Ratite Eggshells and Phylogenetic Questions

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The questions of the origin and the affinities of the ratite birds "have caused more controversy among ornithologists and anatomists than any other problem in avian classification" (Bock, 1963). The proponents of a polyphyletic origin are confronted with new and substantial evidence to the contrary. Bock (1963) showed that homologous cranial structures justify the grouping of the ratites as a "single taxonomic unit". Meise (1963) listed ethological evidence for the monophyly of the ratites. Parkes and Clark (1966) found that ratites and tinamous singularly share a conformation of the rhamphotheca which they attribute to a monophyletic origin rather than to convergence.

In discussions about the origin of the Old World ratites I heard the opinion strongly advocated that the Malagasy Aepyornithidae or elephant birds were not directly or closely related to the ratites on the African continent but had an isolated insular origin, which might have happened similarly in other giant flightless birds in other parts of the world. Uncertain geological evidence was commonly mentioned in support of these speculations: Madagascar had been separated from the African continent much too long, and no land-bridge had existed at the right time to account for an immigration of this island by flightless birds. Madagascar is separated from the African mainland by more than 400 km of ocean. This separation is thought to date from Mesozoic times, which ended about 60 million years ago. If the ancestral aepyornithid birds were flightless when they reached the region of the present day Madagascar, they could have reached it on foot in late Cretaceous times. However, Madagascar may have become separated in the Oligocene. Hence early Tertiary terrestrial species could have invaded it.

My inquiry into the phyletic system of the Old World ratites is based on comparative studies of eggshells (Sauer, 1966, 68, 69). Originally I meant to trace some questions on the origin and species succession within the Struthionidae. But the studies yielded also information beyond the family range. Certain eggshells from outside Madagascar showed features otherwise typically associated with the shells of aepyornithid rather than struthionid eggs. In fact I traced "aepyornithoid" eggshells to Punjab and Inner Mongolia. My search gained new momentum when Peter Rothe (1964) uncovered his original find of ratite eggshells from Lanzarote, one of the eastern Canary Islands.

On the following pages I shall describe the pore patterns and associated structures that characterize the eggshells of the families Struthionidae and Aepyornithidae. Then I shall attempt to clarify some questions concerning the Lanzarote finds and a number of earlier collections from Asia. If we can trust morphological evidence, and I see no reason why the morphology of ratite eggshells should not be used as a reliable means of classification, then the Struthionidae and Aepyornithidae must have more in common than is known to date.

Acknowledgments

Colleagues and institutions provided help, advice, and collections that made this study possible. I am grateful to P. Brodkorb, University of Florida; A. J. Charig, British Museum (Natural History); E. H. Colbert, Museum of Northern Arizona, formerly American Museum of Natural History; C. P. Holton, American Museum of Natural History; L. Marden, National Geographic Society; E. Mayr, Museum of Comparative Zoology; P. Rothe, University of Heidelberg; A. Wetmore, Smithsonian Institution, U. S. National Museum; and to my wife Eleonore M. Sauer.

The scanning electron microscope was made available through Prof. H. K. Erben, Department of Paleontology, University of Bonn, and operated by Mrs. M. Leipelt who also prepared the specimens.

Financial aid was provided from the National Science Foundation, Washington, D. C. (Grant GB-5077), from the University of Florida, and from the Zoological Research Institute and Museum Alexander Koenig.

Abbreviations

AMNH The American Museum of Natural History, New York

BMNH British Museum (Natural History), London

MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

SEM Scanning Electron Microscope (Stereoscan, Cambridge Instrument Company, Ltd.) at the Department of Paleontology, University of Bonn

"type A" eggshells = aepyornithoid (explanation p. 22)

"type S" eggshells = struthious

The Pore Pattern of Struthionid Eggshells

The use of avian eggshells in systematics was introduced in the last century through the pioneering work of Landois, Blasius, and W. v. Nathusius (see Sauer, 1966). Schönwetter (1927) based the subspecific classification of the recent ostriches, except *Struthio camelus syriacus*, on differences in the pore pattern of their eggshells (Fig. 1). He showed that these features are subspecifically distinct. The shells of two subspecies possess tiny circular pore openings which are solitary and scattered diffusely *(S. c. camelus)* or grouped with irregular grooves *(S. c. spatzi)*. These pores and grooves are so small that they are invisible to the naked eye. In the other races the eggshell surfaces show visible pits in which the pore canals open through multiple circular pores and irregular grooves that form more or less distinct patterns *(S. c. australis, S. c. massaicus, S. c. molybdophanes)*.

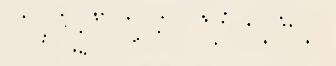
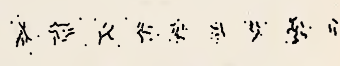
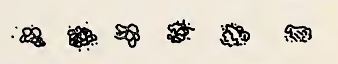
Struthio c.	pattern	n/cm^2	⌀ mm	pores and grooves ⊢⊣ 1 mm
1 camelus	single pores	100	.02–.03	
2 spatzi	groups of pores + grooves	70 2	.01–.02 .5	
3 australis	reticulate grooves	12	.5	
4 massaicus	composite of 3 & 5	8	.8	
5 molyb–dophanes	clusters of 30–70 pores	10	1.0	

Fig. 1 Pore patterns of struthious eggshells after Schönwetter (1927). n number and ⌀ diameter of solitary pores and pore pits, respectively.

Porenmuster der Eierschalen rezenter Strauße nach Schönwetter (1927); n Anzahl und ⌀ Durchmesser der Nadelstichporen oder, wo vorhanden, der Porenhaufen.

Schönwetter laid a sound foundation for a system that identifies subspecies of the recent ostriches according to the pore patterns of their eggshells, but his findings must be supplemented. Although he partly depicts it, he does not mention that the tiny circular pore openings in the smooth-surfaced shell from *S. c. camelus* occur not only as solitary pores in diffuse distribution but also typically in small groups and rows of mostly two and three, or occasionally a few more openings. Also the subspecific occurrence of the circular pores and the variation in the pattern of the pore grooves are greater than indicated by Schönwetter. Eggshells of *S. c. australis,* for example, may show patterns that Schönwetter restricts to *S. c. spatzi* and *S. c. massaicus.*

A few remarks will clarify the features of the pore canals known from struthionid eggshells (Fig. 2). The diagram is a composite as regards the pore canal morphology; however the shell layers are drawn from a single piece of *S. c. australis* eggshell. The pore canals extend from between the tops of the mammillae through the spongiosa and the two cuticular layers to the outer surface of the shell. They are either unbranched or branched. The unbranched ducts may be solitary or grouped; in the latter case they are aligned parallel (Fig. 2) or first diverging and then converging as they penetrate to the surface. Occasionally two parallel canals may fuse in the outer spongy layer and form a common duct the shape of a figure-eight in cross-section (Fig. 3 c). The branches of a pore canal form a well-defined canal system. In addition to the canal type shown in the scheme, a canal may branch at different depths, even close to its base near the mammillary layer.

The pore canals open through circular or oval pores either directly on the smooth surface of the shell or in grooves that are irregular in shape

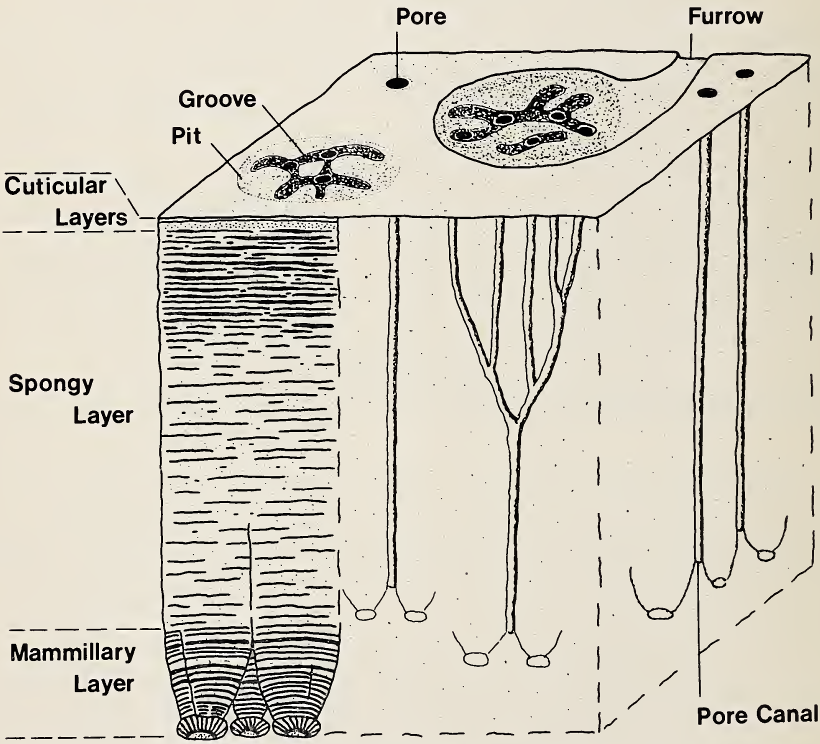


Fig. 2. Scheme of the struthionid pore canal systems and eggshell layers. Further information in the text.

Schema des struthioniden Porenkanalsystems und des Aufbaues der Eischale. Erklärungen: Pit = Grube, groove = Rille, pore = Pore, furrow = Furche, pore canal = Porenkanal; cuticular layers = Cuticularschichten, spongy layer = Sponginschicht, mammillary layer = Mammillarschicht.

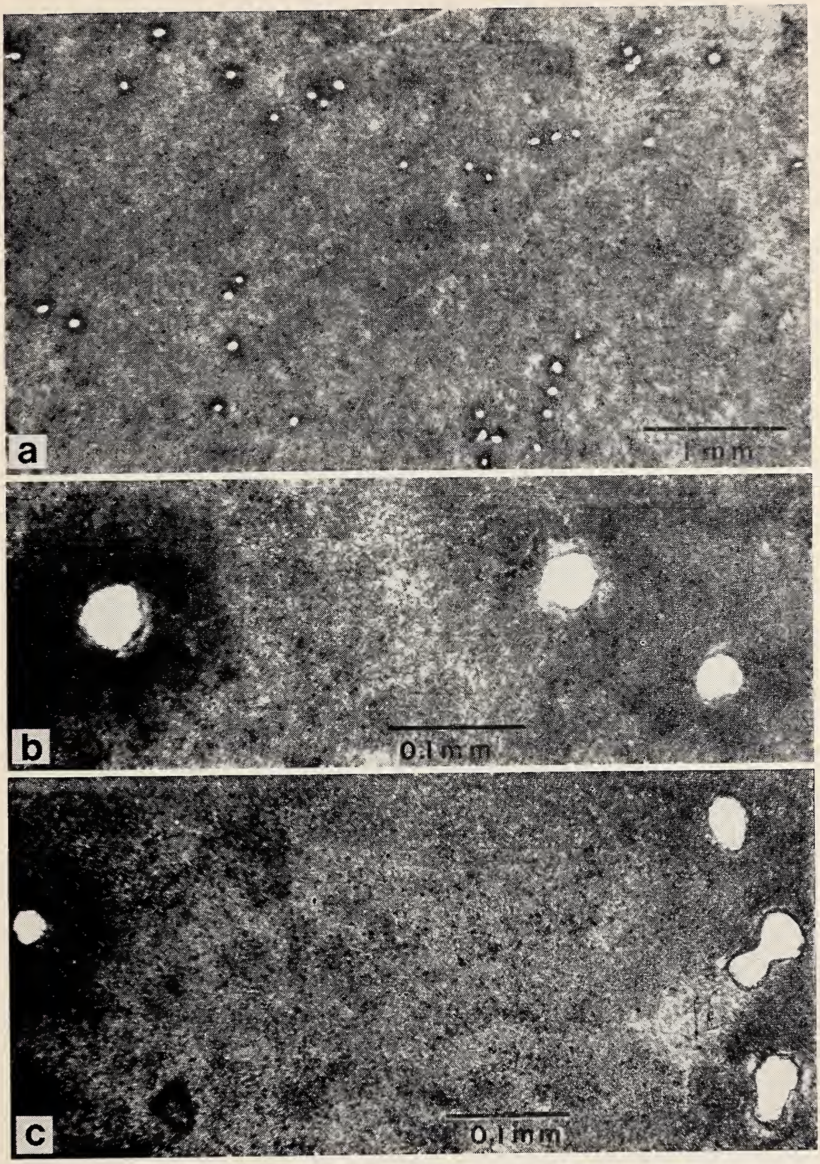


Fig. 3. Pore pattern of a *S. c. camelus* eggshell (BMNH, No. A 2173) revealed in a tangential section through the outer part of the spongy layer; a) distribution, b, c) enlarged solitary and fused pores.

Porenmuster einer Eischale von *S. c. camelus,* dargestellt anhand eines Dünnschliffes tangential durch die äußere Sponginschicht; a) Verteilung, b, c) Vergrößerung solitärer und verschmolzener Nadelstichporen.

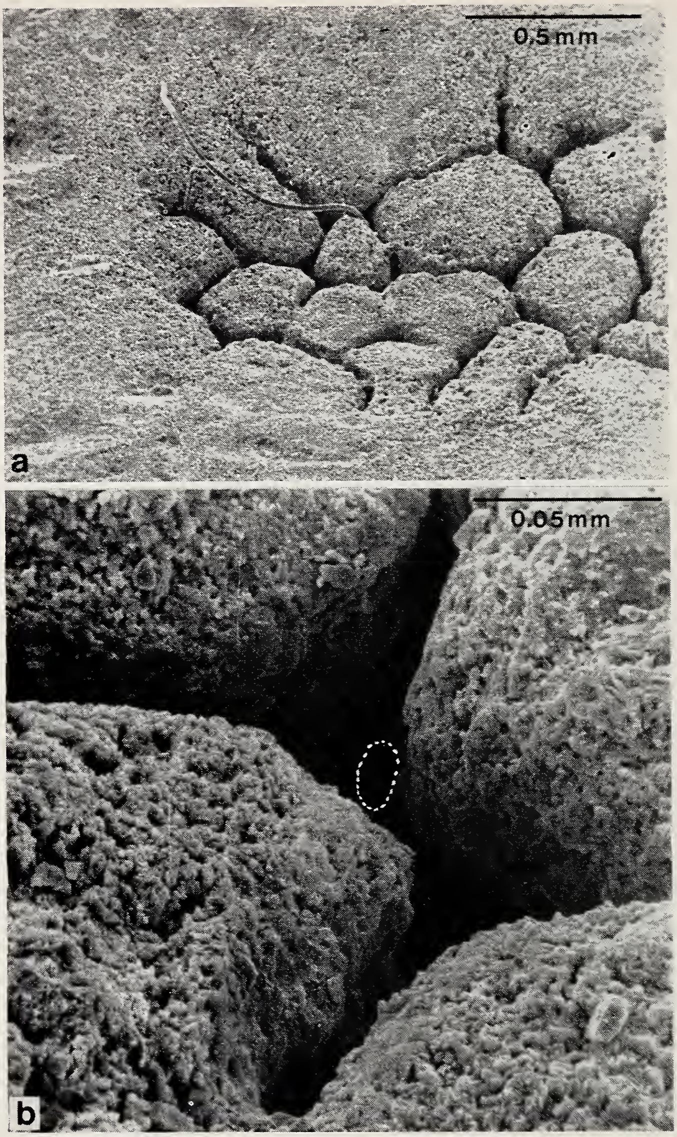


Fig. 4. Pore grooves of a *S. oshanai* eggshell seen in SEM-micrograph; a) pit with grooves arranged in a rosette pattern, b) enlarged section with pore opening (marked with dotted line) at the bottom of the groove.

