Taxonomic revision of the extinct avian oospecies *Diamantornis karingarabensis* (Senut *et al*., 1998) from the Latest Miocene of Namibia

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Abstract :- Restudy of the fossil eggshells originally identified as *Struthio karingarabensis* indicates that they are more likely to belong to the extinct oogenus *Diamantornis* than to *Struthio*. Re-measurement of the entire sample of eggshell fragments from the type locality reveals that the range of variation in thickness is slightly different from previously published estimates. In particular the holotype is thinner than originally reported.

Keywords :- Struthionidae, Eggshells, Late Miocene, Systematics, Ootaxa

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Introduction

Fossil eggshells of struthious birds have proven to be useful for biostratigraphy in Afro-Arabia (Pickford and Dauphin, 1993; Senut and Pickford, 1995; Senut *et al*., 1998; Senut, 2000; Harris and Leakey, 2003; Stidham, 2004, 2008; Harrison and Msuya, 2005; Bibi *et al*., 2006; Stewart and Beech, 2006; Pickford, 2014; Louchart *et al*., 2022; Pickford *et al*., 2023).

New discoveries of fossil eggs in Oman (Pickford *et al*., 2023) prompted a restudy of the previously described material from Namibia, during which it was noticed that some of the published measurements are erroneous.

The aim of this paper is to amend the description of the relatively poorly known oospecies *Struthio karingarabensis*, in particular to provide illustrations of the available sample from the type locality, and to provide more accurate measurements of the thickness of the eggshells.

Previous Work

The extinct avian oospecies *Struthio karingarabensis* was erected by Senut *et al*. (1998) and the oxygen and carbon isotopes of the eggshells were analysed by Ségalen *et al.* (2002). Further mention of the species was made by Pickford (2014).

The species is known from its type locality in the middle section of the Karingarab aeolianite succession and from the Awasib Cliffs in the Namib-Naukluft Park (Senut *et al.*, 1998). The age of the deposits has been estimated to be Latest Miocene.

Material and Methods

GSN KG 26'95, 25 eggshell fragments from the middle section of the Karingarab aeolianite succession, Namibia. The holotype and paratype are labelled 'A' and 'B' respectively (Fig. 1), and the remainder of the fragments are numbered from 1 to 23 (Fig. 2). The fossils are curated at the National Earth Science Museum, Geological Survey of Namibia, Windhoek.

Measurements were taken with sliding calipers to the nearest tenth of a mm. Images were captured with a Sony Cybershot Camera and treated with Photoshop Elements 15 to remove unwanted background and to enhance the contrast. The holotype and paratype were each measured at three points along the edges of the fragments (Fig. 3), while the other fragments were measured at one point only.

Systematic Palaeontology

Order Struthioniformes Latham, 1790

Family Struthionidae Vigors, 1825

Genus *Diamantornis* Pickford and Dauphin, 1993

Diagnosis (translated from French). Avian oogenus with large eggs (16 x 13.3 cm) with the external surface ornamented with large circular pore complexes (megapores) ranging in diameter from 2 to 8 mm. Each pore complex contains multiple smaller pores. In section the pore canals are ramified.

Species *Diamantornis karingarabensis* (Senut *et al*., 1998)

Original diagnosis (translated from French). Pore structure – the outer surface ornamented with pore complexes ranging in diameter from 2.4 to 2.7 mm, forming shallow depressions with an irregular outline; thickness – ranging from 2.95 to 3.2 mm (measured on a single fragment); description of the microstructure – in transverse section, the limit of the internal mammillary layer is generally unclear, not only in naturally fractured sections but also in polished section, due to diagenetic effects; in effect, the cleavage of the calcite tends to obscure the divergent fibres, this cleavage is also present in the columnar and spongy layers; the disposition in columns is visible, but the edges of the columns have become unclear; the complex, ramified structure of the pores, as well as their overall funnel-like shape are preserved; the spherolites on the internal surface are usually eroded.

Emended diagnosis. As above except that the thickness of the shells, measured on 25 fragments from the type locality, ranges from 2.0 to 2.9 mm (Table 1; Fig. 3).

Holotype and Paratype. GSN KG 26'95 'A' and GSN KG 26'95 'B' respectively (Fig. 1).

Other material. GSN KG 26'95, 1-23, eggshell fragments from the same locality as the holotype (Fig. 2).

Locality and Age. Karingarab (28°12'16.2"S : 16°21'34.7"E), middle section of the aeoliantes, Latest Miocene.

