New Ratite Eggshells from the Miocene of Namibia

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Namibian Neogene deposits have yielded a remarkably comprehensive register of fossil ratite eggshells spanning the entire Miocene and Plio-Pleistocene. Previous studies recognised three genera of struthious egg types, from oldest to youngest named *Namornis* (1 species) *Diamantornis* (4 species) and *Struthio* (3 species) and one of aepyornithoid type, older than the struthious ones, hitherto left undetermined on account of the relatively poor preservation of the available material.

A palaeontological and geological survey carried out in November, 2010, in the Tsondab Valley and the Tsondab Flats to the west of the end point of the valley, led to the discovery of good samples of two hitherto unrecognised extinct taxa of eggs, one aepyornithoid, and the other, struthionid, from overlying strata. Neither of the samples fits into the previously established taxonomic schema, indicating that we are in the presence of undescribed taxa. We here analyse the eggshells and discuss their systematic and phylogenetic implications. A small, primitive pedetid tooth, found with the aepyornithoid shells, indicates an Early Miocene age for the deposits. This estimate is supported by comparing the new eggs with the established eggshell biochronology of Namibia, itself calibrated by mammalian biostratigraphy.

Keywords: Early Miocene, Namibia, Aeolianite, Ratite, Eggshell, Biostratigraphy

Introduction

Fossil ratite eggshells from the Neogene of Namibia are useful biochronological and palaeoclimatic resources (Dauphin *et al*., 1996, 1998; Pickford & Dauphin, 1993; Pickford & Senut, 1999; Pickford *et al*., 1993, 1995; Ségalen *et al*., 2002, 2004a, 2004b, 2006a, 2006b; Senut & Pickford, 1995; Senut *et al*., 1995, 1998, 2009). Work by other researchers has extended the Namib eggshell biochronology to other countries, notably Malawi (Stidham, 2004), Tanzania (Harrison & Msuya, 2005), Kenya (Harris & Leakey, 2003), and the Arabian Peninsula (Bibi *et al*., 2006), in cases providing refinement of the initial age estimates.

Previous studies of the Namibian eggs left several questions unanswered. In particular the aepyornithoid type of shell was left undetermined, mainly because of the relatively undiagnostic nature of the available material (Senut *et al*., 1995). It was noted that specimens from Elim attributed to *Namornis oshanai*, were appreciably thinner than material from the type locality, Beisebvlakte, Etosha, Namibia, and other fossils from Rooilepel and Awasib. However, given that the Elim fossils came from only two localities it could not be ruled out that the specimens represented particularly thin examples of *N. oshanai* (Pickford *et al*., 1995).

We are now in a position to address the above uncertainties, due to the collection of good samples of two types of eggshells in the Tsondab Vlei and the Tsondab Flats which lie from 3 to 35 km west of the end point of the Tsondab Valley. At Tsondab Vlei, it has now been established that the aepyornithoid eggs come from stratigraphic levels beneath those that yield eggs of *Namornis* (Fig. 1-3). It is confirmed that the Tsondab aepyornithoid eggs are thicker than those from the Sperrgebiet, whereas eggs from the northern part of the Namib-Naukluft Park previously attributed to *Namornis oshanai* are uniformly thinner than those from the type locality at Etosha and sites in the Sperrgebiet and the southern half of the Namib-Naukluft Park (Fig. 8).

The aim of this report is to describe and analyse the new samples of fossil eggs from Tsondab within the context of previous studies on Namibian ratite eggshells and to refine the biostratigraphy of the Tsondab Sandstone Formation which yielded them.

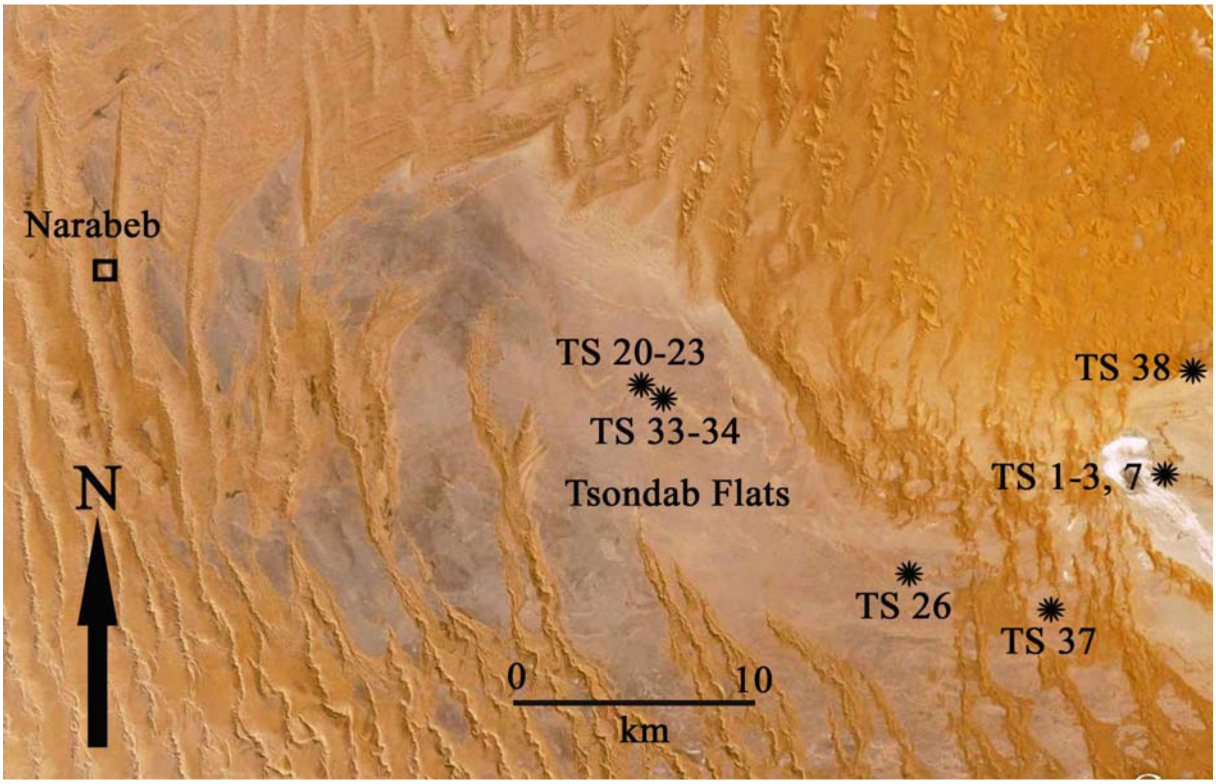

Figure 1: Fossil eggshell localities in the Tsondab Flats and near the end point of the Tsondab Valley, Namib-Naukluft Park, Namibia. TS 7 is the type locality of *Tsondabornis psammoides*, gen. et sp. nov., and of the Tsondab Formation (image modified from Google Earth).