Porenrillen einer Eischale von *S. oshanai* in einer Aufnahme mit dem Raster-Elektronenmikroskop (REM); a) Grube mit Porenrillen in rosettenförmiger Anordnung, b) vergrößertes Teilbild mit einer Porenöffnung (gestrichelte Hilfslinie) am Boden der Porenrille.

and frequently branched. The pattern of the grooves varies from simple to complex. It can be described as irregular, reticulate, and rosette. According to Schönwetter (1927) the pore grooves of *S. c. spatzi* are located right in the smooth surface of the shell. In the other struthionids they are commonly arranged in pits. The pits may be deepened into furrows which connect two or several neighboring pits. The pore pits are mostly scattered diffusely over the shell surface; here and there they can be variously arranged in loose clusters or lined up in irregular rows.

Examples of the patterns of circular pore openings in the smooth shell surface and in grooves illustrate the struthionid systems. The pictures of the Asiatic eggshells (Figs. 5, 6, 23 and 24) and of the Lanzarote eggshells of the "type S" (Figs. 14, 15) present the typical surface pattern of irregularly distributed circular pore openings that corresponds closely with that of a *S. c. camelus* eggshell. The pattern of the latter is shown in a traditional way by a thin section through the outermost part of the spongy layer which reflects the distribution and shape of the pores on the shell surface (Fig. 3). The scattered pores are solitary or arranged in short rows and groups of two to five. The ducts are mostly circular in shape; occasionally two are fused into one forming a common passage the shape of a figure-eight in cross-section.

The pore pit of a shell from the fossil Oshana Ostrich, *S. oshanai*, provides an excellent example of the grooved struthionid eggshell (Fig. 4). The grooves form a rosette pattern. Located in their depth are the openings of the circular pore canals.

In order to present a sufficiently comprehensive picture of the known struthionid eggshells, I refer the reader also to the typically struthious "*Psammornis*" eggshells (see Sauer, 1969) with their fine needle-point pores. The same pore pattern is also revealed in those eggs which are collectively attributed to the Pliocene-Pleistocene genus "*Struthiolithus*" (Figs. 5, 6). Actually there is no need to separate these specimens from the genus *Struthio*. The pore pattern is not the same in all specimens correctly or incorrectly labeled "*Struthiolithus*". However, the pattern of the typical shells compares well with that of the *S. c. camelus* eggshell. Circular pore openings reach the smooth surface of the shell and form an irregular pattern of distribution. Many of the "*Struthiolithus*" eggs from Pleistocene times were recovered unbroken. Their shape is convincingly struthious (Sauer, 1968). Most of the egg surfaces are affected by erosion, which enlarged and even obscured the pores in various ways (Figs. 5, 6). These effects are illustrated to point out that erosion does not create a pattern that might resemble a type of eggshell which I categorize as aepyornithid or aepyornithoid.

Aside from the typical "*Struthiolithus*" eggshells there are collections of shell fragments which the collectors firmly or questionably labeled

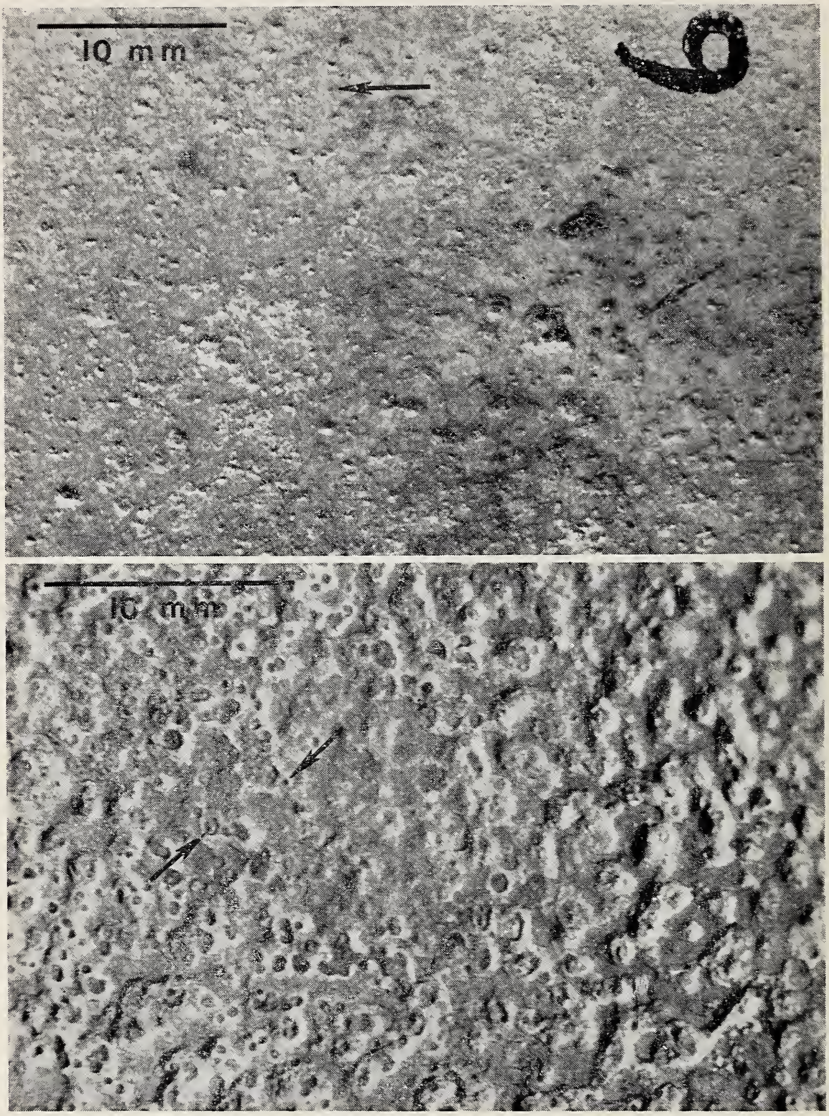


Fig. 5. Pattern of needle-point pores of a "*Struthiolithus*" egg from Pleistocene loess deposits of north China (AMNH, No. 6688); partial views of the whole eggshell with a) slightly, b) heavily eroded surface. Arrows in Figures 5 and 6 point out some representative pores of the obscured pore pattern.

Nadelstichporen eines „*Struthiolithus*"-Eies aus pleistozänen Lößablagerungen in Nordchina; Teilansicht des Eies mit a) leicht und b) stark erodierter Oberfläche. Die Pfeile in den Abbildungen 5 und 6 erleichtern das Auffinden einiger typischer Poren.

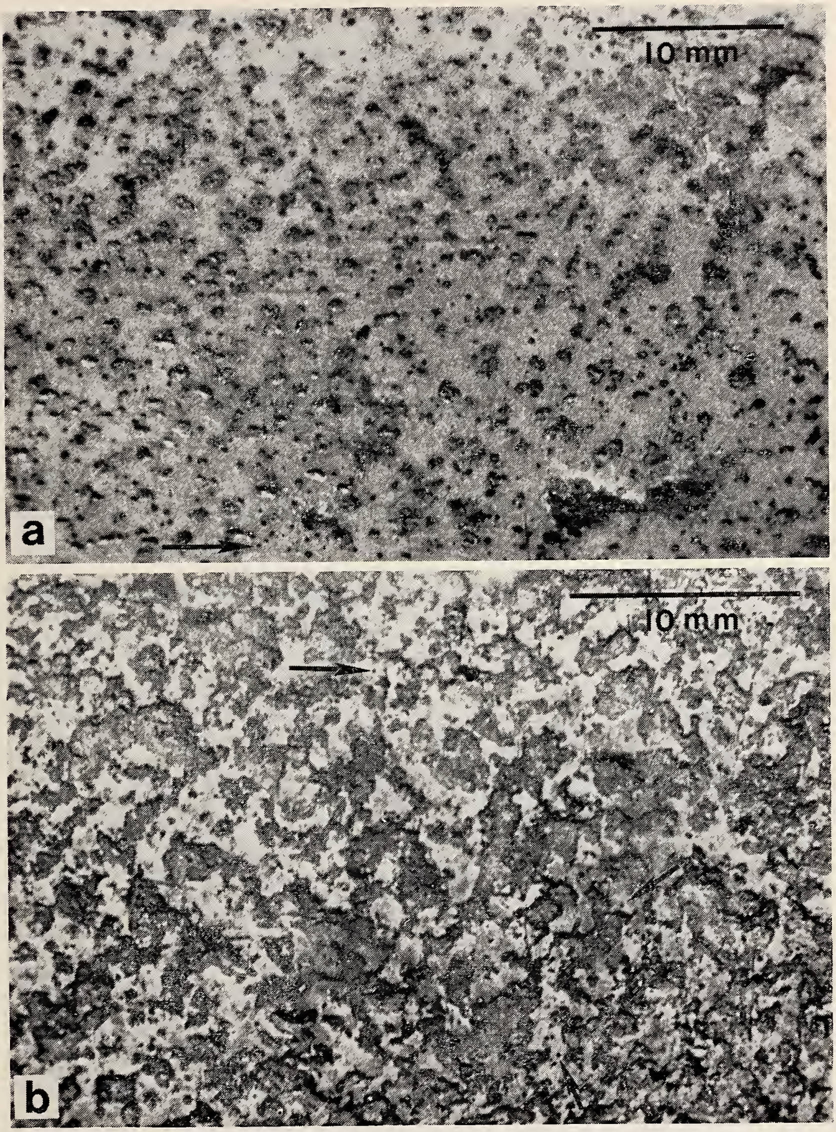


Fig. 6. Pattern of needle-point pores of a "*Struthiolithus*" egg from the Pleistocene of "Honan or Shantung, China" (AMNH, No. 6815), a) slightly, b) heavily obscured by erosion.

Nadelstichporen eines „*Struthiolithus*"-Eies aus pleistozänen Lößablagerungen von Honan oder Shantung, China; a) leicht, b) stark erodierte Schalenoberfläche.

"Struthiolithus". It will be pointed out that not all of these collections are representative of the *"Struthiolithus"* type eggshell (p. 24 ff.).

Pore Patterns of Aepyornithid Eggshells from Madagascar

The morphologically conspicuous feature of aepyornithid eggshells is the alignment of the linear, here and there bent and forked pore grooves, the short "dagger-point" or "comma" pores, and the oval "sting" pores. They are predominantly oriented parallel to one another and to the longitudinal axis of the egg (Figs. 7—9). Some eggs in which the short dagger-point and sting pores prevail, may have some areas in which the pore openings form localized diffuse or "whirlpool" patterns. This occurs particularly on the poles of the eggshell. As the shape of the pores remains unmistakably distinct, and as the pattern of parallel alignment of the pore openings is preserved in other parts of the same egg, it can still be recognized as aepyornithid.

It is the pronounced linear pattern that marks the aepyornithid eggshells as unmistakingly different from the struthionid eggshells with their diffusely scattered micropores and the irregularly curved and frequently branched grooves.

The linear arrangement of the aepyornithid pore openings remains recognizable in the different shell types which range from those with a pronounced presence of linear grooves to those in which the number of grooves is variously reduced in favor of the short dagger-point and sting pores. Additional family-specific features are mentioned below. The material which is discussed and compared here comes from different sites on Madagascar and varies in age. The shell fragments from Tulear (Belalande) and Ampamalora are radiocarbon-dated, based upon the Libby half life (5570 years) for C^{14}. I obtained the dated material from Alexander Wetmore through the generosity of Louis Marden from National Geographic Society.

The *Aepyornis* shell fragment from St. Augustine, southwest Madagascar, reveals the prominence of long linear pore grooves (Fig. 7). This pattern is characteristic of many *Aepyornis* eggshells and seems to characterize one particular group of elephant birds. The piece is on the average 3.30 mm thick.

Nine pieces of eggshell from the Ampamalora locality are collectively dated 1970 $\pm$ 90 years B. P. The fragments are diverse in the type and thickness. The latter varies from 2.88 to 3.55 mm. Two pieces (3.32 mm thick) possess the pronounced long pore grooves (Fig. 8 a). The remaining fragments from different eggs are of the kind characterized by a majority of dagger-point and sting pores, many of which are strung in short longitudinal rows (Figs. 8 b, c).

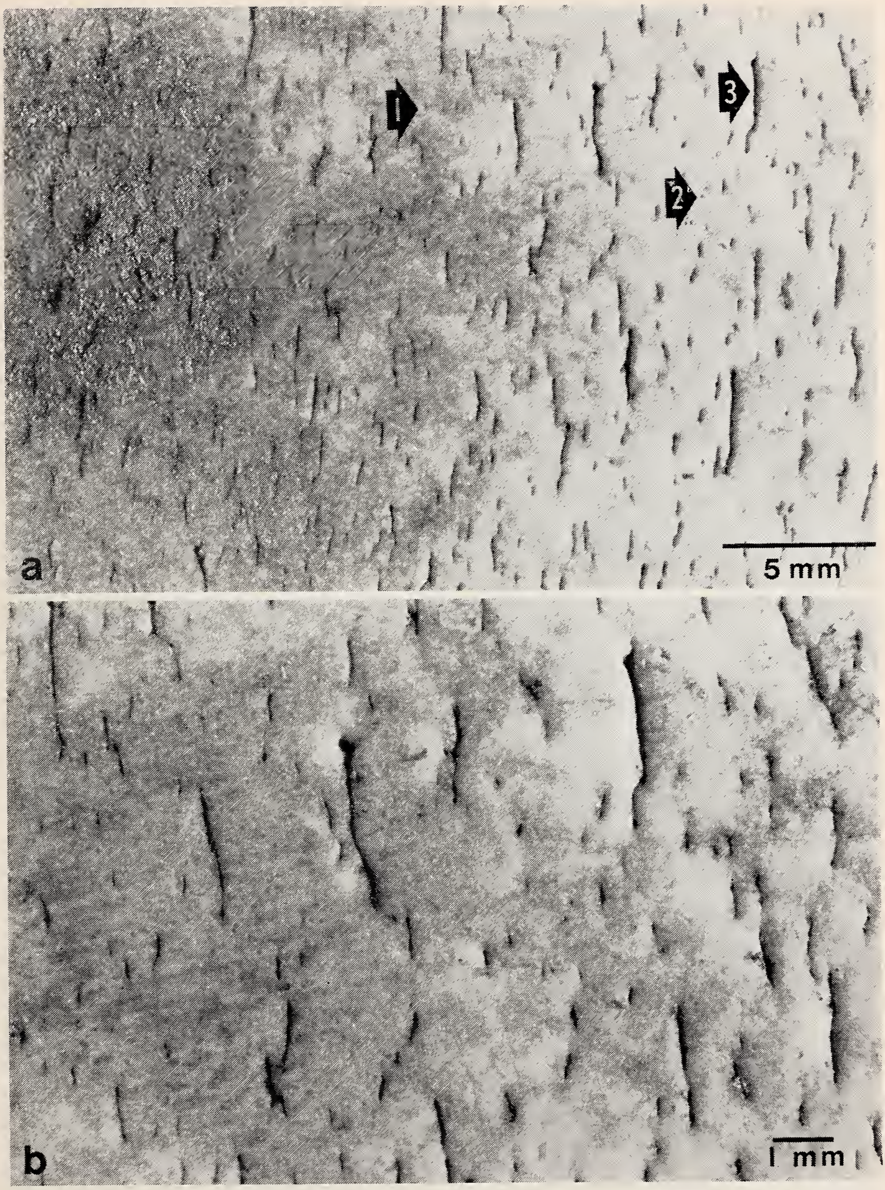


Fig. 7. Pore pattern of an *Aepyornis* eggshell from St. Augustine, southwest Madagascar, (MCZ, No. 3692). Examples of dagger-point pores (1), sting pores (2), and linear grooves (3) are marked in (a) and are easily relocated in the enlarged section (b).

Porenmuster einer *Aepyornis*-Eischale von St. Augustine, Madagaskar. Beispiele von Dolchstichporen (1), Stichporen (2) und linearen Porenrillen (3); a) Übersicht, b) Vergrößerung.

