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CLASSIFICATION OF FOSSIL EGGSHELLS OF AMNIOTIC VERTEBRATES

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Fossil avian and reptilian eggs and eggshells, from the Cretaceous of Mongolia and USSR (Kazakhstan, Zaisan basin) as well as samples of dinosaurian and the Eocene avian eggshells from USA, China, France and Argentina were studied. Methodological, terminological and biomineralization aspects of eggshell structure are discussed. Considered are different classifications of eggshell according to the structural levels of eggshell matter organization (texture, general histostructure, superficial morphology). Basic types, morphotypes, types of pore system and types of surface ornamentation are the main structural categories employed in the systematic description of fossil material. About 18 groups of fossil eggshells referred to turtles, geckoes, crocodiles, and to 14 "families" or dinosaur and bird oological remains are described. Their composition, occurrence, paleobiology and systematics are shortly presented.

Key words: fossil and Recent eggs, eggshells, Reptilia, Aves parataxonomy, classification, paleobiology.

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INTRODUCTION

Nathusius von Koenigsborn (1821—1899) was the first to employ fossil material in his study of the eggshell structure (Tyler 1964). Serious investigations of fossil eggs and eggshell remains started in 1923, after the sensational finds of the American Museum of Natural History Expedition to Mongolia. At that time, the dinosaurian eggs were already known from Southern France (Provence Basin) and in the following few decades numerous new finds were made in China, Mongolia, Southern Europe, Kazakhstan, the Western Interior of North America and, finally, in India, Soviet Asia (Kirghizia) and South America (for a historical review see Hirsch 1989).

A lot of descriptive papers were published during this period (for review see Hirsch 1989, Hirsch and Packard 1987) and most recently (Nesov and Kaznyshkin 1987; Zhao 1988; Hirsch *et al.* 1987, 1989; Hirsch and Bray 1988, Hirsch and Harris 1989, Hirsch and Quinn 1990; Mohabey and Mathur 1989; Jain 1989; Sahni 1989, and others). Karl F. Hirsch, in particular, has considerably increased public and scientific awareness of the value of fossil eggs and their shells.

The abundance and diversity of fossil eggs and eggshells as known recently has arised problems of their identification and classification. These problems have emerged since the first attempts to create a comprehensive classification were made (Jensen 1966; Sochava 1969, 1971; Zhao 1975, 1978, 1979b; Erben *et al.* 1979). They were recently summarized by Hirsch (1989). But up to now, despite these separate efforts the descriptive literature remains spotty and regionally orientated and the

descriptive language only just formalized. The lack of diversity of fossil material available to individual workers, on the one side, and the objective limits of light microscope techniques, on the other (Mikhailov 1987b), seem to be responsible for the inadequate morphological interpretations of fossil eggshell remains. But as I understand the situation, the principal limitation common to all the referred approaches seems to be inadequate focus on the biological aspects of eggshell mineralization.

All the classifications referred to were based on the model of crystal growth, here referred to as "Schmidt's model" (the formation of the shell unit is completely identified with growth of abiogenic spherocrystals; for the taxonomic limitations of this model see below, and for details, Mikhailov 1987b). Meanwhile, another model in which the eggshell can be understood as a "tissue", have already been introduced by von Nathusius (Tyler 1964) and accepted by Tyler and some other workers (Tyler 1969). The results of these classic works, along with the later data on histochemistry, biochemistry and the ultrastructure of eggshell matter (Erben 1970; Erben and Newesely 1972; Simons 1971, Pooley 1979; Krampitz 1982) as well as the data on eggshell formation (Richardson 1935; Wyburn *et al.* 1973; Georgievskiy and Zablotskaya 1973; Fujii 1974; Creger *et al.* 1976) constitute the conceptual and methodological framework beyond which our present understanding of the nature of eggshell matter and its genesis seem unable to proceed. It is only on this basis that we can understand the biological (physiological) meaning of the shell structural features and define their taxonomic status.

An attempt to classify the fossil amniote eggshells from a biomineralogical viewpoint is undertaken in this paper. The chief aim is to show how recent models of biomineralization can work as models of eggshell crystal growth. Before answering this question I shall try to give a short account of the reasons together with principles of biomineralization (see page...). Such a methodological approach to eggshell structure interpretation has already been applied by Erben (1970) and Simons (1971) and was employed in my studies of the eggshell matter organization (Mikhailov 1987a, b). Erben (1970) was the first to provide a micro- and ultrastructural analysis of amniotes eggshells. His results are valid with respect to extant sauropsid groups, but owing to the scantiness of fossil material, and some false interpretations of the ultrastructural patterns in avian eggshell, his groupings of dinosaurian eggshells seem doubtful.

Taking Erben's experience into account, this study was focused on interpreting of the nature of ultrastructural patterns (the most complicated question judging from descriptive papers) and, as the next step, on making a strict hierarchical classification of eggshell characteristics according to their origin and taxonomic stability. As a result, a parataxonomic classification, employing categories of family, generic and specific ranks, has been suggested.

TERMINOLOGY AND NOMENCLATURE

The terminology employed by authors applying various concepts and techniques reflects the multifaceted aspects of eggshell genesis and structure (Mikhailov 1987b). This makes the nomenclature of eggshell characteristics strongly complicated. In the paper the nomenclature is ordered in accordance with the hierarchy of the structural levels of eggshell matter organization (page 199). The general terminology (fig. 1), based on extensively described avian eggshells, is according to Tyler (1969). The description of ultrastructural elements and zones follows Erben (1970), but with some changes (Mikhailov 1987b). A special note is included in the text whenever a new term or nomenclatural category is introduced. Note that in the English edition of Mikhailov (1987b) the terminology employed was a literal translation of the Russian terms and is in some respects inadequate.

MATERIALS AND METHODS

The systematic part of the study involved the examination of the large collection of fossil avian and reptilian eggshell remains, eggs and clutches (mainly dinosaurian) from the Cretaceous of the Mongolian People's Republic (Gobi Desert) and the USSR (Kazakhstan, Zaisan Basin). The material was collected by the Joint Soviet-Mongolian Paleontological and Geological Expeditions (in the 1960s—1980s); by the Mongolian Paleontological Expedition of the USSR Academy of Sciences (guided by I. A. Efremov) in 1946—1948; and by the USSR Academy of Sciences Expeditions in the Zaisan Basin.

In all, more than 80 specimens (whole clutches, eggs and numerous fragments) of Cretaceous eggshells from Mongolia and 5 specimens from the Zaisan Basin were studied. The entire material is housed at the Paleontological Institute, USSR Academy of Sciences (Moscow).

Additional studies were made of some samples of dinosaurian and Eocene avian (*Ornitholithus*) eggshells from USA, China, France and Argentina. A large collection of Neogene ostrich and Holocene ratite eggshells was investigated earlier (Mikhailov and Kurochkin 1988; Mikhailov 1988). This work is also based on studies of the rigid eggshells of the following Recent reptiles and birds: crocodiles (3 genera, 7 species), turtles (3 families, 6 genera, 11 species), geckoes (*Gymnoductilus caspicus?*), birds (35 families, 50 genera, 54 species).

The specimens were studied by ULM (more than 300 thin sections of fossil shells and 150 sections of Recent shells) and SEM (more than 300 samples, about 1000 photographs). Examined with SEM were chiefly radial fractures of eggshells (fig. 1) and broken bases of shell units

(without chemical treatment). For understanding the fine interactions of organic and mineral components, polished sections of eggshells were treated chemically. To etch the mineral phase weak acid solutions (EDTA and HCL) were used; to destroy the intercrystalline organic membranes —

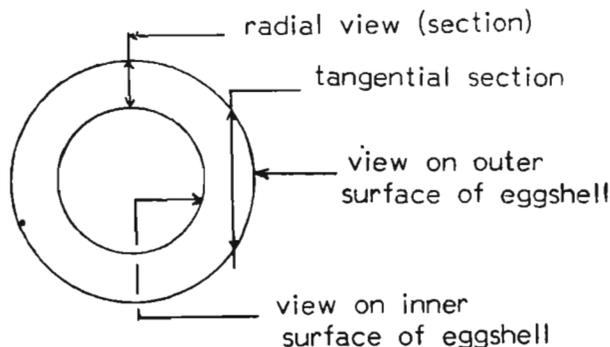


Fig. 1. Schematic drawing of various sections and views of an egg.

hot solutions of alkalis (5—10% KOH) and hydrogen peroxide (30% H_2O_2 — for control). Details of the techniques are described in Erben (1970), Pooley (1979) and Mikhailov (1987a, with precautions(!) in 1987b).

Abbreviations used:

- GI — Institute of Geological Science, Mongolian Academy of Sciences, Ulan Bator;
- HEC — K. F. Hirsch's Egg Catalogue;
- PIN — Paleontological Institute, USSR Academy of Sciences, Moscow;
- PLM — polarizing light microscope;
- SEM — scanning electron microscope;
- TEM — transmission electron microscope;
- ULM — usual light microscope;
- ZPAL — Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

ORGANIZATION PRINCIPLES OF EGG SHELL MATTER

BIOMINERALIZATION AND EGG SHELL FINE STRUCTURE

Taxonomically important features of the polycrystalline "skeletal forms" are determined by the geometrical interrelations between the mineral and organic phases. These ratios are manifested at different levels of the "skeletal" organization (see below). The body of large crystal units is pierced by a three-dimensional network of organic membranes. In general, crystallites of all sizes have organic "sheaths" of their own (Travis 1970, Golubev 1988), but these interrelations may degenerate. The "sheaths" do not represent any special secreted membranes, but only unmineralized external zones of the organic matrix. Any "skeletal form"

may finally be disintegrated to fine elementary crystallites. Usually, however, this does not happen because of a partial fusion of crystals (Golubev 1988).

The structure of the organic matrix is similar to a three-dimensional network: in one direction (which coincides with the direction of crystal growth) extend elongated fibrils (and fibres at higher levels of organization) of structural proteins; a sub-two-dimensional mucopolysaccharide network (discrete plates?) corresponds to the two other directions (Golubev 1988: fig. 56).

Biomineralization proceeds on several levels (Barskov 1988): crystal nuclei appear inside protein fibrils (nucleation of mineral phase); elementary crystallites grow along fibrils (primary growth of mineral phase), then mineralization may proliferate within the limits of the discrete polysaccharide plates (Golubev 1988; secondary growth of mineral phase). Naturally, it suggests a high stereochemical affinity of the mineral lattices and "skeletal" proteins (Golubev 1988).

It is of importance, that polycrystalline elements, joining with each other, form, in a crystallographic aspect, a highly ordered structure which behaves, when observed in PLM, as a monocrystal. For these reasons a higher rank order is suggested to exist in the biomineralization system (Golubev 1988).

To what extent can these statements be applied to the organization of eggshell matter? As is well known, calcium-binding proteins were extracted from the organic matrix of both Recent bird and Cretaceous dinosaur eggshells (Krampitz 1982). The SEM evidence for the eggshell structure (Erben 1970; Simons 1971; Krampitz 1982; Mikhailov 1987*a, b*) makes us accept that, in birds, material of the spongy layer has a polycrystalline structure (for the external zone this was shown earlier by petrographic methods (Favejii *et al.* 1965). Especially revealing are the results obtained by Simons. His TEM micrographs seem to leave no doubt that the structural elements in the spongy layer, 3—15 μm in size, ("squamous units", see below) have their own organic "sheaths" and a network of "intracrystalline" matrix (Simons 1971: figs. 35—37 and 75; see also pl. 16:4 in this paper). Details of the wedges structure still remain problematical — see description of the tabular ultrastructure.

The smallest structural elements of Recent eggshells revealed with SEM (without chemical treatment) are thin plates (0.5—1 μm in size) of a prismatic or subrhombohedral shapes (Erben 1970, Mikhailov 1987*a*). Destruction of the shell organic matrix by hot solutions of hydrogen peroxide also reveals smaller fibril-like crystalline element whose size, shape and elongation correspond to those of organic matrix fibres (pl. 36: 6). The direction of the latter coincides with the preferred orientation of the calcite *c*-axis in the eggshell (*c*-axis is parallel to the normal to the surface of growth; Silyn-Roberts and Sharp 1986). Thus, here an impor-

tant principle of biomineralization might have been expressed, that of the growth of crystals on the fibrils of structural proteins. However, in fossil eggshell even a find of platy elements is hardly possible due to diagenetic processes.

STRUCTURAL LEVELS

Different levels of biomineralization are adequately interpreted in terms of structural levels of the "skeletal material" organization. One can distinguish between the molecular, ultrastructural, microstructural, textural and macrostructural levels (Barskov 1988). In terms of macrostructure of the skeletal element is referred to as "morphological unit"; in terms of microstructure and texture (structural stratification of element) it is regarded as "tissue". The ultrastructure and molecular interactions characterize more fundamental relations of the mineral and organic phases (Golubev 1988). This nomenclature of structural levels can be applied to any morphological element. To avoid ambiguity, I prefer to use a more precise nomenclature for eggshell matter organization.

The following levels are distinguished within the eggshell structure (table 1):

Table 1

Nomenclature and terminology: structural levels of eggshell organization, structural types and their characteristics (see fig. 1)

Structural level	Name of type	Characteristics
Histostructure Texture	nbasic type	sequence of horizontal ultrastructure zones
General histostructure — morphology of shell unit (shell unit macrostructure)	morphotype	proportions; morphology and arrangement (direction of growth) of subunits
— arrangement of pore canal system	type of pore system	size, form and branching of pore canals; arrangement among shell units
Superficial (general) morphology	type of ornamentation	patterns of ornamentation, morphology of sculpture elements pore patterns, thickness of shell, size and form of egg

1) superficial features (general morphology of egg and shell: egg shape and size; shell thickness, surface sculpture (ornamentation) and pore patterns) and 2) histostructural features (exposed on fractures and polished surfaces).

At the histostructural level one can differentiate:

a. General histostructure of an eggshell (commonly called "microstructure"; "eggshell unit macrostructure" in Mikhailov 1991).

b. Texture of an eggshell — a sequence of horizontal ultrastructural zones ("eggshell unit microstructure" according to Mikhailov 1991).

The description of fossil eggshells is generally based on the various macro-features of vertical shell growth units ("shell units" hereinafter) and of the pore canal system. These features describe shell units and pore systems as structural components of eggshells and thus define eggshells on the basis of structural morphotypes and types of pore systems. The features important at this level are: shape, proportions, size, and orientation of shell units and their larger subunits; shape, size, and arrangement of pore canals.

Aggregation of the platy elements of the shell material differs at different stages of shell growth, which is the main property, enabling us to recognize the ultrastructural zones.