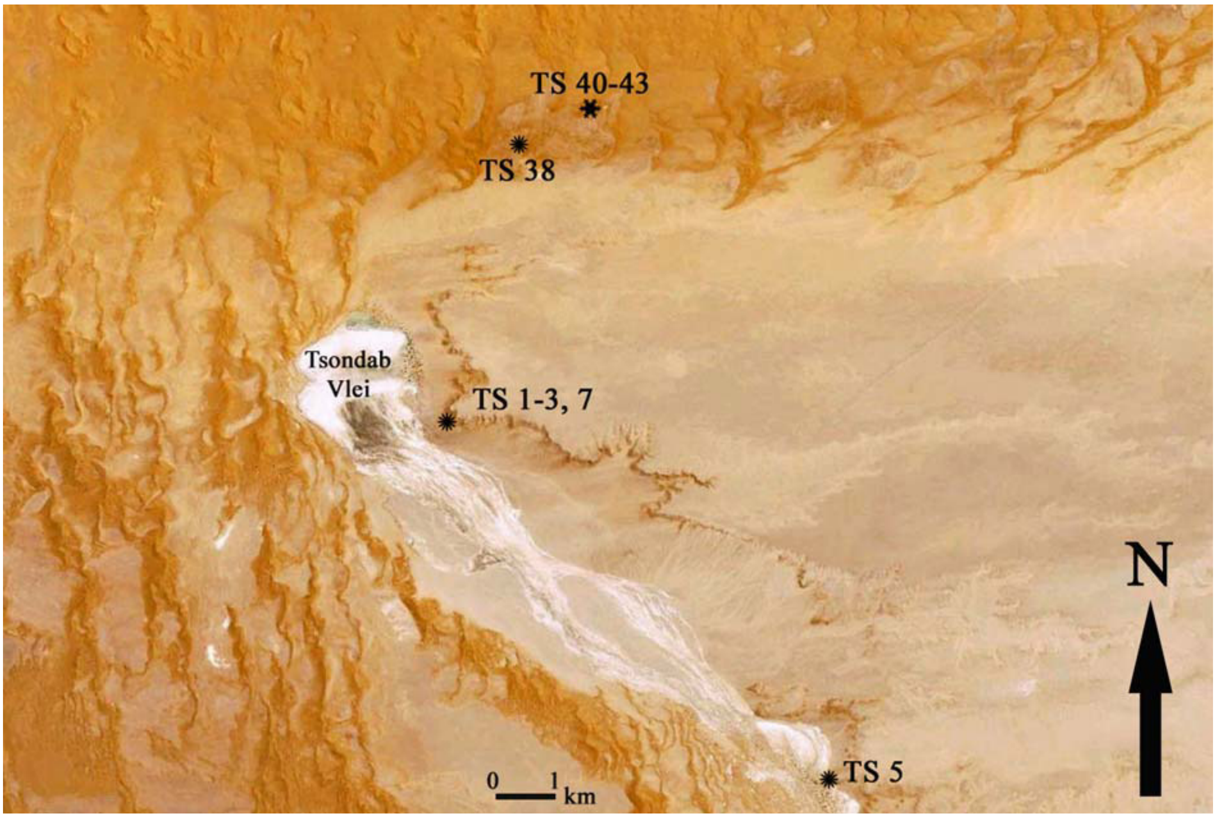

Figure 2: Fossil eggshell localities in the lower reaches of the Tsondab Vlei, Namib-Naukluft Park, Namibia. Localities TS 1-3, 5, 7 and 38 yield eggshells of *Tsondabornis psammoides*, whereas the younger localities TS 40-43, yield eggshells of *Namornis elimensis* (image modified from Google Earth).

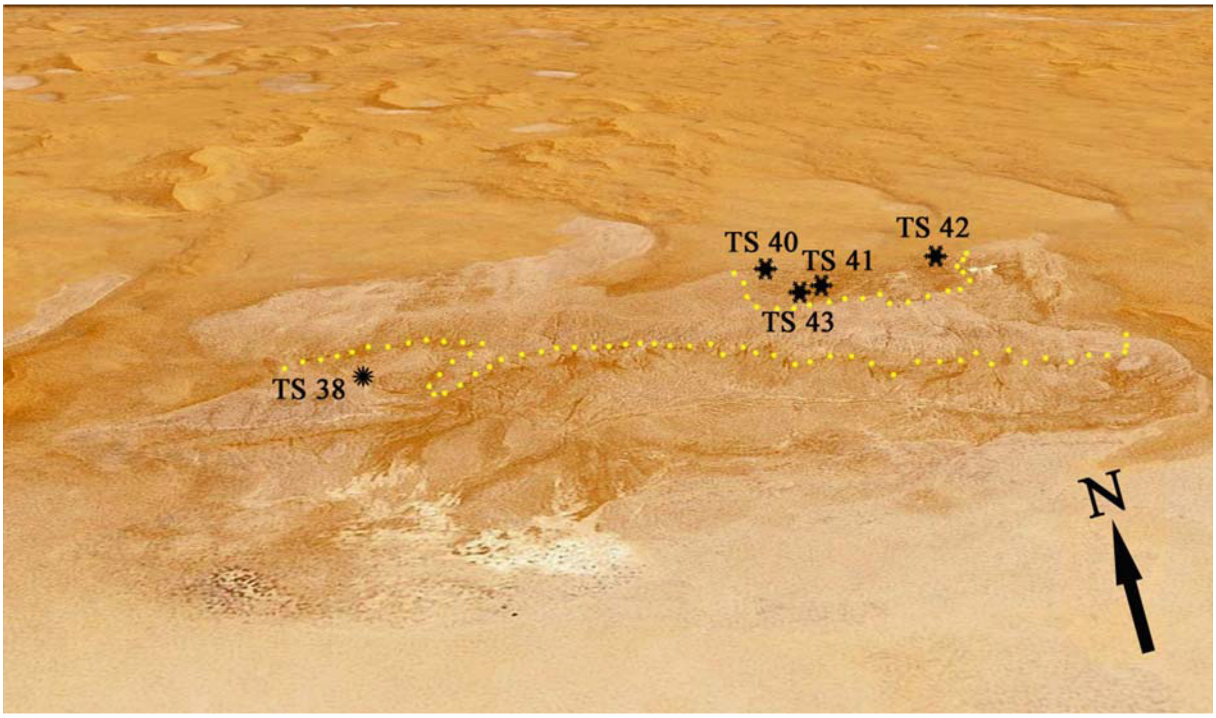

Figure 3: Ratite eggshell localities on the north flank of Tsondab Vlei. Super-bounding surfaces have been highlighted by dotted lines. TS 38 yielded *Tsondabornis psammoides* eggshells, whereas the younger sites TS 40-43 yielded only eggshells of *Namornis elimensis*. Oblique view from the south, extracted from Google Earth - the distance between TS 38 and TS 43 is ca 1 km. Note the Sossus Sand Sea in the background reposing unconformably on the Tsondab Sandstone.

Geological and stratigraphic context

The geology of the northern part of the Namib-Naukluft Park relevant to understanding the Cenozoic deposits, has been studied by numerous researchers (Besler, 1996; Besler & Marker, 1979; Heine, 1985; Lancaster, 1983, 1984a, 1984b; Lancaster & Teller, 1988; Lancaster *et al*., 1984; Marker, 1977, 1979, 1980-81; Pickford & Senut, 1999; Rust & Wienecke, 1980; Seely & Mitchell, 1986; Selby *et al*, 1979; Teller & Lancaster, 1986, 1987; Teller *et al*., 1990; Walter, 1986; Ward, 1987a, 1987b, 1988). In brief, overlying the Namib Unconformity Surface (NUS of Ward, 1987a) is a thick and varied sequence of sands and related deposits attributed to the Tsondab Sandstone Formation which accumulated under arid to hyper-arid palaeoclimatic conditions, with intercalated deposits indicative of periods of sub-humid conditions. Overlying the Tsondab Formation there is the Karpfenkliff Conglomerate which is usually cemented by the Kamberg Calcrete. Incision of the Kuiseb and neighbouring rivers to the north and to the south into their current channels followed the formation of the Kamberg Calcrete. In these valleys there occurs a suite of fluvial deposits ranging from conglomerates to silts dating from the Pleistocene and Recent (Ward, 1987a). Finally, younger than all other deposits are the mobile sands of the Sossus Sand Sea underlain by loose gravel and granule lags.

