <sub>predicted</sub> [cm <sup>2</sup> ] <sup>c)</sup>	450	400	241	270	170	191	117	62	54	20			12.7	16.5	8	7
A <sub>s</sub> /A <sub>predicted</sub>	1.05	1	1	1.2	1.4	1.2	1.2	1.1	1.2	1.2			1.2	1.1	1.2	1
V <sub>cyt</sub> [cm <sup>3</sup> ]	909	736	337	411	197	233	95	43	37.3	7.8			4.8	6.1	2.2	1.7
V <sub>frust</sub> [cm <sup>3</sup> ]	914	740	339	420	213	237	104	45	38.2	8.1			4.8	6.2	2.2	1.7
V <sub>ellips</sub> [cm <sup>3</sup> ]	887	760	348	420	220	229	110	45	30	8			4.4	6	2.2	1.6
V [cm <sup>3</sup> ]	900	750	340	420	220	230	100	45	38	8			4.4	6	2.2	1.7
W = 1.08 V [g]	970	810	375	440	235	260	110	49	40	8.1			4.5	6.7	2.3	1.9
L [mm]	2.3	2.3	1.5	1.3	1.25	1.2	0.3	0.7	0.15	0.14			a) Zhao 1979			
L <sub>pred</sub> = 5.126 · 10 <sup>-2</sup> W <sup>0.456 d)</sup>	1.2	1.1	0.78	0.8	0.62	0.7	0.43	0.3	0.26	0.14			b) Sochava 1969			
L/L <sub>pred</sub>	2	2.1	2	1.7	2	1.7	0.7	2.3	0.6	1						
N	646000	32000	40000	17500	9200	7000	2600			25900						
N <sub>pred</sub> = 1449 W <sup>0.42 e)</sup>	26000	24130	17000	18700	14500	14600	10350			3600			c) Hoyt 1976			
N/N <sub>pred</sub>	25	1.3	2.4	0.95	0.6	0.5	0.25			1.6						
A	203	14.5	12.8	1.3	0.5	0.35	0.1			70.04			d) Ar et al. 1974			
A <sub>pred</sub> = 9.89 · 10 <sup>-5</sup> · W <sup>1.236 f)</sup>	0.5	0.4	0.15	0.2	0.08	0.09	0.03			0.0015						
G <sub>H<sub>2</sub>O</sub> = (A/L) D <sub>H<sub>2</sub>O</sub> 0.56 · 10 <sup>9</sup> / 6.24 · 10 <sup>4</sup> T <sup>9)</sup>	7580	540.3	734	91	32	25	29			22.4			e) Tullett and Board 1977			
G <sub>H<sub>2</sub>O pred</sub> = 0.384 W <sup>0.814 h)</sup>	104	89.5	47	55	33	34	17.4			2.7			f) Rahn et al. 1976			
G <sub>H<sub>2</sub>O</sub> /N	0.01	0.017	0.02	0.005	0.0035	0.0035	0.01			0.004						
l <sub>1</sub> = 11.64 · W <sup>0.221 i)</sup>	53	51	43	45	39	40	33			19						
l <sub>2</sub> = 5.13 · W/G <sub>H<sub>2</sub>O</sub> h)	0.7	8	3	25	38	51	19			13						
l <sub>3</sub> = 0.22 · W · L / A h)	0.3	3	1	9	14	19	7			5						
ΔP <sub>H<sub>2</sub>O</sub> = M <sub>H<sub>2</sub>O</sub> / (l <sub>1</sub> G <sub>H<sub>2</sub>O</sub> ) g)	0.00005	0.0007	0.0006	0.005	0.016	0.02	0.021			0.05						

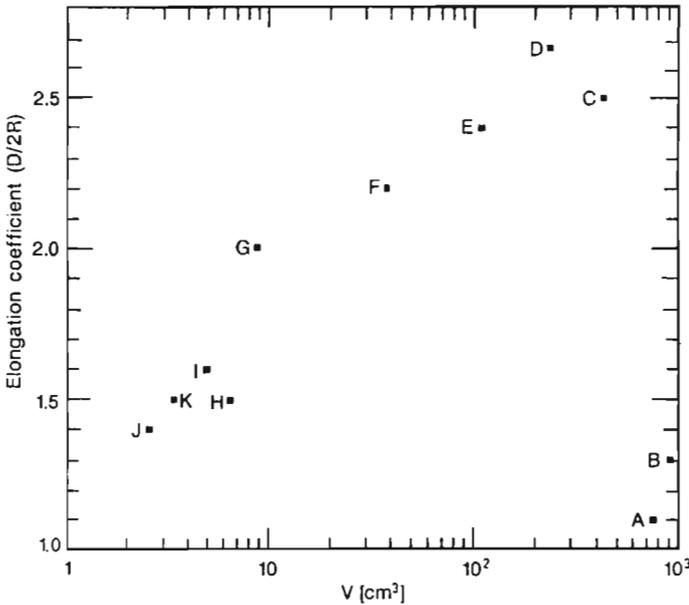


Fig. 7. Volumes and elongation coefficients of studied eggshells. Egg types: the same as in fig. 6.

perature of incubation ranges from about 25°C in some reptiles to more than 35°C in birds (see, e.g., Seymour and Ackerman 1980). This temperature range means about three-fold difference in metabolic rates of the embryo and significantly influences duration of incubation if we assume  $Q_{10} = 2.8$  (Seymour 1979).

Paladino *et al.* (1989) presented some possible consequences of temperature changes to temperature-sex-determination dependent dinosaur populations, suggesting even that the climatic changes could affect the sex ratio of the dinosaur populations, leading to their extinction (exploring the idea of Ferguson and Joanen 1982). Of course, this theory assumes that the parents were unable to control the incubation temperature (via nest location, structure, or active maintenance of the optimum temperature).

Also the oxygen content in the Upper Cretaceous atmosphere could be higher than the present level (Bernier and Canfield 1989), thus altering the diffusive balance of eggs. Visschedijk (1980), and Black and Snyder (1980) described influence of altered partial pressure of oxygen on embryos incubated at different altitudes. Oelofsen (1978) presented a hypothesis to explain the extinction of the dinosaurs. This hypothesis was based on assumed inability of dinosaurs to adapt to changing atmospheric gas content. Experiments made by Carey (1980), however, show that differences in partial pressure of respiratory gases on different altitudes

are successfully compensated for by changed porosity of the eggshells even in non-migratory birds like domestic chicken.

All the above mentioned factors make any estimates of dinosaur, egg physiology imprecise. It is, however, tempting to try some further intelligent guesses about their peculiar adaptations.

