

Review

# The Enigmatic Avian Oogenus *Psammornis*: A Review of Stratigraphic Evidence

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**Abstract:** *Psammornis rothschildi* is an avian taxon established by Andrews in 1911 on the basis of eggshell fragments surface-collected near the city of Touggourt, in the north-eastern part of the Algerian Sahara. Since the initial discovery, a number of *Psammornis* specimens have been reported from various localities in North Africa (Algeria, Tunisia, Libya, Mauritania) and the Middle East (Saudi Arabia, Iran). Most of the finds lack a stratigraphic context, which has resulted in considerable confusion about the geological age of *Psammornis*, with attributions ranging from the Eocene to the Holocene. A review of the available evidence shows that only two groups of localities provide reasonably reliable stratigraphic evidence: the Segui Formation of SW Tunisia, apparently of latest Miocene age, and the Aguerguerian (Middle Pleistocene) of NW Mauritania. This suggests a fairly long time range for *Psammornis*. *Psammornis* eggs are, in all likelihood, those of giant ostriches, although the lack of associated skeletal material makes it difficult to interpret the eggshell fragments in evolutionary terms. However, the oological record suggests that giant ostriches have been present in Africa since the late Miocene, which leads to the reconsideration of some hypotheses about the palaeobiogeographical history of the Struthionidae. The lack of *Psammornis* eggs transformed by humans suggests that this giant ostrich did not survive until Epipalaeolithic or Neolithic times.

**Keywords:** *Psammornis*; ostrich; eggs; Africa; Miocene; Pleistocene



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## 1. Introduction

The genus *Psammornis* was established in 1911 by Andrews [1], with *P. rothschildi* as the type species, on the basis of eggshell fragments collected in southern Algeria in the course of one of Lord Rothschild's expeditions to North Africa [2]. Since then, more eggshell material collected at a number of localities in Africa and the Middle East has been attributed to *Psammornis*; this rather enigmatic taxon has been the subject of much speculation, both because it is represented solely by fragmentary eggshell material not clearly associated with any skeletal remains, and because the stratigraphic provenance of the specimens is often very uncertain due to many of them being surface-collected rather than found in situ in sedimentary formations. Despite these uncertainties, *Psammornis* is still often mentioned in works on ostrich evolution [3] as well as in papers on fossilisation [4], with different geological age estimates—Pleistocene, according to Mikhailov and Zelenkov [3], and Holocene, according to Wiemann et al. [4].

The systematic position of *Psammornis* has been the subject of much debate [5]. Although aepyornithid affinities have been suggested [6,7] and Dughi and Sirugue [8,9] thought that the microstructure of *Psammornis* eggshells was closer to that of rheas and moas, it is now widely accepted that the *Psammornis* eggs are probably those of giant ostriches [1,3,5,10]; according to Mikhailov and Zelenkov [3], they belong to their "non-specialised type S", and are similar to both the thin-shelled eggs of the modern subspecies *Struthio camelus camelus* and the thick-shelled eggs of the Pliocene *S. chersonensis* from

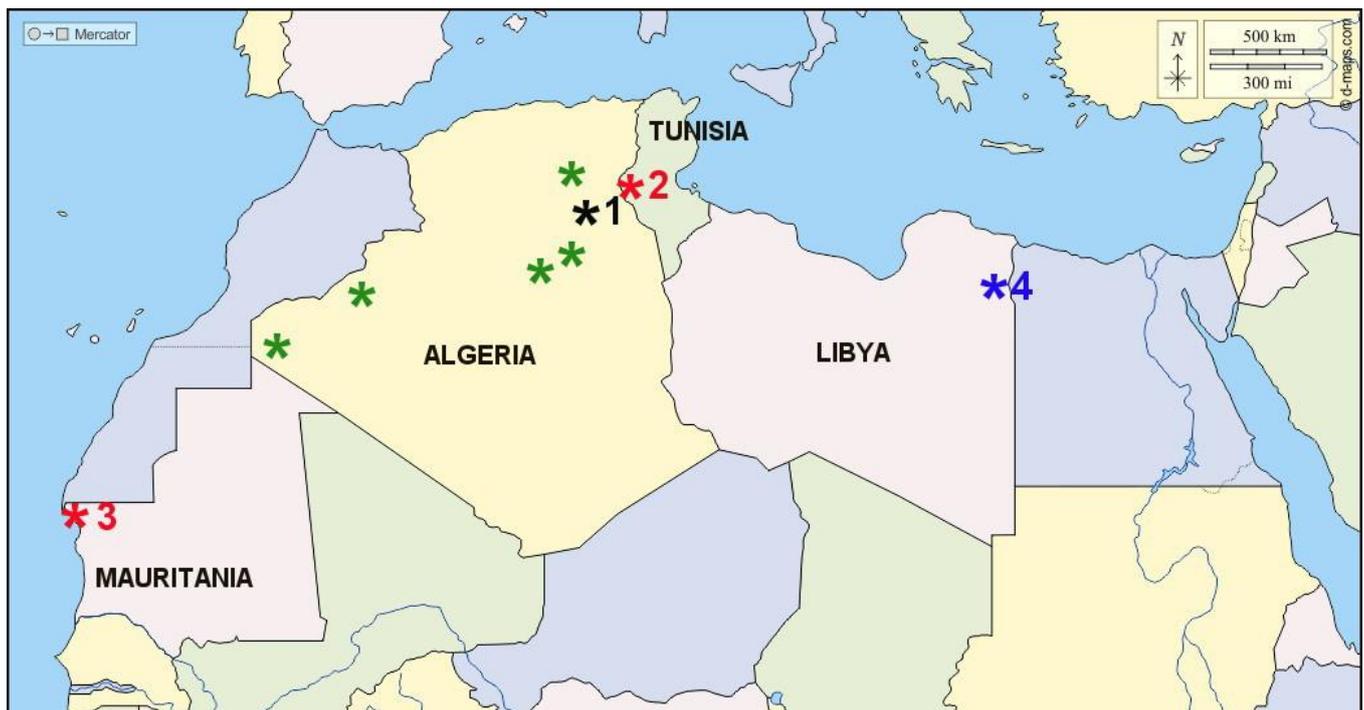
Europe. However, the purpose of the present paper is not to discuss systematic issues or morphological and microstructural characteristics, but to review whatever solid evidence may be available about the stratigraphic provenance of *Psammornis* eggshells, on the basis of a survey of the available literature; this includes papers, mainly in French, which have been overlooked by many authors dealing with the question. Bearing in mind that the geological age of the type material of *Psammornis rothschildi* can rightly be considered as uncertain [11], widely different opinions have been expressed about the geological age of *Psammornis* specimens from various localities; this, in turn, has resulted in divergent interpretations of ratite evolutionary history in Africa and other continents.