The fossil eggshells described in this report come from the Mio-Pliocene Tsondab Sandstone Formation. All the eggshells derive from the aeolian facies of the Tsondab Formation, the other facies (fluvial, lacustrine) being poorly fossiliferous. Fossil and sub-fossil eggs of *Struthio camelus* were found but are not included in this analysis.

The Tsondab Vlei and Tsondab Flats to the west comprise a topographically varied landscape consisting of various granule or gravel covered "terraces" cut into extensive aeolianite deposits of Tertiary age (Marker, 1977, 1979, 1980-81), overlain by loose sands of the Sossus Sand Sea. The

Locality	Co-ordinates WGS 84	Altitude	Taxon
TS 01	23°55’20.4”S : 15°23’00.9”E	641 m	*Tsondabornis psammoides*
TS 02	23°55’19.3”S : 15°23’03.0”E	648 m	*Tsondabornis psammoides*
TS 03	23°55’22.0”S : 15°23’07.8”E	670 m	*Tsondabornis psammoides*
TS 05	23°59’01.5”S : 15°26’44.3”E	672 m	*Tsondabornis psammoides*
TS 06	23°58’16.8”S : 15°26’38.3”E	691 m	*Struthio camelus*
TS 07	23°55’19.0”S : 15°23’09.7”E	694 m	*Tsondabornis psammoides*
TS 10	23°57’36.1”S : 15°20’32.9”E	622 m	*Struthio camelus*
TS 20	23°52’36.0”S : 15°10’12.3”E	542 m	*Tsondabornis psammoides*
TS 21	23°52’43.5”S : 15°10’03.5”E	549 m	*Tsondabornis psammoides*
TS 22	23°52’42.8”S : 15°10’02.9”E	546 m	*Tsondabornis psammoides*
TS 23	23°52’37.2”S : 15°10’09.5”E	543 m	*Tsondabornis psammoides*
TS 28	23°57’19.0”S : 15°16’31.9”E	600 m	*Tsondabornis psammoides*
TS 33	23°52’59.2”S : 15°11’10.6”E	565 m	*Tsondabornis psammoides*
TS 34	23°52’56.5”S : 15°11’09.0”E	556 m	*Tsondabornis psammoides*
TS 37	23°58’01.5”S : 15°20’12.0”E	622 m	*Tsondabornis psammoides*
TS 38	23°52’40.9”S : 15°24’02.4”E	686 m	*Tsondabornis psammoides*
TS 40	23°52’25.3”S : 15°24’37.5”E	720 m	*Namornis elimensis*
TS 41	23°52’29.8”S : 15°24’40.9”E	716 m	*Namornis elimensis*
TS 42	23°52’24.9”S : 15°24’53.4”E	720 m	*Namornis elimensis*
TS 43	23°52’31.3”S : 15°24’58.6”E	711 m	*Namornis elimensis*
Gamsberg Pass (Paradys)	23°21’02.3”S : 15°54’00.5”E	1025 m	*Tsondabornis psammoides*
Elim	24°24’45.7”S : 15°45’07.0”E	900 m	*Namornis elimensis*
Diep Rivier Cliffs	24°07’56”S : 15°53’44”E	1075 m	*Namornis elimensis*
Zebra Hill, Kamberg	23°37’40”S : 15°38’43”E	828 m	*Tsondabornis psammoides*
Tsauchab	24°30’14.0”S : 15°43’02.1”E	772 m	*Diamantornis laini*
North of Sesriem Airstrip	24°28’59”S : 15°44’21”E	784 m	*Diamantornis wardi*
Tsondab South	24°00’47”S : 15°29’24”E	723 m	*Diamantornis wardi*
Narabeb	23°49’12.4”S : 14°57’11.8”E	414 m	*Diamantornis wardi*
Narabeb	23°49’12.4”S : 14°57’11.8”E	414 m	*Tsondabornis psammoides*
West Pan	23°34’10.1”S : 14°48’31.6”E	309 m	*Diamantornis corbetti*

Table 1: Fossil eggshell localities mapped during the 2010 field season in the Tsondab region (TS) and previously known localities in the northern part of the Namib-Naukluft Park, Namibia.

most extensive of the “terraces” is the conglomeratic Kamberg Calcrete (Ward, 1987a), a duricrust that varies in character depending on its distance from the Great Escarpment (Fig. 4). Proximal to the scarp it contains large boulders and cobbles and is up to 30-40 metres thick in places close to valleys, thinning in the interfluves (Pickford & Senut, 1999). The calcrete thins westwards away from the scarp and its clastic content becomes finer grained. At the current end point of the Tsondab Vlei, the calcrete is about 1 metre thick with cobbles up to 5 cm in diameter. 25 km further west the duricrust directly overlies indurated white silts and its clastic component is sand-sized to silt-sized. Here the duricrust is only 2-5 cm thick and it eventually pinches out completely about 40 km west of Tsondab Vlei. In its proximal parts the Kamberg Calcrete is of pedogenic facies (Yaalon & Ward, 1982) but at its western edges where it is only a few cm thick it was formed at the surface during many cycles of condensation and evaporation of dew. The Kamberg Calcrete is a composite unit, but is useful as a geomorphological marker level, as it provides evidence for a widespread, stabilised, almost planar landscape prior to a phase of deep incision, comprising the Kuiseb, Tsondab, Tsauchab and other rivers that currently drain the Great Escarpment.