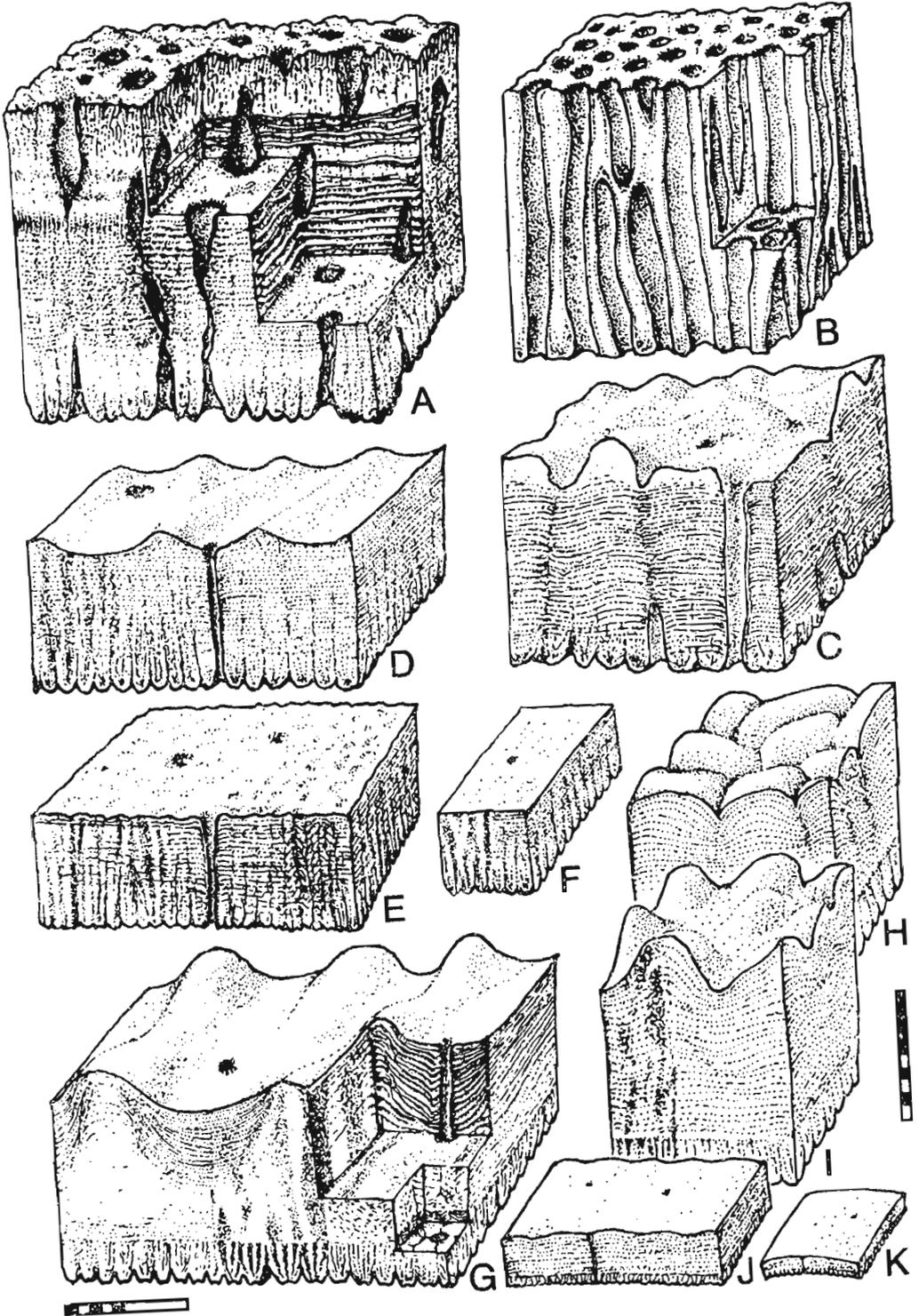
There are several common features of the bigger, dinosaur eggs in which they differ from expectations based on extant birds' eggs comparisons. The eggs are strongly elongated (except for the largest subspherical eggs). The elongation coefficient of angusticanalicate eggs is usually more than 2 and in the largest eggs in this group sometimes closer to 3). Thus the eggs have bigger volume than predicted by an extant bird average formula (Hoyt 1976). Also the surface area is greater, and thus the area/volume (A/V) ratio is higher by about 15%—20% in the elongated eggs than in typical bird eggs of given mass (calculated e.g. according to Paganelli *et al.* 1974). Data shown in fig. 7 seem to suggest a positive correlation of elongation of the eggs with their mass. Probably larger eggs, incubating in underground nests, faced more severe gas exchange problems than did the smaller ones, and so excess surface would have been more advantageous. The only exception to the rule are the largest dinosaur eggs belonging to Faveoolithidae, Spheroolithidae and Dendroolithidae, of subspherical shape (Mikhailov 1991). They have, however, extremely porous shells (multicanalicate and prolatocanalicate pore systems), contrary to the other types, having "normal" angusticanalicate pores.

The eggshell thickness (and thus the pore length) is also almost doubling the values expected for the bird eggs of the same mass (see table 1) (contra Coombs 1989, who regards dinosaur eggs as relatively thin shelled).

Both of these tendencies (excess eggshell surface area and thickening of the eggshell) necessitated much greater amount of calcium carbonate to be excreted by female per egg mass unit (about two- to threefold as compared with extant bird species). Only a small fraction of it was used by an embryo (the resorption craters at the tops of mamillae do not significantly reduce the shell thickness; pl. 12:3, 18:1, 19:1; Bond *et al.* 1988), but the thicker eggshell made the hatching more difficult for the embryo. Thus, it may be expected that such cost (relatively higher for smaller dinosaurs, having higher clutch/female mass ratio; Dunham *et al.* 1989; usually much lower than in extant birds; Rahn *et al.* 1975) resulted from the action of some selective forces.

What could the meaning (adaptive role) of these shared differences be? Which factor(s) could shape them so uniformly?

The synopsis of possible advantages of those feature is presented below. I assume a pan-adaptationist view, implying that intraspecific variability



allowed for modifications of egg shape, eggshell thickness and porosity, limited only by physical constraints, so that the observed values were at least close to the optimal ones.

**A.** Some possible explanations of greater area/volume ratio in elongated dinosaurian eggs:

I. Greater A/V ratio was the selected character itself — e.g. because of easier diffusion per unit mass.

II. The greater A/V ratio is a by-product of greater elongation, which was favored by selection:

1. The highly elongated egg maximizes volume, given the diameter of oviduct/hipbone canal of a female:

a) more yolk was available to the embryo, thus improving the hatchling's fitness;

b) more albumen and thus more water was available to the embryo, thus enabling it to survive incubation in very dry conditions.

2. The elongated shape, resembling almost cylindrical frustum ended with hemispheres, was advantageous:

a) the shape helped to establish regular and stable spiral-conical arrangement of the eggs in the nest, allowing them to incubate in the optimal conditions;

b) the elongated shape, together with the longitudinally oriented ridges on the outer surface of eggshells protecting the pore openings from blocking by the nest material, induced air convection along the grooves, thus improving the aeration of eggs;

c) such shape was more suitable for elongated dinosaur hatchling.

**B.** Possible explanations for the greater thickness of the dinosaurian eggshells than predicted for bird eggs of the same weight:

I. The thickness (and possibly the ornamentation, too) reflects the calcium balance of the female, and thus is not adaptive for the offspring, but just serves as ionic dump for the parent.

II. The shell had to be thicker because its microstructure made it weaker (per unit of thickness) than birds' eggshell.

III. The elongated shape of the eggs induced higher mechanical stresses than more spherical shapes of birds' eggs.

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Fig. 8. Comparison of the examined Upper Cretaceous Mongolian eggshells. A prolatocanaliculate dendroolithid eggshell; B multicanaliculate faveoololithid eggshell; C prolatocanaliculate spheroolithid eggshell; D—K angusticanaliculate eggshells: D, E, F protoceratopsid: ornamented (D equatorial part), and smooth (E typical, F thin) eggshells; G elongatoolithid eggshell (equatorial part); H, I two variants of dispersituberculate ornamentation pattern of elongatoolithid eggshell; J larger ?avian eggshell; K "*Gobipteryx minuta*" eggshell. Scale bars equal 1 mm. In H and I the horizontal scale is compressed by approx. 1.5 to show the ornamentation patterns. The pictures show schematic oblique view of the eggshell fragments, oriented like in fig. 3, and based on observations in transmitted and polarized light, and in SEM. Extinction pattern (polarized light) is superimposed onto the front surface of D, E, F, G and I to show the similarities and differences among the thicker angusticanaliculate eggshells.

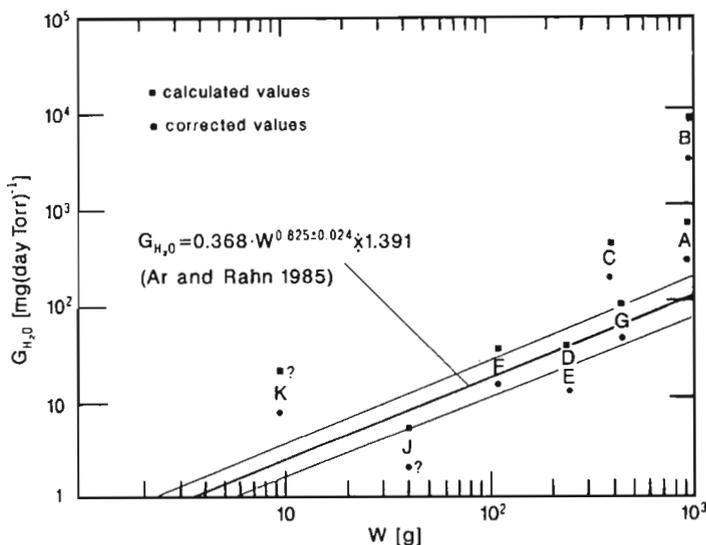


Fig. 9. Plot of eggshell conductance versus egg mass. The lines show regression curve (and standard error range) for extant bird eggs (from Rahn and Ar 1985). The estimates for dinosaur eggs show the highest calculated value and the value corrected down for the pore plugs. Egg types as in Fig. 8.

IV. The external forces acting on the shell of incubating eggs were greater than similar loads of birds' eggs, and thus the eggshells had to be stronger. Possible stresses could have resulted from the amount of overlying nest material, or weight of incubating parents or of other animals crossing the nesting ground during incubation if the chance of stepping on a buried nest was high.

V. The main role of a double-thick eggshell was elongating the pores (and reducing the diffusive permeability of eggshell):

1. to compensate for greater A/V ratio;
2. to reduce water loss;

3. because of a greater-than-present oxygen content in the atmosphere the diffusive constraints for successful incubation were different from those met by extant birds.

Some of the aforementioned possible explanations can be tentatively rejected:

A.I. is rather improbable, because the improvement of A/V ratio is only by factor of 1.1 to 1.2 and the thickening of eggshell necessary to compensate greater fragility of subcylindrical shell vs subspherical one would reduce the enhancement of diffusion permeability to an even less significant level.

A.II.1.a. could be achieved by enlarging the equatorial diameter, not by elongating the egg (yolk forms a sphere, and thus its size is limited by a lesser radius of eggshell); elongating an egg reduces the yolk to whole egg ratio.