## 2. The Discovery of *Psammornis* and the Beginning of the Stratigraphic Conundrum

In 1909, during a visit to southern Algeria, Lord Rothschild and Ernst Hartert explored the area around the city of Touggourt [2], in the north-eastern part of the Algerian Sahara. They found abundant fragments of ostrich eggshell on the ground in various places. While picking up some of them about 22 miles east of Touggourt, Hartert found “three pieces of a very much thicker egg-shell of a much browner colour” ([2], p. 550). Rothschild immediately thought that they must belong to “an extinct large Struthionid bird”. The fragments were handed over for study to C.W. Andrews, a palaeontologist at the British Museum (Natural History), who described them as *Psammornis rothschildi* [1]. Andrews gave a detailed, but not illustrated, description of the microstructure and surface features of the eggshell, noting its considerable thickness (3.2 to 3.4 mm), much greater than that of eggs of the living ostrich (up to 2.10 mm) and second only to that of the eggshell of *Aepyornis titan*, from Madagascar. His conclusion was that the fragments were evidence of a “hitherto unknown bird which laid an egg considerably larger than the largest produced by any modern ostrich” and that, although there were some similarities with *Aepyornis*, “with *Struthio* the relationship was probably very close” ([1], p. 172).

Besides the lack of associated skeletal material, which made precise identification difficult, Andrews also noted uncertainties about the geological age of the specimens. Although they had been surface-collected and had been abraded by drifting sand, they were highly mineralised and had been found in the vicinity of a well. Andrews suggested that they might have been brought up from a considerable depth when digging the well. This gave no clue as to the exact antiquity of the eggshell fragments. Hartert [12], discussing *Psammornis*-like eggshell fragments found in the western Algerian Sahara, questioned Andrews’ suggestion, pointing out that the *Psammornis* fragments often had the same preservation as *Struthio camelus* eggshell fragments and, everywhere, were found together with the latter.

Since the initial discovery in Algeria, many eggshell fragments (but no complete eggs) attributed to *Psammornis* have been reported from various parts of North Africa (including Algeria, Tunisia and Mauritania; Figure 1) and the Middle East (Saudi Arabia, Iran), but many of them were surface-collected and lack details about their stratigraphic origin. In addition, some of these purported *Psammornis* specimens appear to be significantly different from the fragments described by Andrews [1], and their attribution to the genus seems dubious.



**Figure 1.** Distribution map of *Psammornis* localities in North Africa: black star (1)—type locality of *Psammornis rothschildi* Andrews, near Touggourt, Algeria; red stars—localities with *Psammornis* eggshells in situ in a stratigraphic context: 2—Segui Formation (latest Miocene), Chebket Safra near Moulares, south-western Tunisia, 3—Aguerguerian (Middle Pleistocene), Lévrier Bay area, north-western Mauritania; blue star (4)—type locality of *Psammornis libycus* Moltoni (a probable synonym of *Struthio camelus*), near Giarabub, Libya; unnumbered green stars—*Psammornis* finds without a stratigraphic context in the Algerian Sahara.

### 3. An Eocene Age for *Psammornis*?

Rothschild [13] (1911) listed *Psammornis* among what he called the Heterornithes, a loosely defined group of large birds which he considered as “fore-runners or ancestral forms of the Ratite section of the Palaeognathae” ([13], p. 148). This highly heterogeneous group contained birds as different as gastornithids, phorusrhacoids and even the Jurassic *Laopteryx* (now considered a pterosaur). *Psammornis* was listed together with *Eremopezus eocaneus* as an Eocene representative of the Heterornithes from North Africa. *Eremopezus eocaneus* was described by Andrews [14] on the basis of the distal end of a tibiotarsus from the Upper Eocene Jebel Qatrani Formation of the Fayum, in Egypt. It was long believed to be an early ratite, but Rasmussen et al. [15] considered it a representative of an endemic group of large African birds.

Why Rothschild chose to associate *Psammornis* and *Eremopezus* is obscure. In his description of *Psammornis*, Andrews [1] mentioned *Eremopezus*, mainly to remark that it was only the size of a small ostrich (and, therefore, unlikely to have produced eggs the size of *Psammornis* eggs). Moreover, there was no solid reason to believe that the type material of *Psammornis* from Algeria came from an Eocene deposit, despite the fact that Andrews had suggested that the fragments might have been brought up to the surface from a considerable depth by a well. However, as mentioned above, as early as 1913, Hartert [12] had doubted that the Algerian *Psammornis* fragments could have been brought up to the surface by a well, and in 1918, Geyr von Schweppenburg [16] had noted that it was geologically unlikely that they were Eocene in age. The hypothesis that the Algerian specimens may have originated from Eocene deposits was dismissed on geological evidence by Dughi and Sirugue [8,9]. Sauer [5] reviewed, at some length, the question of the possible relationships

between *Psammornis* and *Eremopezus* and concluded that there was no reason to believe they were related.