The biocrystalline ultrastructure might be better understood in terms of mineralogy. The microstructure of crystals is often related to their defective structure. The network of organic membranes and other elements of the organic matrix may be considered as ordered in large volume systems of significant defects (slits). However, these defects in the mineral crystal body by no means change the preferred crystallographic development of calcite (Mikhailov 1987b: fig. 3). This system of biogenetic defects determines a special sensitivity of the mineral phase to mechanical or chemical exposure, which results in the presence of a set of cleavage and etching patterns, peculiar to a definite zone. These patterns are taxonomically important.

The most significant and difficult tasks in the study of eggshells using SEM is to ascertain the nature of the patterns reflecting the biogenic "defective structure". The specific effects of the reagent (including effect of mechanical pressure) on the crystallographic parameters of the mineral's lattice should be considered (see below about the "fish-bone pattern").

The texture of eggshell has a far greater taxonomic significance than the general histostructure and in defining the basic (principal) types of eggshell organization (hereinafter referred to as "basic types"). They are determined by differences in secretory phenomena in the oviduct which are peculiar to higher taxonomic categories (usually above the order level (Mikhailov 1991). Similar morphotypes can be distinguished within the various basic types of hard vertebrate eggshells (avian-like in dinosaurs vs. some carinate birds: large prisms, but of a different texture, in the upper half of the eggshell). Correspondence of the ultrastructural zones with the elements of the general histostructure is shown in table 2.

HISTOSTRUCTURE OF EGG SHELL

General histostructure

The following elements and subunits are usually distinguished at the general histostructural level (fig. 2):

Organic core — a discrete organic body at the very base of the shell unit, with its own distinctive ultrastructure (pl. 21: 2, pl. 38: 5).

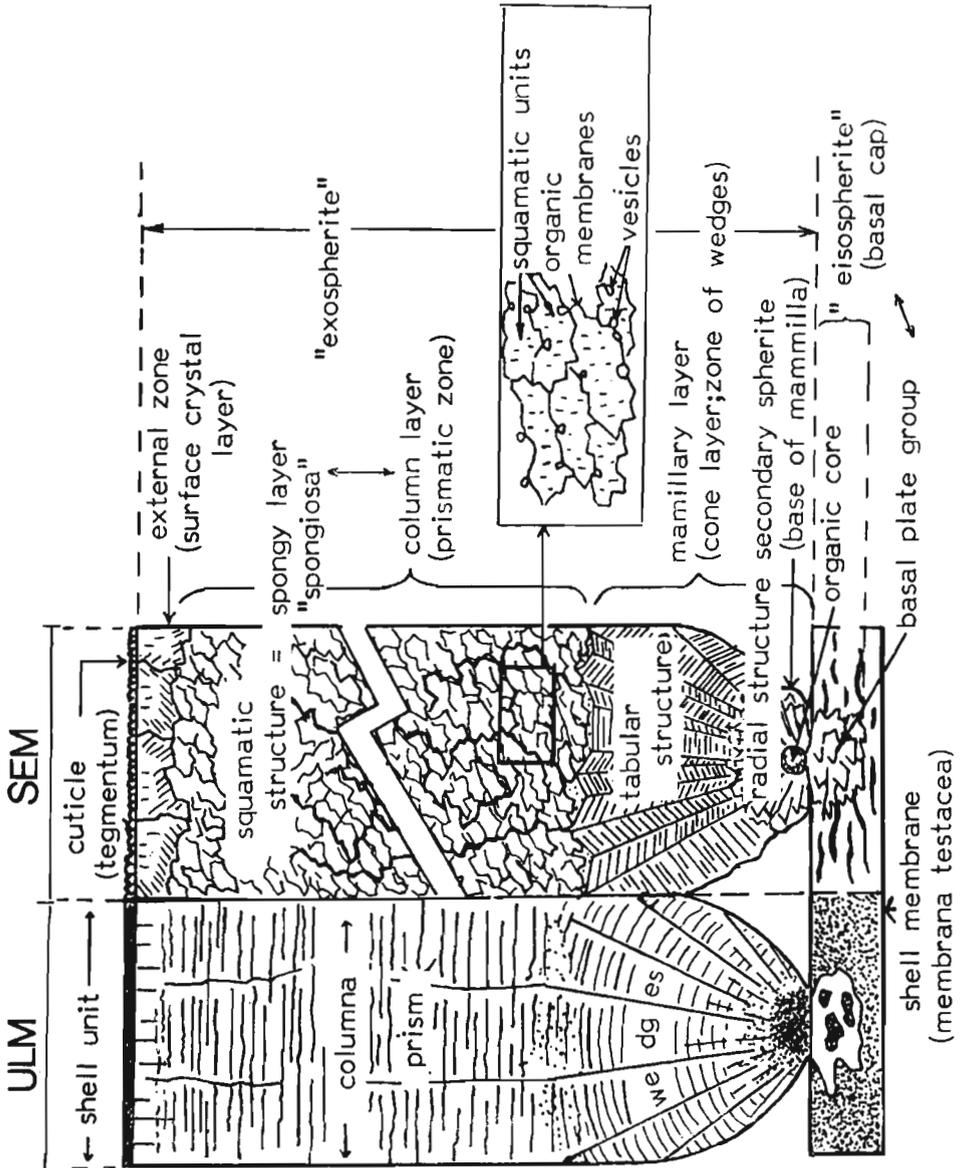


Fig. 2. Terminology of eggshell structure based on avian eggshell. Sketch drawings of radial sections in ULM (thin section) and in SEM (fracture).

Eisospherite — a subcircular crystalline body which lies within the uppermost fibers of the shell membrane below the organic core (pl. 38: 4, pl. 39: 6).

“Base of mammilla” — a more or less expressed apical part of the cone which encloses the organic core and contacts the eisospherite. This element is distinct in avian eggshell.

Mammilla (cone) and column — the lower and the upper parts of the shell unit having a characteristic shape (also distinct in avian eggshell).

Long (large) subunits of the shell unit:

Wedges — long subunits wedge-like in longitudinal section and polygonal or trigonal in transverse section, which radiate upwards from the organic core or base of the mammilla. In the avian eggshell the wedges make up most of the mammilla; this zone is traditionally called the mammillary layer (pl. 37: 1, 5—7; pl. 31: 1—2).

Prisms — long and broad subunits (broader than the wedges) which are prismatic in longitudinal section and roughly polygonal in transverse section and grow vertically. Prisms as well as columns form a zone of prisms which is known as the prismatic, columnar, or palisade layer in the avian eggshell (pl. 27: 7, pl. 29: 1—4; pl. 36: 1).

Single or continuous layer — continuous material covering the mammillary layer. Columns and prisms are either absent, or have hardly traceable vertical boundaries (pl. 30: 2—3; pl. 31: 1—2; pl. 37: 1, 2, 5, 7). Crystallographically controlled cleavage lines cross the apparent boundaries of shell units (columns) (pl. 32: 1, 3).

Remarks. — Prisms are considered here as morphologically discrete elements with well traceable (in SEM) boundaries (true “discontinuities” in shell matter) and a characteristic habitus; they frequently, but not always, coincide with “optical prisms” which can be seen with PLM both in eggshells having a palisade and in those with a single layer (e.g. — in ratite eggshells) and, perhaps, are under strict crystallographic control (Mikhailov 1987b).

The distinction of “macrostructural zones” (zone of prisms, zone of wedges) is often conventional: a distinct structural border between such zones is usually absent, except for the case when it coincides with abrupt changes in the ultrastructure (compare pl. 26: 5, 6 and pl. 29: 1 with pl. 31: 1, 2 and pl. 37: 1, 2).

I believe that the term “(true) spongy layer” should only be used descriptively for the ultrastructure of eggshells (by analogy to the zone with a squamatic ultrastructure). This would be in accordance with the primary meaning given to it by von Nathusius (Tyler 1964).

Table 2

Structure of shell unit in the different groups of amniotic vertebrates (see fig. 1 and 2)

Type and mineral composition	Taxon	Texture: sequence of zones with different ultrastructures	General histostructure (morphology of shell unit)
„Testudoid” aragonite	Chelonia	— shell membrane — organic core (OC) — zone of spherulithic growth of needle aragonite crystals (zone with aragonite ultrastructure (ZRAC))	— spherulite with fine radial striation
„Geckoid” calcite		— shell membrane — zone with bunches of organic elements — one or two zones of vertical growth of calcitic crystals zone of crystallite? aggregates	— zone of narrow calcitic columns
„Crocodiloid” calcite	Crocodylia	— shell membrane — platy crystallite aggregates among fibres of shell membrane (BPG) — zone of irregular radial growth of tabular crystallite? aggregates (zone with tabular ultrastructure (ZTA))	— basal plate group in form of rosette (BPG) — rough unit with rough large wedges
„Dinosauroid” calcite	Dinosauria: Sauropoda Ornithischia	— shell membrane — organic core (OC) — zone of more or less regular spherulithic and prismatic growth of long calcite crystals (or? aggregates) (zone with „tabular” ultrastructure (ZTA))	— elongated spherulithic unit with thin wedges or with prisms (zw; zw+zp)
„Ornithoid” calcite	Aves Theropoda	— shell membranes — platy crystallite aggregates among fibres of shell membrane (BPG) — organic core (OC) — zone of spherulithic growth of platy calcite crystallites (zone with radial calcite ultrastructure (ZRP)) — zone of subspherulithic growth of calcite crystals (or their tabular? aggregates) (zone with tabular ultrastructure) (ZTA) — zone of fast polycrystalline growth of granular (squematic) aggregates (zone with squematic ultrastructure (ZSA)) — zone with compact vertical crystals (EZ)	— basal plate group (BPG) in form of eisospherite (es) discrete part of unit (mammilla) — secondary spherite (base of mammilla) (ss) — zone of wedges (most part of mammilla) (zw) — single (continuous) layer or zone of prisms (prismatic layer) (zp, pl) — external zone (EZ)

Ultrastructural zones (fig. 1, table 2)

Four general ultrastructural zones were distinguished in sauropsidian eggshells by Erben (1970): zone of radial crystallites, zone of tabular crystallite aggregates, zone with a "fish-bone pattern" and external zone. Since, contrary to the earlier opinion (Erben 1970, Erben and Newesely 1972), aragonite has not been found for certain in avian eggshells including the base of the mammilla (Sauer *et al.* 1975; Silyn-Roberts and Sharp 1986), it seems reasonable to distinguish between the aragonite radial ultrastructure (turtle eggshells) and the calcite radial ultrastructure (avian eggshells); both also differ sharply in their crystal morphology. The zone referred to as "fishbone pattern" was renamed "the zone of squamatic ultrastructure" (Mikhailov 1987b, 1991).

Descriptions of fossil eggshells often employ the term "fish-bone pattern". But the interpretation of this character is very ambiguous and misleading. It is obvious that Erben, contrary to Schmidt (1962), understood the "fish-bone pattern" in a histostructural sense, but in practice he used this term for two different patterns: the squamatic one (organic matrix control) and, in most cases, for the crystallographically controlled cleavage and etching pattern of calcite (along (104) planes) (pl. 23: 3; pl. 25: 6; pl. 26: 2; pl. 27: 6; pl. 32: 1; pl. 33: 3, 4; see also Hirsch and Paccard 1987: fig. 36, 52, 56; for details see Mikhailov 1987b). Naturally, the latter type has no histostructural and, thus, taxonomical significance. Its expression strongly depends on the treatment of the eggshell and the extent of recrystallization. But, when well developed, it may obscure the true squamatic pattern and lead to a misinterpretation of the shell ultrastructure. That is why Erben (1970) misinterpreted the ultrastructure in the dinosaurian eggshells from Provence (type A) as corresponding to the squamatic ultrastructure in the true spongy layer of the avian eggshell.

The term "basal plate groups" (applied earlier to crocodylian eggshells) is here used for any crystallite aggregates in the shell membrane.

The eggshell ultrastructural zones have already been described in detail (Erben 1970; Mikhailov 1987a—c). Below I present their short diagnoses and focus on the problem of distinction between the squamatic ultrastructure (in the spongy layer of the avian eggshell) and the tabular ultrastructure (in the wedges), which poses many difficulties to the students of fossil material (see figs. 1, 3 and table 2).

1. Basal plate group (BPG). Platy crystallite aggregates of discrete calcite crystals among the uppermost fibres of the shell membrane. They form eisospherites (in avian and some dinosaurian eggshells, pl. 38: 4, pl. 39: 6) or rosette-like structures in the base of the shell unit (in crocodylian eggshell, pl. 22: 2, 3). In thin sections (ULM, PLM) the structure of an eisospherite is practically nonidentifiable.

2. Aragonite radial ultrastructure (zone with radial aragonite cry-

stals, ZRAC). Narrow aragonite crystals which radiate from the organic core and form the shell unit with a fine granular surface and a fine spherocrystal pattern on radial section (chelonian eggshell; pl. 21).

3. Calcite radial ultrastructure (zone with radial calcite plates, ZRP). Platy calcite crystallites, needle-prismatic in form, which radiate from the organic core and make up the secondary spherite (the base of mammilla in terms of general histostructure, pl. 35: 2, 3; pl. 37: 4; pl. 38: 2). This zone is rich in organic matter. Petal-like aggregates of these crystallites form characteristic "corolla" which are distinctly visible on the inner surface of the shell after the removal of the shell membrane (pl. 34: 2, 3; pl. 39: 3, 6). In thin sections of eggshell (in ULM) this ultrastructure is hardly distinguishable from that of radial aragonite (avian and some dinosaurian eggshells).

4. Tabular ultrastructure (zone of "tabular crystallite aggregates", ZTA). This ultrastructure is characteristic of wedges and, in some dinosaurian eggshells, of prisms. The main feature shown by the radial sections is a regular transverse striation (cleavage and etching lines) of shell subunits (pl. 23: 2a; pl. 25: 10; pl. 29: 2—4; pl. 37: 1, 3). There is still no general agreement on the nature of the tabular ultrastructure: is it a rouleau-like aggregate of tabular crystallites (Erben 1970; Mikhailov 1987a) or is it entirely under crystallographic control (Erben and Newesely 1972; Pooley 1979; Silyn-Roberts and Sharp 1986)? In addition, the homology of the zones of tabular ultrastructure in the wedges of avian, dinosaurian, and crocodilian eggshells is still uncertain (Erben and Newesely 1972).

