Avian Eggshells: an Atlas of Scanning Electron Micrographs

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This book is dedicated to the memory of Ivan A. Sadov, who was one of the first to recommence comparative studies of avian eggshell structure after the end of World War II.

EDITOR'S FOREWORD

Ornithologists have used the shape and colour of birds' eggs to identify the ownership of nests, discuss crypsis, marvel at parasitic adaptations and theorise about many other evolutionary phenomena. Most such studies have until recently relied on information from superficial characters of the eggs' shells. The advent of the Scanning Electron Microscope (SEM) has permitted the structure of eggshells at very high magnifications to be visualised. Dr Mikhailov has been compiling photographs of these images for many years, with a view to examining what can be learnt from them about the relationships between different groups of birds. He has now synthesised his findings and presents them together with his interpretations of their significance in this Atlas. Whilst some of the conclusions may be controversial, and perhaps lie awkwardly next to phylogenies based on morphological characteristics of the birds themselves or on their DNA, it is a pleasure for the British Ornithologists' Club to publish this book as a major contribution to the current debate on avian taxonomy. That this debate is a lively one was witnessed by the discussions, including Konstantin Mikhailov's own contribution, at the joint meeting between the British Ornithologists' Club and the Linnean Society of London, held in March 1996 and published in the *Bulletin of the British Ornithologists' Club* this year.

The British Ornithologists' Club has a long history of publishing papers on birds. The *Bulletin of the British Ornithologists' Club* has been published without interruption since the founding of the Club in 1892. In the Club's centenary year, 1992, a decision was taken to publish a series of *Occasional Publications* in addition to the *Bulletin*. Consideration was to be given to publishing works of scientific significance which workers or their institutions were unable to finance. *Avian eggshells: an Atlas of Scanning Electron Micrographs* appears as the third title of the series and the first by a worker at a scientific institution outside Britain.

Robert A. Cheke
British Ornithologists' Club

January 1997

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INTRODUCTION

Birds' eggs undoubtedly occupy a special place in ornithology: they have inspired many generations of naturalists to accumulate them in remarkable collections (Walters 1993). These eggs – through the great diversity of their shapes and colours – were always assumed to be of particular use for avian systematics. Indeed they serve well as a simple means for separating some species and genera. However, application of general characteristics of eggs to the higher taxonomy of birds has appeared to be limited, although indices of egg shape are stable at the family level (Preston 1969).

The development of scanning electron microscope (SEM) techniques, enabling the precise imaging in three dimensions of micro-ultrastructures of biocrystalline materials, opened up new possibilities for using bird eggs in taxonomic investigations. Micrographs of the radial (=cross) fractures of avian eggshells are not merely fascinating pictures, but also contain important information on the fundamental biological characteristics of birds. Furthermore, these characteristics have turned out to be stable at order / suborder levels.

Data on microscopic eggshell structures are relevant to problems in understanding embryonic development and may also shed light on taxa-specific microhabitat preferences. For example, eggshells possessing a cuticle, or other covering, protect embryos from microbial and fungal infections, whereas the pore canals are directly exposed to rain-water in eggs whose shells lack a covering. Apparently the only solution which has evolved to cope with this problem is hole-nesting, although some hole-nesters do lay eggs possessing a cuticle. Whether the pore canals pierce the whole eggshell thickness or terminate at some shallower level, is thought to have important implications for the embryo's gas exchange mechanisms.

The purpose of this book is to provide ornithologists with both descriptive and illustrative comparisons of eggshell structures for most of the extant higher bird taxa (traditional orders and suborders). In addition to the taxonomic and ecological implications already mentioned, this data-base can provide comparisons for the identification and classification of fossil avian eggshells. The eggs of most traditionally-accepted extant orders, suborders and families of birds and some fossil material have been studied with SEM and are presented in concise descriptions. The unstudied exceptions include the Mesitornithidae, Heliornithidae, Pedionomidae, Dromadidae, Thinocoridae, Chionididae, Tytonidae, Steatornithidae, Aegothelidae, Hemiprocnidae, Brachypteraciidae, Leptosomatidae, Upupidae, Phoeniculidae, Galbulidae, Bucconidae, Capitonidae, Indicatoridae and some passerine families.

The Atlas is organised simply. It begins with a general outline of basic eggshell structure, and briefly discusses some structural trends in the diversity of avian eggshells. This should familiarise the reader with the subject and make it easier to find a way through the taxonomic section which follows. The latter task is facilitated by the glossary, and abbreviations used in the illustrations are listed. The complete list of all genera and species examined is given in Appendix 1, which also serves as an index. Some quantitative characteristics of eggshell structure are presented as graphs in Appendix 2.

The higher taxonomy of birds is currently in a state of flux and discussion of it is beyond the scope of this Atlas, so I have followed the traditional Wetmore arrangement of avian orders and suborders. Minor changes in this sequence merely relate to the convenience of the comparative descriptions and hopefully will be excused by readers. The species and generic scientific names follow Walters (1980).

Acknowledgements

This long-term work could not have been accomplished without the extensive support of many institutions, oological curators and private researchers who provided me with the comprehensive eggshell material for various higher taxa. I owe special gratitude to the Natural History Museum (Tring), Forschungsinstitut Senckenberg (Frankfurt on Main), Museum d'Histoire Naturelle (Paris), National Museum of Natural History (Smithsonian Institution, Washington), State Darwin Museum (Moscow), Western Foundation of Vertebrate Zoology (Los Angeles), Zoological Museum of Moscow State University and Moscow Zoo. Heartfelt thanks to H. Alvarenga, Ph. Janvier, the late S. M. Kudryavtsev, A. Ya. Kondrat'yev, S. L. Olson, M. Walters, B. Farmer and many other colleagues for their valuable contributions.

Most of the material was studied using the facilities and equipment of the Paleontological Institute of the Russian Academy of Sciences, and partly those of the Geological Department of the University of Bristol. I am grateful to S. Powell, N. Evseyenko and A. Kuzmin for assistance with the SEM and with processing of photographs. This work could not have started or been completed without the encouragement and every possible help from Evgeny N. Kurochkin, and it has been made easier through the kind collaboration of Karl F. Hirsch who sadly died in June 1996. The preparation of the manuscript was supported by PalSIRP grant-1995 and RFBR grant N 96-04-50822. For publishing the SEM-Atlas the author is obliged to the British Ornithologists' Club and is particularly indebted to the special interest shown in this work by Dr. Robert A. Cheke, Chairman of the BOC Publications Committee. My thanks are also extended to Dr. Geoffrey H. Harper for improving my English and to the editorial and printing staff.

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August 1996

PART I

INTRODUCTION TO AVIAN EGGSHELLS

HISTORICAL BACKGROUND

The shell of the avian egg, with its fabric of crystalline and organic structures, has been the subject of scientific enquiry from as early as the beginning of the 19th century (e.g. works of Purkinje and Blasius, see Tyler 1969a). The first to undertake an extensive comparative study of avian eggshells using a light microscope was von Nathusius (1821–1899) (see von Nathusius 1868, 1869 and Tyler 1964a), and Romanoff & Romanoff (1949) summarised a number of studies on eggshell structure from the first half of the 20th century.

During the 1950s and 1960s a series of intensive studies introduced a number of novel techniques (e.g. histostructural, biochemical, petrologic and diffractive methods). Eggshell microstructural research at the time was dominated by the work of Tyler and Schmidt, whose controversial results were discussed in detail by Tyler (1969a). While Schmidt emphasised the crystallographic aspects of eggshell crystalline structure, Tyler examined various physical, histochemical and biochemical attributes of eggshell matter. His results are comprehensive for attributes such as eggshell density (weight per unit area), reactivity to acid etching, nitrogen content, staining reactions of organic matter, and structure of pore canals.

The first results of the investigation of eggshell structure by using scanning and transmission electron microscopy (Erben 1970, Simons 1971) marked a new phase of interest in this aspect of oological research and were soon followed by papers outlining the possibilities of SEM techniques (Becking 1975, Pooley 1979, Board 1982, Mikhailov 1987a,b,c, Solomon 1991). An important contribution to the understanding of avian eggshell adaptive properties was made by Board and his collaborators (Board 1982, Board & Sparks 1991) who also initiated a new SEM-based phase in the comparative investigation of eggshell structures in different bird taxa. A detailed analysis of the distribution of colours within eggshells among avian families was conducted by Harrison (1966), and some comments on eggshell superficial structures were published by Shönwetter (1960).

Interest in fossil avian eggshells has for some time been limited to those of Neogene and Holocene ostriches and other large ratites (aepyornises and moas). Remarkable progress in this field is attributable to the inspirational papers of F. Sauer (Sauer 1972, Mikhailov & Kurochkin 1988, Mikhailov 1992). In addition, intriguingly thick eggshells from the Eocene of France have been described by Dughi & Sirugue (1962). A large number of new avian fossil eggs and their shells have been discovered during the last two decades in the Cretaceous – Tertiary of Asia, Europe and North America (Hirsch 1994, Mikhailov 1996) and these have attracted considerable scientific attention. In particular, numerous eggs of possibly extant bird taxa are known from the Palaeocene-Oligocene of the American Western interior and the Oligocene-Miocene of France and Germany. This material has yet to be examined in detail.

BASIC SHELL STRUCTURE OF AVIAN EGGS

GENERAL REMARKS

As in other amniotic vertebrates which lay hard-shelled eggs, the eggshell of birds starts to grow as a palisade of macro-units which are generally known as *basic shell units* (henceforth termed shell units; Fig. 1). The crystallisation commences from more or less round organic bodies, called the organic cores, and at first develops upwards and downwards, slightly penetrating the upper fibres of the outer shell membrane. In late stages, the shell units grow strictly in one direction, towards the surface of the secretory epithelium of the oviduct. In hens and quails (the only birds studied) the organic cores are secreted and the first stage of mineralization proceeds in the terminal (red zone) part of the isthmus. Most of the shell develops in the next portion of the oviduct known as the shell gland. Further details of chronological and cytological aspects of egg membrane formation in birds (based on studies of *Gallus domesticus*) can be found in Richardson (1935), Fujii (1974), Creger (1976), Georgievsky & Zablotskaya (1974) and Board & Sparks (1991). For possible pathological changes and their causes see Erben (1972) and Solomon (1991).

In contrast to reptilian eggshells (except theropod dinosaurs) the shell units in bird eggs are visible as discrete units (mammillae) only in the lower 1/6–1/2 of eggshell thickness (Fig. 2). Above this level the vertical boundaries of the shell units may be ill-defined or not recognised at all in scanning electron micrographs. The more or less regular mammillae turn out to be overlaid with loosely arranged continuous material (continuous layer in Fig. 1C). This general eggshell arrangement is known as the ornithoid type, and is characteristic of all birds and also theropod dinosaurs (Mikhailov 1992). Structural classifications

Figure 1. General structure and terminology of the avian eggshell (two-dimensional sketches). A realistic view seen in radial section (see Fig. 4): A – in polarised light; B – in non-polarised light; C – in SEM. D – E, squamatic ultrastructure at high magnifications; D – 'fish-bone pattern' superimposed on a pattern of the squamatic shell units; E – organic matrix consisting of large membranes, fine fibrils and vesicles.

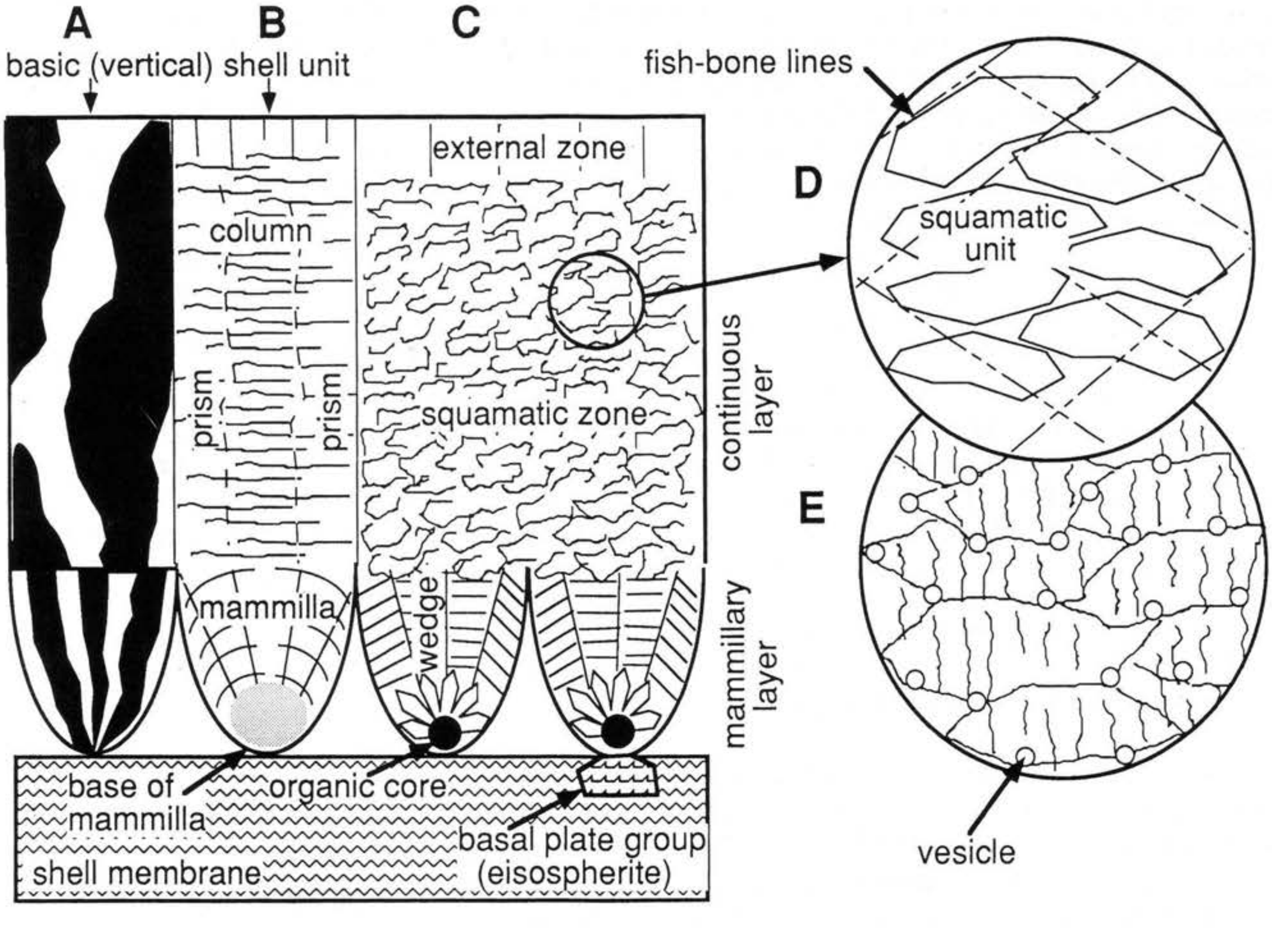
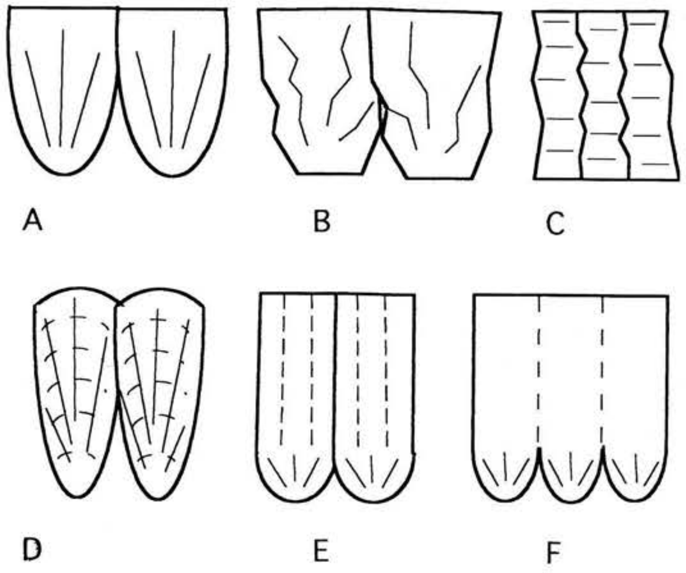


Figure 2. Morphology of basic shell units of sauropsid eggshells in radial section. A – turtles; B – crocodiles; C – geckos; D – sauropod dinosaurs; E – protoceratopsian and hypsilophodontid dinosaurs; F – theropod dinosaurs and birds.



of fossil and recent sauropsid eggshells are summarised in Mikhailov (1991, 1997); illustrated reviews of Recent reptilian eggshells and shell membranes can be found in Packard & Hirsch (1987) and Schleich & Kaestle (1988).

The whole eggshell is pierced by pore canals that enable gas exchange for the embryos. The pore canals can be single (most birds), bifurcating (emu, cassowaries, rheas, moas, swans), or branching in a complicated manner (ostriches, elephant birds). They are generally hollow, but can be plugged or overlaid with organic or amorphous mineral matter (see Accessory material). The formation of these pore canals is intriguing and controversial (Board 1982, Board & Sparks 1991, Mikhailov 1986, 1994) and the porosity of avian eggshells, and its relation to the different aspects of embryo gas exchange, has been the focus of numerous special studies (Carey 1983, Ar & Rahn 1985).

With regard to inorganic components, avian eggshells consist of calcium carbonate in its stable crystallographic form (calcite), which is also true for all reptiles except turtles, the eggs of which contain aragonite (the other, unstable, form of calcium carbonate). Magnesium and phosphates have been found in avian eggshells in residual concentrations (Board & Sparks 1991). For details of the crystallographic analysis of avian eggshells see Erben (1970) and Sauer *et al.* (1975). Taylor (1970) discussed the provision of the growing eggshell with calcium and how this process is regulated.

The crystalline matter, particularly in the continuous layer (i.e. above the mammillae), is penetrated by an ordered continuous network of organic matrix ("spongiosa" of von Nathusius) consisting of rather large membranes, fine fibrils and spherical films (vesicles; Fig. 1E). The organic cores and possibly the strange "triangulars" recognised in the mammillae of some avian eggshells are usually the only macro-organic elements. The organic matrix has a complex muco-polysaccharide-protein composition (Tyler 1969a, Leach 1982) and can absorb liquid plastic (Tyler 1969a). The distribution of the polysaccharides and fats in the shell unit and the amino acid composition of the organic matrix in various taxa of birds have also been examined (Simkiss 1968, Tyler 1969a, Krampitz *et al.* 1972, 1974).

STRUCTURAL ZONES AND LAYERS

In radial sections seen in non-polarised light, and particularly in the scanning electron microscope, the avian eggshell structure is recognised as a sequence of horizontal strata with a specific fine arrangement of biocrystalline material and/or with a differing morphology of the basic shell units in each strata (Fig. 1A,B,C). The strata are distinguished as (micro)structural layers or (ultra)structural zones depending on how sharply they are separated at various magnifications.

The fine arrangement of biocrystalline material appears as a characteristic pattern of figured cleavages (or etching when the eggshell is chemically treated) which cannot be accounted for by the simple crystallography of the calcite, but instead reflects a specific three-dimensional interaction of the mineral component and organic matrix. This arrangement (eggshell ultrastructure) results from the particular cytochemical, biochemical and crystalochemical conditions of biomineralization during consecutive phases of the secretory activity of the oviduct epithelium. Controversies concerning this biomineralization and the nature of crystal-organic interactions in the avian eggshell are discussed by von Nathusius (1868, 1869), Schmidt (1962), Tyler (1969a), Erben (1970), Erben & Newesely (1972), Pooley (1979), Krampitz (1982), Silyn-Roberts & Sharp (1986), Board & Sparks (1991) and Mikhailov (1987a, 1994).

Three general ultrastructural strata can be distinguished in most avian eggshells: a zone of radiating crystallites (mammillary layer), a squamatic zone (zone with squamatic ultrastructure) and an external zone. The name continuous layer (single, prismatic, palisade, spongy layer; see Glossary) is applied to the whole integrated crystalline part of the eggshell above the more discrete mammillary layer and therefore covers both the squamatic and external zones. The tiny portion of the shell unit, which is developed below the organic core between the fibres of the shell membrane, is generally known in avian eggshells as a basal cap or eisospherite. The level of the separate basal caps can be considered as a fourth ultrastructural zone in the shell of the egg. Sometimes two different ultrastructural zones, with radial and tabular ultrastructure, are recognised within the mammillae of some avian taxa (Erben 1970, Mikhailov 1987a, 1991).

ACCESSORY MATERIAL

The sequence of crystallised layers in the shell of the egg is known as a "true eggshell" (Fig. 3). In avian eggs this is usually overlaid with noncrystallised materials, called "covering" or accessory material. When present, these materials also cover the orifices of the pore canals so that the pores usually cannot be seen on the egg surface.

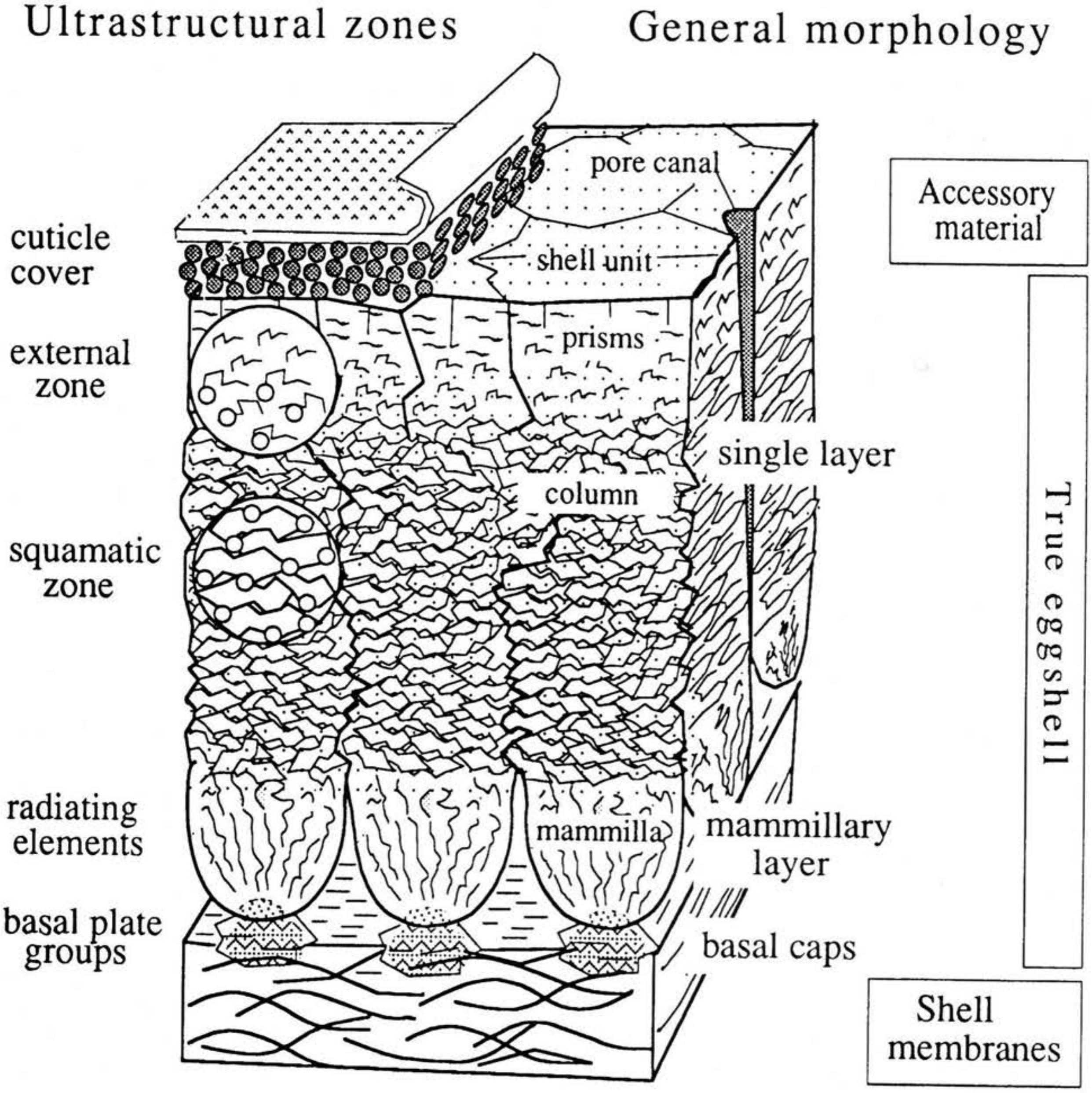
In many avian higher taxa the covering is present only as a thin (1–3 µm) organic cuticle (tegmentum) which is waterproof. However, because of its polysaccharide composition it can easily be consumed by fungi (Board & Fuller 1974, Board 1982). In a few taxa (many species of waders and rails, some auks, geese and bustards) the cuticle is rather thick (5–8 µm). Boiling the egg in a weak alkaline solution, or even in water, results in the cuticle being destroyed and the pores being exposed on the eggshell surface.

The other sort of accessory material, deposited directly on the surface of the true eggshell (always under the cuticle) is a microglobular layer, or "cover". This consists of tiny globules (0.3–1 µm in diameter) either of amorphous calcium carbonate (vaterite) or amorphous calcium phosphate (Plates 2B,D; 3C; 5A,B; 14C,D). Eggs with a thick cover often have a dull chalky surface, some of which can in many cases easily be scratched off with a needle. The cover is clearly absorbent, since eggs with the cover are white when laid, but soon become stained buff or brown by nest material.

A thick (20–100 µm) carbonate cover has been found on the eggs of pelecaniform birds, penguins and non-parasitic cuckoos, while a phosphate cover is present on the eggs of grebes, flamingos, megapodes, curassows and guans. In the other taxa of birds whose eggs possess a cover (Hamerkop *Scopus umbretta* and Shoebill *Balaeniceps rex*) its chemical composition has not yet been analysed, but is likely to be composed of calcium carbonate. In the Boatbill *Cochlearius cochlearius*, egrets and some anseriform and galliform birds (*Egretta*, *Bubulcus*, *Ardeola*, *Anser*, *Branta*, *Cygnus*, *Coscoroba*, *Dendrocygna*, *Anseranas*, *Numida*) only a very thin (1–3 µm) and often discontinuous microglobular covering or its traces (separate patches of microglobules) has been found on the surface of the eggs. Microtraces of granular to globular material, whether under the cuticle or encrusted in it, have been detected in some cranes, caracaras and ibises.

In many cases the microglobular material of the cover not only overlays, but also fills up the funnels of the pore canals (Plate 5B), as well as any gaps on the shell surface, in what are often described as pore "plugs", although no special organic plug material seems to be secreted in the oviduct. This phenomenon is also characteristic of eggs possessing only traces of cover (e.g. some cranes, swans and geese). The prisms of the external zone can also occasionally overlay the developing pore canals during eggshell

Figure 3. General structure and terminology of the avian eggshell (true eggshell and accessory material) in a stylised three-dimensional diagram (see explanations in text and in the Glossary).



formation, and this also results in the deceptive appearance of "crystalline plugs" seen in some eggshell radial sections (e.g. kiwis, rheas and other avian eggs where a dense external zone is formed after an interruption in mineralization).

In two large groups of birds, parrots (Psittacidae) and pigeons (Columbidae), but also possibly in petrels (Procellariidae), swifts (Apodidae) and some auks (Alcidae), the true eggshell lacks any covering, including the cuticle, and the pore canals are directly exposed to the environment of the nest. However, this needs to be checked in fresh material for the open-nesting pigeons and doves, for more species of petrels and swifts and also for hummingbirds and woodpeckers. More detailed data and the sources for the structure of the accessory material can be found in Board (1982), Board & Sparks (1991) and Mikhailov (1995b). The possible adaptive significance of the covering, as an external defence-barrier against microbe and/or fungal intrusion through the pore canals, and the arbitrary classification of avian eggshells in relation to differences in the accessory material, are discussed in Board *et al.* (1977), Board & Perrott (1982) and Board (1982).

VESICULATION

The vesicles (0.3–1.5 μm in diameter) are one of the characteristic elements in the ultrastructure of avian eggshells (Fig. 1E). They are not just air bubbles, but spherical films attached to the fibrils of the continuous network of the eggshell organic matrix (Pooley 1979). The organic fibrils and membranes cannot be detected without chemical treatment of the crystalline matter, but the vesicles are easily recognised in eggshell fractures and form taxon-specific patterns of distribution (vesiculation) in eggshell radial sections. When they occur throughout the eggshell thickness, the vesicles can obscure the horizontal boundaries between structural zones. Striking vesiculation (both large and abundant vesicles) is characteristic of the eggshells of jacanas and parrots (Plates 11E and 13A,B).

DISTRIBUTION OF COLOURS WITHIN THE SHELL THICKNESS

Most of what we know about this subject comes from the data of von Nathusius (Tyler 1964a), Sadov (1940) and especially Harrison (1966). According to Harrison (p. 538), "the only aspect of this pigmentation which appears to be consistent enough to be of possible use in higher taxa is the difference between those species having patterned eggs with superficially applied colour, and those in which pigment patches are present at different depths within the shell". These aspects have been included in the following characterisation of taxa under the heading "Distribution of pigment patches". The different states of this character are: (i) no pigment patches anywhere; (ii) patches of pigment on the egg surface only; (iii) patches of pigment at varying depths within the shell.

TERMINOLOGY AND NOMENCLATURE

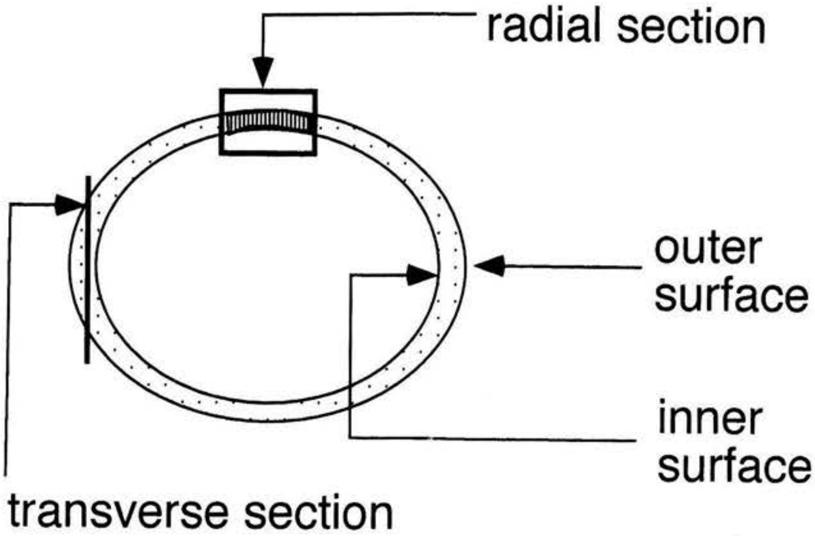
In the history of research on avian eggshells two opposing terminological systems have been developed. The "horizontal" approach, emphasised by von Nathusius in the 19th century (Tyler 1964a, 1969a), reflects recognition of the eggshell as a sequence of layers and zones, while the "vertical" system, developed by Schmidt (Tyler 1969a), reflects recognition of the eggshell as a palisade of large vertical crystals (exospherites or basic shell units) as seen in polarised light (Fig. 1A,B,C). These terminologies are not to be regarded as "old" and "new": each contributes to the general understanding of eggshell biomineralization, but they are also mutually exclusive in some respects concerning eggshell development.

