

**FIGURE 1.** Location map of the Western Region, Abu Dhabi Emirate, United Arab Emirates, plotting sites mentioned in the text. The Baynunah Formation outcrops predominantly along the coast of the Western Region. International boundaries shown are approximate.

## INTRODUCTION

Renewed survey efforts targeting the Late Miocene deposits of the United Arab Emirates have recovered new vertebrate fossil remains from this relatively poorly known period in the Arabian subcontinent's geological history. Whybrow and Hill (1999) led the first efforts to methodically collect and identify fossils from the Baynunah Formation deposits of the Western Region of Abu Dhabi Emirate (map, Figure 1). Their approach included work on the stratigraphy, diagenesis, paleomagnetism, and isotopic composition of the local deposits, as well as descriptions of the invertebrate and vertebrate fossils collected (Whybrow and Hill 1999). The total published faunal list from the Baynunah included over 20 vertebrates identified at the generic level, with three new species (Whybrow and Clements 1999b). The Abu Dhabi Islands Archaeological Survey (A.D.I.A.S.) has, over the last few years, conducted paleontological work at several localities threatened by development. The Baynunah fossil record clearly merits further con-

tinued investigation. Modern climatic conditions along the southern Persian Gulf coast make for extremely poor fossil preservation conditions, and the rapid rate of development in the UAE has meant that, increasingly, access to fossiliferous outcrops is being restricted. Any additional diagnostic specimens collected from the Baynunah Formation become vital towards augmenting our understanding of the deep history of Arabia, the geographical crossroads between the European, Asian, and African continents.

Field work was undertaken by F.B., A.B.S., and B.P.K. and consisted of a total of nine weeks of survey in the Western Region. Most significant among the newly collected mammalian material are specimens of Proboscidea, Artiodactyla (Bovidae and Giraffidae), and Perissodactyla (Equidae and Rhinocerotidae). Important avian fossils include several osteological specimens tentatively referable to genera not previously described from the region, in addition to a large amount of fossilized eggshell representing two dis-

tinct ratite eggshell morphotypes. These fossil eggshells, here identified as the oogenus *Diamantornis* and a form described as aepyornithid-type, are the focus of this paper, while the remaining avian and mammalian material will be described at a later time. Included in our description are 10 eggshell fragments collected by Andrew Hill and accessioned into the Yale Peabody Museum (YPM) collections. Specimens with the Abu Dhabi prefix (AUH) are currently housed at survey quarters on Shuwaihat, and are curated with A.D.I.A.S.

### GEOLOGICAL SETTING

The Baynunah Formation consists primarily of fluvial sands and clays. Its sediments have been studied thoroughly and detailed stratigraphic, sedimentological, and diagenetic information is presented in Whybrow et al. (1999), Ditchfield (1999), Friend (1999), and Peebles (1999). The Baynunah sediments are interpreted as deposits of a shallow braided stream system, with occasional playa lake formation. Fossils are typically found resting on lenses of intraformational conglomerate and are often covered by unconsolidated intermixed sands and clays or arenitic sands that probably represent bar deposits. The eggshell remains described here were all collected from outcrop surfaces and not *in situ*. Their fossil status was determined by their spatial distribution as restricted to outcrops of the Baynunah Formation, their association at these outcrops with remains of vertebrate fossils, and their reddish-brown color, indicative of prior burial in the Baynunah sediments.

The Baynunah Formation lacks any volcanic rocks that may be dated radioisotopically. As a result, the maximum and minimum ages assigned to the Baynunah are based on the composition of the fossil fauna recovered from within it. The presence of faunal elements in common between the Baynunah and radiometrically dated sequences in East Africa has permitted the assignment of an age of between 6 and 8 Ma for the Baynunah fauna (Whybrow and Hill 1999).

Detailed information on most localities mentioned in this paper is provided in Whybrow and Clements (1999b). Further locality data are on file with A.D.I.A.S. and are available upon request from the corresponding author.

### NOMENCLATURE NOTE: PARATAXONOMY

The study of fossil eggshell has prompted the development of an eggshell parataxonomy, or 'ootaxonomy'. Parataxonomic-nomenclatural approaches toward the naming of fossil eggshell taxa (ootaxa) were recently outlined by Mikhailov et al.

(1996), Mikhailov (1997), and Hirsch et al. (1997) among others. These workers recognized that the fossil remains of eggs can rarely if ever be confidently identified with osteological remains of the animal that produced them, necessitating a separate nomenclatural classification for egg and skeletal remains. The parataxonomic approach suggests that fossil eggshell taxonomic ranks incorporate the prefix *oo-* (e.g., ootaxa, oogenus, oospecies) and that generic names end in the suffix *-oolithus* (Mikhailov et al. 1996; Hirsch et al. 1997). Under a parataxonomic framework, avian eggshell is described and discussed separately from avian osteological remains. Ichnotaxonomy provides an analogous case of nomenclatural parallelism, whereby the fossil traces described are rarely able to be associated with the animal species that created them. Ichnotaxa are widely recognized, and ichnotaxonomy (a form of parataxonomy) has become formalized (ICZN 2000: Article 42.2.1) and is well-developed (for a review, see Prothero 1998).

