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ULTRASTRUCTURE AND TAXONOMY OF OSTRICH EGGSHELLS FROM UPPER PALAEOLITHIC SITES OF INDIA

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ABSTRACT

This paper deals with the taxonomy and ultrastructure of isolated ostrich eggshell fragments from several Late-Pleistocene (Palaeolithic) sites reported by Kumar *et al.*, (1988) and records the discovery of a new locality for these *Struthio* eggshell fragments near Anjar, Kachchh. The extensive occurrence of these eggshells in over 40 widespread localities in Peninsular India reopens the question of whether these ratite birds represent the last remnants of *Struthio* lineages known from the Siwalik or whether they were reintroduced into the Indian landmass from East Africa in the Late Pleistocene. This aspect involves precise taxonomic identification based on shell ultrastructure using Scanning Electron Microscopy (SEM), a feature dealt with in the current year.

INTRODUCTION

The earliest systematic description of ostrich remains in India is that of Lydekker (1884) who recorded the occurrence of its bones from Upper Siwalik (Dhok Pathan) and assigned them to *Struthio asiaticus* (Milne-Edwards). Besides, he (op. cit.) also recorded certain other taxa from several unspecified levels in the Siwalik Group belonging mostly to aquatic forms. Apart from the isolated bones assigned to *Struthio*, other Siwalik records relate only to eggshell fragments. Some of these eggshells, collected by Aienger in 1935 from the Upper Siwalik (Dhok-Pathan) near Hasnot, Punjab (now in Pakistan) and presently stored in the American Museum of Natural History, were questionably referred to *Struthio*. Later, Sauer (1972) assigned these specimens to *Aepyornis* on the basis of their pore structure.

Apart from the Siwalik occurrences, the only other record of ostrich remains in India is that of eggshell fragments which are known to occur in over 40 Upper Paleolithic sites in the Peninsula (Kumar *et al*., 1988). Earlier reports on these eggshells, some of which bear engravings supposedly made by Upper-Palaeolithic man (Kumar *et al.*, 1988) have dealt only with their archaeological implications. An Upper Palaeolithic age has been inferred for the eggshells in most of these localities, based either on associated Upper Palaeolithic implements or on radiocarbon dates which vary between 25,000 to 40,000 years B.P. (Sali, 1978; Agrawal, 1987 : in Kumar *et al.*, 1988).

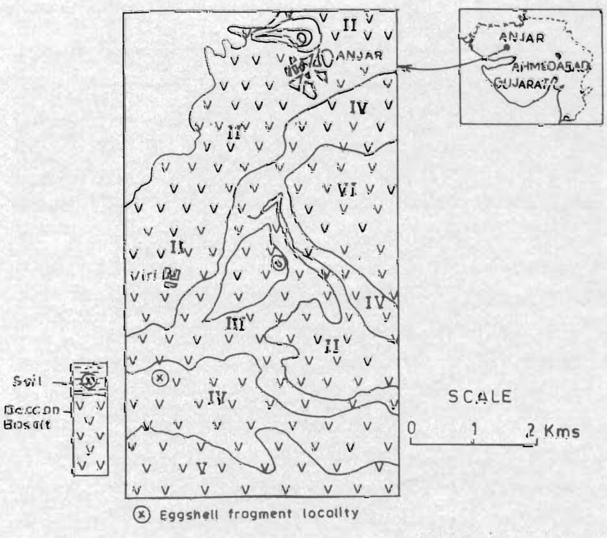


Fig. 1. Geological map of the area around Anjar, Kachchh district, Gujarat Showing Ostrich eggshell locality.

A new locality for ostrich eggshells was discovered recently by two of us (SB and SS) which is situated about 1.5 km South of the village Viri (70° 30″ N : 23° 4′50″ E) near Anjar in district Kachchh, Gujarat. These eggshell fragments, including one which is 5 cm in length, were obtained by surface picking from a pale yellow topsoil occurring above the Deccan basalts. In a nearby section, the fossiliferous intetrappean beds have recently been recognised (Ghevariya, 1988). It is possible that future work may reveal *in situ* occurrences of eggshell fragments in the area. The exact locality is shown on Fig. 1. The age of Anjar eggshells is, however, hard to establish because of absence of associated tools and the fact that all specimens were found on the surface. Similar taxonomically unassigned eggshell fragments which the present authors believe to be identical to the Anjar specimens, have recently been reported from the Kothara Formation (Pleistocene) exposed south of Naliya in the Kachchh district (Mohabey, 1989) and from Kunwargram-nanukchhorna (Wakankar, 1985 in Kumar *et al.*, 1988).