The terminology of von Nathusius is most informative for comparative taxonomic purposes, since the fine arrangement of biocrystalline material is under biological control and the sequence of horizontal strata in avian eggshells differs in various higher taxa. Schmidt's terminology mainly reflects crystallographic regularities in the growth of the eggshell macro-crystals, which is similar in all birds (Mikhailov 1987a). The terminologies clash with respect to the properties of the continuous stratum above the mammillary layer, which is "palisade" (prismatic, column) in terms of eggshell macro-arrangement but "spongy" (i.e. having squamatic ultrastructure) in terms of the three-dimensional interaction of organic and mineral components. Yet the continuous stratum does not always show a clear palisade arrangement, and not all its zones have a squamatic ultrastructure. To avoid confusion it will be referred to by the neutral term *continuous* (or *single*) *layer*. The terms used in this Atlas are summarised in Figs. 1 & 3 and in the Glossary.

METHODS

For the comparative purposes of this study there is no need for any chemical treatment; the boiling of eggshell fragments in weak (5–10%) alkaline solution being required only for special purposes, such as removing the cuticle to examine the orifices of the pore canals. When making comparisons, radial (cross) sections of eggs are the most informative since they exhibit the development of the eggshell material from the earliest (shell membrane) to the latest (egg surface) stages (Fig. 4). The mechanical preparation of eggshell fragments and glueing them to the surface of the stub upon which they are viewed in the Scanning Electron Microscope, are simple procedures although they require some training. The main ways of preparing biocrystalline materials (shells, teeth, bones, scales, etc.) for SEM examination are the same and can be found in many modern handbooks; for sophisticated methods of preparation see Pooley (1979) and Board & Sparks (1991).

Figure 4. Schematic drawing of various sections through the eggshell.



GENERAL TRENDS IN EGGSHELL STRUCTURE WITHIN THE CLASS AVES

Eggshell structure is a taxonomically very stable character. Eggshells of different species within large genera (e.g. *Anas*, *Aquila*, *Calidris*, *Columba*) may differ by no character other than thickness. All genera and subfamilies of one family also have a similar general eggshell structure (the only exception is the Cuculinae within the Cuculidae), but can differ in thickness ratio between structural strata, proportions of the mammillae, some details of the eggshell surface, and the development of the cover. This is also true for most of the traditional avian suborders, within well-defined orders, although there are clear differences between the unrelated orders and the suborders of the less well defined orders. However, these can be united in several structural assemblages.

Generally, at the family level, the relative thickness of the single layer and squamatic zone correlates positively with eggshell thickness. The ratio between the thicknesses of the continuous and mammillary layers (CL:ML), which falls within the range 2–4, can be accepted as normal for neognathes (Figs. 17–19). The smaller eggshell thickness in smaller birds (species) of a genus is usually accounted for by the continuous layer, in particular the squamatic zone (CL:ML ratios may decline from 3:1 to 2:1).

As to the true eggshell, two general structural types can be recognised among avian taxa: the ratite-like and heron-like types (Fig. 5). In the ratite-like eggshells, the continuous layer consists of two distinct and sharply separated ultrastructural zones (SqZ+EZ); the vertical boundaries of the basic shell units are ill-defined or even unrecognisable. In the squamatic zone the scaly elements of the ultrastructure (squamatic units) are mainly large (10–30 µm), regularly shaped (clearly seen) and more or less arranged in a dry-stone-wall pattern (see Plates 1, 8, 9). The external zone is recognised as a separate layer of vertical crystals, very dense (highly translucent in thin sections), and lacking vesicles (Plate 8F). The mammillary layer is also sharply separated from the continuous layer and lacks vesicles. The mammillae are densely packed and exhibit two ultrastructural parts: a small prominent base of the mammilla with radial ultrastructure, and above it highly developed regular wedges with a tabular ultrastructure (Plates 1J, 8H).

This general arrangement of the true eggshell is characteristic of all orders of paleognathe birds as well as anseriform and galliform birds (groups 1 and 15); among extinct groups, it is present in a simpler variant among enantiornithine birds (group 27). A similar arrangement of the continuous layer (but not of the mammillae) can be recognised in the eggshells of penguins and divers and also in those of cuculiform, coraciiform and piciform birds.

In the eggshells of the heron-like type (the "typical" neognathe condition), the palisade macro-arrangement of the continuous layer is very pronounced. In addition, the two zones (SqZ and EZ) of the continuous layer are noticeably less defined and exhibit a gradual ultrastructural transition from one to another (Plates 3A, 4A, 5, 6). The squamatic units of the squamatic zone are clearly less regular and more loosely arranged, often with more abundant vesicles; they never show a dry-stone-wall pattern. The ultrastructure of the external zone is more similar to rather weakly-expressed ("compressed") squamatic material than to the dense and "highly crystalline" material of the ratite-like type. The mammillae in these eggshells do not show a clear subdivision into two ultrastructural parts, and exhibit small radiating elements throughout (Plates 3, 6, 11, 13, 15, 16). The vesicles usually penetrate both the external zone and the upper parts of the mammilla.

Such a "typical" heron-like arrangement of the true shell is characteristic of the eggs of many neognathe birds (herons, ibises, Hamerkop *Scopus umbretta*, Shoebill *Balaeniceps rex*, pelecaniforms, cathartids, falcons, gulls, auks and some others). However, there are also various deviations from this "typical" condition involving the clarity and thickness of the external zone, shape of the mammillae, and the details of the pattern of vesiculation. In some taxa (e.g. cranes, bustards, cariamas, rails) the external zone is still less well defined, while in others (e.g. waders, pigeons, sandgrouse, sunbitterns), it is rather more clearly expressed and exhibits a particular "crystal-splitting" effect (Plates 2G, 11A). In owls, many goatsuckers and parrots the continuous layer generally lacks the external zone; eggshells of parrots and jacanas are also unusual because of the presence of the abundance of large vesicles throughout their structure. In passerine birds, parrots and some other families of mostly arboreal birds, normal squamatic units are replaced by fine-scaled material. There are peculiar ultrastructures (conuli and corimbi) in the eggshells of penguins, divers and grebes (Plate 2B).

Finally, some avian taxa (orders and suborders) exhibit striking and fundamental deviations from both the ratite-like and heron-like conditions. An "aberrant" arrangement of the true eggshell has been found in emus and cassowaries (Casuariiformes), storks (Ciconiidae), hawk-like raptors (Accipitridae and Pandionidae) and hornbills (Bucerotidae; note: Upupidae and Phoeniculidae have yet to be examined in this respect).

Differences in chemical composition of the cover (phosphate or carbonate) apply only to well-defined orders. In cases where the cover is present, all members of a particular taxon (suborder or order) show a predisposition to its development, at least in the form of traces. This implies a phylogenetic basis for this feature (Mikhailov 1995b) in addition to its adaptive significance (Board 1982).

GLOSSARY (see Figs. 1 and 3).

Basic, or vertical, shell unit (shell unit). A basic vertical element of the microstructure in the eggshells of amniotic vertebrates, 0.1–0.5 mm in height and up to 0.5 mm in width. In avian eggshells they are not so clearly recognisable throughout the entire eggshell thickness as in most reptilian eggshells. The vertical shell unit is best seen in polarised light and – with regard to the crystallographic aspects and development of the eggshell structure – is known as an *exospherite* (outward-growing part of the spherocrystal).

Basal cap (basal plate group). An irregularly shaped small body lying below the base of the mammilla within the uppermost fibres of the outer shell membrane; with reference to the crystallographic aspects and development of the eggshell structure it is known as an *eisospherite* (inward-growing part of the spherocrystal).

Column. An extended vertical portion of the basic shell unit above the mammilla; not clearly recognisable in some avian eggshells. The column is roughly polygonal in cross-section, and always lacks a radial arrangement of biocrystalline material (see also *prism*).

Continuous layer. The upper and continuous stratum of mostly scaly biocrystalline material, covering and strictly separated from the mammillary layer (a hiatus in eggshell formation is assumed). The term *single layer* is an unsatisfactory synonym, while *prismatic layer* (*palisade layer*) and *spongy layer* are controversial older terms for the same stratum (see Terminology and Nomenclature).

Conuli. Particular conical microcrystals in the outermost part of the external zone, slightly penetrating the cuticle from below.

Corimbi. Needle microcrystals found in clusters, in the outermost part of the external zone, slightly penetrating the cuticle from below.

Diagenesis. A stage in the transformation of sediment into rock, followed by physico-chemical alterations to the composition of its constituents, including any remnants of organisms, involving dissolution, re-crystallisation and replacement.

External zone. The upper zone of the continuous layer in most modern avian eggshells, sharply separated from or gradually passing into the squamatic zone.

Fish-bone pattern. The pattern of cleavage of the eggshell biocrystalline matter along the crystallographic planes of the calcite. This pattern can be superimposed on the pattern of the squamatic ultrastructure, which it masks to some extent.

Mammilla (cone). A lower, roughly cone-like portion of the basic shell unit with generally radial arrangement of the biocrystalline material; the lowermost part of the mammilla that includes the organic core, often called the *base of the mammilla*.

Mammillary layer. The lower and discrete stratum of separate macro-units (i.e. the mammillae) below the continuous layer.

Oofamily. Name for parafamilies (see below) based on fossil eggs and their shells (see Mikhailov *et al.* 1996).

Organic core (primary spherite). A more or less round organic entity at the base of the mammilla and in contact with the fibres of the outer shell membrane.

Parafamily. Families described in paleontology based on separate parts of organisms rather than on direct taxonomic identifications of known families. A parataxon derives from Greek for near (para) and for an order (taxis).

Prisms. The vertical subunits within the column (assumed to be a continuation of the wedges). In many cases recognised only in polarised light (i.e. as zones of a particular crystallographic orientation).

Radial ultrastructure. The fabric of the biocrystalline material arranged as fine crystallites – needle, prismatic and petal-like in shape – which radiate from the organic core; comprising the entire mammilla or only its base.

Squamatic ultrastructure. The fine fabric of the biocrystalline material that is characterised by a particular scaly pattern called the *squamatic pattern*; the irregular units of these patterns (each 5–30 mm in size) are known as the *squamatic units* (Fig. 1C).

Squamatic zone. The lower zone of the continuous layer with pronounced squamatic ultrastructure; borders the mammillary layer (below) and the external zone (above).

Tabular ultrastructure. The most homogenous ("crystalline") structure of the biocrystalline material with, occasionally, recognisable transverse striations; characteristic of the wedges of the mammillae.

'Triangulars'. Strange triangular structures about 5–30 μm in size, seen in the transverse sections of the mammillae in ratite, galliform and some other eggshells.

Vesicles. Tiny spherical entities unevenly distributed within the eggshell thickness, in particular throughout the continuous layer.

Wedges. Large, robust and regularly shaped radiating subunits of the mammilla in some avian eggshells (in ratite, galliform, anseriform, gruiform birds and some other taxa) where they occupy much of the mammilla.

ABBREVIATIONS

CL	continuous layer
Cov	cover
Cu	cuticle
EZ	external zone
GL	granular layer
McZ	microcanaliculated zone
ML	mammillary layer
RL	resistant layer
SEM	scanning electron microscope
SqZ	squamatic zone
T	eggshell thickness

PART II

TAXONOMIC SURVEY OF SHELL STRUCTURE DIVERSITY WITHIN THE CLASS AVES (HIGHER TAXA: ORDERS – SUBORDERS)

RECENT AND HOLOCENE EGGSHELLS (GROUPS 1–26)

Group 1a

Order Struthioniformes
Order Rheiformes
Order Aepyornithiformes
Order Apterygiformes
Order Tinamiformes

Figs. 5 (p. 15), 6A,D (p. 15), 20 (p. 82); Plate 1A–H (p. 17)

Shell thickness. 0.1–5.0 mm.

Distribution of pigment patches. None.

True shell. Typical ratite-like condition (ML+SqZ+EZ; see General trends). The external zone is a comparatively narrow and clearly separate stratum of vertical crystals (relatively thicker and more discrete in the thinner eggshells of the kiwis and tinamous). The squamatic zone occupies most of the continuous layer; its palisade arrangement is indistinct (*Aepyornis*) or ill-defined (*Struthio*, *Rhea*); the dry-stone-wall pattern is usually clearly shown. The mammillae are very densely packed and with a distinct shape, with strongly developed regular wedges clearly separated from the base of the mammilla with radial ultrastructure (Plate 1J). CL:ML = 2:1 to 3.5:1; in thick ratite eggshells (T = 0.8–5.0 mm) EZ/SqZ = 0.02–0.2 and the mammillae are strong and elongated (h/w = 2–3); in thinner tinamou and kiwi eggshells (T = 0.1–0.3 mm) EZ/SqZ = 0.2–0.6, the mammillae are isomorphic and keg-like in shape (h/w = 1).

Vesiculation. Weakly developed and limited to the squamatic zone; the vesicles are small and sparse.

Accessory material. Only a thin cuticle which lines the complex orifices of the pore canals (Plate 1B). It is the structure of the external zone and the cuticle that make the eggshell surface look very smooth with a glossy appearance like porcelain. Traces of microglobular material have been revealed in the funnels of the pore canals of some tinamou and kiwi eggshells (Board & Perrott 1979a, Board 1982).

Remarks. The pore canals are both single and branching; in the latter case they form complex pore patterns on the egg surface, which are diagnostic for different ratite higher taxa and different species and subspecies of Neogene and Recent ostriches.

Comparison. Most similar to the anseriform and galliform birds (Group 15a,b); sharply differs from the Pelargo-Herodii, Laro-Limicolae and Ralli-Grues divisions.

References. Tyler & Simkiss (1959), Sauer (1966, 1972, 1976), Sauer *et al.* (1975), Sauer & Sauer (1978), Tyler & Fowler (1979), Board & Perrott (1979a), Board (1982), Mikhailov (1986, 1987a, 1988, 1992), Mikhailov & Kurochkin (1988).

Group 1b

Order Casuariiformes
(Casuariidae and Dromaiidae)

Fig. 6C (p. 15); Plate 1I,J (p. 17)

Shell thickness. 0.7–0.8 mm.

Figure 5. General eggshell structure of the heron-like type ("typical" neognathe condition; left) and ratite-like type (right) in three-dimensional diagrams (see explanations in text).

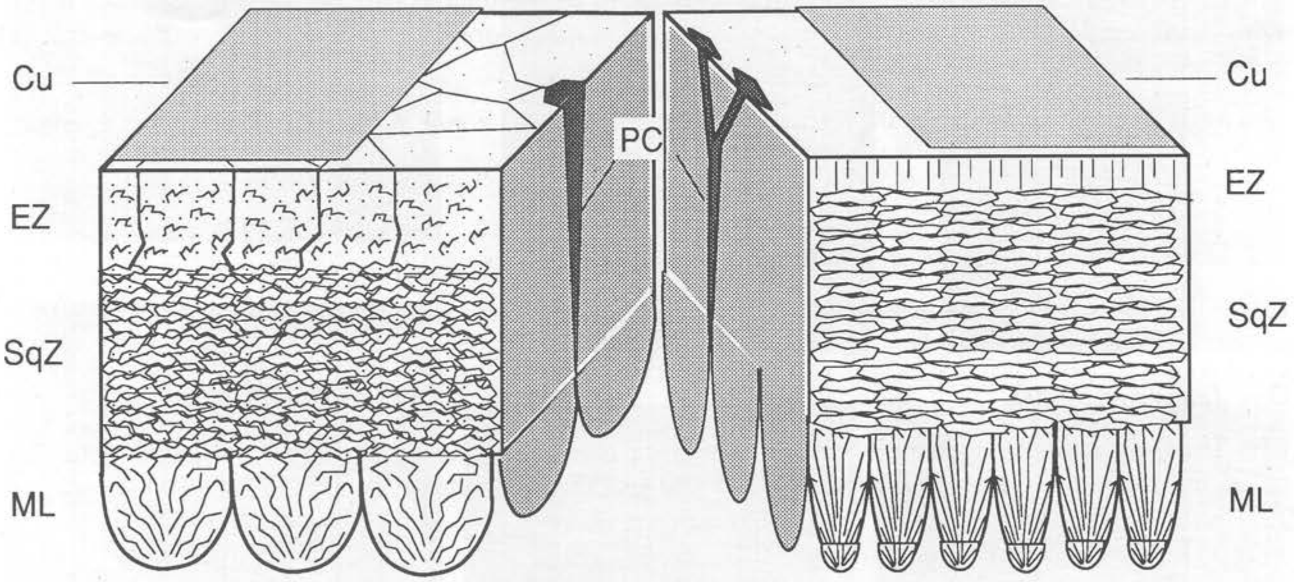


Figure 6. Stylised two-dimensional diagrams of the eggshell structure of the ratite-like type in radial sections: A – Struthioniformes, Rheiformes, Aepyornithiformes (group 1a); B – Dinornithiformes (group 1c); C – Casuariiformes (group 1b); D – Apterygiformes and Tinamiformes (group 1a); E – Enantiornithes (oofamily Laevisoolithidae; group 27); F – theropod dinosaurs (oofamily Elongatoolithidae; for comparison).

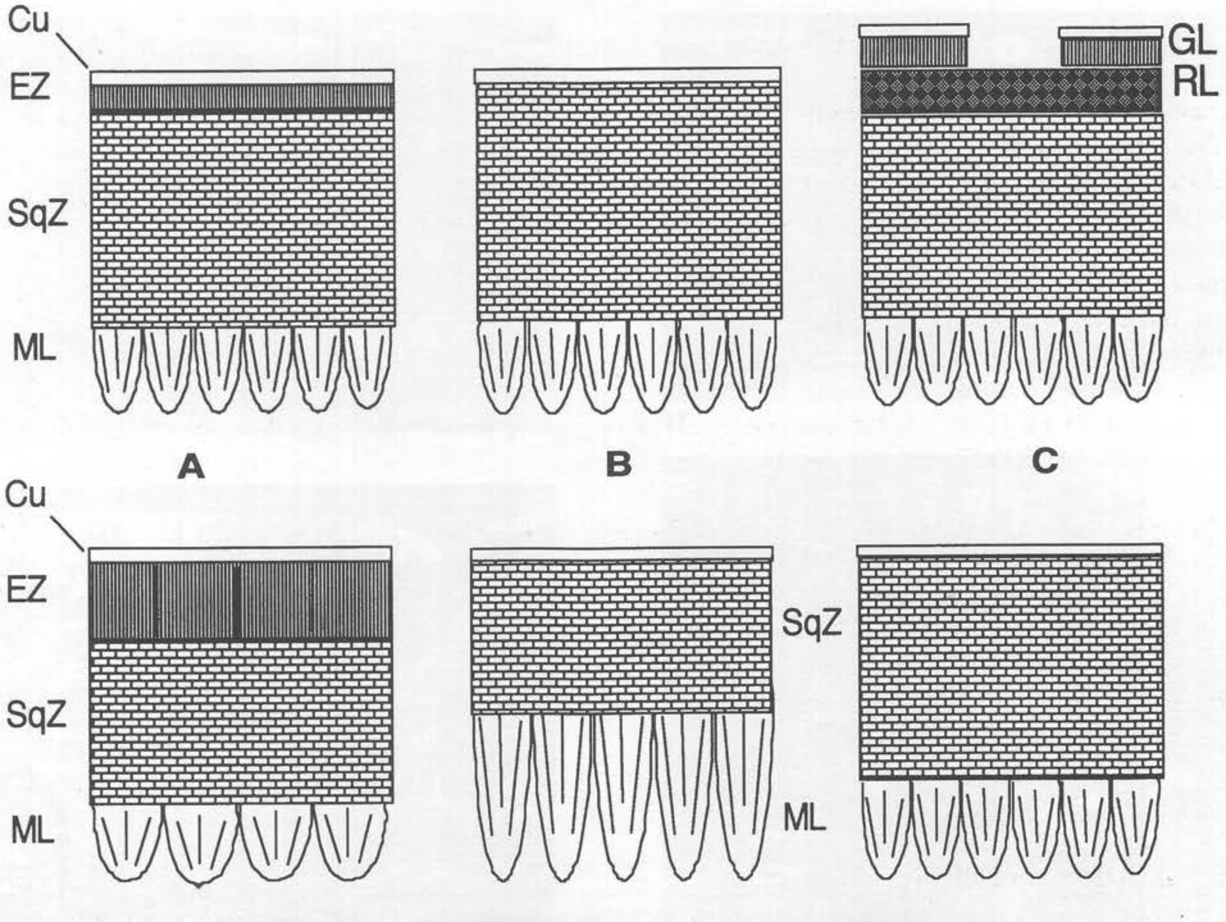


Plate 1. Eggshell structure in the ratites (groups 1a–c) (A,D,E,G,H,I – radial fractures, general view).

A,B – *Struthio camelus*: A – note branching pore canal in the middle part of the eggshell, ×20; B – a view (at an angle) of the polished radial surface: branching pore canals form a distinctive rosette of grooves on the shell surface, ×300;

C – *Rhea americana*; thin layer of vertical crystals (the external zone) in the outer part of the eggshell, ×500;

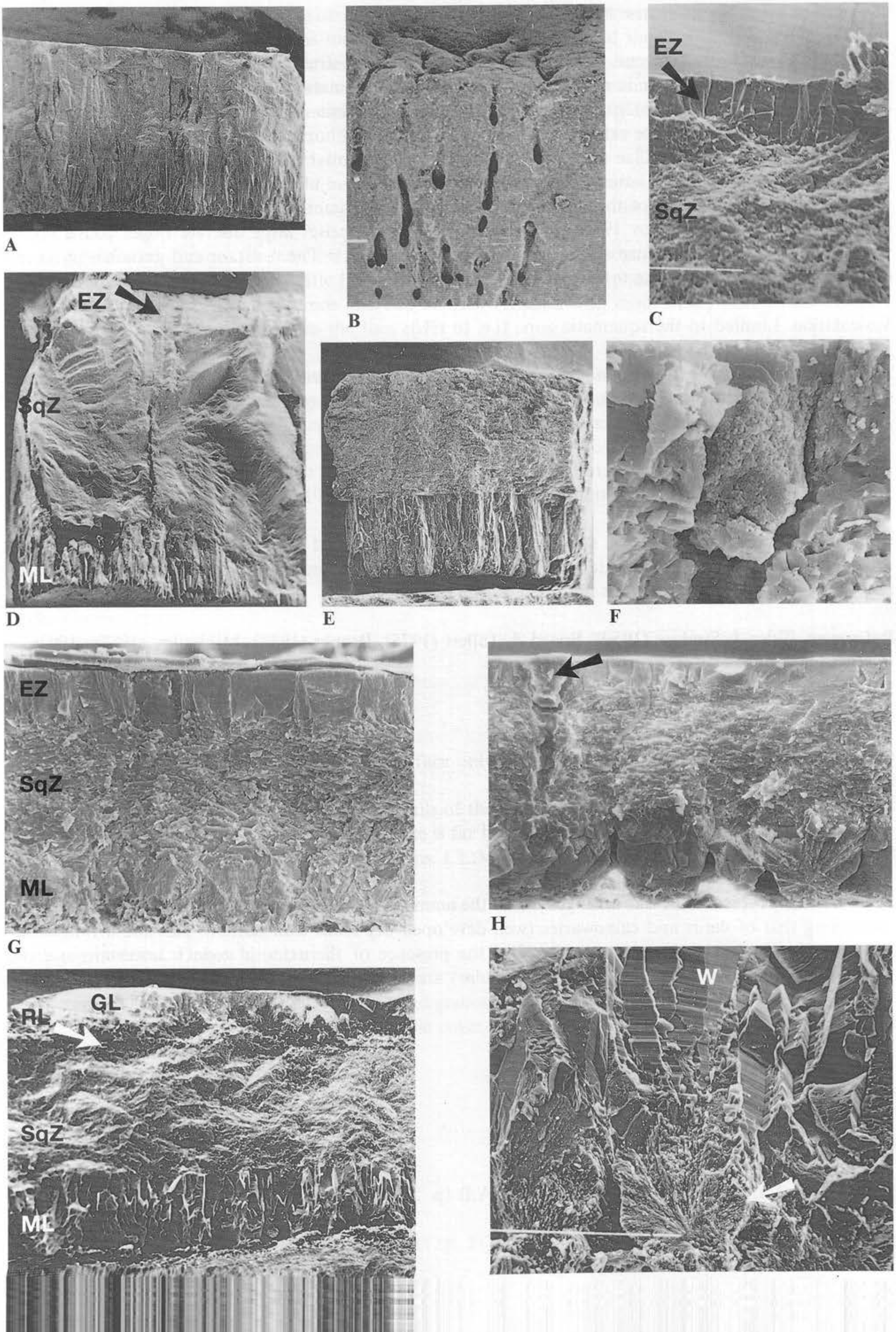
D – *Aepyornis* sp., ×10;

E – *Moa* sp. (?*Anomalopteryx* sp.), ×30;

F,H – *Tinamus* sp.: F – enlargement of H; note the plug within the orifice of the pore canal at the level of the external zone, ×1300, H – ×200;

G – *Apteryx* sp., ×200;

I,J – *Dromaius novaehollandiae*: I – ×30: J – the lower part of the mammilla; note a spherulite with fine radial ultrastructure (arrow) below more solid wedges (W) with tabular ultrastructure, ×500.


A
B
EZ
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EZ
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ML
D
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SqZ
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G
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GL
RL
SqZ
ML
W

Distribution of pigment patches. None.

True shell. Most 'deviant' variant of the ratite eggshell, with four structural layers (ML + CL + two other strata). The continuous layer is entirely composed of the squamatic ultrastructure (i.e. = SqZ) and is overlain by the unique "resistant layer" which is, in turn, overlain by the "granular layer" (possibly a peculiar transformation of the external zone of other ratites); all horizontal boundaries are pronounced. The structure of the mammillae and the continuous layer is similar to Group 1a, with no recognisable palisade arrangement in the latter. The resistant layer has a loose ultrastructure, rich in organic matter and consisting of aggregates of the crystalline plates and large organic bodies which resemble the organic cores (see Fig. 2 in Mikhailov 1987c). The granular layer comprises large discrete ridges consisting of vertical crystals; it is very dense and lacks vesicles. CL:ML = 3:1. The resistant and granular layers are equal in thickness, both being 0.1 of the squamatic zone.

Vesiculation. Limited to the squamatic zone (i.e. to CL).

Accessory material. Only a thin cuticle. Due to the macro-arrangement of the granular layer, the eggshell surface shows a particular network-like pattern of dense vermiform warts between which the parts of the greenish resistant layer can be seen clearly.

Remarks. The pore canals are generally bifurcating and do not reach the shell surface, terminating instead at the boundary between the continuous and resistant layers.

Comparison. In all aspects of the structure of the mammillary and continuous layers these are typical ratites, but the structure of the external zone (i.e. granular layer) and the presence of the resistant layer easily separate both families from the other Ratitae.

References. Tyler & Simkiss (1959), Board & Tullett (1975), Penner (1984), Mikhailov (1987c, 1992).

Group 1c

Order Dinornithiformes

Fig. 6B (p. 15); Plate 1E (p. 17)

Shell thickness. 0.9–>1.0 mm.

Shell structure. Typical ratite-like arrangement of the mammillary layer and the squamatic zone, particularly resembling that of emus and cassowaries (well developed dry-stone-wall pattern, palisade arrangement not recognisable, bifurcating pore canals). But the presence of the external zone is uncertain and the peculiar structural layers (e.g. resistant or granular) are absent. CL:ML = 2.5:1.

References. Tyler (1957), Mikhailov (1992).

Group 2

Order Sphenisciformes

Figs. 7A (p. 22), 24 (p. 83), 25 (p. 84); Plate 2A,B (p. 21)

Shell thickness. 0.6–0.9 mm.

True shell. The continuous layer consists of two distinct and sharply separated ultrastructural zones (SqZ + EZ). The squamatic zone occupies most of the continuous layer, and shows a dry-stone-wall pattern of large squamatic units and an ill-defined palisade arrangement. The external zone is seen as a thin and dense layer of vertical crystals; certain ultrastructures – the conuli and corimbi – are characteristic of its outermost region (Plate 2B). The mammillae are keg-like in shape, sharply separated from the continuous layer and more loosely packed than in Group 1, and do not exhibit a clear subdivision into two ultrastructural parts. CL:ML = 3.5:1 to 4:1; EZ / SqZ = 0.1.

Vesiculation. Expanded from the squamatic zone to both the external zone and upper parts of the mammillae.

Accessory material. Besides the cuticle a thin (2–10 μm) ?carbonate microglobular cover clearly separated from the external zone is characteristic (Plate 2B). Because of the amorphous cover, the eggshell surface is dull white and chalky in appearance and can be easily stained with mud. Many pore canals contact with the air through large fissures in the thin cover.

Comparison. In the structure of the mammillae and the squamatic zone this group is similar to the grebes and divers, but is fairly easily distinguishable by the details of the external zone (from divers) and by the features of the microglobular cover (from grebes); does not show any particular similarities with procellariiform birds and the Pelargo-Herodii and Laro-Limicolae divisions.

References. Tyler (1965), Schmidt (1968a).

Group 3

Order Gaviiformes

Figs. 7B (p. 22), 25 (p. 84)

Shell thickness. 0.2–0.5 mm.

Distribution of pigment patches. On eggshell surface only.

True shell. The general arrangement and the details of the mammillae and the squamatic zone are similar to those of the previous group. The external zone is far better developed (1/4–1/6 T), exhibits very dense ultrastructure, and consists of rather large prisms. CL:ML = 2.5:1.

Vesiculation. Limited to the squamatic zone.

Accessory material. Only a thin cuticle.

Comparison. This group differs from penguins and grebes in the development and structural details of the external zone and in the complete absence of the cover.

Reference. Tyler (1969b).

Group 4

Order Podicipediformes

Figs. 7C (p. 22), 8 (p. 23), 25 (p. 84); Plate 2C,D (p. 21)

Shell thickness. 0.2–0.3 mm.

Plate 2. Eggshell structure in penguins, grebes and procellariiforms (groups 2,4,5) (A,C,E,F,G – radial fractures, general view).

