



## NOMINATION OF A LECTOTYPE FOR THE AVIAN OOSPECIES *PSAMMORNIS ROTHSCILDI* ANDREWS, 1912

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**Abstract:** *Psammornis rothschildi* is an avian oospecies, the type material of which was collected from the desert surface in 1909 (i.e., without stratigraphic context), 20 miles east of Touggourt, Algeria. At 3.2–3.3 mm thick, the eggshell is considerably thicker than those of extant ostriches. Thin sections of the eggshell have been illustrated, and descriptions of the surface features are available, but these have not included images of the external and internal surfaces. This lack has caused uncertainty among authors who have dealt with other occurrences of the taxon, because it has rendered it difficult to compare specimens from other localities with the type material. In order to rectify the situation, images of the original specimens are provided, their curation history is summarised, and a lectotype is nominated so as to stabilise the nomenclature.

**Key words:** ootaxonomy, lectotype, Struthionidae, late Neogene, North Africa, Middle East

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### Introduction

The avian oogenus and species *Psammornis rothschildi* ANDREWS, 1912, was based on two fragments of struthious eggshells collected in 1909 from a locality 20 miles east of Touggourt, towards El Oued, Algeria (Text-fig. 1). Thin sections of the fragments (NHMUK PV A 1334) were illustrated by Sauer (1969) but illustrations of the surfaces of the specimens have never been published, although a brief description was provided by Andrews (1912) who noted that they had been subjected to abrasion by sand.

For many years, three eggshell fragments from Touggourt (Rothschild and Hartert 1912) attributed to *Psammornis rothschildi* (as opposed to only two mentioned by Andrews 1912, Hartert 1927, Schönwetter 1929) have been curated by Bird Group at the Natural History Museum, Tring (catalogue # NHMUK E/1963.9.218), whereas four thin sections cut from two of the fragments were kept in the palaeontology collections at the South Kensington site of the Natural History Museum in London (Catalogue # NHMUK PV A 1334; Text-fig. 6), along with plaster casts of two of the fragments (Text-fig. 7). The curation of the original hypodigm at two separate museum sites could explain why

no illustrations of the external and internal surfaces have been published, because researchers visiting London may have been unaware that the original shells were curated at Tring. Sauer (1969) reported that no fragments of the shells of *Psammornis rothschildi* were available for measurement, even though Schönwetter (1929, 1960) listed them as part of the collection in Tring. To rectify the curatorial situation, the thin sections will be transferred to Tring in order to reassemble the original hypodigm of the species.

Because of the possibility, even if remote, that the three eggshell fragments labelled as coming from Touggourt, could represent different species (or potentially specimens from more than one locality), the aim of this note is to nominate a lectotype for *Psammornis rothschildi* and to illustrate the surface features of the specimens.

### Material

#### The Rothschild Bequest

On the death of Lionel Walter Rothschild, 2<sup>nd</sup> Baron Rothschild in 1937, the Rothschild Bequest left the Tring Museum (formerly the Rothschild Museum) and its contents

to the British Museum of Natural History, London (now the Natural History Museum of the United Kingdom, NHMUK). Rothschild's vast entomological collections were subsequently relocated to South Kensington in the late 1960s and the ornithology collections were transferred to a new, purpose-built building at Tring in the early 1970s.

However, the allocation of the Holocene / Pleistocene ornithological material was sometimes unclear, and as a result, some of it was transferred to South Kensington under the care of the then Palaeontology Department and some was kept in Tring under the care of the then Zoology Department. This situation was exacerbated by the research interests of the staff at the time who often worked across the Quaternary.

### Abbreviations

BM(NH) British Museum of Natural History, London  
MNHN Muséum National d'Histoire Naturelle, Paris  
NHMUK Natural History Museum of the United Kingdom (PV A – Palaeontology, Vertebrata, Aves collection; E – Egg collection register)

### Historical review

Sauer (1969) and Buffetaut (2022) provided detailed discussions concerning the naming and interpretations of the poorly known oospecies, *Psammornis rothschildi*. Originally named by Andrews (1912, but often cited as 1911, the date that features on the cover page of the publication), the species, its type material, and discovery context were discussed by Rothschild and Hartert (1912), Rothschild (1912), Hartert (1913, 1927), Bédé (1919), and Schönwetter (1929, 1942).

The genus name *Psammornis* has featured in publications by diverse authors, some of whom attributed other species to it, such as *Psammornis libycus* MOLTONI, 1928; this species is now considered by Buffetaut (2022) to be based on eggshell fragments of *Struthio* sp. The genus has been reported from other localities in Algeria (Heim de Balsac 1930) and from localities in Mauritania (Monod 1951, Tessier et al. 1971, Voisin 1971), Tunisia (Béde 1919, Choumowitch 1951), Saudi Arabia (Lowe 1933a, b, Philby 1933), and Iran (Dughi and Sirugue 1964) but most of these attributions have been contested or lack precise stratigraphic context (Wiemann et al. 2018, Mikhailov and Zelenkov 2020, Buffetaut 2022). The name also features in catalogues of fossil birds by Brodkorb (1963, 1998).

Arambourg and Magnier (1961) made a questionable listing of the genus (as *Psammornis*?) at the Middle Miocene locality in Libya known as Gebel Zelten (in the literature also spelled Jabal Zaltan and Djebel Zelten), but Mlíkovský (2003), who studied the fossil bird bones collected at Gebel Zelten by Oldřich Fejfar, pointed out that details of the fossils that formed the basis of this listing (skeletal remains or eggshell fragments?) were not provided, and that searches for the fossils in the collections by Rich (1974) and himself were not successful. On this basis he rightfully concluded that the materials “from Djebel Zelten cannot be identified even to the order until they are rediscovered and restudied”.

The systematic affinities of *Psammornis rothschildi* were discussed by Andrews (1912), Rothschild (1912), Lambrecht (1933) and more recently by Dughi and Sirugue (1964, 1978), Sauer (1969), Mikhailov and Zelenkov (2020), Buffetaut (2022). The conclusion of Andrews (1912) and most other researchers, has been that the Touggourt eggshells are closer in overall morphological features to those of Struthionidae (true ostriches) rather than to those of Aepyornithidae, as thought by Lambrecht (1933). Affinities to Eremopezinae as proposed by Rothschild (1912) are untestable, because no eggshells of *Eremopezus* ANDREWS, 1904 are known.

### Systematic palaeontology

Class Aves LINNAEUS, 1758

Infraclass Palaeognathae PYCRAFT, 1900

Family Struthionidae VIGORS, 1825

Genus *Psammornis* ANDREWS, 1912

Type species. *Psammornis rothschildi* ANDREWS, 1912.