MATERIAL AND METHODS

The eggshell fragments selected for study in this work are from three localities, namely, Chandresal I, Chandresal III, (Kota, Rajasthan) and Anjar (Kachchh, Gujarat). The specimens were studied both under the optical microscope and the scanning Electron Microscope. For SEM study, both fractured and polished surfaces were used. These were first etched with 10% acetic acid, for 12 seconds, washed in the distilled water and then subjected to ultrasonic cleaning. The specimens were then sputter-coated wih gold and examined in JEOL SEM-25 S at 15 kv.

SHELL MICROSTRUCTURE

The taxonomy and microstructure of ostrich eggshells is known through the pioneering works of Schönwetter (1927), Sauer (1966, 1968, 1972), Sauer and Sauer (1975), Dughi and Sirugue (1964), Erben (1970), Schmidt (1957) and Tyler and Simkiss (1960). As early as in 1927, Schönwetter demonstrated the taxonomic utility of pore pattern in ratite eggshells as a means of differentiating them down to subspecies level. Sauer (1972) later made extensive studies on ratite eggshells and confirmed, with some slight modification, Schönwetter's findings on the use of pore pattern in ratite classification. He also discussed phylogentic and palaeogeographic implications (in "Continental drift" models) of the ratite eggshells.

The present eggshells are aboiut 2.2m thick. The external surface of the eggshell is smooth except for shallow pore pits with an average density of 3.5 pits/cm^2. The pore pits have an average diameter of 1.0 mm and are well separated from each other. They appear to lack orientation, at least in all specimens in the present collection including those obtained from Kachchh. The pits are circular or oval in shape and contain clusters of 25-66 pores (Plate II, Fig. 1.6). A similar pattern is found in *Struthio camelus molybdophanes* (Schönwetter, 1927) from which the Indian specimens (as had been noted earlier, Bidwell, 1910) appear to be indistinguishable except in the density of pore pits. This density is appreciably less in the present specimens (3.5 pits/cm^2) compared with Schönwetter's (1927) typical average of (12 pits/cm^2) for recent struthious eggshells. However, studies by Sauer *et al.*, (1975) have shown that the number of pore pits per unit area varies considerably even in the same eggshell. Hence, the density deduced here is not of significant taxonomic value, based as it is on shell fragments. Also, this difference in the density of pore pits may reflect palaeoecological and palaeoenvironmental modificatios but does not suggest (at least for the present) that a new taxon should be erected.

In transverse sections (Plate I. — 1, 2), the shell is clearly divisible into three layers: an inner mamillary layer which forms about one-third of the total thickness (650 μ), a middle prismatic layer which forms the bulk of the thickness, and an upper exterrnal layer. The junction of the mammillary and prismatic layers is marked by a zone of horizontally discontinuous to continuous growth lines. This feature is well seen by both light and scanning electron microscopy (Plate I. — 1-3).

In transverse section, the mammillary layer shows distinct crystalline structures (Wedges) rising from the mammillary cores towards the prismatic layer (Pl.I — 1, 2). Prominent parallel discontinous growth lines are seen in the entire mammillary layer. These are somewhat convex or curved externally. The prismatic layer as seen under SEM, consists of faint vertically oriented columnar structures arranged parallel to one another and a clear squamous pattern (Pl. I — 4). Numerous more or less horizontal growth lines, better seen under light microscope, are present in the prismatic layer (Pl. I — 1, 2). These growth lines are continuous throughout the length of the eggshells.

The outer or external layer is not uniformly preserved in most of the eggshell specimens in the present collection. It is very thin and discontinuous and consists of well-developed crystallites oriented at right angles to the surfface of the eggshell (Pl. I — 1, 2).