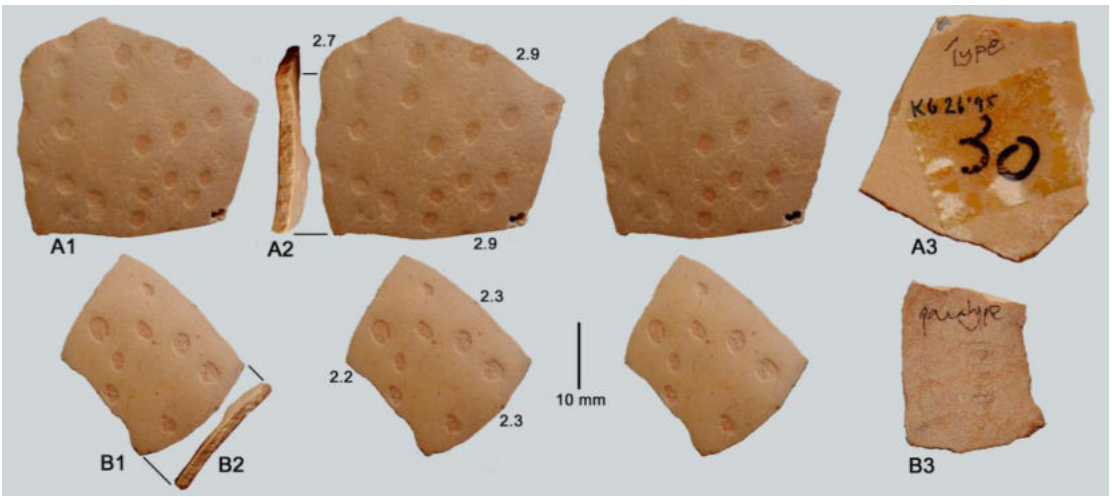

Figure 1. GSN KG 26'95, images of the holotype 'A' and paratype 'B' of *Diamantornis karingarabensis* from Namibia. 1 – stereo views of external surface, 2 – view of naturally broken section, 3 – internal surface. The measurements are of the thickness of the shells

Description

The eggshell fragments attributed to *Diamantornis karingarabensis* range in thickness from 2.0 to 2.9 mm. The external surface of the shells is patterned with abundant shallow ovoid depressions in which the pores are concentrated, the shell between the depressions being smooth and devoid of pores. The depressions range in diameter from 2.4 to 2.7 mm and are randomly distributed over the surface of the shells.

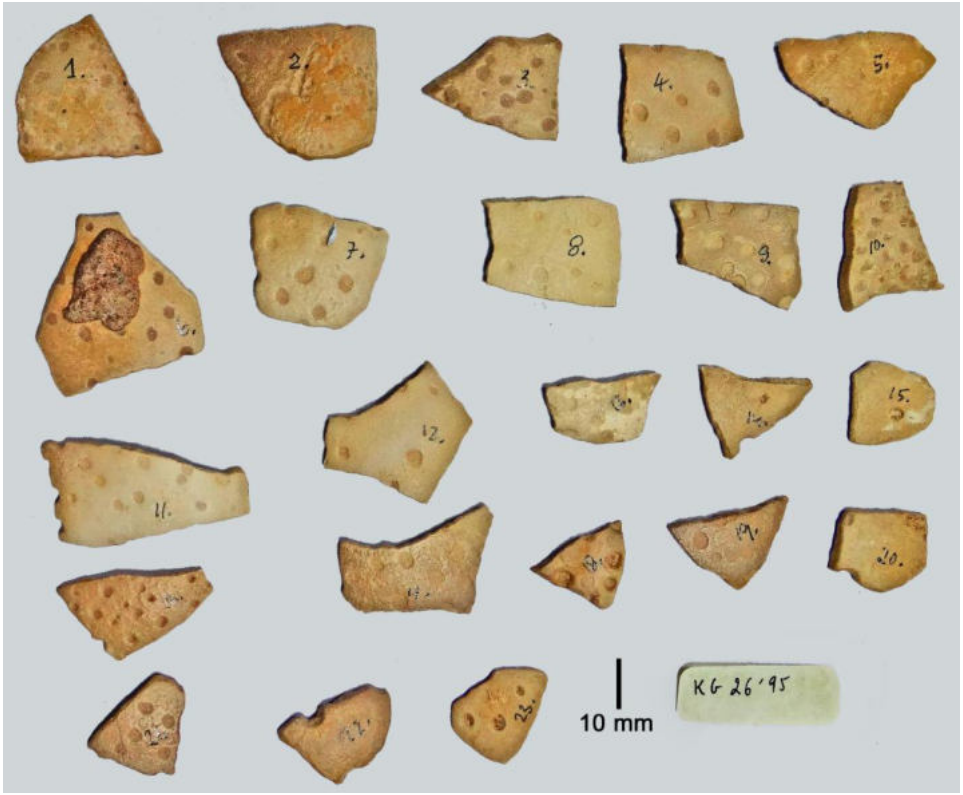

Figure 2. GSN KG 26'95, images of the external surfaces of 23 eggshell fragments of *Diamantornis karingarabensis* from the type locality of the species