Recent work has demonstrated the applicability of cladistic phylogenetic analyses to ratite eggshell (Grellet-Tinner 2000; Zelenitsky and Modesto 2003), possibly doing away with any need for a parataxonomic approach. Grellet-Tinner (2000) conducted a cladistic analysis of eggshell that included fossil and recent palaeognath taxa. His end result included a monophyletic Paleognathae. Zelenitsky and Modesto (2003) found that analyses that included only eggshell characters, only skeletal characters, and both eggshell and skeletal characters produced very similar tree topologies. Although their work included only modern ratites, its implications extend to the fossil record, suggesting that analyses that include eggshells of both fossil ootaxa and recent ratites may provide a basis for the formulation and testing of evolutionary and biogeographic hypotheses. We agree with these workers that cladistic analyses are the best way to test phylogenetic statements regarding eggshell. Yet it is still the case that many taxa have been erected solely on the basis of fossil eggshell, with no association of these specimens to skeletal remains. We maintain that such taxa are more properly referred to as ootaxa and that unless they are either: 1) confidently associated with skeletal remains; or 2) demonstrated cladistically to share synapomorphies with eggs of a skeletally based taxon, their Latin binomials remain parataxonomic. Parataxonomic status does not exclude fossil eggshell from inclusion with skeletal taxa in cladistic phylogenetic analyses, and such analyses do have the capacity to illuminate phylogenetic and evolutionary trends.

In discussing the Namibian eggshell taxa, we employ the taxonomic nomenclature used by the original authors (Pickford and Dauphin 1993; Pickford et al. 1995) purely for simplicity's sake and with the aim of avoiding unnecessary confusion in the literature. These taxa are, however, understood to be ootaxa, and are referred to as such throughout. We elect to replace the commonly used term 'aepyornithoid' with the more meaningful 'aepyornithid-like' (or 'aepyornithid-type', as appropriate), which refers to the actual family-level taxon.

## METHODS

Each preserved edge of each eggshell fragment was measured for thickness, and the average was calculated from the means of each specimen's thickness. Eggshell areas were calculated from digital photographs of the specimens using ImageJ (<http://rsb.info.nih.gov/ij>). For specimens of *Diamantornis*, whole and half-pore complexes (along broken edges) were counted for each specimen. Each preserved whole pore complex was measured for length (greatest diameter) and width (maximal value taken perpendicular to length). Half-pore complex diameters were not computed, but half-pore complexes were included in calculation of pore complex density for each specimen (0.5 pore complex). Pore complex mean diameter was calculated as the combined average of every complete pore complex's mean diameter, calculated as  $(\text{length} + \text{width})/2$ . The 10 Yale Peabody Museum specimens display significant abrasion of pore complex rims and as a result were not included in pore complex diameter measures. For specimens of aepyornithid-type eggshell, the variation in pore morphologies was assessed across specimens. Eggshell cross-sectional microstructure (e.g., Grellet-Tinner 2000), was not considered. Microstructural analysis of *Diamantornis* eggshells was undertaken by Dauphin et al. (1996). The UAE eggshells were assigned on the basis of eggshell thickness, and pore complex shape, size, and density.

## SYSTEMATIC PALEONTOLOGY

### Institutional Abbreviations

AUH: Abu Dhabi, specimens curated with the Abu Dhabi Islands Archaeological Survey, Abu Dhabi, United Arab Emirates. YPM: Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

### AVES

#### PALAEOGNATHAE Pycraft 1900 RATITAE Huxley 1867

## ?STRUTHIONIDAE

### Oogenus *Diamantornis* Pickford and Dauphin 1993

**Type oospecies.** *Diamantornis wardi* Pickford and Dauphin 1993

**Oogenus Diagnosis.** Large eggs (16 x 13.3 cm), the external surface of which is patterned by large (2 to 8 mm) circular (in plan view), funnel-shaped (in section view) pore complexes (or 'megapores') (Pickford and Dauphin 1993). Regions of eggshell between the pore complexes are smooth and devoid of small pores; pore complex density ranges from zero to nine pore complexes per every 4 cm<sup>2</sup>; and eggshell thickness between the different oospecies of *Diamantornis* ranges approximately from 2.1 to 4.3 mm (Dauphin et al. 1996). Microstructural analyses confirm assignment of *Diamantornis* to the ratites (Dauphin et al. 1996).

**Known distribution.** Neogene Tsondab Sandstone aeolianites of the Namib Sand Sea, Namibia (Pickford and Dauphin 1993; Pickford et al. 1995). Lower Member of the Nawata Formation, Lothagam, Kenya (Harris and Leakey 2003; Harrison and Msuya 2005).

