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Taxonomic Evidence and Evolutionary Interpretation of *Psammornis*

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Dedicated to Prof. Dr. G. Niethammer, Museum A. Koenig, Bonn, at the occasion of his 60th birthday.

The question of the taxonomic position of *Psammornis* among the Old World ratites has been so puzzling that some ornithologist jokingly wished the fossil remains of these giant birds had never been found. Rothschild (1911) introduced a first confusion when he noted, without proof, a close relationship between *Psammornis* and *Eremopezus eocaenus,* a bird known by the distal end of a tibiotarsus from the Upper Eocene beds of the Fayum formation north of Birket-el-Qurun in Egypt, and "only about the size of a small ostrich" (Andrews, 1904). Lambrecht (1933) erected the Eremopezinae solely on the basis of this fossil and placed this subfamily in the family Aepyornithidae, which includes the extinct elephant birds of Madagascar. Lambrecht did this against his own better judgement that one can not think of any close relationship between the Eremopezinae, in which he also placed *Psammornis,* and the Aepyornithidae. Brodkorb (1963) followed the system of this authoritative paleontologist only with hesitation and questioned the association of *Eremopezus eocaenus* with *Psammornis rothschildi* from southern Algeria (Andrews, 1911), *Psammornis libycus* from the Cyrenaica (Moltoni, 1928), and the Arabian *Psammornis* spec. from Shuqqat al Kalfat (Lowe, 1933), all believed to date back to the Eocene. Rothschild kept *Psammornis* generically distinct from *Eremopezus* and outside the Aepyornithidae: "In North Africa..... the Eocene forms *Eremopezus* and *Psammornis* had already acquired full Ratite Palaeognathine character of the general type intermediate between *Aepyornis* and *Struthio.*" He considered these birds the forerunners of the Old World ratites that evolved, as he suggested, in the southern Mediterranean basin and thence spread northwards and eastwards as far as China. This, I suggest, is very unlikely. Evidence is accumulating that small forms of ostriches lived in Asia during the Eocene, where they may have shared with the Eocene "cranes" a common carinate ancestor. But Lord Rothschild opened the way for very stimulating discussions when he postulated links between those forms and early representatives of ostriches, namely *Struthio asiaticus, S. chersonensis* (which includes *S. karatheodoris* after Brodkorb, 1963), and *S. wimani.* He also sensed a relationship between *Psammornis* and the Aepyornithidae.

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The question of the age of the *Psammornis* forms is also linked to their unfounded association with *Eremopezus*. Lambrecht (1929) followed Stromer's (1916) dating of the Birket-el-Qurun stage, in which the remains of *Eremopezus* were found, as Lower Oligocene instead of Upper Eocene. Today the Birket-el-Qurun beds are generally dated Upper Eocene, while the fluvio-marine beds of the Qatrani stage, in which *Stromeria fajumensis* was found (below), are Lower Oligocene. This dating appears justified for these two strata, but the remains of *Psammornis* have nothing to do with them. They were all collected on the surface, and thus not definitely attributable to the Eocene. Finally, the *Psammornis* remains are all eggshell fragments which many paleontologists regard as of a dubious nature. This I believe unwarranted, for the *Psammornis* eggshell fragments may provide an even greater wealth of equally reliable structures for taxonomic identification than the distal end of a tibiotarsus. Further, *Psammornis* could not have been conspecific with *Eremopezus;* the slight curvatures of its shell fragments show that the "egg was far larger than that of the modern Ostrich or even than that of *Struthiolithus chersonensis*;" it may have measured as much as "25 cm. in its long diameter and 19 cm. in the transverse direction" (Andrews, 1911). Schönwetter (1929), still not satisfied with this estimate, guessed 280 × 210 mm for the long and short axes of the *P. rothschildi* egg. Even if these dimensions were exaggerated, it appears safe to state that *Psammornis* produced such a large egg that this bird must have been distinct from the relatively small *Eremopezus*. This statement should not exclude the possibility that these two genera might not have been related.

How do we establish the identity of *Psammornis,* the bird whose existence as a taxon has been questioned mostly because of the lack of bony remains? If we concede that eggshell analyses can be as informative as a study of bony fragments, we can place it satisfactorily with the struthionid forms. First, we must show more clearly that *Psammornis* and *Eremopezus* are two different forms.

Eremopezus turned *Stromeria*

While visiting the paleontological collections at Munich, Lambrecht (1929) came upon three bony fragments, a tarsometatarsus, ischium (?), and pubis (?), surprisingly labelled *Eremopezus eocaenus*. The bones had been found in the Qatrani stage of the Fayum formation and were dated Lower Oligocene. Lambrecht's interest was aroused because of the scant knowledge of *Eremopezus*. The ischium and pubis he found unidentifiable; he even questioned that they were avian. The tarsometatarsus, however, revealed an unmistakingly ratite character and came from a bird the size of an ostrich. Lambrecht could detect no resemblance of this bone to that of *Struthio*. On the other hand, its similarity with the corresponding parts

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of a tarsometatarsus of the Madagascan *Muellerornis*, a member of the Aepyornithidae, appeared so striking that Lambrecht did not hesitate to rename the obviously carelessly labelled specimen. He called it *Stromeria iajumensis* and considered it the continental ancestor of the Aepyornithidae

Lambrecht speculated the Aepyornithidae came to Madagascar in the Oligocene or earlier, and he foretold that some day one should find on Madagascar not only Quaternary relics but also Tertiary remains of *Aepyornis*. Lambrecht thought it possible, but left it an open question, that *Psammornis rothschildi* might have been a forerunner of *Stromeria*.

The Identity of *Eremopezus*

The tibiotarsus fragment from the Fayum on which Andrews (1904) based his description of *Eremopezus eocaenus* still remains the only specimen representing subfamily, genus, and species. Lambrecht (1929) relied on Stromer's (1916) dating of the Birket-el-Qurun stage, which yielded this fossil, as Lower Oligocene, but it is now regarded as Upper Eocene. Andrews (1904) noted that the fragment with its pronounced intercondylar groove differed from those of both *Aepyornis* and *Struthio*, and even suggested that it resembled in this respect the tibia of *Casuarius* and *Rhea*. On comparing the fossil with an aepyornithid tibia from Madagascar, Lambrecht (1929) also strongly rejected the notion of a close relationship between *Eremopezus* and *Aepyornis* and emphasized that *Eremopezus eocaenus* must remain excluded from the Aepyornithidae. In 1933 he repeated the same statement, yet unfortunately included the Eremopezinae in the family Aepyornithidae.