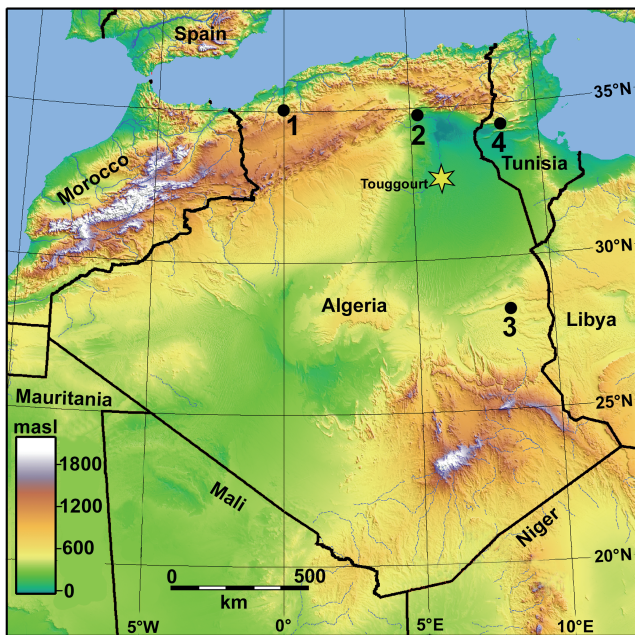
Genus diagnosis. Based on description by Andrews (1912): Eggshells in which the pore canals seem to be for the most part simple and run straight to the outer surface, where they open either singly or in small groups (sometimes in pairs) in very slight depressions. A few of the openings are very much larger than the rest. Outer layer divided into numerous layers by fine laminae of opaque material arranged parallel to the outer surface of the egg. Inner portion of shell ... divided into innumerable small columns separated from one another by narrow cracks and small openings and terminated at the inner surface of the shell in rounded knobs ... Each column may be more or less completely divided into secondary columns by dark vertical lines which tend to curve towards the inner end of the main columns... The whole shell is traversed by pore-canals which originate in the spaces between the columns of the mammillary layer and run to the outer surface of the shell, either as simple straight tubes, or with more or less repeated branching as they approach the surface, where they open as small pores. **Addendum:** the external and internal structured layers of the eggshells are separated from each other by a fine-grained amorphous (spongy) layer. The external layer is about twice as thick as the amorphous layer, which is slightly thinner than the innermost layer.

*Psammornis rothschildi* ANDREWS, 1912

Text-figs 3–6, 8–11

Species diagnosis. Based on description by Andrews (1912): Egg shells 3.2–3.4 mm thick.

Lectotype. (designated herein) NHMUK E/1963.9.218a eggshell fragment and thin sections (NHMUK PV A 1334 a and b) cut from same (mentioned as “the type shell” by Sauer 1969) (Text-figs 3, 6a, b, 8). Sauer (1969) mentioned two specimens as “types” but there is no guarantee that the two fragments came from the same egg, clutch, individual bird to even the same species. To avoid possible confusion, we nominate one of the specimens as lectotype, and refer the other specimen to the species.



**Text-fig. 1.** Location of the type locality of *Psammornis rothschildi* (yellow star) 20 miles east of Touggourt towards El Oued, Algeria. Other localities in Algeria and Tunisia that have yielded eggshell fragments of *Psammornis* spp. are 1 – Bou Hanifia, 2 – 20 miles south of Biskra, 3 – Temassinine, 4 – Chebket Safra.

Tentatively referred specimens. 1) NHMUK E/1963.9.218b fragment of eggshell and thin sections cut from it (NHMUK PV A 1334 c and d), from near Touggourt, Algeria (Text-figs 4, 6c, d, 9). 2) NHMUK E/1963.9.218c (Text-figs 5, 10) fragment of eggshell reportedly collected near Touggourt, Algeria (Rothschild and Hartert 1912) but possibly from Temassinine, Algeria.

**Lectotype locality.** 20 miles east of Touggourt towards El Oued, Algeria (Rothschild and Hartert 1912).

**Age.** Imprecise, probably latest Miocene or Plio-Pleistocene (see Buffetaut 2022, for discussion on the age of the specimens attributed to *Psammornis*); not Eocene as published by Rothschild (1912).

**Etymology.** *Psammornis* – from Greek Ψάμμος (*Psammos*) = Sand + ὄρνις (*ornis*) = bird.

**Date of publication.** With one exception, all scientists who have written about *Psammornis* have cited Andrews as the author and 1911 as the date of publication. The cover page of the congress proceedings (Verhandlungen) gives the date of publication as 1911, but, as was pointed out by Hartert (1927) it was not issued until the beginning of 1912, which, for the establishment of “priority” of zoological names (the case with *Psammornis*) must be the date of publication. Hartert (1927) concluded that the date of creation of the nomen *Psammornis rothschildi* by Andrews was 1912, because, as he wrote, “The volume, though dated 1911, did not appear before January or February 1912”.

The preprint (Sonderabdruck but called Bericht in the literature and on museum labels) of Rothschild’s paper (with Andrews’ paper as its appendix) was reviewed in the January 1912 issue of the *Ibis* (pp. 202–203). These preprints are

usually dated from 1911 (but from 1910 in the *Ibis*). It is thus possible that *Psammornis rothschildi* dates from the Sonderabdruck of 1911 (?1910), not from the Verhandlungen of 1912. However, in view of Hartert’s (1927) statement, we accept the Verhandlungen as the version that established the name of the taxon.

The nomen *Psammornis rothschildi* was “pre-published” by Rothschild and Hartert (1912; the cover page of the issue gives the date as 1911–1912, but the issue was released in 1912). Having evidently seen a preprint or proofs of the Andrews’s paper, the authors (incorrectly) cited its creation as being in the Bericht über den V. Intern. Ornith. Kongress, pp. 150 and 169–73 (Bericht = Report, whereas the Proceedings appeared as Verhandlungen). The incorrect “Bericht” citation was repeated by Bédé (1919) and is written on the labels of the thin section slides (Text-fig. 6).