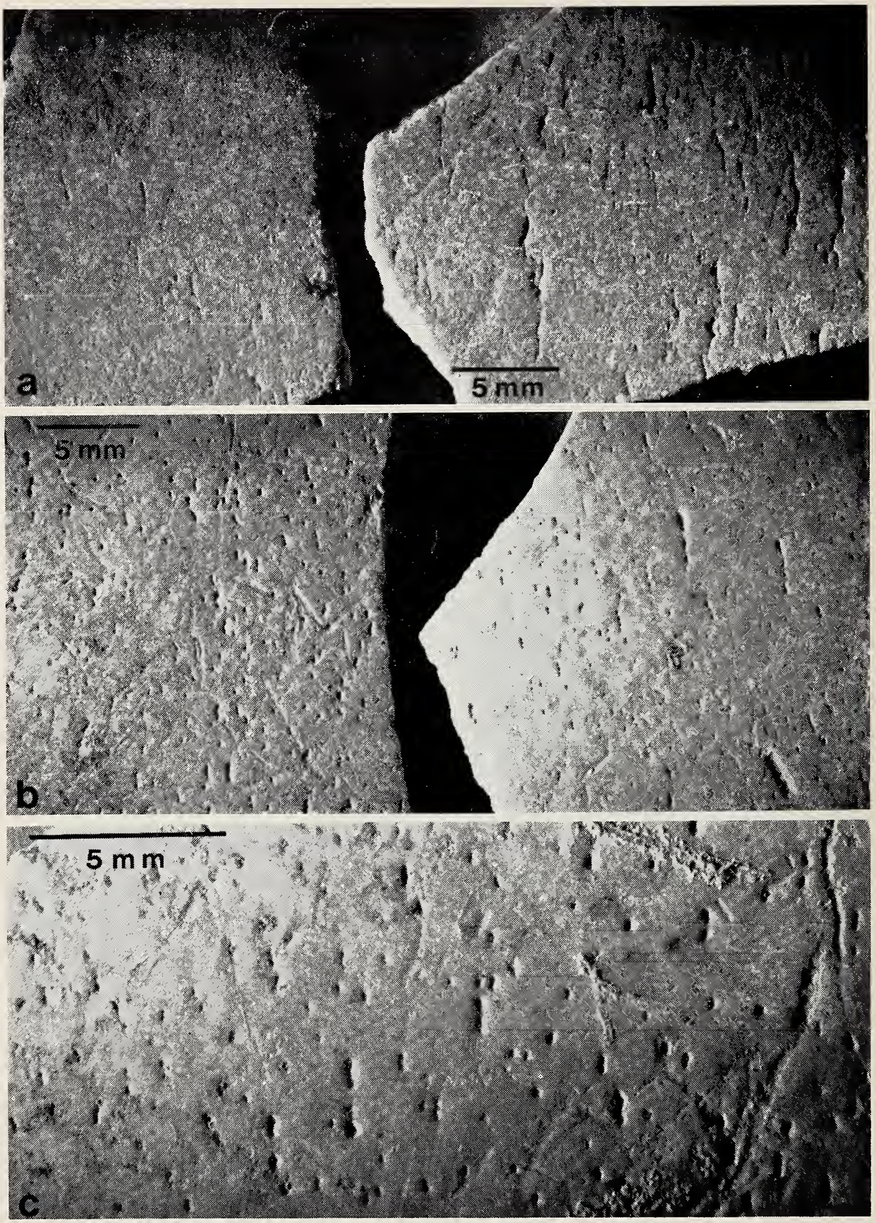


Fig. 8. Aepyornis eggshell fragments from Ampamalora, Madagascar, with majorities of a) grooved and b, c) dagger-point und sting pore openings.

Aepyornis-Eierscherben von Ampamalora, Madagaskar, mit überwiegenden a) Porenrillen, b, c) Dolchstich- und Stichporen.

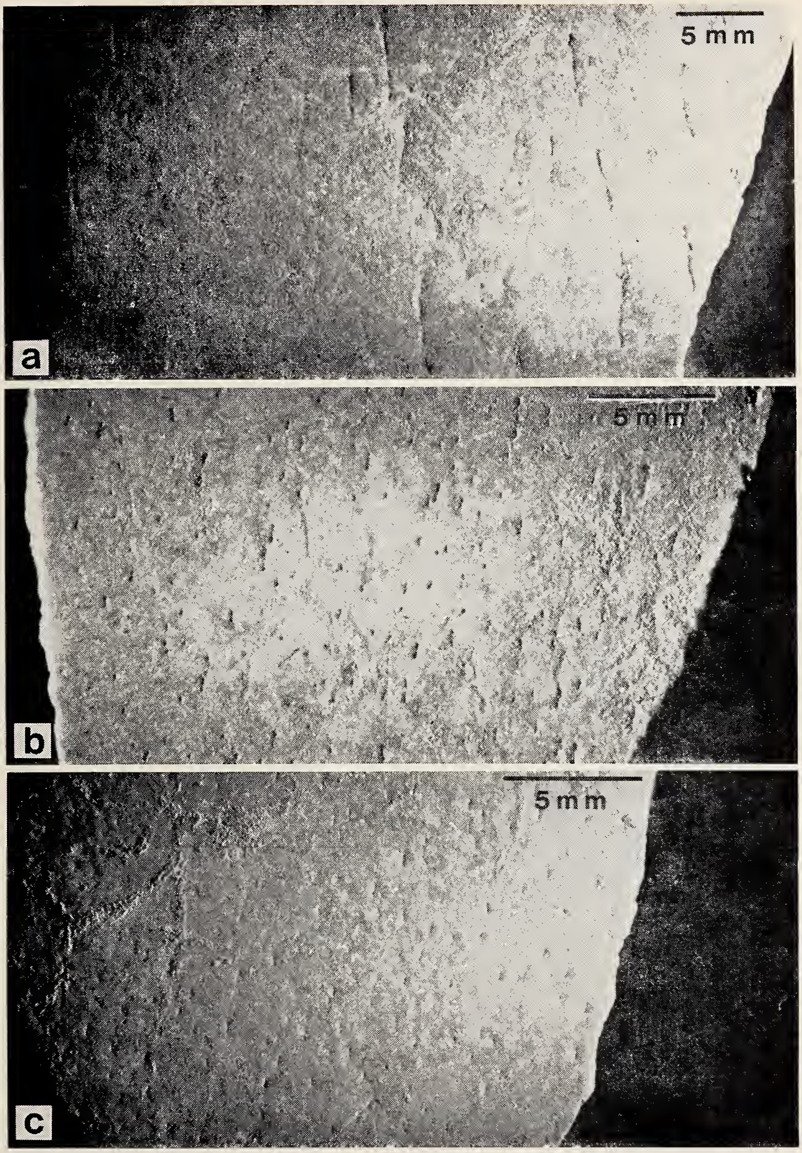


Fig. 9: Aepyornithid eggshell fragments from Tulear, Madagascar. a, b) *Aepyornis* shells with a) pronounced linear grooves and b) sting and dagger-point pore pattern. c) "*Mullerornis*" eggshell with very fine dagger-point and sting pores.

Aepyornithide Eierscherben von Tulear, Madagaskar. a, b) *Aepyornis*-Schalenfragmente mit a) überwiegenden linearen Porenrillen und b) mit Dolchstich- und Stichporen. c) "Mullerornis"-Eierscherbe mit sehr feinen Dolchstich- und Stichporen.

The equally heterogeneous shell collection from the Tulear site is dated 5210 ± 140 years B. P. Among the twelve thick fragments (3.13—4.30 mm) are again some with very long grooves (Fig. 9 a), some with shorter grooves, and others with the pronounced pattern of dagger-point and sting pores (Fig. 9 b). Of particular interest is one exceptionally thin shell fragment, averaging 1.40 mm in thickness, with very fine sting and dagger-point openings (Fig. 9 c). A. Wetmore (pers. comm.) suggested that this shell is "presumably *Mullerornis*".

The elongate shape of the dagger-point and sting pores and the general appearance of the pore openings in *Aepyornis* eggshells are shown in the SEM-micrographs (Figs. 10 and 11). Several of the pore openings are interconnected by tangentially oriented microducts. This is another aepyornithid feature and unknown in struthious eggs. Where they are present, the linear, triangular and complex patterns of these microducts between neighboring pores become very conspicuous when the shell surface is eroded (Fig. 11), or when one makes a tangential section through the outer part of the spongy layer (Fig. 12).

Furthermore, certain *Aepyornis* eggs harbor large, in part interconnected lacunae in the spongy layer (Fig. 13). This feature, whose function is still not fully understood, is also a peculiarity of the aepyornithid eggshell and is unknown in struthious eggs. The lacunae presumably aid in ventilating the particularly thick-shelled eggs of certain species of elephant birds.

In summary, the aepyornithid eggshells possess a number of family-specific and possibly species-specific properties in their pore patterns by which they can be distinguished from the struthious eggshells. It should be noted that most of the aepyornithid eggshells from Madagascar are merely attributed to the genus *Aepyornis* and not to any species.

Rothe's Discovery of Ratite Eggshells on Lanzarote

In 1963, while searching for answers about the much disputed geological origin of the Canary Islands, Peter Rothe unearthed some fossil eggshells on Lanzarote, one of the islands in the northeast corner of the Canary Islands. Rothe (1964) identified the well-preserved material as struthious and concluded that the eggs belonged to Mio-Pliocene ostriches that must have been at least closely related to the recent ostrich. He noted no similarities in eggshell structures with other ratite eggs. Two nearly completely preserved eggshells measured 15 × 12 × 7 cm (laterally compressed from pressures of the embedding matrix) and 15.0 × 11.5 cm. This places the eggs in the range and shape of struthious eggs (see Sauer, 1968). Comparably, the shell fragments were on the average 2 mm thick.

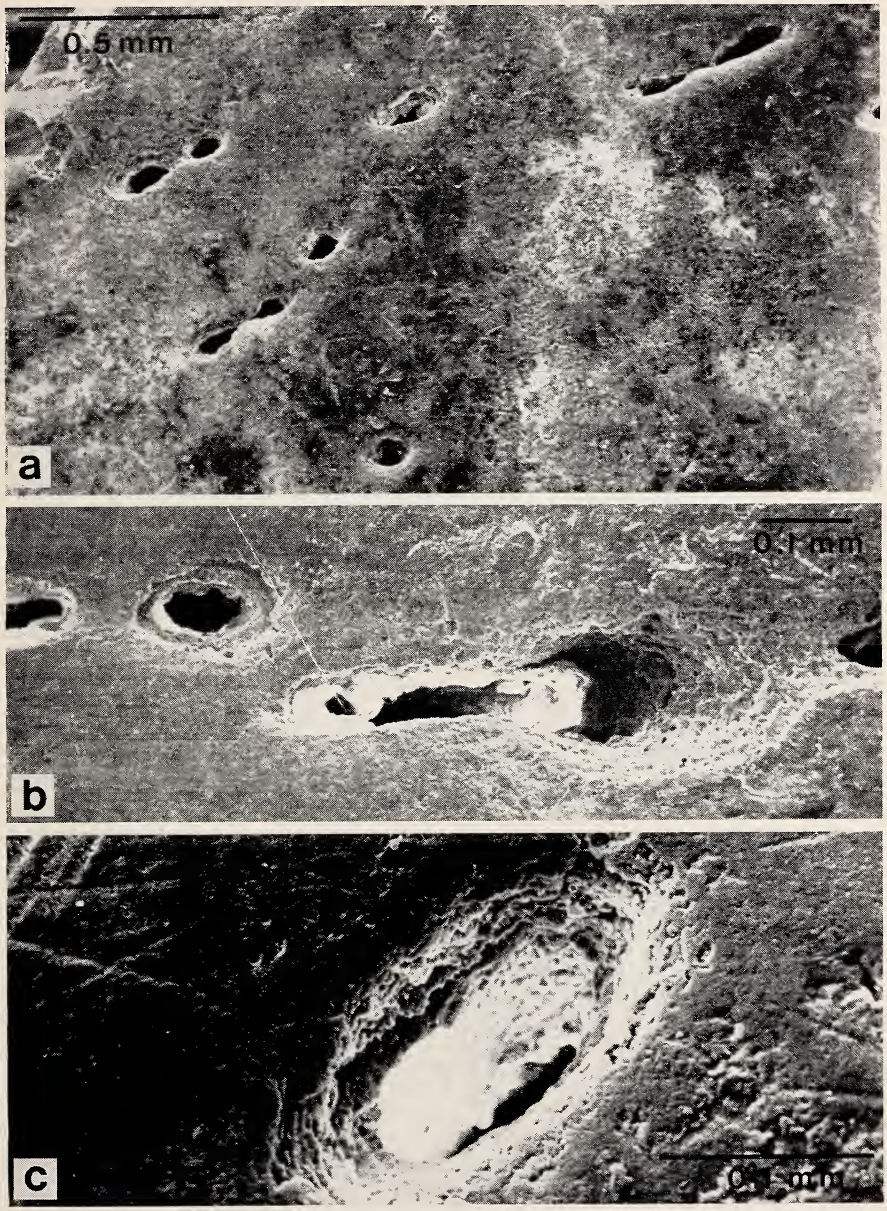


Fig. 10. Pore openings in *Aepyornis* eggshells from Ampamalora seen in SEM-micrographs; a, b) dagger-point and sting pores, c) enlarged sting pore.

Porenöffnungen von *Aepyornis*-Eierschalen von Ampamalora in REM-Aufnahmen; a, b) Dolchstich- und Stichporen, c) vergrößerte Stichpore.

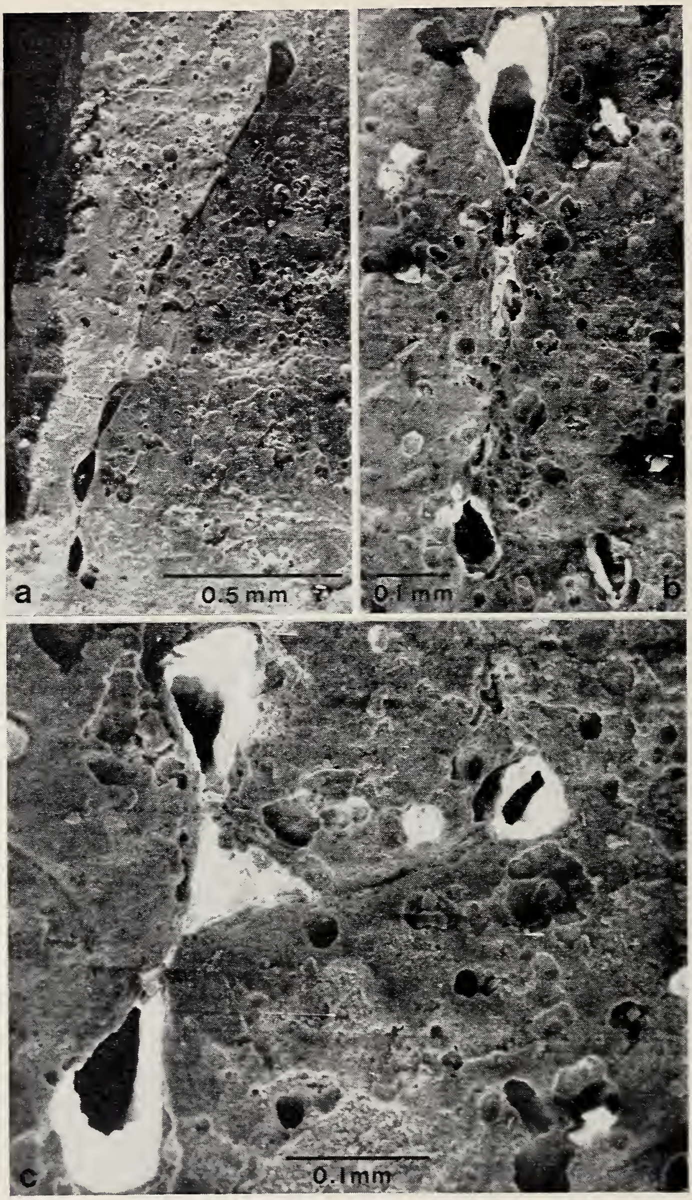


Fig. 11. Pores and interconnecting microducts in surface-eroded *Aepyornis* egg-shells from Tulear; SEM-micrographs a, b) linear systems, c) triangular unit.