The History of *Psammornis*

1. *Psammornis rothschildi*.

Andrews (1911) proposed this genus and species for the fossil shell fragments Lord Rothschild collected in the desert of southern Algeria about 20 miles east of Touggourt.[1]) The mineralized fragments were picked up on the surface near an excavation for a well. It was assumed that they had been brought up from a considerable depth, but Andrews stated cautiously that "the period at which this bird lived is quite unclear." At some time, he noted, the shell fragments had been exposed to drifting sand; they were worn, their edges rounded, and the surface pitted and polished. Andrews remarked that the peculiar pitting is "characteristic of calcareous substances worn by this means," but he seemed not to realize that the shell fragments must have possessed a particular structural pattern in order to

[1]) Strangely, Schönwetter (1942) stated that these fragments were collected by Hartert.

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develop the characteristic pitting when they became sand-worn and beveled.

Andrews (1911) measured the thickness of the worn and cleaned shell fragments as 3.2 to 3.4 mm; Lowe (1931) thought it necessary to correct this to 3.2 to 3.3 mm. Judged from the slight curvature of the fragments, Andrews estimated that the egg must have been very large, possibly as much as 250 × 190 mm.

Andrews's (1911) report on microstructures of the eggshells lacks illustrations; he described the following features studied on thin sections. The outer membrane of the shell fragments is worn off; the spongy layer is like that in eggshells of *Struthio* and *Aepyornis*, and mineralization obscures the region closest to the mammillary layer. The inner ends of the mammillae are worn away, "but the portion remaining is similar to the corresponding part of the egg-shell of *Struthio*, and to some degree to that of *Aepyornis*". The similarity to the eggshell of *Struthio* is evident in the "division of the main columns into secondary ones, and the arrangement of the dark laminae in the accessory columns, in each of which they are convex outwards and concentric round the inner ends of the columns. In *Aepyornis* the columns are less divided and the dark laminae seem to run straight across them". The pore canals are "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." Andrews remarked on the similar arrangement in *Aepyornis* eggs, "except that there is a tendency for the pores to open in irregular rows of four and five, at the bottom of slight grooves." Then he noted the great similarity of the *Psammornis rothschildi* pore pattern with that of the *Struthio c. camelus* eggshell, in which "the pores open singly or in ill defined groups which are not situated in a distinct depression in the surface." The openings of groups of pore canals in surface depressions he saw correctly as characteristic of *S. c. australis*; for examples see Sauer, 1966. In summing up, Andrews recognized similarities between the eggshells of *Psammornis rotschildi, Struthio c. camelus,* and *Aepyornis* (but less than with *Struthio*) and stated, "with *Struthio* the relationship was probably very close."

Schönwetter (1942) reported on ostrich eggshell fragments from southern Algeria, collected by Frommholz and Spatz in 1913 near Fort Flatters (Temassinin) and at Mokrani, Abbon, Djokran, and Khachba. All the fragments were found on the surface of dune sand. The second of three collection groups contained fragments from Temassinin which Schönwetter identified as belonging to *P. rothschildi*. The greyish brown pieces of shell were heavily abraded and eroded, measured 2.50 to 2.90 mm in thickness, and Schönwetter estimated that they must have been more than 3.0 mm thick in their unworn state.

Without further identification Schönwetter also remarked on one larger *Psammornis* shell fragment (5.0×5.25 cm; 3.0 mm thick) from the Iguidi district in Algeria, and on one from Cape Blanco on the Atlantic coast. He noted the distances of these localities from that of the original find at Touggourt as 700 km south and 2800 km southwest respectively.

The Schönwetter collection at the Museum A. Koenig in Bonn, which we viewed only very briefly, includes several shell fragments that appear to be problematical and challenge further investigation; this we plan to do as time permits.

2. *Psammornis libycus.*

Moltoni (1928) described this species from a single shell fragment found in the dunes south of the oasis Giarabub in the Libyan Cyrenaica. The fragment was 2.1 mm thick, considerably thinner than the shell of the *P. rothschildi* egg (above). It was described as well preserved and characterized as hardly sand-worn; it was stained reddish brown, but along a fresh break it was white inside indicating that once it was entirely white. Moltoni did

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not speculate about the possible age of the fossil, nor did he analyze its fine structures or explain why he considered this find congeneric with that identified as *P. rothschildi*. Moltoni's description appears inadequate for generic or specific identification and the fragment should be reexamined.

3. *Psammornis* spec. from Arabia

Lowe (1933) described the one shell fragment collected by St. John Philby at Shuqqat al Kalfat, about 22° N. The fossil came from an old river bed where it was found associated with remains of freshwater mollusks. This suggested that pluvial rather than desert conditions existed at the time the shell was deposited. Lowe considered the bird a member of a fauna that occupied the old land surface of Arabia before it became a desert. He measured the thickness of the "considerably sand-

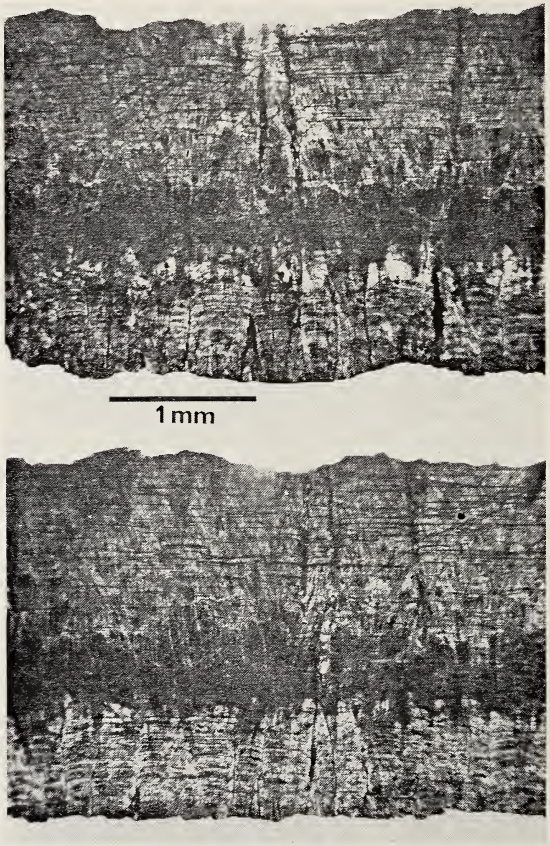

Fig. 1. *Psammornis rothschildi*, British Museum A 1334, section 4; a) solitary pore canal and group of three, b) pair of canals.