5. Squamatic ultrastructure (zone with squamatic aggregates, ZSA). This ultrastructure is characteristic of the spongy layer (both single and palisade) of avian and some dinosaurian eggshells. The main characteristic of radial sections is the squamatic pattern which can be distinguished by different methods of eggshell preparation: on fractures and etched polished sections (SEM), and on thin sections (ULM) (pl. 32: 1; pl. 35: 2; pl. 36: 1, 3; pl. 37: 1, 2; pl. 38: 1). The elements of squamatic pattern are morphologically discrete units (squamatic units — possibly aggregates of smaller plates), up to 10—15 μm in size, which are separated by real discontinuities (pl. 32: 1a; pl. 37: 2). The discontinuities are filled with thick organic membranes which form a complex network within the crystalline matter (pl. 36: 4).

In thin sections (ULM) of fossil eggshells the squamatic ultrastructure is practically indistinguishable from the tabular ultrastructure due to diagenetic changes. In PLM, even in Recent eggshells, changes between the two zones are completely obscured by patterns of light extinction. Examination of fossil eggshells with SEM permits, as a rule, to detect unaltered regions (usually in the central part of the shell), where the squamatic structure is still distinct (pl. 32: 1, 4; pl. 33: 3; pl. 35: 2; pl. 39:

2). In the case of strong recrystallization, one can rely on those features of the general histostructure which correlate with some ultrastructural zones. In the known sauropsidian eggshells, a single layer always has a squamatic ultrastructure, while the zone of wedges displays a tabular ultrastructure. Prisms can have either one or the other, depending on the taxon.

6. External zone (zone with vertical crystals. EZ). This zone is characteristic of the uppermost crystalline part of some avian eggshells and is made up of densely packed crystals which are oriented normal to the shell surface (pl. 36: 1, 2; pl. 39: 1, 2; for details see Mikhailov 1987c). In thin sections, this zone is strongly translucent (due to the poverty of organic component) and displays a regular, fine, vertical stration (fig. 5).

STRUCTURAL CLASSIFICATION OF EGGSHELL

BASIC TYPES OF EGGSHELL ORGANIZATION (SHELL TEXTURE)

Five¹⁾ basic types of hard eggshells of amniotic vertebrates may be distinguished (fig. 3, table 2; Talimaa *et. al.* 1988: 314—319; Mikhailov 1991):

1. Testudoid type (Chelonia) (pl. 21). The shell unit consists of a single ultrastructural zone with regular spherulithic growth of aragonite crystals (radial aragonite structure) and organic core in the base.

2. Crocodiloid type (Crocodilia) (pl. 22). Much of the shell unit consists of a single ultrastructural zone with irregular radial growth of tabular crystallite ?aggregates (tabular structure), and with a basal plate group (rosette of plates) in the base; the organic core is absent.

3. Dinosauroid type (Dinosauria: Sauropoda and Ornithischia) (pl. 23—29). The shell unit consists of one ultrastructural zone with more or less regular spherulithic (or prismatic) growth of tabular crystallite ?aggregates (tabular structure) and organic core in the base; there is possibly a basal plate group in the form of an eisospherite.

4. Ornithoid type (Aves; some Dinosauria: ?Theropoda) (pl. 10—19). The shell unit consists of at least three ultrastructural zones: (i) a zone with spherulithic growth of minute platy crystallites and their petalloid aggregates (radial calcite structure); (ii) a zone with spherulithic growth of tabular crystallite ?aggregates (tabular structure); and (iii) a polycrystalline zone with squamatic elements (squamatic structure, true spongy layer); the external zone (iv) is present in most avian eggshells.

¹⁾ The eggshell of the Recent tuatara (*Sphenodon*) might be also distinguished as a separate basic type (for a general description see Packard *et al.* 1982).

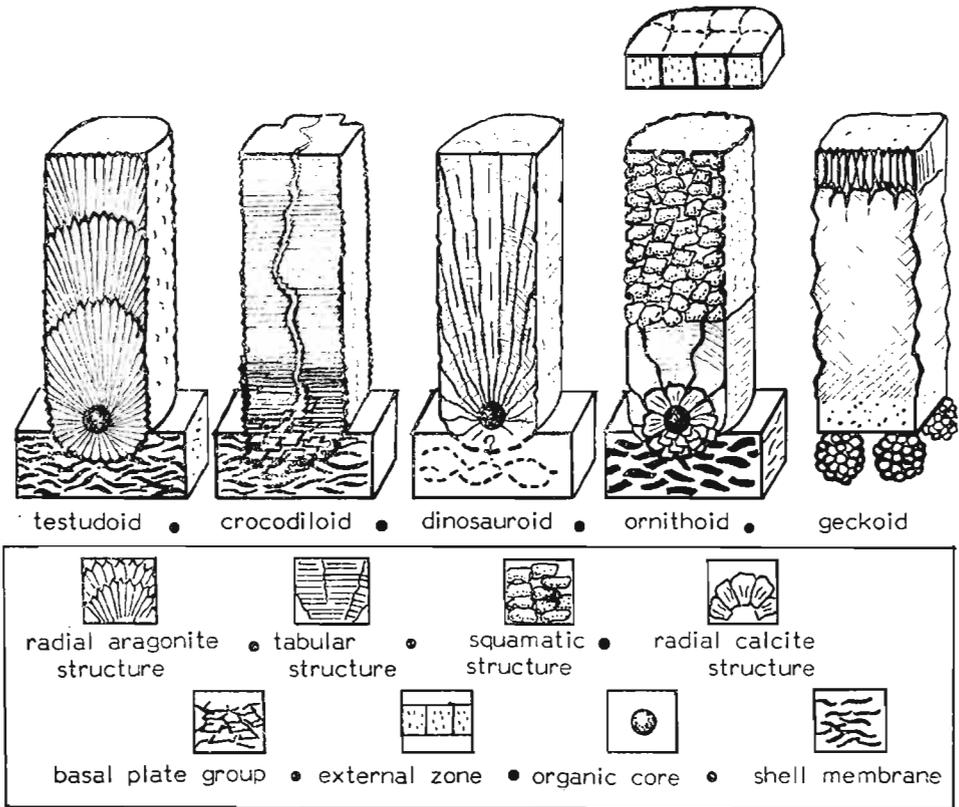


Fig. 3. Basic types of amniote eggshells (sketch drawing, see text).

The organic core and the basal plate group in the form of an eisospherite occur in the base of shell unit.

5. Geckoid type (Gekkota) (pl. 22). The shell unit consists of two or three zones whose ultrastructure is still not understood, the organic core is absent (for general descriptions see Erben and Newsely 1972; Deeming 1988; Schleich and Kastle 1988; Packard and Hirsch 1989).

EGGSHELL MORPHOTYPES

Among the diverse known fossil eggshells, ten distinct morphotypes can be recognized (fig. 4, 5)²⁾:

1. Testudoid morphotype (pl. 21). The eggshell structure is clearly discrete with separate shell units (cylindrical shape with spherical base). In thin section the shell unit looks like an abiogenic spherocrystal (sweeping fine radial striation).

²⁾ In Kurzanov and Mikhailov (1989) the legend referring to illustrations of morphotypes (fig. 12.2) C and D should be reversed.

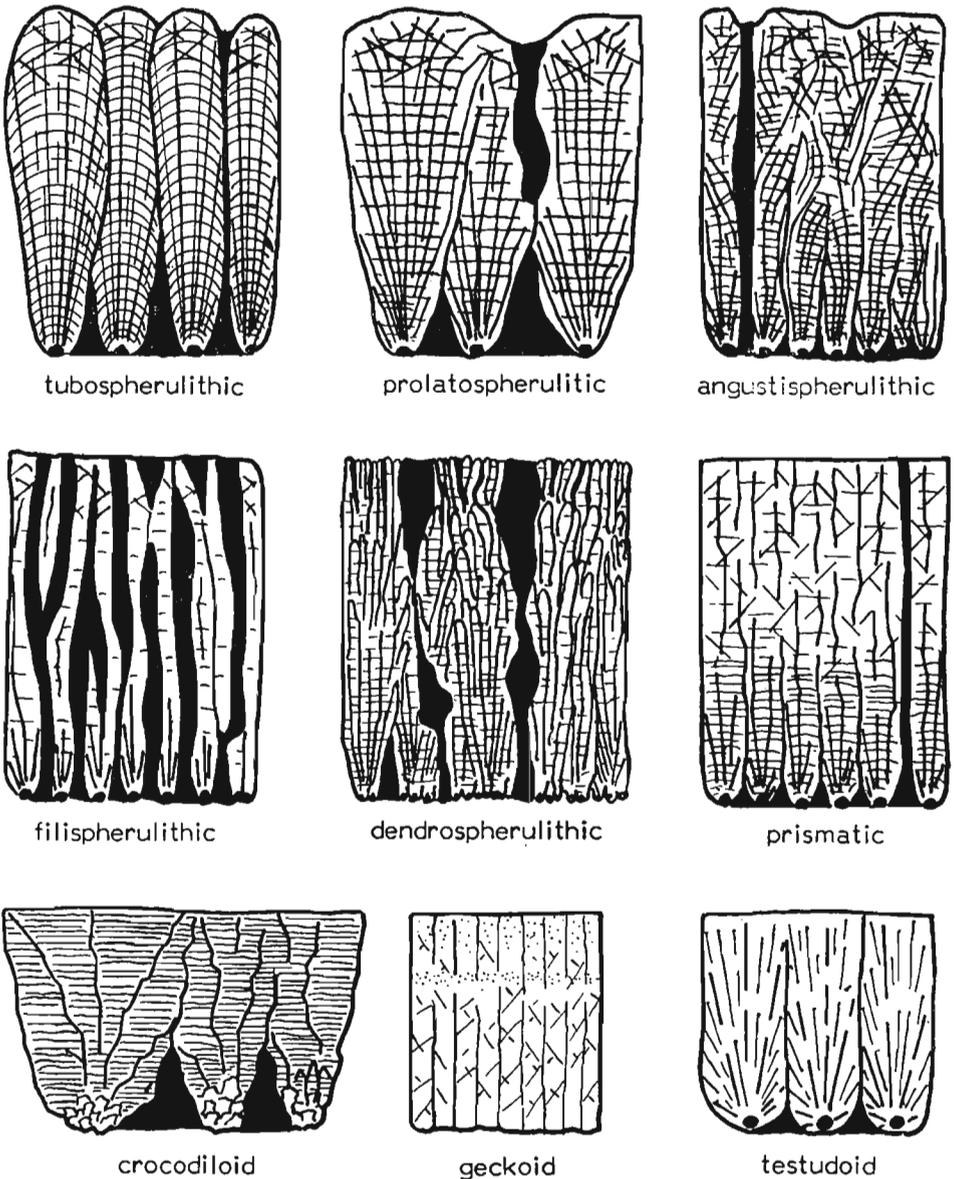


Fig. 4. Morphotypes of amniote eggshells corresponding to dinosauroid, crocodiloid, geckoid and testudoid basic types (see text).

2. Crocodiloid morphotype (pl. 22: 4, 5). The eggshell structure consists of discrete large, rough shell units, which are strongly expanded distally (truncated cone shape with bulbous base and rosette of plates on the inner surface). The not numerous wedges are large and rough, with irregular boundaries (never forming clear fan-like patterns on the radial sections of eggshell).

3—7. Spherulithic morphotypes. The eggshell structure consists of discrete shell units exhibiting thin radiating wedges.

3. Tubospherulithic (discretospherulithic) morphotype (pl. 3: 1—3). The shell units are sharply separated from each other (a fanlike pattern can be traced up to the eggshell surface), have arched accretion lines and exhibit tuberculous elevations on the shell surface (see compactituberculate ornamentation).

4. Prolatospherulithic morphotype (pl. 25: 7—9; pl. 26: 1—3). It is similar to the tubospherulithic morphotype, but the shell units are broader and loosely arranged, less sharply separated from each other; the vertical borders and the fan-like pattern are well displayed only up to $2/3$ — $3/4$ of the eggshell thickness; above, the wedges deviate laterally. Accretion lines are mainly horizontal.

5. Angustispherulithic morphotype (pl. 26: 5; pl. 27: 1, 3). The eggshell structure is less discrete, the shell units are slender and more compact. Their vertical borders and fan-like pattern are displayed only in the inner $1/3$ — $1/2$ of the eggshell thickness; above this level, the wedges diverge strongly and cross one another (the arched cross-striation visible on the radial thin sections looks sometimes like the “fish-bone-pattern” in the spongy layer of the avian eggshell). Accretion lines are horizontal.

6. Filispherulithic morphotype (pl. 24: 2—4). Small spherulites growing in strong competition with one another continue as long narrow prisms. The adjacent prisms touch in such a way that they form a network of irregular crystalline “walls” which surround numerous large pore canals (see multicanalicate pore system).

7. Dendrospherulithic morphotype (pl. 24—27). Small spherulites, united in groups, begin to grow in such strong competition with one another that only a few are capable of further development; wedges pass into bundles of narrow prisms, which grow in a multiplex fashion beginning with the level of about the inner $1/6$ — $1/3$ of eggshell thickness (dendritic pattern is occasionally displayed in thin radial sections). Among the prisms there remains a network of numerous discontinuities (a system of microcanals). This morphotype seems to be genetically closest to the filispherulithic morphotype, on the one hand, and to the angustispherulithic, on the other.

8. Prismatic (spherulitho-prismatic) morphotype (pl. 27: 6; pl. 29: 1—4). The eggshell structure is less discrete than in the spherulithic morphotypes. The shell units are more slender and compact. Slender wedges (zone of wedges) pass into larger prisms (zone of prisms) so that the fan-like pattern is displayed only in the inner $1/5$ — $1/2$ of the shell unit. The boundary between these macrostructural zones is rather arbitrary. In the avian eggshell (ornithoid basic type) this morphotype is sometimes referred to as “neognathous” (fig. 5D).