A,B – *Aptenodytes forsteri*: A – ×50; B – a thin layer of microglobules (arrow) above the external zone and in the mouth of the pore canal, ×350;

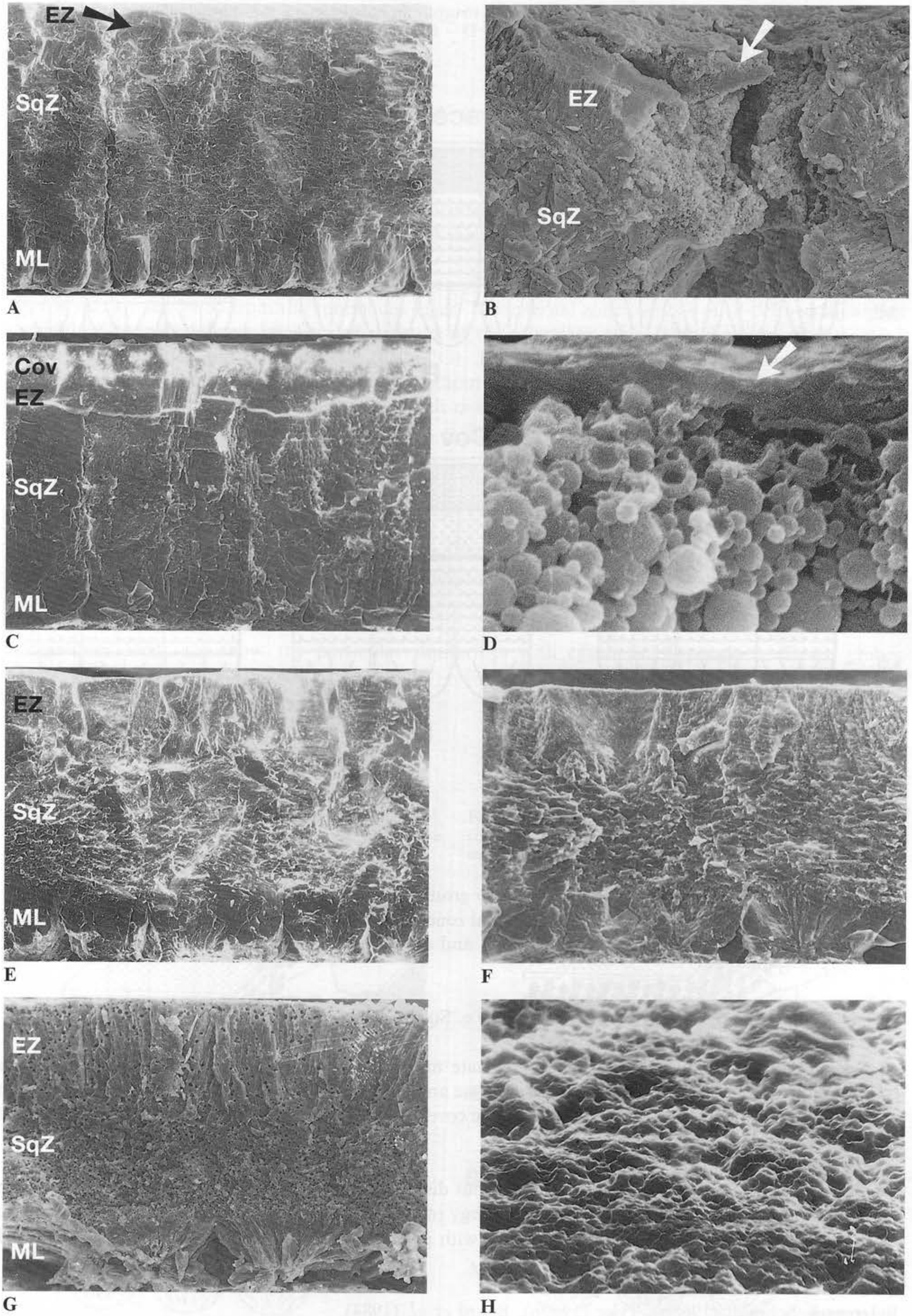
C,D – *Podiceps cristatus*: C – ×200; D – details of C: microglobular cover below the cuticle (arrow), ×7000;

E – *Diomedea nigripes*, ×100;

F – *Puffinus puffinus*, ×200;

G – *Pelecanoides georgicus*, ×400;

H – *Fulmarus glacialis*: the eggshell surface lacks cuticle and the vesicular fine-scaled material of the external zone is clearly seen, ×2800.


EZ
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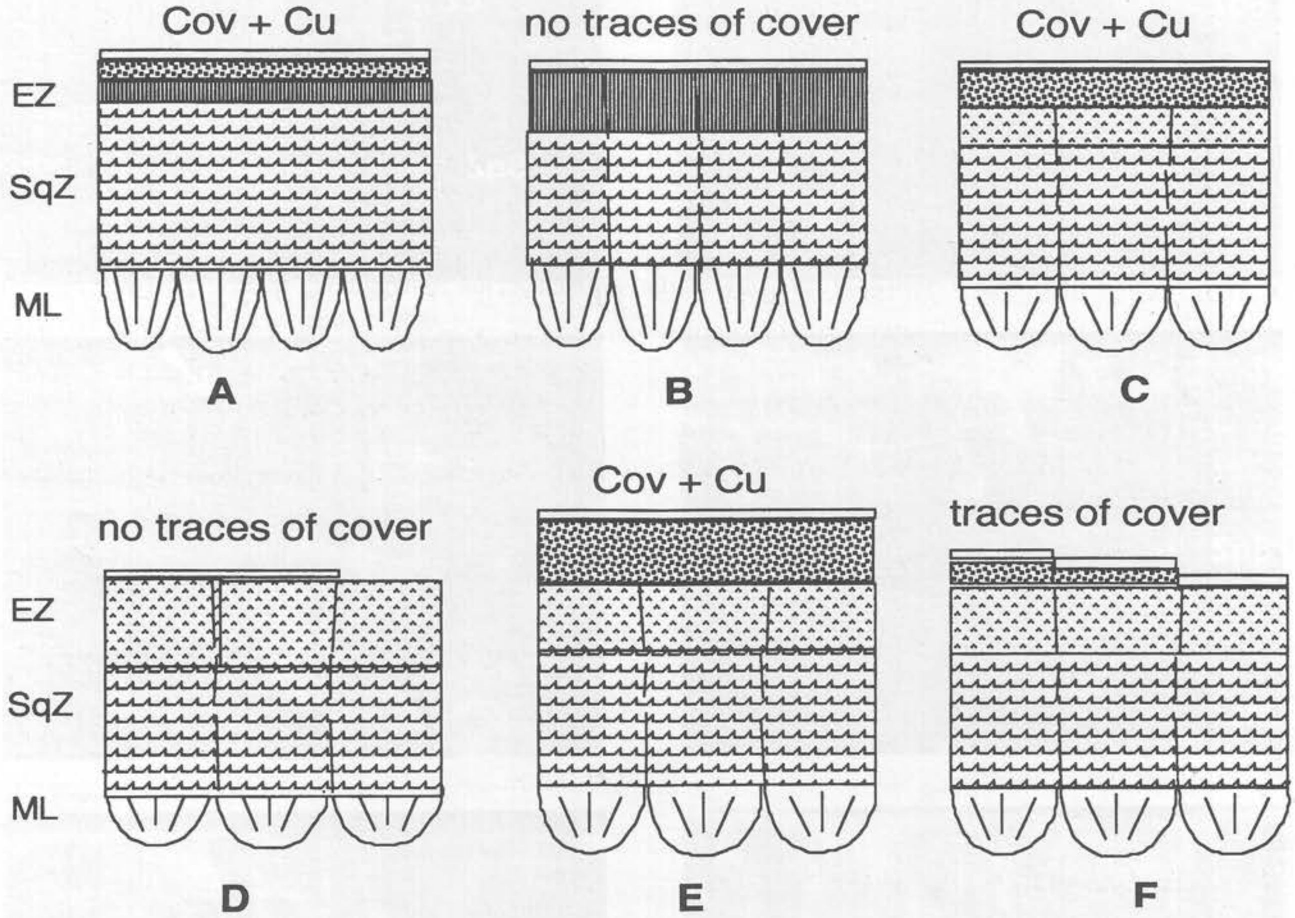
G
H

Figure 7. Stylised two-dimensional diagrams of eggshell structure in radial section: A – Sphenisciformes (group 2); B – Gaviiformes (group 3); C – Podicipediformes (group 4); D – Procellariiformes (group 5); E – Pelecaniformes (group 6; except Phaethontidae); F – Ardeae (group 7).



Distribution of pigment patches. None.

True shell. In general similar to the previous two groups except that the squamatic zone lacks a distinct dry-stone-wall ultrastructural pattern. The external zone is relatively thin, consists of small vertical crystals, and exhibits an outermost microlayer of conuli and corimbi (as in penguins). CL:ML = 3:1 to 3.5:1; EZ / SqZ = 0.2.

Vesiculation. Throughout the continuous layer (i.e. SqZ + EZ).

Accessory material. A thick (30–40 μm) phosphate microglobular cover, plus a thin cuticle. The close interaction between the crystals of the external zone and the amorphous material of the cover (no hiatus) is very characteristic of this taxon. Because of the cover, the surface of grebe eggs appears dull white and is easily stained with nest material.

Comparison. Most similar to penguin eggshells, but distinguished by the thicker cover and details of the structure of the true eggshell (different morphology of the mammillae and the pattern in the squamatic zone); does not show any particular similarities with procellariiform birds and the Pelargo-Herodii and Laro-Limicolae divisions.

References. Schmidt (1968b), Tyler (1969b), Board *et al.* (1984).

Group 5

Order Procellariiformes

Figs. 7D (p. 22), 23 (p. 83), 24 (p. 83); Plate 2E–H (p. 21)

Shell thickness. 0.08–0.5 mm.

Distribution of pigment patches. None in Procellariidae and Pelecanoididae; on the egg surface only in some Diomedeidae; at varying depths of eggshell thickness in Hydrobatidae.

True shell. The continuous layer consists of two zones (SqZ + EZ), not sharply separated; the mammillary layer is sharply separated from the continuous layer. The external zone consists of ill-defined squamatic material (cf. sharply defined, large-scaled structure of the squamatic zone), with a crystal-splitting effect in the Pelecanoididae and Hydrobatidae (Plate 2G). The mammillae are distinctively flattened, highly "crystallised" (very translucent in thin section, without any darkening effect) and loosely arranged; with an homogenous ultrastructure consisting of small radiating crystallites (cf. groups 1–4); occupies 1/3–1/4 of eggshell thickness. CL:ML = 1 to 4:1; EZ = SqZ (Procellariidae, Pelecanoididae, Hydrobatidae) or EZ / SqZ = 0.6 (Diomedeidae).

Vesiculation. Abundant throughout the continuous layer; completely absent from the mammillae.

Accessory material. Neither cover nor cuticle found in petrel, shearwater, storm-petrel and diving-petrel specimens studied; but the cuticle is possibly present in albatross eggshells. More additional fresh material should be carefully checked.

Comparison. Does not show any particular similarities with eggshells of penguins, divers, grebes, pelecaniform and ciconiiform birds.

References. Tyler (1969b), Board (1982).

Figure 8. Stylised three-dimensional diagram of eggshell structure in grebes (group 4), with a thick phosphate cover.

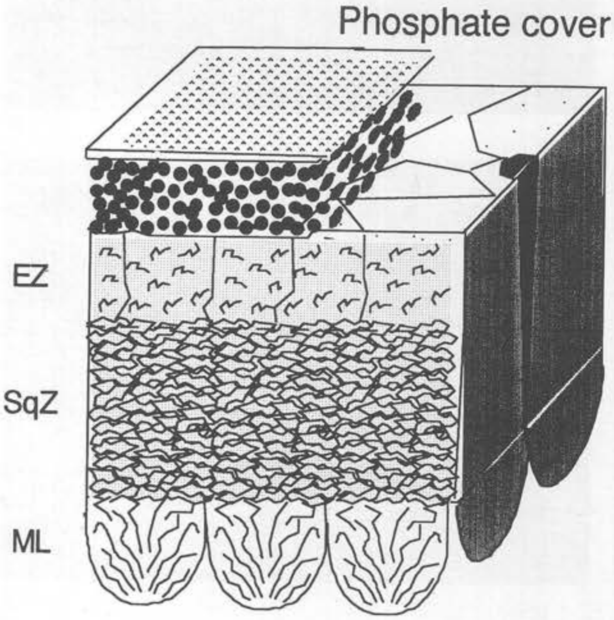


Figure 9. Stylised three-dimensional diagram of eggshell structure in pelecaniform birds (group 6), with a thick carbonate cover (except tropic-birds).

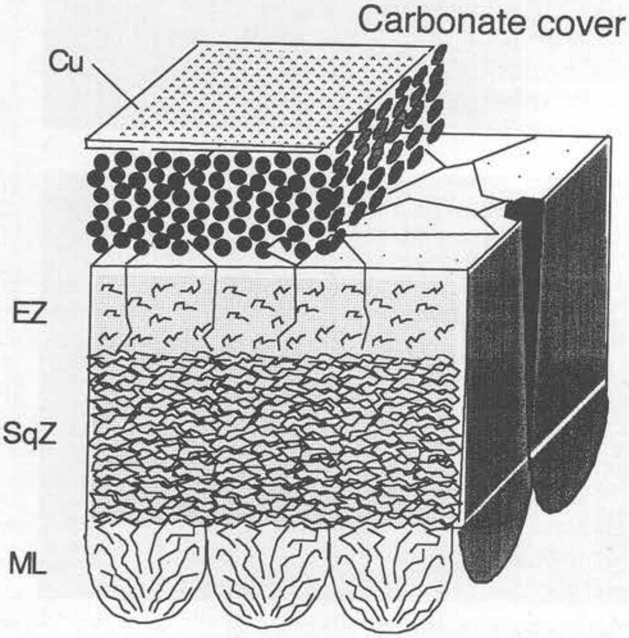


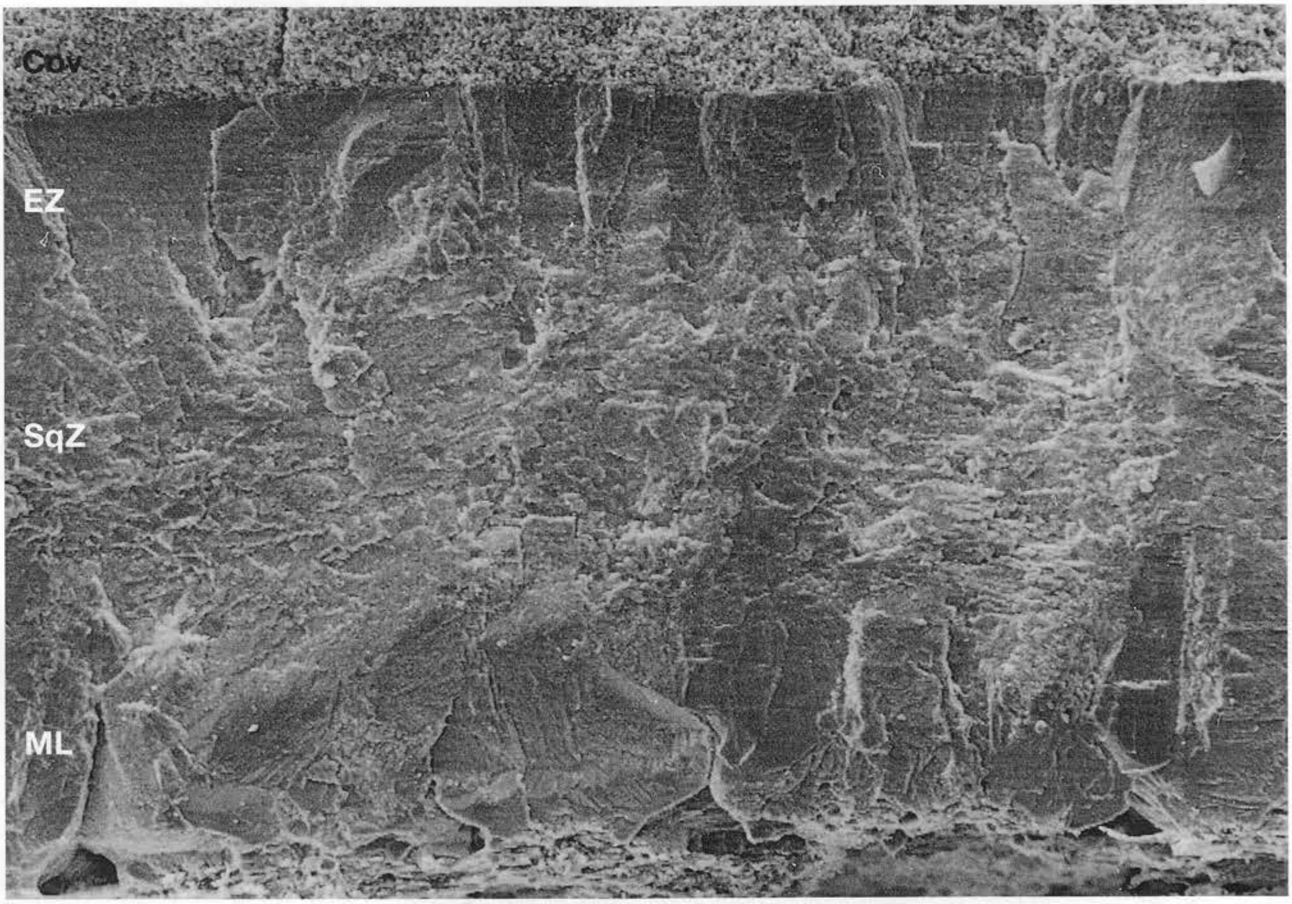
Plate 3. Eggshell structure in pelecaniforms (group 6) (A,B,C – radial fractures, general view).

A – *Sula leucogaster*, ×300;

B,C – *Phalacrocorax auritus*, B – ×170; C – ultrastructure of microglobular cover, ×1200;

D – *Fregata minor*: a chalky appearance of the eggshell surface possessing cover (view from above), ×170;

E – *Phaethon rubricauda*: note development of the prisms and absence of cover, ×170.



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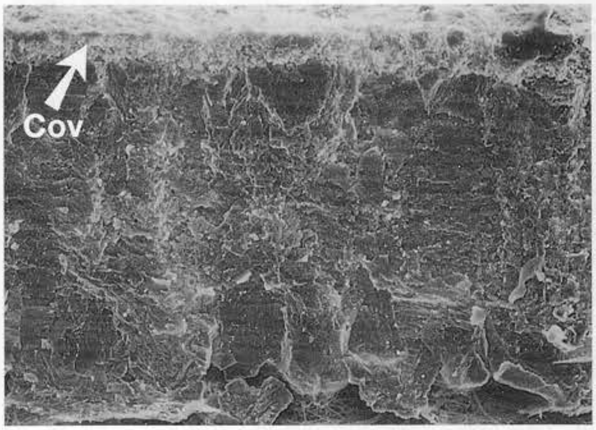

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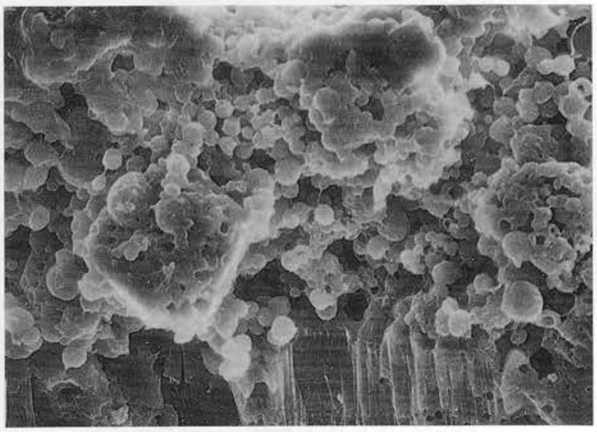

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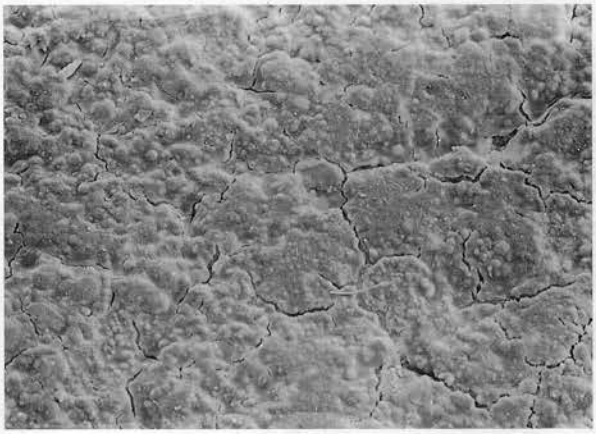
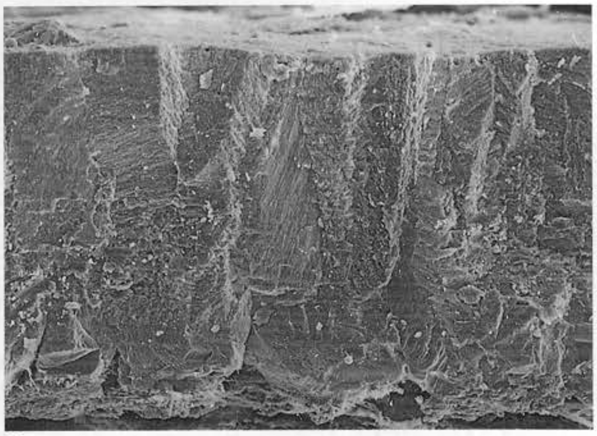


D



E

Group 6

Order Pelecaniformes

Figs. 7E (p. 22), 9 (p. 23), 10A (p. 27), 22 (p. 83), 23 (p. 83); Plate 3A–E (p. 25)

Shell thickness. 0.15–0.4 mm.

Distribution of pigment patches. None in Pelecanidae, Fregatidae, Sulidae and Phalacrocoracidae; tiny surface patches in Phaethontidae; at varying depths within the shell in Anhingidae.

True shell. Of heron-like type (see General trends). The palisade arrangement of the squamatic zone is fairly pronounced and the mammillae are isomorphic (h/w = 1; 1/4 of T) or slightly flattened. CL:ML is generally about 2:1 to 3:1 (1.5:1 in Anhingidae); EZ / SqZ generally about 0.3–0.5 (0.2 in Fregatidae and 0.7 in Phaethontidae).

Vesiculation. Throughout the continuous layer.

Accessory material. A thick to very thick carbonate microglobular cover (30–60 μm; 0.1–0.3 of T) plus a thin cuticle (Plate 3A–D). The cover is sharply separated from the external zone (a hiatus in ultrastructure; cf. grebes). Exceptions are the tropic-birds (Phaethontidae), the eggshell of which lack a cover or cover traces can be found only occasionally, rather as an aberration (Mikhailov 1995b). The cover gives the eggshell surface a crumbled, chalky, appearance.

Comparison. Easily distinguished (except Phaethontidae) from most aquatic and shore-birds and raptors by the presence of a cover; from anseriforms, galliforms and penguins also by the general (heron-like) arrangement of the true eggshell; from grebes and flamingos by the details of structure and different chemical composition of the cover.

References. Tyler (1969b), Tullett *et al.* (1976), Board (1982), Mikhailov (1995b).

Group 7

Families Ardeidae and Cochlearidae
(Ciconiiformes: Ardeae)

Figs. 5 (p. 15), 7F (p. 22), 10C (p. 27); Plate 4A (p. 29)

Shell thickness. 0.1–0.2 mm.

Distribution of pigment patches. None.

True shell. "Typical" neognathe condition (see heron-like type in the General trends). The external zone differs from the squamatic zone only in the fine characteristics of the squamatic material (more dense and weakly-scaled in the former, looser and larger-scaled in the latter) and narrower and more numerous prisms. CL:ML = 2.5:1 to 3:1; EZ / SqZ = 0.7–1.0.

Vesiculation. Throughout the eggshell thickness except for the bases of the mammillae.

Accessory material. Only a thin cuticle in herons and night herons (*Ardea*, *Tigrisoma*, *Botaurus*, *Butorides*, *Ixobrychus*, *Nycticorax*), or with traces of the ?carbonate microgobular cover, or developed into a distinctive thin layer, in egrets (*Egretta*, *Ardeola*) and the Boatbill *Cochlearius*. Note that the pale blue colour of many egret eggs is a result of the thin-coating of the clear blue tint of the true eggshell by cover traces.

Comparison. The "typical" neognathe condition of true ardeiform eggshells are closely comparable with many other avian taxa (e.g. pelecaniforms, falcons, ibises; Hamerkop *Scopus umbretta*); on the other hand, it shows no particular similarities with the eggshells of storks (Ciconiidae) and flamingos (Phoenicopteridae).

References. Mikhailov (1995a,b).

Figure 10. Stylised two-dimensional diagrams of eggshell structure in radial section: A – Pelecaniformes (except Phaethontidae) and Balaenicipitidae (groups 6 and 11); B – Scopidae (group 9); C – Ardeae (group 7); D – Grues (group 16a; see also groups 16b, 16c, 16f, 16g); E – Charadrii (group 17a; see also groups 16d and 16h); F – Threskiornithidae (group 8); G – Phoenicopteriformes (group 12); H – Anseriformes (group 15a, for comparison); I – Ciconiidae (group 10).

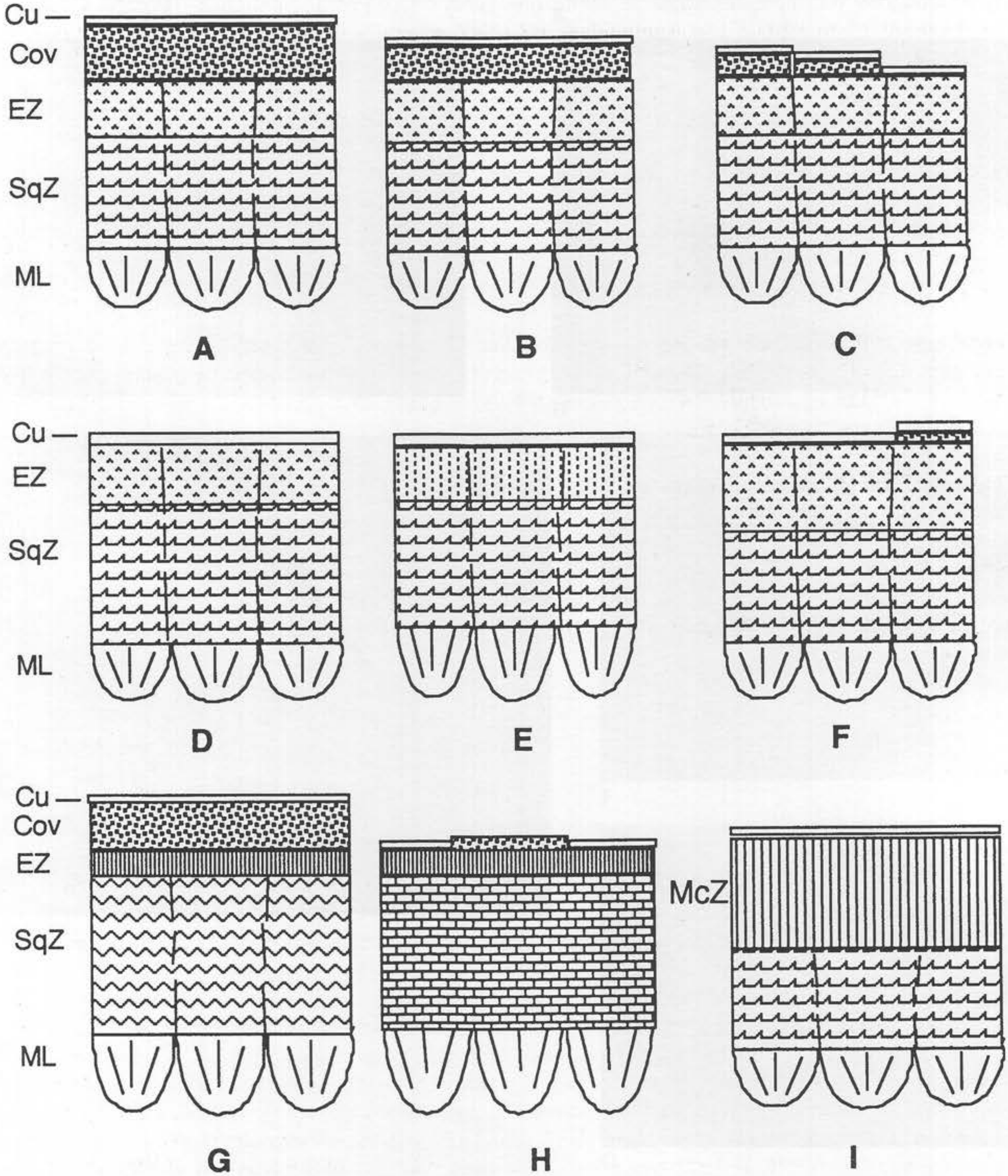


Plate 4. Eggshell structure in ciconiiforms (groups 7,8,10) (A–C,E–G – radial fractures, general view).

A – *Syrigma sibilatrix*, ×300;

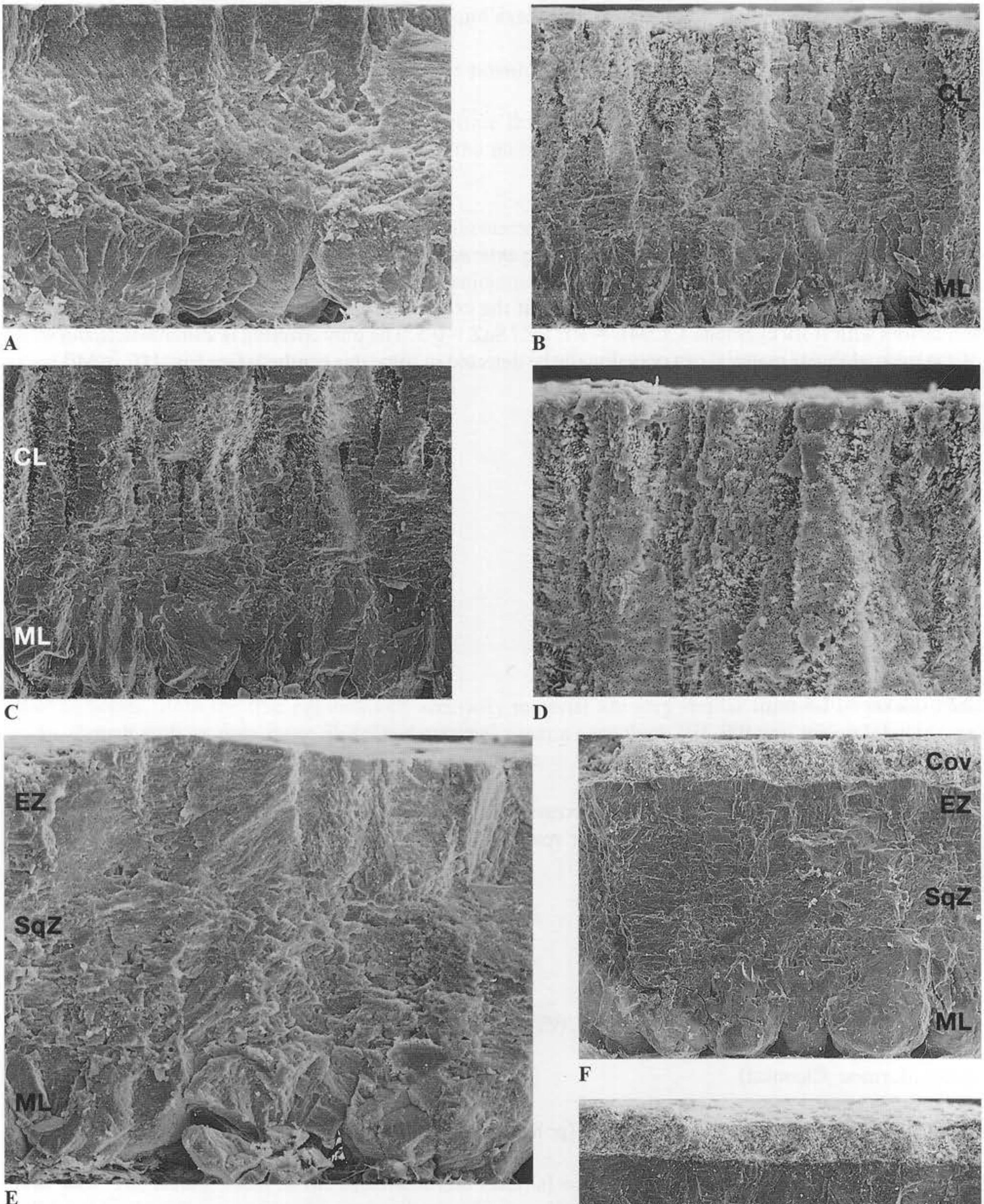
B,D – *Mycteria leucocephala*, B – ×130; D – enlargement of B: note the microcanals in the continuous layer, ×300;

C – *Leptoptilos dubius*, ×120;

E – *Threskiornis aethiopicus*, ×250;

F – *Phoenicopterus ruber*, ×100;

G – *Palaelodus* sp., ×100.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Group 8

Family Threskiornithidae
(Ciconiiformes: Ciconiae)

Fig. 10F (p. 27); Plate 4E (p. 29)

Shell thickness. 0.2–0.3 mm.

Distribution of pigment patches. Throughout the external zone.

Shell structure. Similar to the previous group, but the external zone is often larger; exhibits no particular similarities with stork eggshells. CL:ML = 3:1; EZ / SqZ = 0.5. The only covering is a thin cuticle, but traces of the microglobular material can occasionally be detected in some ibis eggshells (see Fig. 11C in Mikhailov 1995b).