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worn" shell as 3.0 mm and noted that thin sections cut from the fragment revealed structures "remarkably similar in all respects" to those of *P. rothschildi*. He estimated that the size of the egg must have "very greatly exceeded" that of eggs from the recent ostrich.

Examinition of Eggshell Remains Attributed to Psammornis

1. *Psammornis rothschildi*

Our microscopical studies were made on the four thin sections cut from the type shell in the British Museum. The collection is catalogued under No. A 1334 and includes two cross-sections, one tangential section through the spongy layer, and one that cuts from the spongy into the mammillary layer.

a. The shell in cross-section. Both radial sections (Figs. 1 and 5) show heavy abrasions of the cuticular and mammillary surfaces. The greatest thickness comes to 3.23 mm, which must be well below the original thickness of the shell. No trace is left of a cuticle. On the inner side, most of the organic caps of the mammillae are entirely abraded. The outer region of the spongy layer shows a conspicuous tangential arrangement of the coarse laminae; here and there they are interspersed with radial fibers. The section with the more heavily abraded surfaces appears more mineralized than the other; a large part of its outer spongy layer is obscured. The portion of the mammillary region next to the mammillae is also very dense. The mammillae are composed of columns, and their laminae of organic substance shows a pattern (Fig. 2) that Andrews (1911) characterized as struthionid rather than aepyornithid.

The lengths of two free mammillae with the best preserved organic caps came to 772.5 and 875.5 µ. These two values can be considered a close match of the typical length of the mammillae. No further readings were taken, as it would have been of little value to measure heavily abraded mammillae.

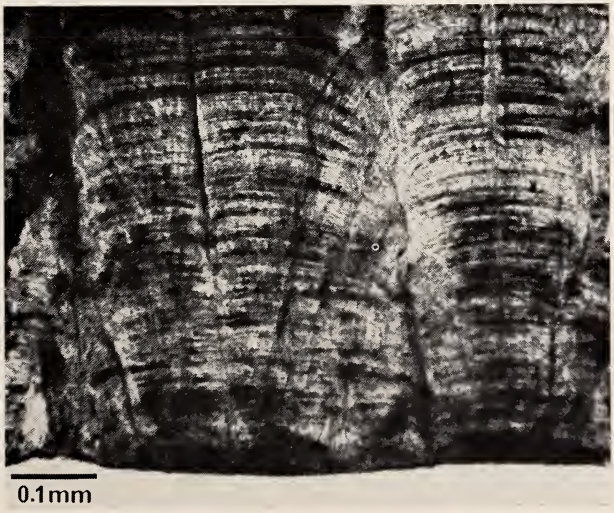

Fig. 2. *P. rothschildi*, B. M., A 1334, section 4, mammillae.

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Fig. 3. *P. rothschildi*, B. M., A 1334, tangential section through the spongy layer; solitary and grouped pore canals in cross-section.

The pore canal system as revealed in the cross-sections is discussed below.

b. The spongy layer in tangential section. The conspicuous features in the spongy layer are the pore canals in cross-section (Fig. 3, and below). The spongy layer and the arrangement of the pore canals are very similar to that of eggshells from the North African Ostrich, *S. c. camelus*. The conspicuous difference from corresponding eggshell structures of the South African Ostrich, *S. c. australis*, is the lack of a pronounced fusion of canals (for examples see Sauer, 1966).

c. The mammillary layer in tangential section. Also the microscopical structures of the mammillary layer (Fig. 4 a) reveal the struthionid character of the shell. The rays of the organic matrix granules are arranged in wedges assembled in more and more irregular patterns as one moves outward in the mammillary layer (Fig. 4 b). On the average the mammillae measure about 336 to 448 µ in diameter, which corresponds to an average area in cross-section of 0.088 to 0.157 mm².

d. The pore canal system. The radial and tangential sections show solitary canals, irregularly distributed, running nearly straight from the outside to the inside of the shell. Interspersed are groups of canals that are composed of two, three, or a few more ducts arranged either parallel, slightly divergent, or convergent. Fusion or branching of grouped canals appears to happen in several places, but this is rare compared to the number of unbranched canals that run straight through the shell (Fig. 5).

The widths of pore canals were measured on both radial and tangential (spongy layer) sections. Measurement was void in places where the ducts were filled and obscured with foreign matter. Forty readings ranged from 12.24 to 61.20 µ; these extremes were measured only once, the former pertaining to an exceptionally fine pore canal, the latter being the diameter of a bigger lumen of a canal near its entrance into the intermammillary space. Fifty percent of the readings came to 20.5 µ, and 70 % ranged between 20.4 µ and 30.6 µ, the latter being the second most frequent value with 15 %. The canals are of circular shape and either quite regular in diameter or varying repeatedly between different values, for example between 30.6 and 20.4 µ.

2. *Psammornis libycus*

Moltoni's (1928) type specimen is preserved at the Museo Civico di Storia Naturale at Genoa, Italy. We examined the fragment, catalogue

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number MSNG 25 172, and found it sufficiently well preserved to identify and measure surface structures (Fig. 6). Its edges and surfaces are sand-worn, the outer surface more than the mammillary side. Wear and erosion of the pore canals on the outside of the shell have reached rather deeply into the spongy layer giving it a pockmarked appearance. The fragment is superficially stained a brownish sand-color; inside it is still white as shown by the relatively fresh break along one of the edges.