The internal surface of the eggshell shows well-developed mammilliary knobs under the SEM (Pl. III,— 1-6). They are circular or subcircular in shape with their diameters ranging between 25-40 μ. Sometimes, the mammillae are separated by irregular spacings which may represent inter-mammillary ventilation duct systems (Pl. III, — 1, 3). Through this inter-mammillary space, ducts pass through the mammillary and prismatic layers and reach the outer surface of the shell pit. In some cases, the mammillary knobs coalesce with each other (Pl. III, — 1,5).

One of the most important features of the eggshells is the pore canal system. These pore canals are almost invariably branches (Pl.I, — 1, 2). Branching of the pore canals is dichotomous and may occur at different depths. In most cases, however, it occurs close to the junction of mammillary and prismatic layers and becomes prominent in the outer half of the prismatic layer. In most of the specimens studied, the pores on the external surface occur within the confines of shallow circular pits and vary in number from 25-66. In each pit there are linearly raised and depressed areas. The pores occur mostly in the depressed portions (Pl. II, 6). Openings are either isolated or linked to each other. It is important to point out however, that the criterion used in the past for taxonomic differentiation of African ostriches (Schönwetter, 1927; Sauer, 1972 and others) are based almost exclusively on pore pattern, i.e. forms and arrangements of the openings of pore canals on the external surface of the eggshell. Sufficient attention has not yet been given to other structural features such as the finer taxonomic assignment. In any case, the pore pattern of the present eggshells as seen on the external surface, is identical to that found in *Struthio camelus molybdophanes*, a present day taxon found in Somalia and Ethiopia (Africa). For a comparison with the pore pattern withknown subspecies of *Struthio camelus*, see Fig. 2.

DISCUSSION AND CONCLUSION

The foregoing account on the morphology of the pore pattern and shell microstructure confirms earlier suggestions (Bidwell 1910, Sauer, 1968), that the ostrich eggshell fragments recovered from Banda and other Pleistocene levels in Peninsular India (Kurnar *et al.*, 1988) have close structural similarity to the Somali and Ethiopian ostrich, *S.c. molybdophanes*.

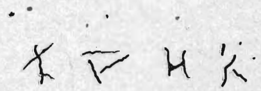
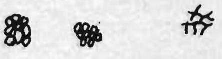
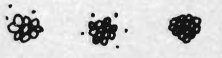
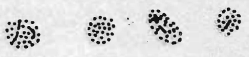
Sub species of Struthio camelus	Pattern	Pores and grooves	Pores/Porepits Per sq cm	Diameter of Pores/Porepits in mm
S. c. camelus	single pores		100	·02 – ·03
S. c. spatzi	groups of pores + grooves		70 2	·01 – ·02 0.5
S. c. australis	reticulate grooves		12	0.5
S. c. massaicus	composite of 3 & 5		8	0.8
S. c. molybdophanes	clusters of 30 - 70 pores		10	1.0
Indian specimens (present work)	clusters of 25-66 pores		3.5	1.0

Fig. 2. Pore patterns of struthious eggshells. Data after Schomwetter (1927) and Sauer (1972).

However, this resemblance has to be viewed in the light of established criteria for taxonomic differentiation at low (specific, intraspecific) levels as well as in a palaeobiogeographical framework. The issues that have to be addressed concern the value of pore structure and distribution as a criterion for taxonomic distinction and furthermore the relationships between the Central and South Asiatic species, *S. asiaticus* and the African species *S. camelus* have also to be considered.

As currently understood (Mikhailov and Kurochkln, 1988), the evolution of ostriches may have taken place sometime during the Eocene in Central Asia. At the start of Neogene, particularly the Lower Pliocene, there was a far ranging dispersal of these primitive ratite birds. The Siwalik occurrences of eggehells recovered by Aiengar 1935 from the Dhok Pathan Formation at Hansot (now in Pakistan) and skeletal remains from unspecified localities in the upper Siwaliks (Lydekker, 1884) have been ascribed to *S. asiaticus* (Milne-Edwards). *S. asiaticus* was a widely distributed taxon in Central, near-West and South Asia and exhibits a wide variety of pore morphologies, ranging from Typa A (aepyornithid) in the early Neogene, through an intermediate Type A-S stage to Type S (struthionid) in the Late Pleistocene. The Hasnot eggshells, originally labelled as *?Struthio*, were later considered to have affinities to *Aepyornis* because of pore structure and morphology (Sauer, 1972). The Siwalik eggshells may reflect the same trend seen in Mongolian *S. asiaticus* in which the early Neogene forms have Type A pores (Mikhailov and Kuruchkin 1988). The great variations in pore morphology within a single species (for example, *S. camelus, S. asiaticus*) suggests that this factor may not be of utility in specific differentiation and is probably palaeoenvironment-dependent. Its use may only be limited to the differentiation of varietal population of the African *S. camelus* as pointed out by Schönwetter (1927) and Sauer (1972). Similarity between the Indian Pleistocene eggshells and *S.c. molybdophanes* may in part be the result of similar responses to increasing aridity and similar environment. Therefore, it would be more appropriate, till shown otherwise by future discoveries, to refer the Indian specimens to *Struthio* cf. *S. asiaticus*.