References. Mikhailov (1995a,b).

Group 9

Family Scopidae
(Ciconiiformes: Ciconiae)

Fig. 10B (p. 27); Plate 5A (p. 33)

Shell thickness. 1.5 mm.

Distribution of pigment patches. None.

Shell structure. Both the true eggshell and accessory material are very similar to those of egrets (Ardeidae); a rather thick (30 μm) microglobular cover results in the white non-crystallised appearance of the egg surface.

References. Mikhailov (1995a,b).

Group 10

Family Ciconiidae
(Ciconiiformes: Ciconiae)

Figs. 10I (p. 27), 22 (p. 83), 26 (p. 84), 27 (p. 84); Plate 4B–D (p. 29)

Shell thickness. 0.25–0.5 mm.

Distribution of pigment patches. None.

True shell. The continuous layer consists of two ultrastructurally ill-defined zones with a gradual transition from clearly-scaled to weakly-scaled squamatic material. The upper zone is remarkable for the numerous microcanals, which exhibit a peculiar brush-needle structure, in its inner walls (Plate 4D). The mammillary layer is clearly separated from the continuous layer and the mammillae are strong and elongated (h / w = 1.5–2), consisting of regularly shaped wedge-like elements, but without a subdivision into two ultrastructural parts. CL:ML = 2.5:1; EZ / SqZ = 1.5:1.

Vesiculation. Throughout the continuous layer and extending to the upper parts of the mammillae.

Accessory material. Only a thin cuticle which is possibly absent from some parts of the egg.

Remarks. Most of the pore canals do not penetrate the upper microcanaliculate zone, and above it the aeration of the egg must generally depend on the numerous microcanals that are exposed on the shell surface as bunches of micropores.

Comparison. The development of the microcanaliculated zone is very unusual for the class Aves (see also groups 14 and 24). This group does not show any particular similarities in eggshell structure with Ardeidae, Threskiornithidae, Scopidae or Balaenicipitidae.

References. Mikhailov (1995a,b).

Group 11

Suborder Balaenicipites
(Ciconiiformes: Balaenicipitidae)

Fig. 10A (p. 27); Plate 5B (p. 33)

Shell thickness. 0.5 mm.

Distribution of pigment patches. None.

Shell structure. Both the true eggshell and accessory material are very similar to those of pelecaniform birds, though with an even more ill-defined external zone; a very thick (60–100 µm) microglobular cover results in a rough chalky appearance of the egg surface.

Reference. Mikhailov (1995b).

Group 12

Order Phoenicopteriformes
(Phoenicopteridae and Palaelodidae)

Figs. 10G (p. 27), 26 (p. 84), 27 (p. 84); Plate 4F,G (p. 29)

Shell thickness. 0.3–0.5 mm.

Distribution of pigment patches. None.

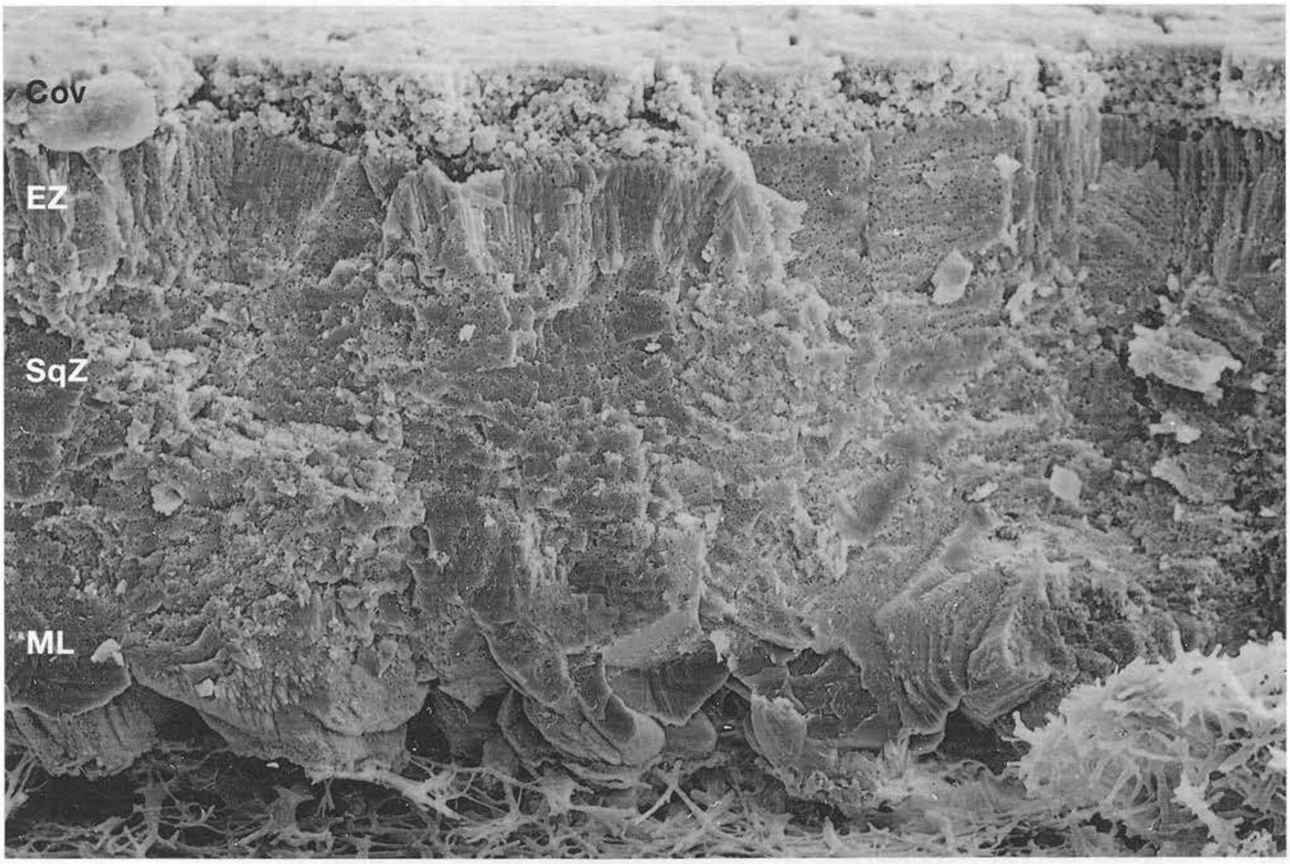
True shell. The arrangement of the squamatic and external zones is very similar to that of anseriform and galliform birds (EZ appears as a separate layer of vertical crystals and has no vesicles; pronounced dry-stone-wall pattern of the squamatic units; cf. group 15). The structure of the mammillae is similar to that of gruiform birds (no clear subdivision into two ultrastructural parts; vesicles penetrate the upper parts of the mammillae; the boundary between the mammillary and continuous layers is rather obscure). CL:ML = 3:0; EZ / SqZ = 0.1–0.2.

Accessory material. Besides the thin cuticle, there is a very thick phosphate microglobular cover (50–60 µm; 0.1 T) sharply separated from the external zone (cf. grebes and pelecaniform birds). Because of the cover the egg surface appears non-crystalline and chalky-white. The pore canals are overlain by the cover.

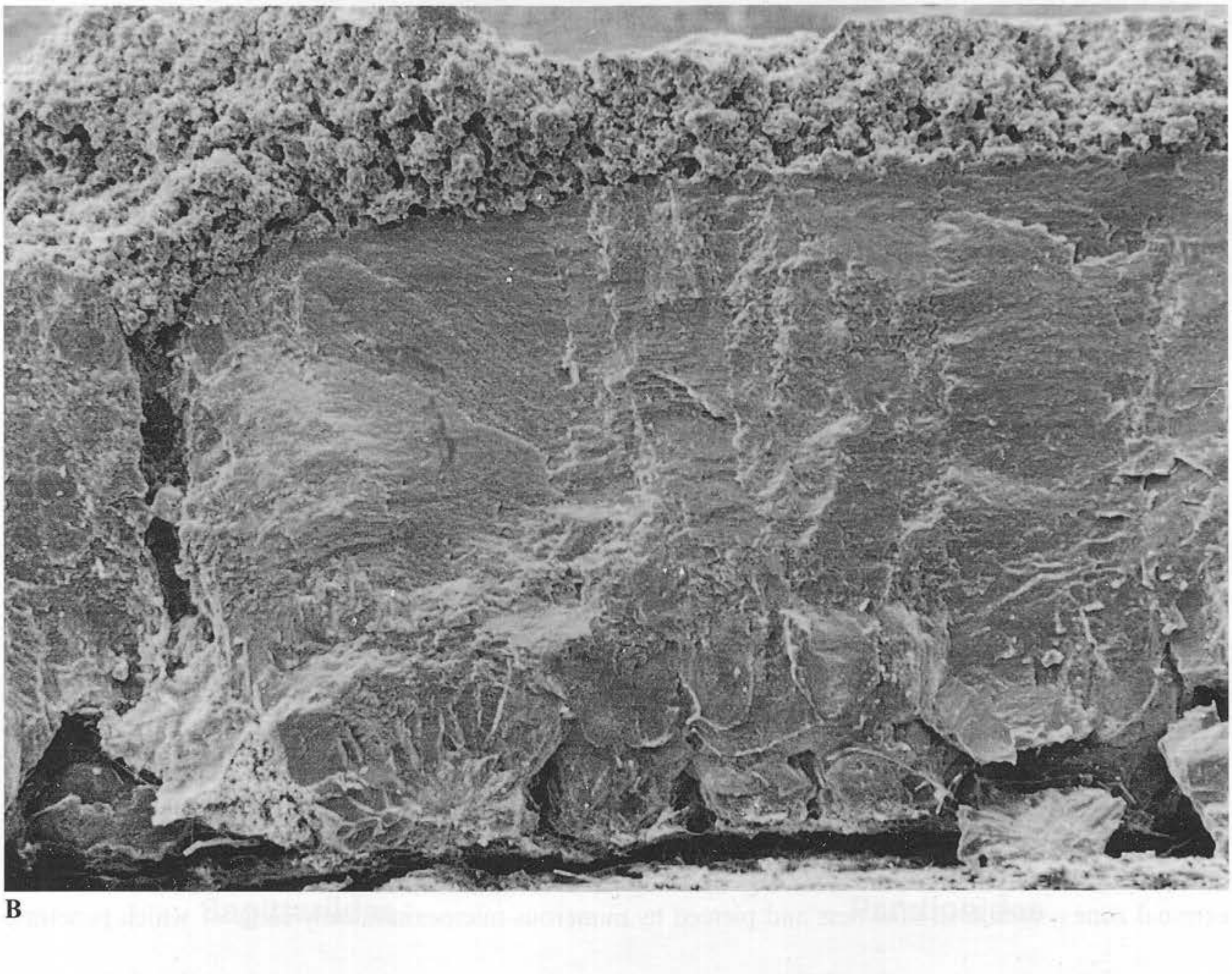
Plate 5. Eggshell structure in Hamerkop and Shoebill (groups 9,11) (radial fractures, general view).

A – *Scopus umbretta,* ×450;

B – *Balaeniceps rex*: note the pore canal (at left) plugged with material of cover, ×200.



A



B

Remarks. The shell structure of *Palaelodus* eggs from the Miocene of France is identical with that of Recent flamingo species, and the microglobular cover is in particular perfectly preserved (Plate 4G).

Comparison. Does not exhibit any particular similarities with ardeiform, ciconiiform and charadriiform eggshells.

References. Mikhailov (1995b).

Group 13

Families Cathartidae, Sagittariidae, Falconidae
(Falconiformes)

Fig. 11 (p. 35); Plate 6 A–E (p. 37)

Shell thickness. 0.15–0.6 mm.

Distribution of pigment patches. None in Sagittariidae; surface patches at varying depths within the shell in Cathartidae; in Falconidae, pigment patches form a definite layer within the external zone – considered by Harrison (1966) as one of the three deviating patterns within the class Aves.

True shell. Of heron-like type ("typical" neognathe condition; cf. group 7) except that in Cathartidae the external zone has rather more dense (solid) ultrastructure; its large prisms form a mosaic pattern on the eggshell surface. CL:ML = 2.5:1 to 5.5:1 (Cathartidae); 2.0:1 to 2.5:1 (Falconidae and Sagittariidae). EZ / SqZ = 0.2–0.3 (Cathartidae) and 0.7–0.8 (Falconidae).

Vesiculation. Almost throughout the eggshell except for the outermost part of the external zone and the lower part of the mammilla (Falconidae and Sagittariidae); completely absent in the external zone in Cathartidae.

Accessory material. Only a thin cuticle.

Comparison. Closely comparable with any avian taxon exhibiting the typical heron-like condition and easily distinguished from the eggshells of hawk-like raptors (Accipitridae and Pandionidae). Cathartid eggshells do not show any particular similarities with those of storks (Ciconiidae).

References. Tyler (1966), Mikhailov (1995a).

Group 14

Families Accipitridae and Pandionidae
(Falconiformes)

Fig. 11 (p. 35); Plate 7A–E (p. 39)

Shell thickness. 0.15–0.5 mm.

Distribution of pigment patches. On the egg surface or at varying depths within the shell thickness.

True shell. The continuous layer consists of three (instead of the usual two) distinct and sharply separated ultrastructural zones. The squamatic zone is strongly reduced to a thin stratum (about 20–50 μm) just above the mammillary layer. Above this is a "stony layer" – unique among avian eggshells – with distinctly separated prisms having a homogenous solid ultrastructure. Above this, in turn, is the external zone – similar in thickness and pierced by numerous microcanals, only some of which penetrate the surface of the shell. The mammillae are more elongated (h / w = 1.5) than in the previous group and consist of rather stronger and more wedge-like radiating crystallites. CL:ML = 2:1 to 3:1.

Vesiculation. The vesicles are common in the outermost parts of the mammillae, in the narrow squamatic zone and external (microcanaliculated) zone, very rare in the 'stony layer'.

Accessory material. Only a thin cuticle: only some of the pore canals seem to penetrate the eggshell surface.

Comparison. The whole arrangement of the true eggshell is unique within the class Aves; the microcanaliculation in the external zone is also seen in the Ciconiidae (group 11), and in a weakly expressed variant in Cariamidae (group 16e); see also Bucerotiformes (group 24).

References. Tyler (1966), Mikhailov (1995a).

Group 15a

Order Anseriformes
Figs. 12A (p. 40), 21 (p. 83), 28–31 (pp. 84–85); Plate 8A–F (p. 43).

Shell thickness. 0.15–0.7 mm.

Distribution of pigment patches. None.

True shell. Distinctively ratite-like in its general arrangement. The continuous layer consists of two distinct and sharply separated zones (SqZ + EZ); EZ is recognised as a dense thin layer of vertical crystals. The mammillary layer is sharply separated from the continuous layer, and the mammillae possess two ultrastructural parts (cf. Plate 8H). The squamatic zone does not generally exhibit a perfect dry-stone-wall pattern (cf. Group 1). CL:ML ranges from 4:1 (some *Cygnus* species) to 1:1 (some *Anser* and *Chen* species), generally from 2:1 to 3:1; the usual range of EZ / SqZ is 0.1–0.3 (up to 0.4–0.5 in some Anatinae). There are consistent differences in the ranges between different subfamilies (Table 1, p. 41). The mammillae are strongly developed (elongated) and densely packed (up to 1/2 T; h / w = 2–3) in Cygninae and Anserinae, but rather keg-like (h / w = 1) in many Anatinae (Table 1).

Figure 11. Stylised three-dimensional diagram of eggshell structure in hawks (Accipitridae and Pandionidae right, and other raptors left).

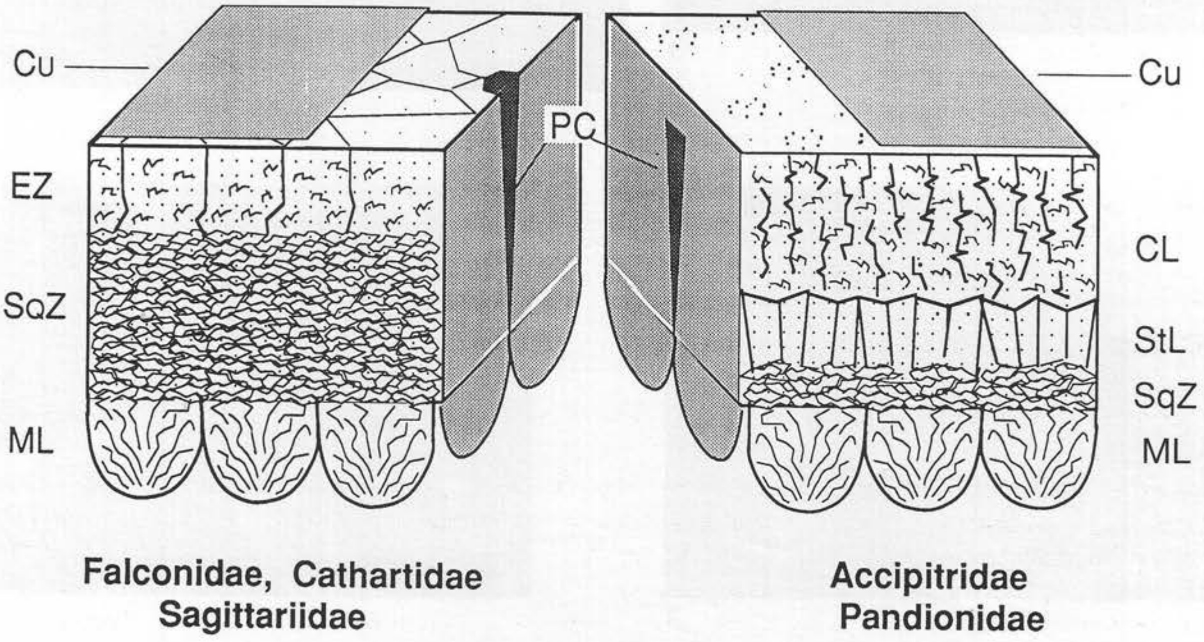


Plate 6. Eggshell structure in falconiforms (group 13) (radial fractures, general view).

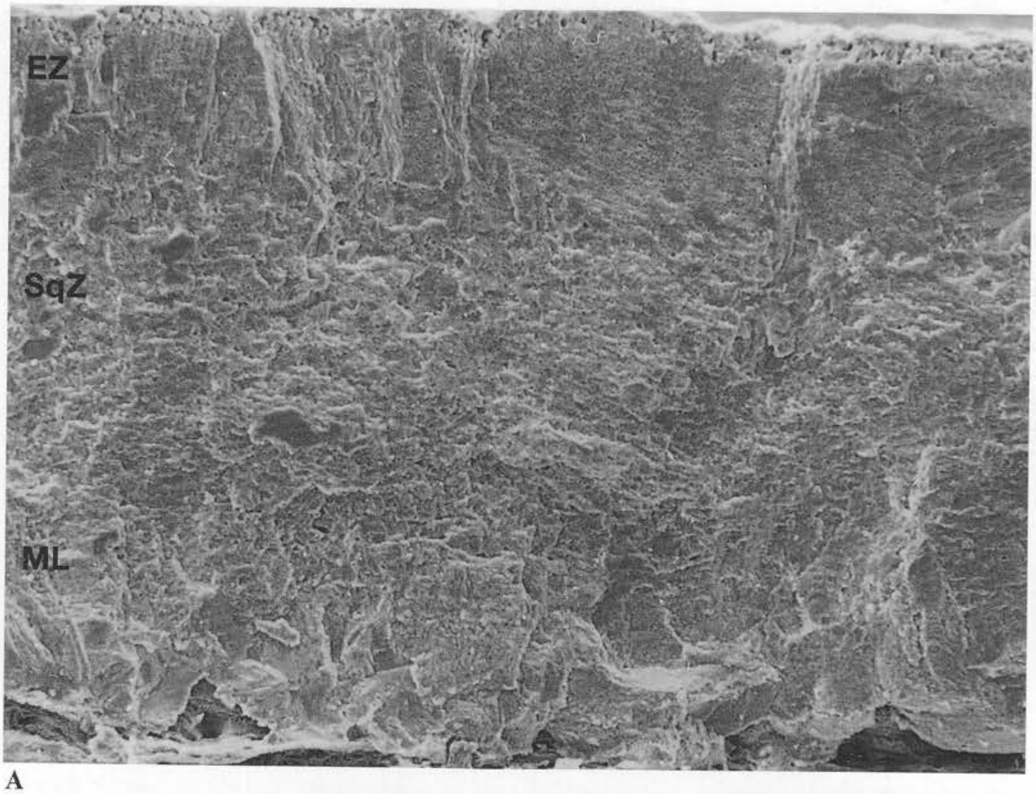
A – *Polyborus plancus*, ×300;

B – *Falco peregrinus*, ×350;

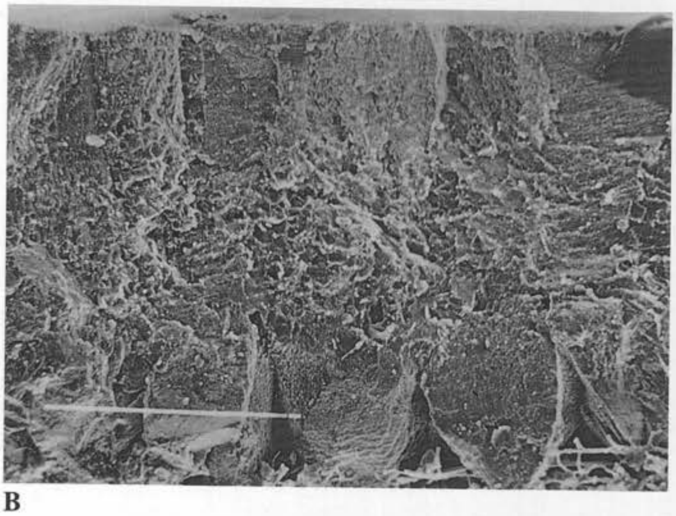
C – *Sagittarius serpentarius*: note the pore canal (arrow) plugged with cuticular material, ×100;

D – *Coragyps atratus*, ×170;

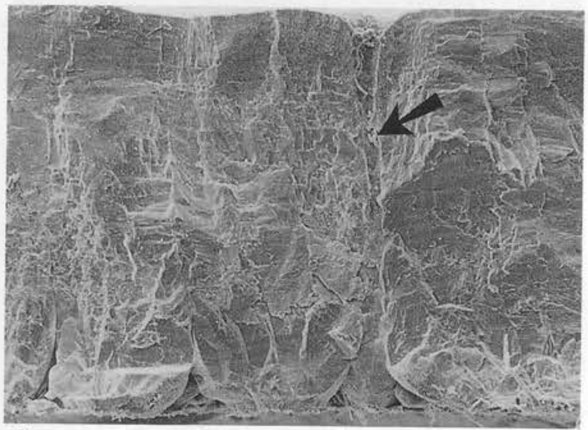
E – *Cathartes aura*, ×170.



A

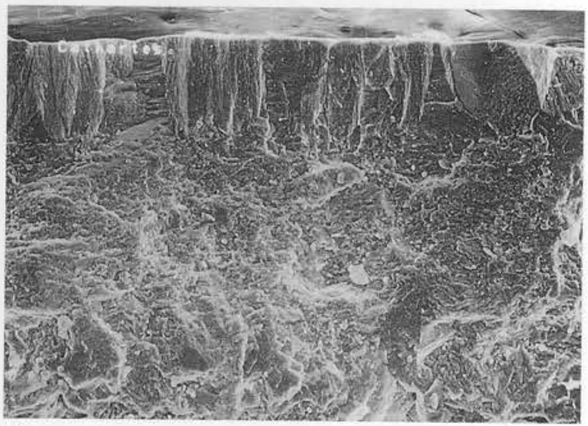


B



C

D



E

Plate 7. Eggshell structure in falconiforms (group 14) (A,B,C,D – radial fractures, general view; 1 – 'stony layer', 2 – microcanaliculate zone; note reduced squamatic zone – arrow).

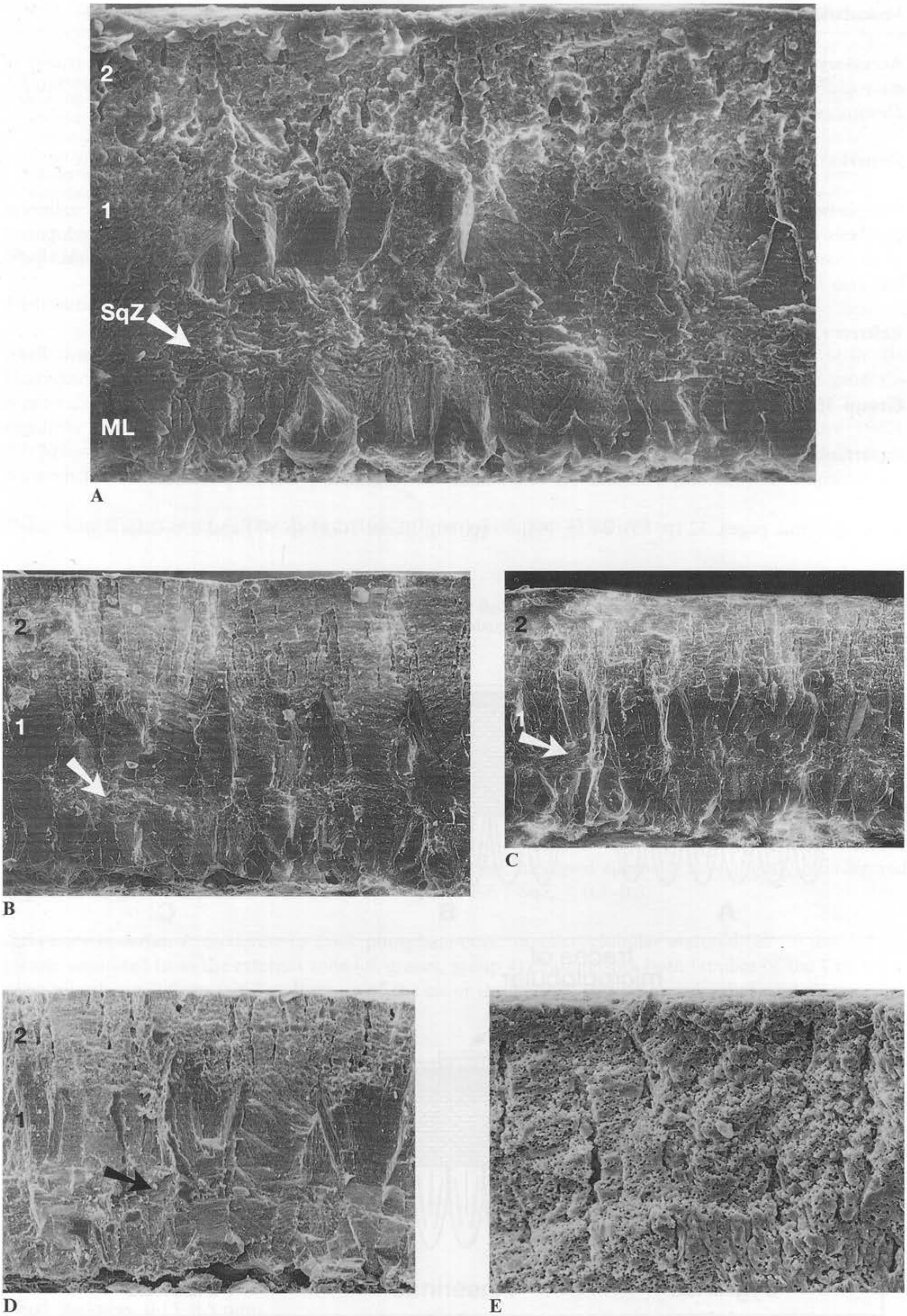
A – *Pandion haliaetus*, ×230;

B – *Gypaetus barbatus*, ×120;

C – *Haliaeetus albicilla*, ×90;

D – *Polyboroides radiatus,* ×400;

E – *Machaerhamphus alcinus*: microstructure of the microcanaliculate zone, ×1500.


2
1
SqZ
ML
A
2
1
B
2
1
C
2
1
D
E

Vesiculation. Limited to the squamatic zone.

Accessory material. The cuticle is thin to thick (up to 8–10 μm in *Anser* and *Branta*); traces of microglobular material have been found in subfamilies Anserinae and Cygninae (*Cygnus*, *Branta*, *Dendrocygna*, *Anser*, *Coscoroba*) (Plate 8E,F).

Remarks. Pore canals are generally simple but some are bifurcating in thick *Cygnus* eggshells.

Comparison. Anseriform eggshells form a single structural assemblage with paleognathe and galliform eggshells, and differ markedly from those of Pelargo-Herodii and Laro-Limicolae. The equal development of the mammillary and continuous layers (CL / ML = 1) is shared by anseriform and galliform taxa only, but also found in Cretaceous avian eggshells (enantiornithine birds; Group 27).

Reference. Tyler (1964b).

Group 15b

Superfamily Phasianoidea
(Galliformes: Tetraonidae, Phasianidae, Numididae, Meleagrididae, Odontophoridae)

Figs. 12B (this page), 32 (p. 85), 34 (p. 86), 35 (p. 86); Plates 8G,H (p. 43) and 9A–C (p. 45)

Figure 12. Stylised two-dimensional diagrams of eggshell structure of ratite-like type in radial section: A – Anseriformes (group 15a); B – Phasianoidea (group 15b); C – Cracoidea (group 15c).

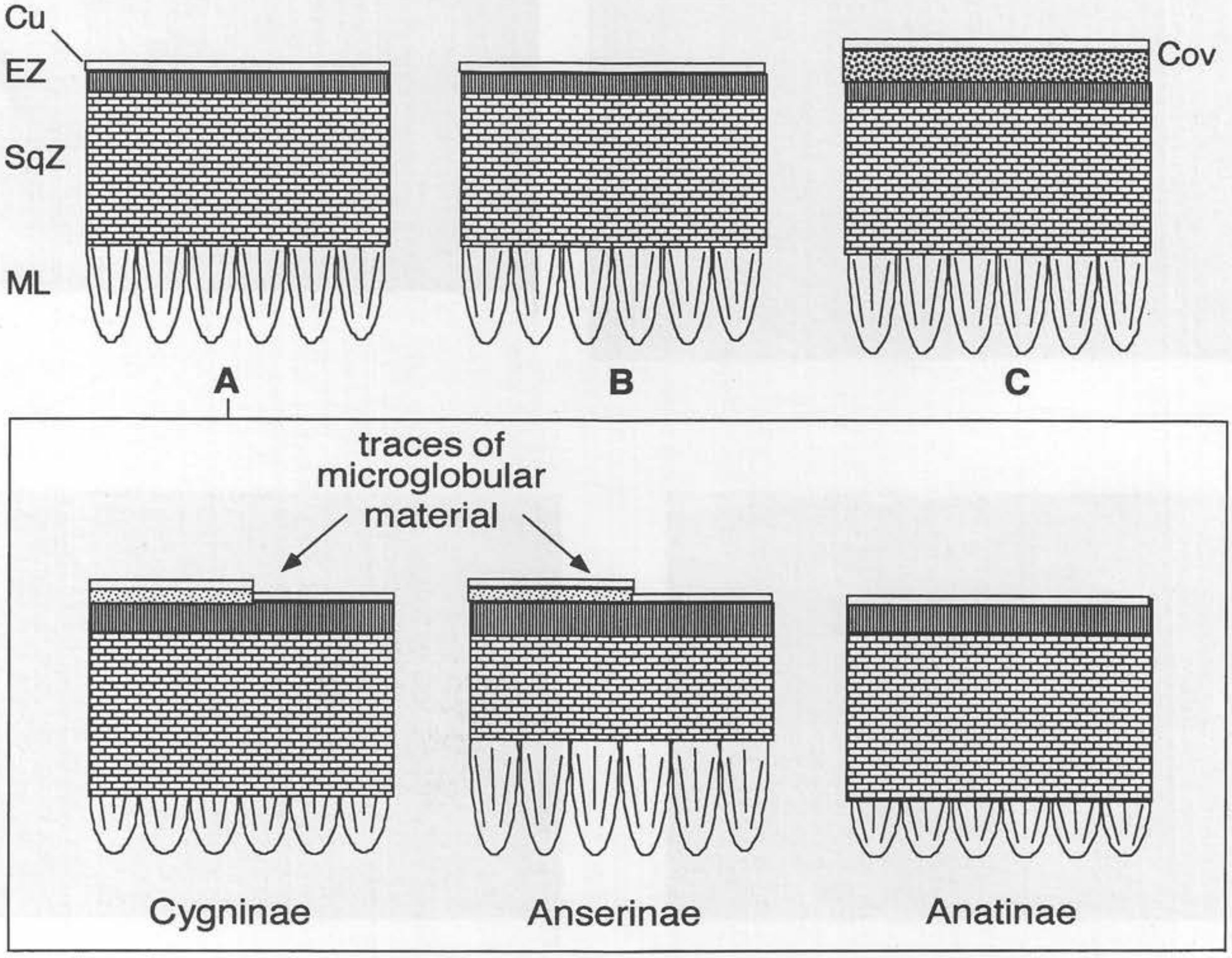


Table 1: The details of eggshell structure within families/subfamilies of the orders Anseriformes and Galliformes.