Nonetheless, Rothschild's idea of an Eocene age for *Psammornis* was taken up first by Abel [17] and then by Lambrecht [6], who placed it together with *Eremopezus* in the family Eremopezinae within the Aepyornithiformes. In 1933, Lambrecht [7] still placed *Psammornis* close to *Eremopezus* but as a genus *incertae sedis*, and gave it an Eocene age with a question mark. More recently, Piveteau [18] noted that *Psammornis* had been discovered in the Eocene of Touggourt. Brodkorb [19] still considered *Psammornis* as a possible synonym of *Eremopezus*, and also attributed it to the Eocene, with a question mark. Dementiev [20] used question marks concerning the placement of *Psammornis* among the "Eremopezidae" and its attribution to the Eocene. As late as 1965, Swinton [21] wrote that *Psammornis* had been found in the Eocene of southern Algeria. Obviously, Rothschild's ill-founded assertion that *Psammornis* was an Eocene taxon has had long-lasting consequences. There is, in fact, no convincing stratigraphic evidence anywhere suggesting that *Psammornis*-type eggshells have been found in Eocene deposits.

#### 4. *Psammornis* Outside Africa

##### 4.1. Saudi Arabia

In 1933, Lowe [22] attributed to *Psammornis* a thick eggshell fragment collected by the explorer and secret agent St John Philby at Shuqqat al Khalfat in Saudi Arabia. He compared it with Andrews' original material from Algeria and found close similarities in thickness and microstructure. The specimen had been surface-collected and lacked accurate information about its geological origin.

In this connection it should be noted that Bibi et al. [23] attributed eggshell fragments from the Upper Miocene Baynunah Formation of the United Arab Emirates not to *Psammornis*, but to *Diamantornis*, previously described from Namibia and Kenya. The pore complexes of the specimens from the United Arab Emirates are clearly different from what has been described in *Psammornis*, and Philby's specimen from Saudi Arabia, whatever its age, may indicate a bird different from that from the Baynunah Formation.

##### 4.2. Iran

Dughi and Sirugue [8] reported on eggshell fragments collected at several localities in the Lut desert of eastern Iran by the geographer Jean Dresch and the naturalist Théodore Monod in 1969 and 1970. Although these fragments were significantly thinner (1.8 to 2.3 mm) than the *Psammornis* material described by Andrews, Dughi and Sirugue attributed them to *Psammornis* on microstructural evidence, considering that they belonged to an early, less advanced form than that from North Africa. However, the Iranian specimens seem to have been collected in a sand dune environment without a well-defined stratigraphic context. Caution should be urged when trying to use the putative *Psammornis* specimens from Iran for evolutionary interpretations. In connection with these specimens, Dughi and Sirugue mentioned the large ostrich eggs known from the Neogene and Quaternary periods of China [3,24–26], which may indeed be more relevant than the African *Psammornis*.

#### 5. African Records of *Psammornis* of Doubtful Identification or Stratigraphic Position

##### 5.1. Algeria

In addition to the type material of *Psammornis rothschildi* from the Touggourt region in the north-eastern part of the Algerian Sahara, Rothschild and Hartert [2] reported that in 1911, Hilgert had surface-collected a number of large eggshell fragments, rather different from the type of *P. rothschildi*, near Biskra, north of Touggourt. Schönwetter [27] discussed the fragments found by Hilgert and found them similar to the type material from Touggourt. He also mentioned eggshell fragments collected at Ouargla and El Golea (SW of Touggourt) by Hilgert and Hartert and at Temassin (S of Touggourt) by Fromholz and found them different from the type material. In 1960, Schönwetter [28] came back to the topic of

*Psammornis* and mentioned additional material from the Iguidi region, in the southern part of the Algerian Sahara, collected by Colonel Le Pivain.

Le Pivain also collected thick eggshell fragments at various points during a trip across the western Algerian Sahara in 1930; they were referred to *Psammornis* by Heim de Balsac [29].

Dughi and Sirugue [8] mentioned additional *Psammornis* eggshell fragments collected at various localities in the north-eastern Algerian Sahara (Souf region). No indications about the geological context were provided.

Apparently, all of the above-mentioned Algerian specimens were surface-collected and do not provide any reliable stratigraphic evidence about the age of *Psammornis*.

## 5.2. Libya

*Psammornis libycus* was described by Moltoni [30] on the basis of brownish-red eggshell fragments found in the dunes south of Giarabub (al-Jaghbug), a town in the eastern Libyan desert. No stratigraphic information was available. Moltoni established a new species because the fragments were significantly thinner (2.1 mm) than those of *Psammornis rothschildi* eggs. Schönwetter [28] concluded that these fragments had nothing to do with *Psammornis* and were reminiscent of specimens from Algeria possibly belonging to *Struthio camelus*. Sauer [5] described the type specimens of *Psammornis libycus* in detail and found similarities with *Struthio camelus*, wondering whether they could be the earliest *S. camelus* (or a link between *Psammornis* and *Struthio*). However, nothing is known about the geological age of *P. libycus*. Although this species was mentioned by some authors (e.g., [7,19]), there seems to be no reason to attribute it to *Psammornis*. The fragments described by Moltoni are more likely to belong to *Struthio*.