Sauer (1968, p. 48) assumed that the skeletal material recovered from the Siwalik (Lydekker, 1884) and the Banda eggshell fragments (Bidwell, 1910) belonged to *S. asiaticus* even though recent magnetostratigraphic studies (Johnson *et al.*, 1983) have shown that the Lower Pliocene and Late Pleistocene Struthio-bearing horizons may be separated in time by more than 6 my. The correspondence of association is forthcoming. At presnt, however, no final verdict can be given regarding associations in which either only bones are known (Lydekker, 1884), or in which only eggshell fragments have been recognized as in the case of Dhok Pathan eggshells and the Late Pleistocene specimens (Kumar *et al.*, 1988). In fact, a consideration of the taphonomic factors suggests that differing burial conditions hinder the preservation of bones in association with eggshells, a feature which has been well demonstrated in the cases of the Indian dinosaur eggehslls (Srivastava *et al.*, 1986, Vianey-Liad *et al.*, 1987). Nonetheless, additional efforts in Palaeolithic sites have to be made to find skeletal material of *S. asiaticus* to establish unequivocally, the presence of the species based on both types of material.

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REFERENCES

BIDWELL, E. 1910 Remarks on some fragments of the eggshell of a fossil Ostrich from India, *Ibis.* **9** (4); 759-761.

DUGHI, R & SIRUGUE, F. 1964 Sur la structure des coquiles des ceufs des sauropsides vivants ou fossiles: le genre *Psammornis. Bull. Soc. Geol. France* **7**: 240-252.

ERBEN, K.H. 1970 Ultra strukturen und mineralisation rezenter und fossiler Eischalen bei Voegeln und Reptilien. *Biomineralisation* **1**: 1-66.

GHEVARIYA, Z.G. 1988 Intertappean dinosaurian fossils from Anjar area, Kachchh district, Gujarat. *Curr. Sci.*, **57**: 248-251.

JOHNSON, G.D., OPDYKE, N.D, TANDON, S.K. & NANDA, A.C. 1983 The magnetic polarity stratigraphy of the Siwalik Group at Haritalyangar (India) and a new last appearance datum for *Ramapithecus* and *Sivapithecus* in Asia. *Palaeogeog., Palaeoclimatol., Palaeoecol.*, **44**: 223-249.

KUMAR, G., NARVARE, G. & PANCHOLI, R. 1988 Engraved ostrich eggshell objects - New evidence of Upper-Palaeolithic art in India. *Rock Art Research* **5**(1): 43-53.

LYDEKKER, R. 1984 Siwalik birds, *Mem. Geol. Surv. India.* **10**(3): 136-202.

MIKHAILOV, K.E. & KUROCHKLN, E.N. 1988 The eggshells of Struthioniformes from the palearctic and its position in the system of views on ratitae Evolution. The joint Soviet-Mongolian Palaeontological Expedition. *Trans.* **34**: 43-109.

MOHABEY, D.M. 1989 Avian eggshells from Pleistocene of

Kutch. *Jour. Geol. Soc. India* **33**: 477-481.

SAUER, E.G.F. 1966 Fossil eggshell fragments of a giant Struthious bird *(Struthio oshanai*, sp. nov.) from Etosha Pan, South West Africa, *Cimbebasia* **14**: 1-52.

SAUER, E.G.F. 1968 Calculations of Struthious egg sizes from measurements of shell fragments and their correlation with phylogenetic aspects. *Cimbebasia* **1**: 27-55.