The outer surface shows numerous very fine pores of circular shape; a number of canals are opened up through wear and erosion. The pores are neither grooved nor fused but rather isolated, solitary and arranged in small groups. Their distribution is mostly irregular, but here and there they are lined up in short rows (Fig. 6). Erosion has altered the surface pattern. For a full understanding of the remaining canal system thin sections must be made from the fragment. Less eroded and worn areas reveal that the shell in its original state was probably

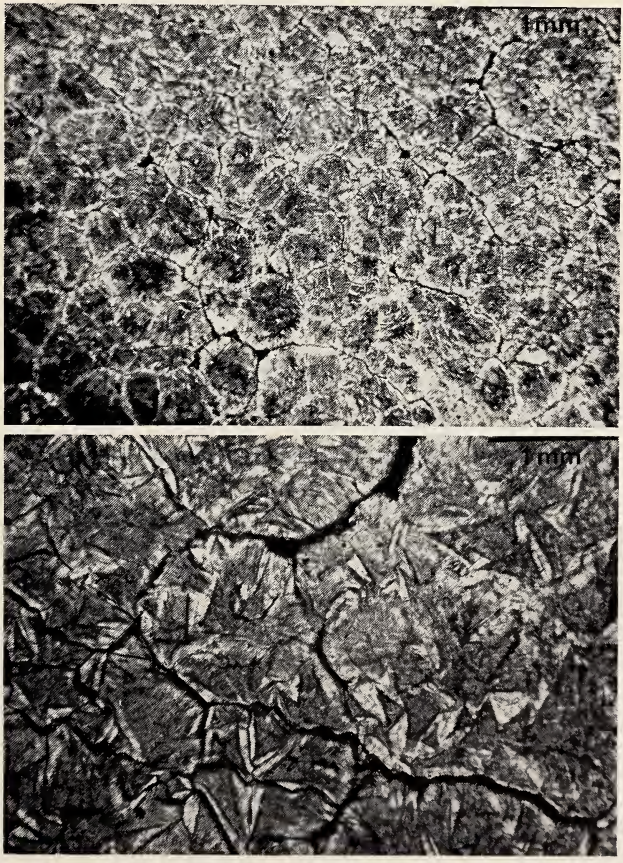

Fig. 4. *P. rothschildi*, B. M., A 1334, tangential section through the mammillary layer; a) arrangement of mammillary cores, b) enlarged section showing wedges of the granular organic matrix.

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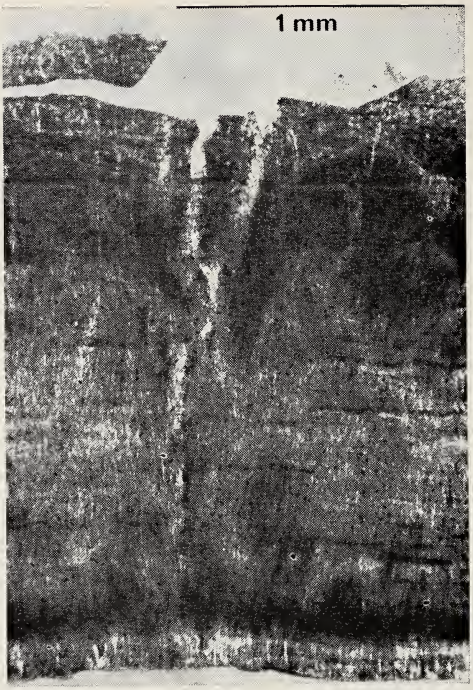

Fig. 5. *P. rothschildi*, B. M., A 1334, radial section 3; segment indicating branched pore canals.

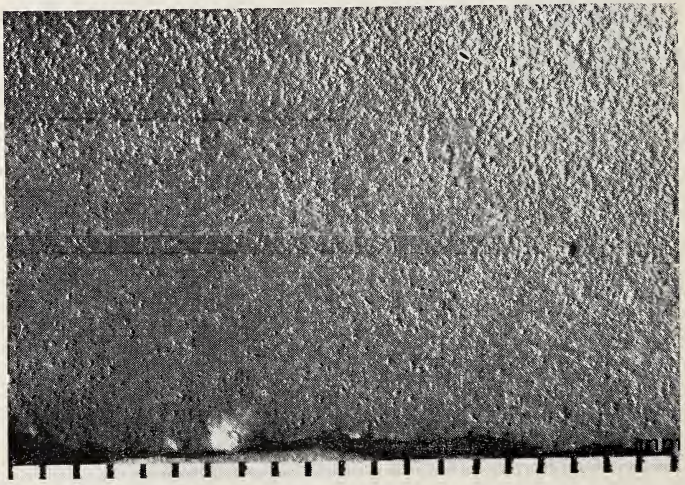

Fig. 6. *P. libycus*. Part of the fragment seen from its outer surface, showing the arrangement of pore openings.

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quite smooth without pore grooves and pits or pronounced furrows. It may have resembled the surface of the *S. c. camelus* eggshell. If the now visible faint and shallow furrows with several solitary, round pore openings in a row are still indicative of the original surface pattern, it may have shown a superficial resemblance to shells of *S. c. australis,* in which a similar pattern is made up of surface furrows with pits of multi-branched reticulate pore grooves rather than solitary round pore openings (for examples see Sauer, 1966).

The exact diameters of pore canals and their number per surface area must be studied on thin sections, which are unavailable at present. The surface appears littered with pore openings (Fig. 6). Erosion has exposed more of the canals than their original surface openings. Measurements in less eroded areas show the most frequent diameters of pores to be approximately 34 and 45 µ; less frequent are very fine canals of about 23 µ and larger ones around 57 µ. I expect that these readings are slightly on the large side because erosion widened the pores. Independent of this, the measurements fall right into the range characteristic for *Struthio* eggs. In sample counts in less worn areas of 1 mm² the number of pore openings varies between 28 and 42. This is an excessive number of pores, and some of them may not be pores but only pockmark products of erosion; thin sections will tell.

The mammillary surface shows a mostly severe abrasion of the organic mammillary caps (Fig. 7), but the weathering has affected this side less than the outer surface of the shell. In places where individual mammillae can still be identified, 30 to 45 main and secondary mammillae fill areas of 1 mm².

The average thickness of the abraded shell fragment is 2.08 mm; the maximum of 23 measurements reads 2.10 mm, the minimum 2.05 mm. The curvatures of the cuticular and mammillary surfaces were measured with a Geneva lens measure (see Sauer, 1968). The great variations in lengths of the radii of curvature measured in four different directions in 17 planes on each of the two surfaces (Fig. 8), indicate that the piece of shell comes from an area nearer the equator than to one of the poles of the egg. A completely satisfactory evaluation of these measurements of curvature is not possible, but the following attempts have been made to obtain a learned guess as to the probable thickness of the shell and the size of the egg.