Poren verbunden mit Mikrokanälen dargestellt an erodierten *Aepyornis*-Eierscherben von Tulear; REM-Aufnahmen. a, b) lineare und c) trianguläre Verbindungen.

The shell remains were located in Tertiary calcareous sediments, which Rothe identified as an old land surface older than the volcanic formations below and above. The basalt above the shell-bearing sediments is aged about 12 million years, as indicated by physical dating methods. Associated with the shells were remains of terrestrial Gastropoda and nests of what were possibly mining bees related to the recent species of the genus *Anthophora.*

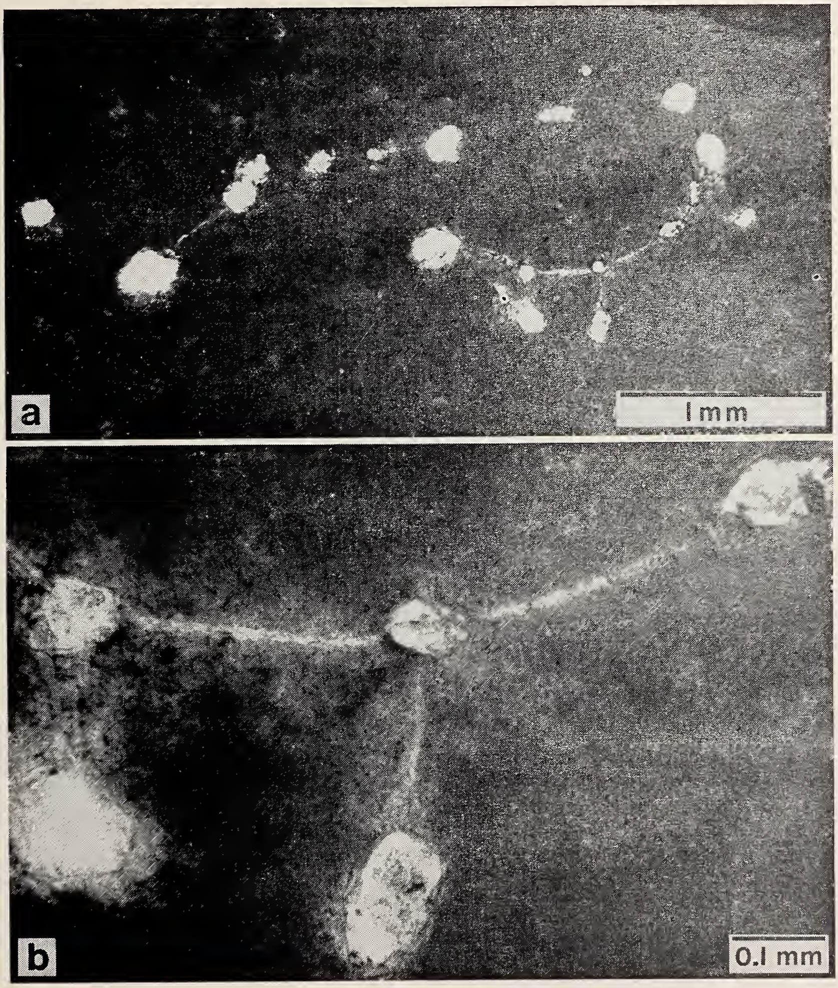


Fig. 12. Tangential section through the outer part of the spongy layer of an *Aepyornis* eggshell (BMNH, No. A 3645; slide No. 4). The pores, seen in cross-section, are interconnected by microducts

Tangentialschliff der äußeren Sponginschicht einer *Aepyornis*-Eierscherbe zur Darstellung des durch Mikrokanäle verbundenen Porensystems.

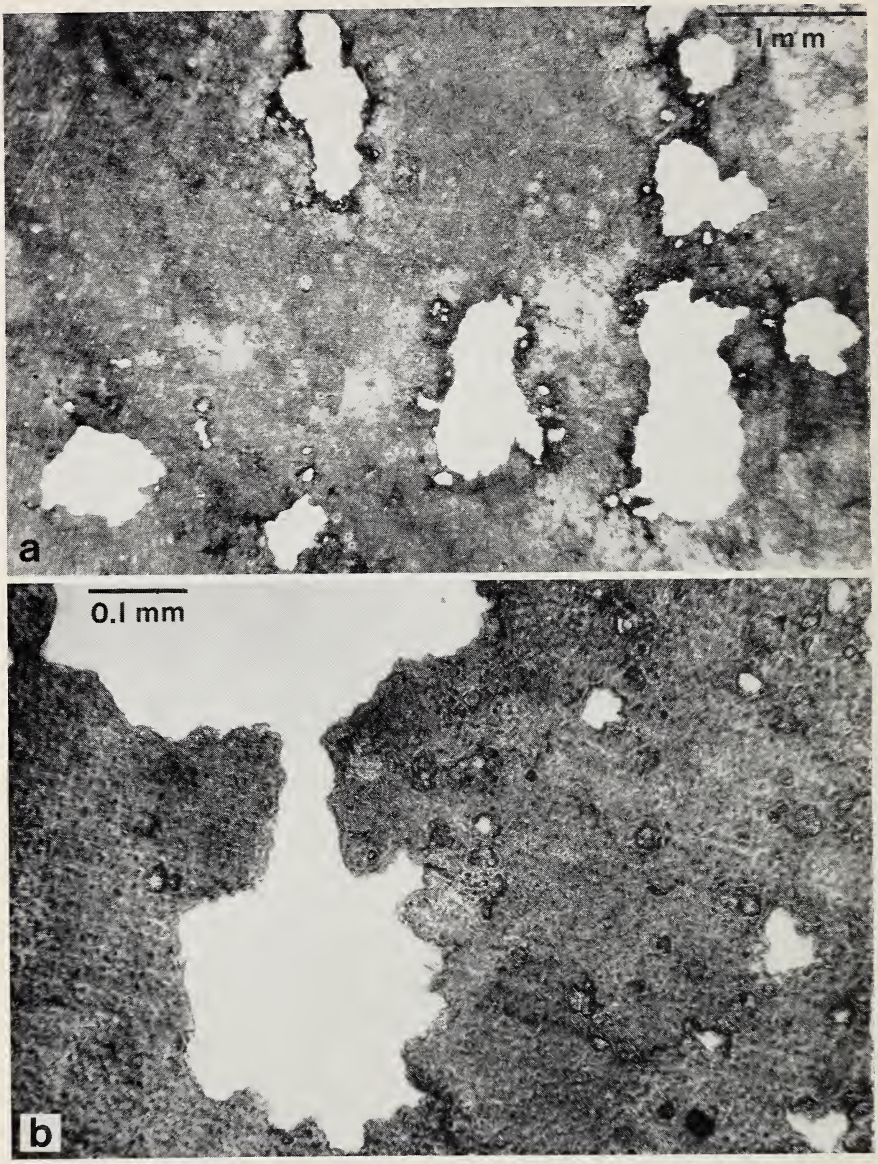


Fig. 13. Tangential sections through the spongy layer of an *Aepyornis* eggshell with lacunae (BMNH, No. A 3645; slide No. 5).

Tangentialschliff der äußeren Sponginschicht einer *Aepyornis*-Eierscherbe mit Lakunen.

Based on the dating and structure of the geological formations, Rothe thinks his find of struthious shells provides further evidence of an old land connection between Africa and the eastern Canary Islands. It must have still existed in the Tertiary (Rothe, 1966, 67 a, b, 68 a, b, c; Rothe and Schmincke, 1968; Evers et al., 1970). While the eastern islands of Lanzarote and Fuerteventura are underlain by the continental crust, the western Canary Islands may be oceanic in origin (Rothe and Schmincke, 1968). Dietz and Sproll (1970) suggest that the East Canaries form a microcontinent or sialic continental fragment which became detached from the African margin of what is known as the "Ifni Gap" in the Africa—North America continental drift fit (p. 43).

The Challenge of Rothe's Discovery

Rothe (1964) compared thin sections of some of his Lanzarote eggshells with corresponding shell sections made from *Struthio camelus* eggs. He found the general morphology of the spongy and mammillary layers sufficiently alike to identify the Lanzarote eggshells as struthious. There is no doubt that Rothe uncovered struthious eggshells on Lanzarote. However, the material he pictured for identification in his 1964 publication proved the ratite character of the shells and not more. In addition, he dug up shell remains in different places (below).

For these reasons I suggested further investigation to provide proof of the familial character of the Lanzarote eggshells. Rothe's reaction was swift and determined; he claimed to be neither an ornithologist nor a paleontologist and requested that I take over. The shipment of eggshells followed at once, and at first glance the shell fragments proved my suspicions. Years passed until I had an opportunity to investigate the two "complete" eggs in the Senckenberg Museum and in Rothe's possession, respectively.

The ratite character of the Lanzarote eggshells is sufficiently proved by Rothe (1964). The placement of the fragments into a family requires a close scrutiny of the pore system.

The Pore Patterns of the Lanzarote Eggshells

Rothe noticed eggshells distributed over most of the calcarenite horizon at the northern tip of Lanzarote and collected shell remains in Valle Chico (29° 13′ 08″ N, 9° 46′ 40″ W) and on the north slope of Valle Grande (29° 12′ 38″ N, 9° 46′ 20″ W). He collected two nearly complete eggshells and 302 shell fragments. The whole calcarenite horizon can be considered one locality. The nearest village to the east is Orzola, and the locality is situated approximately 150 km from the nearest point on the African continent.

The Lanzarote eggshells reveal two very different pore patterns. This suggests that the eggs came from at least two kinds of ratites. Presently I recognize two shell types. Judged from their pore patterns, one of them has to be attributed to a struthious species. The second pattern matches that known from *Aepyornis* eggs. I call it *"aepyornithoid"*, *i. e.* resembling the pore pattern of Malagasy aepyornithid eggs. In the following descriptions and discussions I shall label the Lanzarote shell material "type S" (struthious) and "type A" (aepyornithoid), respectively.

a) The Pore Pattern of the "Type S" Eggshells

Some of the shell remains recovered in Valle Chico and Valle Grande are of the struthious type. This includes the two "complete" eggs. All of these shells have tiny round pores, the so-called needle-point pores, which open singly and which are scattered diffusely over the shell surface. Here and there the pore openings are grouped in small assemblies of two and three (Figs. 14, 15). Some pores have become enlarged, possibly under the influence of chemical erosion.

In contrast to Moltoni's (1928) more densely pored struthious eggshells attributed to *"Psammornis"* (see Sauer, 1969), the "type S" eggs from Lanzarote have relatively few pores. Compared with the pore patterns of the recent ostrich eggs, the "type S" pattern resembles most closely that of the *S. c. camelus* egg.

Some of these fossils, including the egg in the Senckenberg collections, are blackish. The others are of a light to dark ochre. As Rothe (pers. comm.) noticed a sulfurous odor when he cut thin sections from the black shell fragments, one might assume that these eggs became fossilized either in a wet-rotten condition, or that they might have been affected by certain external volcanic events. The ochre-stained shells were probably in a dry state and clean when they became buried.

b) The Pore Pattern of the "Type A" Eggshells

Like the "type S" shell remains, Rothe sampled "type A" fragments (Figs. 16—18) in Valle Chico and Valle Grande. From the material so far collected it is not clear if these aepyornithoid eggshells belonged to one single species of bird. The pore pattern shows a variation which covers about the spectrum of variability typical of the aepyornithid eggshells from Madagascar (p. 12), most of which are not specifically identified but thought of belonging to several species. Apart from the pieces characterized by the conspicuous pattern of elongated, longitudinal pore grooves, the collections contain fragments in which the short dagger-point and sting pores prevail.

Further, the "type A" shells are not uniformly thick. Some range from 2.10 to 2.15 mm, others from 2.25 to 2.50 mm, and a third sample reaches from 2.60 to 2.90 mm. This seems more than an intraspecific range of modification.

Several shell fragments came from the equatorial region of the respective eggs. Although these shells were not more than 2.10 to 2.15 mm thick, some preliminary surface measurements with a Geneva lens measure (see method in Sauer, 1968) suggest large eggs of possibly twice the size of a full-sized egg from a present day ostrich.

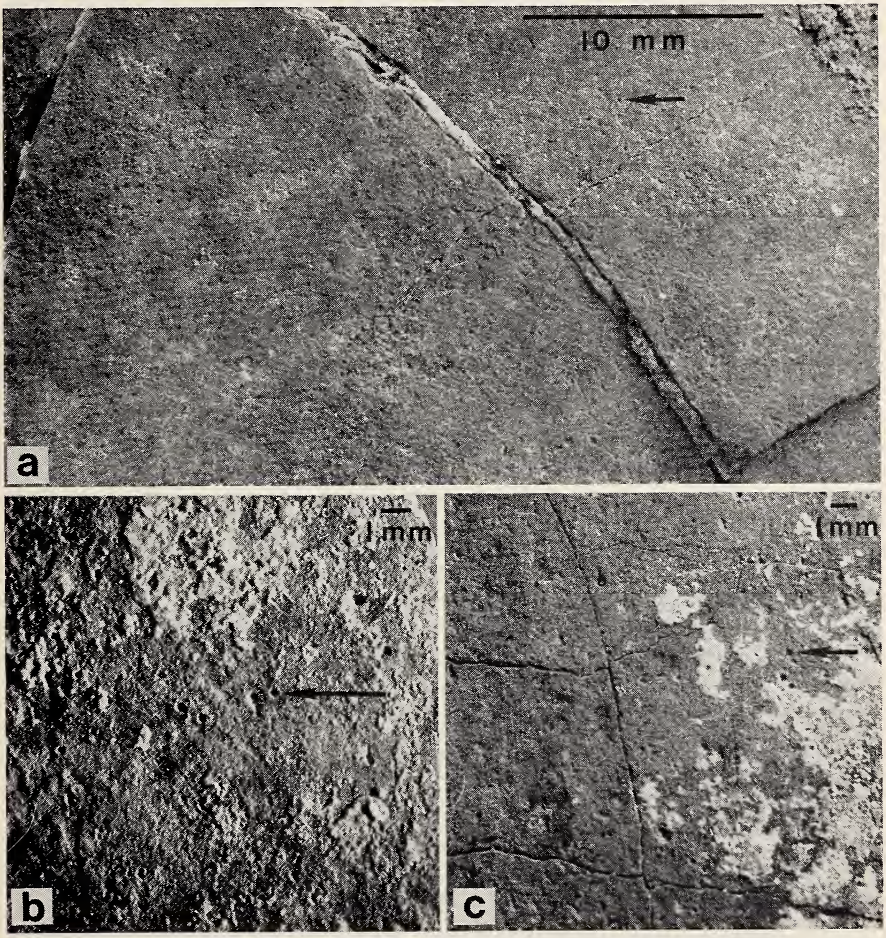


Fig. 14. Pore pattern of "type S" eggshells from Valle Grande, Lanzarote. Partial views of a, c) Rothe's complete egg and b) shell fragment, all showing the fine needle-point pores.

Porenmuster struthionider Eierscherben aus dem Valle Grande, Lanzarote (Kanarische Inseln). Die Teilansichten von a, b) Rothes vollständigem Ei und b) einem Schalenfragment zeigen die feinen, runden Nadelstichporen.