Taxon	(No. of gen.; spp.)	T range, µm	CL:ML	EZ / SqZ	Traces of cover
Cygninae	(3; 7)	350 – 700	2.5 – 4	0.1 – 0.2	present
Anserinae	(5; 8)	200 – 520	1 – 2	0.1 – 0.2	present
Anatinae	(10; 15)	180 – 310	2 – 3	0.2 – 0.5	not found
Tetraonidae	(4; 4)	140 – 310	1 – 1.5	0.1 – 0.2	not found
Phasianidae	(10; 10)	90 – 290	1 – 1.5	0.1 – 0.3	not found
Meleagrididae	(1; 1)	320	1.5	0.1	?not found
Numididae	(1; 1)	380	2.5	0.1	present

Shell thickness. 0.1–0.4 mm.

Distribution of pigment patches. On egg surface only.

Shell structure. Very similar to the anseriform birds with often even more clearly expressed ratite-like characters in the structure of the mammillae and the squamatic zone. The accessory material is generally represented only by a thin cuticle, but traces of a microglobular cover have been found in *Numida* eggshells and some of the microglobular "plugs" in the pore canals of hen eggshells (Board 1982). CL:ML = 1:1 – 1.5:1 (2.5:1 in *Meleagris gallopavo*); EZ / SqZ = 0.1–0.3. Some quantitative differences between the families are summarised in Table 1.

References. Tullett *et al.* (1976), Board (1982), Board & Perrott (1982).

Group 15c

Superfamily Cracoidea
(Galliformes: Cracidae and Megapodiidae)

Figs. 12C (p. 40), 33 (p. 86); Plate 9D–H (p. 45)

Shell thickness. 0.2–0.6 mm.

Distribution of pigment patches. None.

True shell. Similar to the previous group in many details; megapod eggshells have slightly broader and loosely arranged mammillae. CL:ML = 1:1 – 1.5:1; EZ / SqZ = 0.1–0.3.

Accessory material. A moderate to thick phosphate cover of microglobular material (15–20 µm; 0.1 T), clearly separated from the external zone (cf. grebes, group 4) distinguishes both families of the Cracoidea from all other galliform families. Because of the cover the eggshell surface appears dull whitish and non-crystalline.

References. Board (1982), Board *et al.* (1982).

Group 16a

Suborder Grues
(Gruiformes: Gruidae, Aramidae, Psophiidae).

Fig. 10D (p. 27); Plate 10A–C (p. 49)

Shell thickness. 0.15–0.5 mm.

Plate 8. Eggshell structure in anseriforms (A–F) and galliforms (G,H) (groups 15a,b) (A,B,C,D,G – radial fractures, general view).

A – *Anser albifrons*: note the cuticle covering the orifice of the pore canal (arrow), ×150;

B – *Branta ruficollis*, ×200;

C – *Mergus serrator*, ×180;

D – *Chauna torquata*, ×140;

E – *Anser fabalis*: note thin layer of cover (arrow) above the external zone, ×350;

F – *Cygnus atratus*, ×350;

G – *Tetrao urogallus*, ×150;

H – *Gallus domesticus*: the base of the mammilla: note small spherulite with radial ultrastructure (arrow) below radiating wedges with more solid ultrastructure, ×1800.

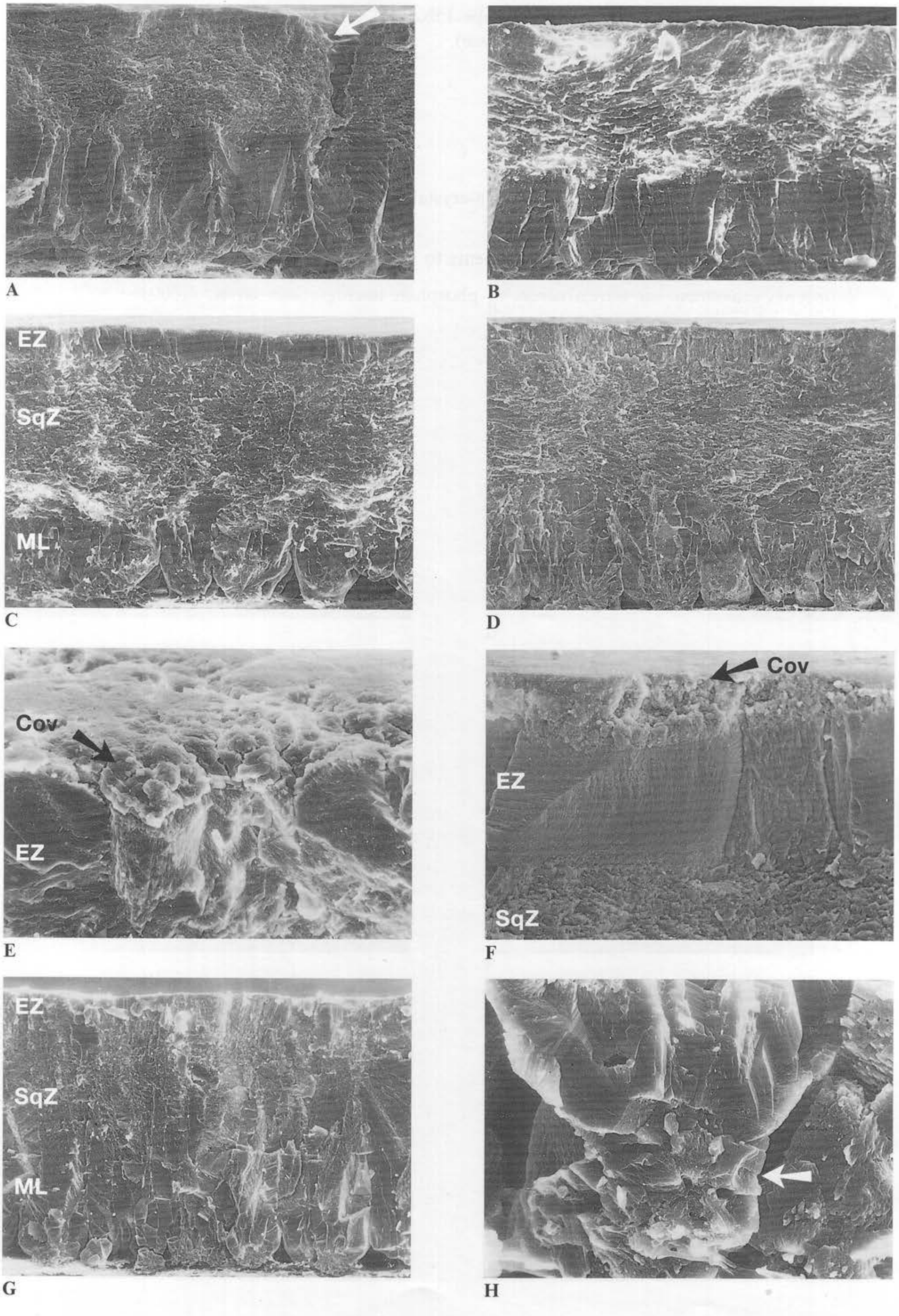

A
B
EZ
SqZ
ML
C
D
Cov
EZ
E
Cov
EZ
SqZ
F
EZ
SqZ
ML
G
H

Plate 9. Eggshell structure in galliforms (groups 15b,c) (A,B,C,D,E – radial fractures, general view; G,H – a view from above on the eggshell surface).

A – *Meleagris gallopavo*, ×180;

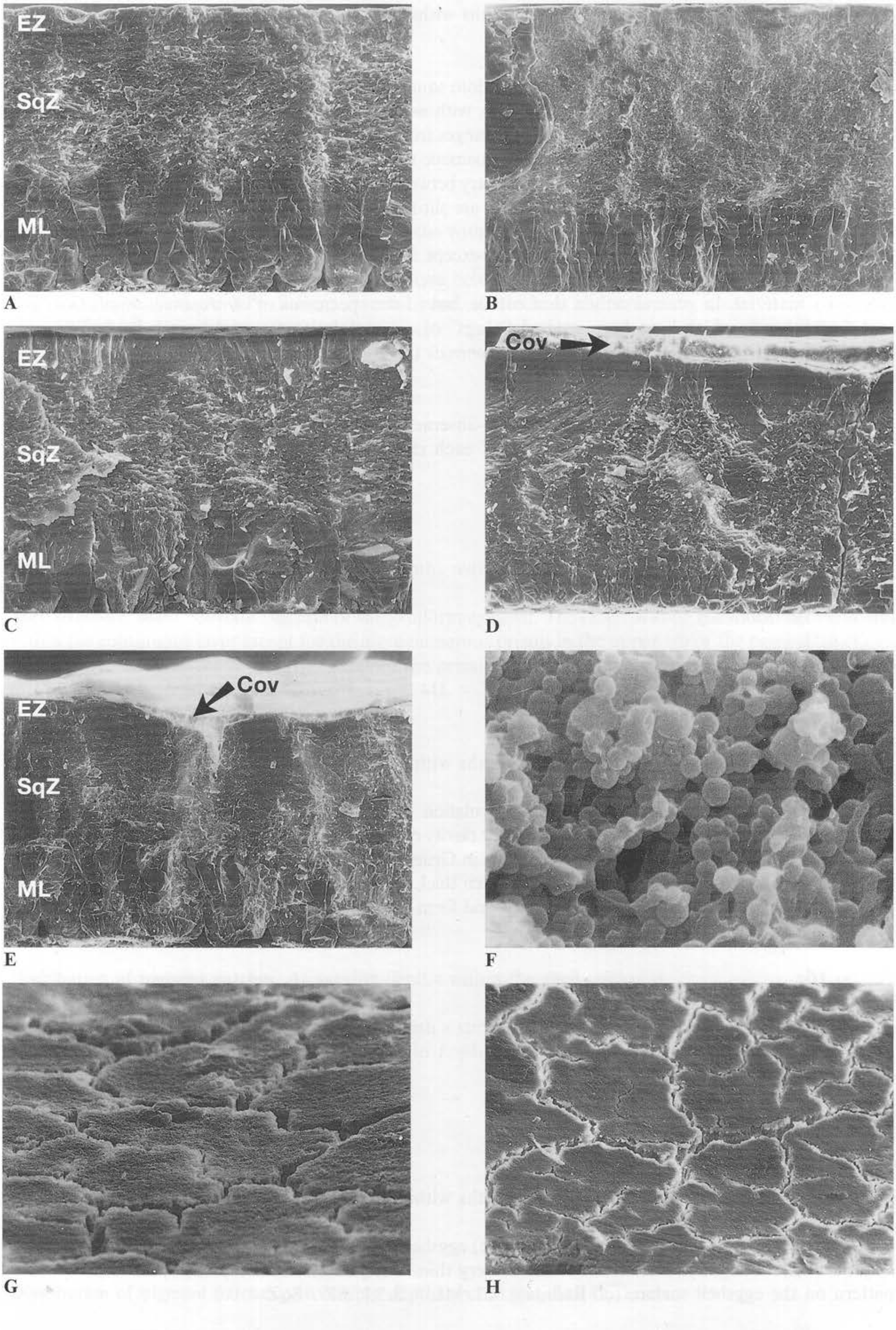
B – *Numida meleagris*, ×120;

C – *Chrysolophus pictus*, ×250;

D,H – *Megapodius freycinet*: D – ×200; H – non-crystalline appearance of the egg surface possessing a cover, ×300;

E,G – *Crax fasciolata*, E – ×70; G – see comments to H, ×800;

F – *Nothocrax urumutum*: the ultrastructure of phosphate microglobular cover, ×10000.


EZ
SqZ
ML
A
B
EZ
SqZ
ML
C
Cov
D
Cov
EZ
SqZ
ML
E
F
G
H

Distribution of pigment patches. At varying depths within the shell thickness in Gruidae and Aramidae; absent in Psophiidae.

True shell. The subdivision of the continuous layer into squamatic zone and external zone is still less clear than in the "typical" neognathe condition (cf. group 7), with no separation between them at all. The mammillae are generally strong and slightly elongated (h / w ranges from 1 to 2) with distinctive wedge-like subunits, the upper parts of which also exhibit weakly-scaled squamatic ultrastructure. This, together with the plain pattern of the vesiculation, results in a very obscure boundary between the mammillary and continuous layers. CL:ML = 2:1 – 2.5:1; EZ / SqZ = 0.2 – 0.4. Many pores are slit-like or crescent-like in cross-section.

Vesiculation. Throughout the eggshell thickness except the lower parts of the mammillae.

Accessory material. In general only a thin cuticle, but in the specimens of *Antropoides virgo*, *Grus grus* and *G. japonensis* which have been studied "plugs" of microglobular material have been found in the funnels of the pore canals (Plate 10B). In *G. japonensis* this material forms a network-like pattern on the eggshell surface.

Comparison. Differ clearly from ratite and gallo-anserae eggshells and from those of the penguin-diver-grebe family assemblage by the arrangement of each structural zone and obscure boundaries between zones.

Group 16b

Suborder Ralli
(Gruiformes: Rallidae)

Plate 11D (p. 53)

Shell thickness. 0.1–0.3 mm.

Distribution of pigment patches. At varying depths within the shell thickness.

Shell structure. In general arrangement and vesiculation pattern similar to Grues, but often with a more pronounced external zone. In this character and the clarity of the mammillae, rather similar to Charadrii (note: this cannot be explained merely by a thinner (than in Grues) range of eggshell thickness which is comparable with Psophiidae and Aramidae). The cuticle is often thick. CL:ML = 2:1 to 3.5:1; EZ / SqZ = 0.4–0.6. The prisms of the external zone are perfectly joined and form a smooth eggshell surface; cf. Charadrii.

Group 16c

Suborder Rhynocheti
(Gruiformes: Rhinochetidae)

Fig. 10D (p. 27); Plate 10D (p. 49)

Shell thickness. 0.18 mm.

Distribution of pigment patches. At varying depths within the shell thickness.

Shell structure. Looks like trumpeter (Psophiidae) eggshells but the boundary between the squamatic and external zones is slightly clearer. The cuticle is very thin. The prisms of the external zone form a mosaic pattern on the eggshell surface (cf. Rallidae). CL:ML = 3.5:1; EZ / SqZ = 0.3.

Group 16d

Suborder Eurypygae
(Gruiformes: Eurypygidae)

Fig. 10E (p. 27); Plate 10G (p. 49)

Shell thickness. 0.1 mm.

Distribution of pigment patches. At varying depths within the shell thickness.

Shell structure. More similar to charadriiforms (see below), though this is not merely due to the thinner shell (cf. Psophiidae). A very distinct external zone, as thick as the squamatic zone CL:ML = 2.5:1; EZ / SqZ = 0.9.

Group 16e

Suborder Cariamae
(Gruiformes: Cariamidae)

Plate 10H (p. 49)

Distribution of pigment patches. At varying depths within the shell thickness.

Shell structure. Most "deviant" variant of the gruiform eggshell. The external zone is almost unrecognisable within the continuous layer except for the more numerous prisms in the upper 1/6 of the eggshell thickness (cf. Otides). Many of the boundaries between the prisms are short microcanals similar in microstructure to those in stork eggshells (see Group 11). CL:ML = 3:1; EZ / SqZ = 0.2.

Group 16f

Suborder Otides
(Gruiformes: Otididae)

Fig. 10D (p. 27); Plate 10E (p. 49)

Shell thickness. 0.2–0.4 mm.

Distribution of pigment patches. At varying depths within the shell thickness.

Shell structure. Very similar to crane eggshells with a still less pronounced external zone (indistinguishable in *Otis tarda*); the cuticle is thick, up to 7 μm in *Lophotis*. CL:ML = 2:1 to 3:1; EZ / SqZ = 0.1.

Group 16g

Family Burhinidae
(Gruiformes or Charadriiformes)

Shell thickness. 0.2 mm.

Distribution of pigment patches. At varying depths within the shell thickness.

Plate 10. Eggshell structure in gruiforms (groups 16a,c–f,h) (A,C–H – radial fractures, general view).

A – *Grus grus*, ×120;

B – *Grus japonensis*: the pore orifice plugged with microglobular material (arrow), ×250;

C – *Aramus guarauna*, ×250;

D – *Rhynochetus jubatus*, ×250;

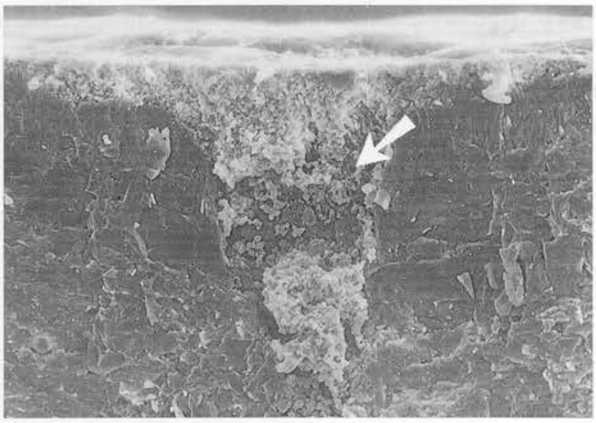
E – *Lophotis ruficrista*, ×250;

F – *Turnix suscitator*, ×250;

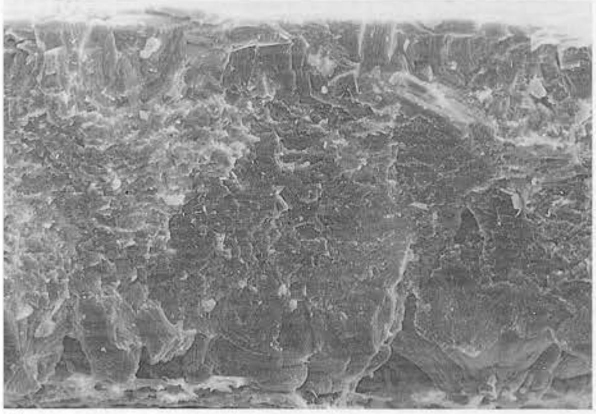
G – *Eurypiga helias*, ×300;

H – *Cariama cristata*, ×120.

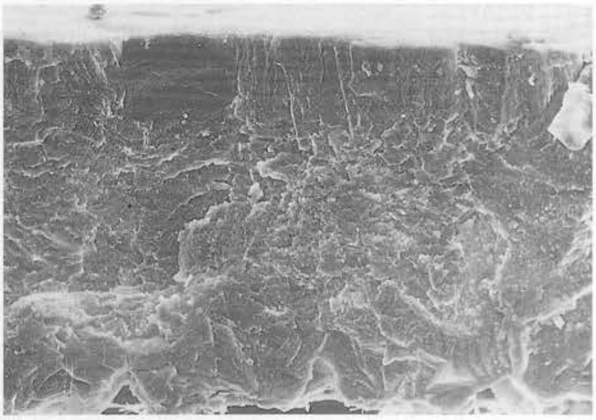
A



B

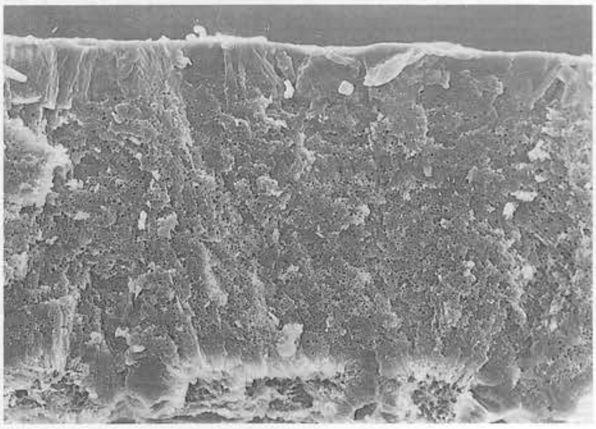


C

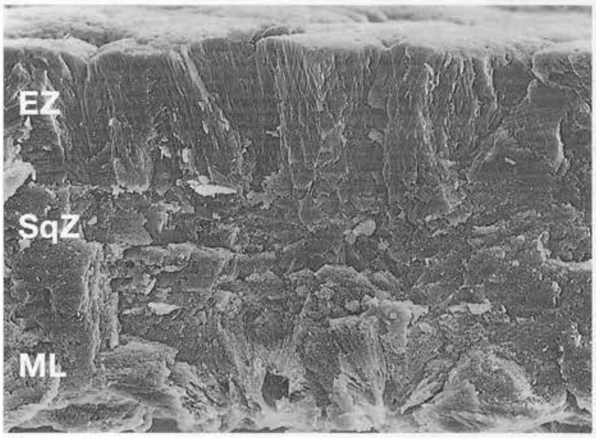


D

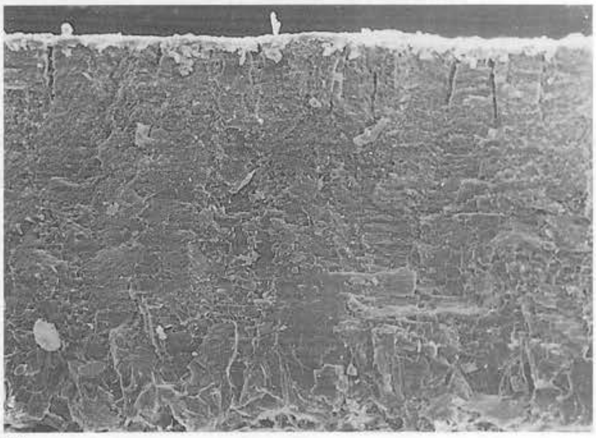
E



F



G



H

Shell structure. Similar to crane eggshells in all details (cf. charadriiform birds). CL:ML = 2:1; EZ / SqZ = 0.6.

Group 16h

Suborder Turnices
(Gruiformes: Turnicidae)

Plate 10F (p. 49)

Shell thickness. 0.08 mm

Distribution of pigment patches. At varying depths within the shell thickness.

Shell structure. Similar to that in Charadrii and some Ralli (but CL is larger). CL:ML = 3.5:1; EZ / SqZ = 0.5.

Group 17a

Suborder Charadrii
(Charadriiformes: all families except Jacanidae)

Figs. 10E (p. 27), 26 (p. 84), 27 (p. 84); Plate 11A–C (p. 53)

Shell thickness. 0.05–0.25 mm.

Distribution of pigment patches. At varying depths within the shell thickness with exceptions in Dromadidae and Thinocoridae (none).

True shell. In general similar to gruiform eggshells, but the mammillary layer and especially the external zone are noticeably more pronounced and with a sharper border. The mammillae consist of fine and irregular radial crystallites and are loosely arranged so that the intermammillary spaces are 1.5–2 times the width of the mammillae. In many genera the external zone shows a "crystal-splitting" effect in subvertical directions and, rather as in Lari, its prisms form a mosaic pattern on the eggshell surface (cf. also Ralli and Rhynocheti). CL:ML = 2:1 to 3:1; EZ / SqZ = 0.3 to 1.0. Some differences in structure between charadriiform and most gruiform eggshells are not merely the consequences of different ranges of eggshell thickness, since they overlap.

Vesiculation. Throughout the squamatic zone and extending to the upper half of the mammillae; penetration of vesicles to the external zone varies among the families and genera being absent (e.g. *Haematopus*) through "partial" (most cases) to reaching the eggshell surface (e.g. *Vanellus*, *Tringa*, *Actitis*, *Calidris*). This may change the external zone's clarity of definition slightly.

Accessory material. Only the cuticle, which is thick in many genera.

Comparison. Together with the gruiform and lariform families form a single assemblage of avian eggshells with quite a simple structure of the heron-like type.

Group 17b

Family Jacanidae
(Charadriiformes)

Plate 11E (p. 53)

Shell thickness. 0.15–0.2 mm.

Distribution of pigment patches. A definite layer within the external zone at the eggshell surface which is considered by Harrison (1966) as one of the three deviant patterns within the class Aves.

Shell structure. Most distinctive charadrian eggshell in the stronger development of the continuous layer (5/6 T), generally consisting of "flaky" squamatic material, and strikingly abundant vesiculation. The external zone is rather thin and all the horizontal boundaries are less pronounced. The eggshell surface is smooth (without a mosaic pattern of the prisms) and covered with a thick cuticle. CL:ML = 5:1; EZ / SqZ = 0.1.

Reference. Board & Perrott (1979a).

Group 17c

Suborders Lari and Alcae
(Charadriiformes)

Fig. 5 (p. 15); Plate 12A–D (p. 55)

Shell thickness. 0.08–0.5 mm.

Distribution of pigment patches. At varying depths within the shell thickness.

True shell. Of heron-like type ("typical" neognathe condition) and closely comparable with both gruiform and ardeiform eggshells, but the continuous layer and the external zone appear to be thicker (the latter is rather denser in Alcae than in Lari); the mammillae lack (Alcae) or almost lack (Lari) vesicles. CL:ML = 3:1 to 4.5:1; EZ / SqZ = 0.3–0.6 (except in *Pagophila eburnea,* 2.5 and 0.7 respectively). The eggshell surface is slightly rough and has a mosaic pattern of unevenly joined large prisms of the external zone (cf. Charadrii, Ralli, Rhynocheti).

Accessory material. No microglobular cover, but a large variation in the cuticle is found in Alcidae eggshells. In *Synthliboramphus* and *Aethia* the eggshell surface lacks the cuticle. In *Fratercula*, *Lunda*, *Cyclorhynchus* and *Ptychoramphus* the cuticle has not been identified for certain, at least as a continuous covering; only some cuticular patches and scattered "crumbles" of crystalline grains can be seen. In *Cepphus* and *Uria* the eggshell surface has a thick (8–10 μm) cuticle with crystalline grains and separate microglobules (Plate 12D). The surface of gull, tern, stercorariid and skimmer eggs is covered with quite a thick cuticle (5 μm).

Comparison. See Charadrii.

Group 18

Order Columbiformes

Fig. 14B (p. 57); Plate 11G,H (p. 53)

Shell thickness. 0.05–0.15 mm.

Distribution of pigment patches. None in Columbidae; at varying depths within the shell in Pteroclididae.

True shell. Of heron-like type ("typical" neognathe condition), i.e. with only slight differentiation of the continuous layer into squamatic and external zones, and with an homogenous radial arrangement of the

Plate 11. Eggshell structure in charadriiforms and columbiforms (groups 16b;17a,b;18) (A–H – radial fractures, general view; note clearly seen eisospherites – arrow – and 'crystal-splitting' effect in the external zone).

A – *Actitis hypoleucos*, ×600;

B – *Calidris alpina*, ×700;

C – *Haematopus ostralegus*, ×200;

D – *Crex crex*, ×400;

E – *Actophilornis africana*, ×250;

F – *Glareola pratincola*: note pore canal covered with the cuticle (double arrow), ×500;

G – *Syrrhaptes paradoxus*, ×350;

H – *Columba palumbus*; ×350.