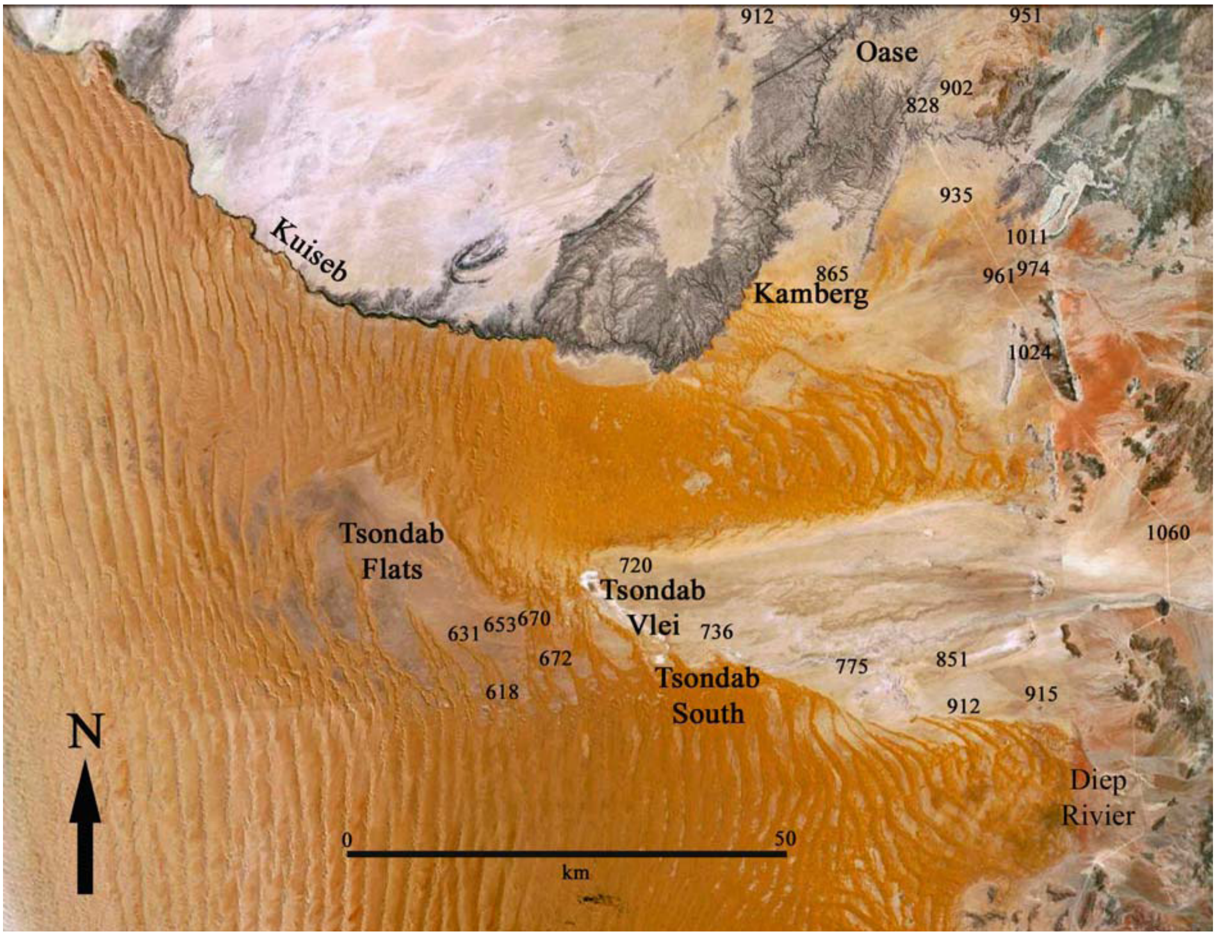

Figure 4: Spot heights (in metres) on calcrete in the northern part of the Namib-Naukluft Park and neighbouring farms. Note the decrease in altitude from the Great Escarpment in the east with spot heights of over 1000 m, decreasing to altitudes of just over 600 metres 80 km to the southwest. At Tsondab South and Elim (see fig. 11), these calcretes contain Pleistocene fossils and stone tools (image modified from Google Earth).

In detail, the Kamberg Calcrete has an undulating surface, draping down into shallow valleys and gullies and up the other side. In its proximal parts, close to the Great Escarpment, it formed under a thin (generally less than 50 cm) vegetated sand cover (grassy plains for the most part), but over much of its present extent it is exposed at the surface and is in the process of being dissolved by rainwater and especially by dew. Cobbles of carbonate rocks (limestone, dolomite, calcrete) often show a runnelled surface which is formed by dew condensing on exposed surfaces of the rocks and trickling down their sides to the ground. Repeated many times, such dew produces a surface that is patterned by runnels dissolved into the surface of the rock. The same happens to fossil eggshells that are exposed for extended periods.

After a long phase of landscape stability (Ward, 1987a, estimated the duration to be about 0.5 million years, but it could have been much shorter than this, perhaps as little as 40,000 years (Leeder, 1975)) fluvial incision started, culminating in the present day drainage network of the region. In the Tsondab Valley, Marker (1979) recognised seven terraces resulting from various phases of incision. Later workers tended to recognise fewer terraces. Nevertheless there are at least three widespread “terraces”, not only in the Tsondab Valley, but also close to the base of the Great Escarpment, where at least three flights of calcreted terraces have been noted (Pickford & Senut, 1999).

The importance of this geomorphological development for understanding the palaeontology of the region is that post-Kamberg incision cut into the Tsondab Sandstone Formation, thereby exposing different layers from which fossils may be collected. It should be noted that at Diep Rivier, there are impressive cliffs of sandstone (summit at ca 1000 m) which stand proud of the Kamberg Calcrete horizon, and which, at the time of calcrete genesis, comprised bornhardts rising a 80-90 metres above the generally planar Kamberg Plains (altitude in the vicinity ca 915 m (Fig. 4).

The fossils collected by the Namibia Palaeontology Expedition reveal that sedimentation patterns in the Tsondab Formation were complex, with wind driven cut and fill on large and small scales. Super-bounding surfaces are common in the Tsondab region, as are the usual smaller scale dune cross-cutting features. Nevertheless, outcrops are sufficiently informative that the sequence of fossil horizons can in most cases be established by superpositional criteria. By this means we can be sure that the eggs of *Tsondabornis* are older than those attributed to *Namornis* (Fig. 3) which are in their turn older than those of *Diamantornis* and finally those of *Struthio*.

Systematic descriptions

Family Struthionidae Vigors, 1825
Genus *Tsondabornis* nov.

Diagnosis - Eggshells with smooth to lightly undulating external surface, pores arranged in sub-parallel slits and dagger point depressions.

Differential diagnosis - *Tsondabornis* differs from *Namornis*, *Diamantornis* and *Struthio* by possessing pores arranged in sub-parallel slits and dagger point depressions, and not in clumps or clusters. Its outer shell surface is smooth to slightly undulating, which differentiates it from other aepyornithoids and the above taxa. *Tsondabornis* differs from *Psammornis* by its thinner shells and its slit-like pore structures.

Derivatio nominis - The genus name refers to the *Tsondab* area where the material was collected and *ornis*, Greek for bird.

Synonymy - Pending the discovery of diagnostic specimens, in previous literature these Namibian eggs were referred to "aepyornithoid".

Type species - *Tsondabornis psammoides* sp. nov.

Species *Tsondabornis psammoides* nov.

Diagnosis - Eggshells ranging in thickness from 1.5 to 2.2 mm, mode 1.8 mm, some fragments showing incipient vermiform or undulating sculpture of the outer shell surface.

Derivatio nominis - The species name *psammoides* refers to the fact that all the specimens were found in sandstone.

Holotype - TS 7, eggshell fragment associated with dozens of other fragments many of which are *in situ* in the Tsondab Sandstone.

Type locality and age - TS 7, Tsondab Sandstone Formation (type area of the formation) ca 18 Ma.

Material - Numerous eggshell fragments (see Table 1 for complete list of localities).

Description - The eggshells of *Tsondabornis psammoides* generally possess a smooth to slightly undulating outer surface, in which the pores are usually subtle, best viewed in slanting light with a low power lens (4x – 10x). Some specimens have more obvious slits arranged in a sub-parallel pattern, with scattered dagger point depressions scattered here and there.

The eggs attributed to *Tsondabornis psammoides* range in thickness from 1.3 to 2.3 mm, discounting obviously eroded specimens (Fig. 6D, 6E). The mode varies from 1.8 to 2 mm in the different samples.