Aepyornithoid and Struthionid Eggshells from Asia

During my studies of fossil struthionid remains in the collections at the American Museum of Natural History, I came upon two samples of ratite eggshells that showed little resemblance to the known struthionid eggs.

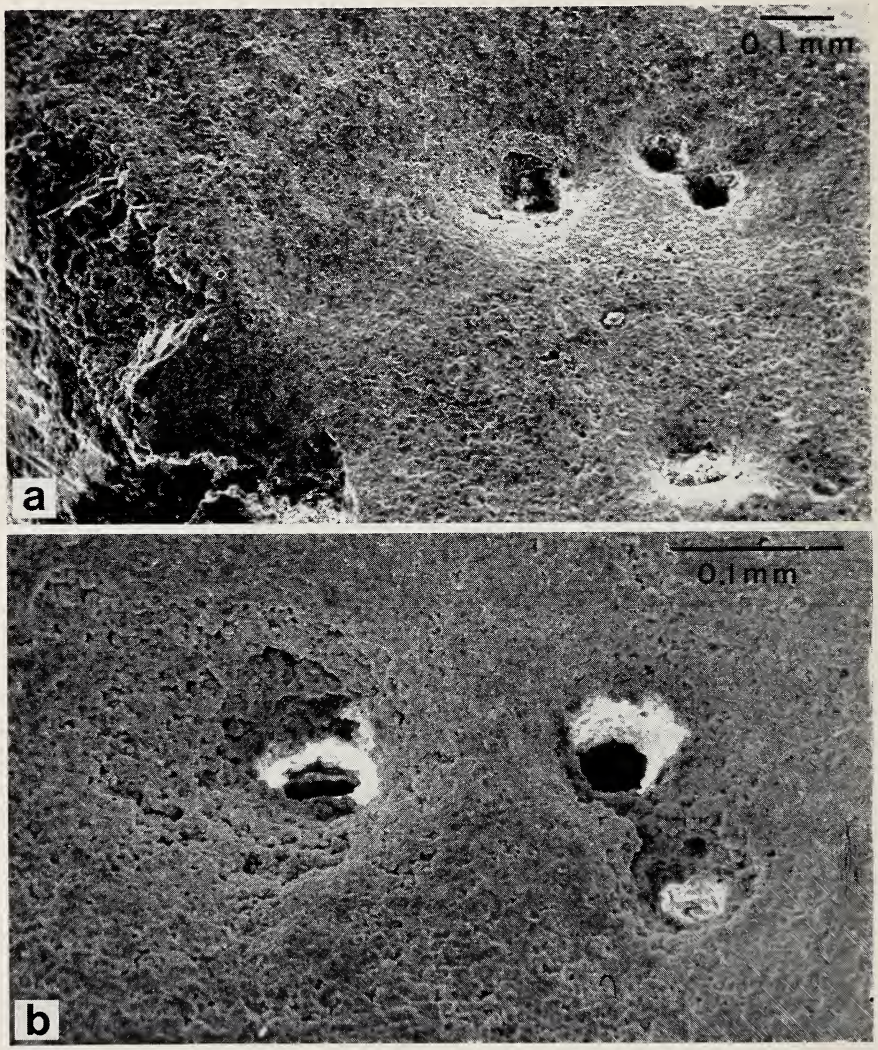


Fig. 15. Needle-point pores in a "type S" eggshell from Valle Chico, Lanzarote; SEM-micrographs. The pore at the lower right in (a) is clogged with debris.

REM-Aufnahmen von Nadelstichporen struthionider Eierscherben aus dem Valle Chico, Lanzarote.

The shell fragments revealed instead the distinct "type A" pattern of pore openings. One of these samples came from northern India and the other from Inner Mongolia. The Mongolian collections contained also some struthious shell remains and some "problem" shells.

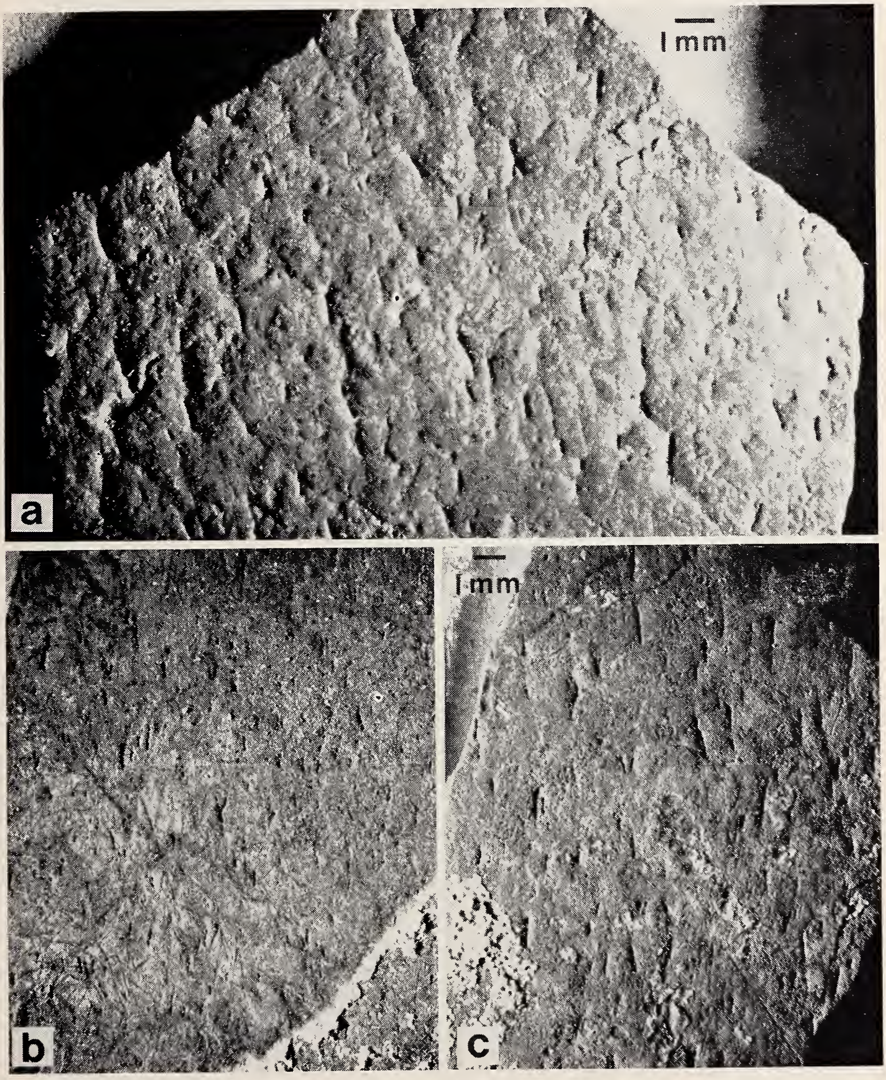


Fig. 16. Pore patterns of "type A" eggshells from Valle Grande, Lanzarote; a—c) three different fragments; b) and c) same scale.

Porenmuster aepyornithoider Eierscherben aus dem Valle Grande, Lanzarote; a—c) drei verschiedene Fragmente; b) und c) im gleichen Abbildungsmaßstab.

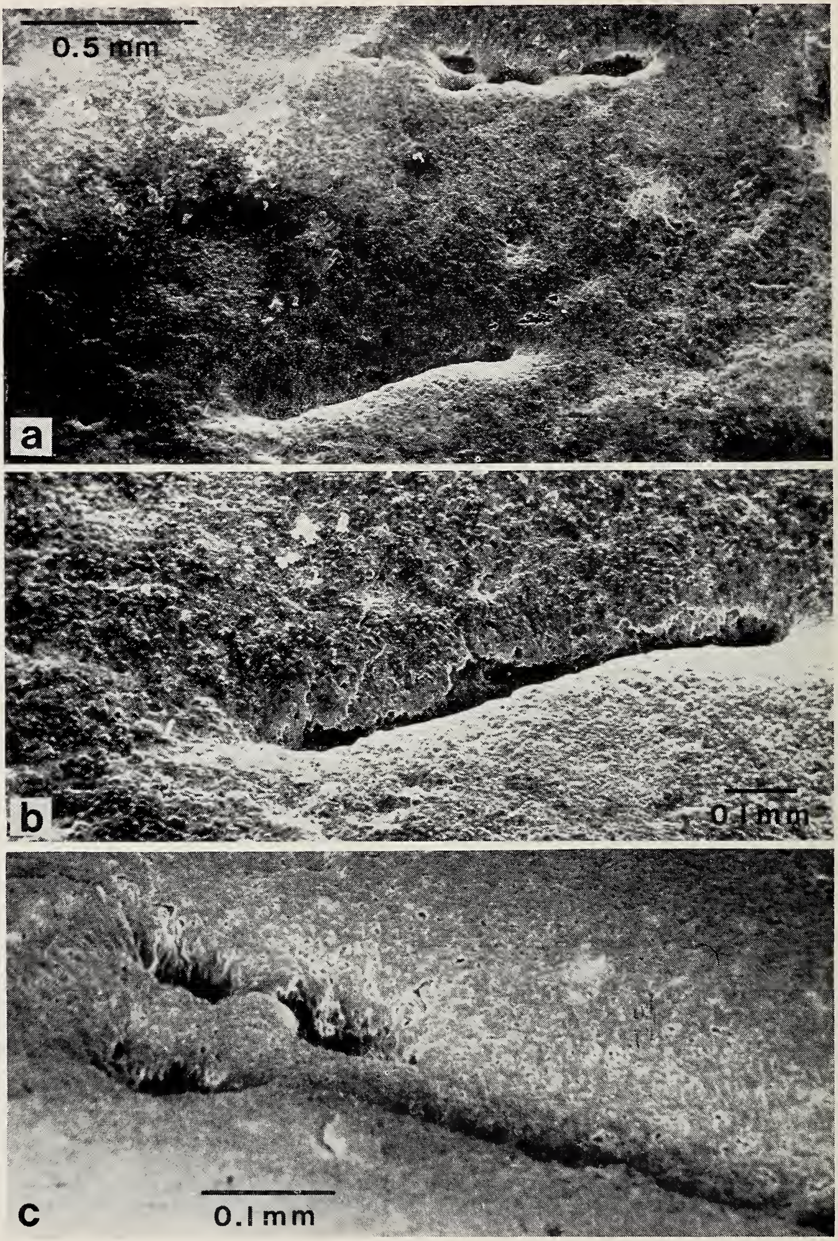


Fig. 17. Linear pore grooves, sting and dagger-point pores in "type A" eggshells from Valle Grande, Lanzarote; SEM-micrographs; b) enlarged segment of (a).

Lineare Porenrillen, Dolchstich- und Stichporen aepyornithoider Eierscherben aus dem Valle Grande, Lanzarote, in REM-Aufnahmen.

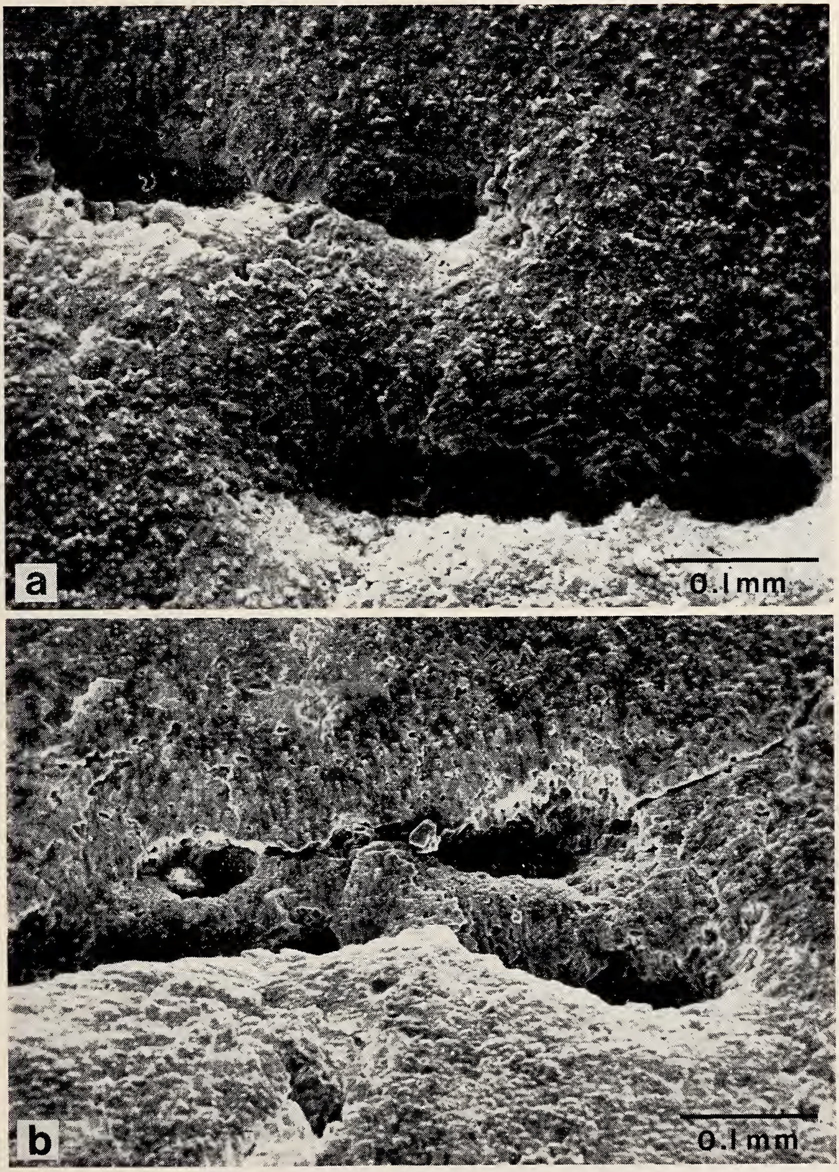


Fig. 18. Pore openings and interconnecting microducts in "type A" eggshells from Valle Grande; SEM-micrographs.

REM-Aufnahmen von Poren mit verbindenden Mikrokanälen in aepyornithoiden Eierscherben aus dem Valle Grande, Lanzarote.

In the context of this paper I shall briefly describe the Asiatic shell collections as far as they contribute to the discussion on the shell types by providing additional samples for comparison. The Eocene and Oligocene fossil-bearing strata and localities in Inner Mongolia are described by Radinsky (1964).

a) Ratite Eggshell Remains of the "Type A" from Punjab, India

The Siwalik Collection of the AMNH contains a sample of 34 well preserved eggshell fragments from Hasnot, Punjab:

AMNH No. 903, Siwalik Collection
? *Struthio*
egg-shell fragments
Horizon: Dhok Pathan
Loc. Nr. 43 C/15, Hasnot, Punjab. Aiengar, 1935.

The material appears to be uniform. The fragments are yellowish in color, and some are covered with remnants of red sand from the stratum in which they were embedded. In general their surface is smooth; several fragments are somewhat rough as a result of abrasion. The shells possess linear pore grooves which are either simple or forked and aligned parallel to one another in the direction of the polar axis of the egg (Fig. 19). Short dagger-point pores and a few sting pores are also noticeable.

By their pattern of pore openings the eggshells from Hasnot, Punjab, resemble those known from *Aepyornis* species and bear no similarity with "*Struthiolithus*" or *Struthio* eggshells. The forking of pore grooves appears slightly more pronounced than in most of the Malagasy aepyornithid eggshells and resembles most closely that of the *Aepyornis* shell from Ampamalora shown in Fig. 8 a. The shell fragments are on the average 2.76 mm thick. Some pieces are thinner than the other; 51 measurements on 15 fragments range from 2.50 to 2.90 mm.