### Oospecies *Diamantornis laini* Pickford et al. 1995

#### Figure 2

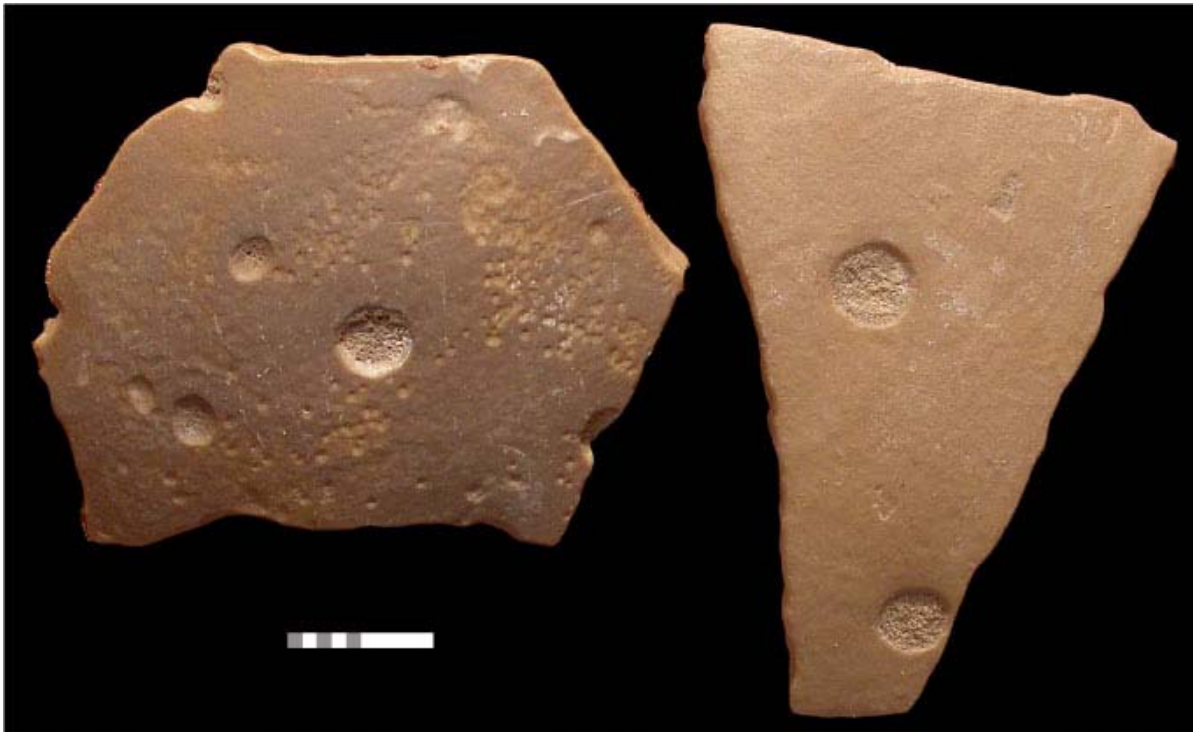
**Holotype.** Target Pan 3a'93 housed at the Geological Survey of Namibia, Windhoek.

**Oospecies Diagnosis.** Pore complexes circular in shape, having a diameter of about 5 mm (see below). These complexes tend to be well separated from each other by areas of smooth eggshell. Pore complexes are funnel shaped in section. Pore complex density is zero to four pore complexes per 4 cm<sup>2</sup>. Eggshell thicknesses range from 2.1 to 2.9 mm, mode = 2.4 mm (n=22) (Pickford et al. 1995, shell thickness means are unpublished).

The original diagnosis (Pickford et al. 1995) for this oospecies describes the pore complexes as having an approximate diameter of about 9.5 mm, a value inconsistent with the illustrations in the paper in which the pore complexes of *D. laini* eggshells appear to be closer to 5 mm in diameter. Later publications (Dauphin et al. 1996; Senut 2000) more accurately referred to *D. laini* pore complexes as being about 5 mm in diameter.

**Known Distribution.** As for *Diamantornis* above with the inclusion of *D. cf. laini* from Lothagam (Harrison and Msuya 2005).

**New Material.** Eighty-four eggshell fragments from the Late Miocene Baynunah Formation, Abu Dhabi Emirate, United Arab Emirates (AUH 922, 923,



**Figure 2.** Two fossil eggshell fragments representative of *Diamantornis laini* from the Baynunah Formation. AUH 931 (left), and AUH 990. AUH 931 exhibits moderate weathering, evidenced by pore complexes with rounded edges, and texturing of the otherwise smooth surface between pore complexes. Scale bar equals 1 cm total.

926, 929–931, 934, 940–943, 947–952, 954–993, 995–1010, YPM 56709–56718).

**Localities Present.** Hamra (H3-1, H5-0), Baynunah Municipality Site (MU1-2), Ras al-Qal'a (Q1-1), Shuwaihat (S2-0, S2-1, S2-5, S3-0, S4-0, S8-1).

**Description.** The eggshell fragments vary in preservation. In general, the AUH specimens vary from greatly eroded to very well preserved. The 10 YPM specimens are greatly eroded. We consider highly weathered specimens to be those that exhibit rounding of broken edges, smoothing of pore complex rims, texturing of the surface between pore complexes, and exposure of the pore complexes on the internal surface of the eggshell. Fresh cross-sectional breaks clearly exhibit the abrupt transition between the mammillary and squamatic layers diagnostic of Palaeognathae (Grellet-Tinner 2000). Maximal fragment length ranges between about 1 cm and 6 cm. The eggshell fragments likely derive from multiple eggs and clutches, although it is a possibility that certain specimens may be from a single egg or a single clutch. The thickness of the eggshells ranges from 2.11 to 3.46 mm with a mean thickness of 2.77 mm (standard deviation 0.28). Pore complex diameter ranges from 1.43 to 6.17 mm with a mean diameter of 4.1

mm (66 measurements from 36 specimens; standard deviation 1.05). Mean pore complex density is 0.26 pore complexes/cm<sup>2</sup> (73 specimens measured; standard deviation 0.20).