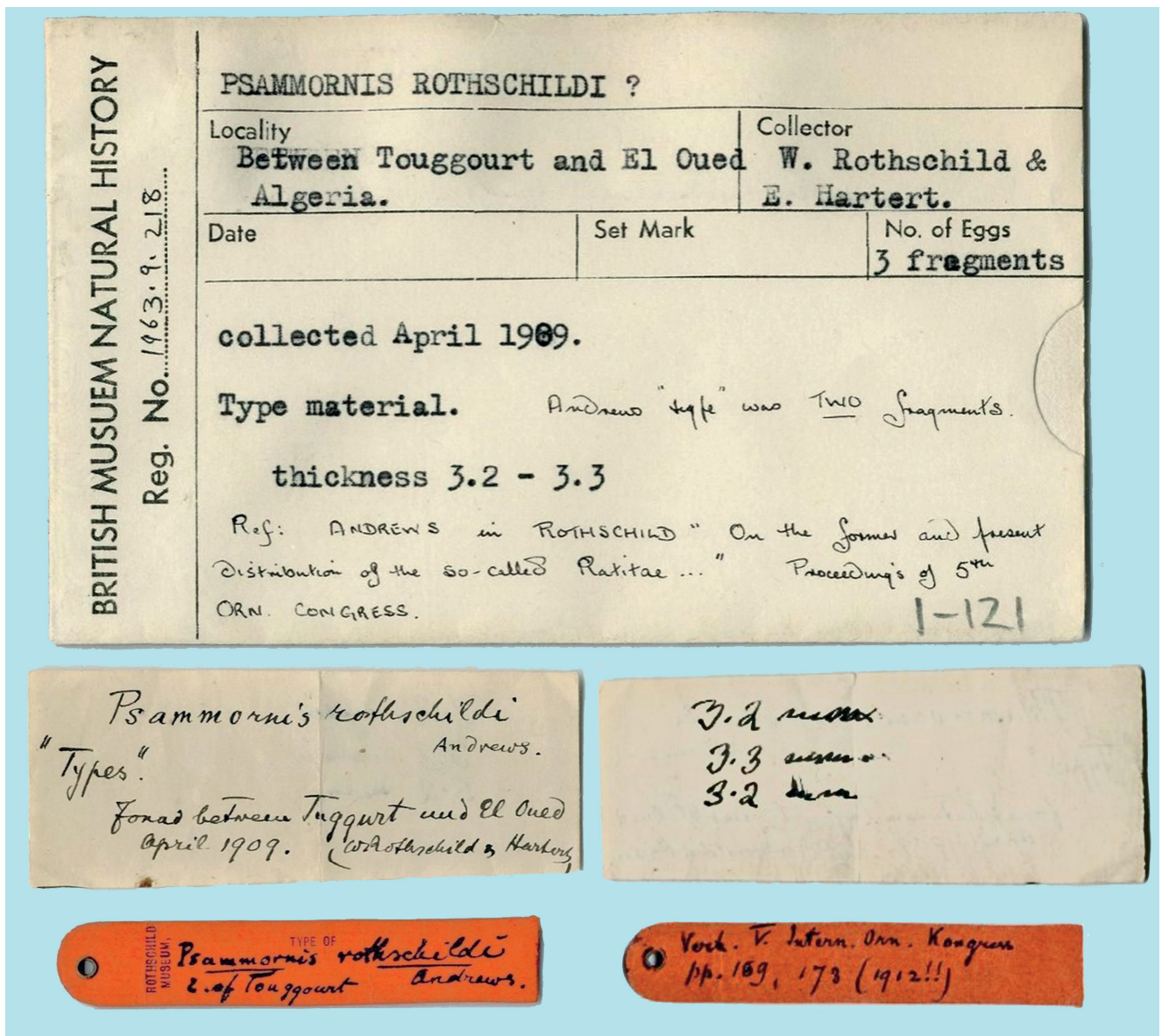
*Psammornis rothschildi*, as cited by Rothschild and Hartert (1912) is a nomen nudum because it was not accompanied by any description or designation of type material. Furthermore, the citation of the name (variously as *Psammornis* or *Psammornis rothschildi*) by Rothschild (1912) on pages 144, 146, 147, 150 and 167 of the congress proceedings (i.e., in the article in the Verhandlungen) does not give the author page priority because all these mentions are nomina nuda. The valid erection of the genus and species was by Andrews 1912, on page 173 of his article (pp. 169–174) in the proceedings.

**Documentation and curation.** The original hypodigm of *Psammornis rothschildi* consisted of two fragments of eggshell (Andrews 1912) even though Rothschild and Hartert (1912) reported that there were three fragments from the site. Andrews (1912) also mentioned the presence of thinner eggshells from the same location attributable to the extant ostrich, *Struthio*, but no details of their morphology were provided.

At the Natural History Museum, Tring, three eggshell fragments labelled “Type material” *Psammornis rothschildi* ? are curated under the register No. NHMUK E/1963.9.218 (i.e., entered in the register 54 years after the year of collection). The main label (Text-fig. 2) refers to the fact that Andrews’ “type” was **TWO** fragments but that the sample consists, in fact, of three fragments. The thin sections made from two of the fragments that were previously kept in London, have the register No. NHMUK PV A 1334 (Sauer 1969). Note that the main label in the Tring Museum articulates doubts about the precise nature of the type material, and it is for this reason, among others, that it is necessary to nominate a lectotype for the species. Small red cardboard labels with the fossils give the date of publication of the genus and species as 1912 (Text-fig. 2).

Inspection of the table at the end of Schönwetter’s (1929) paper shows that he listed two shards of “*Psammornis rothschildi* Andr.” from Touggourt (3.40 and 3.30 mm thick, that he specified as *typus*), and several shards (mehrere Scherben) from South of Biskra, 3.20 mm thick (labelled as having been collected by Hilgert). The locality data of the latter specimen(s) is probably erroneous, as explained below.

In a separate entry in the same table published by Schönwetter (1929), is the mention of several shards of eggshells from South of Biskra that measure 2.50 mm thick



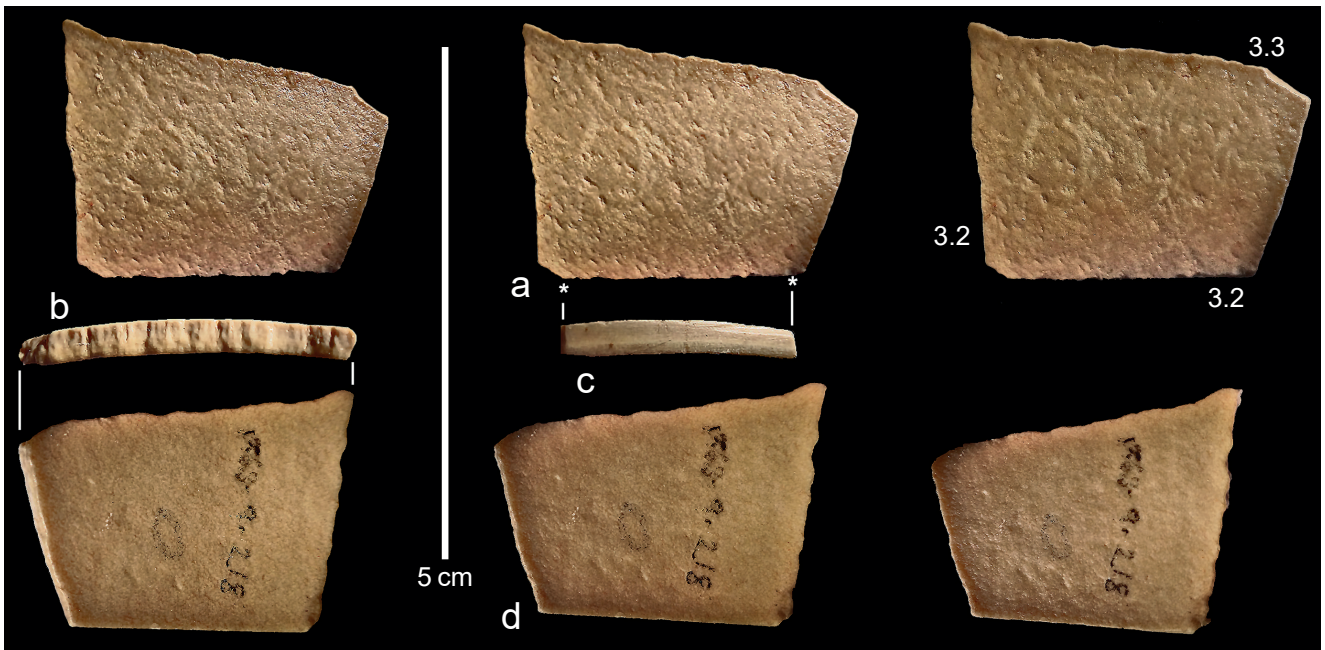
Text-fig. 2. Labels associated with 3 fragments of the "Type material" of *Psammornis rothschildi* ANDREWS, 1912 curated at the Natural History Museum, Tring (previously called the Rothschild Museum). Note the question mark after the species name, the comment about the type material and the publication date as 1912.

listed as "*Struthio* spec. extinct?". Our own measurements of the thickness of 41 fossil eggshell fragments from South of Biskra curated at Tring (NHMUK E/1963.9.236), give a range of variation of 1.8 to 2.6 mm, with the commonest measurement (15 fragments) at 2.5 mm. It appears that, at the time of Schönwetter's visit to Tring, there may have been a mix-up such that the supposed "third" specimen from Touggourt had become mixed in with the thinner shells from Biskra, and that it was subsequently re-associated with the other two fragments from Touggourt. The preservation characters of the specimen (Text-fig. 5) differ from the fossils from Biskra, which are darker chocolate coloured and show a greater degree of erosion of the shell surfaces. However, the fact that the third specimen labelled Touggourt has some aeolianite adhering to it suggests that it may have been collected at Temassinine, Algeria (see taphonomy section below).