SAUER, E.G.F. 1972 Ratite eggshells and phylogenetic questions. *Bonn. Zool. Beitr.* **23**: 3-48.

SAUER, E.G.F., SAUER, E.N. & GEBHARDT, M. 1975 Normal and Abnormal Patterns of Struthious Eggshells from South West Africa. *Biomineralization* **8**: 32-54.

SCHMIDT, W.J. 1957. Ueber den Aufbau der schale des vogeleies nebst Bemerkungen veber Kalkige Eischalen anderer Tiere. *Ber. Oberhess. Ges. NatureHelik, Giessen, Naturw. Abt.* **28**: 82-108.

SCHÖNWETTER, M. 1927 Die Eier von *Struthio camelus spatzi Stresemann. Orn. Mber.* **35**: 13-17.

SRIVASTAVA, S., MOHABEY, D.M., SAHNI, A. & PANT, S.C. 1986 Upper Cretaceous Dinosaur egg clutches from Kheda district (Gujarat, India). *Palaeontographica Abt. A.* **193**: 219-233.

TYLER, C. & SIMKIES, K. 1960 A study of the eggshells of Ratite birds. *Proc. Zool. Soc. London.* **133**: 201-243.

VIANEY-LIAD, M., JAIN, S.L. & SAHNI, A. 1987. Dinosaur eggshells *(Saurischia)* from the Late Cretaceous Intertrappean and Lameta Formation (Deccan, India).*Jour. Vert. Palaeon.* **7**(4): 408-424.

EXPLANATION OF PLATES

PLATE I

1,2 Transverse section of eggshell showing network of pore canals and well differentiated mammillary and prismatic layers and afaint outer layer. Also note horizontal growth lines throughout the shell width. Anjar (Kachchh, Gujarat), base-width 7.5 mm (optical microscope).

3. Transverse section showing coneshaped structure in the mammillary layer. Chandesal I (Kota, Rajasthan), base width 4.10 mm (SEM).

4. Transverse section showing a clear squamous pattern in the prismatic layer. Chandesal III (Kota, Rajasthan) base width 0.38 mm (SEM).

5,6. Transverse section showing well-developed spongiose columns in the mammillary layer. Chandesal III (Kota, Rajasthan), base width 1.3 mm and 0.11 mm respectively (SEM).

PLATE II

1. Complete pore pit Anjar (Kachchh, Gujarat) base width 40.74 mm (SEM).
2. Enlarged view of a pore Anjar (Kachchh, Gujarat) base width 0.83 mm (SEM).

3,6. Enlarged view of pore pit showing isolated as well as coalescing pore Anjar (Kachchh, Gujarat) base width 0.28 mm and 1.17 mm respectively (SEM).

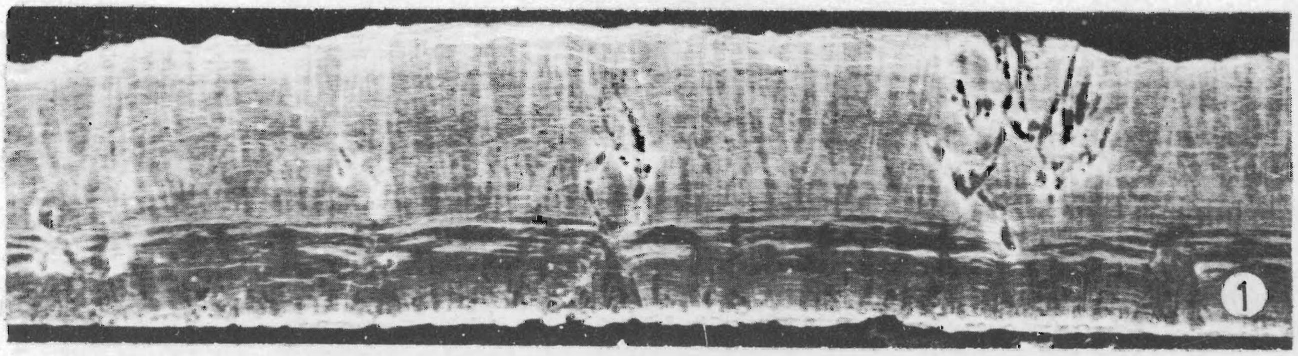
4. Eggshell in external view showing subrounded pore pits Anjar (Kachchh, Gujarat) maximum width 11.4 cm.
5. Eggshell in internal view showing aggregate of mammillae Anjar (Kachchh, Gujarat) maximum width 11.1 cm.