9. “Ratite” (ratite-like) morphotype (pl. 30: 2, 3; pl. 31: 1, 2; pl. 37:

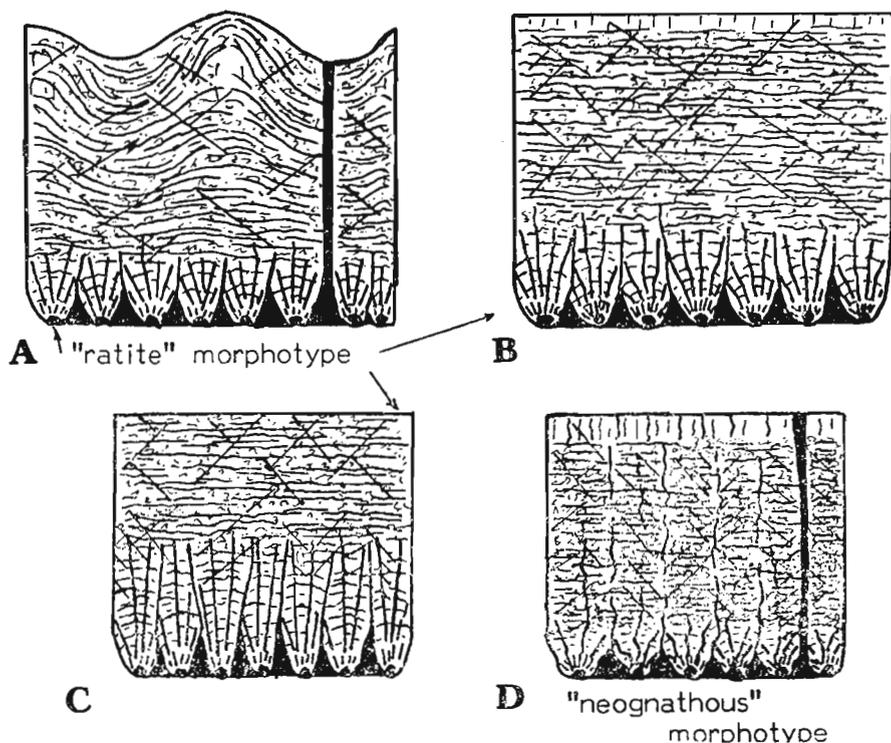


Fig. 5. Morphotypes of amniote eggshells corresponding to ornithoid basic type (see text); a Elongatoolithidae, b ratite birds, c Subtiliolithidae, d majority of neognathous birds.

5, 7). The eggshell structure is discrete only in the inner $1/6$ — $1/2$ of the shell thickness (mammillary layer). Most of the eggshell is formed of a single, continuous layer.

10. Geckoid morphotype (pl. 22: 7). The eggshell consists of very slender, numerous, densely packed vertical columns; spherulithic part is entirely absent.

TYPES OF THE PORE SYSTEM

Classification of the eggshell pore system, introduced by Sochava (1969) and developed by Erben *et. al.* (1979) (angusticanaliculate, prolato-canaliculate, multicanaliculate and tubocanaliculate types; fig. 6: A, E—G), is acceptable for the systematic description of fossil material.

New material permits recognition of an additional type — rimocanaliculate (from *rimus*, Lat. — slit), with predominating slit-like pore canals, 0.01—0.03 mm wide and 2—5 mm long (fig. 6D; pl. 27: 2, pl. 13: 6). These canals form a characteristic pore pattern of grooves on the outer surface of the eggshell (pl. 27: 4; pl. 33: 5). Within the angusticanaliculate type it is possible to distinguish single and branching pore

canals, and the latter can be subdivided into multibranching ("struthioid") canals and those branching in a single plane ("aepyornithoid") (fig. 6: A—C). In some special cases we can use a more detailed classification of

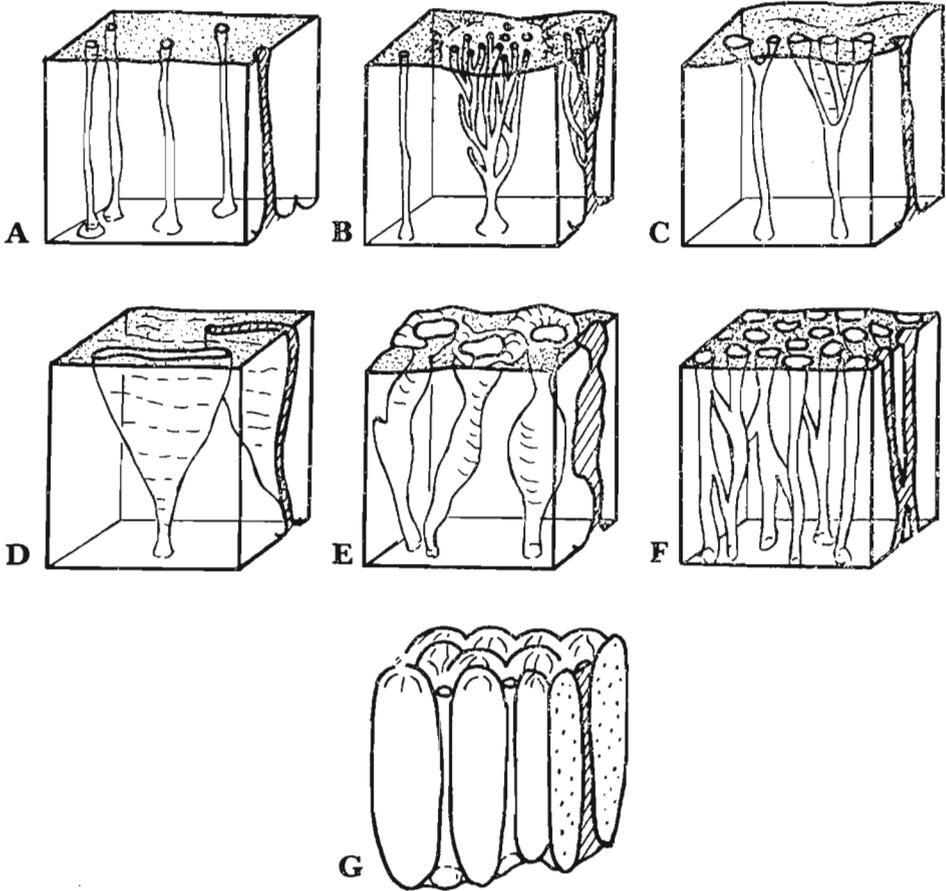


Fig. 6. Types of pore system of amniotes eggshells (sketch drawings). A—C angusticanaliculate type: A non-branching pore canals, B multibranching pore canals ("struthioid" type), C branching in one direction pore canals ("aepyornithoid" type); D rimocanaliculate type; E prolatocanaliculate type; F multicanaliculate type; G tubocanaliculate type.

the pore canals and the surface pore patterns. Such a classification was established for the eggshell remains of Neogene ostriches (Mikhailov and Kurochkin 1988).

Two variants, foveocanaliculate and lagenocanaliculate, were distinguished within the prolatocanaliculate type (Nesov and Kaznyshkin 1986). Though these categories may be useful for the morphological description of pore canals, I have failed to distinguish them as distinct types of the eggshell pore system within the eggshells of the prolatocanaliculate type examined.

GENERAL MORPHOLOGY. TYPES OF ORNAMENTATION PATTERNS

Zoologists and paleontologists have considerable experience in the evaluation of the taxonomic significance of some general morphological characteristics of eggs and eggshells. As was shown by von Nathusius, such features as the size and density of mammillae and shell thickness may broadly overlap in different taxa (Tyler 1964). But they can still be

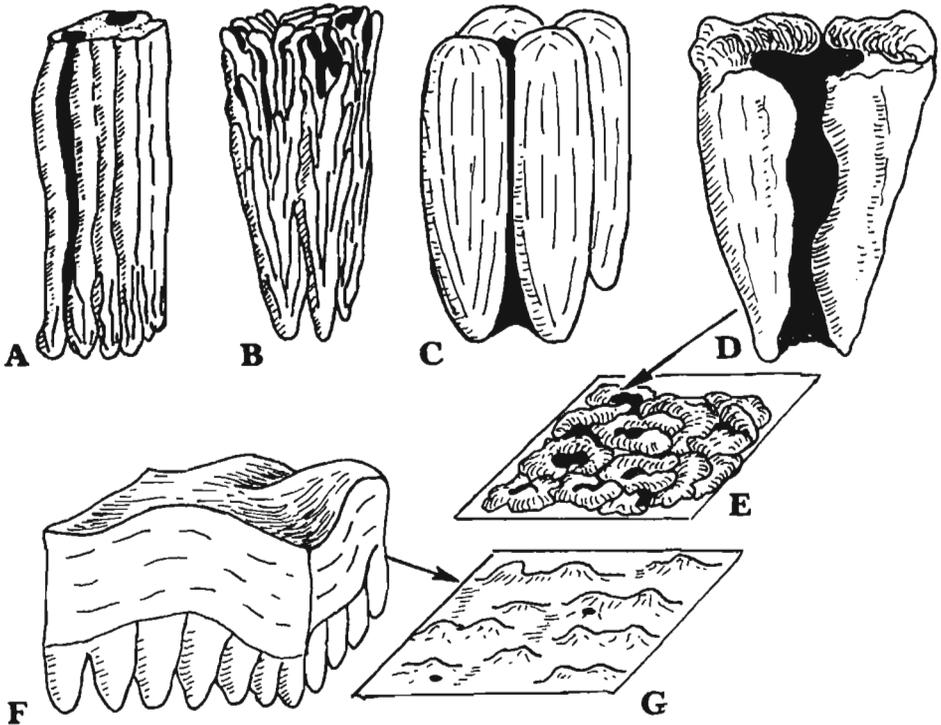


Fig. 7. Correlation between the types of surface ornamentation and characters of shell unit growth types and pore systems (sketch drawings, see text). A Faveoolithidae (filispherulithic morphotype — smooth surface); B Dendrospheroolithidae (dendrospherulithic morphotype — rough surface); C “Megaloolithidae” (tubospherulithic morphotype — compactituberculate ornamentation); D, E Spheroolithidae (prolatospherulithic morphotype — prolatocaniculate pore system — sagenotuberculate ornamentation); F, G Elongatoolithidae (ratite morphotype — linearituberculate ornamentation).

used as subsidiary characteristics within the limits of particular taxa (on familial or generic levels).

One of the most valuable external features of the dinosaurian eggshell is its surface ornamentation. Three main categories of eggshell surface can be distinguished: smooth surface (sometimes with microsculpture), rough surface (verruculate, rugose; nodes are sparse and irregular, ornamentation pattern is absent) and sculptured surface (elements of sculpture are regular and form a distinct ornamentation pattern).

Different types of ornamentation in sculptured eggshells appear to be connected with the character of the shell unit growth (fig. 7):

A. Ornamentation derived from accretion lines of the single layer: elements of sculpture cover few shell units (fig. 7F, G):

a) Linearituberculate ornamentation (fig. 8C, pl. 27: 8; pl. 30: 1C) — called so because of the linear arrangement of tubercular nodes (“ridged eggshell”: Kurzanov and Mikhailov 1989: fig. 13.3B—D). The elements of sculpture (ridges, heteromorphic hillocks or nodes) are elongated in parallel to the long axis of the egg. Typical of equatorial portions of elongated eggs.

b) Ramotuberculate ornamentation (fig. 8D; pl. 30: 1B) — called so because of the ramous arrangement of tubercles. Derived from the line-

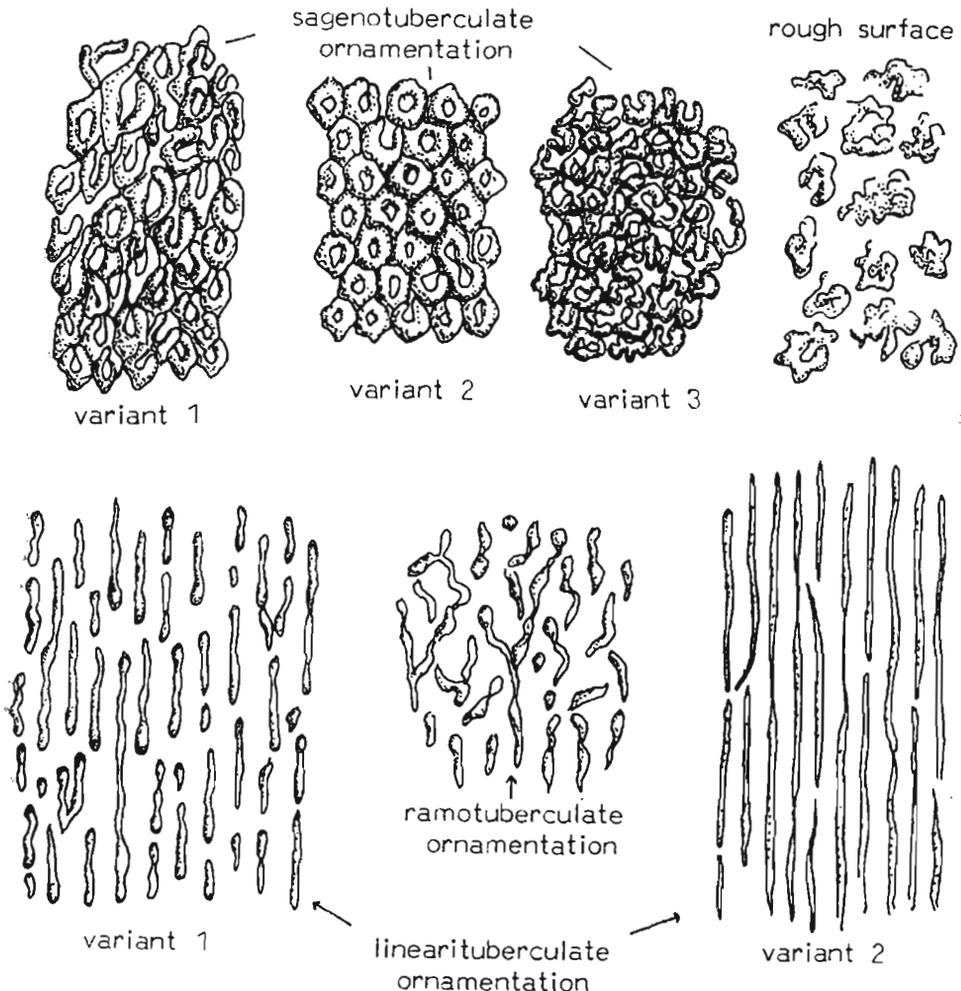


Fig. 8. Types of the eggshell outer surface ornamentation in the dinosaurian eggs (see text).

arituberculate ornamentation, the orientation of ridges and hillocks is blurred; they ramify. Typical of the portions of elongate eggs, transitional between the equatorial zone and the poles.

c) Dispersituberculate ornamentation (pl. 30: 1A) — called so because of dispersed turbeclles (“nodose eggshell”). Spherical, isomorphic nodes or hillocks are scattered over the shell surface. Typical of the poles of elongate eggs.

B. Ornamentation connected only with the growth of separate shell units and their subunits (fig. 7A—E):

a) Compactituberculate ornamentation (fig. 7D; pl. 23: 5) — called so because of the dense tuberculation (“shagreen eggshell”, “tuberculous eggshell”). Shell surface completely covered with spherical tubercles, each tubercle forming a dome-shaped roof of the spherulithic shell unit. Typical of some spherical eggs.

b) Sagenotuberculate ornamentation (fig. 8A; pl. 25: 3—5; pl. 27: 4) — called so because of its net-like sculpture (Lat. *sagena* — fishing net); “nodular eggshell”; “reticulate patterns of nodes” (Kurzanov and Mikhailov 1989: fig. 12.3A). The elements of sculpture (irregular nodules, worm-like ridges and microridges) form faveolate, ramiform, “mottled” or multigyrate ornamentation patterns, with pits (meshes) and grooves, some of which represent the orifices of the prolatocanaliculate pore canals. Typical of some spherical and ellipsoid eggs.