**T a p h o n o m y.** Andrews (1912) and subsequent authors (Schönwetter 1929, Sauer 1969) reported that the inner and

outer surfaces of the eggshells of *Psammornis rothschildi* had been abraded by sand blasting, thereby reducing their thickness, but our own examination of the surfaces of the shells suggests that such is not the case, the polishing and abrasion is weak and has not greatly affected the thickness of the shells (Text-figs 8–10).

The two specimens from Touggourt studied by Andrews (1912) are free of matrix, but the third specimen labelled as coming from Touggourt, retains small patches of indurated, slightly reddened aeolianite. The aeolianite adhering to this specimen resembles that which occurs on several of the specimens from Temassinine (Fort Flatters) southern Algeria, collected by Fromholz. In addition, the shell is lighter in colour than the other two specimens from Touggourt. These observations raise the possibility that the "third" Touggourt specimen came from a different locality, possibly Temassinine. Hartert (1927) and Schönwetter (1929) briefly mentioned the material from the site (as Temassin (sic) by the latter author). The 12 specimens from Temassinine

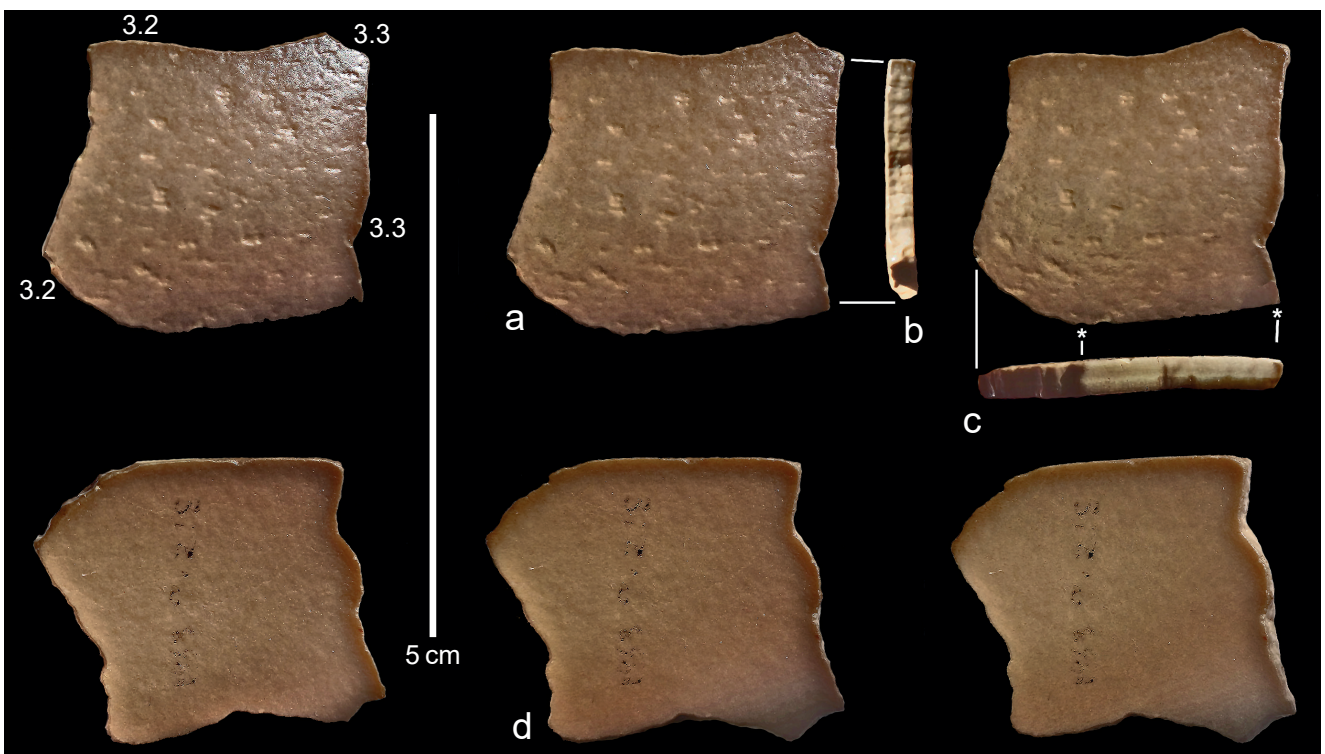


Text-fig. 3. NHMUK E/1963.9.218a, avian eggshell fragment from 20 miles east of Touggourt, Algeria, herein nominated lectotype of the oospecies *Psammornis rothschildi* ANDREWS, 1912. a: stereo external views, b: edge view, c: edge view of cut section from which thin sections were prepared, d: stereo internal views. Stars show the cut surface from which thin sections were made. Thickness measurements in three places.