A.II.1.b. is doubtful, as extant crocodile eggs, though elongated, do not show adaptations to drier nesting conditions than e.g. spherical turtle eggs.

B.I. The comparative studies (Ar and Rahn 1985, Calder 1978, Seymour and Rahn 1978) have shown that the shell thickness in close to predicted by allometric equations in birds of different size but similar incubating conditions, and alters appropriately when these conditions are atypical (hole nesting, mound nesting). It is also rather improbable that only the female and precisely during the oviposition period should suffer from calcium stress. The adaptive role of the character, which could be expected on theoretical grounds, is also a necessary prerequisite for the following discussion.

B.II. The eggs having microstructure closely resembling the avian (ornithoid) microstructure have also much thicker shell than bird's eggs of similar weight. It seems also that the eggshell strength could be improved by continuous ridges, parallel to the long axis. This is the case in the ornamented protoceratopsid eggs, but the other eggs have ornament consisting of isolated hillocks (Elongatoolithidae) or not visible at all. It does not affect the degree of "overthickening", however.

B.III. is obviously true, but does not explain the degree to which the shell is thicker (the shell at the hemispherical ends of an egg is still thicker than a predicted mean).

B.V.1. could be true but the dinosaur eggshells are much thicker than it would be needed for compensating for the greater A/V ratio.

B.V.2. and 3. are likely the most appealing explanation of excessive thickening of the dinosaurian eggshells, but they urge to raise two questions:

1. If reducing the diffusive permeability by elongating pores were the main advantage, couldn't the same be achieved at lesser calcium carbonate expenditure by merely locating the pore openings at the prominent hillocks instead of situating them in the grooves? Such an egg was illustrated by Hirsch and Packard (1987: fig. 41—42; superficially alike ornamented egg, reported by Dobie 1978, had, however, pores opening between hillocks).

2. If the reduced permeability as such was advantageous, why was not the total pore area reduced by minimizing pore density and/or diameter?

The answer to the first question is simpler: locating the pore openings at the protruding hillocks, though saving much shell material, would make the pore orifices susceptible to occlusion by the nest material. Developing such a morphological type of eggshell as illustrated by Hirsch and Packard (1987) would also require rather deep changes in the process of shell formation, so we may except that probability of its appearance

in different groups of reptiles is low. Since the distance between neighboring ridges and hillocks exceeds mean diameter of predominantly fine sand grains in the sediment, it seems that the eggshell surface was adapted to protect the pore openings from being blocked by objects larger than sand grains, most probably vegetation (fig. 5A). So the eggshell ornamentation may reflect properties of nest material. Thus, the coarsely sculptured eggs would have been incubated in vegetation mounds and the smooth-shelled ones — in sand mounds, holes or on the surface of ground (the latter is most probable for the "*Gobipteryx*" eggs). This interpretation is further corroborated by the notion, that smooth-shelled eggs are seldom crushed and flattened, and tend to be preserved in parallel subvertical orientation (blunt ends pointing upwards) — e.g. ZPAL MgOv-I/3 (Lefeld 1971: fig. 14; pl. 20: 2), MgOv-II/7, MgOv-II/25. This indicates little disturbance after deposition, so that the eggs were only covered by excess sand in their upper part, which is not always preserved. The ornamented eggs do not exhibit such differences in preservation potential of both ends of an egg. Their nests seem to be secondarily flattened and destroyed after vegetation decay, so the collapsing sediment have crushed the eggshells (fig. 5E, F). The functional significance of the ornament is also indicated by the fact that otherwise similar eggs of smooth and ornamented protoceratopsid type differ in that the former lacks the prominent ridges, which should be interpreted as resulting from different mode of nesting. Since the smooth eggs were obviously positioned vertically with no less care than the ornamented ones, we may leave out another possible explanation, that the sculptured surface was an adaptation for facilitating parental manipulations with slippery eggs.

The hypsilophodontid *Orodromeus makelai* eggs are also found preserving their subvertical arrangement with upper ends mostly lost (Horner 1987, Coombs 1989). This makes their nests similar to the aforementioned Mongolian nests of smooth-shelled elongated eggs, interpreted here as originally positioned in warm and humid sand. The hypsilophodontid eggs do show longitudinal ornamentation on their outer surfaces. The pattern, however, consists of fine parallel longitudinal striations, with density exceeding 15 per millimeter (Horner 1987: fig. 5c). This value is much greater than in ornamented Mongolian eggs, where the distance between neighboring ridges varies between 1 and 2 mm. Thus the hypsilophodontid eggs, though "ornamented", fit well within the scenario, developed here for the Gobi eggs, and assuming taphonomy-morphology correlation. Their taphonomy indicates that they were incubated in sand, and the size of their grooves seems to match sand grains dimensions rather than elements of dead vegetation. *Maiasaura* eggs, on the other hand, should have been incubated in the vegetation mound instead (not like illustrated in Horner 1984: 134).

The second question is more challenging. The porosity of the thickest dinosaur eggshells is much greater than predicted for bird eggs of that size. Why then did the dinosaurs spend so much excess calcium carbonate for double-thick eggshells, at the same time perforating it with multiple pores, making the diffusive permeabilities orders of magnitude higher than those observed in avian eggs today?

Perhaps the pore orifices were capped with organic filling, common in avian (Board 1982) and crocodylian (Ferguson 1982) eggs incubating in a hole- or mound-nests, thus reducing the water loss but not the oxygen diffusion. The other possibility is that the thick eggshell was necessary for mechanical reasons (B.III.) rather than for impairing gas exchange rate. Another argument against thickening of the eggshell as the way of reducing permeability of the shell is that extant birds achieve this by reducing porosity (Carey 1980).

There, of course, another problem remains: how can it be explained that the sauropods, living in the same area, laid down not elongated, but subspherical eggs? Do the inferences apply to them?

The sauropod and ornithopod eggshells were still thicker than in the other dinosaur eggs. This could be attributed to some extent to the microstructure of the shell which was probably less resistant to tangentially oriented tensions. This could also explain the subspherical shape of these eggs, making them mechanically more resistant. The shell was extremely porous, especially in the inner layer, so that the permeability was almost ten times greater than expected for bird eggs of similar size. Since water loss from such shell would exceed lethal level of 20—25% in a few days (2—6) and the estimated incubation time for egg of that mass was longer than a month (see table 1), we must assume that incubation took place under very high humidity and/or that the pores were plugged with some organic matter, reducing the actual permeability. In fact, partial removal of calcite from a ?sauropod eggshell preparation (ZPAL zpOv.-I/8), from Los Alamitos Fm, Patagonia (Andreis 1987), revealed possible traces of a pore plug in the outer part of a pore. These eggs are attributed to Titanosauridae (Powell 1987). Organic fillings of the pores of tubospherulitic eggs were also described earlier by Williams *et al.* (1984). Such structures could have been present also in the angusticanaliculate eggs (pl. 12: 4).

In France, superficially similar eggs belonging probably to the tubospherulitic morphotype (their exact microstructure was not described nor illustrated), were found forming large circular nests (Breton *et al.* 1986, Cousin *et al.* 1989, Coombs 1989). Cousin *et al.* (1989) claimed that similar eggs at Rennes-Le-Chateau belong to two different species of dinosaurs: a sauropod and an iguanodontid. The only criterion given by these authors relies solely on the arrangement of eggs (eggs that can be regarded as laying on somewhat arbitrarily chosen circles are regarded

to be laid by *Hypselosaurus*, and identical eggs forming clusters intertwined with circles are regarded as representing *Rhabdodon*). Moreover, Cousin *et al.* reported lack of differences in shape, size or eggshell microstructure, that could support the two-species interpretation.

Such far-reaching conclusions seem to be unfounded, especially regarding variability of eggs and eggshells of roughly similar age from the Gobi desert. Thus rejecting the explanation of Cousin *et al.* (1989), constructed on assumption that sauropod and iguanodontid eggs after more than 100 million years of independent evolution were still morphologically identical and that the female sauropod made the circles moving around her anchored tail, I propose another, functional, explanation of the two modes of nesting.

Gas diffusion parameters limit clutch size in underground or vegetation covered nest. Seymour (1979) calculated this limit for *Hypselosaurus* as being ca. 13 eggs. This is a small fraction of adult *Hypselosaurus* body mass, so we may not only infer that one female shared out the eggs into several nests (Seymour 1979), but also that she used one mound of vegetation for placing two spatially separated clutches. The incubation temperature differences among the two groups of eggs could induce developing embryos into male or female hatchlings, like in extant crocodiles and other reptiles (Bull 1987). Given the close phylogenetic relationship between crocodiles and dinosaurs it seems very probable that the temperature-induced sex determination mechanism was present among dinosaurs (Paladino *et al.* 1989).