CLASSIFICATION OF FOSSIL EGGS AND EGGSHELLS

GENERAL REMARKS

A system of fossil eggs and their shells should be established in terms of a structural eggshell classification (structural types and characteristics). Eggshells of different basic types can now be reliably assigned to natural taxa of the ordinal, and higher levels; but there is hardly any sense to use formal names in this case. For eggshells assigned to lower taxonomic categories, it should be reasonable, in some cases, to use the parataxonomical group names (family, genus, species).

As experience and literature show, not only species and genera, but also families of turtles and crocodiles are in fact, indistinguishable as far as the eggshell histostructure is concerned. On the contrary, the dinosaurian and avian eggshells vary widely in their histostructure and superficial characteristics, hence they may be given familial and generic names. I provide here a general description of fossil eggshell groups of amniotic vertebrates. A more detailed systematic description of fossil eggs and eggshells from the PIN collection will be given in future papers.

I accept here the family group names introduced by Zhao (1975, 1978, 1979). But the diagnoses are essentially new and formalized. All of them are arranged in the same way: basic type, morphotype, type of pore system, type of ornamentation and subsidiary characteristics (overall shape of egg, main range of shell thickness values, type of pore pattern).

In the diagnoses of the parataxonomic genera and species the following characters should be used: variations in ornamentation and pore patterns (with quantitative characteristics), exact form and size of egg, shell thickness, etc.

The names applied here are not intended to be used in a formal sense as determined by the International Code of Zoological Nomenclature. The classification of avian and dinosaurian fossil eggshell groups is intended to be of practical stratigraphic and zoogeographic application, and should be subordinated to a natural system.

CRITERIA OF SYSTEMATIC INTERPRETATION

The classification presented in this paper employs the following criteria:

1. The availability of valid taxonomic identifications, based on identifiable embryos and hatchlings or mass-burials of associated egg clutches and skeletal remains.

2. High systematic rank of eggshell basic types (Mikhailov 1991): eggshells of diverse basic types cannot belong to the same natural family.

3. High taxonomic stability of eggshell morphotypes (above the order-family level) in recent turtles, crocodylians and birds.

4. Discontinuities between morphotypes in fossil material.

5. Additional criteria: stratigraphic and geographic distribution of families; correlation of the beds with bone and eggshell remains; assumptions about physiology, mode of life and nesting behavior based on the functional interpretation of the pore system and the structure of clutches (mode of incubation).

SYSTEMATICS

Fossil chelonian eggshells

(pl. 21: 7—8)

Diagnosis. — Eggshell of testudoid basic type; testudoid morphotype; pore canals consist of widely separated simple tubes; smooth surface; spherical to ellipsoid eggs.

Occurrence. — Jurassic (Colorado); Cretaceous (England, Mongolia, Kirghizia?); Palaeocene (Belgium); Oligocene (Western Interior of America, Mongolia); Miocene-Pliocene (Yugoslavia?, Canary Islands, Western Interior of America).

Main references. — Milosevic 1967, Hirsch 1983, Hirsch and Lopez-Jurado 1987, Hirsch and Packard 1987, Hirsch *et al.* 1987a, Hirsch and Bray 1988, Nesov and Kaznishkin 1986 (variants 1, 2, 5?), Schleich *et al.* 1988, Schleich and Kästle 1988.

Fossil gecko eggshells

(pl. 22: 6—7)

Diagnosis. — Eggshell of geckoid basic type; geckoid morphotype; very fine and widely separated funnel-shaped pore canals (Packard and Hirsch 1989); smooth surface; ellipsoid or round eggs.

Occurrence. — Cretaceous of India(?); Eocene of Wyoming; Miocene of Kenya.

Main references. — Sahni *et al.* 1984, Hirsch and Packard 1987, Hirsch *et al.* 1987.

Fossil crocodylian eggshells

(pl. 22: 1—5)

Diagnosis. — Eggshell of crocodyloid basic type; crocodyloid morphotype; pore canals consist of wide tubes with large funnels; smooth surface (unincubated shell) or mottled with "craters of resorption" (incubated shell, Ferguson 1981); ellipsoid eggs.

Occurrence. — Upper Cretaceous of France; Eocene of Colorado (*Krokolithes wilsoni* Hirsch, 1985) and East Germany.

Main references. — Hirsch 1985, Hirsch and Packard 1987, Kerourio 1987.

Remarks. — Fossil crocodylian eggshells are as yet unknown from the Asian continent.

DINOSAURIAN EGGSHELLS

Eggshells of dinosauroid basic type (possibly Sauropoda and Ornithischia; Mikhailov 1991)

Family "Megaloolithidae" Zhao, 1979³⁾ [Sauropoda]

(pl. 23)

Type genus: "*Megaloolithus*" — Cretaceous eggs from Aix-en-Provence (France) region, attributed to *Hypselosaurus*.

Synonymy. — A-type and C-type, Erben 1970; testudoid type, Sochava 1971; Megaloolithidae Zhao, 1979; tubocanaliculate eggshell, Erben *et al.* 1979; spherulithic type with tubocanaliculate pore canals, Kurzanov and Mikhailov 1989; fig. 12.2.B.

Diagnosis. — Tubospherulithic morphotype; tubocanaliculate pore system; sculptured surface: compactituberculate ornamentation; subspherical eggs; "thick" eggshell: 1.5—2.5 mm (possibly more).

Remarks. — An analogue of the spongy layer (with a squamatic ultrastructure),

³⁾ This parataxon is invalid because Zhao (1979) did not observe the ICZN rules (art. 11) failing to assign any definite genus (nor species) to his Megaloolithidae. As a formal revision of taxonomy is beyond the scope of this paper, this familial name is here provisionally accepted; the generic name "*Megaloolithus*" is also informally here introduced.

characteristic of avian eggshells is undoubtedly absent in "megaloolithid" eggshells (see above concerning the "fish-bone pattern"); distinction of two types (A and C, Erben 1970) in the records of spherulithic eggshells in Provence is incorrect (see also Vianey-Liaud *et al.* 1987: 409).

Occurrence. — Triassic(?), Argentina; Upper Cretaceous: South Europe (France, Spain), Peninsular India, Peru(?).

Composition. — "*Megaloolithus*" from France and Spain; two types of eggshells from India very similar to "*Megaloolithidae*" and a departing type from South America.

Examined material. — "*Megaloolithus*" eggshells from Aix-en-Provence (5 specimens from 3 sites); a sample of eggshell from Argentina.

Main references and illustrations. — Erben 1970: pl. 17—20; Erben *et al.* 1979; Bonaparte and Vince 1979, Sige 1968, Penner 1983, Williams *et al.* 1984; Beetschen 1985; Vianey-Liaud *et al.* 1987; Jain 1989, Jain and Sahni 1985; Mohabey and Mathur 1989; Hirsch 1989; fig. 10.1D—E.

Paleoecological and systematic interpretation. — Nesting: underground nests near water (Kerourio 1981, Erben *et al.* 1979), "humid" incubation conditions (Seymour 1979, Williams *et al.* 1984). The eggs from France have been assigned to a sauropod dinosaur *Hypselosaurus priscus* — on the basis of their close association with bones (Erben *et al.* 1979, Breton *et al.* 1986). The eggs from India were assigned to the sauropods *Titanosaurus* and *Antarctosaurus* (Vianey-Liaud *et al.* 1987); the bones of a juvenile sauropod were found in one of the egg specimens (Mohabey 1987). In similar(?) eggs from Argentina two juvenile dinosaurs with mixed pro-sauropod and sauropod features were found (Bonaparte and Vince 1979).

Family *Faveoolithidae* (Zhao et Ding, 1976) (Sauropoda?)

(pl. 24)

Synonymy. — Multicanalicate eggshell, Sochava 1969, Kolesnikov and Sochava 1972, Erben *et al.* 1979; "spherulithic" type with multicanalicate pore system, Kurzanov and Mikhailov 1989; fig. 12.2D.

Diagnosis. — Filispherulithic morphotype; multicanalicate pore system (pore canals have organic walls); smooth or slightly rough surface (the heads of prisms are densely packed); spherical and ellipsoid eggs; "thick" eggshell (≥ 2 mm).

Remarks. — The strict separation of the Mongolian multicanalicate eggshells from the tubocanalicate eggshells from France (Sochava 1971) is based on taxonomically inconsistent features. The eggshell is similar to the "*Megaloolithidae*" eggshell; both lack a true spongy layer with a squamatic ultrastructure.

Occurrence. — Lower(?) and Upper Cretaceous of Asia (Mongolia and China).

Composition. — *Faveoolithus* (Zhao et Ding 1976) and *Youngoolithus* (Zhao 1979).

Examined material. — *Faveoolithus* remains: four complete clutches, unbroken eggs and numerous eggshell fragments from three localities in the Gobi Desert (Mongolia) (PIN 4225—I, 2970, no #; GI and ZPAL materials).

Main references and illustrations. — Sochava 1969: pl. 11: 1, pl. 12: 11—13; 1971: pl. 9: 8—10; Kolesnikov and Sochava 1972: pl. 16: 1—13; Zhao and Ding 1976: pl. 1: 1—3; Zhao 1979, pl. 1, 2: 1—4.

Paleoecological and systematic interpretation. — Turtle-like nesting type: underground nests near water; very "humid" incubation conditions (Seymour 1979). Correct taxonomic assignment unknown. The size of eggs (largest after "*Megaloolithus*"), the mode of the nesting and incubation conditions allow to assign tentatively the *Faveoolithidae* material to sauropod dinosaurs.

Family Dendroolithidae (Zhao, 1988) [Sauropoda? or Ornithopoda?]

(pl. 24: 7)

Diagnosis. — Dendrospherulithic morphotype; prolatocanaliculate pore system (pores are widely distributed) with a network of microcanals among the prisms in the upper part of the eggshell; rough surface (the heads of prisms are protruding in oblique directions); spherical and slightly ellipsoid eggs; “thick” eggshell (≥ 2 mm).

Monotypic(?) family.

Remarks. — To avoid the ambiguity the terms “cone layer” and “columnar layer” should not be used for the eggshells of the dinosauroid basic type.

Occurrence. — Upper Cretaceous of Asia (China and Mongolia).

Examined material. — *Dendroolithus*(?) material from the Gobi desert (Mongolia): one clutch of eggs (GI), one whole egg and numerous eggshell fragments (PIN).

Paleoecological and systematic interpretation. — Nesting: underground? nests near water. Correct systematic assignment unknown. Basing on eggshell structure and the mode of nesting the *Dendroolithidae* material should be tentatively attributed to some ornithopod or sauropod dinosaurs.

Family Spheroolithidae (Zhao, 1979 [Ornithopoda: some hadrosaurs])

(pl. 25, pl. 26: 1–4)

Synonymy. — Partly prolatocanaliculate type, Sochava 1969, 1971, Erben *et al.* 1979; spherolithic type with prolatocanaliculate pore canals, Kurzanov and Mikhailov 1989: fig. 12.2A.

Diagnosis. — Prolatospherulithic morphotype; prolatocanaliculate pore system; smooth, rough and sculptured surface (sagenotuberculate ornamentation — variants 1, 2 at fig. 8A and fig. 8B); subspherical and ellipsoid eggs; “thick” (> 2 mm) and medium thick (> 1 mm) eggshells.

Occurrence. — Lower Cretaceous: USA (Utah), Mongolia?; Upper Cretaceous: Asia (Mongolia, China, Kirghizia), North America (Western Interior).

Composition. — Asia: *Spheroolithus* Zhao (1978, 1979; = *Oolithes spheroides* Young, 1954), undescribed material from Mongolia. North America: eggs of *Maiasaura peeblesorum* Horner et Makela, 1979 (Hirsch and Quinn 1990); “*Oolithes carlinensis*” and another still undescribed eggshell remains from the Western Interior (Jensen 1966, 1969).

Examined material. — Two whole clutches, unbroken eggs and numerous eggshell fragments from seven localities in the Gobi Desert (Mongolia) (PIN 2970/3, 4216–400, 4228–2, 522–400, 614–606, 607; 3142–454, 466; 4216–401; GI and ZPAL materials); two specimens from Laiyang (China) (eggshells from the clutches “*Oolithes spheroides*” V-721 and V-733); some specimens from Utah and Montana (USA), including eggshells of *Maiasaura*.

Main references and illustrations. — Jensen 1966: pl. 4: 4–5; 1970; Sochava 1969: pl. 12: 6–8; Chao and Chiang 1974: pl. 1: 1–6, pl. 2: 1–5; Shuvalov 1982: 27, 29; Nesov and Kazniskin 1986: variants ?9, 12; Hirsch and Packard 1987: fig. 10.2C, J, I; Hirsch and Quinn 1990.

Paleoecological and systematic interpretation. — Colonial nesting with possible parental care, open(?) or halfopen(?) nests constructed of plant material (Horner 1982, 1987); “semihumid” incubation conditions. One of the most common groups of dinosaur eggs and eggshells in Mongolia and China (in China, about 85% well

preserved eggs belong to the spheroid eggs of this group: Chao and Chiang 1974: 82). The hatchlings of a hadrosaur *Maiasaura peeblesorum* from colonial nesting sites in Montana, USA, were described (Horner and Makela 1979). *Spheroolithus* eggs from China (Laiyang) have been repeatedly assigned to hadrosaurs; the *S. irenensis* eggs were found in association with *Bactrosaurus* remains (Chao and Chiang 1974: 81).

Family **Ovaloolithidae** nov. (**Ornithopoda?**)

(pl. 26: 5, 6, pl. 27)

Synonymy. Partly prolatocanaliculate type, Sochava (1969).

Diagnosis. — Angustispherulithic morphotype; pore system of mixed type, mainly rimocanaliculate + angusticanaliculate; sculptured surface: sagenotuberculate ornamentation (often variant 3: fig. 8), or smooth surface; ellipsoid — sub-spherical eggs; “thick” (>2 mm) and “medium” (>1 mm) eggshell.

Occurrence. — Upper Cretaceous, Asia (Mongolia, China, Kirghizia), ?North America (Western Interior).

Composition. — *Ovaloolithus* (Zhao 1978, 1979), undescribed material from Mongolia (PIN).

Examined material. — Complete eggs and numerous eggshells from four localities in the Gobi Desert (Mongolia) (PIN 4231—1, 2970/7, 3097—502, 3225—150, 151, 152). Eggshell fragments from the clutch V-736 (“*Oolithes chinkangkouensis*”, China, Laiyang).