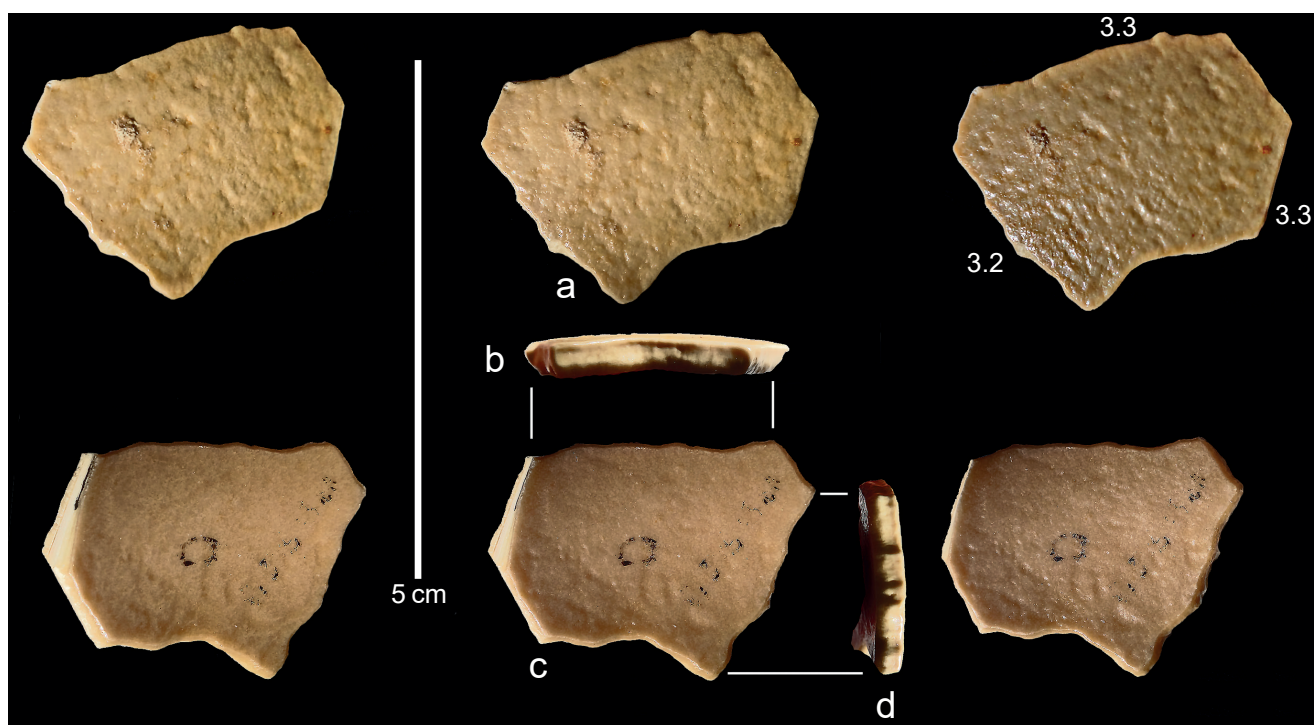
curated at Tring (NHMUK E/1963.9.221) range in thickness from 2.5 to 3.0 mm, and the third specimen supposedly from Touggourt is 3.2 to 3.3 mm thick, slightly greater than the thickest shell from Temassinine. Given the uncertainty, we prefer to refer the third specimen labelled as coming from

Touggourt to *Psammornis rothschildi*, but not to include it in the type series.

Sauer (1969) estimated that the original thickness of the Touggourt shells could have been about 4 mm, which, if correct would imply that about 0.7–0.8 mm of matter has



Text-fig. 4. NHMUK E/1963.9.218b, avian eggshell fragment from 20 miles east of Touggourt, Algeria, paralectotype of the oospecies *Psammornis rothschildi* ANDREWS, 1912. a: stereo external views, b: edge view, c: edge view of cut section from which thin sections were prepared, d: stereo internal views. Stars show the cut surface from which thin sections were made. Thickness measurements in four places.



**Text-fig. 5.** NHMUK E/1963.9.218c, avian eggshell fragment labelled as having been collected from 20 miles east of Touggourt, Algeria, herein tentatively referred to the oospecies *Psammornis rothschildi* ANDREWS, 1912. a: stereo external views, b: view of edge, c: stereo internal views, d: edge view. Thickness measurements in three places.

been removed from their surfaces. However, the lectotype shows well preserved pore slits and the pores in their depths are clearly visible over much of the shell (Text-fig. 8). The paralectotype shows some effects of abrasion, including superficial scratches, and some enlargement of the pore slits and depressions, possibly due to repeated exposure to dew (Text-fig. 9), but the damage has not greatly altered its thickness. The third specimen labelled as coming from Touggourt is well preserved and even retains small patches of indurated aeolianite on its external surface (Text-fig. 10). The pore slits are moderately well preserved, as are the pores in some of the depressions. Our measurements of the thicknesses taken at three to four places on each of the three eggshells labelled Touggourt, are 3.2 and 3.3 mm.

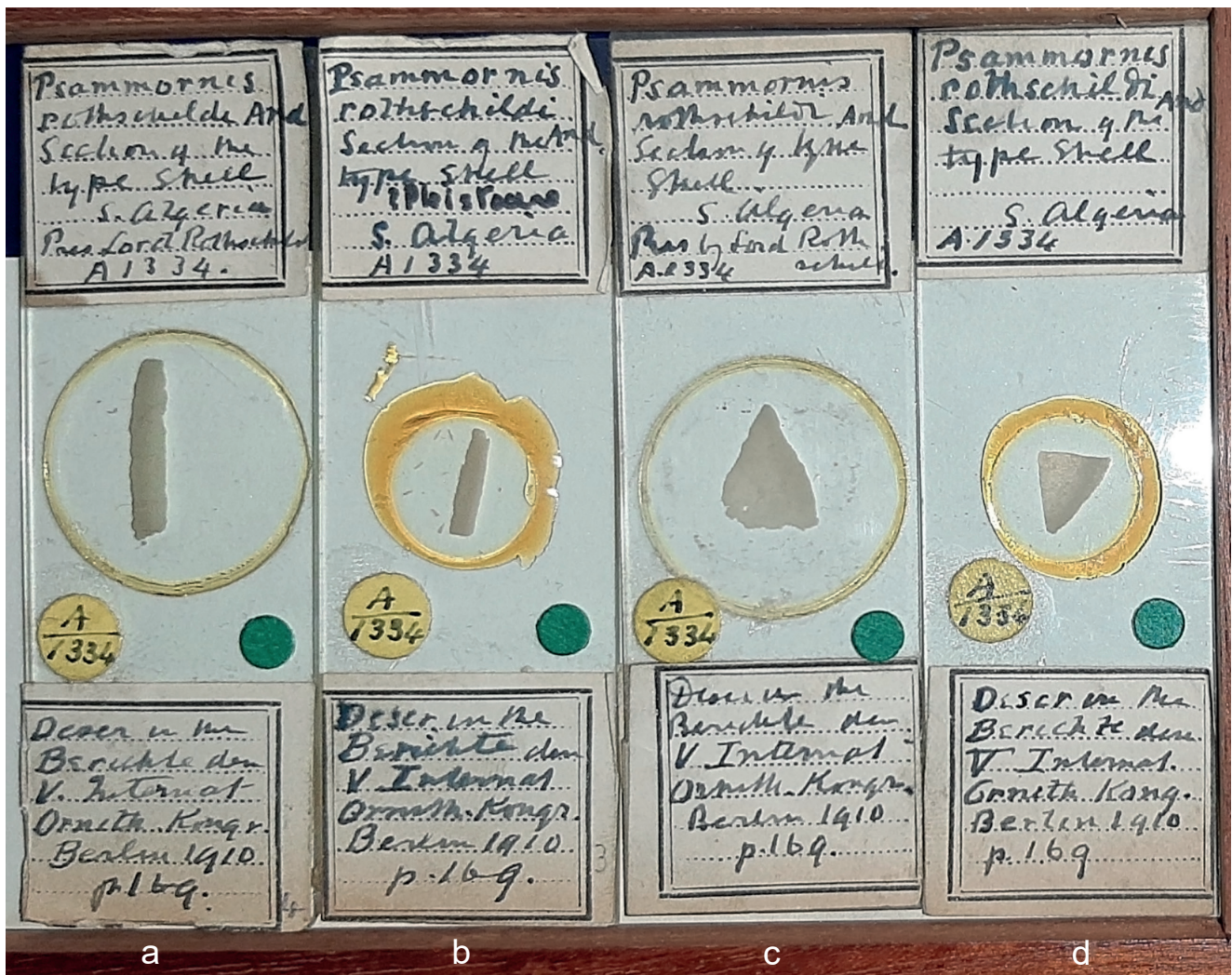
**Morphology.** The external surfaces of the eggshell fragments from Touggourt show irregularly spaced straight to slightly angular, quite short, slit-like depressions arranged with their long axes sub-parallel to each other or in a meandering pattern. The slits or depressions usually contain two or three pores, sometimes as many as four or five. Some of the depressions have been modified post-mortem by erosion, but the alteration does not affect the entire surface. However, care needs to be taken to avoid interpreting some depressions as pore complexes when that might not be the case.