The longest and shortest radii among the 34 readings were 80.91 and 63.47 mm for the outside, 77.94 and 60.92 mm for the inside of the shell. The maxima and minima are corresponding pairs of measurement; they can be used for a theoretical determination of the original thickness of the shell. The difference between

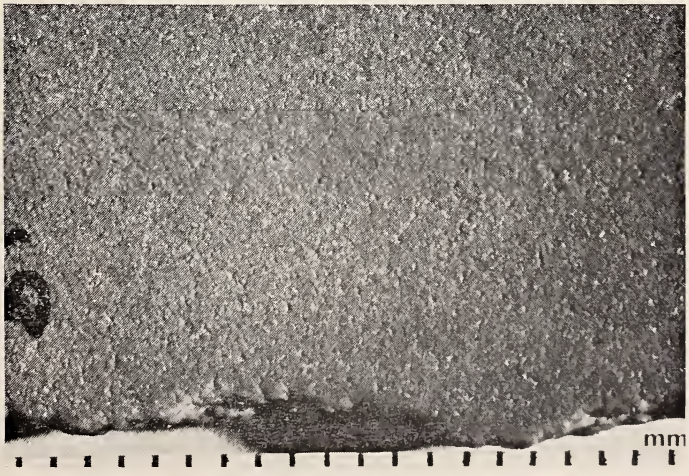

Fig. 7. *P. libycus,* mammillary surface of the fragment.

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the longest radii yields a thickness of 2.97 mm, that of the shortest radii comes to 2.55 mm. Similarly, comparisons of the groups of relatively uniform outside and inside curvatures yield values of 2.89 mm (Fig. 8, vertical readings) and 2.81 mm (horizontal readings). These figures are higher than the average thickness of 2.08 mm derived from the measurements of the worn fragment. This one would expect. While the wear of the shell probably affected its curvatures too, the average theoretical value of 2.80 mm, which is the mean of the four calculated thicknesses, may yet be considered the best approximation to the thickness of the shell in its original state.

For an estimate of the size of the egg we refer to the measurements of curvature. In a piece from the equator of the egg the radii of curvatures are maximally different and occur at right angles. As only one piece of shell is available, which does not show the equatorial radius unequivocally, its longest and shortest radii on the two surfaces can be used only as crude approximations to the lengthwise and crosswise radii at the egg's equator. How much they differ from the real dimensions may be judged from the result, particularly from a comparison of radial indices. As the mammillary surface is less worn than the outer surface, the maximally different radii of 77.94 and 60.92 mm from the measurements of the inner surface are chosen for a first approach. The long radius is made equal to the lengthwise radius of the egg, a^2/b, and the short radius becomes the semiaxis b, both

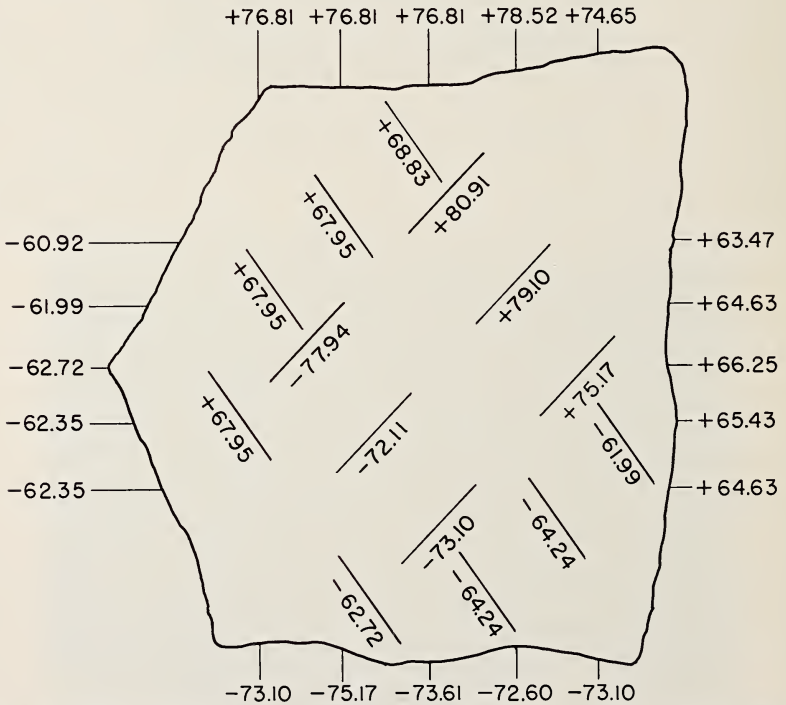

Fig. 8. *P. libycus*. Geneva lens measure readings of curvatures in millimeters on the outer (+) and inner (—) surfaces of the shell fragment.

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for the inside of the shell. Taking the latter value to determine a, and using 2.80 mm for the theoretical thickness of the shell, the outer axial dimensions of the egg come to 143.41 × 127.44 mm. The short axis expressed in percent of the long axis yields an axial index of $I_a = 88.8$. For a control, the same calculation is repeated with the maximally different radii, 80.91 and 63.47 mm, from the more worn outer surface of the shell. This process leads to axial dimensions of 143.36 × 126.94 mm ($I_a = 88.5$), which are 1/20 and 1/2 mm below the former.

3. *The Arabian Psammornis spec.*

At the British Museum we examined the fragment of eggshell described by Lowe (1933) and labelled: ? *Psammornis,* Pleistocene, Freshwater De-

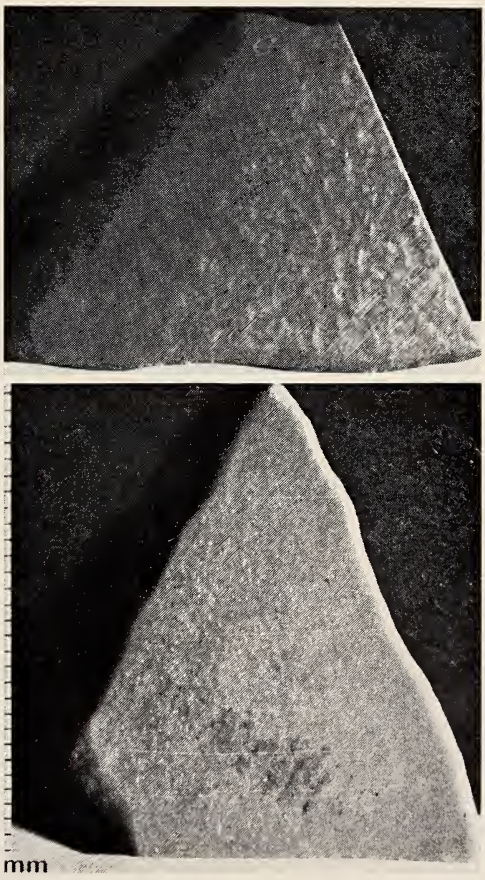

Fig. 9. *Psammornis* sp. from Arabia; shell fragment viewed from the outer (a) and mammillary (b) surface.