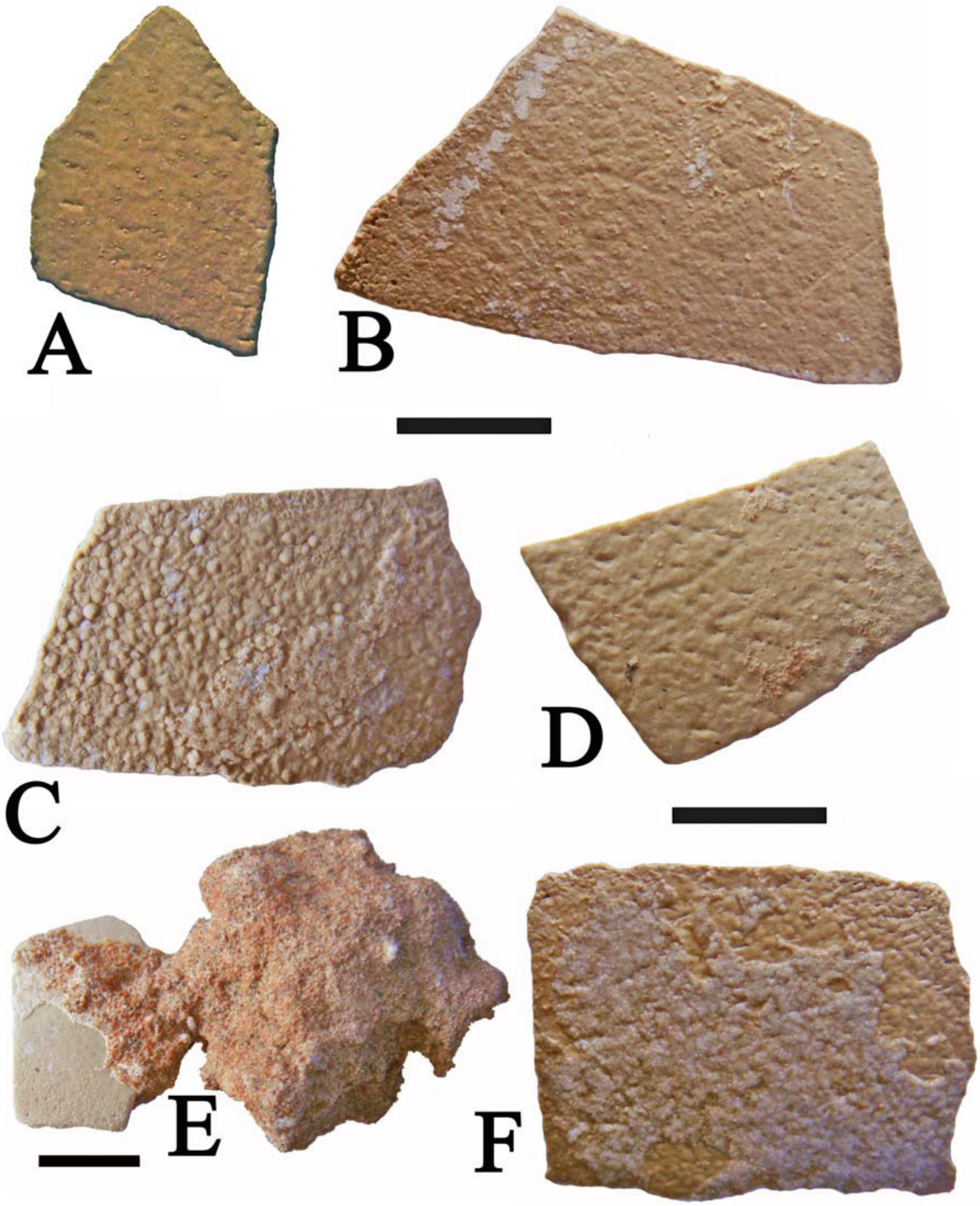

Figure 5: Eggshell fragments of *Tsondabornis psammoides* gen. et sp. nov. from the type locality, TS 7, Tsondab Cliffs, Namib-Naukluft Park. A) holotype showing sub-parallel slits and a few dagger point pits, B) a particularly smooth example in which it is difficult to make out the pores, C) example in which the outer surface either did not form, or has been removed by erosion, exposing the external part of the mammillary layer, D) specimen with sub-parallel slits, dagger point pits and a slightly undulating external shell surface, E) egg-

There were about 200 pores per 4 cm² counted on one specimen which possessed many pores. Some fragments appear to have fewer pores, which could be due either to variability of pore density over the egg, a well known variation in extant ostriches (Sauer, 1966) or to variation between eggs. It is also probable that some pores are so small that they are easily missed during counting.

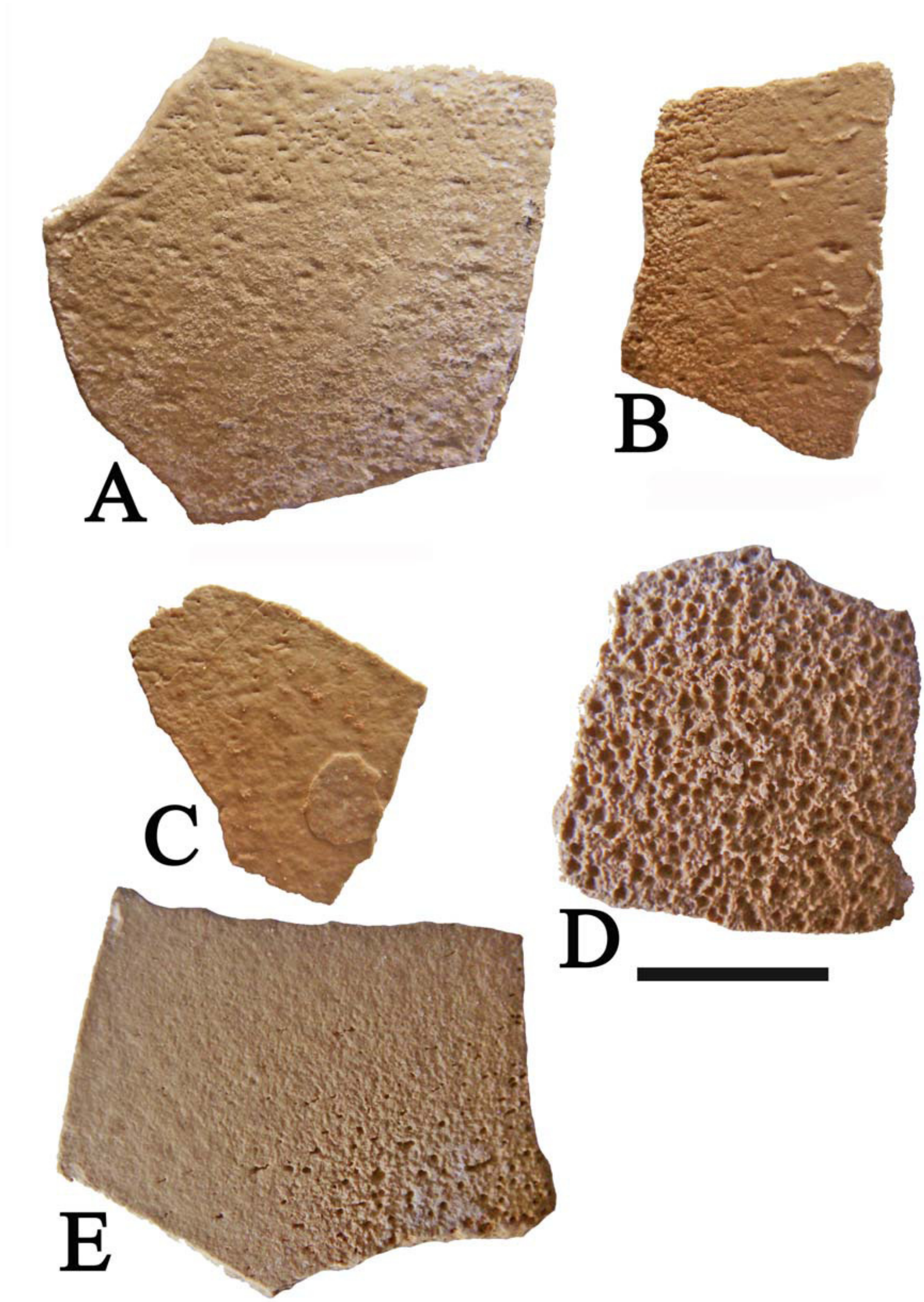

Figure 6: Eggshell fragments of *Tsondabornis psammoides* gen. et sp. nov. from the type locality TS 7, Tsondab Cliffs in the northern part of the Namib-Naukluft Park, Namibia. A) specimen showing sub-parallel slits and dagger point pores, B) specimen with some slits running into each other, C) a specimen with slightly undulating surface with slits and dagger point pore complexes, D) eroded specimen in which the outer layer has been completely removed, exposing the inner parts of the mammillary layer, E) a specimen in which a gradient of erosion exposes deeper and deeper parts of the external surface of the eggshell. Note how the slits are more easily observed in the eroded part than in the fresh part of the shell (scale – 10 mm).