Catalogue GSN	Thickness	Comment	Catalogue GSN	Thickness	Comment
KG 26'95 'A'	2.7	Holotype	KG 26'95 '10'	2.5	
KG 26'95 'A'	2.9	Holotype	KG 26'95 '11'	2.5	
KG 26'95 'A'	2.9	Holotype	KG 26'95 '12'	2.7	
KG 26'95 'B'	2.2	Paratype	KG 26'95 '13'	2.9	
KG 26'95 'B'	2.3	Paratype	KG 26'95 '14'	2.4	
KG 26'95 'B'	2.3	Paratype	KG 26'95 '15'	2.2	
KG 26'95 '01'	2.6		KG 26'95 '16'	2.0	
KG 26'95 '02'	2.5		KG 26'95 '17'	2.5	
KG 26'95 '03'	2.8		KG 26'95 '18'	2.2	
KG 26'95 '04'	2.6	Fig'd Pickford 2014	KG 26'95 '19'	2.6	
KG 26'95 '05'	2.6		KG 26'95 '20'	2.4	
KG 26'95 '06'	2.5		KG 26'95 '21'	2.3	
KG 26'95 '07'	2.5		KG 26'95 '22'	2.7	
KG 26'95 '08'	2.6		KG 26'95 '23'	1.8	Damaged
KG 26'95 '09'	2.8				

Table 1. Measurements (in mm) of the thickness of eggshell fragments of *Diamantornis karingarabensis* from Karingarab, Latest Miocene, Namibia