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posit, Shuqqat al Khalfat, Lat. 22° N Rub 'al Khali, S. Arabia. Catalogue Number A 2043.

Seen from the outer surface (Fig. 9 a), the fragment appears heavily worn and its two long edges sharply bevelled. The sand-worn outer surface looks irregularly reticulate, resembling the pattern of hammered copper, which is possibly a result of the action of the sand. With the unaided eye one can see neither linear pore grooves nor circular pore pits or openings. Thus, other structures being comparable, one gets the impression that the shell must have been quite smooth with tiny pore openings resembling the eggshell of *S. c. camelus*.

Also the mammillary surface of the fragment (Fig. 9 b) presents a faint reticulate pattern. On this side the longest edge is heavily bevelled. The question arises, but remains unanswered, if the reticulate pattern and the heavy bevelling of the edges are the result of natural forces or if they were possibly man-made. In the collections of the Museum A. Koenig in Bonn we noticed shell fragments from the Algerian Sahara, identified by Schönwetter (1942) as *Psammornis*, that show the same kind of bevelling. It is also present in two other shell fragments at the British Museum that are labelled *Struthio ?syriacus* (No. 2056), also from Rub 'al Khali. Yet other shell fragments from the same location have no such bevelled edges. As most of those fragments with knife-blade edges are roughly triangular in shape, it is conceivable that men may have bevelled the pieces for use as tools. Naturally, this could have happened long after the eggs were laid and broken up when the shell had become hardened through fossilization.

The thickness of the shell fragment, measured with a Vernier caliper, came to 3.1 mm, with the lowest value at 3.05 mm. Lowe's (1933) reading was 3.0 mm. In addition, we measured curvatures of the shell fragment with the Geneva lens measure. The radii of the inside curvatures ranged from 82.81 to 124.70 mm, those of the outside curvatures from 85.91 to 127.80 mm. These readings lead to a theoretical value of the average shell thickness of 3.1 mm which coincides exactly with our caliper readings. Judged from the immense variation of curvatures in different directions, the fragment came probably from the equator of the egg. This opens an avenue for a reliable calculation of the size of the egg. The short outside radius of 85.91 mm would equal the short semiaxis b, and the long outside radius of 127.80 mm would be $a^2 b$, in which the factor a corresponds to the long semiaxis of the egg. From this information one can calculate a long axis of 209.56 mm and a short axis of 171.82 mm for the Arabian *Psammornis* egg. While these calculated figures derived from a single shell fragment must be treated with

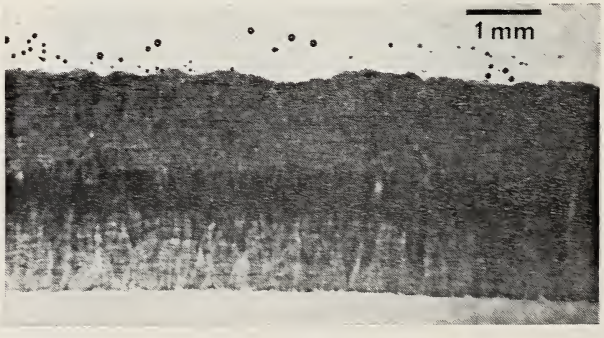

Fig. 10. *Psammornis* sp. from Arabia; shell fragment in cross-section.

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great caution, they are most likely quite reliable and appear to be grounds for an interesting comparison (below).

An examination of a thin radial section made from this fragment, slide No. A 2044 from the British Museum, reveals a great resemblance with the *P. rothschildi* eggshell (Fig. 10). The outer surface is heavily abraded and eroded. Most of the mammillary structures are well preserved, but the organic caps of the mammillae are mostly gone. The greatest thickness of the shell comes to 3.09 mm, corresponding with our reading of 3.1 mm taken from the shell mentioned above, and also calculated from the measurements of the radii of its curvatures.

None of the pore canals shown in the section is complete, but the parts of 15 identifiable canals present sufficient clues for a reconstruction of the internal pore canal system. Canals are solitary or arranged in groups of two, in one place possibly three. The fine canals lead right through the shell with few bends and without branching. In one place two converging canals may have met and fused. Diameters of canals were measured in the nine best identifiable places. They ranged from 20.4 to 51.0 µ, with a typical canal lumen in the depth of the spongy layer measuring 30.6 µ. Like these canals, the mammillae also compare well with those of other struthionid eggshells.

Discussion

The Sizes of *Psammornis* Eggs and Thicknesses of their Shells.

Our preliminary attempt to gain information on the probable sizes of *Psammornis* eggs is based on the assumption that they are typically struthionid, *i. e.* ellipsoid in shape. Andrews (1911) realized that the *P. rothschildi* egg must have been very large and guessed that it may have measured as much as 250 × 190 mm. Our calculation of the axes of the Arabian *Psammornis* sp. egg led to 209.56 × 171.82 mm, which we consider a good approximation. The corresponding axial index of 81.99, which is the length of the short axis expressed in percent of the long axis, puts the egg into the center of the range of axial indices characteristic of ostrich eggs from the past and the present (Sauer, 1968). This calculated size exceeds all of that of the fossil and recent eggs from the different species of ostriches listed in that publication, save the estimate for the Hungarian *S. pannonicus* egg.

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 useable.

The readings for the *P. libycus* egg are tentative. With 143.41 × 127.44 mm (I_a = 88.8) they compare to the size of a typical *S. camelus* egg. The axial index is typically struthionid, on the round side of the range. If the fragment came from the equator, one might have found the axial index to be slightly below this value. But as it is still inside the range, little more can be added than the fact that the roundest ostrich egg listed in our graph (Sauer, 1968) comes from *S. c. spatzi* with axes of 140 × 126 mm and an index of 90.0 (Schönwetter, 1927). Judged from the widely differing radii of curvatures of the shell fragment, they must approximate the equatorial

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dimensions and the result of our calculation is probably close to the original egg axes. One may assume that the *P. libycus* egg was not much larger if it was at all larger.

For an evaluation of the thicknesses of the *Psammornis* eggshells we turn to the caliper measurements of the worn fragments, the micrometer readings of the thin cross-sections, and the theoretical values deducted from the readings of the surface curvatures.