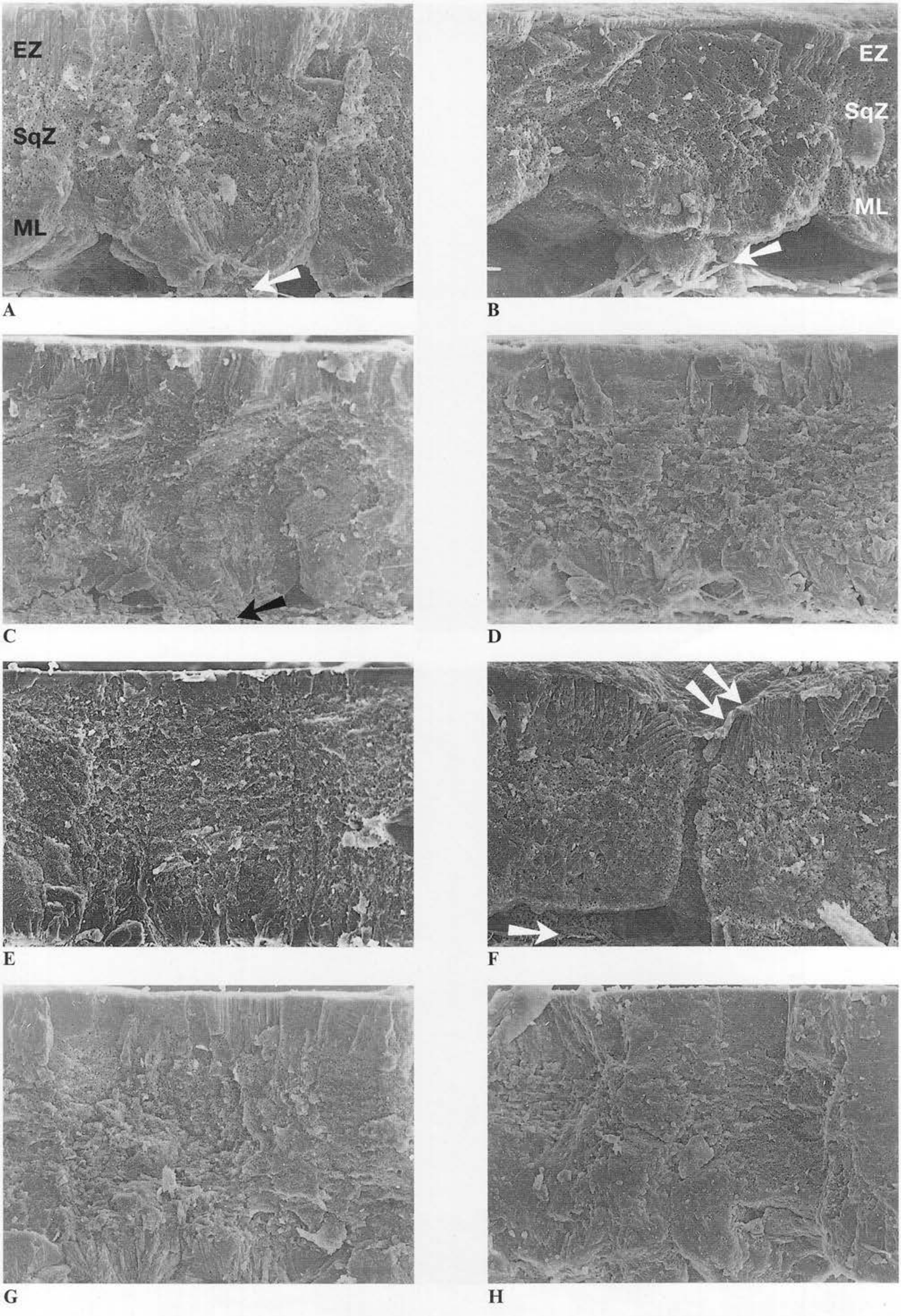
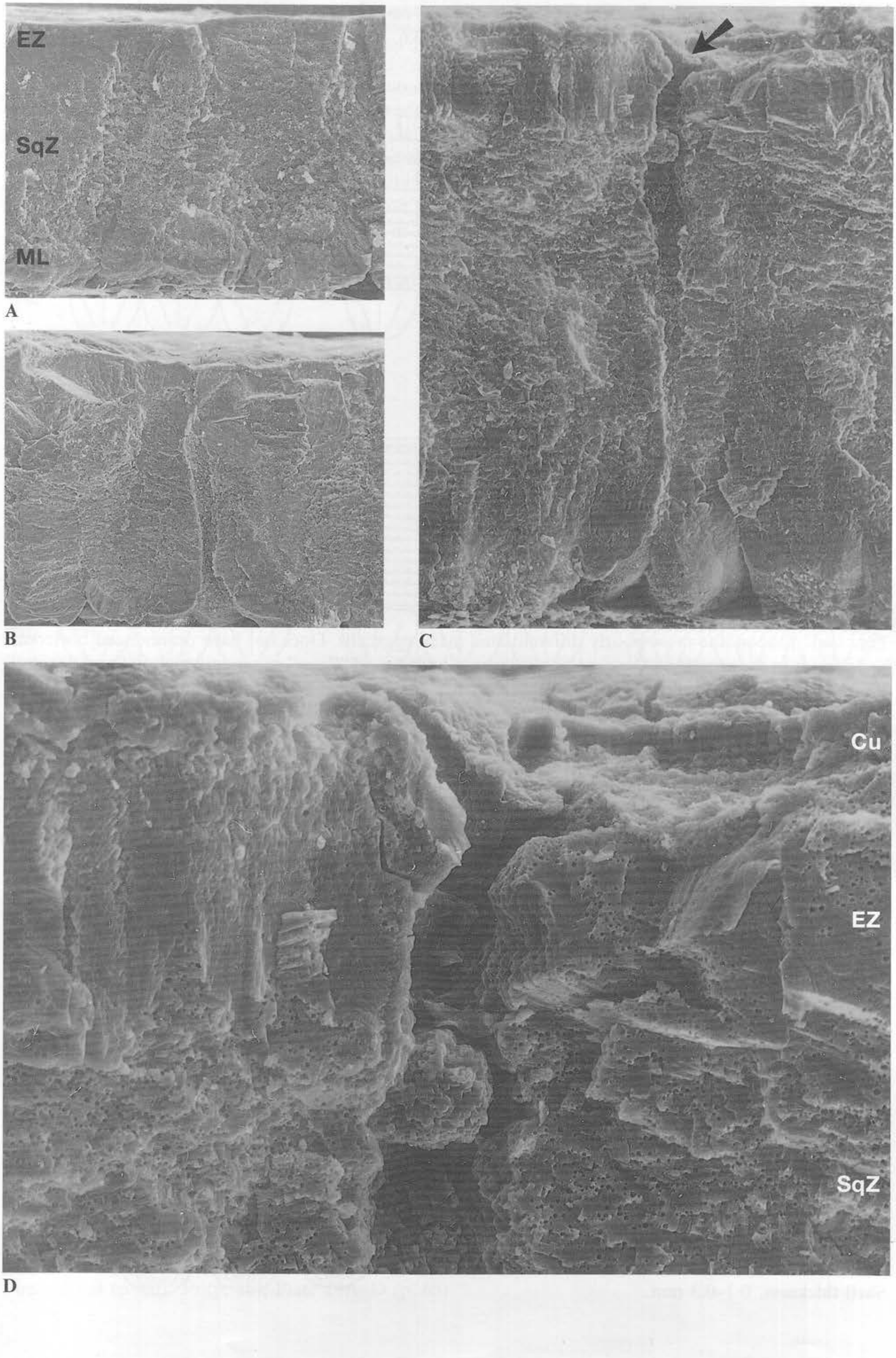

EZ
SqZ
ML
A
EZ
SqZ
ML
B
C
D
E
F
G
H

Plate 12. Eggshell structure in charadriiforms (groups 17c) (A,B,C – radial fractures, general view).

A – *Larus ridibundus*, ×300;

B – *Stercorarius longicaudus*, ×180;

C,D – *Uria aalge*; C – note pore canal covered by cuticle, ×250; D – enlargement of C; note complex ultrastructure of the thick cuticle encrusted with a granular and/or globular elements, ×800.


EZ
SqZ
ML
A
B
C
Cu
EZ
SqZ
D

isomorphic mammillae. Eggshell surface fairly smooth due to perfect joining of the prisms within the external zone. CL:ML = 2:1 to 5:1; EZ / SqZ = 0.4–0.6.

Vesiculation. In pigeon eggshells, throughout the continuous layer (decreasing in the external zone up to the eggshell surface) and penetrating the upper parts of the mammillae; in sandgrouse the mammillae and upper half of the external zone lack vesicles, and this makes the boundary between the mammillary and continuous layers slightly clearer. Vesicles are small and not abundant (cf. Psittacidae).

Accessory material. Only a thin cuticle in Pteroclididae; no covering in Columbidae. Pore canals exhibit cuticular "plugs" in Pteroclididae, but are mostly open in specimens of Columbidae studied.

Comparison. No particular similarities with parrots (Psittacidae) except in the absence of a cuticle in Columbidae.

References. Board (1974, 1982).

Group 19

Order Psittaciformes

Figs. 13 (this page), 14D (p. 57); Plate 13A,B (p. 59)

Shell thickness. 0.05–0.25 mm.

Distribution of pigment patches. None.

True shell. One of the most poorly differentiated avian eggshells. Does not have pronounced horizontal boundaries in the structure; the continuous layer is built up of "flaky" squamatic material and generally shows no subdivision into the squamatic and external zones (an exception is the egg of a captive *Nymphicus*). The mammillae are small (generally 1/5–1/6T), flattened and loosely arranged. CL:ML = 3:1 to 5:1.

Vesiculation. Throughout continuous layer, up to the eggshell surface (but not in *Nymphicus*) and penetrating the mammillae; abundant and large vesicles give a very distinctive appearance (cf. Jacanidae).

Accessory material. None, including the cuticle.

Comparison. No particular similarities with columbiform eggshells (except for the absence of cuticle); much more similar in structure to Strigiformes and Caprimulgiformes.

Reference. Board (1982).

Group 20

Order Strigiformes
Order Caprimulgiformes
(Note: Tytonidae, Steatornithidae and Aegothelidae have not been examined)

Fig. 14E (p. 57); Plate 13C,D (p. 59)

Shell thickness. 0.1–0.3 mm.

Figure 13. Stylised three-dimensional diagram of eggshell structure in parrots (Psittaciformes; group 19).

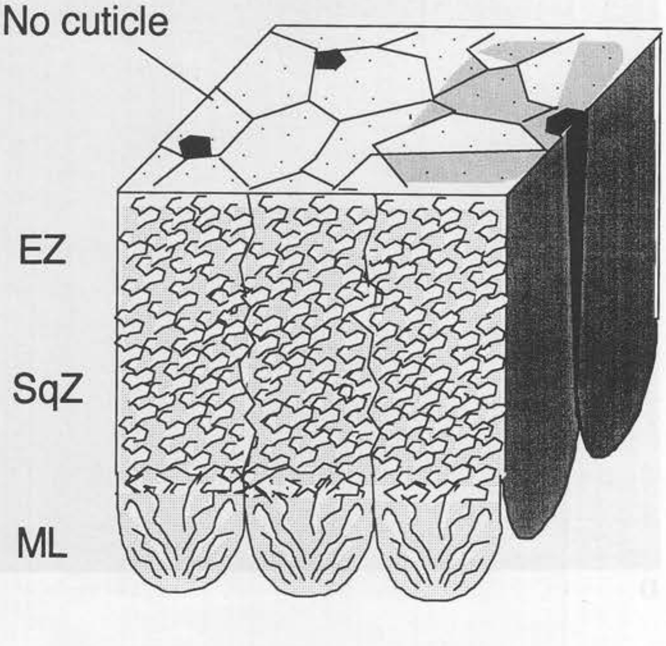
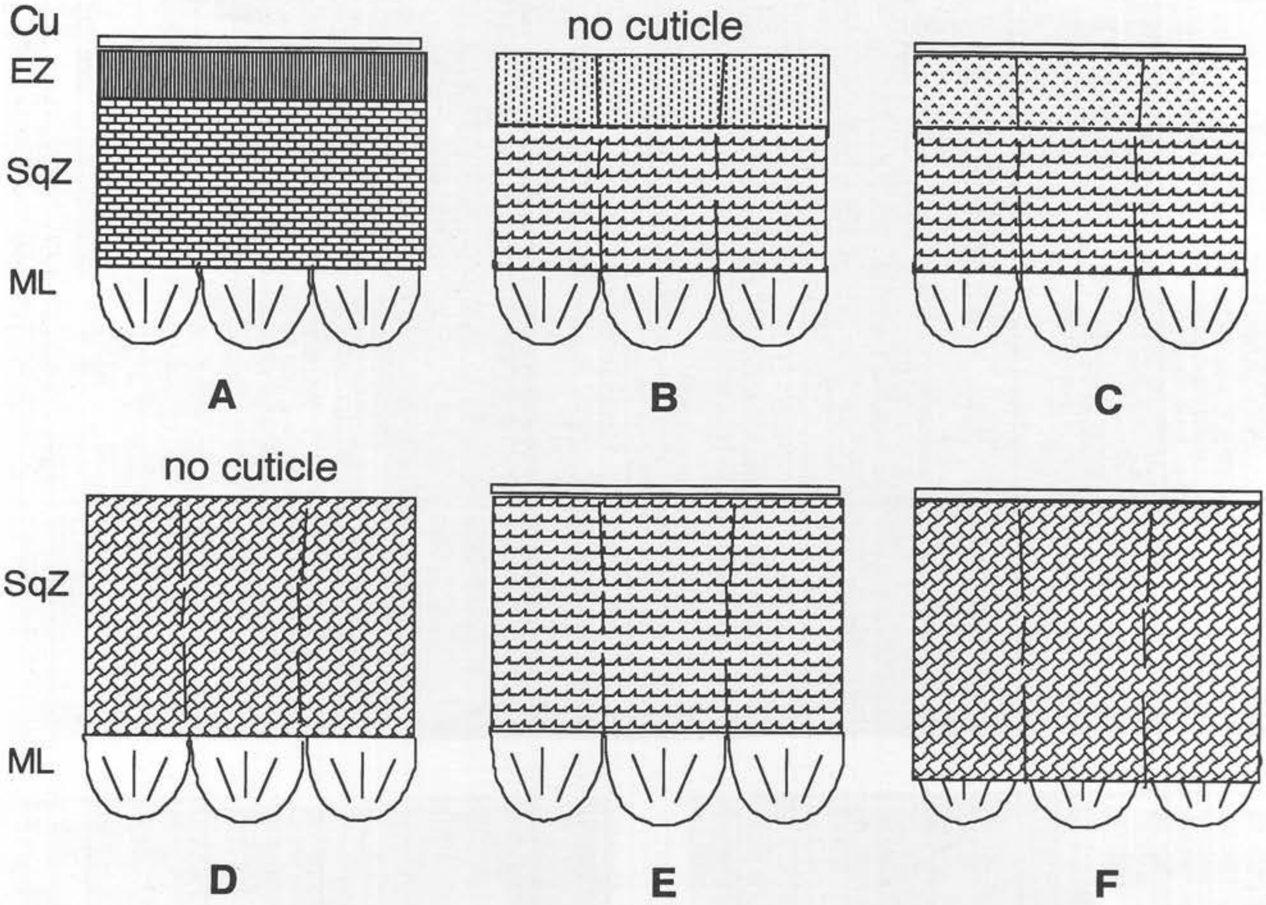


Figure 14. Stylised two-dimensional diagrams of eggshell structure in radial section: A – Coraciiformes (group 23) and Piciformes (group 25); B – Columbiformes (group 18; note that there is a thin cuticle in Pteroclididae); C – Apodiformes, Trochiliformes, Coliiformes and Trogoniformes (group 22; very stylised); D – Psittaciformes (group 19); E – Strigiformes and Caprimulgiformes (group 20); F – Passeriformes (group 26).



Distribution of pigment patches. None in any family (including Tytonidae, Steatornithidae and Aegothelidae) except Caprimulgidae where the patches occur at varying depths within the shell (no data seem to be available for Nyctibiidae).

True shell. In general similar to the previous group, but the squamatic material in the continuous layer is coarser, not "flaky" (except Podargidae; see Vesiculation). The external zone is poorly-defined in some owls and in caprimulgiforms. CL:ML = 3.5:1 – 4:1 (Strigiformes) or 2.5:1 – 3.5:1 (Caprimulgiformes).

Vesiculation. Similar to parrots in the pattern of distribution, but the vesicles are smaller and not so abundant.

Accessory material. Only a thin cuticle.

Comparison. The eggshell structures in orders Strigiformes and Caprimulgiformes are almost identical in their deviant heron-like condition and share many similarities with Psittaciformes.

Group 21a

Non-parasitic cuckoos (subfamily Couinae has not been examined)
(Cuculiformes)

Figs. 15A,B (p. 60), 36 (p. 86); Plate 14A–D (p. 63)

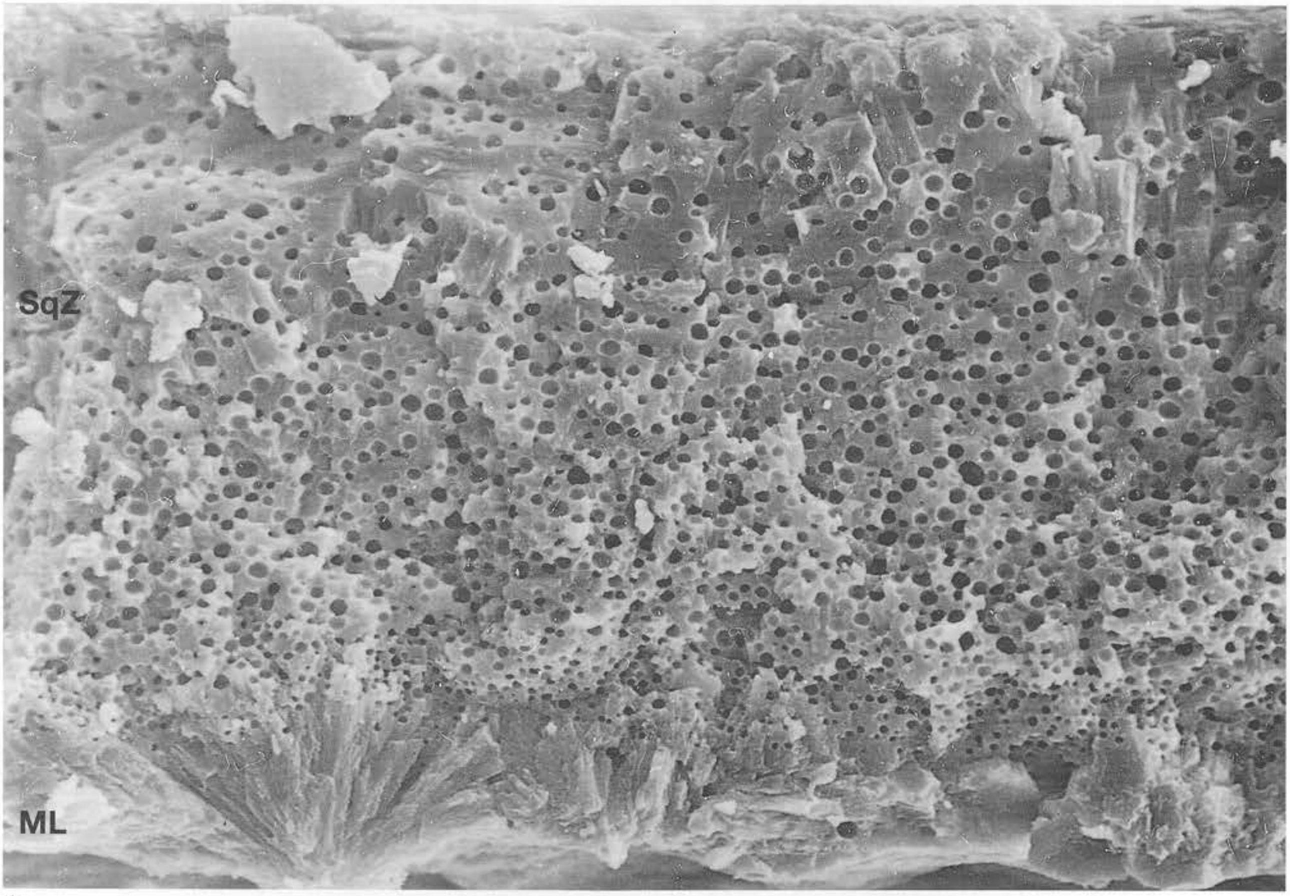
Plate 13. Eggshell structure in parrots, caprimulgiforms and owls (groups 19,20) (A–D – radial fractures, general view).

A – *Agapornis* sp., ×1500;

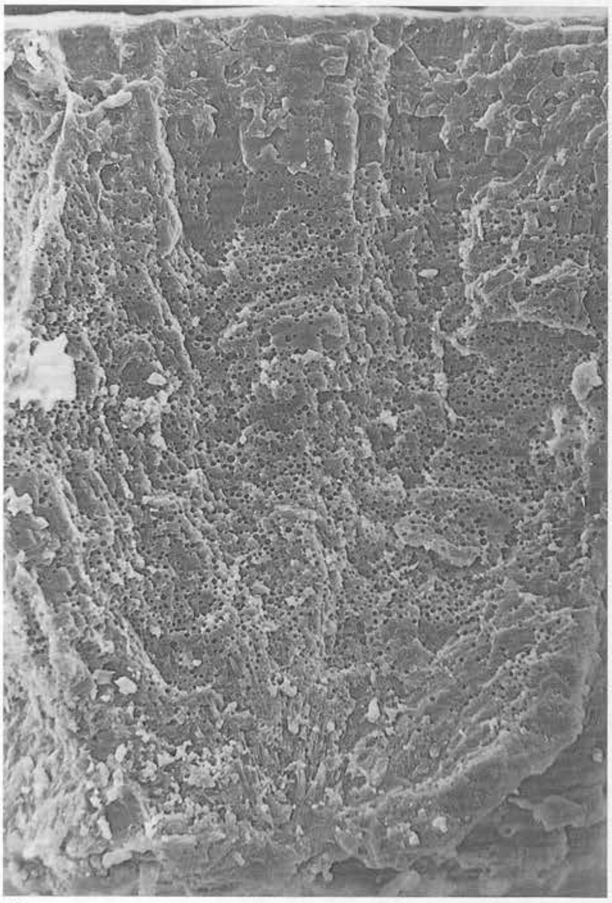
B – *Cacatua moluccensis*, ×500;

C – *Podargus* sp., ×500;

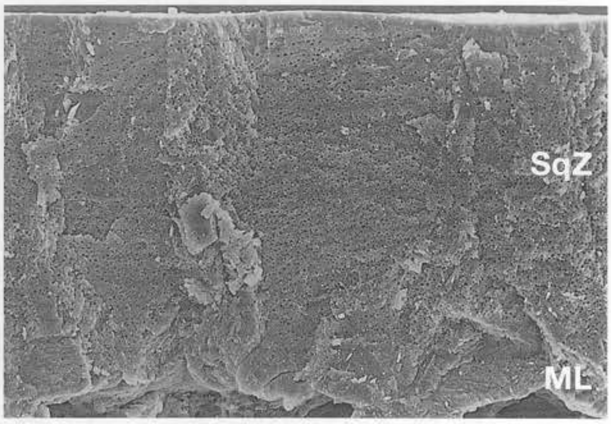
D – *Ketupa blakistoni*, ×200.



A



B



C

D

Shell thickness. 0.1–0.2 mm.

Distribution of pigment patches. None.

True shell. Strikingly different from the "typical" (heron-like) neognathe condition, in particular having the ratite-like arrangement of the continuous layer subdivided into two distinct and sharply separated zones (SqZ + EZ). The squamatic zone exhibits a perfect dry-stone-wall pattern of large squamatic units, while the external zone is relatively thin and recognised as a dense stratum of vertical crystals. The mammillary layer is sharply separated from the continuous layer; the mammillae are keg-shaped (h/w = 1), densely arranged, and unlike "typical" ratite-like eggshells do not have two ultrastructural parts. CL:ML = 3:0; EZ / SqZ = 0.2–0.3.

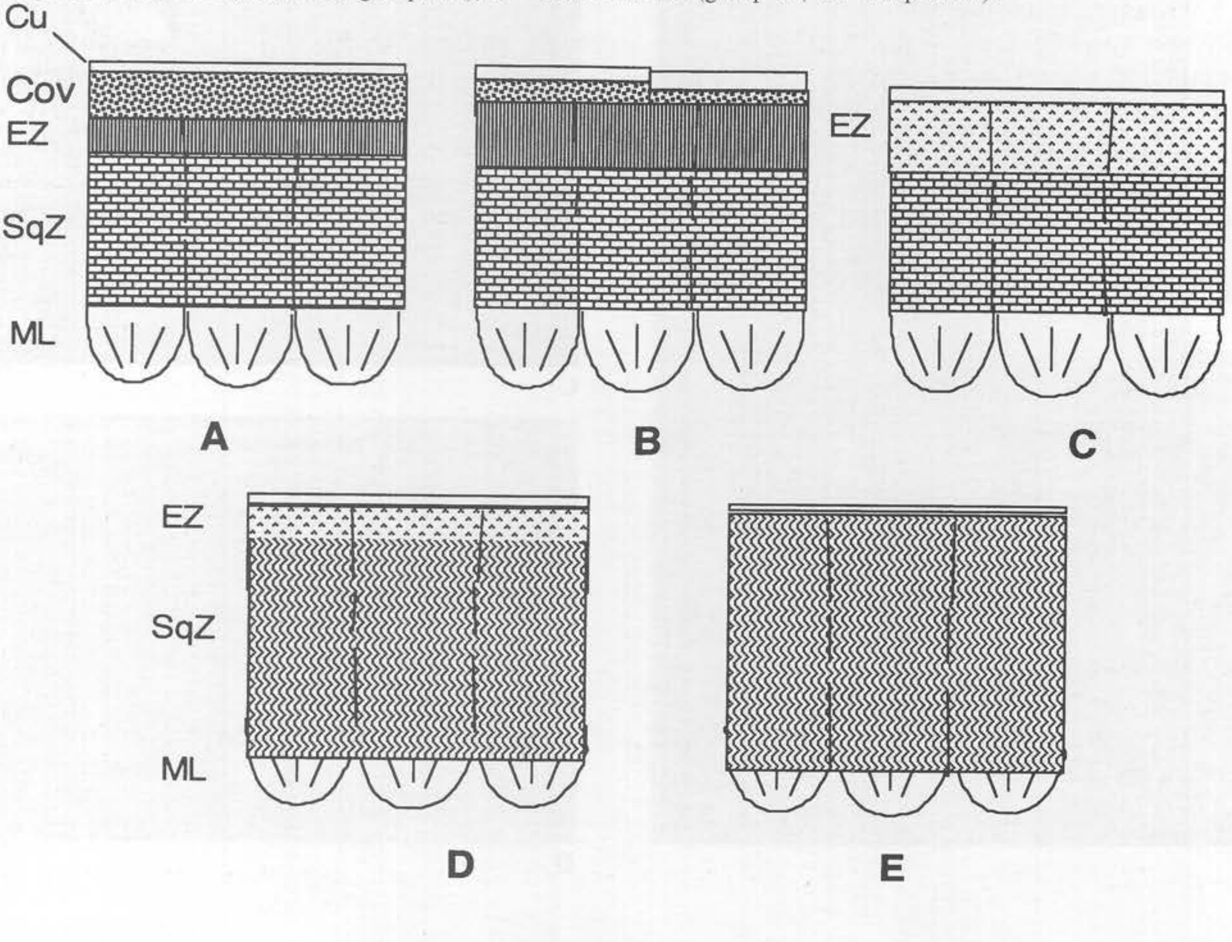
Vesiculation. Generally limited to the squamatic zone; rarely may be completely absent (*Crotophaga*).

Accessory material. Besides the cuticle, the carbonate microglobular cover is characteristic. It is thick or of moderate thickness (40–15 μm) in *Crotophaga*, *Guira*, *Geococcyx* and thin to very thin (10–3 μm) in *Coccyzus* and *Centropus* (Plate 14C,D). It is because of the cover that the shell surface of the eggs of non-parasitic cuckoos looks so dull and non-crystalline (crumbled-chalky in *Crotophaga*, *Guira* and *Geococcyx*). In some eggs of *Centropus* and *Coccyzus* only a very thick (up to 10 μm) cuticle with microglobular and granular inclusions has been identified.

Comparison. Form a single structural assemblage with the coraciiform and piciform eggshells, which is separate from other arboreal neognathe orders.

Reference. Board & Perrott (1979b).

Figure 15. Stylised two-dimensional diagrams of eggshell structure in radial section: A, B – nonparasitic cuckoos (group 21a): A – *Crotophaga, Guira, Geococcyx*; B – other genera; C – Opisthocomidae and Musophagidae (group 21b); D – parasitic cuckoos (Cuculinae; group 21c); E – Passeriformes (group 26; for comparison).



Group 21b

Families Musophagidae and Opisthocomidae
(Cuculiformes)

Fig. 15C (p. 60); Plate 14E,F (p. 63)

Shell thickness. 0.1–0.15 mm.

Distribution of pigment patches. None in Musophagidae; patches at varying depths in Opisthocomidae.

Shell structure. The true eggshell is generally similar to the previous group, but the external zone is larger and exhibits vesiculation in lower 1/2 to 3/4, the microlayer (3 μm) of conuli forms the outer edge of the external zone in radial section. Accessory material is represented only by a thin cuticle. CL:ML = 3:1; EZ / SqZ = 0.6.

Group 21c

Parasitic cuckoos (subfamily Cuculinae)
(Cuculiformes)

Fig. 15D (p. 60); Plate 15F (p. 67)

Shell thickness. 0.05–0.1 mm.

Distribution of pigment patches. At varying depths within the shell thickness.

Shell structure. Strikingly different from the other cuckoos, turacos and hoatzin, and similar in its structural simplification to some other arboreal avian orders, in particular Passeriformes. The mammillae are still noticeable (approximately 1/3T), but the boundaries between ultrastructural zones are not pronounced; the external zone differs only slightly from the squamatic zone in a sort of "crystal-splitting" effect and denser ultrastructure. The squamatic zone has a "flaky" ultrastructure (cf. groups 19, 20, 26). The vesiculation extends some way from the squamatic zone to both the external zone and mammillae. The accessory material is represented only by a thin cuticle. CL:ML = 2:1 – 2.5:1; EZ / SqZ = 0.3–1.

Group 22

Order Apodiformes
Order Trochiliformes
Order Coliiformes
Order Trogoniformes

Fig. 14C (p. 57); Plate 15A–C (p. 67)

Shell thickness. Generally 0.04–0.08 mm (*Calypte anna* – 0.02 mm).

Distribution of pigment patches. None in Apodidae, Hemiprocnidae and Trochilidae; blotch pigment layers at surface in Coliidae; data apparently not available for Trogonidae.

True shell. In general, represents a similar deviation from the "typical" heron-like type as do waders and pigeons. The boundary between the mammillary and continuous layers is distinct, but the latter exhibits

Plate 14. Eggshell structure in cuculiforms (groups 21a,b) (A,B,C,F – radial fractures, general view; C and D – microglobular cover above the external zone (EZ) and below the cuticle (arrow)).

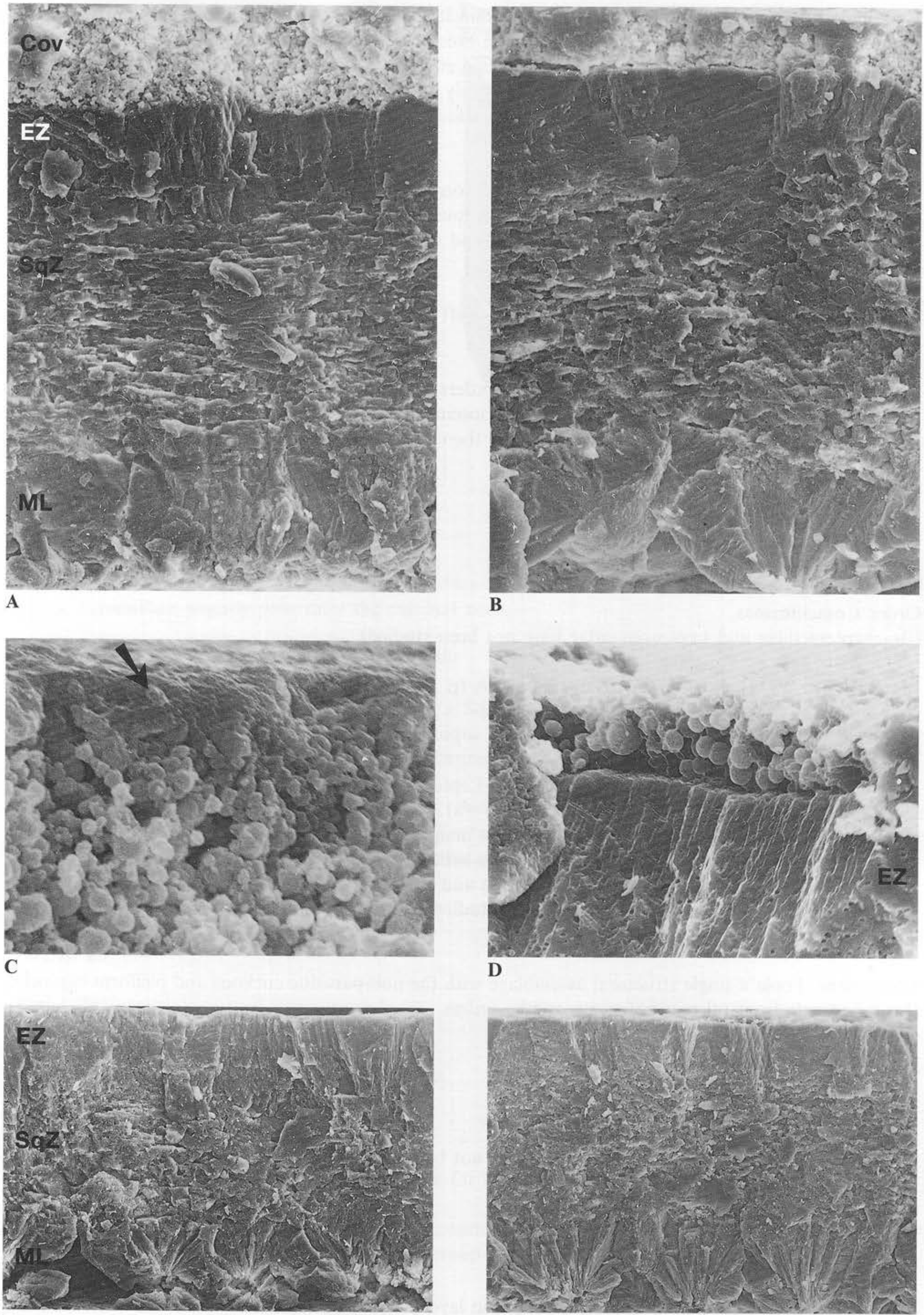
A,C – *Crotophaga ani,* A – ×550; C – ×3000;

B – *Geococcyx californiana*, ×600;

D – *Coccyzus erythropthalmus*, ×2000;

E – *Opisthocomus hoatzin*, ×400;

F – *Tauraco persa*, ×400.