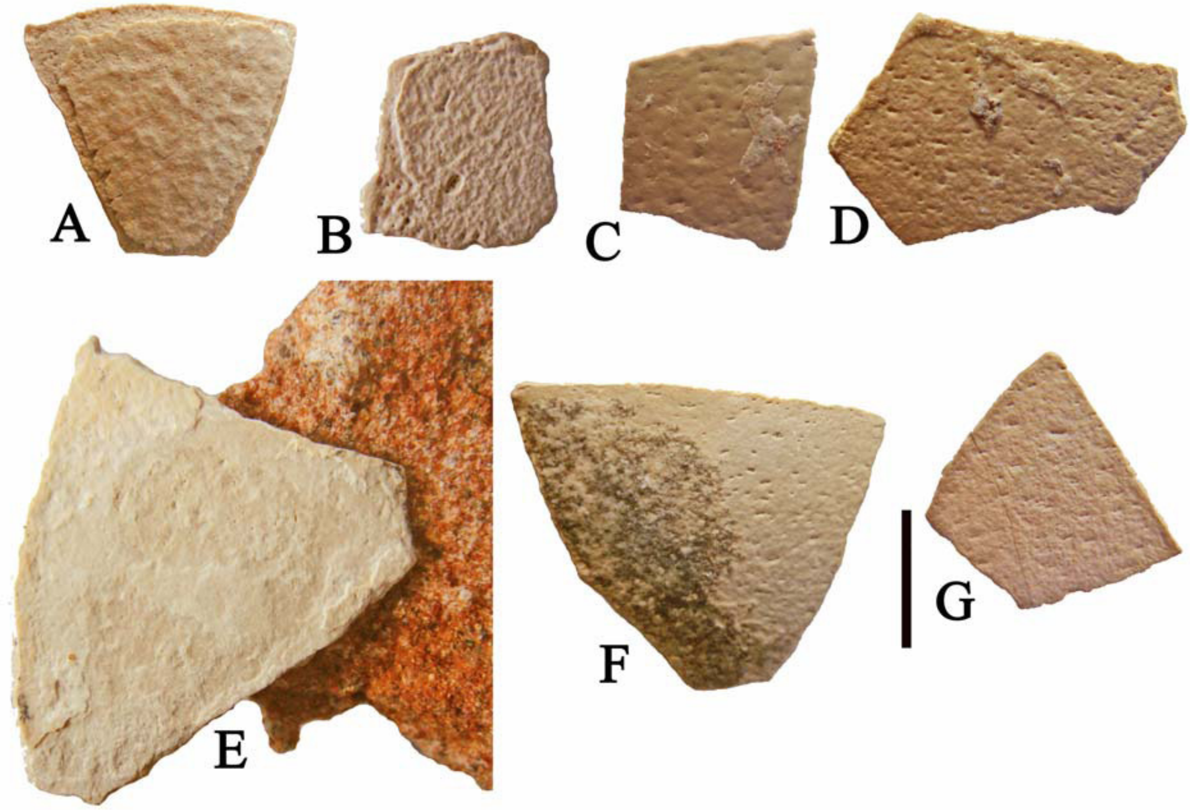

Figure 7:*Tsondabornis psammoides* eggshell fragments from various localities in the Tsondab Vlei and Tsondab Flats, Namib-Naukluft Park, Namibia. A) TS 20, B) TS 22, C) TS 28, D) TS 33, E) TS 23, specimen

Discussion - *Tsondabornis psammoides* eggshells occur widely in the northern part of the Namib-Naukluft Park, but are seldom common save at Zebra Hill. They occur in dark red aeolianites which have been pervasively affected by bioturbation, mostly plant root systems, but also hives (*Namajenga mwichwa* Pickford, 2008a) and foraging tunnels of the termites *Hodotermes* and more rarely *Psammotermes* (Seely & Mitchell, 1986). The same levels of sandstone often yield clumps of white nodules, resembling coprolites, although the true nature of the nodules remains to be determined. In several places, fossil roof webs of the buck-spoor spider, *Seothyra* were found (Pickford, 2000).

The combination of the trace fossils, red colouration of the sands and the widespread outcrops of the Oase Member (fluvial facies of the Tsondab Formation) suggests that the palaeoenvironment at the time of deposition was one of summer rainfall with a semi-arid to arid palaeoclimate.

Species *Tsondabornis minor* nov.

Diagnosis - Eggshells ranging in thickness from 1.0 to1.7 mm, mode 1.3 mm, external surface of eggs generally smooth, without undulating or vermiform sculpture.

Derivatio nominis - The species name *minor* refers to the fact that all the specimens of eggs are appreciably thinner than those of the type species, implying a smaller species.

Holotype - EF 95'01, eggshell fragment.

Type locality and age.- Elisabethfeld, Sperrgebiet, Namibia, Early Miocene ca 21 Ma on the basis of mammalian biochronology.

Other localities - Grillental, Langental, Fiskus

Description - The eggshells of *Tsondabornis minor* are usually smooth with little or no sign of undulations, save in wind-eroded specimens or material in which the shell surface has been dissolved by dew. Pores are arranged in sub-parallel slits with dagger point pits scattered here and there.

Shell thickness ranges from 1.0 to 1.7 mm, the mode ranging from 1.2 to 1.5 mm at different localities. In the holotype specimen there are about 100 pores per 4 cm², but other specimens have fewer, reflecting within-egg and between-egg variation.

Discussion - The fossil eggshells from the fluvio-paludal deposits of the Sperrgebiet were previously attributed to an unidentified bird species with "aepyornithoid" egg morphology. Elisabethfeld has yielded bones of a diminutive ostrich (*Struthio coppensi*) (Mourer-Chauviré *et al.*, 1996a, 1996b) which could well be the bird responsible for the eggs (they are compatible in dimensions).

The fact that eggshells of *Tsondabornis minor* are common at all four localities in the Northern Sperrgebiet, suggests that the species was well adapted to the palaeoenvironment, which was sub-humid to semi-arid with indications of both summer and winter rainfall. The terrestrial gastropods *Trigonephrus* and *Dorcasia* are common in deposits at Grillental and Elisabethfeld (Pickford, 2008b) as are hives of the harvester termite *Hodotermes*. The mammalian fauna, frogs and tortoises also indicate that the fluvio-paludal deposits of the northern Sperrgebiet accumulated under sub-humid to semi-arid palaeoclimatic conditions close to a winter rainfall zone or within the belt that experienced both winter and summer rainfall.