*Psammornis* has also been reported from the important early Miocene Jebel Zelten vertebrate locality in north-central Libya. However, this record is not based on oological evidence, and therefore, is completely unreliable. In a preliminary report, Arambourg and Magnier [31] initially mentioned a giant bird belonging to the Aepyornithidae, without specifying what kind of material this identification was based on. In 1961, this was clarified by Arambourg [32], who briefly attributed to an aepyornithid an incomplete large tibia (more properly, a tibiotarsus) lacking both ends, which in terms of size, shape and proportions was supposed to be reminiscent of *Aepyornis*. Arambourg then mentioned that large eggshell fragments from “Mio-Pliocene” deposits in the northern Sahara had been described as *Psammornis rothschildi*, but refrained from clearly attributing the Jebel Zelten giant bird to that genus. In 1967, however, in a list of the Jebel Zelten fauna, he mentioned: “Aepyornithide [sic] (*Psammornis*)”, without specifying what kind of material this was based on [33]. This mention obviously caused some confusion among subsequent authors who appear to have been unaware of Arambourg’s 1961 paper, in which it is clearly stated that the evidence for the presence of a giant bird at Jebel Zelten is based on a fossil bone. Curiously enough, Savage and Hamilton [34], who cite Arambourg’s 1961 paper, list “*Eremopezus*” among the fossil vertebrates from Jebel Zelten; this is probably a consequence of the above-mentioned confusion, initiated by Lord Rothschild, between *Eremopezus* and *Psammornis*. Vickers-Rich [35], not being aware of Arambourg’s 1961 paper, was not sure on what material the mention of *Psammornis* was based. Mlíkovsky [36], who apparently was not aware of Arambourg’s 1961 paper either, misquoted Arambourg and Magnier (his quote clearly refers to Arambourg’s 1967 paper, not cited in his list of references) and noted that the material on which a giant bird was identified at Jebel Zelten was “unknown” but probably consisted of eggshell fragments, since it was attributed to *Psammornis*. This, of course, is erroneous, since Arambourg’s mention of a giant bird was based on a tibiotarsus.

To sum up, there is no evidence of *Psammornis*-type eggshell material from Jebel Zelten. The large tibiotarsus from Jebel Zelten mentioned by Arambourg [32] was never described in detail or illustrated. It is of potentially considerable importance for our understanding of the evolution of giant birds in Africa, but it cannot provide much reliable

evidence concerning the question of the geological age of *Psammornis*, and cannot be used as evidence for the presence of this egg-based taxon in the early Miocene of Libya.

#### 6. *Psammornis* from Tunisia: A Late Miocene Record?

As early as 1911, Rothschild and Hartert [2] reported that the German naturalists Erlanger and Hilgert had found many fragments of large eggshells in the South Tunisian desert. Bédé [37] noted that he had found eggshell fragments of a brownish colour and thicker than those of the “ordinary ostrich” at Mezzouna, 100 km SW of the city of Sfax; he thought they belonged to *Psammornis*.

A stratigraphically more significant discovery of *Psammornis* specimens was reported by Choumowitch (not ‘Choumwitch’ as erroneously printed in his paper) in 1951 [38]. The eggshell fragments mostly came from outcrops SW of the city of Moularès, in south-western Tunisia. They were found in abundance in red beds deeply dissected by erosion (Figure 2) in an area known as Chebket Safra (“yellow network”). The brown-coloured eggshell fragments were attributed to *Psammornis* because of their thickness (3 mm). Choumowitch also noted that they were less convex than ostrich eggshells, thus indicating larger eggs.



**Figure 2.** The *Psammornis*-bearing red clays on the southern flank of the Chebket Safra, SW of the city of Moularès in south-western Tunisia. The level containing remains of broken eggs preserved in situ is shown by the yellow asterisk. Photo by E.G. Gobert, modified after Choumowitch (1951).

As emphasised by Choumowitch, contrary to previous *Psammornis* finds, the eggshell fragments from Chebket Safra came from well-dated sediments. They were found in palaeosols containing calcareous concretions and fossil helioid gastropods, notably *Leucochroa tissoti*, considered as indicating a Pontian age. Choumowitch’s investigations showed that the eggshell fragments did not come from Quaternary pebble deposits topping the hills. Digging into the red clays to a depth of one metre below the surface, he found an accumulation of eggshell fragments (weighing altogether more than 11 kg) arranged into small groups, each of which apparently corresponded to an egg. The whole accumulation was interpreted as a nest.

According to the geological map, the egg-bearing red beds were Pontian in age, overlying fluvial sands. Choumowitch noted that similar *Psammornis* eggshell fragments occurred at other localities in the area. Other records from Tunisia (Metlaoui, Gabès) were listed by Dughi and Sirugue [8] on the basis of information provided by Gobert.

More details about the geology of the localities were sent to Dughi and Sirugue by Gobert and published by them [8,9]. He mentioned that within the Pontian red marls, the eggshell fragments were concentrated in a well-defined zone about 50 cm in thickness, containing abundant helicid gastropods and calcareous concretions, which were interpreted as having formed around grass roots. The egg-bearing deposit was considered a paleosol formed in a dry steppe environment.

The observations made by Choumowitch and Gobert thus indicate that at Chebket Safra, the *Psammornis* eggshells were found in situ, and not reworked.

Dughi and Sirugue [8,9] gave detailed descriptions of the morphology and microstructure of the eggshells from Chebket Safra (Figure 3A). They had no hesitation about attributing the Tunisian specimens to *Psammornis rothschildi*. However, they noted that Andrews' description of the pores and canals of the *Psammornis* eggshell had to be significantly modified. This raises the question of whether the Tunisian specimens can really be attributed to *Psammornis rothschildi*. The comparison between Andrews' material from Algeria and the Tunisian fragments is made difficult by the fact that the former have suffered aeolian abrasion so that their surface features are somewhat obscured [1]. On the basis of the type material from Touggourt, Andrews [1], and especially Sauer [5], emphasised the similarities between the eggshells of *Struthio* and *Psammornis*. Dughi and Sirugue [8], mainly on the basis of the Tunisian specimens, came to a somewhat different conclusion, viz. that *Psammornis* was more closely related to Rheiformes and Dinornithiformes. In a later paper [9], they found similarities with Aepyornithiformes, Rheiformes, Casuariformes and Dinornithiformes, rather than with ostriches. A detailed comparison between eggshell fragments from Chebket Safra and the type material of *Psammornis rothschildi* from Touggourt would be useful to check whether they can really be attributed to the same ootaxon.