Cov
EZ
SqZ
ML
A
B
C
D
EZ
EZ
SqZ
ML
E
F

a very gradual transition in the ultrastructure within its upper part, so that the external and squamatic zones appear not to be separated at all (possible exception: a trogon specimen studied). The external zone is generally defined here by its "crystal-splitting effect"; the squamatic zone has a "flaky" structure. The mammillae are weak and consist of small, densely packed, radial crystallites. CL:ML = 2:1 to 3.5:1; EZ / SqZ = 0.2–0.3. In *Calypte anna* the eggshell surface is slightly rough and dull; in *Harpactes oreskios* it is smooth and glossy.

Vesiculation. Limited to the squamatic zone in Trogonidae; penetrates (decreasing) the external zone in Apodidae and Trochilidae; throughout the continuous layer in Coliidae. In the single specimen of a hummingbird eggshell studied the upper (3 µm) band of the external zone produces a striking effect of dense vesiculation with large vesicles.

Accessory material. No cuticle at all recognised in swift and hummingbird eggshells examined; the others have a thin (*Harpactes*) or thick (*Colius*) cuticle.

Remarks. Only a few specimens from these four orders have been examined: two species of swifts and a single species from each of the other orders; no specimens of Hemiprocnidae. The slight differences in vesiculation, details of external zone, etc. should therefore be treated as provisional.

Reference. Schmidt (1970).

Group 23

Order Coraciiformes
(Brachypteraciidae and Leptosomatidae have not been studied)

Figs. 14A (p. 57), 16 (p. 65), 36 (p. 86); Plate 16A (p. 69)

Shell thickness. 0.05–0.15 mm.

Distribution of pigment patches. None (including Leptosomatidae).

Shell structure. Similar to non-parasitic cuckoos in many details, i.e. with ratite-like continuous layer (see group 21a). Perfect alignment of the homogenous-solid prisms in the external zone and absence of the cover make the eggshell surface look very smooth and glossy. The cuticle is mainly thin, but quite thick in the specimens of Alcedinidae and Todidae studied (the lustre of the egg surface correspondingly decreased).

Comparison. Form a single structural assemblage with the non-parasitic cuckoos and piciform eggshells; this is separate from other arboreal neognathe orders.

Group 24

Order Bucerotiformes
(Bucerotidae; Phoeniculidae and Upupidae have not been examined).

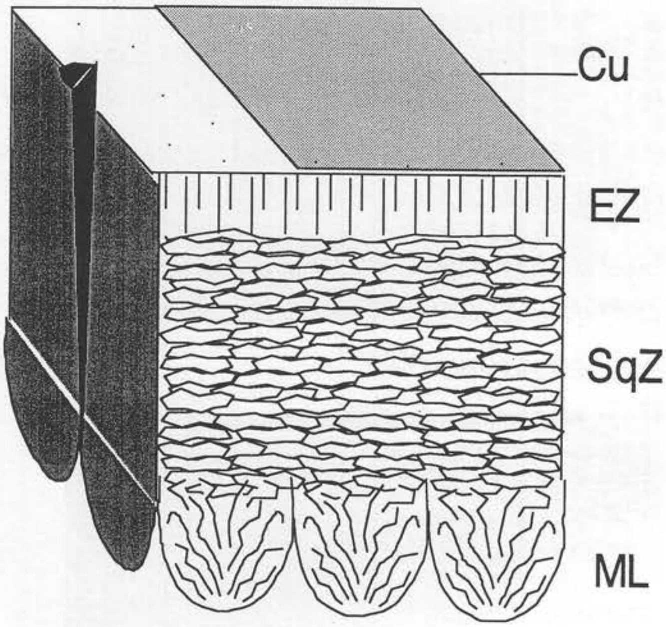
Plate 16B (p. 69)

Shell thickness. 0.2–0.3 mm.

Distribution of pigment patches. None or very thin layer in the eggshell surface (also true for Upupidae and Phoeniculidae).

True shell. The most "aberrant" structure among avian eggshells. The continuous layer is as much as six times as thick as the mammillary layer and consists of three distinct ultrastructural zones. The lower is typically the squamatic zone which occupies here about a third of the eggshell thickness; outside this is a peculiar, loose, organic-mineral layer, equally thick, which may be similar to the so called resistant layer in casuariiform eggshells (see group 1b); the last (outer) zone is a more or less typical external zone exhibiting dense and homogenous ultrastructure. The middle and outer are pierced by short (20–30 μm) vertical microcanals which form a complicated network in the upper half of the continuous layer; between these zones a microlayer of horizontal organic fibres seems to be present. The mammillary and continuous layers are distinct; with pronounced boundary; the mammillae are small and have a loose structure. It is possible that the pore canals do not penetrate the lower and middle zones of the continuous layer.

Figure 16. Stylised three-dimensional diagram of eggshell structure in coraciiform birds (group 23).



Vesiculation. Throughout the lower and middle zones of the continuous layer, extending to the upper half of the mammillae; slightly penetrates the external zone.

Accessory material. A thick (5–7 μm) cuticle only.

Comparison. The lower part of this eggshell (ML + SqZ) is comparable with "normal" eggshells of heron-like type; the upper part, on the contrary, is unique and combines peculiar features found in different avian taxa (in orders Casuariiformes, Accipitriformes, Ciconiiformes).

Remarks. Only one specimen of a single species (*Buceros bicornis*) has been examined and it is possible it exhibits a pathological alteration of its eggshell structure. However, the general descriptions of hoopoe and wood-hoopoe eggs suggest a similar arrangement of the outer part in their shells. Additional specimens of all three families need to be examined.

Group 25

Order Piciformes
(Only Picidae has been studied)

Fig. 14A (p. 57); 36 (p. 86); Plate 16C–E (p. 69)

Shell thickness. 0.05–0.1 mm.

Distribution of pigment patches. None (also true for all other families of the order).

True shell. Similar to non-parasitic cuckoo and coraciiform eggshells in many details, i.e. exhibiting ratite-like characteristics in the continuous layer (see group 21a). The squamatic units are large (5–10 μm) and arranged in a perfect dry-stone-wall pattern.

Accessory material. No cover; the cuticle has also not been detected unequivocally.

Plate 15. Eggshell structure in passeriforms and some other orders (groups 21,22,26) (A–H – radial fractures, general view; the arrows on D,F,H mark the eisospherites).

A – *Apus apus*, ×600;

B – *Calypte anna*: note peculiar external zone (arrow), rich with large globules, ×1800;

C – *Colius striatus:* note very thick cuticle (arrow), ×600;

D – *Turdus hortulorum*, ×500;

E – *Passer ammodendri*, ×600;

F – *Cuculus canorus*, ×700;

G – *Corvus corax,* ×500;

H – *Uragus sibiricus*, ×700.

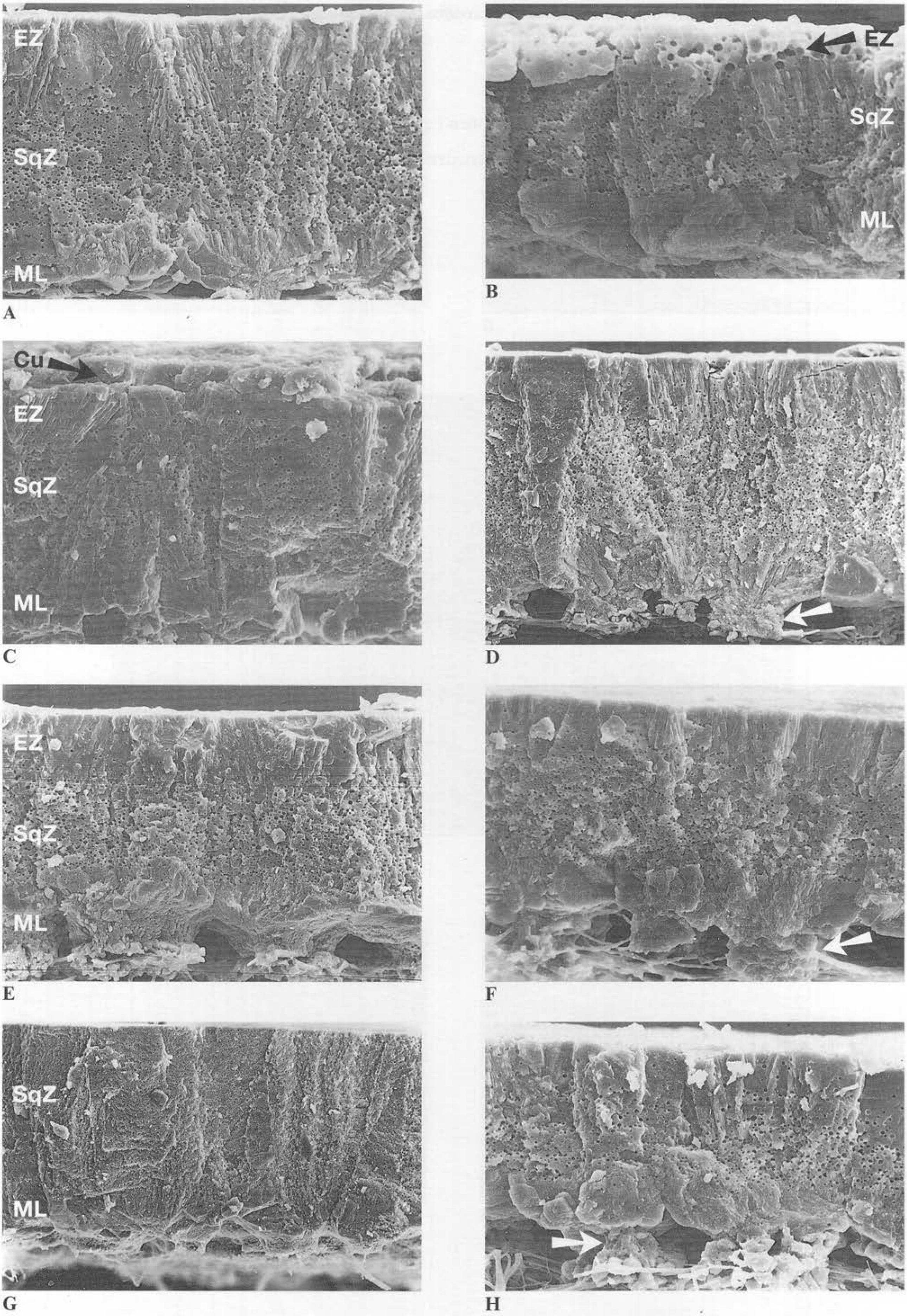

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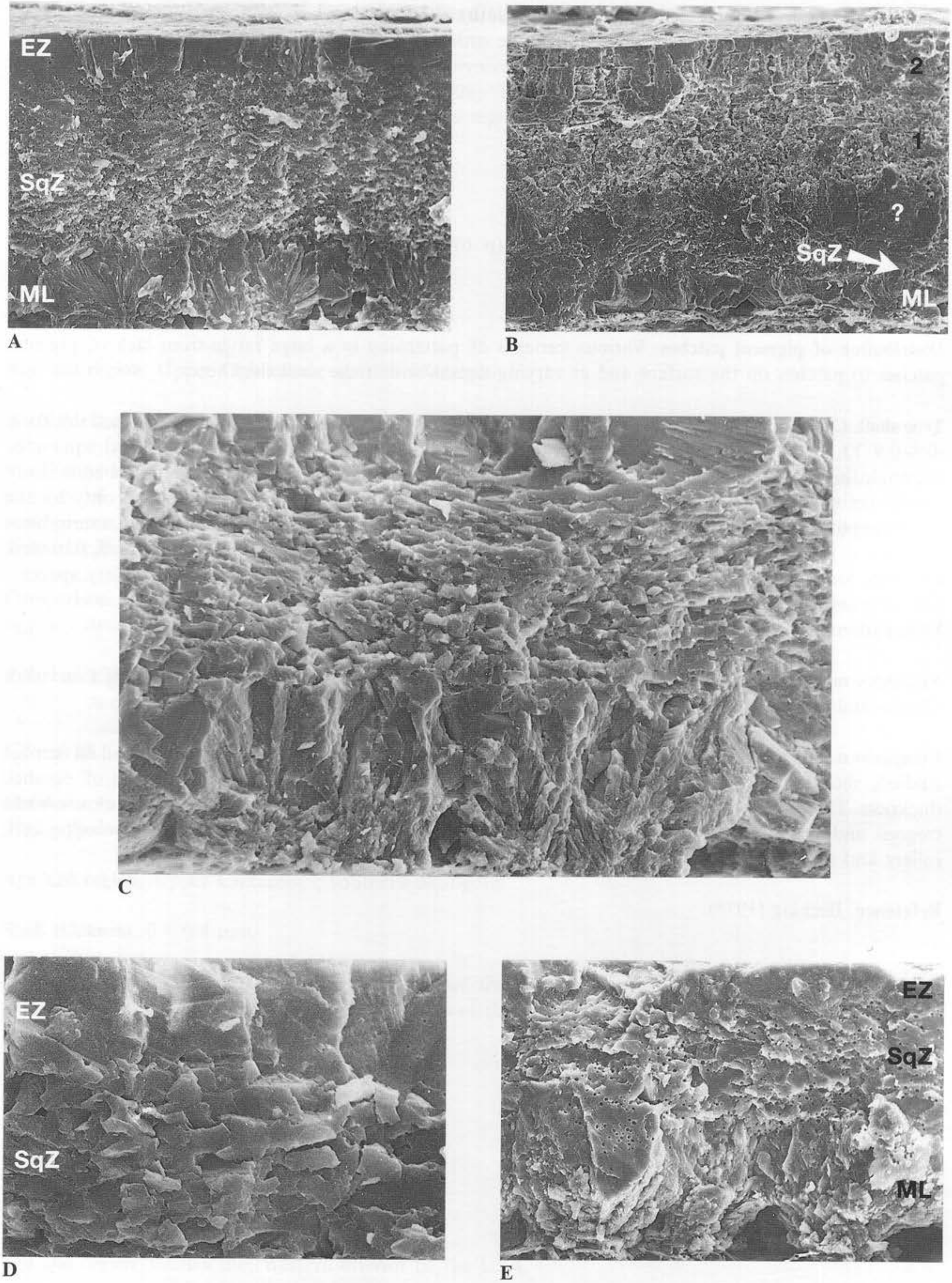
Plate 16. Eggshell structure in coraciiforms, bucerotiforms and woodpeckers (groups 23–25) (A,B,C,E – radial fractures, general view).

A – *Coracias garrulus,* ×320;

B – *Buceros bicornis*: 1,2 – peculiar structural zones (see text), ×150;

C,D – *Dryocopus martius,* C – ×700; D – cf. the ultrastructure in the squamatic and external zones, ×1500;

E – *Dendrocopos minor*, ×600.


EZ
SqZ
ML
A
2
1
?
SqZ
ML
B
C
EZ
SqZ
D
EZ
SqZ
ML
E

Comparison. Form a single structural assemblage with the coraciiform and non-parasitic cuckoo eggshells, which is separate from other arboreal neognathe orders.

Group 26

Order Passeriformes
(29 families studied, see Appendix 1)

Figs. 14F (p. 57), 15E (p. 60); Plate 15D,E,G,H (p. 67)

Shell thickness. 0.025–0.15 mm.

Distribution of pigment patches. Various variants of patterning in a large range from lack of pigment patches to patches on the surface and at varying depths within the shell thickness.

True shell. One of the 'simplified' variants of avian eggshell structure. Almost the entire eggshell thickness (0.8–0.9 T) is occupied by the continuous layer, consisting of "flaky" and well vesiculated squamatic material; the palisade arrangement of the continuous layer is notable. However, the external zone is not clearly defined in many cases (as in the, non-passerine, parrots), or can be recognised only by the "crystal-splitting" effect in the outer part of the continuous layer (as in the, non-passerine, mouse-birds and trogons). The mammillae are strongly reduced as morphological entities (0.1 T), being small, flattened, and very loosely arranged; the squamatic material penetrates into the large intermammillary spaces.

Vesiculation. Absent in mammillae and sometimes in the area of the external zone.

Accessory material. Only a thin cuticle (not found unequivocally in the available specimens of *Cincloides*, *Cinclus* and *Uragus*); in the tit (*Parus*) eggshell examined there are some globular inclusions.

Comparison. The representatives of both suborders (Deutero-Oscines and Oscines), including all 29 families studied, show a great deal of similarity in their eggshell structure within a large range of eggshell thickness. There are similarities with the eggshells of some non-passerines such as parrots, mouse-birds, trogons and swifts, but considerable differences from all other non-passerines including woodpeckers, rollers and non-parasitic cuckoos.

Reference. Becking (1975).

CRETACEOUS-EOCENE EGGSHELLS (GROUPS 27–31)

The parataxonomy of fossil eggs and eggshells involves only oofamily, oogenera and oospecies names without assignation to Order (Mikhailov *et al.* 1996). These groups are arranged according to age, from the Upper Cretaceous to the Eocene; the age and region refer only to the finds of fossil eggshells.

Group 27

Oofamily Laevisoolithidae
(enantiornithine birds)

Fig. 6E (p. 15)

Age and region. Upper Cretaceous; southern Mongolia.

Shell thickness region. 0.3–0.6 mm.

Shell structure. Consists of two distinct and sharply separated layers (ML and CL). The continuous layer consists of squamatic ultrastructure throughout (no external zone) and does not have a palisade arrangement. The mammillae are very distinctive: strong and high (occupy 0.5–0.7 T), densely packed, and exhibiting well developed wedges with tabular ultrastructure.

Comparison. Show similarities with ratite, galliform and anseriform eggshells; the most theropod-like eggshell structure within the class Aves.

References. Mikhailov (1991, 1996).

Group 28

Oofamily Gobioolithidae
(flying ?palaeognathe birds)

Age and region. Upper Cretaceous; southern Mongolia.

Shell thickness. 0.1–0.4 mm.

Comparison. In the ultrastructural organisation of the mammillae similar to ratite and gallo-anserae eggshells (two ultrastructural parts); the structure of the outer half of the eggshell thickness is strongly altered during diagenesis.

References. Mikhailov (1991, 1996).

Group 29

Family Lithornithidae

Age and region. Palaeocene; Western interior of the USA.

Comparison. Ratite-like structure.

Reference. Houde (1988).

Group 30

Family Presbiornithidae

Age and region. Palaeocene; Western interior of the USA.

Comparison. No certain conclusions can be drawn as the primary ultrastructure is completely lost during diagenesis (the pronounced palisade arrangement of the shell is quite different from flamingos and anseriforms and possibly strengthened in the process).

Group 31

Oofamily Ornitholithidae
(?diatrymas)

Age and region. Eocene; France.

Shell thickness. 1.9–4 mm.

Comparison. The mammillae are strong and elongated (as in ratite, anseriform and galliform eggshells), but the horizontal structural boundaries are ill-defined – possibly a result of diagenetic changes in fine biocrystalline structure. In eggshell thickness comparable only with extinct ratites. The most distinctive feature is the slit-like (in cross-section) pore canals which form a particular pore pattern on the undulating surface of the egg.

Reference. Dughi & Sirugue (1962).

CONCLUDING REMARKS

As eggshell ultra-microstructure is a fundamental characteristic of birds, it can be used as an additional criterion in resolving some intriguing questions of avian higher taxonomy. Although discussion of the controversies surrounding different approaches to bird classification are beyond the scope of this Atlas, some general conclusions can be derived from the results presented. These concern (1) cases where unique similarities or lack of any similarities are demonstrated and (2) where eggshell data contrast with phenetic classifications based on DNA hybridisation (Sibley & Ahlquist 1990).

The main conclusion, which can be inferred from the data, is that all members of well defined traditional orders exhibit the same eggshell structure. Another conclusion is that basic structural parallels (as a result of constraints imposed by morphogenesis) are quite common in the class Aves. These conclusions lead to two assumptions. Firstly, two families of birds within the same order will not exhibit different eggshell structures, since such differences indicate substantial biological separation. This is even more true of subfamilies within one family. Secondly, only unique similarities in the basic eggshell structure should be taken to suggest taxonomic closeness amongst families being compared.

Bearing in mind these two assumptions, analysis of the data-base of eggshell structures leads to the following conclusions:

1) Ratite, galliform and anseriform birds all show ratite-like basic eggshell structures. This does not provide reliable information as to their real taxonomic relations with each other (although particular phylogenetic closeness is admittable), but indicates that each of these groups is taxonomically very distinct from the main neognathe bulk of families.
2) Mesozoic enantiornithid birds (oofamily Laevisoolithidae) also had eggshell structures of the ratite-like type, even more similar to the theropod dinosaurs (oofamily Elongatoolthidae), than to ratites or galloanseres. Again, this only suggests them to be a particular stock of the class Aves strongly separated from the neognathe family assemblage.
3) The casuariiform birds (emu and cassowaries) share unique eggshell structures within the ratite-like basic type. This demonstrates their particular taxonomic closeness and separates them as a distinct evolutionary stock within the bulk of the traditional paleognathes.
4) Curassows, guans and megapodes (Cracidae and Megapodiidae) also share an unique eggshell structure and hence are particularly close to each other and form a separate stock within the other galliform birds.
5) Three orders of arboreal neognathes, namely Cuculiformes, Coraciiformes and Piciformes, also exhibit somewhat ratite-like eggshell structures. Although this does not inevitably imply particular relations between them (although this is admittedly possible), it clearly separates each of these orders from the rest of the arboreal neognathe taxa.
6) The group comprising the Psittaciformes, Strigiformes and Caprimulgiformes and another including the Apodiformes, Coliiformes and Trogoniformes form separate structural assemblages of orders, as do the Passeriformes.
7) All gruiforms and charadriiforms (amongst which the jacanas are most distinct) have generally similar eggshell structures, but this does not clarify any particular relationships between their different families.
8) The unusual suborder Ciconii sensu Sibley and Ahlquist (1990) is an assemblage of high ranking taxa, including (a) the Pelecaniformes (which may be separate from the Phaethontes, but allied with the Balaenicipitidae) with the Ardeiformes (Ardeidae, ?Threskiornithidae, Scopidae); (b) Falconiformes; (c) Ciconiiformes (Ciconiidae only); (d) Procellariiformes; (e) Gaviiformes; (f) Sphenisciformes; (g) Podicipediformes and (h) Phoenicopteriformes. Each of a–h are very separate groups with the Falconiformes further divided, as the Accipitridae and the Pandionidae comprise a separate group.
9) Eggshell data do not support a particular closeness of New World vultures (Cathartidae) to storks (Ciconiidae) and stress particular separation of hawk-like raptors (Accipitridae + Pandionidae) from (within?) other diurnal birds of prey.
10) In terms of eggshell structure the Hamerkop appears to be an "advanced" ardeid and the Shoebill a rather unusual pelecaniform.
11) The casuariiforms, hawk-like raptors, storks and hornbills (presumably all Upupiformes) have eggs with the most "aberrant" eggshell structures amongst the class Aves.

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APPENDIX I

A list of species whose eggshell material was examined. The list also serves as an index of the genera and species illustrated.

[**Note**: within orders, the species are listed in the traditional hierarchy of families and subfamilies; within subfamilies in alphabetic order. Scientific names follow Walters (1980). Italicised numbers are eggshell group numbers; numbers in bold are plate numbers (for species) or figure numbers (for orders).]

STRUTHIONIFORMES, *1a,* **6A**
Struthio camelus, **1A,B**

RHEIFORMES, *1a,* **6A**
Rhea americana, **1C**

CASUARIIFORMES, *1b,* **6C**
Dromaius novaehollandiae, **1I,J**

AEPYORNITIFORMES, *1a,* **6A**
Aepyornis spp., **1D**

DINORNITHIFORMES, *1c,* **6B**
Moas (?*Anomalopteryx*), **1E**

APTERYGIFORMES, *1a,* **6D**
Apteryx sp., **1G**

TINAMIFORMES, *1a,* **6D**
Crypturellus parvirostris
Nothoprocta pentlandii
Tinamus sp., **1F,H**

SPHENISCIFORMES, *2,* **7A**
Aptenodytes forsteri, **2A,B**
Pygoscelis adeliae

GAVIIFORMES, *3,* **7B**
Gavia immer
Gavia stellata

PODICIPEDIFORMES, *4,* **7C, 8**
Podiceps cristatus, **2C,D**
Podilymbus podiceps

PROCELLARIIFORMES, *5,* **7D**
Diomedea nigripes, **2E**
Fulmarus glacialis, **2H**
Puffinus puffinus, **2F**
Puffinus pacificus
Oceanithes oceanicus
Hydrobates pelagicus
Pelagodroma marina
Pelecanoides georgicus, **2G**

PELECANIFORMES, *6,* **7E, 9, 10A**
Phaethon rubricauda, **3E**
Pelecanus rufescens
Sula leucogaster, **3A**
Phalacrocorax auritus, **3B,C**
Phalacrocorax carbo
Anhinga anhinga
Fregata minor, **3D**

CICONIIFORMES, *7–11,* **7F, 10B,C,F,I**
Ardea cinerea
Ardeola ralloides
Botaurus stellaris
Bubulcus ibis
Butorides striatus
Egretta alba
Egretta garzetta
Egretta caerulea
Ixobrychus minutus
Nycticorax violaceus
Syrigma sibilatrix, **4A**
Tigrisoma lineatum
Cochlearius cochlearius
Balaeniceps rex, **5B**
Scopus umbretta, **5A**
Ciconia abdimii
Ciconia ciconia
Ciconia nigra
Leptoptilos dubius, **4C**
Mycteria americana
Mycteria leucocephala, **4B,D**
Eudocimus albus
Hadegashia hagedash
Lophotobis cristata
Plegadis falcinellus
Pseudibis papillosa
Threskiornis aethiopicus, **4E**
Ajaia ajaja

PHOENICOPTERIFORMES, *12,* **10G**
Phoenicopterus ruber, **4F**
Palaelodus sp., **4G**

ANSERIFORMES, *15a,* **10H, 12A**
Chauna torquata, **8D**
Anseranas semipalmata
Dendrocygna arborea
Coscoroba coscoroba
Cygnus atratus, **8F**
Cygnus olor
Cygnus buccinator
Cygnus cygnus
Anser anser
Anser albifrons, **8A**
Anser fabalis, **8E**
Anser (*Chen*) *coerulescens*
Anser cygnoides
Anser indicus
Branta leucopsis
Branta ruficollis, **8B**
Chloephaga picta
Alopochen aegyptiacus
Tadorna ferruginea
Anas acuta
Anas crecca
Anas poecilorhyncha
Anas undulata
Somateria mollissima
Aythia ferina
Aix galericulata
Bucephala clangula
Mergus merganser
Mergus serrator, **8C**
Oxyura jamaicensis

FALCONIFORMES, *13–14,* **11**
Cathartes aura, **6E**
Coragyps atratus, **6D**
Vultur gryphus
Pandion haliaetus, **7A**
Pernis apivorus
Elanus caeruleus
Machaerhamphus alcinus, **7E**
Milvus migrans
Haliaeetus albicilla, **7C**
Aegypius monachus
Gypaetus barbatus, **7B**
Gyps fulvus
Neophron percnopterus
Trigonoceps occipitalis
Circaetus gallicus
Polyboroides radiatus, **7D**
Circaetus gallicus
Circus aeruginosus
Accipiter gentilis
Buteo buteo
Aquila clanga
Aquila chrysaetos
Aquila cheliaca
Aquila rapax
Sagittarius serpentarius, **6C**
Phalcoboenus megalopterus
Polyborus plancus, **6A**
Milvago himango
Micrastur semitorquatus
Falco peregrinus, **6B**
Falco tinnunculus

GALLIFORMES, *15b,c,* **12B,C**
Megapodius freycinet, **9D,H**
Leipoa ocellata
Crax fasciolata, **9E,G**
Nothocrax urumutum, **9F**
Ortalis vetula
Lagopus mutus
Lyrurus tetrix
Tetrao urogallus, **8G**
Tetrastes bonasia
Odontophorus sp.
Alectoris chukar
Catreus wallichi
Chrysolophus pictus, **9C**
Exalfactoria chinensis
Gallus domesticus, **8H**
Lophura sp.
Pavo cristatus
Pavo muticus
Phasianus versicolor
Tragopan satyra
Numida meleagris, **9B**
Meleagris gallopavo, **9A**

GRUIFORMES, *16a–h,* **10D**
Turnix suscitator, **10F**
Anthropoides virgo
Grus canadensis
Grus grus, **10A**
Grus japonensis, **10B**
Grus vipio
Aramus guarauna, **10C**
Psophia leucoptera
Crex crex, **11D**
Gallinula chloropus
Fulica atra
Porzana parva
Rallus aquaticus
Rhynochetus jubatus, **10D**
Eurypiga helias, **10G**
Cariama cristata, **10H**
Otis tarda
Lophotis ruficrista, **10E**

CHARADRIIFORMES, *17a–c,* **10E**
Actophilornis africana, **11E**
Haematopus ostralegus, **11C**
Charadrius alexandrinus
Vanellus vanellus
Vanellus leucurus
Numenius phaeopus
Actitis hypoleucos, **11A**
Heteroscelis brevipes
Tringa totanus
Calidris alpina, **11B**
Gallinago media
Scolopax rusticola
Cladorhynchus leucocephala
Himantopus himantopus
Recurvirostra avosetta
Phalaropus lobatus
Glareola pratincola, **11F**
Catharacta skua
Stercorarius longicaudus, **12B**
Pagophila eburnea
Larus hyperboreus
Larus ridibundus, **12A**
Chlidonias nigra
Sterna hirundo
Rhynchops flavirostris
Aethia cristatella
Cepphus carbo
Cepphus grylle
Cyclorrhynchus psittacula
Fratercula arctica
Fratercula corniculata
Lunda cirrhata
Ptychoramphus aleuticus
Synthliboramphus antiquus
Uria aalge, **12C,D**

COLUMBIFORMES, *18,* **14B**
Syrrhaptes paradoxus, **11G**
Pterocles orientalis
Columba livia
Columba palumbus, **11H**
Columba rupestris
Streptopelia turtur

PSITTACIFORMES, *19,* **13**, **14D**
Agapornis sp., **13A**
Cacatua moluccensis, **13B**
Nymphicus hollandicus
Melopsittacus undulatus

CUCULIFORMES, *21a–c,* **15**
Opisthocomus hoatzin, **14E**
Tauraco persa, **14F**
Clamator jacobinus
Cuculus canorus, **15F**
Cuculus micropterus
Cuculus poliocephalus
Coccyzus erythropthalmus, **14D**
Phoenicophaeus sp.
Crotophaga ani, **14A,C**
Geococcyx californiana, **14B**
Centropus sp.