### Discussion

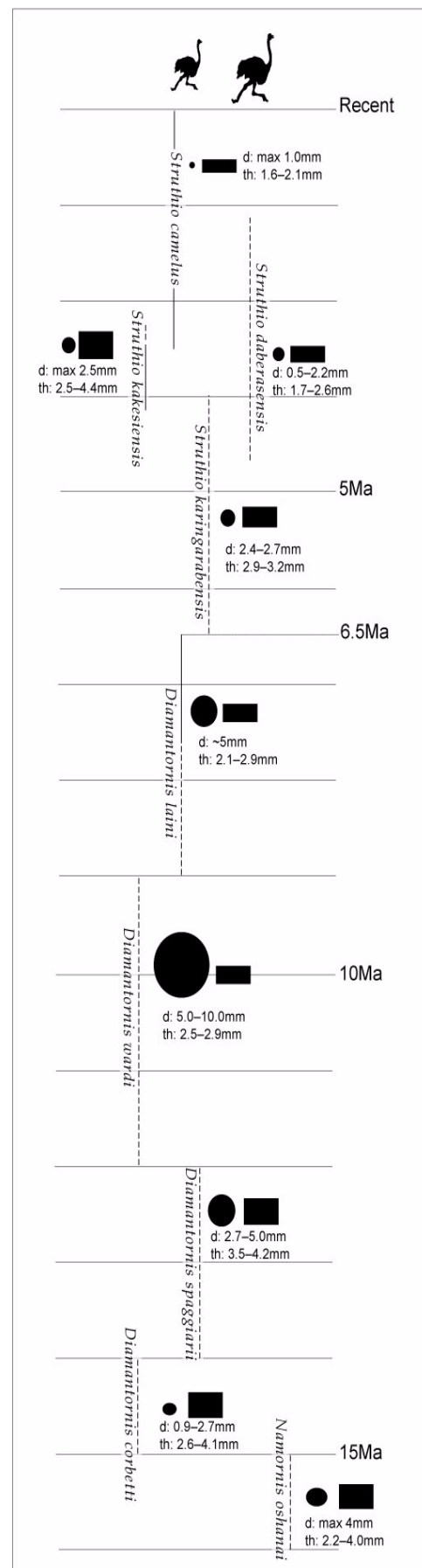
Fossil eggshell fragments of *Diamantornis laini* occur at almost all exposures of the Baynunah Formation in the UAE and in abundance relative to other faunal elements. These ratite eggshells from the Baynunah differ markedly in pore morphology and eggshell thickness from those of all modern ratites, including the genus *Struthio*. In terms of eggshell thickness, pore complex size and density, and overall morphology, the eggshell specimens conform well to the description of *Diamantornis laini* from Namibia. The Baynunah specimens exhibit an upper range of thickness exceeding that noted in the Namibian sample. Pore complex diameters range to just greater than the approximate measure in the Namibian sample. In all, the Baynunah specimens are metrically indistinguishable from specimens assigned to *Diamantornis laini*. Although the microstructure of *D. laini* has been described (Dauphin et al. 1996), no microstructural comparisons were made given the extremely characteristic macromorphology of these eggshells (cf. Stidham 2004; Harrison and Msuya 2005).

### Biostratigraphy

The occurrence of *Diamantornis* in southwestern Africa (Namibia), probably East Africa (Kenya), and now Arabia (UAE) is evidence for the existence in the latter half of the Late Miocene of at least a single form of large ratite bird distributed across this vast region. If *D. laini* dispersed to occupy its total geographic range soon after its origination and then only existed for a relatively short temporal span, then its presence would be of biostratigraphic significance. Pickford, Dauphin, and Senut described a sequence of ratite eggshells from the Neogene fossil record of Namibia that they interpreted as an anagenetic lineage spanning almost 20 million years (e.g., Senut et al. 1998). Beginning with the ootaxon *Namornis oshanai*, originally described as *Struthio oshanai*, and attributed a Pliocene age (Sauer 1966), their eggshell sequence progressed through four oospecies of *Diamantornis* and two of *Struthio* to culminate in *Struthio camelus*, the modern ostrich (Figure 3). In total, two genera and seven species were named, each characterized primarily by discrete differences in eggshell thicknesses and pore complex widths and densities, and with no two forms displaying any overlap in temporal range. These workers proposed that ratite eggshell may be of relatively precise biostratigraphic utility (Senut and Pickford 1995; Senut 2000). Harrison and Msuya (2005) reported the temporal overlap of the oospecies *Struthio* cf. *karingarabensis* and *Struthio kaesiensis* at Laetoli, both of which would overlap with the suggested age range of the oospecies *Struthio daberasensis* (Senut 2000; Stidham 2004). Further discoveries of eggshell from Miocene sites may determine that the different oospecies of *Diamantornis* also exhibited some temporal overlaps. In general, however, all the recent discoveries of fossil ratite eggshell have shown that the proposed biostratigraphic sequence of ootaxa is at least relatively accurate, even if the biochronology is imprecisely resolved.