Knowing the great taxonomic diversity of eggs (e.g. Schleich and Kastle 1988, different works by Hirsch), which allows even for their identification at subspecies level (Sauer 1972), the "*Hypselosaurus/Rhabdodon*" eggs found in the same place and stratum should not have been assigned to two distant groups only by their spatial arrangement, without any indication of morphological or microstructural differences. I argue for the temperature-dependent sex determination as the most plausible explanation for such mode of nesting. Although the precise reconstruction of the nest structure is not possible, three alternative models of the arrangement of eggs can be proposed.

First, it is possible that the preserved pattern reflects quite faithfully the original one, with one set of the eggs occupying the center of the mound (cluster with higher incubating temperature) and the other distributed circumferentially (lower temperature of incubation).

Equally plausible is, however, another taphonomical interpretation: two sets of eggs could have been placed in one vegetation mound in two layers, one above another, like in alligator nests (Ferguson and Joanen 1982). In this case, the eggs from the upper layer could, after partial decay of peripheral plant material, roll down the slope of the mound. Thus they would secondarily stay at the ground level, marking the cir-

cumference of the base of the mound. This would also explain incompleteness of the "circular nests" and irregular gaps between the eggs; the eggs would tend to roll down by chance, depending on the degree of destruction of nest material in a particular sector.

Another possibility is that the same type of nest could have decayed differently: in some cases the outer "walls" of the mound were weaker and they allowed the eggs to roll down or else the eggs may have remained clustered until burial by sediment. Such differences could result from the fact that lethal flooding of the eggs happened at different stages of incubation period each time (Rennes-Le-Chateau eggs seem to represent three successive nesting seasons).

Similarly, the interpretation of collapsed sauropod eggshells as successfully hatched (Cousin *et al.* 1989) is rather unconvincing. The hatching embryo should rather push out the lid or cap from the egg rather than pulling it in, as would be necessary to produce section shown in Cousin *et al.* (1989), unless a unique "implosive hatching" model is assumed for dinosaurs. Hayward *et al.* (1989) have shown instead that similar collapsing occurs in unhatched eggs of extant ground-nesting birds under the pressure of overlying sediment (volcanic ash in the case described) and the forces produced by heavy animals walking upon the sediment and trampling the eggs underneath. It is worth of noting here that also the ?titanosaurid eggs may have been buried by volcanic eruption in Romania (Grigorescu *et al.* 1990). The eggs, attributed to sauropod *Magyarosaurus*, found in clay layer topped by thick bed of volcanic deposits, are clustered in linear rows comprising either four or two eggs. The description of the eggs arrangement given by Grigorescu *et al.* (1990) does not allow for comparing it to the Rennesles-Chateau eggs. Perhaps "a linear row comprising two eggs" could be a part of a "circular nest" or of a "cluster clutch". Moreover, Kerourio (1981) described a hole-buried clutch of "*Hypselosaurus*" eggs, showing neither linear nor circular pattern.

Another interesting problem is the nesting behavior of the primitive birds: how early did they start to use the parents' metabolism as the energy source for the incubating embryo (open nests instead of mound or hole-nests)? Such a behavioral transition should be reflected in synchronous reduction of eggshell porosity to the level predicted by allometric equations calculated for extant birds or even lower (due to higher-than-present atmospheric oxygen content in late Mesozoic). It would be interesting to analyze the Tertiary bird eggs (like *Ornitholithus*) in that respect. The Mongolian Upper Cretaceous avian eggs have strongly recrystallized eggshells with obscured pore pattern. Judging from taphonomic indications incubation, in wet sand seems to be the most probable nesting mode (compare Mikhailov 1991). Thus the reptilian type of

incubation would persist among birds at least to the Late Cretaceous. The ecological consequences of the behavioral shift to incubating by parents themselves would be enormous for birds. They could begin the conquest of habitats farther from beaches and shores of the warmer climatic zones, being probably their original niche.

#### ISOTOPIC STUDIES

The isotopic studies (fig. 10) revealed that all specimens analyzed, originating from different localities, formations and representing different types of eggs show values of  $\delta^{18}\text{O}$  of  $-10$  to  $-13$  (except one eggshell from Bayn Dzak, with the value of  $-7$ ) and  $\delta^{13}\text{C}$  of  $-3.8$  to  $-6$ . These values are close to those reported by Erben *et al.* (1979) for "Protoce-

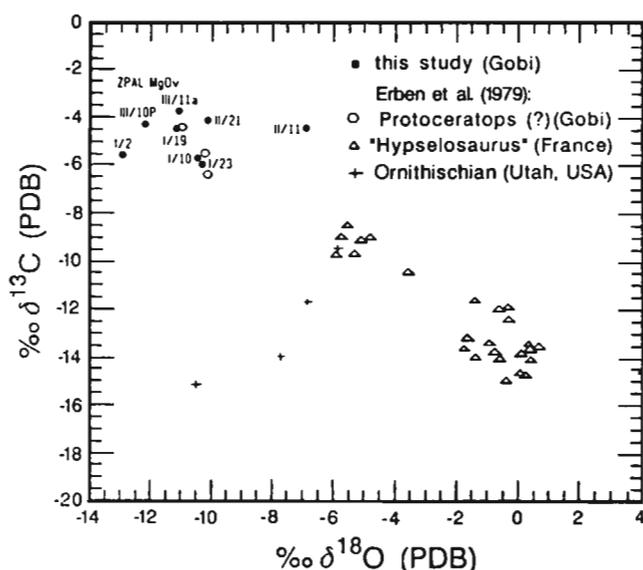


Fig. 10. Isotopic contents of eggshell samples. Data of Erben *et al.* (1979) for comparison.

ratops" eggshells. They differ from values obtained by Erben *et al.* (1979: fig. 14) for other dinosaur eggs, from France and the United States. Values cited by Erben *et al.* (1979: fig 12, tab. 1) for eggshells of chickens from equatorial America, Morocco and Afghanistan, to which the Gobi egg samples are closer than the other dinosaurian eggs, would suggest rather warm and possibly semiarid climate of the paleo-nesting site at Bayn Dzak. Folinsbee *et al.* (1970) attributed the oxygen isotopic ratios met in their samples of dinosaur eggs from Gobi to the physiographical

situation of the area, irrigated by continental water from cool highlands, which would be enriched in the lighter oxygen isotope.

It should be remembered, however, that any simple paleophysiological and paleoenvironmental inferences, based on stable carbon and oxygen isotopic contents in the fossil eggshells, are very uncertain. There are many different factors affecting the isotopic balance. They include: the unknown physiological bias (fossil eggshells, contrary to brachiopod shells, were not simply reflecting the environmental concentrations of C and O isotopes), diet (but both the C<sub>4</sub> and C<sub>3</sub> plants markedly differ from the Gobi egg samples), climate (temperature, precipitation, season of the year, latitude, elevation, type of erosion substrate) as well as the changing global atmospheric balance of isotopes, resulting from even minor changes in their oceanic circulation.

All these usually undetermined factors combine with possible diagenetical alterations of isotopic concentrations. Any attempt to compare and interpret isotopic data concerning samples of various types of eggshells, from different areas and of different age, needs cautious evaluation of all possible biases, that could finally result in observed isotopic content.

That fact, that the isotopic ratios of C and O in fossil Cretaceous eggshells are remarkably more coherent within samples from each area (even though the samples studied here come from different types of eggs: avian to dinosaurian) may indicate that the environmental control over this feature was overwhelming the physiological differences or that the diagenesis markedly biased the isotopic content. The latter interpretation is further corroborated by studies of Dauphin and Jaeger (1990), showing that the stable elements content in French dinosaur eggs is mostly diagenetically controlled (this is, however, mainly a result of extreme porosity and large amount of interfering sedimentary filling in this type of eggshell).

#### SYSTEMATIC PART

The following descriptions employ character typology, nomenclature and taxonomic approach of Mikhailov (1991), who also described ultra- and microstructure of the Mongolian Late Cretaceous eggshells. Thus, the microstructure is not described in detail there; only diagrammatic synopsis of eggshell types studied is given for clarity (figs. 6, 8).

The shell material from the Gobi Desert is distinct from many other European and American fossil eggshells by its pale color: whitish, creamy or pinky.

All the occurrences given in the descriptions below refer to the material collected by the Polish-Mongolian Expeditions.

**Dendroolithidae**

(pls. 12: 1, 13: 2; figs. 6B, 8A)

*Material.* — ZPAL MgOv-I/16 — a half of an eggshell and some shell debris with ?faint traces of embryonic bones on the inner side, several pieces of the broken eggshell from Khulsan.

ZPAL MgOv-III/17, 18a—c, 20 — numerous pieces of eggshells from Khermeen Tsav II.