Dr. Colbert (pers. comm.) informed me that the age of the Dhok Pathan horizon is Lower Pliocene or at least Pliocene.

b) Ratite Eggshell Fragment of the "Type A" from Camp Margetts, Inner Mongolia

Among the eggshells collected during the Third Asiatic Expedition of the AMNH is one shell fragment of the aepyornithoid type:

AMNH No. 6738: Camp Margetts, 10 miles SW 25 miles SW
Iren Dakar
Date: 1930

Camp Margetts, some 25 miles SW of Iren Dakar (syn. Iren Dabasu), is located in the Shara Murum region, Suiyan Province in Inner Mongolia,

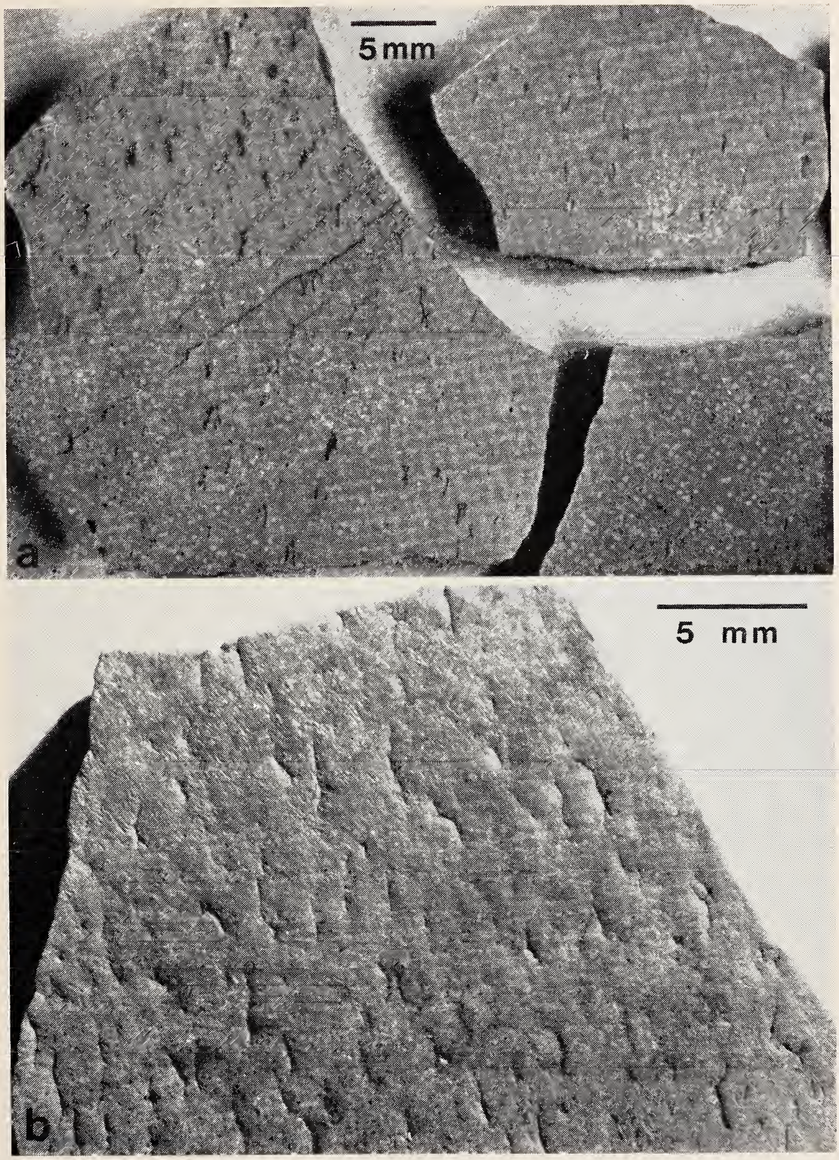


Fig. 19: "Type A" eggshell fragments from Hasnot, Punjab, Siwalik Collection of the AMNH. a) Three pieces with pore grooves, sting and dagger-point pores. b) Enlargement of piece shown at bottom right in (a).

Aepyornithoide Eierscherben von Hasnot, Punjab (Indien), aus der Siwalik Kollektion des Amerikanischen Museums für Naturgeschichte. a) Scherben mit Porenrillen, Dolchstich- und Stichporen; b) Vergrößerung.

The formation (Irdin Manha) is dated Upper Eocene; it yielded *Eogrus aeola* (Wetmore, 1934). Not far from this locality, some 40 miles SE of Iren Dabasu, is also an Upper Miocene formation (Tung Gur) from which Brodkorb (1967) described *Eogrus wetmorei*.

The yellowish fragment, covered with some reddish sand, shows the distinct pattern of parallel and forked pore grooves, as well as dagger-point and sting pores (Fig. 20). By its pattern the piece resembles the eggshells from Hasnot, Punjab, but it has fewer pore openings than these and it is only 2.20 mm thick.

c) Problem Collections from Inner Mongolia

Two of the shell collections gathered during the Asiatic Expeditions of the AMNH may be heterogeneous. Also the determination of the locality and horizon leaves much to be desired. Therefore, no attempt is made at present to unravel these collections. With further clarification and comparative studies, these shells may eventually become identified. I am inclined to think that most if not all of the material will be recognized as aepyornithoid as is suggested by the resemblance of the shape and pattern of the pores with certain *Aepyornis* eggs that combine areas with diffuse pore arrangements and the characteristic longitudinal pattern. For the time being I treat these fragments as problem collections and ignore their "*Struthiolithus*" label.

During the Third Asiatic Expedition, Shackelford collected 34 well preserved pieces of eggshell near Shabarakh Usu at a locality which is now dated Lower Pliocene.

AMNH Collector: Shackelford

Hor. Pliocene or later
Loc. East of Shabarakh Usu. 15 miles
Struthiolithus egg-shell fragments. July 31.

This collection contains fragments with irregularly distributed round to oval pores and those with sting and dagger-point pores and short linear pore grooves (Fig. 21). The latter pieces indicate a clear tendency of a parallel alignment of the pore openings, similarly to that of the *Aepyornis* shells illustrated in Figs. 8 b, c and 9 b. Although the pieces with the round and oval pores may bear a resemblance with the struthious shell type with circular pores, they are more similar to certain *Aepyornis* eggshells with spots of diffuse pore patterns in between the longitudinal pore arrangement.

Comparable are some shell fragments secured by the Central Asia Expedition in 1928. These pieces are also marked "*Struthiolithus*" and were gathered in "Inner Mongolia". As in the Shackelford collection some pieces reveal an irregular arrangement of circular and oval pores while the others show sting pores, dagger-point pores, and linear pore grooves in longi-

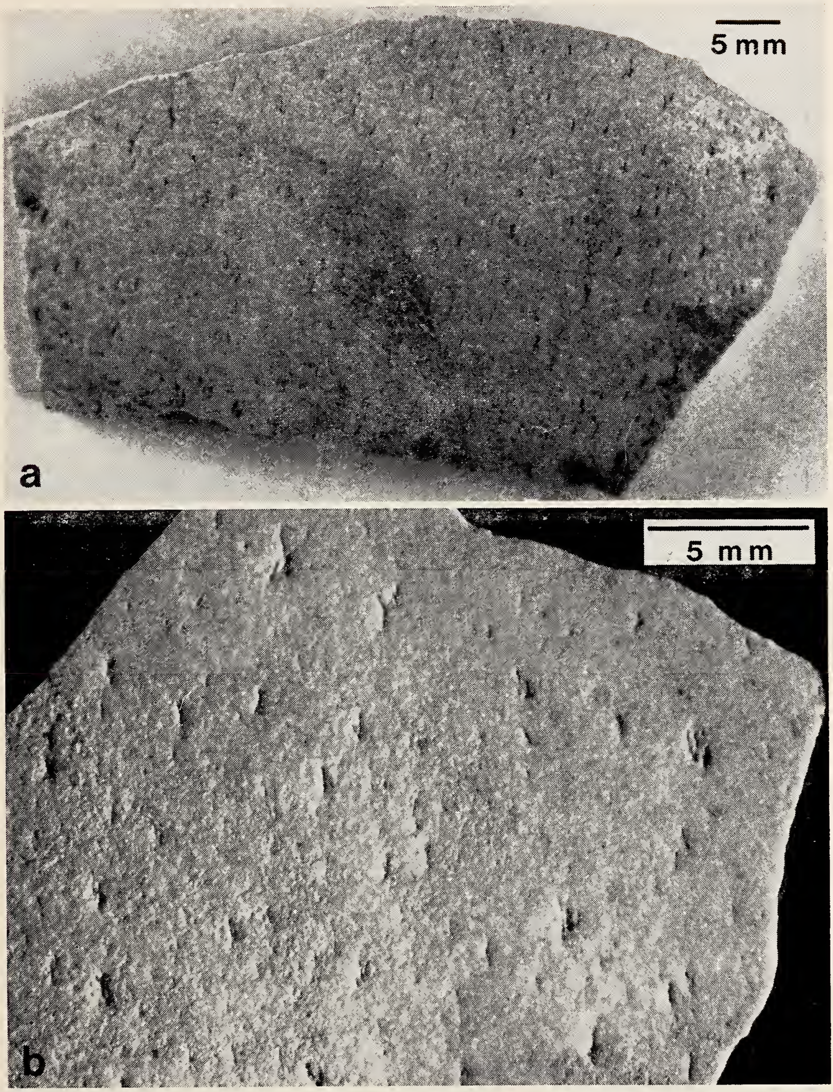


Fig. 20. "Type A" eggshell from Camp Margetts, Inner Mongolia, with pore grooves, sting and dagger-point pores; b) enlarged segment of the fragment shown in (a).

Aepyornithoide Eierscherbe von Camp Margetts, Innere Mongolei, mit Porenrillen, Dolchstich- und Stichporen; b) vergößerte Teilansicht des unter (a) gezeigten Stückes.

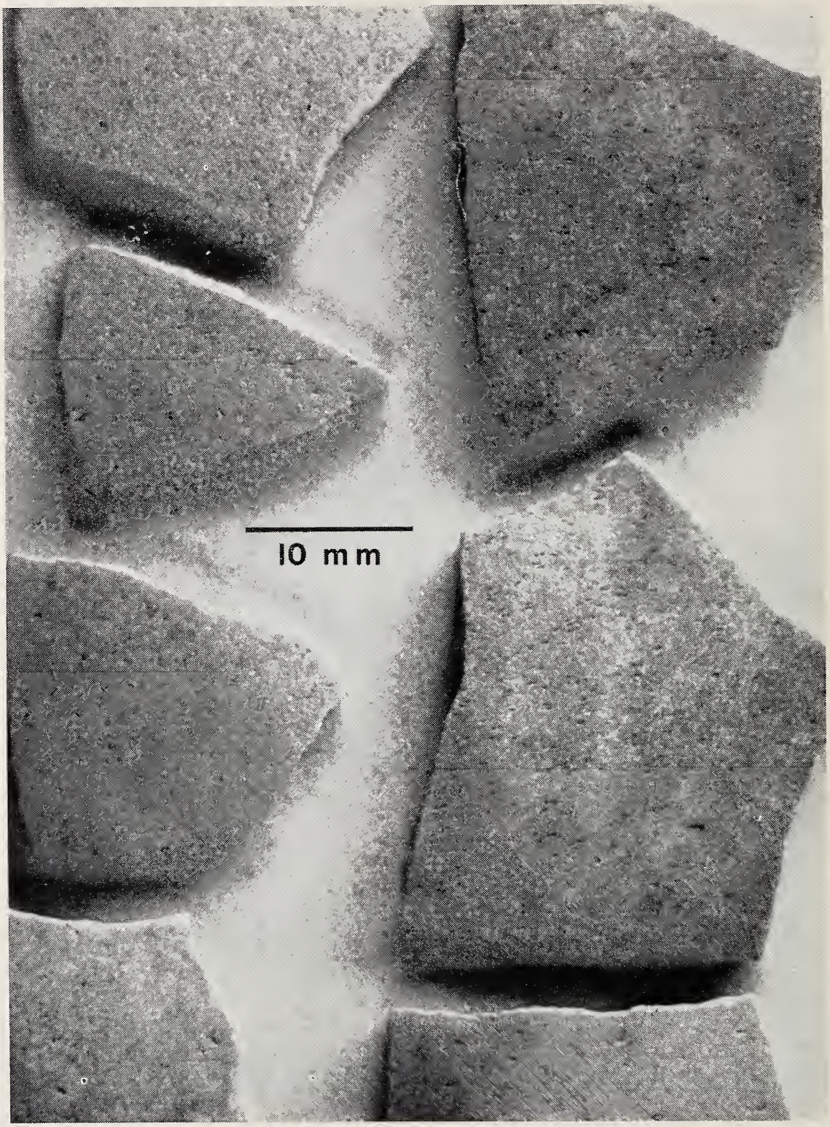


Fig. 21. Eggshells from Shackelford's "problem" collection from Shabarakh Usu, Mongolia.

Unbestimmte Eierscherben aus Shackelfords Sammlung von Shabarakh Usu, Mongolei. Ein Teil der Fragmente weist aepyornithoide Porenmerkmale auf; siehe Text.

tudinal rows (Fig. 22). One finds the same similarities with *Aepyornis* eggshells as mentioned above.

In summary, the majority of shell fragments in these two collections strongly resemble the aepyornithoid eggshell type. A meaningful comparison should become possible when further material can be gathered at the localities where these eggshells were found.

d) Struthious Eggshells from Mongolia

A large number of eggshells from different localities in Asia could be listed to ascertain the existence of a distinctly struthious shell type side

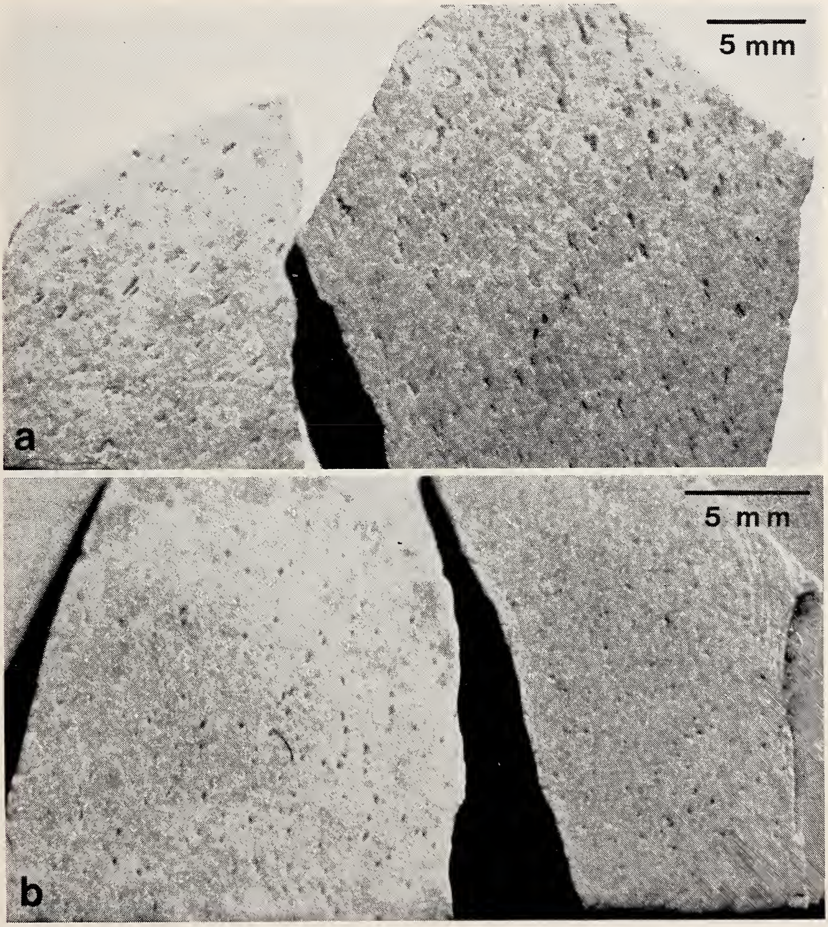


Fig. 22. Eggshell fragments ("problem" collection) from "Inner Mongolia", collected during the Central Asia Expedition of the AMNH in 1928.