Andrews (1911) noted 3.2 to 3.4 mm for the *P. rothschildi* shell. Our reading of the maximum thickness taken from the cross-section comes to 3.23 mm. As the fragments are heavily abraded, one must consider all these values well below the original thickness of the shell, which may have come close to 4.0 mm. No shell fragments were available for calculating the thickness of the *P. rothschildi* shell from measurements of surface curvatures.

Moltoni (1928) gave 2.1 mm for the thickness of the worn *P. libycus* fragment. Our values range from 2.05 to 2.1 mm with an average of 2.08 mm. The calculated thickness, derived from the radii of surface curvatures, is with an average of 2.80 mm well above those readings from the abraded shell. I consider this calculated value a close match of the original shell thickness. As the calculated egg axes make the *P. libycus* egg equal in size to a typical *S. camelus* egg, one can not determine at present whether the egg of *P. libycus* was a relatively small but thick-shelled egg, or comparable in size to the other two *Psammornis* eggs.

Lowe (1933) gave 3.0 mm for the sand-worn shell of the Arabian *Psammornis* sp. Our measurements of the only available piece ranged from 3.05 to 3.1 mm, the latter being most frequent and typical. Our calculation of the theoretical shell thickness confirms the measured thickness of 3.1 mm, but this does not exclude the possibility that the shell might not have been thicker in its unworn state. As size, shell thickness, and microstructures of the *P. rothschildi* and the Arabian *Psammornis* sp. pieces compare well, I am inclined to consider both forms closely related if they were not the same. The one millimeter thinner *P. libycus* fragment, if one refers to the measurements of the worn fragments, is either more worn through longer exposure or stronger action by the sand, or it comes from an egg with a thinner shell but not necessarily smaller in size than the eggs of the other two species. Relationships between struthionid egg sizes and shell thickness are discussed in Sauer, 1968.

The Pore Canal System of the *Psammornis* Eggshells

The radial and tangential sections of all of the *Psammornis* eggshell fragments present a picture of a struthionid system of pore canals; also the size of the canals is identical with that of other ostrich eggs but not

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with those of *Aepyornis* forms. The canal system of the *P. rothschildi* egg is comparable to that of *S. c. camelus* as Nathusius described it in 1885. In the eggshells of these two species we find irregularly distributed solitary canals and groups of two, three, or a few more canals that penetrate the shell either without branching or through fusion with other canals. While the heavily abraded *P. rothschildi* shell fragments leave no image of the outermost surface pattern of the pore canal openings, the pattern on the abraded surface, the typical distribution and arrangement of the pore canals as shown in the thin sections, and the small diameter of the circular lumina of the canals suggest that the surface pattern was similar if not identical with that of the *S. c. camelus* eggshell. Schönwetter (1927) depicted the latter well: The pore canals open singly or in loose groups of two and three in an irregular pattern of distribution, hardly noticeable to the naked eye because of their small size. Schönwetter gave the diameter of the *S. c. camelus* pore canals as 20 to 30 µ and counted 100 of them per cm^2. Judged from the counts of the pore canals in the thin section through the spongy layer of the *P. rothschildi* eggshell, their number comes to about 106 per cm^2, which closely matches that of the *S. c. camelus* eggshell. This figure is tentative; I consider it a crude approximation because of the small size of the section available for the count. The typical size of the pore canals of the *P. rothschildi* eggshell ranges from 20 to 30 µ, which also compares with that of the *S. c. camelus* eggshell. Thus, the study of the pore canal system brings much evidence of structural similarity and identity of the eggshells of *P. rothschildi* and *S. c. camelus*. In fact the pore canal systems of the eggshells of these two species are more similar than that of the only subspecifically different *S. c. camelus* and *S. c. australis*. If it were not for the enormous size of the *P. rothschildi* egg, its pore canal system and other microstructures of the shell would not warrant a specific distinction of this species from *S. c. camelus*.

The eggshell of the Arabian *Psammornis* sp. resembles most closely that of *P. rothschildi*. It is also so worn that the pattern of pore openings remains obscure. The pore structures visible in the radial section show an arrangement of solitary canals, groups of twos and possibly threes. By this and by the way they penetrate the shell with little or no fusion, as well as by their size, they are like the canals in te *P. rotschildi* shell. This could suggest that the surfaces of the two eggs were comparable and as smooth as in the *S. c. camelus* shell. The available evidence leaves little doubt that *P. rothschildi* and the Arabian *Psammornis* sp. were closely related.

The pore canal system of the *P. libycus* eggshell cannot be fully evaluated before thin sections are made. From the study of the surfaces and edges of the worn fragment we must note that this shell differs from that of *P. rothschildi* and the Arabian *Psammornis* sp. in a number of details.

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On the other hand there are similarities; also a resemblance of the *P. libycus* eggshell to that of *S. c. camelus* can not be denied. The sizes of the pore canals and their arrangements as solitary pores or in small groups agree with the structures noticed in the other *Psammornis* shells. The line-up of singly isolated pores in short irregular rows is not found in the former specimens, but it is found in the *S. c. camelus* eggshell as Nathusius (1885) noticed. A resemblance of this feature with the furrows on the surface of eggs from the South African Ostrich, *S. c. australis,* was considered superficial; in the furrows of the latter we find pits of multi-branched reticulate pore grooves. Beyond this the formation of the furrows on the surface of the shells of these two species may be considered comparable and done for the same, still unknown reason. The number of pores per unit area is huge compared to that of the other species, even if our tentative count on the eroded shell fragment exaggerates their number. On the other hand, the large number of pores appears to support the notion that the *P. libycus* egg might have been relatively thick-shelled for its size (p. 304).

None of the *Psammornis* shell fragments shows pore canals of the size and arrangement typical of all of the aepyornithid eggshells known to date. A characterization of the latter and their comparison with corresponding struthionid structures is planned for a separate publication.

Other Microscopic Features of the Shell Fragments

The fine structures of the spongy and mammillary layers, particularly the arrangement of the organic matrix substance and the construction and size of the mammillae, are very similar in the shell remains attributed to the three *Psammornis* forms. As pointed out above, they are struthionid rather than aepyornithid. They can be found practically identical in eggshells from Asiatic ostriches of the Pliocene as well as in those from *S. camelus.* Whether these microstructures can be used as species characters in struthionid eggshells is not known at present.