Measurements:

D(mm)	d(mm)	As(cm <sup>2</sup> )	V(cm <sup>3</sup> )	L(mm)	p·cm <sup>-2</sup>
115	108	350—400	650—800	2.2—3	60—100

*Description.* — Large subspherical egg reaching 12 cm in maximum diameter and volume of ca 0.7—0.8 dm<sup>3</sup>. The shell is thick (2—3 mm, including protruding ornamentation), with shagreen external surface, forming irregular hillocks, nodes and well visible pits: openings of pores. The microstructure of the shell represents dendrospherulitic morphotype, with varying orientations of interlocking prisms, especially well visible on thin sections in polarized light. The prolatocanaliculate pore system makes the shells the second most porous among studied Mongolian material (after multicanaliculate faveoolithid eggshells). The porosity is however less than in similar-sized "*Hypselosaurus*" eggs from Aix-en-Provence Basin (France; ZPAL zpOv-I/1—5) or in "*Titanosauridae*" eggs from Los Alamitos (Argentina; ZPAL zpOv-I/8). The latter two categories of eggs (megalolithid *sensu* Mikhailov 1991) are believed to be laid by sauropods (Dughi and Sirugue 1957, Powell 1987).

*Remarks.* — No nests of these eggs were collected by the Polish-Mongolian expeditions, but in the Chinese, Mongolian and Soviet collections there are clutches of dendroolithid eggs. Their form (irregular clusters), resembling extant turtle nests, indicates hole-nesting.

*Occurrence.* — Khulsan (Barun Goyot Fm.) and Khermeen Tsav II (red beds of Khermeen Tsav).

**Faveoolithidae**

(pl. 15: 1—3; figs. 6A, 8B)

*Material.* — ZPAL MgOv-III/18b — several pieces of eggshell.

Measurements:

D(mm)	d(mm)	As(cm <sup>2</sup> )	V(cm <sup>3</sup> )	L(mm)	p·cm <sup>-2</sup>
ca 150	ca 135?	500—700	900—1200	2.2—2.4	300—1500

*Description.* — Thick, multicanaliculate eggshells of filispherulitic morphotype.

*Remarks.* — The dimensions of the egg roughly estimated from the curvature of preserved fragments fall within the values reported by Kolesnikov and Sochava (1972) and Zhao, (1979). A clutch of 16 eggs of this type described as *Youngoolithus xiaguanensis* (Zhao, 1979) was accompanied by a tridactyl footprint, about 15 cm long (Zhao 1979: fig. 2). This may indicate ornithopod affinities of these eggs.

*Occurrence.* Khermeen Tsav II (red beds of Khermeen Tsav).

**?Spheroolithidae**  
(pl. 15: 4—6; fig. 8C)

*Material.* — ZPAL MgOv-III/17 — few fragments (“S”) of eggshell.  
ZPAL MgOv-III/18b — fragment “F”.

*Measurements:*

L(mm)	p·cm <sup>-2</sup>
1.4—1.8	150—200

*Description.* — Thick eggshell with sagenotuberculate ornamentation and prolatospherulitic morphotype.

*Remarks.* — Due to the scarcity of material, diffusive permeability may be only estimated as being similar to that of dendroolithid eggshells. The eggs were of subspherical shape (Mikhailov 1991).

*Occurrence.* — Khermeen Tsav II (red beds of Khermeen Tsav).

**?Protoceratopsidae**

Mikhailov (1991) does not further subdivide the Late Cretaceous Mongolian eggs with prismatic morphotype and angusticanaliculate pore system. I decided, however, to separate numerous eggs possessing this shell structure into three groups, differing in size, eggshell thickness and ornamentation. Nevertheless it cannot be excluded that the differences are not taxonomically relevant and reflect inter- or intrapopulation variability and secondary changes (e.g. erosion, dissolving of the shell).

Larger smooth-shelled protoceratopsid eggs  
(pls. 11: 2—3; 18: 1—4; figs. 6D, 8E, F)

*Material.* — ZPAL MgOv-II/2, 2a — a nest: 8 eggs embedded in the sandstone and 7 loose egg fragments from Bayn Dzak (Main Field);

ZPAL MgOv-II/3a, 3b — a nest: 6 eggs in one block of sandstone and half of an egg from Bayn Dzak (Dashzeveg Sayr);

ZPAL MgOv-II/20, 21 — several egg fragments and shell debris from Bayn Dzak.

*Measurements:*

D(mm)	d(mm)	As(cm <sup>2</sup> )	V(cm <sup>3</sup> )	L(mm)	p/cm <sup>-2</sup>
<150	<50	ca 230	ca 230	0.6—1.2	20—80

*Description.* — Large, strongly elongated ovate eggs (D/d almost 3). The eggshell is light beige or grayish colored, with no prominent ornamentation. Sometimes faint parallel striation is visible in the equatorial part of the egg. Under a small magnification the pore openings become visible. The eggshell thickness varies from ca. 0.6 mm on poles to twice as much in the equatorial area of the egg.

*Remarks.* — The oblique or subvertical arrangement of eggs resembles rather the nests of larger ?bird eggs from Khulsan and Bayn Dzak, described below (p. 181). Despite some superficial microstructural similarity to extant avian eggs, shape of the eggs of this type made them not suitable for typical incubating procedures common among birds (like turning the eggs while incubating by parents). Their close arrangement in the nest, well visible in preserved clutches, seems to indicate rather immobile condition until hatching. They could have been buried by the female in a deep hole with steep siding, then possibly covered with vegetation. Lack

of ornament and preserved subvertical orientation seems rather to point to filling the hole with sand. Perhaps a different nesting behavior was the cause of the apparent reduction of external ornament. In some cases, eggshells of elongatoolithid type were also lacking their prominent external ornamentation, even in areas protected from erosion by the rock matrix, while internal undulation of accretion lines was preserved. Perhaps this was the result of similar diversification of nesting habits; the internal undulations could have been retained in smooth-shelled variants, as "invisible" for the selection.

The volume estimate of over 500 cm<sup>3</sup> for protoceratopsid eggs given by Bakker (1971) and used by Case (1978) in their calculations of egg/adult mass relationships is twice as high as the highest result obtained in this study. The eight inches (20 cm) long model used by Bakker is larger than protoceratopsid eggs in the Warsaw and Moscow collections (hardly exceeding 15 cm in length). The superficially similar elongatoolithid eggs are slightly larger than protoceratopsid ones, but still well below the value of 0.5 liter.

*Occurrence.* — Bayn Dzak, Djadokhta Fm. ("upper egg-bearing horizon", see Lefeld 1971).

#### Smaller smooth-shelled ?protoceratopsid eggs (pl. 20: 12; fig. 6E)

*Material.* ZPAL MgOv-I/1 — one incomplete egg embedded in sandstone, with imprints of broken eggshell in 2 pieces of red sandstone, from Altan Ula IV.

ZPAL MgOv-I/10 — eroded half of an egg from Khulsan;

ZPAL MgOv-I/25a—b — two polar parts of egg(s) from Khulsan;

ZPAL MgOv-III/9 — two polar parts of eggs from Khermeen Tsav.

Measurements:

D(mm)	d(mm)	As(cm <sup>3</sup> )	V(cm <sup>3</sup> )	L(mm)	p·cm <sup>-3</sup>
120?	50	140—180	110—170	0.1—0.3	20—30

*Description.* — Elongate egg of the shape similar to the previous type, but smaller. Thin, smooth angustispherulitic eggshell.

*Remarks.* — The extremely thin eggshell of these eggs is the most striking difference to the above-described type. It should be stressed that even fractured pieces of equatorial zone of eggshell, embedded in rock matrix, and thus witnessing no weathering process since burial, never exceed 0.3 mm in thickness. It is worth noting, however, that in spite of the thin eggshell the eggs are almost not deformed. This is markedly different from common flattening of the ornamented protoceratopsid and elongatoolithid eggs, which have much thicker shells. This should be probably attributed to the nesting conditions favoring the thin-shelled eggs. The preserved parts were probably the sharp ends, buried in sediment. This kind of preservation constraints would suggest sand-nesting mode, as it was probably the case with other large and medium smooth-shelled eggs described here. Subvertical positioning of these eggs (like in the previous type nests) would reduce the stress perpendicular to the long axis of the egg, enabling it to withstand successfully the forces which could otherwise crush it. The load of material covering the nest had to be remarkably smaller than in the nest of previously described, thick-shelled eggs. Another support for that inference is the incomplete preservation of the eggs — with no blunt ends, which were poorly protected. Thin eggshell indicates also rather humid incubation conditions with low oxygen partial pressure (Calder 1978).

*Occurrence.* — Khermeen Tsav (red beds of Khermeen Tsav), Khulsan (Barun Goyot Fm.), Altan Ula IV (Nemegt Fm.).