The surface microstructure of the eggshells of *Psammornis rothschildi* was described in detail, but not illustrated, by Andrews (1912). In the thin sections illustrated by Sauer (1969) the more structured inner and outer layers of the eggshells are observed to be separated from each other by a layer of finer-grained amorphous material. The amorphous layer corresponds to what was called the “spongy” layer by Andrews (1912), Sauer (1969) and Louchart et al. (2022). The outer layer is about twice

as thick as the amorphous layer, which is slightly thinner than the innermost layer (Text-fig. 11). The relatively great thickness of the spongy layer in *Psammornis* eggs represents a major difference from eggshells of *Struthio* (sensu stricto).

**Biostratigraphy.** When collected, most of the North African and Arabian fossils hitherto attributed to *Psammornis rothschildi* were not found in situ in datable deposits (Andrews 1912, Rothschild and Hartert 1912, Hartert 1927, Lowe 1933a). Because of this, age estimates have varied widely, ranging from Eocene to Pleistocene (Andrews 1912, Rothschild 1912). An exception is the material from Chebket Safra, Tunisia (Choumowitch 1951, Buffetaut 2022) which is likely to be of Messinian age, although previously the deposits (the Segui Formation) from which the eggshells were collected were originally correlated to the Pontian (in the old sense of the term as the continental equivalent of the Pliocene, but in reality of Late Miocene age). Choumowitch (1951) reported that the eggshell fragments from Chebket Safra are regularly 3 mm thick (“Ces fragments ont très régulièrement trois millimètres d’épaisseur, c’est à dire un millimètre du plus que l’œuf d’autruche courant”).

Pickford et al. (2023) described eggshells (2.0–2.7 mm thick) excavated from Bou Hanifia, Algeria, from deposits that were for a long time correlated to the Pontian (Arambourg 1959), but which are more likely to be of Ventian age (Pickford and Chaïd-Saoudi 2024). The Bou Hanifia specimens were initially attributed to *Diamantornis laini*, but following detailed examination of the Omani collection, it is now considered to be more likely that they belong to a small species of *Psammornis*. A similar re-attribution of the eggshells (2.0–3.0 mm thick) from the Marsawdad Formation, Rub al-Khali, Oman, is likely.



Text-fig. 6. Thin sections of the “type” eggshell fragments of *Psammornis rothschildi* ANDREWS, 1912, from S. Algeria (NHMUK PV A 1334). (a) and (b) are from the lectotype (NHMUK E/1963.9.218a), (c) and (d) are from the paralectotype (NHMUK E/1963.9.218b). Note the citation as “Berichte den V. Internat Ornith Kongr. Berlin, 1910”, instead of “Verhandlungen des V. Internat. Ornith. Kongr. Berlin, 1912”.

Even though there remains a wide margin of error in the age determinations of eggshells attributed to *Psammornis*, the specimens from Chebket Safra, Tunisia, suggest that *Psammornis rothschildi* is of latest Miocene (Ventian) age, while the slightly thinner specimens from Bou Hanifia, south of Biskra, and Temassinine (ex Fort Flatters) (Hartert 1927, Schönwetter 1929) in Algeria, and the Marsawdad Formation in the Rub al-Khali, Oman (Pickford et al. 2023) are likely to correlate to the Ventian or Zanclean.

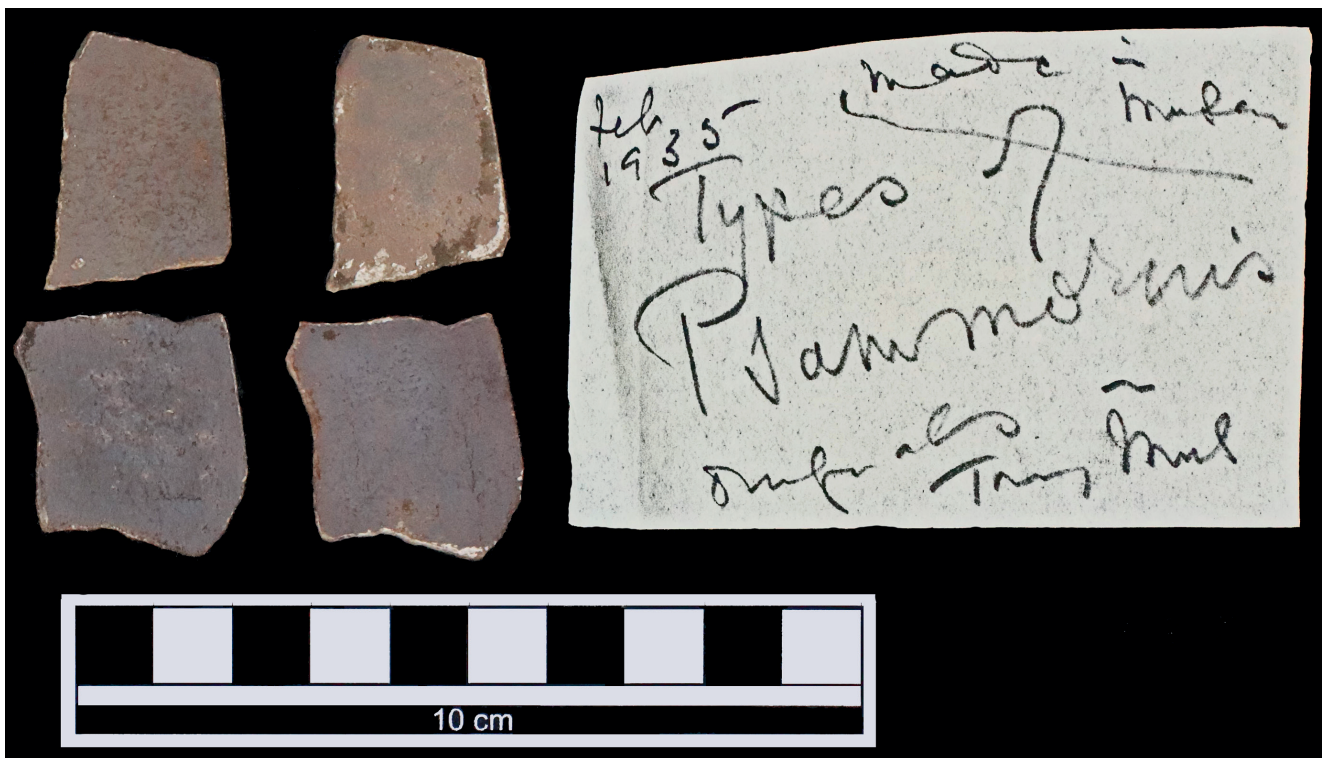
Thus, even though some doubt remains about its stratigraphic range, it is considered that the type material of *Psammornis rothschildi* is likely to be of Ventian age.