By contrast with the various specimens from Algeria, which lack a stratigraphic context, the eggshells from Chebket Safra are of considerable importance concerning the geological age of *Psammornis*. However, the age attributions proposed at the time of the discovery need to be discussed in light of current knowledge.

On the basis of previous work in the area, notably that of Solignac [39], Choumowitch attributed the fossil-bearing red beds to the Pontian. The Pontian is a local stage for the Peri-Tethyan regions around the Black Sea corresponding to deposits close to the Miocene–Pliocene boundary. According to Rybkina and Rostovtseva [40], the Pontian of the Black Sea area can be correlated with the Messinian Salinity Crisis of the upper part of the Messinian stage (latest Miocene). However, correlations of the so-called Pontian of south-western Tunisia with the standard stratigraphic scale is not obvious. Moreover, the red beds of the Chebket Safra lack useful biostratigraphic markers. The abundant helicid gastropods they contain, in particular *Helix (Leucochroa) tissoti*, were once considered valuable stratigraphic indicators for a Pontian age in North Africa [38,41]. However, this has been doubted [42].

The lithostratigraphic characteristics and the abundant helicid gastropods lead to the consideration that the *Psammornis*-bearing red beds belong to the Segui Formation. This is in agreement with the Metlaoui sheet of the geological map of Tunisia at 1/100,000 [43], which shows a great development of this formation (attributed to the Pliocene) SW of Moularès, in the area of the Chebket Safra. Although Robinson and Wiman [42] described the Segui Formation as a temporal enigma, its stratigraphic position is relatively clear. As early as 1910, Roux and Douvillé [41] placed the red clays containing *Helix tissoti* in the upper part of the Miocene series and observed that they overlie white and yellow sands yielding mammal remains. This sandy formation is now called the Beglia Formation and two fossiliferous levels within it have yielded a rich vertebrate assemblage indicative of an age close to the middle–late Miocene boundary ([44] and references therein). The Beglia Formation has yielded skeletal remains of an ostrich [45], *Struthio* sp., which is not larger than the living *Struthio camelus*, and therefore, unlikely to have produced the very large *Psammornis* eggs. The Segui Formation, which in the Moularès region directly overlies the Beglia Formation, was considered Messinian to Pliocene [46], or Mio-Pliocene to Villafranchian [47]. In her reviews of Miocene formations in Tunisia, Mannai-Tayech [48,49]

suggested a late Tortonian–early Messinian age for the Segui Formation. Mannai-Tayech’s lithological description of the Segui Formation suggests that the level with *Psammornis* eggshells is in the upper part of the formation. It is worth noting that Robinson and Wiman [42] mentioned the occurrence of gypsum deposits in the Segui Formation as possible evidence for contemporaneity with the Messinian salinity crisis.

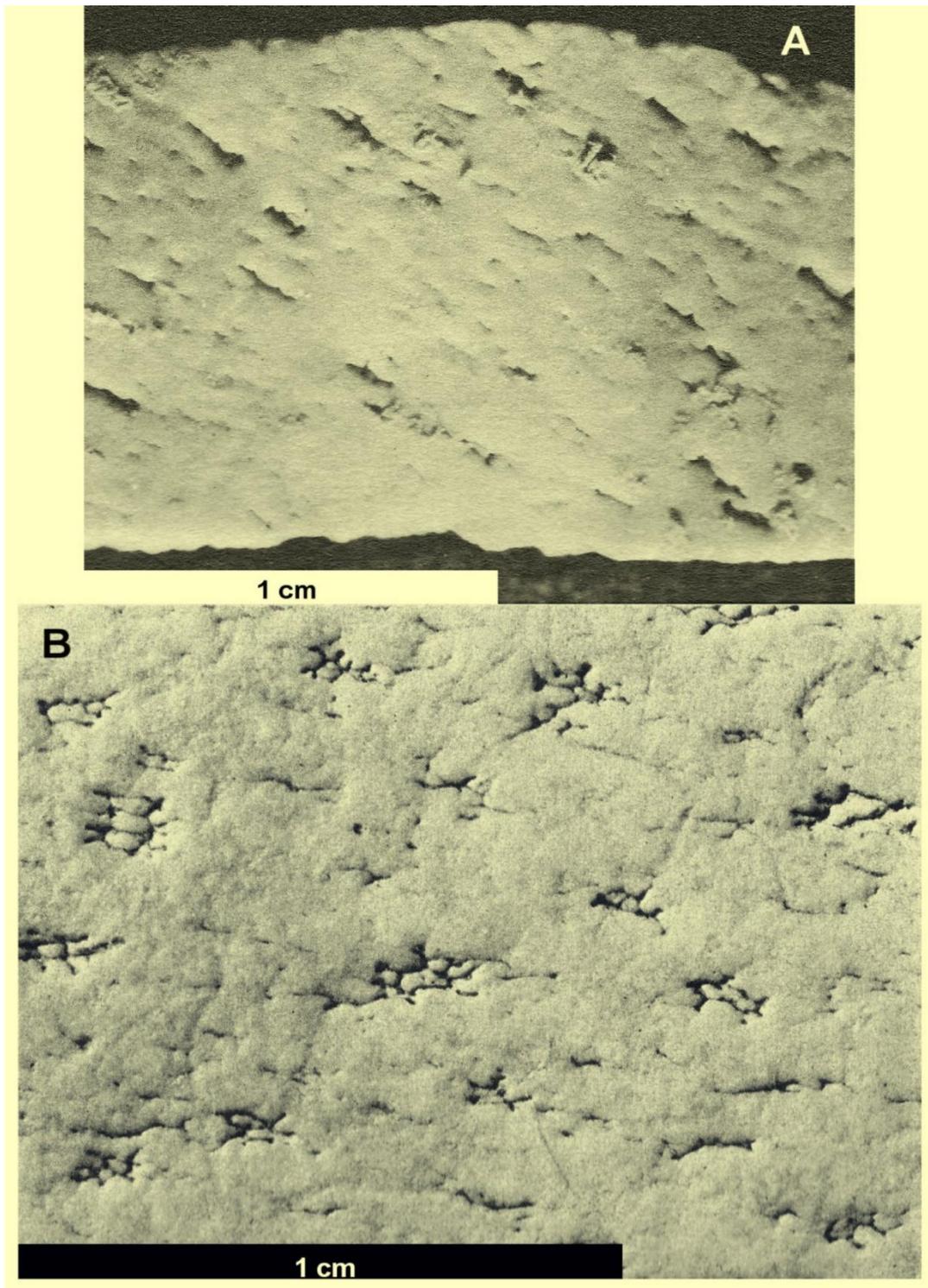
Although some uncertainties remain about the age of the upper boundary of the Segui Formation, the above-mentioned evidence strongly suggests a late Miocene, possibly Messinian age, for the *Psammornis* eggshells from the Chebket Safra.