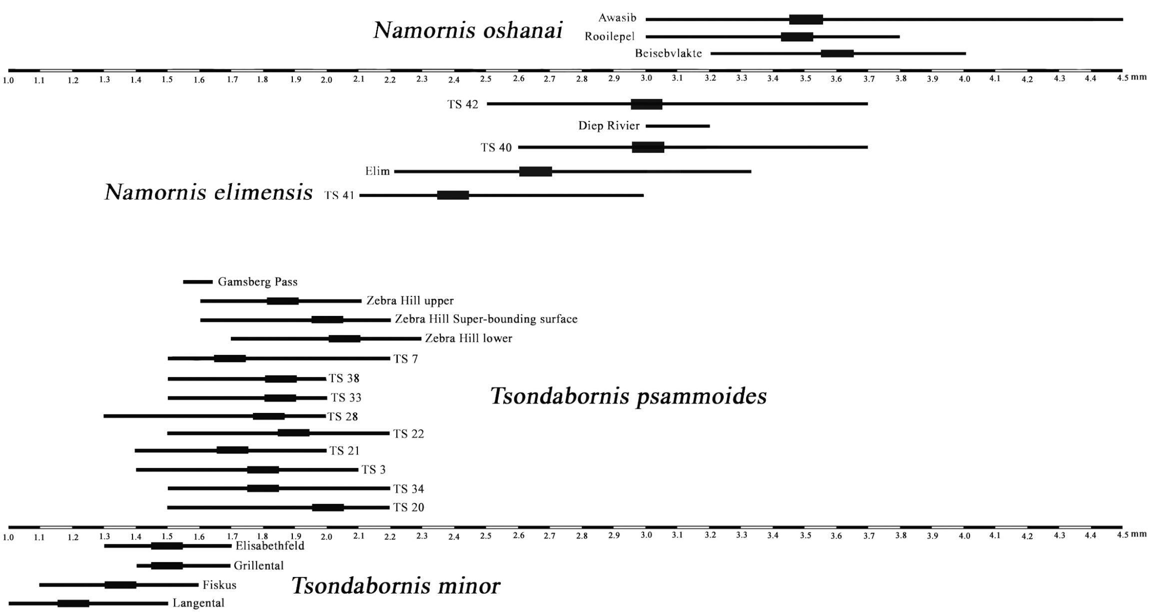

Figure 8: Shell thickness of Early and basal Middle Miocene ratite eggs from Namibia. The thin bar represents the range of variation; the thick bar is the mode.

Genus *Namornis* Pickford, Senut & Dauphin, 1994

Species *Namornis elimensis* nov.

Diagnosis - Eggshells ranging in thickness from 2.5 to3.7 mm, mean 3.2 mm which is less than the type species, *Namornis oshanai*, from Beisebvlakte, Etosha, Namibia (range 3.2 to 4.0 mm, mean 3.6 mm). Pores arranged both in clusters in the depths of vermiform depressions and in sub-parallel slits (like those of aepyornithoids).

Derivatio nominis - The species name refers to the *Elim* Gullies north of Sossus Vlei,

Figure 9: Eggshell (holotype) of *Tsondabornis minor* from Elisabethfeld, Sperrgebiet, Namibia (view of external surface showing sub-parallel slits and dagger point pores (scale - 10 mm).

eroded into the Tsondab Sandstone, where the type series was collected.

Holotype - Eggshell fragment from Elim housed at the Geological Museum, Geological Survey of Namibia, Windhoek (Fig. 10C).

Type locality and age - Elim Gullies, Tsondab Sandstone, ca 17-16.5 Ma.

Description - The external surface of the eggshells of *Namornis elimensis* is patterned by a complex undulating system of depressions and pore complexes (Pickford *et al*., 1995). In addition in some shells there are parts of the surface in which there are slit-like depressions arranged in sub-parallel fashion, recalling the situation in eggs of *Tsondabornis psammoides* but with swollen slit edges.

Eggshells of *Namornis elimensis* range in thickness from 2.1 to 3.7 mm, with modes ranging from 2.4 to 3.0 mm at different localities, thinner than the eggs attributed to *Namornis oshanai* from the Sperrgebiet (range 3.4 to 4.5, mode ranging from 3.5 to 3.6) and Beisebvlakte (range 3.2 to 4.0 mm, mode 3.6 mm).

In *Namornis elimensis* from Tsondab Vlei there are about 40 pore complexes per 4 cm^2. The Elim and Diep Rivier sample were reported to have 24-37 pore complexes per 4 cm^2 (Pickford *et al*., 1995). *Namornis oshanai* possesses between 16 and 44 pore complexes per 4 cm^2 (Sauer, 1966).

Discussion - When fossil eggshells of this species were known from only a single site, it was not clear whether their diminutive thickness should be interpreted as a species character or as a case of a particularly thin egg of *Namornis oshanai*. Now that the same thin egg type has been found at six localities in the northern half of the Namib-Naukluft Park, whereas none of the thicker eggshells of *Namornis oshanai* have been found there (they occur at Awasib in the southern part of the Namib-Naukluft Park and in the Sperrgebiet (Fig. 8)) then it is clear that the eggs from the northern part of the NNP belong to a separate species, here named *Namornis elimensis*.

A striking feature of the eggshells of *Namornis elimensis* is that the pores are arranged not only in clusters in the depths of vermiform depressions, but many of them also occur in sub-parallel slits, as in aepyornithoids. This combination of pore arrangement suggests that the *Namornis* eggshell type evolved from the *Tsondabornis* type, in which the pores are mostly in sub-parallel slits and dagger point depressions. Although the outer surfaces of most of the eggshells of *Tsondabornis* are smooth, there are specimens in which the surface is undulating with shallow vermiform depressions. We interpret these undulations to be precursors of the deeper, better expressed vermiform depressions that occur in eggshells of *Namornis*. If so, then *Tsondabornis* is likely the ancestral group from which *Namornis* evolved.

A strange feature of the eggs of *Namornis elimensis* is that they appear to occur as singletons, or at most in pairs. As a result, the eggs are found in small patches of shell fragments, and not in immense concentrations of broken eggshells such as typify nests of *Diamantornis* and *Struthio*. For this reason, the eggs of *N. elimensis* are more difficult to locate than those of the other genera. It is still unclear whether the pattern of occurrence is due to the fact that the species was laying small clutches of eggs (K-strategy reproduction) or whether the eggs found were "scatter" eggs, much as extant *Struthio camelus* occasionally lays an egg far from the nest, and immediately abandons it. Further field research is required to determine whether the pattern repeats itself at all of the occurrences or not.