## Discussion

The lack of illustrations of the inner and outer surfaces of the fossil eggshells of *Psammornis rothschildi* from near Touggourt, Algeria, has constituted an obstacle that has prevented proper understanding of the taxonomy and systematics of the oospecies (Sauer 1969, Buffetaut 2022). The curation of the samples at two different sites appears to have been the underlying cause of this lack of illustration,

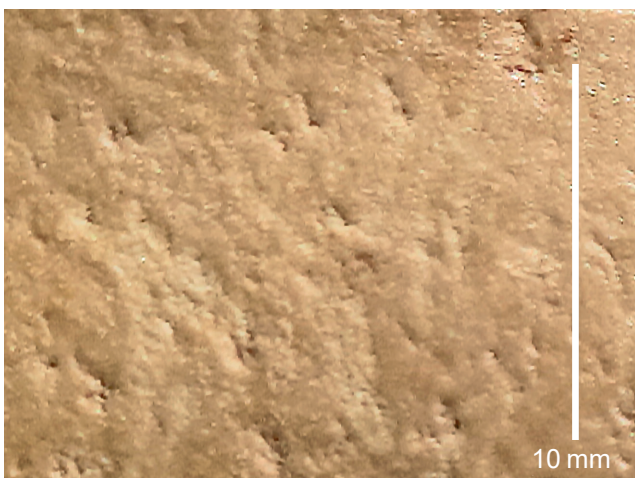
because researchers studying the thin sections (Sauer 1969: figs 1–5) at South Kensington in London may not have realised that the shell fragments themselves were stored at the Tring site. The only published papers that mention the presence of the specimens at the latter locale are by Hartert (1927) and Schönwetter (1929). Of these two publications, the first has seldom if ever been cited. It is absent from Sauer’s (1969) paper on *Psammornis* as well as from Buffetaut’s (2022) detailed discussion of the genus.

The fact that there are three fragments of eggshell from Touggourt referred to the species (Rothschild and Hartert 1912), of which only two were mentioned by Andrews (1912) when he erected the new genus and species, raises questions about the material studied by the latter author. The thin sections (NHMUK PV A 1334) and the two fragments (NHMUK E/1963.9.218a and NHMUK E/1963.9.218b) from which they were prepared were evidently studied by Andrews (1912). Two un-numbered plaster casts kept in London (Text-fig. 7) are associated with a label dated Feb. 1935, which states that the casts are “Types of *Psammornis* originals in Tring Mus”. In the interests of nomenclatural stability, it is considered necessary to nominate formally one of the



Text-fig. 7. Label and duplicated plaster casts of two of the eggshell fragments of *Psammornis rothschildi*, curated at the NHMUK, London. In the upper row are casts of the lectotype NHMUK E/1963.9.218a, in the lower row are casts of NHMUK E/1963.9.218b. The label reads “Feb 1935, Made in Museum, Types of *Psammornis*, Originals in Tring Mus”.

fragments from which the thin sections were manufactured (as well as the thin sections made from it) as the lectotype of the species, and to provide illustrations of its internal and external surfaces (Text-figs 3, 8). The second eggshell fragment that was cut and then cast is a paralectotype of the oospecies (Text-fig. 4), while the third specimen (Text-fig. 5) mentioned by Rothschild and Hartert (1912) is referred to the species but excluded from type series, because, as noted above, there is a possibility that it may have been collected at Temassinine, north of the Hoggar Mountains, southern Algeria.

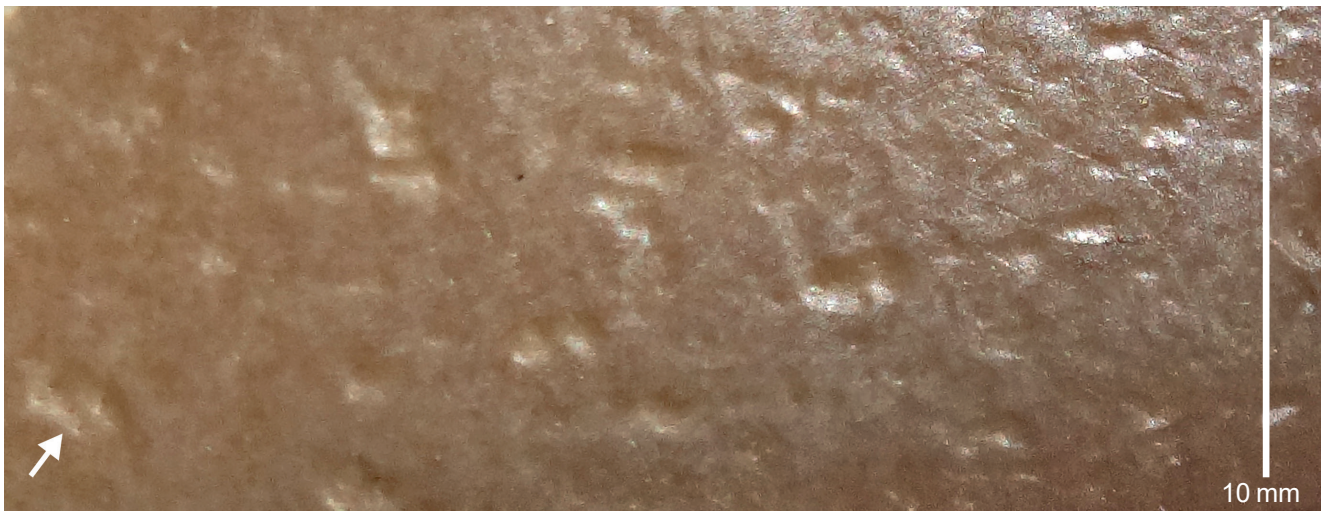


Text-fig. 8. Enlargement of part of the external surface of the lectotype of *Psammornis rothschildi* ANDREWS, 1912, (NHMUK E/1963.9.218a) highlighting the sub-parallel to slightly meandering arrangement of the pore clusters and the depressions or slits in which they occur.

Further research, including better estimates of the dimensions of complete eggs, needs to be carried out, because the previous estimates made by Andrews (1912) and Schönwetter (1929) assumed a constant relationship between eggshell thickness and overall dimensions of the egg, which may not apply to eggs of *Psammornis* because the relatively great thickness of the spongy layer in eggshells of *Psammornis* possibly altered this relationship, and could contribute to an overestimate of shell dimensions. Sauer (1969) discussed the issue but did not resolve it because he did not see the original fossils, reporting that “No size calculations were attempted for the *P. rothschildi* egg, as no shell fragments were available and readings from the short thin sections were not usable”.

The thickness estimate of 3.50 mm of the eggshells of *Psammornis rothschildi* made by Schönwetter (1929: 196, or 3.40 mm in the table at the end of the paper) is, in our opinion, unrealistic. Schönwetter (1960: 12) explained that he measured the thickness of *Psammornis* eggshell fragments as 3.2–3.4 mm, but thought that they were abraded and estimated the original thickness at 3.5 mm. His measurements resulted in him making an exaggerated estimate of the dimensions of the entire egg (axial dimensions of 280 × 210 mm) as was commented on by Sauer (1969). The latter author suggested that the Touggourt eggshells might have been as thick as 4 mm when fresh, but our examination of the specimens indicates that such a high figure is extremely unlikely. Andrews’ (1912) reconstruction of total egg size was 250 × 190 mm. Direct measurements of the curvature of the inner and outer surfaces of the Touggourt eggshells is feasible, on which basis a more reliable estimate of egg size could be calculated, but it is not the aim of this contribution.