The age range of *D. laini* from Namibia has been determined as "late middle Miocene" (Senut et al. 1994), from 11 to 8 Ma (Senut and Pickford 1995), and from 10 to 8 Ma (Pickford and Senut

**Figure 3.** (See right) Biostratigraphy and biochronology of ratite eggshells from Africa. *Diamantornis laini* is here reported from the Arabian Peninsula. Dashed lines represent tentative age ranges. d: pore diameters; th: shell thicknesses. Black circles and rectangles represent maximum pore diameter sizes and maximum shell thicknesses, respectively, at natural size. Data from Senut 2000; Harrison and Msuya 2005; Stidham 2004.



2000; Senut 2000). These estimates were based primarily on the stratigraphic occurrence of the *D. laini* material and its associated fauna. Pickford and Dauphin (1993) and Senut et al. (1994) listed *Parapedetes namaquensis* (Rodentia) and Giraffidae as the mammalian material associated with *D. laini* specimens. However, *P. namaquensis* appears to be present throughout the Namibian Miocene sequence, associated also with other, older *Diamantornis* oospecies (Senut et al. 1994), and the family Giraffidae is well known to have representatives extending as far back as the early Miocene (Churcher 1978). Thus, the biostratigraphic precision of the Namibian eggshell fossils, including *D. laini*, leaves much to be desired. Specimens of *D. cf. laini* from the Lower Nawata Member of Lothagam are dated to between 7.4 and 6.5 Ma. (Harrison and Msuya 2005). Whereas no eggshell is reported from below these levels, *D. cf. laini* is replaced above the Marker Tuff by a more derived form of *Diamantornis* (Harrison and Msuya 2005). Metrically, the Lothagam *D. cf. laini* is almost indistinguishable from Namibian *D. laini* and from the Baynunah sample. The Baynunah fauna has been biostratigraphically constrained to somewhere between 8 and 6 Ma (Whybrow and Clements 1999a). The presence of *D. laini* may suggest that the Baynunah fauna is no younger than 6.5 Ma. In a similar case, the Baynunah hippopotamid *Archaeopotamus cf. lothagamensis* (Gentry 1999; Boisserie 2005) bears affinities with the Lower Nawata *A. lothagamensis*, which occurs between 8 and 6.5 Ma (Weston 2000).

#### Paleobiogeography

The presence of *D. laini* in Arabia serves to strengthen the biogeographical affinity of this region to Africa, to the exclusion of Eurasia. Specifically, it is of interest that fossil eggshell of the Namibian *Diamantornis*–*Struthio* type has been reported from sites in Kenya, Malawi, Namibia, and Tanzania but not from other well-known sequences to the north of the continent such as from the Middle Awash in Ethiopia, the Tugen Hills, Kenya, the deposits of Chad, or from Sahabi, Libya. Boisserie (2005) has found endemic interconnections between the fossil hippopotamids at Lothagam and those from the Baynunah fauna. With the continued lack of reports of fossil eggshell of *Diamantornis* from Central and North African fossil sites, it is possible to propose a hypothesis of a strengthened faunal relationship between the Baynunah fauna and specifically those of southern East Africa and western southern Africa. Models depicting the different stages of the Red Sea's formation and the proximity of the Arabian and African portions of the

Straits of Mendeb allow for a dry route between these two regions across which terrestrial forms could have migrated throughout the Late Miocene, until at least about 6.2 Ma (Redfield et al. 2003).