Main references and illustrations. — Sochava 1969, Chao and Chiang 1974: pl. 3, 4: 1—5; Zhao 1979; Nesov and Kaznyshkin 1986: variants 6, 11(?).

Paleoecological and systematic interpretation. — Colonial nesting near water, “semihumid” incubation conditions. Correct systematic assignment unknown. The histostructure and superficial features of the shells as well as the structure of the clutches are most similar to the Spheroolithidae; presumably attributable to ornithopods.

Remarks. — Four small limb bones adhere to the inner surface of large fragment of an egg (PIN 2970/7). The bones were assigned by Sochava (1972) to a protoceratopsid. A re-examination of the specimen by S. M. Kurzanov showed that the bone originally considered as metatarsal III does not represent a foot element. The diaphyses preserved allow one to identify the bone remains but as the dinosaurian ones. Moreover, as it is now certain, protoceratopsids laid distinctly different eggs, what particularly concerns the shell histostructure (see below).

Eggs and eggshells of protoceratopsids

(pl. 27: 8, pl. 28: 1, pl. 29; fig 7)

Synonymy. — Angusticanaliculate eggshell, Sochava 1969; spherolitho-prismatic type, Kurzanov and Mikhailov 1989: fig. 12.2C.

Diagnosis. — Prismatic morphotype; progressively thinning towards equatorial region; angusticanaliculate pore system; surface smooth or with fine linearituberculate ornamentation (fine, long ridges without nodes, variant 2: fig. 8C, pl. 27: 8ab) in the equatorial region (ornamentation not in accordance with the orientation of the accretion lines, which are horizontal); strongly elongated eggs (slightly asym-

metric; elongation — length/breadth = 2.3—2.7; “thin” eggshell (0.5—1.2 mm), progressively thinning towards equatorial region.

Occurrence. — Upper Cretaceous (Upper Santonian — Campanian) of Asia (Mongolia, ?Kirghizia).

Remarks. — The literature concerning the eggs and shells of protoceratopsids is very confusing. In the description of the angusticanalicate eggshells (Sochava 1969), the *Protoceratops* shell material was confused with the shell remains of Elongatoolithidae (possibly eggs of theropods) from Mongolia and China. All figures of angusticanalicate eggshells in Sochava (1969) and Erben *et al.* (1979) represent the Elongatoolithidae. No unquestionably protoceratopsid egg remains have been described from China so far. Only fragments of the eggshells of “*Oolithes lamino-dermus*” (Chao and Chiang 1974: pl. 4: 6) bear some resemblance to *Protoceratops* eggshells.

Eggshells similar to those of protoceratopsids, with histostructure apparently of a prismatic morphotype, were described from the Upper Cretaceous of Southern France (Kerourio 1982: pl. 1—2).

Examined material. — Four whole clutches, abundant eggs, parts of eggs and shell fragments from 6 localities in the Gobi Desert (Mongolia), (PIN 614—(58, 601, 603), 3142—(415, 429, 447—453, 455, 489, 495, 496), 3143—(121, 122, 123). 4228—1; GI and ZPAL materials].

Paleoecological and systematic interpretation. — Colonial nesting along beaches and estuary marshes. Half-buried (?) or open (?) nests, possibly constructed of plant material; “semihumid” incubation conditions. The eggs were assigned to *Protoceratops* at the time of the Central Asiatic Expedition of the American Museum of Natural History (1923—1924). Essentially, I agree with this conclusion: in at least three Gobi localities (Bain-Dzak, Tugrikeen-Shire, Khermin-Tsav) clutches and numerous eggs under discussion are found in a close association with whole skeletons of protoceratopsids (adults, subadults and hatchlings); see also remarks on the family Ovaloolithidae.

Eggs and eggshells of hypsilophodontids

(pl. 27: 6—7)

Discussion. — The embryonic skeletal remains allowed Horner and Weishampel (1988) to attribute these eggs to the hypsilophodontid dinosaur *Orodromeus makelai*. Detailed descriptions of the clutches, eggs and eggshell remains from the Upper Cretaceous of Montana are now available (Hirsch and Quinn 1990). The diagnosis given below is based on this description and illustrations (see also Hirsch and Packard 1987: fig. 46, 47; Hirsch 1989: fig. 10.2A, B) and also on the examination of eggshell samples.

Diagnosis. — Prismatic morphotype; angusticanalicate pore system with “aepyornithoid” pore pattern (twin-pores in elongated depressions parallel to the long axis of the egg); smooth surface; elongate eggs; “thin” eggshell (0.8—0.9 mm).

Remarks. — Though remarkably similar to the protoceratopsid eggs in the histostructure, form of eggs and the structure of clutches, the hypsilophodontid eggs are well distinguishable by pore patterns and other shell surface features.

The eggshell sample from the Jurassic of Colorado (Hirsch *et al.* 1987, 1989), which I have re-examined, proved to be a dinosaurian eggshell of prismatic morphotype with smooth surface.

Eggshells of ornithoid basic type [Theropoda(?); Mikhailov 1991]**Family Elongatoolithidae (Zhao, 1975)**

(pl. 28: 2; pls. 20—21; pl. 22: 1)

Synonymy. — Angusticanalicate eggshell, Sochava 1969, 1971, Erben *et al.* 1979, Kurzanov and Mikhailov 1989: fig. 12.2.E.

Diagnosis. — “Ratite” morphotype (single to mammillary layer ratio ranging from 3:1 to 5:1); angusticanalicate pore system (simple, non-branching); sculptured eggshell: linearituberculate ornamentation (variant 1: fig. 8C) on equatorial region of eggs, tending to ramotuberculate ornamentation adjacent to the poles and dispersituberculate ornamentation on the poles (sculpturing is in correspondence to the undulating accretion lines); elongate eggs (elongation more than 2); “thin” (up to 1 mm) and of medium thick (1—2 mm) eggshell. From the protoceratopsid eggshells they differ in the texture, details of ornamentation, and in the size and form of eggs.

Occurrence. — Lower and Upper Cretaceous of Asia (Mongolia, China, Kirghizia); Upper Cretaceous of Kazakhstan (Zaisan Basin), ?Southern Europe (France), North America (USA, Montana).

Composition. — Asian material: *Elongatoolithus* („*Oolites elongatus*” (Young 1954), *Macroolithus*, *Nanhsingoolithus* (Zhao 1975), numerous undescribed material from Mongolia. North American material: eggs of ?*Troodon* (Hirsch and Quinn 1990).

Remarks. — The ?*Troodon* eggshell has dispersituberculate ornamentation completely covering the egg and can thus be distinguished as a close, but separate “family”.

Examined material. — More than 20 specimens: three whole clutches and numerous eggshell fragments from 7 localities in the Gobi Desert (Mongolia) PIN 522—401, 614—(59, 604, 605, 610, 611), 2970/2—1, 3097—500, 3142—400, 4216—(402, 404), 4227—1, 4229—1, 4230—(1, 4, 5); GI and ZPAL materials; abundant eggshell remains from Kazakhstan (Zaisan Basin) [2970/8]; two samples from China (Laiyang) (eggshells of “*Oolithes elongatus*” from clutches V-734 and V-788); samples of ?*Troodon* eggshell from Montana.

Main references and illustrations. — Bazhanov 1961, Sochava 1969: pl. 11: 6—8. pl. 11: 1—5; 1971: pl. 9: 1; Chao and Chiang 1974: pl. 4: 7; Zhao 1975: pls. 1, 2; Beetchen *et al.* 1977: figs. 1—5; Nesov and Kaznyshkin 1986 variants ?3, 7, 8, 13, fig. 2A; Hirsch 1989, fig. 10.2D; Hirsch and Packard 1987: figs. 52, 53; Hirsch and Quinn 1990: figs. 9—11; Mikhailov 1987b: pl. 5: 1, 2; 1991; Kurzanov and Mikhailov 1989: fig. 12.1A—D.

Paleoecological and systematic interpretation. — Widely separated clutches (nesting by separate pairs?); very rarely colonial nesting. Open(?) or half-open(?) nests constructed with ?plant material (Kurzanov and Mikhailov 1989); rather “dry” incubation conditions.

The Asian material has yet to be precisely identified, but I, in general, agree with the proposition that the dinosaurian eggshells of the ornithoid basic type are attributable to theropod dinosaurs. Elongatoolithidae shell remains are widely distributed in the Upper Cretaceous deposits of Asia, thus they may belong to one of the three dinosaurian groups: hadrosaurs, protoceratopsids, or theropods. Eggshells of the first two groups are already known, and are of a quite different basic type (dinosauroid), so they may be excluded from consideration (see criteria of taxonomic interpretation: 2—5). The dinosaurian eggs with eggshells of the ornithoid basic type from Montana (representing the same, or a very close group; Hirsch and Packard

1987: fig. 56; Hirsch 1989: fig. 10.2D) which I have examined (sample HEC 240) were found to contain remains of the embryo of *Troodon* (Theropoda; Hirsch and Quinn 1990).

Incertae sedis fossil eggshells of the ornithoid basic type [Theropoda(?), Aves]

Family *Laevisoolithidae* nov.

(pl. 32: 2—4)

Derivation of the family name: after a smooth, sleek egg surface.

Synonymy: partly angusticanalicate eggshell, Sochava 1969: 89, pl. 11: 5 (indication on fig. 3b is incorrect).

Diagnosis. — “Ratite” morphotype (the ratio of single layer to mammillary layer is 2:1.5); angusticanalicate pore system; smooth surface; rather small ellipsoid eggs (less than 7 cm in length); “thin” eggshell (less than 1 mm).

Monotypic group; the same diagnosis for the type genus and species.

Type genus and species: *Laevisoolithus sochavai* gen. et sp. n.

Holotype: PIN 2970/5 (whole egg with partly broken pole, pl. 32: 2).

Derivation of the species name: in honour of the Soviet paleontologist, A. V. Sochava, who was the first to classify fossil eggshells from the Cretaceous of Mongolia.

Occurrence. — Upper Cretaceous (Nemegt Formation, ?Maastrichtian) of Mongolia (Bugeen-Tsav, Gobi Desert).

Examined material. — A single egg (PIN 2970/5).

Systematic interpretation. — Relationship of this egg is unknown, presumably it was laid by a bird or small (theropod?) dinosaur.

Family *Subtiliolithidae* nov.

(pl. 33: 1—4)

Derivation of the familial name: after subtly ornamented, fine eggshell.

Diagnosis. — “Ratite” morphotype (single layer to mammillary layer ratio reverse to the normal one and varying from 1: 2 to 1: 3); angusticanalicate eggshell; smooth surface or with microsculpture (microtubercules); “very thin” eggshell (main range 0.3—0.4 mm).

Monotypic group; the same diagnosis for the type genus and species.

Type genus and species: *Subtiliolithus microtuberculatus* gen. et sp. n.

Holotype: PIN 4230—3 (eggshell fragments, pl. 33: 1, 2).

Derivation of the specific name: after surface with micronobules.

Occurrence. — Upper Cretaceous (?Nemegt Formation, ?Maastrichtian) of Mongolia (Khaichin-Ula-I, red beds Gobi Desert).

Examined material. — Eggshell fragments from remains of several clutches (PIN 4230 — (3, 7, 8).

Systematic interpretation. — Possibly colonial nesting. The true relationship of these remains is unclear; the eggs might have been laid by birds or small (theropod?) dinosaurs.

Fossil avian eggshells

All examined avian eggshells represent the ornithoid basic type.

Eggs and eggshells of "*Gobipteryx*" (Elżanowski 1981)
(pls. 34—35)

Diagnosis. — Prismatic ("neognathe") morphotype (spongy to mammillary layer ratio is 2:1); angusticanalicate pore system; smooth surface; small eggs of elongate — oval shape (elongation 1.8—2.0); "very thin" eggshell (0.1—0.4 mm).

Remarks. — In thin sections (in ULM and PLM), eggshells of "*Gobipteryx*" may be confused with eggshells of protoceratopsid dinosaurs.

Occurrence. — Upper Cretaceous (Barun-Goyot Formation, ?Upper Santonian — Campanian) of Mongolia (Khermeen-Tsav, Khulsan, Nemeget, Gobi Desert).

Examined material. — Numerous intact and broken eggs and their parts (PIN 3142—).

Paleoecological and systematic interpretation. — Long-term colonial nesting along the margins of lakes, estuaries and possibly islands; possibly open nests. Most of the eggs found indicate that the nests were often flooded as a result of fluctuations of the water level. In the eggs collected by the Polish-Mongolian and Soviet-Mongolian paleontological expeditions developed embryos were discovered. They have been attributed to volant palaeognathous birds (Elżanowski 1981), though can not be directly compared (E. N. Kurochkin — personal comm.) with the earlier described from Gilbert locality (Southern Gobi aimak) genus *Gobipteryx* Elżanowski, 1977.

Family Ornitholithidae (Dughi et Sirugue, 1962)

(pl. 33: 5, 6)

Diagnosis. — "Ratite" morphotype with well developed mammillae (with wedges deviating from the radial arrangement in the uppermost part of the mammillary layer); rimocanalicate pore system; hieroglyphic or ramifying pattern of twisted pore grooves on the shell surface (grooves roughly parallel to the long axis of the egg); unsculptured but slightly undulating eggshell surface; "thick" and "very thick" eggshell (1.9—4.0 mm).

Monotypic group.

Remarks. — In thin section, the *Ornitholithus* eggshell may be confused with *Aepyornis* and *Struthio* eggshells, on the one hand, and with angustispherulithic dinosaur eggshells (Ovaloolithidae), on the other hand. But it distinguishes from both by its characteristic pore system and pore pattern.

Occurrence. — Eocene (Sparnacian) of France.

Examined material. — 3 specimens of *Ornitholithus* eggshell from 3 localities of Southern France (PIN 4237—(1, 2, 3)).

Systematic interpretation. — Dughi et Sirugue (1962, 1969) referred *Ornitholithus* eggshells to the avian families Gastornithidae and Diatrymidae, representatives of which have been found in contemporaneous deposits in the Paris Basin. Taking into account the thickness and histostructure of these eggshells, this suggestion seems reasonable.

Fossil eggshells of ratite birds (*Aepyornithidae*, *Struthionidae*, *Dinornithiformes*)

(pl. 37: 5—7)

Diagnosis. — “Ratite” morphotype (single layer to mammillary layer ratio varying from 2: 1 to 3.5: 1); reverse, external zone is very characteristic of all groups, except for the examined moa eggshell; angusticanalicate pore system with single and branching pore canals; complicated pore patterns (“aepyorinthoid” — “struthioid” range) on smooth or undulating shell surface; “thick” and “very thick” eggshell (1.5—5 mm).