PLATE III

1,3. Inner surface showing rounded or shubrounded mammillary knobs Chandresal I (Kota, Rajasthan) base width 0.74 mm and 0.23 mm respectively (SEM).

2,4. Inner surface showing irregularly shaped aggregates of mammillae, with irregular interspace Chandresal III (Kota, Rajasthan), base width 1.21 mm and 0.12 mm respectively (SEM).

5. Englarged view of a single mammllary knobs showing aggregate of crystallites Chandresal II (Kota, Rajasthan) base width 0.05 mm (SEM).
6. Enlarged view of a mamillary knob showing well-developed platy crystals on the wall Chandresal III (Kota, Rajasthan) base width 0.40 m (SEM).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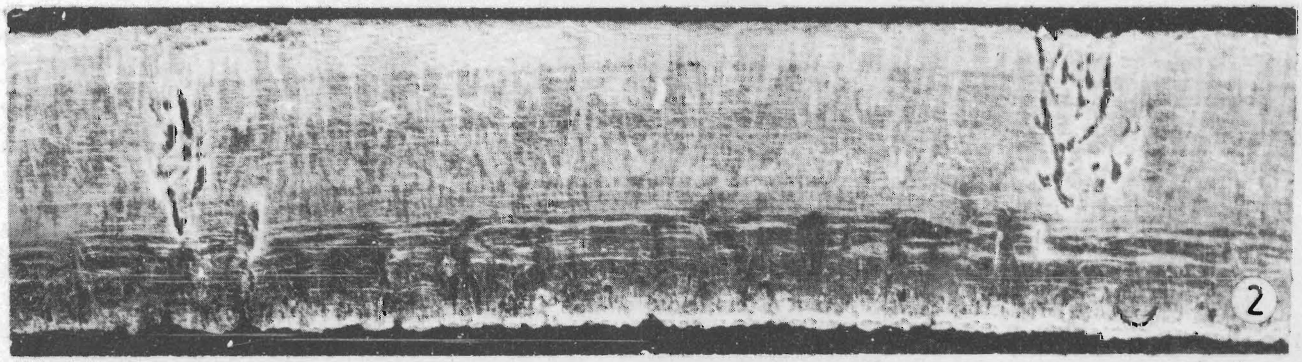
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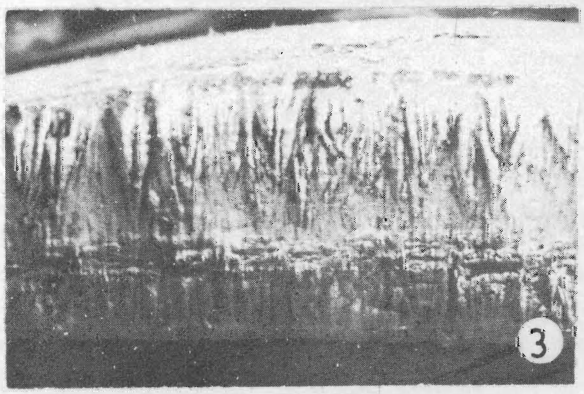
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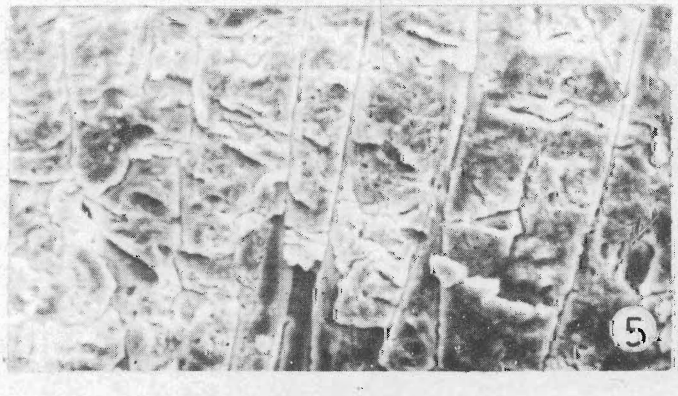
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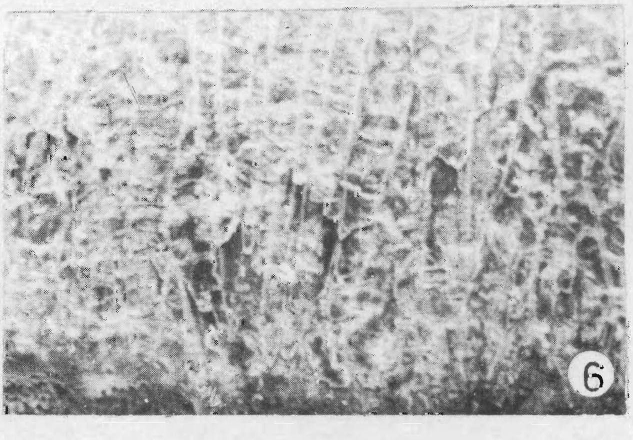
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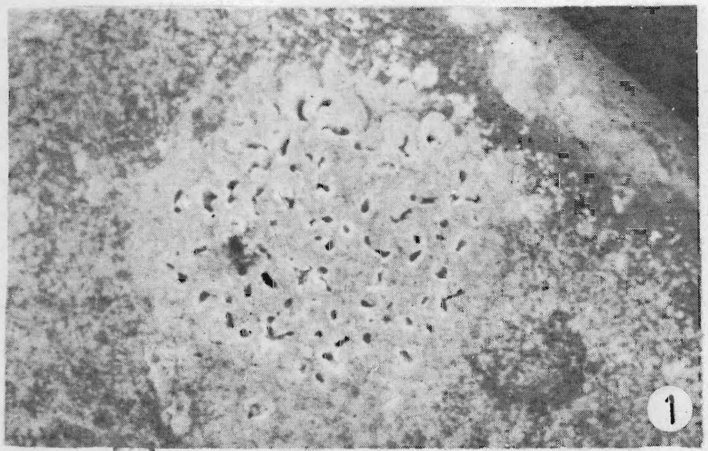
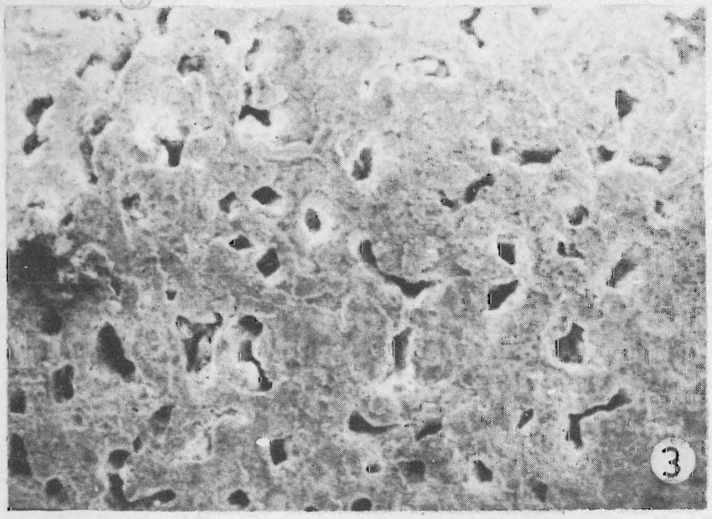
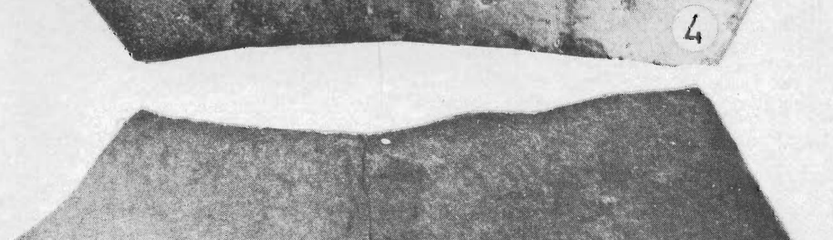
Plate II