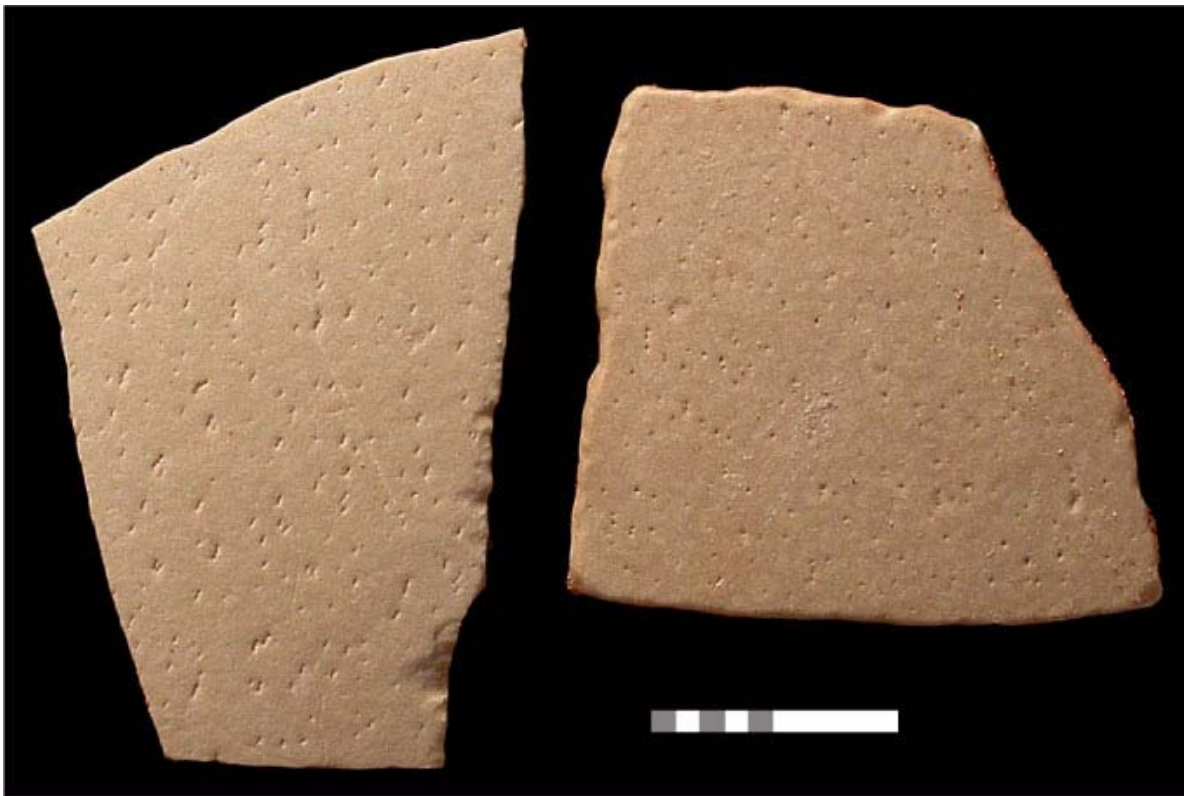
#### Paleoecology

*D. laini* is reported from arid and fluvial environments in Namibia, and fluvial sediments representing variations of wooded to open-grassy and dry habitats from Lothagam, and the UAE. As Stidham (2004) noted for *Struthio daberensis* from Malawi, the wide range of paleohabitats for these extinct ratite forms is well within what is observed for the modern ostrich, *Struthio camelus*.

#### ?AEPYORNITHIDAE

##### Aepyornithid-type Figure 4

**Diagnosis.** A form of fossil ratite eggshell characterized by pores shaped as: 1) linearly aligned long, bent, and forked grooves; 2) shorter groove or comma-shaped pores ('dagger-point'); and 3) tiny, circular to ovoid 'needle-point' or 'sting' pores (Sauer 1972). Under magnification, the long groove pore type typically appears comprised of two ovate pores connected by a superficial groove. Reported eggshell thicknesses range between 1.4 and 3.05 mm (Sauer 1972; 1976; 1978; Sauer and Sauer 1978) with individual samples displaying more conservative thickness ranges. In gross morphology, aepyornithid-type eggshell is extremely similar to eggshell of *Aepyornis*, the extinct Elephant Bird of Madagascar. Aepyornithid-type eggshell differs from that of *Aepyornis* in having generally thinner eggshell [based on measurements of *Aepyornis* of 2.88–4.30 mm given in Sauer (1972), Silyn-Roberts and Sharp (1986), and Hirsch et al. (1997), and our own observations]. Comparison with eggshell of *Mullerornis* and *Paraphysornis* was not possible. Aepyornithid-type eggshell differs from *Diamantornis* in the absence of the large (>2 mm) circular pore complexes characteristic of *Diamantornis*. Aepyornithid-type eggshells are on average slightly thinner (compared to *D. laini*) to significantly thinner (compared to *D. wardi*) than eggshells of *Diamantornis*. Aepyornithid-type eggshell differs from those of *Struthio* in the absence of pore complexes in the aepyornithid-type. It differs from *Struthio*, *Namornis*, and *Struthiolithus* (*Psammornis*) in the presence of long groove pores in aepyornithid-type eggshells, and in the characteristically linear and sub-parallel arrangement of the pores, as opposed to the more random scattering of pores and pore complexes in *Struthio* and *Namornis*. Aepyornithid-type eggshell



**Figure 4.** Two fossil eggshell fragments of aepyornithid-type, AUH 1026 (left) and AUH 1017. Note the variations in pore morphology between the two specimens. The groove pore morphologies of the fragment on the left characterize most fragments assigned to the aepyornithid-type. The circular pore morphologies of the piece on the right indicate it probably derived from one of the polar regions of the egg. Scale bar equals 1 cm total.

differs from *Incognitoolithus* known from the Eocene of North America (Hirsch et al. 1997) by the former's greater eggshell thickness and its stronger resemblance to the *Aepyornis* pore pattern (dominance of the subparallel long groove pores). Aepyornithid-type eggshells differ from those of *Rhea* primarily in their significantly greater thickness. It's worth noting that the pore morphologies of *Aepyornis*, *Rhea*, and aepyornithid-type eggshell are very similar, at least macroscopically. The similarities between eggshells of *Aepyornis*, *Rhea*, *Incognitoolithus*, and aepyornithid-type fossils that are widely dispersed in time and space suggest that the defining characteristics of these eggshells' morphology may be plesiomorphic for the Ratitae as a whole.