### Protoceratopsid eggs with prominent ornamentation

(pls. 11: 4; 16: 3; 17: 2—5; figs. 6D, 8D)

*Material.* — ZPAL MgOv-I/4 — several fragments of eggs embedded in light sandstone from Nemegt (Western Sayr);

ZPAL MgOv-I/5—7, 8a—b, 9a—e, 10a, 12—13, 14a—b, 15a—d, 17, 20, 23—24, 26a—f, — ca 40 eggs and egg fragments from several distorted nests from Khulsan;

ZPAL MgOv-I/27a—b — numerous shell debris from SE Nemegt “Barren series”);

ZPAL MgOv-II/1a—f — poorly preserved remains of a nest (7 partially preserved eggs, numerous smaller fragments and shell debris) from Bayn Dzak;

ZPAL MgOv-II/4, 5a—d, 8, 10, 19, 22 — ca 20 eggs and egg parts from Bayn Dzak (Main Field);

ZPAL MgOv-II/23 — a nest of 19 eggs from Khashaat;

ZPAL MgOv-II/24 — numerous shell debris from Bayn Dzak (Green Sayr);

ZPAL MgOv-III/1—8, 19 — 8 fragmentary eggs and shell debris from Khermeen Tsav II.

#### Measurements:

D(mm)	d(mm)	As(cm <sup>2</sup> )	V(cm <sup>3</sup> )	L(mm)	p·cm <sup>-2</sup>
140—150	50—55	200—260	200—250	0.6—1.4	20—90

*Description.* — Large, asymmetric, strongly elongated egg with linearituberculate ornamentation (the ornament consists of tiny ridges, oriented parallel to long axis of the egg in the equatorial part and meandering in the polar area; the ornament vanishes towards the poles). Nest, of ca 0.5 m in diameter, consists of ca 20 (perhaps up to 30—40) eggs, arranged radially around the center. The eggs are often preserved in pairs (ZPAL MgOv-II/1a, 1d, 8a—b, 23, 26). The eggshell is grayish or beige colored, never white.

*Remarks.* — The presence of twin eggs can be interpreted as resulting from gluing together the eggs from both oviducts during oviposition. If such pairs are still present in the fossil material, then it can be inferred that after being laid, the eggs were not disturbed. Their subhorizontal position may reflect their location *in vivo*, but according to the functional interpretation presented on fig. 5, it is the result of decay of the nest material (plants?). The ornament suggests a coarser-than-sediment incubation environment and subvertical arrangement of eggs, facilitating convection.

Eggs and eggshells of this type have been often confused with those of Elongatoolithidae, described below. In case of the strongly eroded or recrystallized specimens, even the microscopic studies may be not sufficient to assign them correctly to one or the other group (e.g. pl. 12: 2).

*Occurrence.* — Bayn Dzak and Khashaat (Djadokhta Fm.), Khermeen Tsav II (red beds of Khermeen Tsav), Khulsan (Barun Goyot Fm.).

### Elongatoolithidae

(pls. 12: 3, 4; 13: 3—9; 14: 2, 3; 16: 4; 19: 1—4; fig. 6C, 8G, H, I)

*Material.* — ZPAL MgOv-I/2 — hundreds of eggshell fragments from Tsagan Khushu.

ZPAL MgOv-II/12 — a partially preserved egg and shell debris from Bayn Dzak (Dazheveg Sayr);

ZPAL MgOv-II/14a—b — 2 eggs, a few parts and shell debris from Toogreeg.

ZPAL MgOv-II/10—11a—b — voluminous shell debris from Bayn Dzak (Volcano, The Ruins).

ZPAL MgOv-II/16 — an egg from Bayn Dzak;

ZPAL MgOv-III/18a—c — shell debris from Khermenn Tsav;

Measurements:

D(mm)	d(mm)	As(cm <sup>2</sup> )	V(cm <sup>3</sup> )	L(mm)	p·cm <sup>-2</sup>
150—170	55—65	310—350	380—420	0.8—1.6	40—70

*Description.* — Large egg, apparently similar to ornamented protoceratopsid eggs, but slightly longer and with markedly bigger equatorial diameter (elongation coefficient of the protoceratopsid and elongatoolithid eggs is 2.7 and 2.4, respectively); ornamentation pattern consists of distinct hillocks arranged along parallel or bifurcating longitudinal or meandering lines instead of continuous fine ridges (pl. 13: 3—6). The trend of the ornament pattern to change from parallel on equator to irregularly meandering (or vortex-like) on the poles in protoceratopsid and elongatoolithid eggs (linearituberculate → ramituberculate → dispersituberculate in terms of Mikhailov, 1991) can be explained by purely geometrical reasons; the regions of the secretory epithelium with different effectiveness of eggshell formation were elastically stretched by the forming egg advancing along the oviduct. These eggs reveal ornithoid basic type and ratite morphotype with angusticanaliculate pore system. Pore openings appear in the valleys of the ornament, distributed in 1—2 mm intervals. The eggshell is grayish or beige colored.

*Remarks.* — As compared with the externally similar protoceratopsid type, the elongatoolithid morphotype is overrepresented in the eggshell debris, amounting up to 50% of loose eggshell fragments from Bayn Dzak, but rarely preserving as complete eggs or parts. This may reflect different nesting habits of the ovipositing animals (e.g. preferring nesting areas less prone to flooding during incubation season) and/or better hatching success because of parental care (Kurzanov and Mikhailov 1989 attributed similar eggshells to a theropod dinosaur; this may suggest that the parents were less susceptible to predation and probably displayed more bird-like parental care behavior). The ornamentation and porosity data presented here suggest humid, coarse incubation environment (?mound of vegetation).

*Occurrence.* — Bayn Dzak (Djadokhta Fm.), Toogreeg (Toogreeg Beds), Tsagan Khushu (Nemegt Fm.). Similar comparative material comes from Khaichin Ula (equivalent of the ?Nemegt Fm) — ZPAL zp Ov-I/9.

### ?Laevisoolithidae

(pl. 16: 1; fig. 7F)

*Material.* — ZPAL MgOv-I/3 — a fairly complete, but laterally collapsed, egg from Nemegt (Western Sayr);

ZPAL MgOv-II/9e — polar part of an egg from Bayn Dzak.

Measurements:

D(mm)	d(mm)	As(cm <sup>2</sup> )	V(cm <sup>3</sup> )	L(mm)
71	34	55	28—30	0.7

*Description.* — The eggshell is smooth, of the ratite morphotype, and the egg was of elongated ovate shape.

*Remarks.* — The more complete specimen was similar to the larger avian eggs in size, but its shell has been severely crushed. It is strange that the only egg of this size which was found so much deformed is the one having the thickest eggshell (0.7 mm vs 0.2 mm in the following type).

The partially preserved specimen from Bayn Dzak seems assignable to this type of eggs on the basis of shell thickness and structure.

In one part of the MgOv-I/3, apparent duplication of the shell is visible, probably resulting from a "telescoping" collapse of a fractured eggshell.

*Occurrence.* — Nemegt: Western Sayr, (Nemegt Fm. Bayn Dzak (Djadokhta Fm.).

### Larger avian eggs

(pls. 11: 1; 16: 2; figs. 6F, 8G)

*Material.* — ZPAL MgOv-I/19 — 26 egg halves or smaller parts from Khulsan;

ZPAL MgOv-I/21a—c — 3 egg halves and a piece of sandstone with eggshell fragments from Khulsan;

ZPAL MgOv-I/25c—d — an egg half with adhering shell bites of another egg, and equatorial part of second egg from Khulsan;

ZPAL MgOv-II/6a—g — parts of 6 eggs from Bayn Dzak (The Ruins);

ZPAL MgOv-II/7a—e — a nest (3 eggs embedded in sandstone and parts of at least 5 more eggs) from Bayn Dzak (Volcano).

ZPAL MgOv-II/25 — a block of sandstone containing at least one egg (lacking the upper end) and traces of other two, as well as bones in the same bedding plane as the top of eggs.

*Measurements:*

D(mm)	d(mm)	As(cm <sup>2</sup> )	V(cm <sup>3</sup> )	L(mm)
70	30	65—75	35—40	0.1—0.4

*Description.* — Medium size eggs, of elongated ovate shape ( $D/d > 2.2$ ). The shell is thin ( $< 0.4$  mm), smooth, chalky in appearance, white (sometimes with pink tone; e.g. the ones found at the Volcano site). It represents ornithoid type of structure, although strongly changed diagenetically. The eggs were standing subvertically, close to each other in the nest. Since upper ends are not preserved, the estimation of the overall dimension of the egg's long axis may be erroneous by more than 10%.

*Remarks.* — Along with the eggs in the nest ZPAL MgOv-II/7 and close to ZPAL MgOv-II/25, a few hind limb bone fragments were preserved. The size of bones fits well into the expected size range of parents (probably a bird). These cases [supported by a similar association in Moscow collection], if not accidental, could be interpreted as an evidence for very intensive parental care, with even lethal consequences to the parent protecting the nest.

*Occurrence.* — Khulsan (Barun Goyot Fm.), Bayn Dzak: Volcano and Ruins (Djadokhta Fm.).