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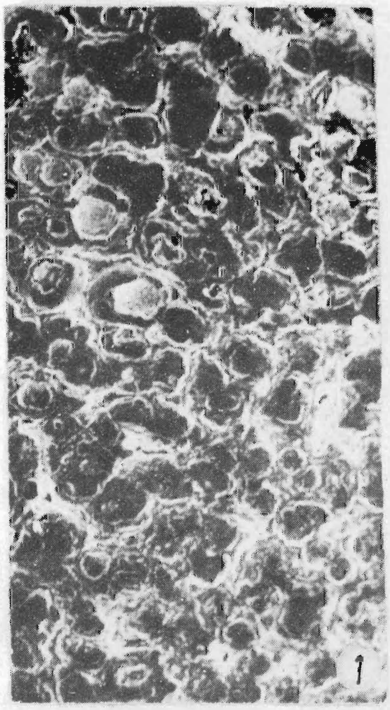
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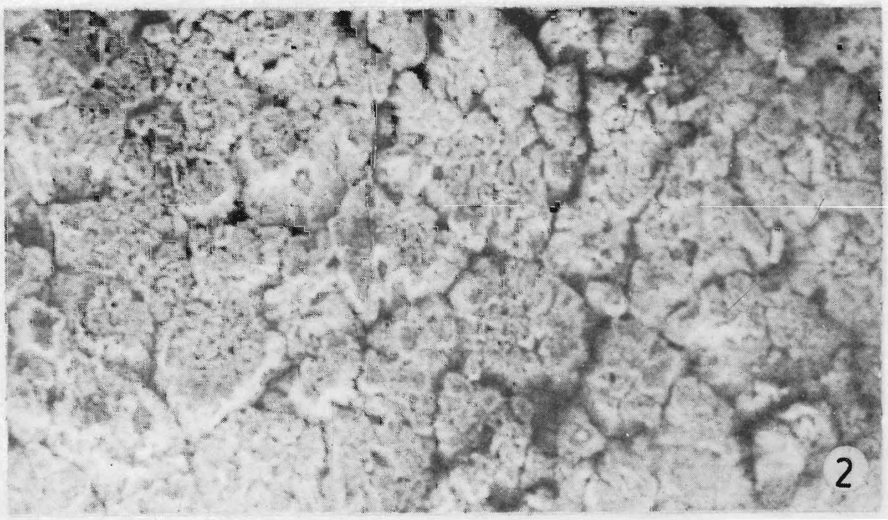
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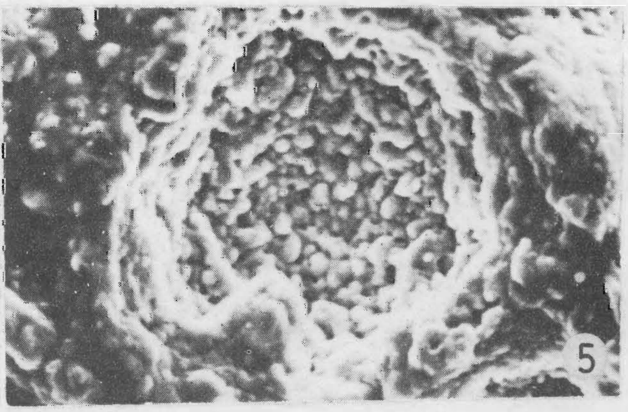
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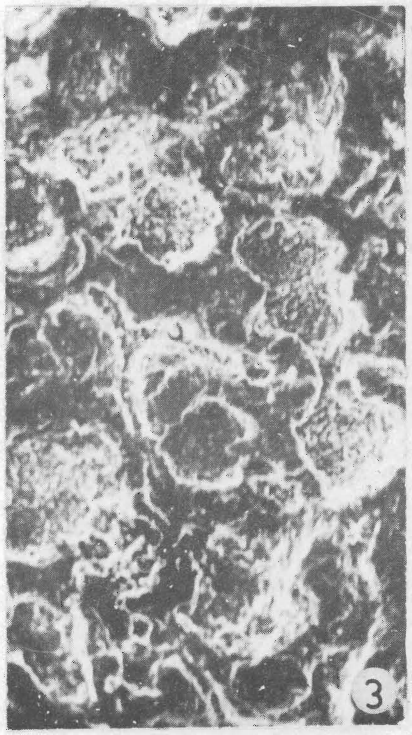
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