It is worth noting that in 1952, Arambourg [50] mentioned that, according to Gobert, *Psammornis* eggshell fragments were relatively frequent in continental deposits, probably Pontian in age, in southern Tunisia. However, he did not cite Choumowitch’s paper and seems to have been unaware of it (or possibly Choumowitch’s paper was published after Arambourg wrote his paper). Vickers-Rich [10] noted Arambourg’s mention of *Psammornis* in southern Tunisia, but she was unaware of Choumowitch’s and Dughi and Sirugue’s papers, so she could not appreciate the real significance of the Tunisian finds.

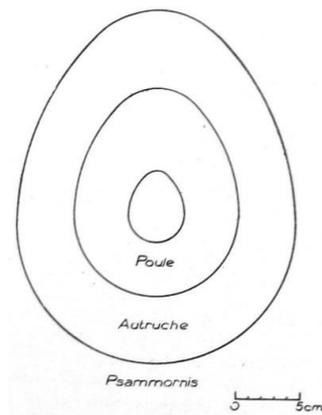
### 7. *Psammornis* from Mauritania: A Pleistocene Record

In 1939, Monod [51] was the first to report the occurrence of *Psammornis* on the Atlantic coast of Mauritania in a semi-popular short paper on eggshell fragments he had discovered at the “root” of the Cap Blanc (Râs Nouâdibhou) peninsula, in the northwestern corner of the country. The specimens were communicated to Schönwetter, who noted that they were 3 to 3.4 mm thick, and provided estimates for the dimensions of the complete shell (28 × 21 cm) and the weight of the egg (7 kg)—all of these figures being much larger than those for the living ostrich (as expressed by a comparative drawing). Monod gave no information about the geological provenance of the eggshell fragments but jokingly mentioned the omelets and water containers the Neolithic people of the Sahara could have made with such eggs, showing that he thought that they were of a comparatively recent date. In a more formal paper, including a better comparative drawing (Figure 4), Monod [52] quoted Schönwetter again; the German oologist had no doubt that the fragments belonged to *Psammornis rothschildi*, the thickness being the same, although he remarked that the disposition of the pores was not exactly similar.

The geological provenance of the Mauritanian *Psammornis* was made clear in 1971, when Tessier et al. [53] showed that the eggshells came from Aguerguerian deposits (the Aguerguerian is a local stage of the Pleistocene). They were found in calcareous and clayey sandstones, which, as in Tunisia, also yielded helioid gastropods. Seven localities (see map in [9]) were mentioned where *Psammornis* eggshell fragments were found in situ, with sharp, unworn edges (unlike the surface-collected specimens showing clear signs of aeolian erosion). Voisin [54] described the surface features (Figure 3B) and microstructure of eggshells collected by Hébrard at three Mauritanian localities, noting that they were extremely abundant at one of them, which seemed to correspond to a nesting site. She found a complete correspondence with *Psammornis rothschildi* and noted great similarities with ostrich eggs in the surface features of the shell. No association with human artefacts was noted. Dughi and Sirugue [9] also gave a description of Mauritanian eggshells, which they attributed to *Psammornis*, noting a certain variability in the eggshell surface.

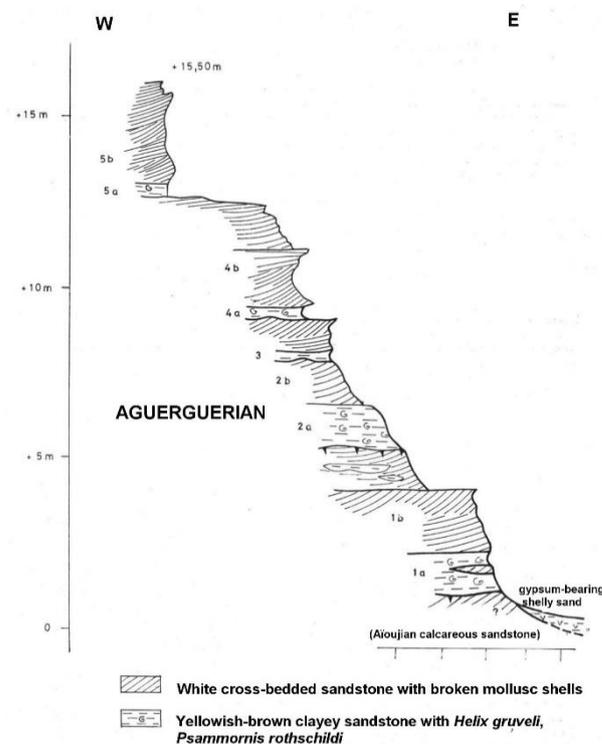


**Figure 3.** Pores on the outer surface of *Psammornis* eggshell fragments from Tunisia, (A) modified after Dughi and Sirugue [8]) and Mauritania (B), modified after Voisin [54].