### "*Gobipteryx minuta*"

(pl. 20: 1—7; figs. 6G, 8K)

*Material.* — ZPAL MgOv-III/10a—b — 2 eggs from Khermeen Tsav;

ZPAL MgOv-III/11a—c — 85 eggs and egg halves from Khermeen Tsav;

ZPAL MgOv-III/12 — 20 eggs and halves from Khermeen Tsav;

ZPAL MgOv-III/13 — 8 eggs and parts from Khermeen Tsav;

ZPAL MgOv-III/14 — 4 eggs and egg halves from Khermeen Tsav.

*Measurements:*

D(mm)	d(mm)	As(cm <sup>2</sup> )	V(cm <sup>3</sup> )	L(mm)
40—45	18—23	25—35	7—12	0.1—0.2

*Description.* — Medium size, ellipsoid rather than ovate eggs ( $D/d < 2$ ), ca 30—50% smaller than the larger avian or laevisoolithid eggs, with relative thickness of eggshell intermediate between the last two types.

*Remarks.* — The abundance of these eggs, occurring on different levels of a weathered slope (Dr. Andrzej Sulimski, pers. comm. 1989), indicates that Khermeen Tsav was a repetitive nesting ground for this species (*Gobipteryx?*). The taxonomic assignment of these eggs relies on the identification of embryonic bird skeletons (Elżanowski 1981). Thus, it is the most credible among attributions of the whole array of the eggs described here to their possible ovipositors<sup>1)</sup>. One of the unhatched embryos was described as possessing double eggshell (Elżanowski 1981: pl. 42: 1h, Mierzejewska 1981: fig. 1). The loose contact between the two shell fragments may indicate accidental overlap of crushed eggshell fragments.

*Occurrence.* — Khermeen Tsav I (red beds of Khermeen Tsav), in the *Protoceratops*-bearing horizon.

### Problematica

In some localities, numerous small ovoid sandstone forms were collected. Mikhailov (1988, personal comm. 1990) refused to describe similar fossils as eggs, quoting Hirsch's (1986) warning that some inorganic forms may mimic eggs in appearance. He regards then the "Problematica" as nodules. The mass occurrences of these objects in some Mongolian egg-bearing localities may suggest, however, that they represent the casts of true eggs: one can distinguish some categories of these fossils by their specific shape and size; besides, they sometimes bear calcareous remains of white ?eggshell contrasting with reddish sandstone matrix filling. These egg-like objects, shortly presented below, are strikingly similar to those illustrated by Schleich and Kästle (1988: 108—111) from Oligocene and Miocene of Germany, considered as the eggs of turtles and/or squamates, or to Tertiary fossils described as possible sea-snake eggs (Hatai *et al.* 1974). If those presumption are true, then the Mongolian ?egg casts may represent fossilized soft-shelled eggs of turtles, crocodiles or lizards, all three groups being represented in the local Late Cretaceous faunas (Osmólska 1980, Efimov 1983, Borsuk-Białynicka 1984). The differences among the types of problematic eggs described below are within the limits of variability of the Tertiary samples of Schleich and Kästle (1988), so they may represent individual variation rather than interspecific or generic one. Schleich and Kästle suggest that the smallest fossil cast may be that of an unfertilized egg. Perhaps this interpretation is also applicable to the Mongolian fossils of parchment-shelled eggs.

#### Small ellipsoid ?eggs

(pl. 20: 8; fig. 6I)

*Material.* — ZPAL MgOv-I/22a—d — 4 partially preserved egg casts from Khulsan;

ZPAL II/9a—c, 17a — 10 partially preserved egg casts, some of them with traces of dissolved eggshells.

ZPAL III/16 — an eroded egg from Khermeen Tsav I.

<sup>1)</sup> Current studies on the palaeognathe bird embryos from similar eggs from the Moscow collection may, however, put this assignment in doubt (Mikhailov personal communication, 1991).

## Measurements:

D(mm)	d(mm)	As(cm <sup>2</sup> )	V(cm <sup>3</sup> )
23—27	14—15	15	4.5

*Occurrence.* — Bayn Dzak (Djadokhta Fm.), Khulsan (Barun Goyot Fm.), Khermeen Tsav I (red beds of Khermeen Tsav).

## Small ovate ?eggs

(fig. 6H)

*Material.* — ZPAL MgOv-II/17b — 3 partially preserved egg casts with ?traces of eggshell.

## Measurements:

D(mm)	d(mm)	As(cm <sup>2</sup> )	V(cm <sup>3</sup> )
22	14	9	2.3

*Occurrence.* — Bays Dzak (Djadokhta Fm.).

## Small asymmetric ellipsoid ?eggs

(pl 20: 11; fig. 6J)

*Material.* — ZPAL MgOv-I/18a—c — 3 egg casts; ZPAL MgOv-III/21 — 1 egg cast.

## Measurements:

D(mm)	d(mm)	As(cm <sup>2</sup> )	V(cm <sup>3</sup> )
22	12	9	2.2

*Occurrence.* — Khulsan (Barun Goyot Fm.), Khermeen Tsav (red beds of Khermeen Tsav).

## ?Unfertilized small ovate eggs

(pl. 20: 10; fig. 6K)

*Material.* — ZPAL MgOv-II/9d, 15 — eroded casts of eggs.

## Measurements:

D(mm)	d(mm)	As(cm <sup>2</sup> )	V(cm <sup>3</sup> )
16	13	5	1

*Remarks.* — If these slightly flattened objects are egg remains, then they may be interpreted as natural casts of unfertilized eggs of one of the two previous types (compare Schleich and Kästle 1988).

*Occurrence.* — Bayn Dzak (Djadokhta Fm.).

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## KOPALNE JAJA OWODNIOWCÓW Z PÓZNEJ KREDY PUSTYNI GOBI

## Streszczenie

Praca zawiera opis kolekcji późnokredowych jaj ptaków, dinozaurów gadzi- i ptasiomiedniczych, oraz prawdopodobnych skamieniałości miękkoskorupowych jaj innych gadów, odkrytych w latach 1963—71 przez Polsko-Mongolskie Wyprawy Paleontologiczne na pustyni Gobi (fig. 1). Kolekcja ta, gromadząca bogaty materiał kopalny, obejmujący kilkanaście typów jaj późnokredowych, należy do najbogatszych w świecie.

Poza przeglądem mikrostruktury skorup (fig. 3, 4, 8) i kształtów jaj (fig. 2, 6; pl. 11—20), przedstawiono szacunkowe wyliczenia objętości, powierzchni, wydłużenia jaj, porowatości skorupy i jej przepuszczalności dla gazów oddechowych, porównując je z równaniami alometrycznymi dla współczesnych jaj ptasich (fig. 7, 9, tab. 1). Zaproponowano funkcjonalne wyjaśnienie roli ornamentacji, kształtu jaj i różnic tafonomicznych między gniazdami jaj ornamentowanych i gładkich (fig. 5) oraz oszacowano warunki i długość trwania inkubacji różnych typów jaj.

Wyniki badań składu izotopowego węgla i tlenu w próbkach skorup (fig. 10) wskazują na przewagę lokalnych czynników diagenetycznych w kształtowaniu proporcji trwałych izotopów, nie pozwalając na wiarygodne wnioskowanie o klimacie lub diecie dinozaurów i ptaków kopalnych.

Pracę wykonano w Instytucie Paleobiologii PAN w ramach problemu CPBP 04.03.

## EXPLANATION OF PLATES 11—20

## Plate 11

Nests from Bayn Dzak, Djadokhta Fm. (2—4: ?protoceratopsid nests)

1. ZPAL MgOv-II/7. Nest of ?avian eggs: *a* top and *b* side views. Note the bone (?avian crus) atop of the nest (arrows).
2. ZPAL MgOv-II/2. Smooth-shelled eggs (reversed museum specimen, prepared from below).
3. ZPAL MgOv-II/3a. Smooth-shelled eggs in a block of sandstone: exposed side (section: see Lefeld 1971: fig. 14).
4. ZPAL MgOV-II/23. Ornamented eggs: *a* the nest *in situ* (1970 expedition; photo: W. Skarżyński), *b* an egg from this nest, with attached matrix.

Scale bars: 1, 4 — 10 mm; 2, 3 — 5 cm

## Plate 12

1. ZPAL MgOv-I/16: *a* preserved half of a dendroolithid egg from Khulsan, *b* radial thin section of the eggshell (Prep. No. Ov-9/C<sub>2</sub>); polarized light, *c* tangential section (Prep. No. Ov-9/C<sub>1</sub>). Note numerous wide pore canals.
2. Radial thin section of ?protoceratopsid egg (Prep. No. Ov-4/5<sub>2</sub>). Polarized light.
3. ZPAL MgOv-II/1. Radial thin section of elongatoolithid (?theropod) egg (Prep. No. O-18/1<sub>3</sub>). Note pore canal (arrow) opening into a groove. Polarized light.

4. ZPAL MgOv-I/2. Elongatoolithid eggshell from Tsagan Khushu: radial section embedded in epoxy, treated with HCl (Prep. No. SOv-2/4); *a* note pore plug between mamillae with resorption craters (arrow; the circular structure is an air bubble in epoxy), *b* an enlarged detail. SEM.