Unbestimmte Eierscherben aus der Inneren Mongolei, gesammelt während der Zentralasiatischen Expedition des Amerikanischen Museums für Naturgeschichte 1928; einige Fragmente mit aepyornithoiden Porenmerkmalen; siehe Text.

by side with the "type A" shells. The examples given here were also obtained during the Asiatic Expeditions of the AMNH. The collections do not show an altogether uniform pattern of pore openings. Some shells possess the irregularly distributed fine needle-point pores and compare with the *"Struthiolithus"* eggs (Figs. 5, 6) or with the recent *S. c. camelus* eggs (Fig. 3). The other eggshells reveal needle-point pores as well as fine pencil-mark pores which are more oval than circular in shape. This latter type may represent a phylogenetically older eggshell. A large number of different samples is needed before one can attempt a classification of these shells.

Three of the collections of struthious eggshells come from Tsagan Nor out of the Hung Kurek. Although one of the labels (No. 542) reads "? Pleistocene", the Hung Kurek is dated Lower Pliocene. In this case one

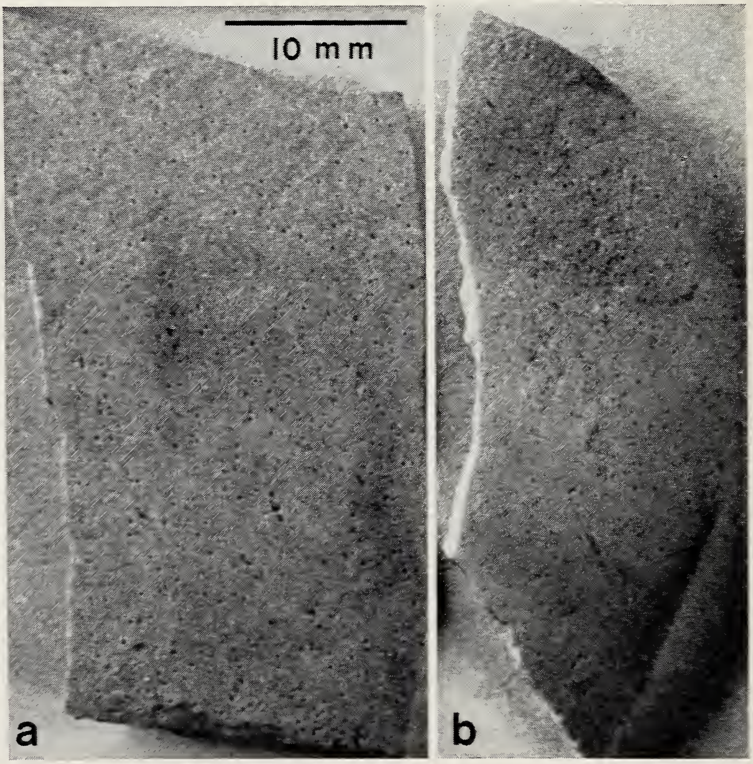


Fig. 23. Struthious eggshells from Tsagan Nor, Mongolia; No. 541; a) and b) same scale. Pattern of needle-point pores.

Struthionide Eierscherben mit Nadelstichporen von Tsagan Nor, Mongolei; a) und b) im gleichen Abbildungsmaßstab.

can not rule out the possibility that the whitish eggshells are younger in origin than the shells from the other two collections. The latter ones were attributed to the Hung Kurek period without any question.

1. AMNH *Struthiolithus,* fragment of eggshell
   Pliocene, Hung Kurek
   Loc. Tsagan Nor, Mongolia. Am. Mus. Exp. 1922.

This find consists of one fragment, 2.35 to 2.40 mm thick, which shows fine needle-point and pencil-mark pores.

2. AMNH No. (541) *Struthiolithus* ? Eggshell fragments.
   Period: Hung Kurek
   Loc. N'r. e. end Tsagan Nor, Mongolia. 1925.

Seven of these 16 fragments show "pock-mark" erosion on the cuticular surface. The fine needle-point pores reveal very clearly the struthious pore pattern of these shells (Fig. 23). Two representative pieces are 2.05 mm thick.

3. AMNH No. 542. Collector: Granger. Found by chauffeur Wong.
   Loc. ? Pleistocene (Hung Kurek)
   East end of Tsagan Nor
   Egg-shells of *Struthiolithus*
   from a stratum in yellow gravels. June 1925.

This largest of all collections contains 1,171 fragments from various eggs. Most of the pieces are in excellent condition, some have an eroded outer surface with pock-mark erosion pits up to 1 cm in diameter, and a few fragments are covered with "worm-marks," the result of tunneling invertebrates. The shells are withish and have a smooth surface with fine needle-point pores (Fig. 24). Some of the pores are slightly enlarged by erosion. Apart from one questionable piece, which may erroneously have found its way into this collection, the shell fragments are uniform in character and distinctly of the struthious type. The average thickness of these shells, determined from 80 measurements on 17 pieces, comes to 1.98 mm; the variation ranges from 1.80 to 2.25 mm.

The following two collections come from Shabarakh Usu (Lower Pliocene):

4. AMNH No. 6682 *"Struthiolithus"* Fragments of egg-shells
   Quaternary
   Loc.: Shabarakh Usu, near Chovji Cliffs, Mongolia
   Exp. 1925; Field No. 516.

Some of these 54 fragments are heavily eroded on both the cuticular and mammillary surfaces. The shells reveal the typical needle-point pores and coincide with those of the Nos. 541 and 542 samples. Measurements of the shell thickness of some unabraded pieces range from 1.95 to 2.30 mm.

5. AMNH F. 255 *Struthiolithus* eggshell fragm.
from Shabarakh Usu
Coll. 1923.

These 5 pieces bear needle-point and very fine pencil-mark pores and are from 1.95 to 2.20 mm thick.

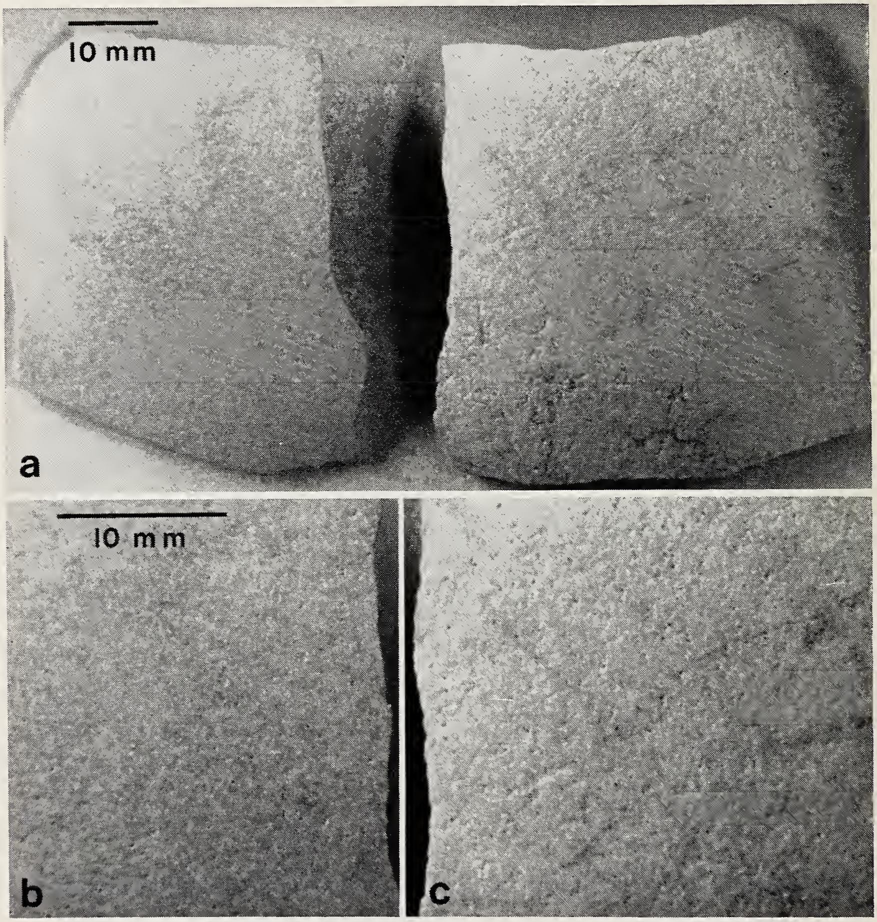


Fig. 24. Struthious eggshells from Tsagan Nor, Mongolia; No. 542; b) and c) same scale enlargements of fragments shown in (a). The shells possess very fine needle-point pores.

Struthionide Eierscherben mit sehr feinen Nadelstichporen von Tsagan Nor, Mongolei; b) und c) Vergrößerungen des unter (a) gezeigten Schalenstückes im gleichen Abbildungsmaßstab.

6. AMNH Collector: G. O.

Loc. Loh
Fragment of? eggshell found on surface of
Hsanda Gol beds. June 21, 1925.

This single, well preserved fragment, 2.00 mm thick, is identical in pore structure with the 5 pieces (F. 255) from Shabarakh Usu.

7. AMNH Collector: Horwarth

Hor. ? Pleistocene
Loc. Shara Marun region. North Mesa
From wash on SW face of mesa — 1 mile
Desc. SW of Chimney Butte Camp.
Struthiolithus eggshell fragments. April 27, 1928.

These two eggshells, uniformly 2.25 mm thick, possess needle-point pores and are of the "*Struthiolithus*" type.

Discussion

The Family-specific Pore Patterns of the Struthionid and Aepyornithid Eggshells

The discussion of eggshell features in this paper is largely restricted to the pore pattern, that is to the forms and arrangements of the openings of the pore canals on the cuticular surface of the eggshell. These features appear sufficiently reliable to identify a ratite eggshell as either struthionid (=struthious, as there is only the one genus *Struthio)* or aepyornithid. Additional features can be used to recognize and classify ratite eggshells, for example the system of the pore canals, the surface texture of the shell, or the shape of the egg (Sauer, 1966, 68).

The morphological investigation and comparison of the pore patterns of known struthionid and aepyornithid eggshells reveal several family-specific features:

The Struthionid Pore Pattern

1. Shells possess small circular or somewhat oval pore openings, the so-called needle-point and pencil-mark pores; their distribution is irregular, *i. e.* there is no alignment with the axes of the egg.
   a) The pores appear solitary or in small groups of two to three, occasionally a few more.
   b) The pores occur in clusters of about 30 to 70.
2. Shells possess pore grooves, into which the pore ducts open, and may additionally be equipped with circular pore openings. The grooves are

irregularly bent and branched and may form reticulate and rosette patterns of varying complexity.

3. The clustered pores and grooves are mostly located in pits that may be interconnected by furrows. The pits are mostly distributed diffusely over the shell surface; here and there a few of them may be arranged in loose clusters or lined up in irregular rows.

The Aepyornithid Pore Pattern

1. The shells possess linear, here and there bent and forked pore grooves, short dagger-point or comma pores, and sting pores. They are predominantly conspicuously oriented parallel to one another and to the longitudinal axis of the egg. Narrowly localized diffuse or whirlpool patterns of pore openings occur on the poles of the egg. Occasionally they appear in other small areas of individual eggs, particularly in those with a preponderance of sting and dagger-point pores. They do not obscure the predominant parallel alignment of the pore openings.
   a) Linear pore grooves prevail in some eggshells.
   b) Other eggshells possess a majority of dagger-point and sting pores, often strung in short longitudinal rows.

2. Neighboring dagger-point pores and pore grooves may be interconnected by microducts.

3. Lacunae may occur in the spongy layer and are probably a part of the ventilation system.

The formation and occurrence of the lacunae is not fully understood. But for the purpose of identification of a ratite eggshell no weight must be placed on the presence or absence of the lacunal feature. The other characters suffice for a clear placement of an eggshell. As the description of the shapes of the pores as "needle-point," etc., follows largely a subjective terminology, the reader is referred to the illustrations depicting the pores.

The Ratite Eggshells from Lanzarote and the Question of the Aepyornithoid Shell Type

Rothe's discovery of ratite eggshell remains on Lanzarote and his evidence of a Tertiary land connection between continental Africa and the eastern Canary Islands of today contribute new information and cause for speculation on the history of the Old World ratite birds. One can discard the notion that the Lanzarote eggs had drifted in an ocean current from the continent to the island. The clues of a direct land connection are undeniable, and the eggshell remains in the buried land surface of Tertiary Lanzarote are so plentiful that one must accept the suggestion that ratite birds reached the region of the present-day Lanzarote on foot and that they lived and nested there. The expanse of the habitat occupied by these birds remains unknown. It may have been limited, bordered by mountains and ocean, and it was surely the westernmost range of these ratites. From a comparative view it can be mentioned that the recent ostrich, often characterized as a cursor of the plains, is a highly flexible opportunist. In South West Africa this bird pioneers into rugged mountain ranges and lives there quite successfully. It roams through the Namib Desert to the barren Atlantic coast. Though a cursorial runner in arid habitat, it has been seen swimming unhesitatingly and succesfully in inland bodies of water (references to the ostrich's behavior are given in Sauer, 1971).

Rothe's geological evidence suggests that ratite birds roamed the Lanzarote region until more than 12 million years ago. As the onset of the Pliocene is dated to 13 million years ago, the Lanzarote ratites might have had their roots in the Miocene or still earlier (p. 43).

It is remarkable that Rothe unearthed two types of eggshells which, on the basis of their morphology, are struthious and aepyornithoid. With regard to the latter type I suspect eventual proof of their place within the Aepyornithiformes. I am tempted to see the Aepyornithidae expanded in time, the number of species, and geographically from Madagascar to Lanzarote and eastward to India and Inner Mongolia. However, we may patiently wait for the "bony evidence" in support of the prophecy cast by "mere" eggshell remains.

The Aepyornithiformes with the one family Aepyornithidae are grouped in two subfamilies (Brodkorb, 1963). That of the Eremopezinae is known from a single distal end of a tibiotarsus from Birket-el-Qurun, Fayum formation, in Egypt. It is dated Upper Eocene, and since the eggshells tentatively attributed to this subfamily have been recognized as struthious (Sauer, 1969), it remains the only eremopezinine specimen known. Even the classification of *Eremopezus eocaenus* has created some pains and remains debatable (see Sauer, 1969).

The fossils of the subfamily Aepyornithinae contain also only one piece from outside Madagascar, a distal third of a right tarsometatarsus from the Fayum north of Dimeh, Egypt. Lambrecht (1929) described this Lower Oligocene find as *Stromeria fayumensis* and considered it the continental ancestor of the Malagasy Aepyornithidae. Of the latter, one recognizes at present seven species that are all grossly dated Quaternary. Eggshell finds have been plentiful, and a number of the 10 to 12 liter eggs were dug up unbroken. Wetmore (1967) reported on one which contained a mumified embryo.

It appears to me that Madagascar was not the original homeland but rather the last refuge of the Aepyornithidae. Here they survived longer than in any other place of their range, probably until less than 2,000 years ago. The radiocarbon-dated shell material from Tulear and Ampamalora is about 5,000 and 2,000 years old. One could imagine that aepyornithid birds were more common 12 million years or so before the time when the last ones became extinct. The Lanzarote region was probably another refuge for the possibly predator-ridden and ecologically upset large ratites. In their Lanzarote refuge the relatively sluggish and elephantine birds must have become even more endangered as their numbers and habitat decreased. If any of them had survived the separation of the small island from the continent, they had little chance to survive. If any of their bony remains were preserved to the present day, they should be searched for and found to piece together a more detailed and complete story of these unusual birds.