**Known Distribution.** Africa: Mio-Pliocene of Lanzarote, Canary Islands (Sauer 1972); Mio-Pliocene of Ouarzazate, Morocco (Sauer and Sauer 1978); Early Miocene localities of the Tsondeb Sandstone Formation, Namibia (Pickford et al. 1995); Late Miocene locality of Lothagam, Kenya (Harris and Leakey 2003); Asia: Late Miocene and Pliocene of Turkey (Sauer 1976); Late Miocene localities of the Baynunah Formation,

United Arab Emirates (this paper); and ?Pliocene Hasnot Locality, Dhok Pathan Horizon, Siwaliks, Punjab, India (Sauer 1972). We also include a ?Pliocene locality east of Bayan Zag (Shabrakh Usu), Mongolia, from which exists a collection that Sauer (1972) felt probably represents the 'Aepyornithoid' type.

**New Material.** Twenty-five eggshell fragments from the Late Miocene Baynunah Formation, Abu Dhabi Emirate, United Arab Emirates (AUH 924, 925, 927, 932, 935, 936, 938, 939, 945, 994, 1012–1026).

Localities Present: Jebel Barakah (B5–0), Hamra (H3–1 H5–0, H5–2), Shuwaihat (S2–5), Talahafa (TL1–0).

**Description.** Most of the specimens derive from a single site (TL1–0) and are relatively well preserved, exhibiting only moderate weathering. Maximal fragment length ranges between about 2 and 4.5 cm. The thickness of the 25 eggshells ranges from 1.65 to 2.29 mm with a mean thickness of 1.93 mm (standard deviation 0.16). Pore morphologies are dominated by long groove-pores in subparallel arrangement, along with shorter groove

pores, and small ovate to round pores. Some specimens exhibit a predominance of small ovate to round pores with areas of eggshell devoid of the long groove pores.

### Discussion

Here we present a new fossil sample for a type of ratite eggshell that had previously been referred to as 'Type A' or 'Aepyornithoid' type (for example, Sauer 1972). We include in our assessment of the aepyornithid-type all forms classified by Sauer and other workers as Aepyornithoid or Type A eggshell, marked particularly by its relative thickness and the presence of subparallel groove pores, and we include eggshell fragments from these same assemblages that display what Sauer termed to be Type A–Type S transitional morphologies (explained below).

Two of us (F.B. and B.P.K.) found and collected eggshell fragments from the Oligocene (Early Oligocene?) locality of Tashgain Bel, Hsanda Gol Formation and the Late Miocene locality of BUK–A, Loh Formation, Mongolia. These fragments appear to be aepyornithid-type, exhibiting an eggshell thickness of about 2.5 mm and variations of groove and circular pore morphologies. In addition, Sauer (1972) described eggshells supposedly derived from the Eocene Irdin Manha Formation, Camp Margetts near Iren Dabasu, Inner Mongolia, China. If the taxonomic attribution and the stratigraphic provenance, respectively, of these two records can be confirmed, the age of the earliest aepyornithid-type eggshell would extend into the Oligocene and Eocene. Nevertheless, Aepyornithid-type eggshell has been well documented from deposits extending from the Early Miocene to the Pliocene and is known to have occurrences from areas as far apart as Central Asia and southwestern Africa. Thus, aepyornithid-type eggshell, known cross-continually and throughout most of the Neogene, does not currently seem to be of any precise biogeographic or biostratigraphic utility. Further work on the different samples, particularly microstructural comparisons (e.g., Grellet-Tinner 2000; Zelenitsky and Modesto 2003), may help establish a taxonomic and phylogenetic framework against which a biostratigraphy may be constructed. At the moment, it is likely that more than one species of extinct ratite produced the egg type that we and other workers include within the aepyornithid-type. It is a point of great interest that aepyornithid-type eggshell is found with very little variation across such vast temporal and spatial distributions. This is in contrast to the Namibian *Namornis*–*Diamantornis*–*Struthio* egg-

shell oospecies that appear to have had relatively restricted geographical and temporal spans.

### SYSTEMATIC RELATIONSHIPS: A REVIEW

Sauer (e.g., Sauer 1972) recognized a form of fossil eggshell displaying pore morphology that he identified as struthious (Type S) in structure, specifically in that it resembled eggshells of *Struthio camelus camelus*. Other fossil eggshells displaying a similar pattern had been referred to as *Psammornis* (see in Sauer 1969) or *Struthiolithus* (see in Mikhailov 1997), and Sauer (1972:9) felt that "actually there is no need to separate these specimens from the genus *Struthio*." Sauer distinguished this struthious Type S eggshell from the aepyornithid-type (Type A) by the fact that the pore structure in Type S eggshell was dominated solely by small circular pores, with a total absence of groove-type pores. Later, in describing the eggshells from the Mio-Pliocene of Ourzazate, Morocco, Sauer and Sauer (1978) presented their discovery of fossil eggshell intermediate in pore morphology between the previously recognized Type A and Type S eggshells. This interpretation came about with the discovery at Ourzazate of eggshell fragments that exhibited areas occupied solely by singular, small round pores, along with areas occupied by the typical subparallel groove pores, and with a gradational zone in between. In fact, among the specimens from the Baynunah Formation, several pieces can be seen which capture a transition zone between an area populated purely by small circular pores to one expressing primarily the subparallel bent and forked groove pores. The eggshell fragments shown in Figure 3 have been chosen to represent these variations in pore morphology. Pore morphology is known to vary across different regions of an egg (personal observations on eggs of *Rhea* and *Aepyornis*), making it possible that Sauer's Type A and Type S morphologies, and those similar variations represented among the Baynunah aepyornithid-type specimens, simply reflect fragments from different parts of the egg (see also Sauer and Sauer 1978).