STRIGIFORMES, *20,* **14E**
Asio otus
Athene noctua
Bubo bubo
Ketupa blakistoni, **13D**
Otus scops
Strix aluco
Strix nebulosa

CAPRIMULGIFORMES, *20,* **14E**
Podargus sp., **13C**
Nyctibius griseus
Chordeiles minor
Caprimulgus europeus

APODIDIFORMES, *22,* **14C**
Apus apus, **15A**
Chaetura pelagica

TROCHILIFORMES, *22,* **14C**
Calipte anna, **15B**

COLIIFORMES, *22,* **14C**
Colius striatus, **15C**

TROGONIFORMES, *22,* **14C**
Harpactes oreskios

CORACIIFORMES, *23,* **14A**, **16**
Dacelo novaeguineae
Megaceryle sp.
Todus subulatus
Momotus momota
Merops apiaster
Coracias garrulus, **16A**

BUCEROTIFORMES, *24*
Buceros bicornis, **16B**

PICIFORMES, *25,* **14A**
Jynx torquilla
Dendrocopos major
Dendrocopos minor, **16E**
Dryocopus martius, **16C,D**

Picus virides
Picoides tridactilus

PASSERIFORMES, *26,* **14F, 15E**
Cinclodes sp.
Myiozetetes sp.
Alauda arvensis
Hirundo rustica
Dicrurus sp.
Oriolus oriolus
Corvus corax, **15G**
Corvus cornix
Corvus corone
Corvus monedula
Garrulus glandarius
Pica pica
Podoces panderi
Gymnorhina tibicen
Paradisea sp.
Chlamydera cerviniventris
Parus major
Suthora webbiana
Cinclus cinclus
Troglodytes troglodytes
Mimus polyglotus
Turdus hortulorum, **15D**
Luscinia calliope
Acrocephalus arundinaceus
Phragmaticola aedon
Phylloscopus occipitalis
Sylvia curruca
Muscicapa striata
Prunella modularis
Motacilla alba
Motacilla flava
Bombicilla garrulus
Lanius cristatus
Sturnus vulgaris
Nectarinia reichenowi
Pardalotus substriatus
Vireo solitarius
Passer ammodendri, **15E**
Icterus galbula
Uragus sibiricus, **15H**

EXTINCT FAMILIES AND OOFAMILIES

LAEVISOOLITHIDAE, *27,* **6E**
Subtiliolithus spp. (oospecies)
Laevisoolithus sochavai (oospecies)

GOBIOOLITHIDAE, *28*
Gobioolithus minor (oospecies)
Gobioolithus major (oospecies)

LITHORNITHIDAE, *29*
Lithornis sp.

PRESBIORNITHIDAE, *30*
Presbiornis sp.

ORNITHOLITHIDAE, *31*
Ornithoolithus spp. (oospecies)

APPENDIX 2

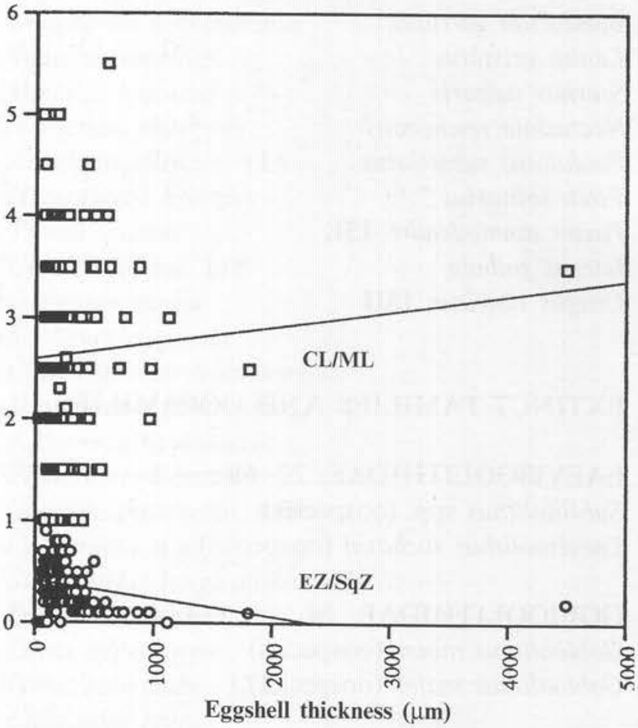


Figure 17. Thickness ratios of structural strata (CL / ML and EZ / SqZ) plotted against eggshell thickness: *y*-axis – values (0–6) of the ratio between the continuous and mammillary layers (CL / ML, squares), and between the external and squamatic zones (EZ / SqZ, circles); *x*-axis – eggshell thickness (μm). Lines are fitted regressions. Data for the class Aves.

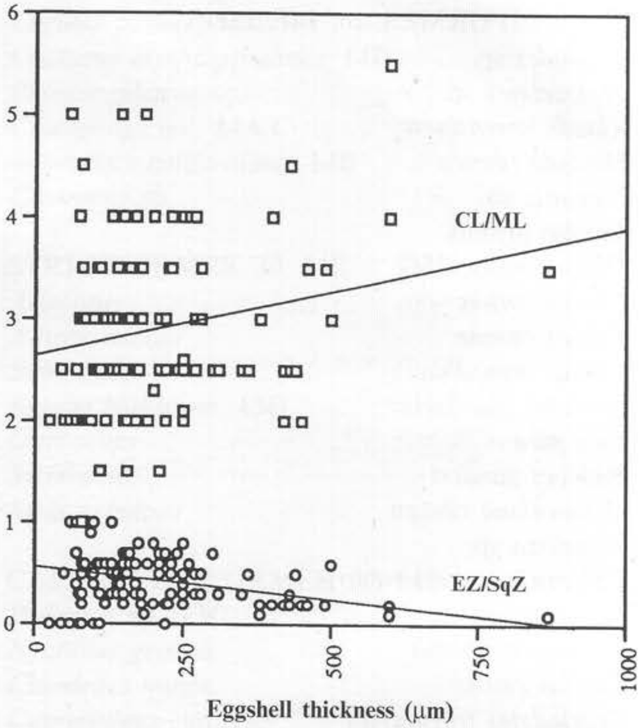


Figure 18. As for Fig. 17. Data for Neognathae.

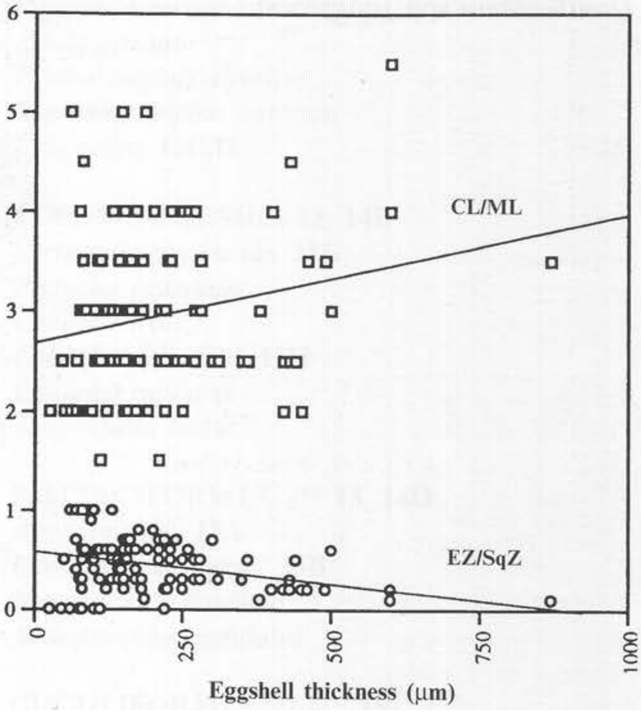


Figure 19. As for Fig. 17. Data for the class Aves but excluding the Ratitae and the Gallo-Anserae.

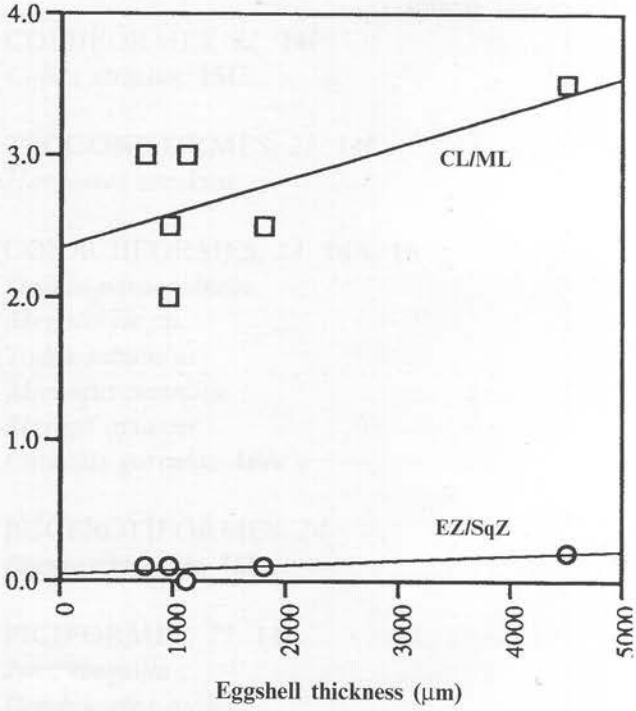


Figure 20. As for Fig. 17. Data for the Ratitae.

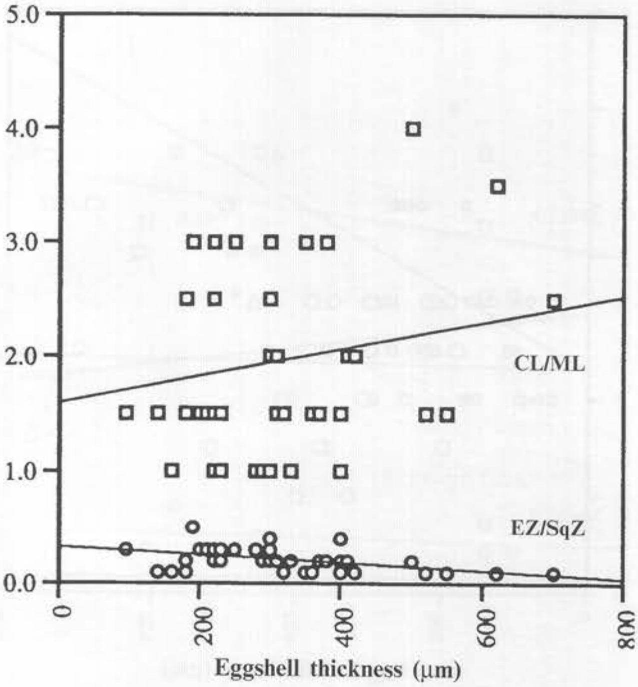


Figure 21. As for Fig. 17. Data for the Gallo-Anserae.

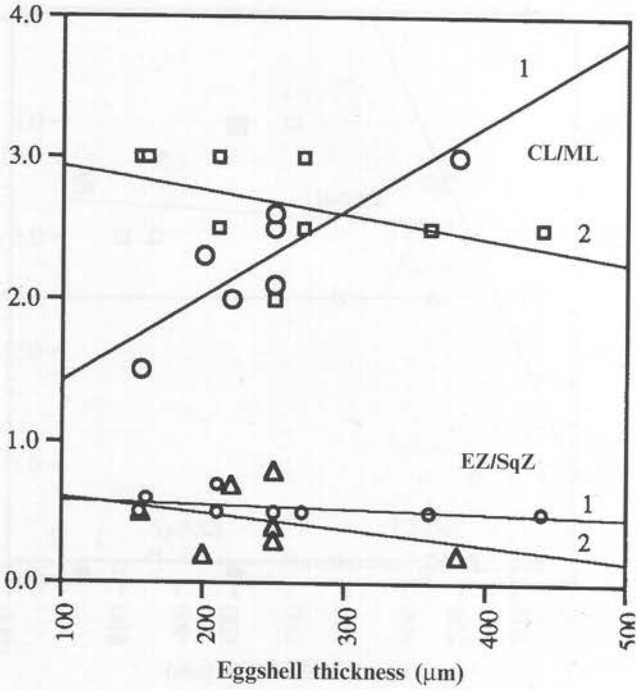


Figure 22. As for Fig. 17. Data for the Pelecaniformes (1) and the Ciconiiformes (2).

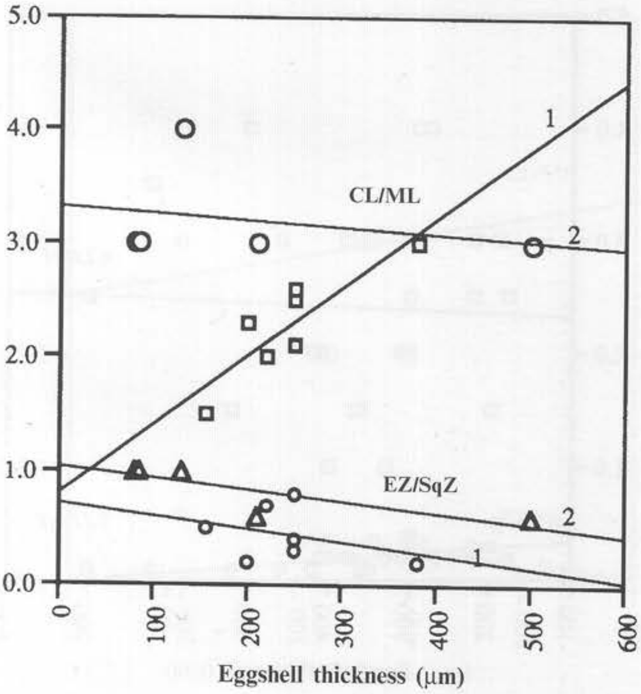


Figure 23. As for Fig. 17. Data for the Pelecaniformes (1) and the Procellariiformes (2).

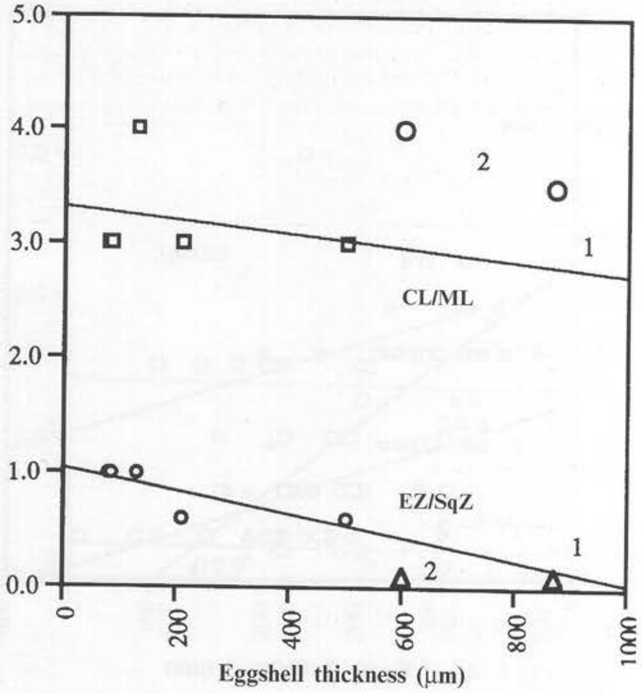


Figure 24. As for Fig. 17. Data for the Procellariiformes (1) and the Sphenisciformes (2).

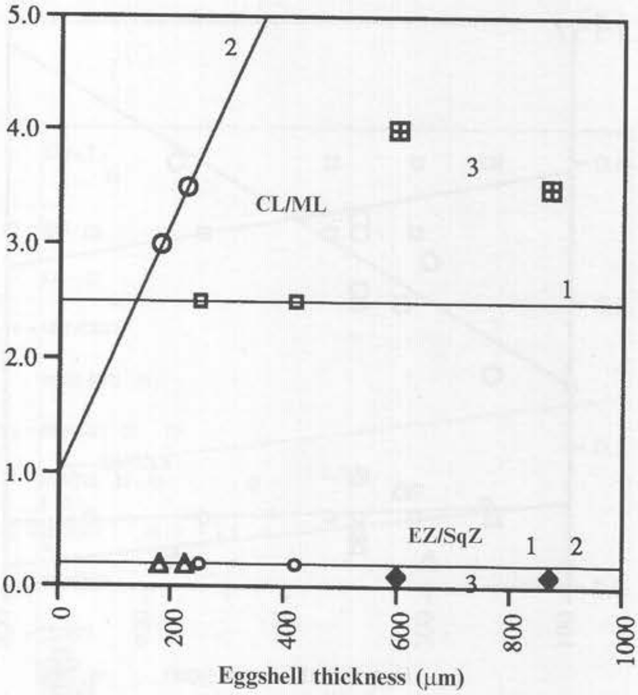


Figure 25. As for Fig. 17. Data for the Gaviidae (1), Podicipedidae (2) and the Spheniscidae (3).

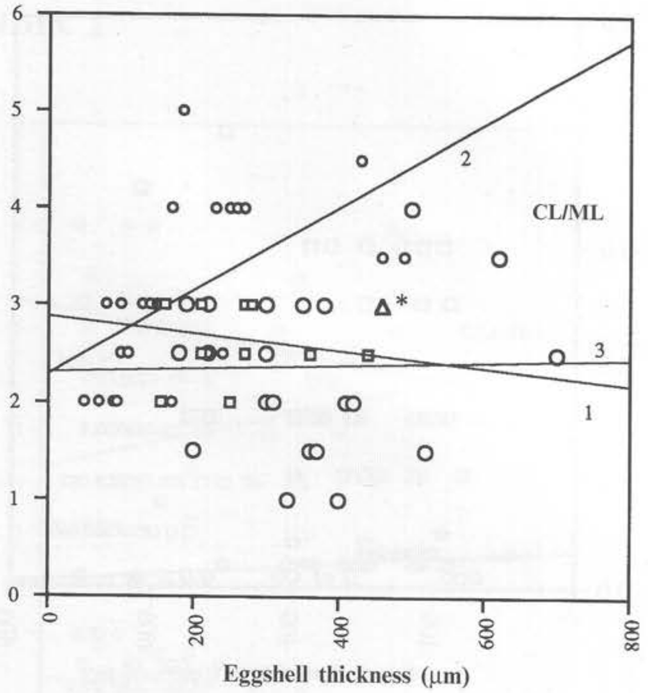
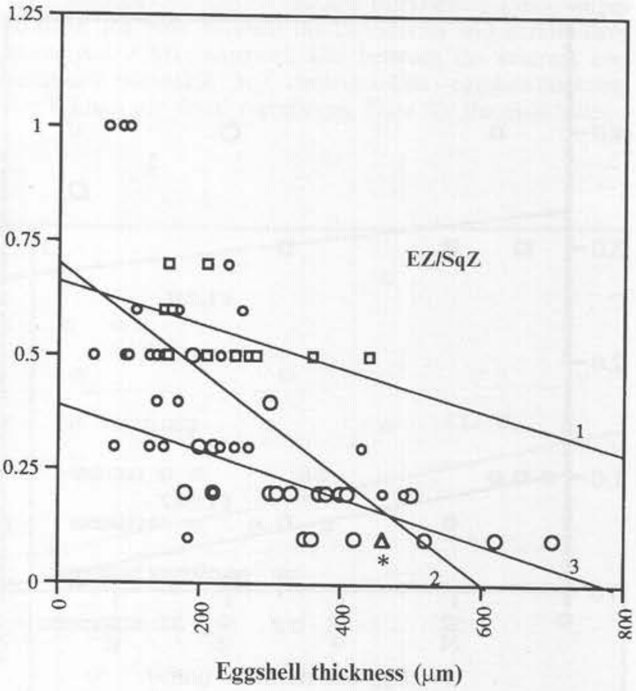


Figure 26. As for Fig. 17 but CL/ML data only for the Ciconiiformes (1), Charadriiformes (2), Anseriformes (3) and *Phoenicopterus* sp (*).



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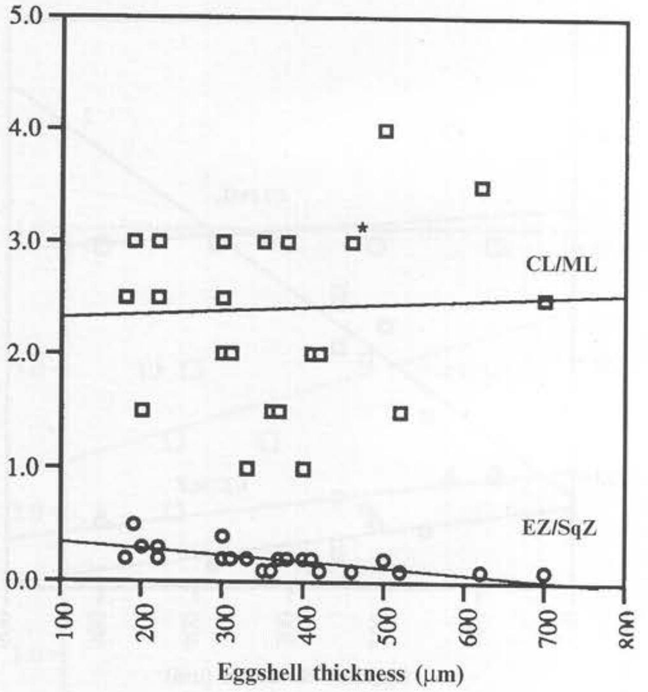

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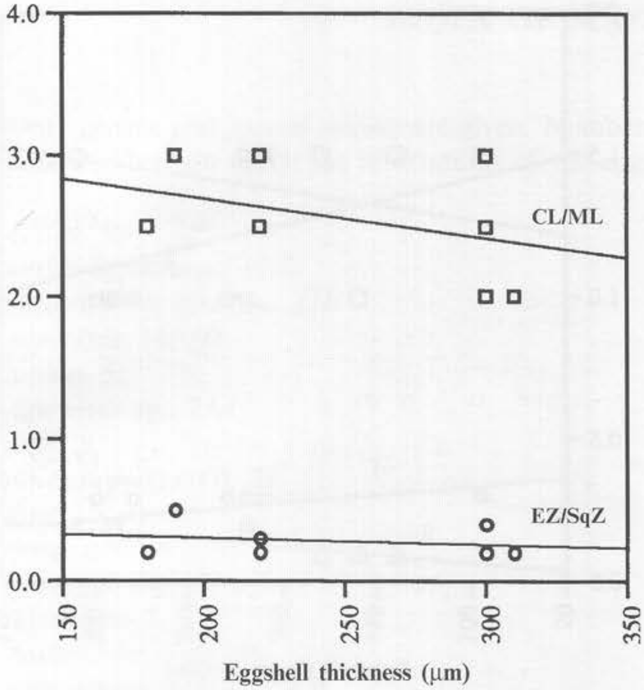

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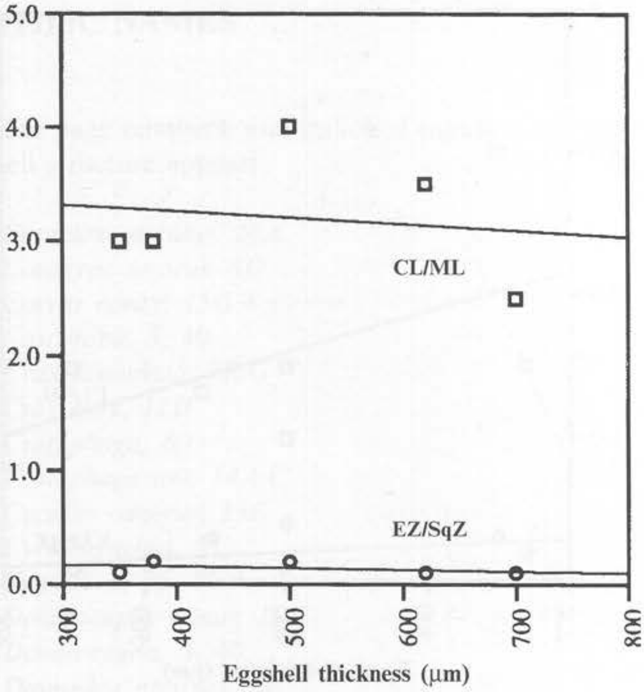

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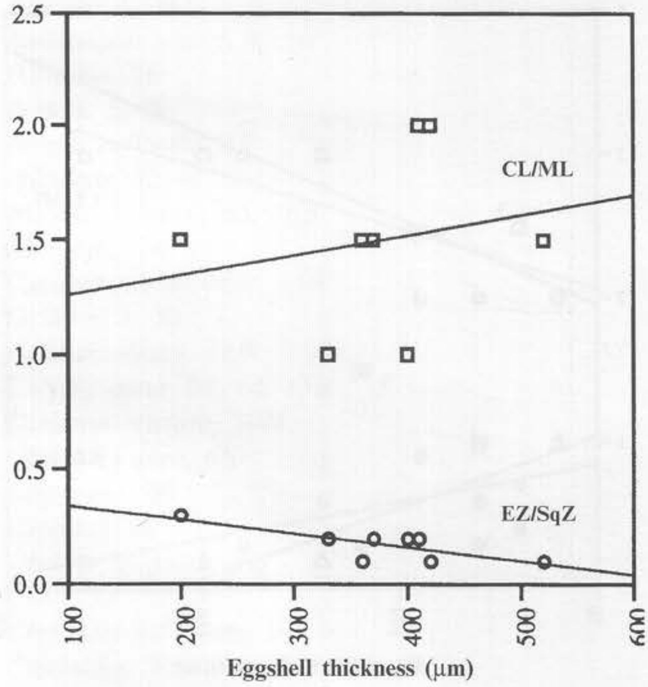

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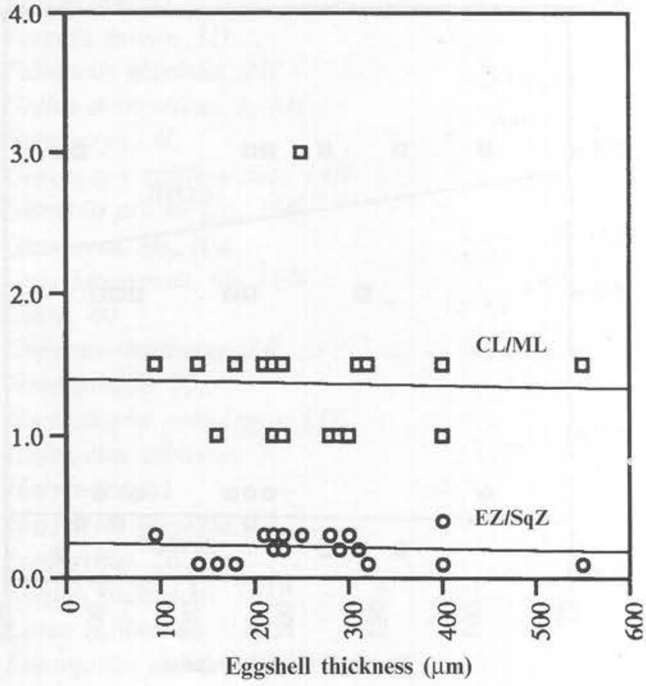

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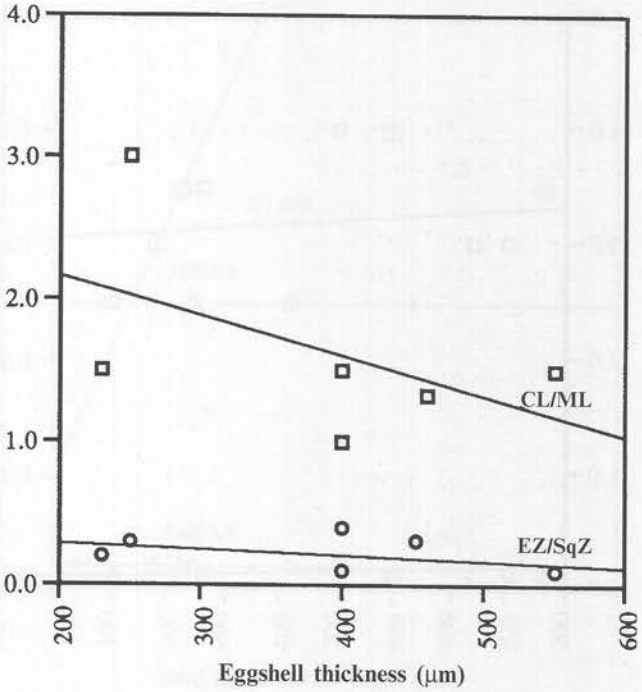

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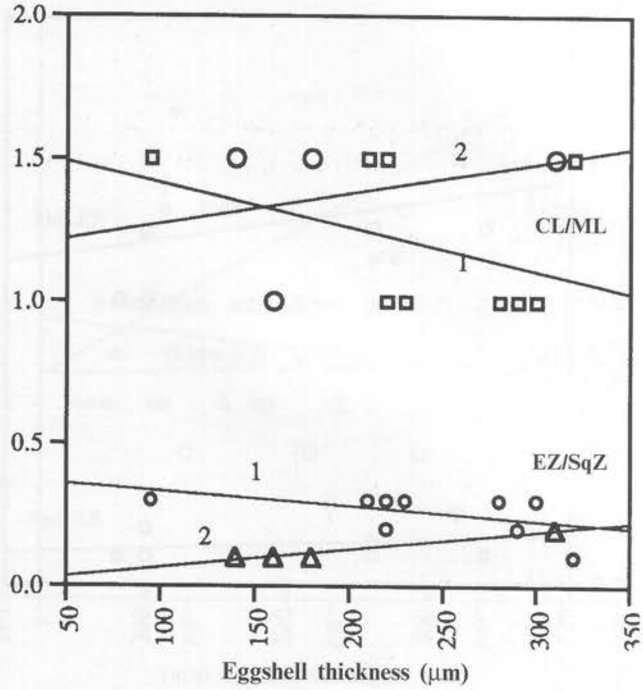

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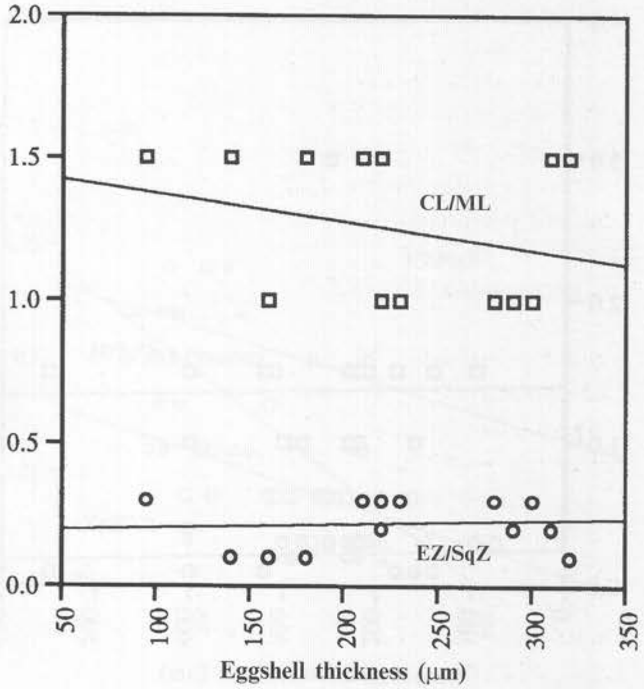

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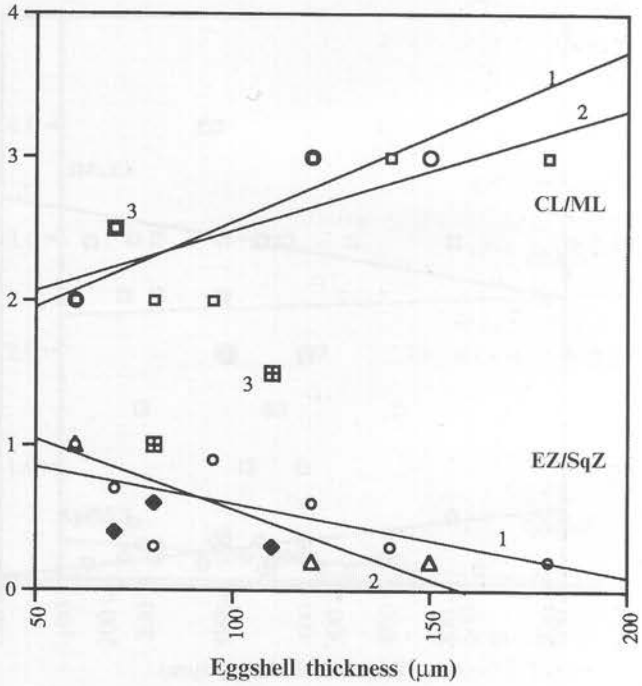

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