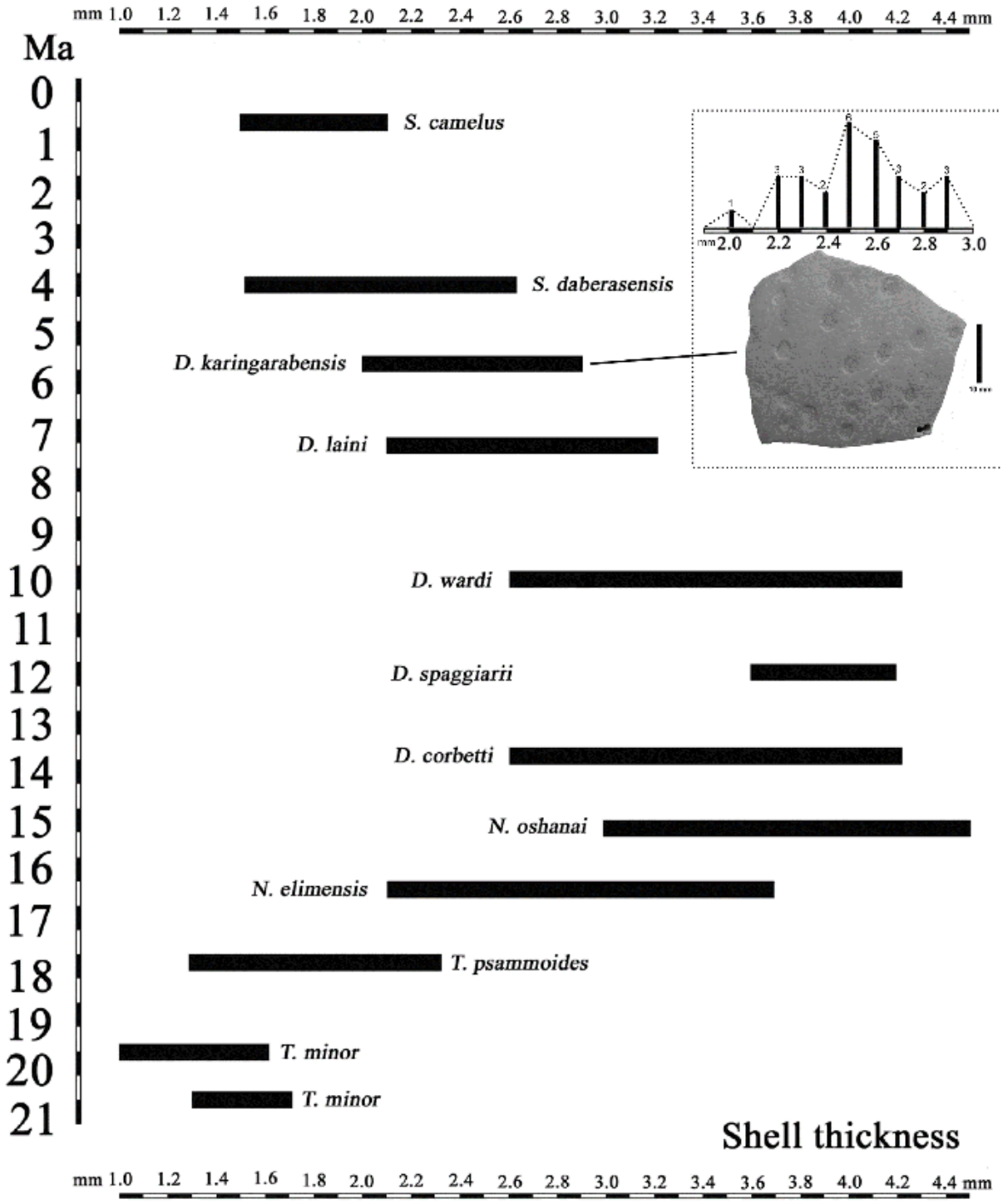

Figure 3. Ranges of thicknesses of fossil struthious eggshells from Namibia (Early Miocene to Recent), highlighting the new intrepretation of *Diamantornis karingarabensis*. The illustrated eggshell fragment is the holotype of the species (GSN KG 26'95 'A') and the inset is a frequency histogram of the thicknesses of eggshells from the same locality – mode 2.5 mm. (*T - Tsondabornis, N - Namornis, D - Diamantornis, S - Struthio*). Figure modified from Pickford (2014)

Discussion

Restudy of the entire sample of eggshell frragments from the type locality of *Struthio karingarabensis* (25 fragments) reveals that their thickness is somewhat less than previously reported, ranging in thickness from 2.0 to 2.9 mm (mode 2.5 mm) (Fig. 3). Furthermore,

the pore complexes are morphologically similar to those that occur in species of *Diamantornis*, even though they are of smaller diameter than them and are more irregular in outline, as originally reported by Senut *et al*. (1998). The pores are clustered close together in the depths of shallow depressions with well-marked margins, as in *Diamantornis corbetti*, *Diamantornis spaggiarii*, *Diamantornis wardi* and *Diamantornis laini*, and the shell between the pore complexes is smooth and devoid of pores, also as in these species. In species of *Struthio*, in contrast, the pores are generally scattered over the surface of the eggshell, not forming clusters of many closely-packed pores in clearly defined shallow ovoid depressions but forming groups of a few pores in shallow linear or curved grooves. It is therefore logical to transfer the Karingarab species to *Diamantornis* as the combination *Diamantornis karingarabensis*.

Previous attribution of the Karingarab eggshells to the genus *Struthio* reflected the rather irregular outlines of the pore complexes as well as their relatively diminutive dimensions when compared with those present in *Diamantornis wardi* which are larger and more circular in outline (Pickford and Dauphin, 1993; Pickford, 2014). As such the form of pore complexes of the eggshells of *D. karingarabensis* is intermediate between those of *D. wardi* and *Struthio camelus*. The specimens are also intermediate in thickness and age between *D. wardi* and *S. camelus* (Fig. 3) so it is plausible that *D. karingarabensis* eventually gave rise to *Struthio*. However, on the basis of the morphology of the pore complexes and the thickness of the shells, it is considered that the Karingarab fossils are better classified in *Diamantornis* than in *Struthio*.

The pores in eggshells are channels via which gases are exchanged between the developing chick inside the egg and the surrounding atmosphere, with carbon dioxide and water vapour being 'exhaled', and oxygen 'inhaled'.

By concentrating the pores in shallow depressions in the external surface of the eggshell, species of *Diamantornis* effectively reduce the distance between the inner surface of the eggshell and the atmosphere, while maintaining an overall thick shell related to the greater dimensions of the egg. Eggs of *Struthio*, in contrast, are thinner and smaller than those of *Diamantornis*, so even though the pores penetrate similar thicknesses of shell as they do in the latter genus, they are not concentrated into depressions in the outer surface of the eggs, but are scattered liberally all over the egg, often in shallow grooves.

In view of the usefulness that fossil struthious eggshells have shown for Afro-Arabian Neogene biochronology, it is deemed necessary to refine the data base concerning the dimensions of the eggshells in *Diamantornis karingarabensis*, because previous reports on their thickness (Senut *et al*., 1998; Pickford, 2014) differ slightly from the new measurements (Table 1; Fig. 3).

Conclusion

Re-examination of the sample of eggshell fragments from the type locality of *Struthio karingarabensis* Senut *et al*. (1998) reveals that the specimens are morphologically closer to those of the oogenus *Diamantornis* rather than to those of *Struthio*. For this reason they are herein classified as the combination *Diamantornis karingarabensis*.

A few published measurements of the material, in particular of the holotype, overestimated the upper end of the range of variation of eggshell thickness, so a revised compilation of measurements of the entire sample of eggshell fragments from the type locality is provided.

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