If the clues provided by the eggshell remains from Asia prove to be correct, the aepyornithid ancestors like their struthionid counterparts were driven out of Asia or they became extinct in their ancestral home for various other reasons. Still more traces should be uncovered along their routes of adaptive radiation and migrations from the steppe regions of Asia through the Near East and through Africa. It might also be worthwhile to check the museum stores of fossil ratite bones from Asia for signs of aepyornithid features.

These speculations can be countered with the suggestion that parallelism may have been rampant among the ratite birds. This may have been. But I can not conceive of the idea that Mio-Pliocene ostriches in the region of Lanzarote or in Inner Mongolia should have evolved, side by side, a struthious and an aepyornithoid pore pattern. The distinct struthious eggshell with its round pores that open on the smooth surface of the shell seemed a very useful design, as it was maintained successfully through the ages, from the Lower Pliocene (and probably much longer) to modern times, and throughout the range from Inner Mongolia to North and West Africa. Only in Africa, it appears, did it become modified along the known lines of struthious eggshell modification, and possibly only after the long line of ancestors from the Far East had become severed and extinct. One may even see this change as the result of environmentally favored genetic events that affected small and disjunct populations.

In the same way one can explain the stability of the family-specific aepyornithid eggshell pattern and its range of modification. It seems conceivable that the newly described aepyornithoid pore pattern with the predominance of rows of dagger-point and sting pores (in contrast to the one with the long linear pore grooves) is identical with the phylogenetically old aepyornithid shell pattern that was present before eggshells with long pore grooves came into existence. In fact, it is this trend in which I see processes of parallel evolution in the Struthionidae and Aepyornithidae, namely the departure from small pores through the development of increasingly longer pore grooves, which each family accomplished in its own specifically patterned way.

I realize that this is all trying speculation, for my purpose and pleasure desirable speculation, which may stir up opinion and call for future research.

The Aepyornithoid and Problem Eggshells from Asia

The "type A" eggshells from Hasnot, Punjab, and from Camp Margetts in Inner Mongolia seem to have originated at least in the Lower Pliocene and possibly as early as in the Upper Eocene (p. 30). They may bear a direct relationship with those shells tentatively treated as problem collections probably from the Lower Pliocene. As mentioned above, I strongly suspect that the Asiatic aepyornithoid eggshells from India and Mongolia are in reality traces of aepyornithiform ancestry. If one can rely on the relative dating of the aepyornithoid eggshells from Inner Mongolia, Punjab, Lanzarote, and the aepyornithids from Madagascar, and if one adds the radiocarbon-dated samples from the latter island, then emerges a crude picture of a temporal succession of these forms. It spans the scale from possibly the Upper Eocene, to the Upper Miocene, to the Lower Pliocene and into the Quaternary as recently as about 2,000 years ago.

It should be understood that this temporal sequence is not meant to represent a phylogenetic time scale or one useful for speculating on the dispersal rates of ratite birds. We must bear in mind that the ancestors of the Aepyornithidae may have come to Madagascar in late Cretaceous times or still in the early Tertiary (p. 3) and that we know particularly little about the evolution of birds during the 72 million years of the Cretaceous period. However, with the few available scraps of information it is gratifying that the aepyornithoid and aepyornithid shell remains from the localities mentioned above can be listed roughly according to a progressive time scale. It can be aligned with the presumably progressive movements of the ratites from Inner Mongolia or some other place in the steppe regions of central Asia to Madagascar by way of India and West Africa (Lanzarote), and it is neither reverse nor scrambled. What worth this speculation is must still be proved.

It seems safe to assume that neither one of the eggshell finds mentioned in this paper is the oldest of its kind. Therefore, the fitting of the fossils into a system of time-correlated adaptive radiation can become possible only as more information becomes available with new and more fossil evidence. I suggest, for a working hypothesis, that we stop thinking of elephant birds being insularly restricted to Madagascar and to the Quaternary period, and that we begin searching for further evidence of their ancestry on Lanzarote, in Africa (northwest Africa must be particularly promising), and in Asia as far as Inner Mongolia.

The Struthious Eggshells from Lanzarote and Mongolia

Perhaps the most conspicuous feature of these old eggshells is the fact that their pore patterns resemble most closely that of the eggs from the recent *S. c. camelus*. Indeed, the pore pattern of the "type S" eggshells from Lanzarote matches that of the *S. c. camelus* eggs so perfectly that one might think that Rothe held one of these specimens in his hands when he concluded that his Mio-Pliocene ostriches must have been at least closely related to the recent ostrich. However, as I pointed out, the pattern of the irregularly distributed tiny circular pores is an ancient and stable struthious pore system that has served ostrich embryos for at least 13 million years and over a considerable range of their geographic distribution, from the continental Inner Mongolia to the maritime Lanzarote region.

It occurs that the thickness of all of these struthious eggshells is on the average significantly less than that of the thick *Aepyornis* eggshells and also less than that of the aepyornithoid specimens. The old struthious eggshells with the needle-point pores are little thicker than the present day *S. c. camelus* shells. This may have a certain bearing on the stability of the pore pattern, although it can be only one facet of a more complex mechanism. On the contrary, the thickest ostrich shells known to date, that of the fossil Oshana Ostrich from South West Africa, reached up to 4.00 mm and possessed the most complex pattern of struthious pore grooves (Fig. 4).

The well-defined needle-point pattern of the pore openings of the "type S" eggshells from Lanzarote and from Mongolia makes it also easy to distinguish these shells from the "type A" shells secured from the same regions and, on Lanzarote, from the same stratum and locality.

It must be left an open question whether the struthious eggshells from the Tertiary land surface of Lanzarote are of the same age as the aepyornithoid eggshells from the same sediments. I can imagine that the latter might turn out older than the struthious remains and that the birds that laid the "type A" eggs had made it to the Lanzarote region before the advent of the struthious birds that laid the "type S" eggs. If the old sediments preserved the eggshells well, and the evidence proves that they did, and if the sediments formed a thin layer on solid bedrock, then the remains from different ages must have been closely packed. Indeed, they must have been pushed even more tightly together when the sediments were squeezed under the geological events that affected Lanzarote some 12 million years ago.

One is reminded of the peculiar pore pattern of the eggs from *S. c. spatzi* of Rio d'Oro (Fig. 1). It seems, so to speak, wedged between the two conforming patterns of needle-point pores of the present *S. c. camelus* and the Lanzarote "type S" egg. Apart from the time element involved, one can envision that the shell pattern of the *S. c. spatzi* egg must have evolved in a group of isolated birds aside from the mainstream of ostrich evolution.

Continental Drift and the Isolation of the Lanzarote Ratites

The question if the distribution patterns of certain species of birds might be attributed to continental drift has been an ornithological discussion of long standing and seemingly unsatisfactory results. However, Wolfson's (1948) heavily criticized paper on bird migration and the concept of continental drift can not be rejected on the grounds of a temporal discrepancy between drift and migration. In relation to the Lanzarote ratites one must point out that new geological data combined with the fossil biological evidence suggest new answers to the old problem. As has been mentioned on p. 21, Dietz and Sproll (1970) view the East Canaries as a microcontinent or sialic continental fragment that was detached from the African continent as a result of the rifting between North America and Africa. The time and duration of these events are by no means clearly determined. It may take millions of years from the initial opening of a gap to the complete separation of an affected land segment from its mother continent. Baja California of today may be an excellent example of how slowly such an event can take place. If the opening of the Ifni Gap, according to the continental drift concept, happened some 200 million years ago, the corresponding East Canaries block might not have become completely separated from Africa until millions of years later, at a time when the giant ratites had long been fully emerged and when the struthious and aepyornithoid birds had established themselves in the Lanzarote region.

Dietz and Sproll (1970) do not force the issue of a mid-Triassic detachment of the East Canaries block. They rather suggest that, alternatively, this event might have taken place, "in the early Cenozoic, associated with the Alpine orogeny and the creation of the Atlas foldbelt".

Rothe (1968 a, b) and Rothe and Schmincke (1968) present good evidence in support of the concept of a Tertiary detachment. They have pointed out similarities in the Cretaceous stratigraphy on Lanzarote and neighboring Africa, and Rothe found the ratite eggshells on Lanzarote in Tertiary calcareous sediments. According to Rothe (1968 a) a land connection between Lanzarote and continental Africa might have still existed some 12 million years ago. As it is most likely that the ratites had reached Lanzarote long before that time, their isolation by continental drift can be noted as equally probable (Sauer and Rothe, 1972).

Geological and biological evidence brings new validity to the hitherto controversial concept of bird distribution in relation to continental drift.

It makes it plausible that the isolation of the struthious and aepyornithoid ratites of Lanzarote might have been the direct result not of the initial rifting process but of the eventual detachment of the East Canaries block from the African mainland and its subsequent drift in a southwesterly direction.

The question arises if the Malagasy ratites might not have experienced a similar fate.

Studies of other faunistic elements, though less clear, suggest old faunal connections between the Canary Islands and the African continent. For example, Pinker (1960, 61, 62, 63, 65, 68, 69) investigated the Lepidoptera of the Canary Islands, including the Lanzarote fauna. He noted that many species, originally thought to be endemic, are represented by subspecies on the African mainland. He considers the faunistic link as very old rather than recent. Avifaunistic records and peculiarities of Lanzarote are listed by W. D. C. Trotter and commented upon by R. de Naurois in Trotter (1970).

Summary

A morphological investigation of ratite eggshells from Africa and Asia, their family-specific identification, and their phylogenetic placement are the subject of this study.

The familial characters of the pore patterns of struthionid and aepyornithid eggshells are described. They form the basis for the identification of fossil ratite eggshells from Lanzarote (Canary Islands), Punjab (India), and Inner Mongolia.

The small circular pore openings, clusters of pores, and clusters of irregular pore grooves of struthionid eggs are irregularly distributed over the surface of the eggshell and show no particular alignment with the axes of the egg. The grooves form irregular, reticulate, or rosette patterns, and like the clustered pores they are mostly located in pits that may be interconnected by furrows.

The aepyornithid eggshells possess dagger-point and sting pores and linear, often bent and forked pore grooves. These pore openings are conspicuously oriented parallel with the longitudinal axis of the egg. Small deviations from this norm may occur but do not obscure the general pattern. Microducts and lacunae may be present as parts of the ventilation system.

Eggshells from Tertiary calcareous sediments of Lanzarote are recognized as struthious and aepyornithoid. The former possess a pore pattern that coincides with that of the *S. c. camelus* egg. The pore openings of the latter resemble those known from Malagasy *Aepyornis* eggs.

Further aepyornithoid eggshells are described from Hasnot, Punjab, and from Inner Mongolia. They originated at least in the Lower Pliocene; the Mongolian remains may be as old as Upper Eocene. Other eggshells from Mongolia that resemble the aepyornithoid shell type are left as problem collections for further investigations of their origins. Struthious eggshells from the Pliocene and Pleistocene of Asia are listed and illustrated for comparison.

The discussion focuses on the familial aspects of the pore patterns. The presence of pore grooves in certain struthionid and aepyornithid eggshells is seen as the results of phylogenetic developments derived from eggshells with patterns of irregularly distributed circular pores (Struthionidae) and longitudinally oriented daggerpoint and sting pores (Aepyornithidae).

In a way of constructive speculation it is suggested that the ancestors of the Aepyornithidae, just like those of the Struthionidae, radiated from Asia to Africa.

It is probable that the Lanzarote ratites were separated from the African continent and thereby from their ancestors by continental drift. This interpretation is based on threefold evidence. (1) The struthious and aepyornithoid eggshell remains were found on Lanzarote in Tertiary calcareous sediments representing an old land surface. (2) Pronounced similarities exist in the Cretaceous stratigraphy of the eastern Canary Islands and the neighboring parts of Africa. (3) The North America — Africa continental drift pattern provides a distinct place (Ifni Gap) for the East Canaries block in the margin of the African continent.

Zusammenfassung

Eierschalen altweltlicher Ratiten von Afrika und Asien, Fragen ihrer Familienzugehörigkeit und ihre stammesgeschichtlichen Beziehungen sind die Objekte und Problemstellungen dieser morphologischen Untersuchung.

Als Basis für die Vergleiche werden Merkmale der Porenmuster struthionider und aepyornithider Eier beschrieben. Danach werden fossile ratite Eierscherben von Lanzarote (Kanarische Inseln), Punjab (Indien) und aus der Inneren Mongolei identifiziert.

Struthionide Eierschalen besitzen je nach Art und Unterart kleine rundliche Poren, Porengruppen und Gruppen von irregulär, netz- und rosettenförmig angeordneten Porengruben, die überwiegend diffus über die Eierschale verteilt sind. Die Gruppen von Poren und Gruben liegen meistens in Vertiefungen, die durch Furchen verbunden sein können.

Aepyornithide Eierschalen weisen längliche Poren, Stichporen und lineare, mitunter gebogene und gegabelte Porengruben auf. Sie verlaufen auffällig in der Richtung der Längsachse des Eies. Eng lokalisierte Abweichungen von diesem Muster verwischen nicht den Gesamteindruck der parallelen Porenanlage. Quer verlaufende Mikrokanäle und Lakunen in der Sponginschicht der Eierschale können als Besonderheiten des Ventilationssystemes auftreten.

Eierschalen aus tertiären Kalkareniten von Lanzarote werden als struthionid und aepyornithoid beschrieben. Das Porenmuster der struthioniden Eierscherben stimmt mit dem von *S. c. camelus* überein. Die Porenöffnungen der als aepyornithoid, d. h. als dem aepyornithiden Eityp ähnlich, bezeichneten Eierscherben sind denen der *Aepyornis*-Eier Madagaskars vergleichbar.

Ratite Eierscherben von Hasnot (Punjab) und aus der Inneren Mongolei werden ebenfalls als aepyornithoid erkannt. Sie stammen wenigstens aus dem frühen Pliozän, die ältesten vielleicht aus dem oberen Eozän. Die Bestimmung einiger ratiter Eierscherben aus der Mongolei, die ebenfalls dem aepyornithoiden Schalentyp ähneln, wird bis zur Kenntnis ihrer genauen

Herkunft und der Bereitstellung eines größeren Vergleichsmaterials ausgesetzt. Asiatische Straußeneierschalen aus dem Pliozän und Pleistozän werden vergleichsweise angeführt. Bereits im frühen Pliozän gab es in der Mongolei sowohl einen struthioniden als auch einen aepyornithoiden Eierschalentyp, deren Entstehungen wahrscheinlich noch weiter zurückreichen.

In der Diskussion wird die Brauchbarkeit der Porenmuster zur Charakterisierung altweltlicher Ratiteneier nach ihrer Familienzugehörigkeit unterstrichen. Auf die mutmaßlichen stammesgeschichtlichen Entwicklungen und Veränderungen der Porenöffnungen struthionider und aepyornithider Eierschalen wird hingewiesen. Eier mit Porengruben, im Gegensatz zu denen mit rundlichen und länglichen Einzelporen, werden als stammesgeschichtlich abgeleitet aufgefaßt.

Spekulativ wird die These aufgestellt, daß die Vorfahren der Aepyornithidae genau so wie die der Struthionidae aus Asien stammen und sich von dort nach Afrika ausbreiteten.

Verschiedene Hinweise sprechen dafür, daß die Ratiten von Lanzarote durch Kontinentalverschiebung von ihrem afrikanischen Herkunftsland und damit von ihren Vorfahren isoliert wurden. Es sind dies das tertiäre Alter der Kalksedimente auf Lanzarote, stratigraphische Übereinstimmungen mit dem benachbarten Kontinent aus der Kreidezeit, die Rekonstruktion des Abbruchs und der Verdriftung des ostkanarischen Landblockes.

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Zeitschrift/Journal: Bonn zoological Bulletin - früher Bonner Zoologische Beiträge.

Jahr/Year: 1972

Band/Volume: 23

Autor(en)/Author(s): Sauer Edgar Gustav Franz

Artikel/Article: Ratite Eggshells and Phylogenetic Questions 3-48