**Text-fig. 9.** Enlargement of part of the external surface of the paralectotype (NHMUK E/1963.9.218b) of *Psammornis rothschildi* ANDREWS, 1912, from Touggourt, Algeria. Note the superficial scratches (top right) and the cluster of pores in a depression (arrow). Some of the other depressions show bevelled edges possibly as a result of repeated exposure to dew.

A notable difference between eggs of *Struthio* (sensu stricto) and those of *Psammornis* is that, in the latter genus, the spongy layer between the external and internal layers of the shell is appreciably thicker than it is in *Struthio*. Nevertheless, overall, the eggshell structure of *Psammornis* is closer to that of *Struthio* than to those of aepyornithoids on the one hand, or to genera such as *Diamantornis* PICKFORD et DAUPHIN, 1993, and *Namornis* PICKFORD et al., 1995, on the other. This observation suggests that *Psammornis* is most closely related to *Struthio*, and could potentially be a subgenus of it (or even a synonym of it, as was discussed briefly by Sauer 1969).

Sauer (1969) considered whether *Psammornis* should be subsumed into *Struthio* or not, but opted to retain it as a distinct genus. As he explained “If it were not for the enormous size of the *P. rothschildi* egg, its pore canal system and the other microstructures of the shell would not warrant a specific distinction from *S. c. camelus*”. He mentioned that “On the basis of the struthionid structures of the shell fragments, separating the *Psammornis* birds generically

from *Struthio* becomes questionable” but he eventually concluded that “For the sake of convenience the generic name of *Psammornis* may be maintained at present”.

## Conclusion

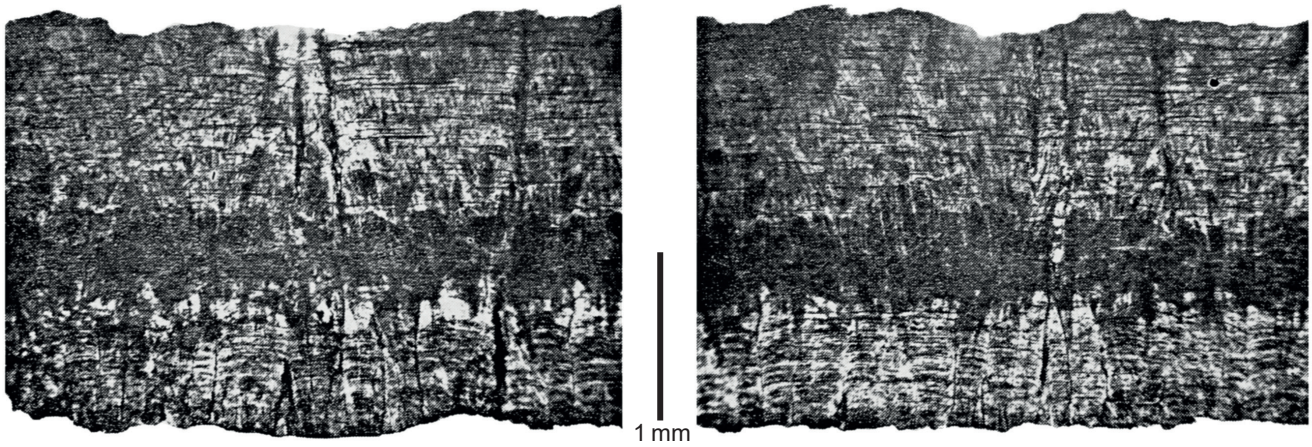
There has been a measure of doubt about which specimens formed the basis for Andrews’ (1912) description of the avian oospecies *Psammornis rothschildi* (he mentioned only two of the three specimens collected near Touggourt (Rothschild and Hartert, 1912)). One of the fragments, from which thin sections were manufactured, is herein nominated the lectotype of the species and, for the first time, illustrations are provided of the internal and external surfaces of the eggshells, in the hope that they will contribute to resolving the taxonomic and systematic issues that have persisted about the oospecies for more than a century.

Partly because the external surface of the eggshells has never been illustrated, the oospecies *Psammornis rothschildi* has been the subject of a great deal of debate and uncertainty, recently summarised by Buffetaut (2022) who concluded that its taxonomic position and systematics remain enigmatic.

Andrews (1912) considered *Psammornis* to be closer to *Struthio* than to any other group of birds, including aepyornithoids, a suggestion that has been largely accepted by recent students of fossil eggs, but uncertainties persist about its stratigraphic context and its palaeobiogeographic distribution, and whether the genus *Psammornis* is, or is not, a synonym of *Struthio* (Sauer 1969, Mikhailov and Zelenkov 2020, Buffetaut 2022). Further research on all the available fossil eggshells from northern Africa, the Middle East, Hungary, Ukraine, Russia, Kazakhstan and Iran may resolve the doubts, but is not the focus of the present paper. However, it is noted that the disposition of the pores and the depressions in the external surface of eggshells of *Psammornis* accords with a *Struthio*-like bird rather than an *Aepyornis*-like one. The available evidence indicates a closer relationship between *Psammornis* and *Struthio*, than between the former genus and any other described oogenus,



**Text-fig. 10.** Enlargement of part of the external surface of the eggshell tentatively referred to *Psammornis rothschildi* ANDREWS, 1912, labelled as having been collected at Touggourt, Algeria (NHMUK E/1963.9.218c). Note the indurated, slightly reddened aeolianite adhering to the shell (star symbol). The pore slits tend to be elongated and sub-parallel to each other with the pores in their depths (arrow).



**Text-fig. 11.** Cross sections of the “type” eggshells (NHMUK PV A 1334) of *Psammornis rothschildi* from Touggourt, Algeria. Note the relatively thick amorphous or “spongy” layer (dark grey in images) between the thicker external layer above and the thinner internal layer at the bottom of the images. Images modified from Sauer (1969: fig. 1).

including *Diamantornis* and *Namornis*. The relationship is perhaps close enough that *Psammornis* could be a subgenus of *Struthio* rather than a distinct genus.

Concerning estimates of overall egg size, the three fragments kept in Tring are well-enough preserved and are potentially large enough that, direct measurements of curvature of the inner and outer surfaces could yield pertinent results. Previous calculations of egg size (Andrews 1912, Schönwetter 1929) may have over-estimated the axial dimensions of complete eggs.

The precise stratigraphic distribution of *Psammornis rothschildi* remains to be determined, but currently available estimates suggest that it is likely to be of Ventian age (latest Miocene).

Fossilised eggshell fragments from a wide geographic area (from Mauritania in West Africa to Iran in Asia) have been attributed to *Psammornis* (Béde 1919, Heim de Balsac 1930, Lowe 1933a, b, Philby 1933, Choumowitch 1951, Monod 1951, Dughi and Sirugue 1964, Tessier et al. 1971, Voisin 1971) and the genus is thus potentially of palaeobiogeographic and biostratigraphic interest, but all these reports need to be re-examined in light of a better understanding of the type material of the type species *Psammornis rothschildi* from Algeria (Andrews 1912).

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