Scale bars: *1a* — 10  $\mu$ m, *1b*, *c*, *2*, *3* — 1 mm, *4a* — 0.1 mm, *4b* — 0.05 mm

### Plate 13

1. ZPAL MgOv-III/18b. Dendroolithid eggshell from Khermeen Tsav II: outer surface of the eggshell. Rough, shagreened surface with large pore openings. Do not confuse with the sagenotuberculate ornamentation of Dendroolithidae.
2. ZPAL MgOv-III/20 dendroolithid eggshell, radial thin section (Prep. No. Ov-19/17). Polarized light.
3. Polar part of elongatoolithid eggshell from Bayn Dzak: *a* upper view, dispersituberculate ornamentation; *b* radial section (Prep. No. Ov-1/4<sub>2</sub>). Polarized light.
4. Polar part of elongatoolithid eggshell from Tsagan Khushu. *a* upper view, *b* radial section (Prep. No. Ov-7/3<sub>2</sub>); Polarized light.

### Equatorial parts of elongatoolithid eggshells from Bayn Dzak

- 5, 6 — upper views, egg axis horizontal, reflected light; 7—9 — transverse radial sections, polarized light
5. Ramotuberculate ornamentation.
6. Nodular variant of linearituberculate ornamentation.
7. Well preserved ornamentation. (Prep. No. Ov-7/9<sub>2</sub>).
8. External surface eroded. Note prominent undulation of accretion lines in the upper layer (white arrow) and sharp boundary between both layers (black arrow).
9. Eggshell eroded from outside (Prep. No. Ov-2/10<sub>1</sub>). Note extinction pattern in the spongy layer.

Scale bars: all 1 mm, except for *4a* — 2 mm

### Plate 14

Recent (1) and fossil (2, 3) ornithoid eggshell: SEM, radial views of fracture (1) or sections embedded in epoxy (2, 3)

Treatments: Cr<sub>2</sub>(SO<sub>4</sub>)<sub>3</sub> (*1a*, *b*), EDTA (2, 3)

1. ZPAL zpOv-I/14. Emu (*Dromiceius novaehollandiae*) eggshell (Prep. No. SOv-4/1): *a* general view, note pore canal and thick external zone (arrows); *b* boundary between spongy and mamillary layers, note squamatic ultrastructure in the upper and intermamillary fissure in the lower part; *c* mamillary layer, note the polygonal plates forming wedges (tabular ultrastructure) and the underlying egg membrane.
2. ZPAL MgOv-I/2. Elongatoolithid eggshell from Tsagan Khushu (Prep. No. SOv-4/2): *a* general view; *b* boundary between continuous and mamillary layers (arrow), note different ultrastructure of both layers and oblique cleavage cracks (herring-bone pattern).
3. ZPAL MgOv-II/10. Elongatoolithid eggshell from Bayn Dzak (Prep. No. SOv-4/3): mamillary layer, note wedges, adjacent matrix.

Scale bars: 1 mm, except for *1b* — 0.05 mm, *1c* — 0.1 mm, *2b* — 0.5 mm

Plate 15  
Multicanalicate faveoolithid eggshells

1. ZPAL MgOv-III/18b, fragment "1": a radial section (Prep. No. Ov-9/1<sub>2</sub>), b tangential section (Prep. No. Ov-9/1<sub>1</sub>). Reflected light.
- 2, 3. ZPAL MgOv-III/17, fragments "M": outer views of shell fragments.

Spheroolithid eggshells

- 4, 5. ZPAL MgOv-III/17, fragment "S": outer views of shell fragments. Note prolato-canaliculate pores; in 5, where erosion revealed deeper layer of the shell, large pore cavities are visible.
6. ZPAL MgOv-III/18b, fragment "F": a outer view, note sagenotuberculate ornamentation; b radial section (Prep. No. Ov-4/6<sub>2</sub>); c tangential section (Prep. No. Ov-4/6<sub>1</sub>).

Scale bars: 1 mm, except for 2, 3, 4 and 5 — 1 cm

Plate 16

1. ZPAL MgOv-I/3: a radial section showing overlap of collapsed eggshell fragments (apparent double eggshell); polarized light (Prep. No. Ov-22/1<sub>3</sub>) b whole ?laevisoolithid egg, note location of section.
2. ZPAL MgOv-II/25. Note the ?avian egg (upright and not flattened), fragment of another one (e) and the bone next to the nest (arrow).
3. ZPAL MgOv-II/4. Flattened ornamented protoceratopsid egg in a lower and b upper view.
4. ZPAL MgOv-II/16. Elongatoolithid egg: a general view; note typical flattening of the egg; b imprint of the eggshell with prominent dispersituberculate ornamentation.

Scale bars: 10 mm, except for 1a — 1 mm

Plate 17

1. Thick protoceratopsid eggshell from Bayn Dzak. Radial thin section (Prep. No. Ov-2/5<sub>3</sub>). Polarized light.
2. ZPAL MgOv-II/1. Longitudinal radial section of ornamented protoceratopsid eggshell from Bayn Dzak (Prep. No. Ov-18/1<sub>2</sub>).
3. Tangential section of the deeper layer of protoceratopsid eggshell from Bayn Dzak (Prep. No. Ov-18/1<sub>1</sub>).
4. ZPAL MgOv-II/10, fragment "P". Upper view of linearituberculate ornamentation of the equatorial area of protoceratopsid eggshell (compare pl. 13: 4—6).
5. ZPAL MgOv-I/2, fragment "P". Radial views of ?protoceratopsid eggshell from Tsagan Khushu: a treated with HCl (Prep. No. SOv-7/5a), b non-treated fracture (Prep. No. SOv-7/5b), c treated with EDTA (Prep. No. Ov-7/5c). SEM.

Scale bars: 1 mm, except for 5b — 0.5 mm

Plate 18

Smooth protoceratopsid eggshells from Bayn Dzak

1. ZPAL MgOv-II/21: a oblique upper view, EDTA treatment (Prep. No. SOv-7/1a); b oblique lower view, HCl treatment, note resorption craters; c radial view, HCl

treatment (Prep. No. SOv-8/1b; d lower part of nontreated eggshell (Prep. No. Ov-8/1d) in radial view (slightly from below).

2. Transverse radial section (Prep. No. Ov-5/2<sub>2</sub>). Note pore canal. Reflected light.
3. Transverse radial section (Prep. No. Ov-2/3<sub>4</sub>). Polarized light.
4. Transverse radial section embedded in epoxy, EDTA treatment (Prep. No. SOv-8/4): a general view, b a detail; note herring-bone pattern. SEM.

Scale bars: 1 mm, except for 4b — 0.1 mm

#### Plate 19

#### Elongatoolithid eggshells from Bayn Dzak (1) and Tsagan Khushu (2—4)

1. ZPAL MgOv-II/10, fragment "B" (Prep. No. SOv-9/1): a radial fracture showing partially preserved structure of mamillae (spreading wedges) and resorption craters (arrows); b oblique lower view, note resorption craters (indicating substantial pre-burial incubation period) and pore openings; c radial view, note pore canal and linearituberculate ornamentation typical of equatorial parts of the eggs. Non-treated, SEM.
2. ZPAL MgOv-I/2 "B" (Prep. No. SOv-9/2). Polar part, oblique radial view. Note pore canals (arrows) and dispersituberculate ornamentation. Non-treated, SEM.
3. Oblique tangential thin section (Prep. No. Ov-7/1<sub>1</sub>). Note pore canals and transition between mamillary layer (left) and continuous layer (right). Reflected light.
4. Tangential thin section through upper continuous layer of equatorial part of the eggshell (Prep. No. Ov-7/5<sub>1</sub>). Note pores situated exclusively in the grooves between the ridges. Reflected light.

Scale bars: 1a, 1b, 4 — 0.5 mm, 1c, 2, 3 — 1 mm

#### Plate 20

#### "Gobipteryx" eggs

- 1, 2. ZPAL MgOv-III/10a, b.
3. ZPAL MgOv-III/11b. "B—R". Radial section through "Gobipteryx" eggshell and adjacent matrix (Prep. No. Ov-10/3). Note growing crystal size inwards and high degree of diagenesis.
- 4—7. ZPAL MgOv-III/11b. Natural cast (4) and eggs (5—7).

#### Problematica

- 8, 9. ZPAL MgOv-I/22c, d.
10. ZPAL MgOv-II/9.
11. ZPAL MgOv-/18a.

Thin shelled ?protoceratopsid egg

12. ZPAL MgOv-III/9.

Scale bars: 1 cm, except for 3 — 1 mm

#### Note added in proof:

A review of all Mongolian egg-bearing localities, including a map and emended toponomy, will be given in: Mikhailov, K., Sabath, K. and Kurzanov, S., "Eggs and nests from the Cretaceous of Mongolia", in: Carpenter, K. and Horner, J. (eds.), "Dinosaur eggs and babies" Cambridge University Press (in press).