Occurrence. — *Struthio* eggshell: Miocene — Holocene of Palaearctic; Upper Pliocene — Pleistocene of South Africa; ?Miocene of North India. *Aepyornis* and *Dinornis* eggshell: Holocene of Madagascar and New Zealand respectively.

Main references and illustrations — Sauer 1972; Mikhailov 1988, 1991; Mikhailov and Kurochkin 1988).

Remarks. — On the basis of histostructure and superficial characteristics, it is possible to identify eggshells of diverse ratite taxa (down to the species or subspecies level for Neogene ostriches; for review see Mikhailov 1991).

Dromornithid eggshells have been described from the Late Pleistocene of Australia (Williams 1984).

Fossil eggshells of neognathe birds

(pl. 39: 1—3)

Remarks. “Thin” (<1 mm) avian eggshell remains (ornithoid basic type; prismatic (“neognathe”) morphotype; angusticanalicate pore system; smooth surface) have been reported from numerous places all around the world, especially from the Tertiary (Hirsch and Packard 1987: 389; Stephan 1977, 1984). Such eggshells are also known from the Upper Cretaceous of the USSR (Kazakhstan, Zaisan Basin; pl. 39: 2). At present, identification of this material is difficult, because of the lack of a comprehensive SEM-atlas of the Recent eggshells.

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KLASYFIKACJA KOPALNYCH SKORUP JAJ OWODNIOWCÓW

Streszczenie

Praca zawiera przegląd budowy skorup jaj gadzich i ptasich oraz propozycję ujednoczonej terminologii oologicznej (fig. 1—8, tab. 1—2). Zbadany materiał obejmuje szczątki kredowych i kenozoicznych jaj gadzich i ptasich z Mongolii, Chin, Azji Środkowej, Francji, USA i Argentyny (pl. 21—39). Autor podaje kryteria klasyfikacji jaj na podstawie skorupy. Wyróżnia kilka poziomów organizacji strukturalnej skorup jaj: teksturę (ultrastrukturalne postaci biomineralizacji), histostrukturę ogólną i ogólną morfologię. Omawia i nazywa typy systemu porów oddechowych i ornamentacji zewnętrznej powierzchni skorupy. Na tej podstawie wyróżnia zasadnicze typy i morfotypy, oparte przede wszystkim na kryteriach ultra- i mikrostrukturalnych, jako najbardziej stabilnych i użytecznych diagnostycznie u grup współczesnych. Parataksonomiczny podział jaj kopalnych obejmuje 14 „rodzin” jaj dinozaurów i 18 grup jaj przypisanych krokodylom, żółwiom i gekkonom. Formalne opisy zawierają obok omówienia swoistych cech budowy skorup zaliczonych do poszczególnych grup także dane o ich występowaniu, spostrzeżenia paleobiologiczne i próbę powiązania parataksosów z grupami naturalnymi organizmów rodzicielskich.

EXPLANATIONS OF PLATES 21—39

Plate 21

Eggshells of Recent (1—6) and fossil (7, 8) turtles

1. Shell unit with organic core (oc) in the base. Note regular zones of growth of aragonite crystals. Recent, *Dohyma* sp., SEM, $\times 300$. Polished surface treated with 1% HCl for 6 sec.
2. Broken base of shell unit within shell membrane (sm). Note “hole loculi” of organic core (oc), radiating aragonite crystals and organic fibres (f). Recent, *Testudo graeca*, SEM, $\times 1000$.
- 3—6. Thin radial sections of the eggshell. Note secondary (pathological) layer (sl) observed in 3. ULM: 3 *Testudo radiata*, $\times 50$; 4 *T. pardalis*, $\times 120$; 5 *T. horsfieldi*, $\times 120$; 6 *Trionyx sinensis*, $\times 120$.
- 7—8. Fossil turtle eggshells: bases of shell units (partly recrystallized in 7). Note site of the organic core (oc) and fine spicular aragonite crystals (A). PIN 4225—2, Lower? Cretaceous of Mongolia: 7 inner surface, SEM, $\times 350$; 8 thin radial section, ULM, $\times 200$.

1, 3—6, 8 radial views and 2, 7 inner surfaces

Plate 22

Eggshells of Recent crocodiles (1—5) and geckoes (6—7)

1. Broken surface, crocodyloid basic type. Note large shell units (*su*), rough wedges (*w*), basal plate group (*bp*) and crater of erosion (*ce*). *Alligator mississippiensis*, SEM, $\times 40$.
2. Base of shell unit (normal to shell surface is parallel to the right diagonal of photo). Note plates of basal plate group (*bp*) among uppermost fibers of shell membrane and cross-fracture of wedge (*w*). *Alligator mississippiensis*, SEM, $\times 300$.
3. Inner surface of eggshell, bases of discrete shell units. Note characteristic rosettes of plates (= basal plate groups, *bp*). *Alligator mississippiensis*, SEM, $\times 30$ (bar = 100 μm).
- 4, 5. Thin sections of crocodylian eggshells. Note large shell units (*su*) rich in organic material at their bases (dark pits) and very regular horizontal accretion lines. ULM: 4 *Alligator sinensis*, $\times 80$; 5 *Crocodile* sp., $\times 80$.
6. Broken surface, geckoid basic type. Note bulbous organic forms (*b*) in the base and four ultrastructural zones above: 1 amorphous material, 2 compact crystalline columns, 3 subgranular material, 4 vertical polycrystalline? plates (like "cunei" in avian eggshell); distinct border (arrow) between zones 2 and 3 corresponds to the dark line observed in fig. 7. Recent, *Gymnodactylus caspicus*?, SEM, $\times 1200$.
7. Thin section of gecko eggshell. Note dark horizontal line (arrow) of organic? material, corresponding to the border between zones 2 and 3 in fig. 6. Recent, *Gymnodactylus caspicus*?, ULM, $\times 220$.

1, 2, 4—7 radial views

Plate 23

Eggshells of dinosaurs (sauropods), Upper Cretaceous of France: family "Megaloolithidae"

1. "*Megaloolithus*" eggshell, broken surface: discrete tubospherulithic shell units, broken (upper and lower fragments) and with unbroken walls (at the middle), $\times 10$.
2. Broken surface, dinosauroid basic type: *a* upper parts of shell units lacking squamatic ultrastructure — compare with pl. 31: 1a, b, pl. 32: 1, 3, 4, pl. 36: 1; indicated are diagenetically crystallized pore canals (*pc*) and spherulites (*s*) of secondary pathological layer, SEM, $\times 80$; *b* a detail: note cross-sections of wedges (arrow) in the very centre of spherulite and tabular ultrastructure of wedges (*w*), SEM, $\times 300$.
3. Polished and etched radial section. Note organic "sheaths" of pore canals (*pc*); fine "fish-bone pattern" (*fb*) represents a crystallographically controlled micro-etching pattern of calcite, SEM, $\times 30$. To compare with squamatic pattern see pl. 31: 2a, b. Treated with 0.1% HCl for 24 h.
4. Transverse thin section of eggshell. Tubocanalicate pore system. Pore canals (*pc*) have dark organic walls, ULM, $\times 56$.
5. Eggshell outer surface, compactituberculate ornamentation, $\times 5$.

1—3 radial views and 4, 5 transverse views

Plated 24

Eggshells of dinosaurs (sauropods?): family Faveoloolithidae (1—6) and Dendroolithidae (7)

- 1—6. *Faveoloolithus ningxianensis* Zhao, Upper? Cretaceous of Mongolia, Gobi Desert:
1. Clutch of eggs (its upper layer), PIN 4225—1, Ologoi-Ulan-Tsav locality, $\times 1/25$.
 2. Broken surface, filispherulithic morphotype, multicanalicate pore system. Arrows indicate numerous pore canals among long prisms; τ rock matrix; $\times 10$.
 - 3, 4. Broken surface. Note recrystallized large prisms (*p*) and pore canals (*pc*) filled with secondary calcite. SEM: 3 $\times 100$ (bar = 100 μm), 4 $\times 50$.
 5. Polished and etched section: base of shell unit; note remnants of organic core (*oc*) and organic "sheaths" (*os*) of prisms in the beginning of their growth; SEM, $\times 100$. Treated with 0,1% HCl for 24 h.
 6. Thin transverse section: prisms form "walls" between pore canals (*pc*); note dark organic membranes of prisms (arrows) which constitute organic walls of pore canals, ULM, $\times 56$.
 7. Dendrospherulithic eggshell showing shell units (*s*) with branching off subunits in their upper part (zone 2), as well as lacunae and surface depression of prolatocanalicate pore system (arrows). *Dendroolithus* sp., PIN #, Upper Cretaceous of Mongolia, Gobi Desert, $\times 10$.

2—5 and 7 radial views

Plate 25

Eggshells of dinosaurs (?ornithopods): family Spheroolithidae except 10; Upper Cretaceous

- 1—2. Whole clutches of eggs differing in structure: 1 *Spheroolithus chiangchungtingensis*, China, Laiyang; clutch V-731, PIN, $\times 1/6$; 2 *Spheroolithus* sp., PIN 4216—400, Gurilin-Tsav locality, Mongolia, Gobi Desert, $\times 1/6$.
- 3—5. Eggshell outer surface, sagenotuberculate ornamentation, variant 1: 3 hadrosaur *Maiasaura peeblesorum*, USA (Montana), $\times 2$; 4 — PIN 614—600, Mongolia, Gobi Desert, $\times 1.5$; 5 — PIN 3142—454, Mongolia, Gobi Desert, $\times 1.5$.
6. Broken surface in radial view. Note crystallographically controlled cleavage pattern of calcite (arrow) well developed in upper parts of spherulithic shell units (*s*). *Spheroolithus chiangchungtingensis*, V-731 (PIN), China, Laiyang, SEM, $\times 40$.
- 7—9. Thin radial sections of prolatospherulithic eggshells. Note poorly separated shell units (*su*) and canals (*pc*) of prolatocanalicate pore system as well as an evident lack of differentiation into two structural layers (compare with pl. 30: 2, 3). ULM: 7 hadrosaur *Maiasaura peeblesorum* (with permission of K. F. Hirsch), small arrows indicate diagenetic calcite layers $\times 30$; 8 PIN 614—606, Mongolia, Gobi Desert (from unpublished materials of I. A. Sadov), $\times 15$; 9 PIN 2970—3, Mongolia, Gobi Desert, $\times 20$.
10. Radial fracture of spherulithic shell unit showing tabular ultrastructure (without chemical treatment). "*Megaloolithus*" eggshell, Upper Cretaceous of France, $\times 350$.

Plate 26

Eggshells of dinosaurs (?ornithopods): family Spheroolithidae (1—4) and Ovaloolithidae (5, 6); Upper Cretaceous

- 1—3. Broken surface of prolatospherulithic eggshells. Note large shell units (*su*), fan-like pattern of wedges and diagenetically crystallized pore canals (*pc*); squamatic ultrastructure is lacking (compare with pl. 31: 1, pl 32: 1—4, pl. 37: 1, 2); “fish-bone pattern” (*fb*) represents a crystallographically controlled cleavage pattern of calcite. 1 hadrosaurian eggshell (*Maiaosaura*, Montana), $\times 30$; 2 *Spheroolithus* sp., PIN 2970/3, Mongolia, Gobi Desert, $\times 30$; 3 PIN 3142—454, Mongolia, Gobi Desert, $\times 25$.
4. Base of spherulithic shell unit in polished and etched section. Note remnants of organic core (*oc*) and “sheaths” of shell unit (arrow) as well as borders of wedges (small arrows); note also lack of ultrastructural transition along the wedges (compare with pl. 35: 2, pl. 37: 4); fine radial pattern within wedges seems to represent the pattern of microetching along crystallographic c-axes of calcite. PIN 3142—454, Mongolia, Gobi Desert, $\times 200$. Treated with EDTA for 2 h.
5. Broken surface of angustispherulithic eggshell. Note the differentiation of the shell structure into two zones: inner zone of regular subvertical growth of wedges and upper zone, where development of wedges is laterally declined conventional border of zones is marked by two arrows); a small arrow indicates a fine slit — interruption in mineralization (see also 6); PIN 4231—1, Mongolia, Gobi Desert, $\times 30$.
6. Enlarged detail from 5 (marked by a small arrow). In the slit, no general change of the ultrastructure can be observed (compare with pl. 31: 2b, pl. 33: 3, pl. 37: 2); fine radial elements seem to result from diagenetic microetching — compare with pl. 26: 4, and notice the contrast with pl. 25: 10, $\times 350$.

All SEM, radial views

Plate 27

Eggs and eggshells of dinosaurs: family Ovaloolithidae (1—4), protoceratopsid (5,8) and hypsilophodontid (6,7) remains; Upper Cretaceous

- 1, 3. Angustispherulithic eggshell. Note two zones differing in structure: inner zone of compact spherulithic shell units and upper zone with declining wedges intertwined with one another (borderline indicated dashed line). No features of squamatic ultrastructure can be observed (compare with pl. 30: 3, pl. 31: 1, pls. 32 and 33). Colour changes in 3 are of diagenetic origin: 1 broken surface, PIN 3225—150, Mongolia, Gobi Desert, SEM, $\times 15$; 3 thin section, Y-736 (“*Oolithes chinkangkouensis*”, PIN), China, Laiyang, ULM, $\times 15$.
2. Rimiform pore canal, transverse thin section of eggshell, V-376 (PIN), China, Laiyang, ULM, $\times 60$.
4. Eggshell outer surface, sagenotuberculate ornamentation, variant 3, and pore pattern (grooves) of rimocanaliculate pore system, $\times 5$.
5. Clutch of eggs of protoceratopsian dinosaur, PIN 3142—496, Mongolia, Gobi Desert, Khermeen-Tsav locality, $\times 10$.
- 6—7. Hypsilophodontid eggshell (prismatic morphotype), USA, Montana: 6 broken surface in oblique radial view; note a lack of squamatic ultrastructure in

prisms; "fish-bone pattern" (arrows) represents a crystallographically controlled cleavage pattern of calcite, SEM, $\times 30$; 7 thin section (with permission of K. F. Hirsch), an arrow indicates angusticanalicate pore canals, ULM, $\times 30$.

- 8a, b. Eggshell outer surface of protoceratopsian dinosaur, observed in the equatorial part of egg and showing a linearituberculate ornamentation with fine ridges; PIN 3142—451 (8a) and #N (8b), Mongolia, Gobi Desert, $\times 1.5$.
1, 3, 6, 7 radial views

Plate 28

Eggs of dinosaurs: protoceratopsian (1) and ?theropod eggs of the family Elongatoolithidae (2); Upper Cretaceous of Mongolia, Gobi Desert

1. Three eggs from clutch of *Protoceratops andrewsi*; note smooth surface of eggshell, PIN 614—58 (1—3), Bayn Dzak locality, $\times 1/2$.
2. Clutch of eggs of *Elongatoolithus?* sp., PIN 3143—126, Tugrikiin-Shire locality, $\times 1/3$.