The Age of *Psammornis*

No C-14 dating has been made for any of the *Psammornis* eggshell fragments. As Andrews (1911) suggested, the age of *P. rothschildi* remains in doubt. There is no evidence for the notion expressed repeatedly in ornithological literature that this bird dates back to the Eocene. The large size of the eggs of *P. rothschildi* and *Psammornis* sp. from Arabia, as well as the considerable thickness of their shells, suggest from a comparative point of view that these birds were of pre-Pleistocene age (the date for the beginning of the Pleistocene, however, is not fixed and seems to be still shifted back). They were probably members of the giant Pliocene (less

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likely still earliest Pleistocene) ostriches. But they could have lived at any period of the long history of the giant ostriches prior to the advent of the smaller Pleistocene neospecies *S. camelus*. It is unlikely that the large *Psammornis* birds were contemporaries of the earliest *S. camelus*. One may reasonably speculate that the *Psammornis* forms could have been forerunners of *S. camelus*, as may be derived from the similarity of their eggshell structures. The microstructures of the *Psammornis* eggshells show also great similarities to those of eggshells attributed to Pliocene representatives of *Struthio* from Asia. At present we do not know the phylogenetic lineages between the pre-Pleistocene ostriches nor those that lead from them to their Pleistocene descendants. The remains of the *Psammornis* forms, other still unidentified Arabian and North African struthionid fossils, that of *S. oshanai* from South West Africa (Sauer, 1966), and struthionid shell remains from Lanzarote, Canary Islands (Rothe, 1964, 66) indicate that it might well have been that ratites invaded the Mediterranean basin and Africa in several waves separated by considerable periods of time.

Schönwetter's (1942) shell fragments, which he attributed to *P. rothschildi*, were collected on the surface too and do not provide a clue to their age from this. The shell of the Arabian *Psammornis* sp. was found in a place that suggested the bird might have lived in a pluvial environment. Lowe (1933) thought this bird a resident of the old land surface of Arabia before it became a desert. His specimen was labelled tentatively „Pleistocene", and it might have been that this ostrich lived in an early pluvial period of this epoch before it was replaced by *S. camelus*.

The *P. libycus* fragment was also collected on the surface in dunes. As the arrangement of the pore canals is more similar to that of the *S. c. camelus* eggshell than to that of the other *Psammornis* remains, one might speculate that *P. libycus* could have formed a link between the two if, in fact, it was not the earliest *S. camelus*. We had completed these studies and came to these conclusions about *P. libycus* when we finally obtained the long requested article by Schönwetter (1942), in which he noted to our delight the same consideration.

Generic Rank and Taxonomical Position of *Psammornis*

On the basis of the struthionid structures of the shell fragments, separating the *Psammornis* birds generically from *Struthio* becomes questionable. Taxonomists have not hesitated to place into the latter genus Pliocene ostriches that were widely distributed from Asia to Africa. And some of them were probably older than *Psammornis*. Eggshell structures of several of the Asiatic species are hardly distinguishable from those of the *Psammornis* shells. For example, the pore canal systems of the *Psammornis* and *S. mongolicus* shells look alike; the latter species is dated Lower Pliocene and found in Mongolia.

If the generic identification of the Pliocene ostriches from Asia is correct, *Psammornis* seems as good a fossil ostrich of the genus *Struthio* as any other assigned to the genus. For the sake of convenience the generic

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name of *Psammornis* may be maintained at present. But one must understand that *Psammornis* cannot be considered an isolated genus outside the main stream of struthionid evolution. And still more important, *Psammornis* is not an intermediate form linking the Struthionidae with the Aepyornithidae. Our comparative studies show the remains of these birds as typically struthionid as any eggshell from the present day ostriches. Further, the existence of other Asiatic and African ratite shell remains that show great similarity in structure with those of the Madagascan Aepyornithidae brings to our attention that the ancestors of the elephant birds were others than *Psammornis*. These continental ancestors may prove to form links between these two families of Old World ratites.

While the shell fragments of all of the three *Psammornis* forms tie these birds closely to the extinct ostriches recognized as *Struthio*, the *P. libycus* appears to have the closest association with *S. camelus* if it is not indeed the earliest representative of this species. Further comparative studies of still unidentified or tentatively labelled fossil struthionid shell material from North Africa and an analysis of the fine structures of the *P. libycus* eggshell could clarify this point.

In retrospect, it appears that the guess of an impressive size of the egg of *P. rothschildi* and the unfounded notion of a relationship with *Eremopezus* were the major features that encouraged early workers to consider this bird a link between the Struthionidae and Aepyornithidae. Coming back to our introductory discussion, the *Psammornis* forms are struthionid and can not be associated with *Eremopezus eocaenus*. Further, the Eremopezinae can not be listed with the Aepyornithidae, and they should not be included, at present, in the Struthionidae. Lambrecht (1929) did not consider the features and identification of the tibiotarsus fragment of *Eremopezus eocaenus* from the Lower Oligocene of the Fayum (now considered Upper Eocene) sufficient to associate it with either family. At present, related fossil bone structures that could allow a better identification and classification of the *Eremopezus* find are still wanting. It now appears that the Lower Oligocene *Stromeria fajumensis* is the one African fossil sufficiently identified (Lambrecht, 1929) to justify its association with the Aepyornithidae. On the other hand, I consider Lambrecht's (1929) notion that *P. rothschildi* might have been a forerunner of *Stromeria* highly improbable.

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Zusammenfassung

Untersuchungen an fossilen Eierscherben von *Psammornis rothschildi, Psammornis* sp. von Arabien und *P. libycus* zeigen, daß diese Vögel in den Artenkreis der Strauße der Gattung *Struthio* gehören und weder als Zwischenglieder für die Struthionidae und Aepyornithidae noch als Angehörige der letzten Familie aufzufassen sind. Für die Schalenstrukturen von *P. rothschildi* und dem arabischen *Psammornis* sp. sind keine Artunterschiede festzustellen. Die Eierschale von *P. libycus* ist in ihrer Mikrostruktur der von *S. c. camelus* ähnlicher als der der beiden anderen *Psammornis*-Arten. Es ist möglich, daß *P. libycus* der früheste Vertreter von *S. camelus* war. *Psammornis* kann weder mit *Eremopezus eocaenus* vergesellschaftet noch als Vorläufer von *Stromeria fajumensis* aufgefaßt werden. Keinerlei Nachweise gibt es für das postulierte Eozän-Alter von *Psammornis*, und das Alter der Eierscherben sollte durch C-14-Datierung festgestellt werden.

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