**Figure 4.** Outline reconstruction of a *Psammornis* egg by Monod on the basis of Schönwetter's size estimates, with outlines of the eggs of an ostich and a hen for comparison. After Monod [51].

The specimens from Mauritania, like those from the Chebket Safra, are of especial importance because they were found in situ in a stratigraphic context, and therefore, provide evidence about the geological age of *Psammornis*. As noted by Tessier et al. [53], Ortlieb [55] and Hébrard [56], they occur in the Aguerguer sandstones, attributed to the Aguerguerian stage. A section of one of the localities was published by Hébrard [56] (Figure 5). As noted by Hébrard et al., [57], the Aguerguerian is, in fact, a regressive facies of the Middle Pleistocene Aioujian stage, and the clayey sandstones containing helioid gastropods and *Psammornis* correspond to paleosols.



**Figure 5.** Section showing Aguerguerian deposits at 'point kilométrique 52' at the north-eastern end of Lévrier Bay, north-western Mauritania. White cross-bedded sandstones alternate with yellowish-brown clayey sandstones containing the snail *Helix gruveli* and in situ *Psammornis* eggshells. The main *Psammornis*-bearing horizon is at the bottom of the section. Modified after Hébrard [56].

Although the Aguerguerian has long been considered as Middle Pleistocene, its exact age remained uncertain until radiometric dates became available. C14 ages of more than 39,900 years were obtained for *Psammornis* eggshell fragments [55], but this was a minimum

age. Giresse et al. [58] published U/Th dates from fossil mollusc shells from geological formations corresponding to several Pleistocene local stages along the Mauritanian coast. No ages were provided for the Aguergerian; however, ages ranging from 241,000 to 258,000 years were obtained for the underlying Aioujian, and of up to 111,000 years for the overlying Inchirian. Since the Aguergerian is considered a facies of the Aioujian, an age of about 200,000 years seems likely (Middle Pleistocene, Chibanian). As noted by Hébrard [56], *Psammornis* does not occur in the Inchirian deposits.

It is worth noting that engraved ostrich eggshells and ostrich eggshell beads are found in some abundance at prehistoric (Epipalaeolithic and Neolithic) sites in Mauritania [59]. Vernet et al. [59] mentioned that at the Cansado prehistoric site, many *Psammornis* eggshell fragments were collected in addition to fragments of *Struthio camelus* eggs; they noted that *Psammornis* had disappeared well before the occupation of the site by humans. More generally, there does not seem to be any record of the use of *Psammornis* eggs (for ornamentation or other purposes) by prehistoric humans, in Mauritania (R. Vernet, pers. com.) or elsewhere. Nevertheless, the presence of *Psammornis* eggs in the Middle Pleistocene Aguergerian deposits of coastal Mauritania implies that this giant bird must have been contemporaneous with early humans, even though no early Palaeolithic industries have been found in Aioujian and Aguergerian sediments [56,60]. This absence may possibly be linked to unfavourable climatic conditions, since the Aguergerian climate appears to show an evolution towards greater aridity [56,61].

## 8. The Stratigraphic Record of *Psammornis* and its Implications

(1) Most reported occurrences of *Psammornis* lack a reliable stratigraphic control. This applies to all records from the Algerian Sahara, including the type material from Touggourt. They correspond to surface finds, often in a sand dune environment, and the geological origin of the fragments could not be ascertained. This also applies to finds from Saudi Arabia (which may belong to *Psammornis*) and Iran (unlikely to be *Psammornis* in view of the thinness of the shell).

(2) The attribution to *Psammornis* of various eggshell fragments is dubious. This applies mainly to fragments which are significantly thinner than the original specimens from Touggourt and do not seem to be much thicker than normal *Struthio camelus* eggshells. A case in point is the material of "*Psammornis libycus*" from Libya which, in all likelihood, can be attributed to *Struthio*. As pointed out by Dughi and Sirugue [8], the unusual thickness of *Psammornis* eggshells was one of the main defining characteristics used by Andrews [1] to establish the taxon *Psammornis rothschildi*. However, among thick eggshells, differences in the pore system have been noted. This is reflected by the divergences between the interpretations of Andrews [1], Sauer [5] and Voisin [54], who find great similarities between *Psammornis* and *Struthio*, and that of Dughi and Sirugue [8,9], who conclude that *Psammornis* is related to Rheiformes, Casuariformes, Aepyornithiformes and Dinornithiformes. A revision of the material from Chebket Safra, on which Dughi and Sirugue's conclusions were largely based, would help to clarify the question.

(3) Only two groups of localities seem to provide reliable stratigraphic evidence concerning the geological age of *Psammornis*:

- The Segui Formation of south-western Tunisia, where *Psammornis* 'nests' have been discovered in situ in red sandy clays apparently containing paleosols. Although some uncertainties remain, the likeliest age for the Segui Formation seems to be latest Miocene (about 6 My ago);
- The Aguergerian of the Mauritanian coast, especially in its northern part, where what are apparently *Psammornis* nesting sites have been discovered in situ in sandstone formations showing evidence of paleosols. The Aguergerian is placed in the Middle Pleistocene and may be about 200,000 years old.