Grellet-Tinner (2000) described and coded 22 eggshell characters, most of which are based on the radial microstructure of the eggshell. His cladistic analysis indicated that aepyornithid-type eggshell (his *Struthiolithus*) shares autapomorphies with *Aepyornis*, and that both of these are sister taxa to *Struthio*. We note that the sister-relationship of Aepyornithid-type eggshell with *Aepyornis*, as based on characters of the cross-sectional microstructure, is in congruence with the gross morphology of the eggshells. Grellet-Tinner (2000) refers

Aepyornithid-type eggshell to the oogenus *Struthiolithus*. It is not clear why this is done as he does not justify a similarity between all Aepyornithid-type eggshells and all those of *Struthiolithus* (e.g., Brandt 1874; Lowe 1931; Sauer 1968; Mikhailov 1997). Although we agree with Grellet-Tinner (2000) that many samples of Aepyornithid-type and *Struthiolithus* eggshell are indistinguishable, we do not at this point feel it is justified to refer all Aepyornithid-type eggshell to *Struthiolithus*. Furthermore, it would not be advantageous to refer Aepyornithid-type eggshell to *Aepyornis* nor to ascribe a new ootaxon name to aepyornithid-type eggshell type without a comprehensive study and revision of its representative samples in relation to those of all the other ratites.

Skeletal remains from Namibia identified as *Struthio coppensi* (Mourer-Chauviré et al. 1996a) extend the age of the genus *Struthio* to the Early Miocene. Mourer-Chauviré et al. (1996a) claim that the didactyl tarsometatarsus of *Struthio coppensi* is associated with eggshells of aepyornithid-type from Namibia. If aepyornithid-type eggshells represent a non-monophyletic cluster diagnosed on the basis of primitive pore characters, then it remains possible that the Struthionidae developed their characteristic eggshell morphology from an aepyornithid-type ancestor.

Eggshells from Plio-Pleistocene deposits are generally attributed to *Struthio asiaticus*, skeletal remains of which were described by Lydekker (1884). These eggshells display a pore morphology that is reportedly indistinguishable from that of *Struthio camelus molybdophanes* (Bidwell 1910; Sauer 1968; Sahni et al. 1990). As noted by Sahni et al. (1990), the attribution of the eggshell material to *Struthio asiaticus* is a product of practicality rather than a statement of phylogenetic affinity. Other fossil ratite eggshell have been included in the following taxa or ootaxa: *Struthio pannonicus* (includes skeletal remains, Kretzoi 1954); *Struthiolithus chersonensis* (Brandt 1873, 1874); *Struthio asiaticus* (includes skeletal remains, Milne-Edwards 1871); *Struthio wimani* (founded on skeletal remains, Lowe 1931); *Struthio anderssoni* (Lowe 1931); *Struthio mongolicus* (Lowe 1931). See Sauer (1968) for a review of these forms. The validity and systematic relationships of these and other ratite ootaxa are in need of study.

Fossil skeletal remains of ratites have been discovered and described (Lowe 1931, 1933; Kretzoi 1954; Kurochkin and Lungu 1970; Mourer-Chauviré et al. 1996a, 1996b) although it still remains to coherently synthesize all the available evidence and revise the different conflicting evolutionary hypotheses established on the basis of

these remains. Further comparative work, particularly cladistic work including both eggshell and skeletal material, should illuminate the evolutionary history of the Ratitae.

## CONCLUSION

Field work targeting the Late Miocene Baynunah Formation deposits of Abu Dhabi, UAE, has resulted in the recovery of two types of fossil ratite eggshell. These are described here as *Diamantornis laini* and an unnamed aepyornithid-type eggshell. *D. laini* is a well-diagnosed ootaxon that has been reported only from eastern and southern African sites. The age of *D. laini* from the Baynunah may be correlated to that from the Lower Nawata Member at Lothagam, dated at 7.4–6.5 Ma (Harrison and Msuya 2005). Such an age accords with previous biostratigraphic estimates of the Baynunah fossil fauna. The discovery of fossilized eggshells attributable to *Diamantornis laini* in the Late Miocene Baynunah Formation of the UAE serves to: 1) provide an additional biostratigraphic index fossil for estimating the age of the Baynunah fauna; and 2) further strengthen the paleobiogeographic affinities of the fossil Arabian biota with that of Africa, to the exclusion of Europe and Asia, during this time. Further discovery and study of remains of *D. laini* from radiometrically dated sites in Africa should refine the temporal range of this ootaxon, allowing for more precise statements of biostratigraphy founded on its occurrence in paleofaunas.

The aepyornithid-type eggshell is known from Africa and Asia and spans at least the entire Neogene, certainly in Africa and most likely in Asia. Its pore morphology is exceedingly similar to that of the Malagasy elephant bird *Aepyornis*, although these similarities may be a product of characters plesiomorphic for the Ratitae.

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