Plate 29

Eggshells of protoceratopsian dinosaurs Upper Cretaceous of Mongolia, Gobi Desert

1. Broken surface, prismatic morphotype. In prisms of shell units (*su*), the squamatic ultrastructure is lacking — compare with pl. 31: 1, pl. 32: 1, 3, 4, pl. 36: 1. PIN 614—58(1), SEM, $\times 50$.
2. Base of shell unit. Note a crystallized site of organic core (*oc*) and unchanged ultrastructure of growing radial elements (wedges — *w*) — compare with pl. 6: 4 and notice the contrast with pl. 35: 2, pl. 37: 4, pl. 39: 3. PIN 614—58(1), SEM, $\times 700$.
- 3—4. Thin radial sections of eggshell (prismatic morphotype). Well seen vertical borders of shell units (arrow). ULM, $\times 80$: 3 relatively thick fragment from the polar area; 4 relatively thin fragment from equatorial part; when prisms are short the shell structure resembles that of the crocodiloid morphotype (compare with pl. 22: 4, 5).
5. Polished and etched section. Note that the squamatic ultrastructural zone is lacking — compare with pl. 31: 2a, b pl. 32: 4a, b; fine rhombohedral elements and their "prints" (arrows) result from crystallographically controlled microetching of calcite. PIN 4228—1, SEM, $\times 250$. Treated with EDTA for 1.5 h.

All in radial view

Plate 30

Eggshells of dinosaurs (?theropods): family Elongatoolithidae, Upper Cretaceous

1. Fractured egg and shell fragments from diverse parts of egg (outer surfaces). *Elongatoolithus?* sp., PIN 3143—126, Tugrikiin-Shire locality, Mongolia, Gobi Desert, $\times 2$: A — dispersituberculate ornamentation, polar area; B — ramotuberculate ornamentation, transitions to polar area; C — linearituberculate

ornamentation (ridges and hillocks, compare with pl. 27: 8a, b), equatorial part of egg.

- 2—3. Thin radial sections ("ratite" morphotype). Note the presence of two layers lacking prisms — a mammillary layer (*ml*) and a single layer (*sl*) as well as an angusticanaliculate pore canal (*pc*); note also undulation of accretion lines corresponding to surface ornamentation, compare with pl. 29: 3, 4. ULM: *Elongatoolithus?* sp., PIN 614—59, Mongolia, Gobi Desert, $\times 25$; 3 — *Macroolithus?* sp., PIN 4014—5, Kazakhstan, Zaisan Basin, $\times 25$.

Plate 31

Eggshells of dinosaurs (?theropods): family Elongatoolithidae

- 1—2. Radial views of eggshell (ornithoid basic type, "ratite" morphotype). Note a distinct structural border (arrows) between the mammillary (*ml*) and single layers (true spongy layer, *sl*) with squamatic material (*sq*) as well as a lack of prisms in the latter. *Macroolithus?* sp., PIN 2970/8, Upper Cretaceous of Kazakhstan, Zaisan Basin, SEM: 1a broken surface showing characteristic cavernous surface on fracture of true spongy layer, $\times 30$ (bar = 100 μm); 1b a detail, showing bulbous base of mammillae (*mm*) with fine crystals and overlying wedges, $\times 100$; 1c a detail of 1b with remnants of organic core (*oc*), $\times 300$; 2a polished and etched section, treated with EDTA for 1.5 h, $\times 25$; 2b a detail, $\times 100$, with characteristic etching pattern of true spongy layer.
3. Inner surface of eggshell showing the base of mammilla with crystallized site of organic core (*oc*). Note fine calcite plates typical of radial ultrastructure in avian eggshell — compare to the ultrastructure in pl. 34: 4, pl. 38: 2, pl. 39: 3, 4, and notice the contrast with wedges — pl. 26: 4, pl. 29: 2. PIN 4227—1, Lower Cretaceous Mongolia, Gobi Desert, SEM, $\times 2700$.

Plate 32

Eggshells of ?theropod dinosaurs (1a, b) of the family Elongatoolithidae and (2—4) of the family Laevisoolithidae (?theropod dinosaurs or birds); Cretaceous of Mongolia, Gobi Desert

1. a Broken surface of an eggshell of ornithoid basic type, "ratite" morphotype, showing well developed true spongy layer (single layer) with an unaltered squamatic ultrastructure (*sq*) in its inner part and with diagenetic changes in ultrastructure of ridges (arrow), PIN 4227—1, Lower Cretaceous, SEM, $\times 100$; b a detail, showing squamatic ultrastructure (*su* — squamatic units), $\times 500$ (bar = 10 μm) — compare with pl. 36: 3, 4 and pl. 37: 2.
2. Egg of *Laevisoolithus sochavaei* with very smooth surface and shell of ornithoid basic type, PIN 2970—5, Upper Cretaceous, Nemegt Formation (Maastrichtian), Bugin-Tsav locality, natural size.
- 3—4. 3, 4a Broken surface of eggshell from the specimen 2970—5 "ratite" morphotype: note well developed wedges (*w*) in the mammillary layer (*ml*) and unaltered squamatic ultrastructure (*sq*) in the inner part of the single layer (*sl*), SEM, $\times 100$ (bar = 100 μm); 4b a detail of 4a (zone marked with an arrow), $\times 500$; note that squamatic material (*sq*) overlies boundaries between wedges (*w*) (smaller bar = 10 μm).

All in radial view

Plate 33

Eggshells of ?theropod dinosaurs or birds from the family Subtiliolithidae (1—4) and bird eggshells from the family Ornitholithidae (5,6)

- 1—4. Thin eggshell of *Subtiliolithus microtuberculatum*, PIN 4230—3, Upper Cretaceous (Nemegt Formation, Maastrichtian) of Mongolia, Gobi Desert, Khai-chin-Ula-I locality: 1, 2 eggshell outer surfaces; smooth (1 right) and microtuberculated (1 left and 2) ones, 1×2.5 and 2 SEM, ×50; 3, 4 broken surface of eggshells of ornithoid basic type, "ratite" morphotype: note strongly developed wedges (*w*), the border (dashed line, arrows) between mammillary layer (*ml*) and single layer (*sl*), slightly recrystallized inner part of the single layer (*sl*, 1) with remnants of squamatic material and more strongly recrystallized upper part (*sl*, 2); "fish-bone pattern" (*fb*) is crystallographically controlled cleavage pattern of calcite; SEM: 3 ×200, 4×250.
- 5—6. *Ornitholithus* sp., Eocene of France: 5 eggshell outer surface with characteristic pattern of pore grooves (rimocanaliculate pore system), ×2; thin transverse section of eggshell, rimiform pore canal, ULM, ×80.

Plate 34

Eggshells of flying paleognate birds ("*Gobipteryx*") Upper Cretaceous (Barun Goyot Formation) of Mongolia, Gobi Desert

1. Eggs of "*Gobipteryx*", PIN 3142—(462—467), Khermeen Tsav locality, natural size.
2. Inner surface of eggshell with bases of mammillae (*mm*), SEM, ×50.
3. *a* Enlarged part of eggshell inner surface: note mineralized shell membrane (*sm*), eisospherites (*es*) and petal-like crystallites (*pt*) of secondary spherite, SEM, ×200; *b* a detail in SEM, ×500.
4. Very base of mammillae in rock matrix (radial view). Note remnants of organic core (*oc*) and fine radiating plates (*pl*), which constitute the petaloid elements (*pt*) of radial ultrastructure (compare with pl. 37: 4, pl. 38: 2, pl. 39: 3—5), SEM, ×2000.

Plate 35

Eggshell of flying paleognate birds ("*Gobipteryx*") Upper Cretaceous (Barun Goyot Formation) of Mongolia, Gobi Desert

1. General view of eggshell in rock (*r*). Note mammillary layer (*ml*), slightly (1) and strongly (2) recrystallized zones of spongy layer and mineralized remnants of ?cuticle (*cu*); note also crystallographically controlled, well developed cleavage of calcite in strongly recrystallized zone (2), SEM, thickness of shell = 0.2 mm.
2. *a* Fragment of 1, in magnification, showing the ornithoid basic type of structure of the prismatic ("neognathous") morphotype with a clear structural difference between radial elements of secondary spherite (*ss*), wedges (*w*) and squamatic material (*sq*), most of wedges and spongy layer are strongly recrystallized, SEM, ×850; *b* a detail, × 1500: note remnants of organic matrix (black arrow) of secondary spherite and site of organic core (*oc*), SEM, ×1500.
3. Fine radial crystals of secondary spherite in the rock matrix, SEM, ×1500.

All in radial view

Plate 36

Ultrastructure of avian eggshells

- 1—3. 1 Broken surface of an eggshell of ornithoid basic type, prismatic ("neognathous") morphotype: note clear ultrastructural differences between mammillae (*mm*), true spongy layer (*sl*) and external zone (*ez*); note also, that vertical borders of columns (*su* — shell unit), although vague, may be traced in spongy layer (bar = 100 μ m); 2 detail of 1, with compact crystalline blocks (*bl*) of external zone above squamatic ultrastructure (*sq*) of the spongy layer; 3 a detail of 1, with a squamatic ultrastructure (smaller bar = 10 μ m). Recent, *Falco peregrinus*, SEM: 1 \times 200, 2 \times 700, 3 \times 1500.
4. Squamatic ultrastructure. Polished and etched eggshell section showing spongy layer: note that squamatic units (*su*) are separated by membranes of organic matrix ("sheaths" — arrows). Holocene eggshell, *Aepyornis* sp. Madagascar, SEM, \times 1000. Treated with EDTA for 2h.
5. Squamatic ultrastructure, thin radial section of eggshell in spongy layer. Holocene eggshell, *Aepyornis* sp., Madagascar, ULM, \times 80.
6. Ultrastructure of avian eggshell material in spongy layer after treatment with heat H₂O₂ (40 min. decomposition of organic component); picture square corresponds to one squamatic unit from 4. Note fibril-like crystalline elements, oriented along c-axis of calcite in this zone of eggshell. Recent, *Struthio camelus*, SEM, \times 10 000.

All in radial view

Plate 37

Eggshells of Recent (1—4) and fossil (5—7) ratite birds

- 1—4. Ultrastructure of avian eggshell on broken surfaces, Recent, *Dromaius novaehollandiae* (1—3) and *Struthio camelus* (4): 1 mammillary layer adjoining to the shell membrane (*sm*) and single (spongy) layer (above): note a border line (arrows) between wedges (*w*) of mammillae and overlying squamatic material (*sq*), and clear structural differences between wedges and secondary spherite (*ss*) with radial ultrastructure, \times 150 (bar = 100 μ m); 2 a detail showing squamatic ultrastructure, \times 500; note crystallographically controlled cleavage planes of calcite (arrows) in wedges (smaller bar = 10 μ m); 3 transverse fracture of a part of the mammilla showing crystallographically controlled sides of wedges (arrows) and subrhombohedral contour with more loose ultrastructure in the centre of mammilla (dotted line), \times 2000 (right bar = 10 μ m); 4 base of mammilla; note clear structural border (arrows) between radial ultrastructure of secondary spherite (*ss*) and tabular ultrastructure of wedges (*w*), \times 700 (right bar = 10 μ m).
- 5—7. Fossil ratite eggshells; note apparent stratification of eggshell into two layers: a mammillary layer (*ml*) and a single layer (*sl*) with clear borderline between them, and lack of prisms and columns in the single layer — compare with pl. 25: 7—9; pl. 27: 3, 7; pl. 29: 3, 4; an arrow in 7 indicates an angusticanaliculate pore canal which contrasts with rimiform pore canal (*pc*) in 6: 5 thin section of *Aepyornis* eggshell, Holocene, Madagascar, ULM, \times 10; 6 broken surface of moa eggshell, Holocene, New Zealand, SEM, \times 25; 7 thin section of ostrich eggshell (*Struthio asiaticus*), Pleistocene, Transbaikalia, ULM, \times 15.

All in radial view

Plate 38

Ultrastructure of avian eggshell

1. Broken surface of an eggshell of a neognathous bird, ornithoid basic type, prismatic ("neognathous") morphotype. Note apparent structural difference between vesicular squamatic material of spongy layer (*sl*) and wedges (*w*) of mammilla with clear borderline (slit) between wedges (arrows) and vague borders of the column in spongy layer. Recent passerine bird, *Motacilla alba*, $\times 600$.
- 2—5. Ultrastructure of the base of mammilla observed on the eggshell inner surface: 2 radial calcite ultrastructure in secondary spherite, *oc* — site of organic core, Holocene, *Aepyornis* sp., Madagascar, $\times 3000$; 3 organic core with "loculi" and surrounding elements of radial ultrastructure: note first calcitic platy and needle crystals starting their growth from the surface (and within) organic membranes of the organic core (arrows); Recent. *Struthio camelus*, $\times 1800$; 4 platy eisospherites (*es*) with prints of fibres of shell membrane (arrows) and wedges (*w*) in the background. Recent passerine bird, *Oriolus oriolus*, $\times 1000$ (bar = 100 μm); 5 organic cores with loculi after complete demineralization of the bases of mammillae (*glue* in the background); arrows indicate "central spherulithic membrane". Holocene, *Aepyornis* sp., $\times 300$. Treated with 0.1% HCl for 3.5 days.

All in SEM

Plate 39

Eggshells of fossil (1,2) and Recent (3—6) neognathous birds

- 1,2. Broken surfaces in radial views. Note eisospherite (*es*), mammillae (*mm*) with plates of secondary spherite (*ss*) around site of organic core, spongy layer (*sl*) with remnants of squamatic material (*sq*) and compact blocks (*bl*) of external zone (*ez*): 1 Pleistocene, Leningrad region, $\times 640$, 2 Upper Cretaceous, Zaisan Basin (USSR), $\times 200$.
- 3—5. Radial calcite ultrastructure in the base of mammilla, view on inner surface of the eggshell; note sites of decomposed organic cores (*oc*), characteristic corolla of plates of secondary spherite (*ss*) around the cores and bases of wedges (*w*): 3 Pleistocene, Leningrad region, $\times 2000$; 4 Recent tropical cuckoo, *Crotophaga ani*, $\times 900$; 5 Recent penguin, *Aptenodytes forsteri*, $\times 360$.
6. Inner surface of the avian eggshell with eisospherites (*es*) and wedges (*w*). Recent wagtail, *Motacilla alba*, $\times 450$.

All in SEM

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).