These two relatively well dated *Psammornis* records are rather far apart in time, implying that, if the specimens from Chebket Safra do belong to this oogenus, *Psammornis* was present in North Africa over a long time span, covering at least 6 million years. This in

itself is not unlikely for a genus of giant bird. The genus *Struthio* has a record extending from the Early Miocene (*S. coppensi*) to the present. It seems less likely that the Miocene and Pleistocene specimens of *Psammornis* should belong to a single species (*P. rothschildi*). It should be remembered, however, that *Psammornis* is an ootaxon, the evolution of which probably cannot be followed over time with the same precision as that of taxa based on skeletal material. In fact, the distribution of *Psammornis* eggshells mainly shows that very large ratite birds were present in North Africa over a fairly long period of time, from the Late Miocene to the Middle Pleistocene. There is no consensus about the systematic position of these birds, although the idea that they may have been related to the Aepyornithiformes of Madagascar has never been well-supported. Dughi and Sirugue [8,9], on the basis of microstructural characteristics, suggested relationships with rheas and moas. However, following Sauer's revision [5], most authors [3,10,11,62] seem to agree that *Psammornis* was closely related to *Struthio*—if not, in fact, a member of that genus—and this would lead to the possible consideration of *Psammornis* as a junior synonym of the oogenus *Struthiolithus*. Further research is needed to decide whether the specimens from Chebket Safra can, indeed, safely be referred to *Psammornis*.

It may be worth noting that both in Tunisia and in Mauritania the deposits that yield *Psammornis* eggshells apparently show signs of aridity. The giant ostrich may have been adapted to dry environments, and this may, in turn, explain its large size. Size increase in the Australian dromornithids has been interpreted as an adaptation to an increasingly arid environment with decreasing food resources [63,64], and a similar process has been proposed for some of the giant ostriches of Eurasia [65].

(4) When *Psammornis* became extinct remains uncertain. The Mauritanian record indicates that it survived until the Middle Pleistocene, roughly 200,000 years ago; this implies that it was contemporaneous with early humans, although evidence of interactions between hominins and these giant birds has never been reported. Attributions of *Psammornis* to the Holocene (e.g., [4]) are not supported by the available evidence. A point worth noting, as mentioned above, is that apparently no engraved or otherwise transformed (for instance for bead-making) *Psammornis* eggshells have been reported, whereas decorated, cut or perforated *Struthio* eggshells are very common at Epipalaeolithic and Neolithic sites in North Africa [66,67]. This strongly suggests that *Psammornis* was no longer in existence when these cultures flourished in the Late Pleistocene and Holocene.

(5) Although very few *Psammornis* localities are well dated, the available reliable ages are important in terms of the evolution of giant ratites in North Africa. It should of course be borne in mind that ootaxa are more difficult to interpret in terms of evolutionary history than skeletal remains, and that no reliable association between *Psammornis*-type eggshells and fossil bones has been reported. Large ostriches have been reported on the basis of skeletal material from North Africa. They include *Struthio barbarus*, from the 'Villafranchian' (early Pleistocene) of Algeria [68], which is not associated with egg remains. At Ahl al Oughlam (late Pliocene or earliest Pleistocene of Morocco), a few bones of a large ostrich have been erroneously [3] assigned to *Struthio asiaticus* by Moure-Chauviré and Geraads [69]; they are accompanied by eggshell fragments described as being different from *Psammornis*. As long as no clear association between skeletal remains and *Psammornis* eggs is reported, it will remain difficult to interpret the *Psammornis* record in evolutionary terms. However, the stratigraphic evidence yielded by the Tunisian and Mauritanian records leads us to question some assumptions. For instance, Mikhailov and Zelenkov [3] assumed that *Psammornis rothschildi* is late Early Pleistocene to Middle Pleistocene in age and suggested that the *Psammornis* lineage evolved in more northern territories (perhaps from *Struthio chersonensis* from eastern Europe) and then dispersed to North Africa. However, if they actually belong to *Psammornis*, the latest Miocene specimens from Tunisia are not in agreement with this hypothesis. They indicate the presence in North Africa of a giant ostrich at a much earlier date and may even suggest an African origin for the large ostriches of late Neogene Europe, although the direction of dispersal remains uncertain. The whole picture is made even more complicated by the struthionid record

from southern and eastern Africa, consisting of both bone and egg remains (but apparently not including *Psammornis*-type eggs), which is beyond the scope of the present paper and has led to speculations about the evolutionary history of the ostriches [70].

## 9. Conclusions

Ever since the initial description by Andrews in 1911, the egg-based taxon *Psammornis* has been the subject of widely divergent interpretations in terms of both zoological affinities and stratigraphic distribution. There now seems to be a measure of consensus about the fact that the large thick-shelled *Psammornis* eggs were produced by giant ostriches, although the lack of association with skeletal material makes an interpretation in evolutionary terms difficult. The stratigraphic conundrum which began at the time of the initial description, when an Eocene age was suggested without any solid evidence, has proved even more difficult to resolve, because many of the *Psammornis* finds (even when doubtful records are eliminated), consisting of surface finds, lack any solid stratigraphic context. However, a review of the literature, including various important papers which, for some reason, have been ignored by most authors dealing with the topic, shows that eggs attributed to *Psammornis* have been discovered in situ in relatively well-dated formations at two geographically widely separated groups of localities, in south-western Tunisia and on the Mauritanian coast. Interestingly, these sites are also quite distinct in geological age: the Tunisian finds are apparently latest Miocene in age, whereas the Mauritanian occurrences are in Middle Pleistocene deposits. Whether the Tunisian and Mauritanian *Psammornis* really belong to a single taxon is a moot point, but the occurrence in North Africa of large eggs probably produced by giant ostriches at two periods widely distant in time may suggest a long-lasting lineage of large ratites in that region. This should be taken into consideration when trying to reconstruct ostrich evolutionary history. In particular, it seems difficult to accept that giant ostriches dispersed from Eurasia to Africa as late as the Pleistocene, since they appear to have been present on the African continent as early as the late Miocene. The large eggs from Tunisia may even suggest dispersal in the opposite direction, from Africa to Eurasia. A detailed revision of the Tunisian specimens would, therefore, be very welcome.

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