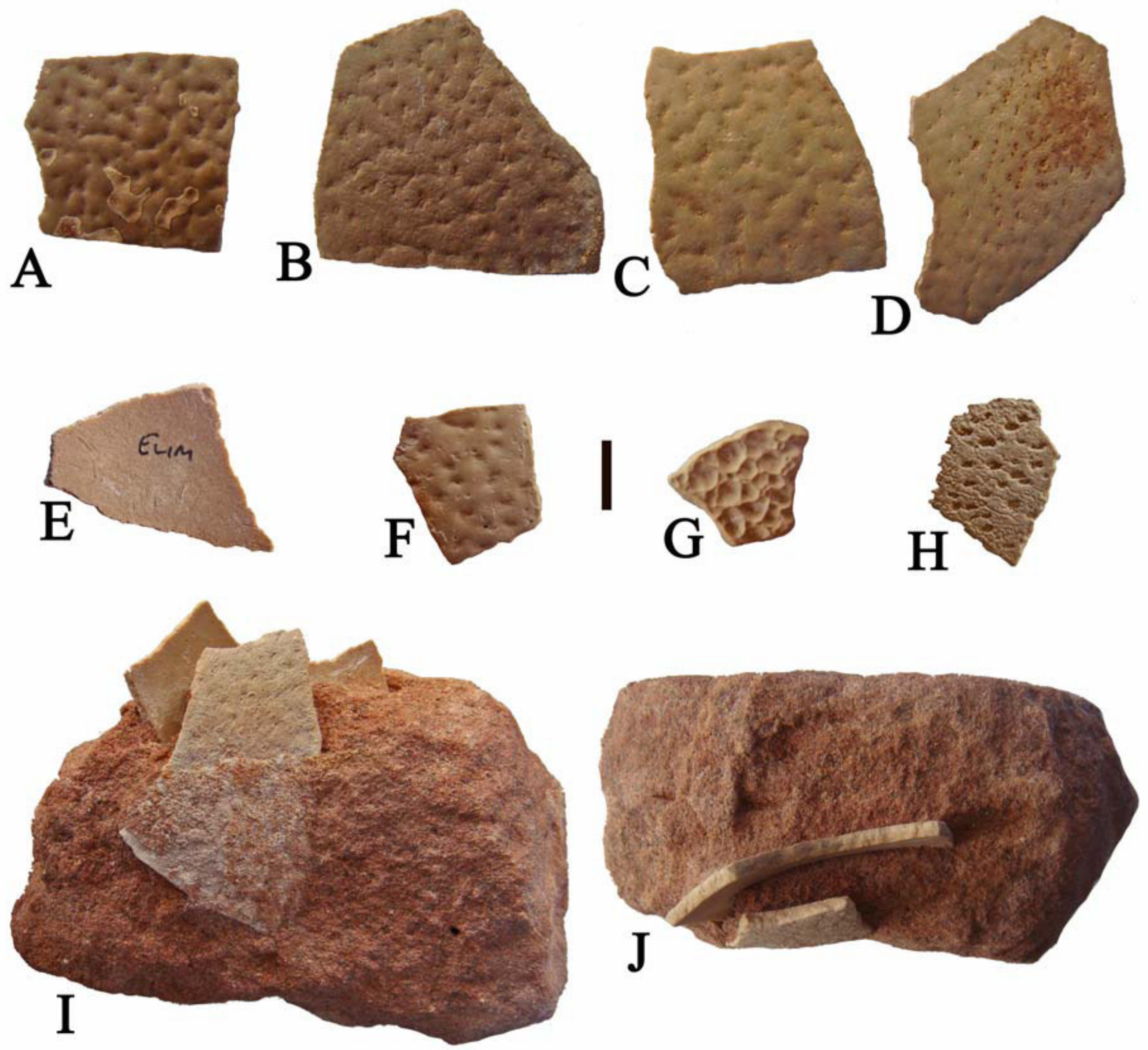

Figure 10: Fossil eggshells of *Namornis elimensis* from the northern part of the Namib-Naukluft Park. A-E, I-J) specimens from the type locality, Elim (C is the holotype, E is the inner surface of the egg); F-H) specimens from TS 40 (Tsondab Vlei) F) un-eroded specimen, G) specimen with wind facetted external surface, H) specimen in which the external layer has been removed by sandblasting, exposing the pore complexes and mammillary layer (scale - 10 mm except I-J, which are reduced).

Discussion on ratite eggshells from the northern part of the Namib-Naukluft Park

The northern part of the Namib-Naukluft Park, north of Sesriem (Fig. 11) has yielded a large variety of fossil avian eggshells spanning much of the Miocene. The samples from this part of Namibia complement and extend downwards the succession of egg types described from the southern part of the park and the Sperrgebiet (Pickford *et al*., 1995) (Fig. 14).

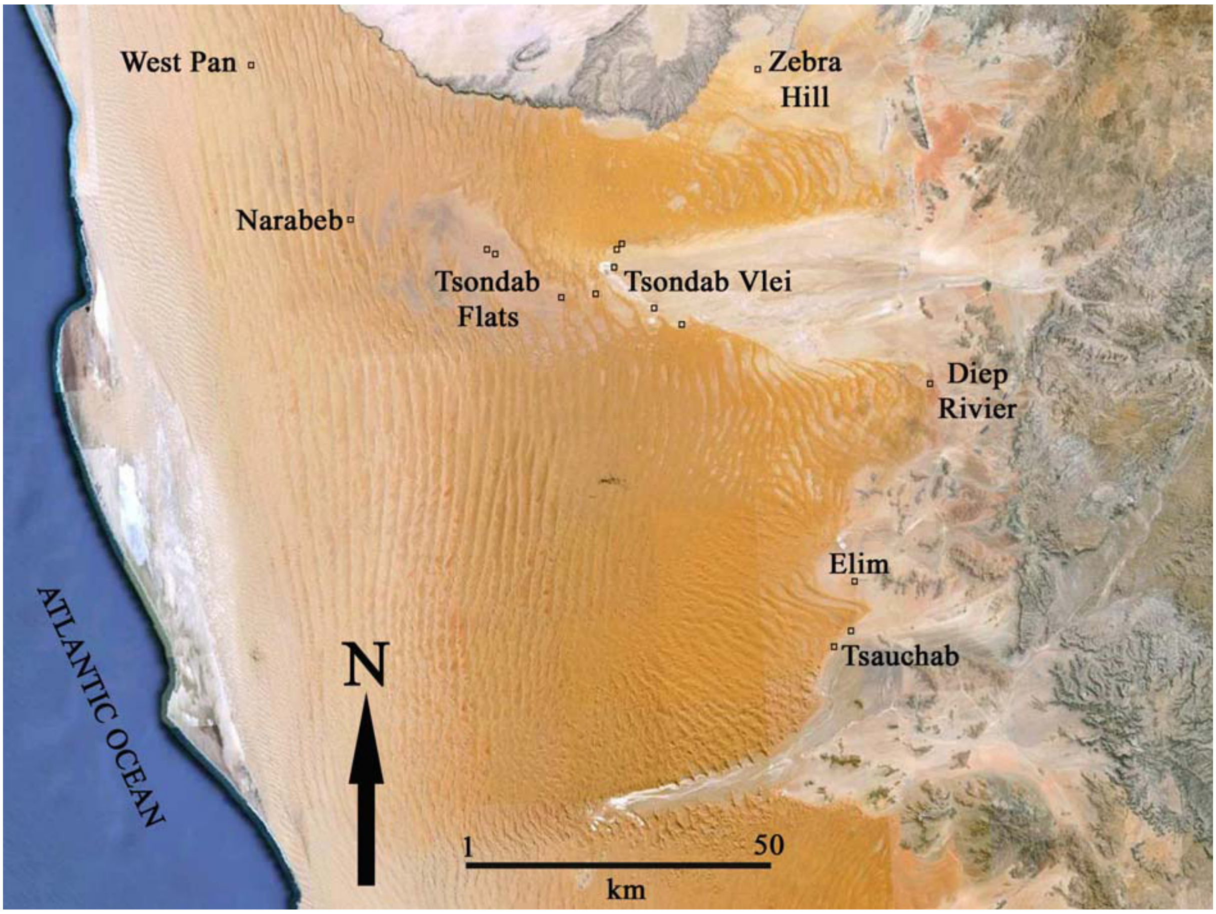

Figure 11: Fossil eggshell localities in the Tsondab Sandstone in the northern part of the Namib-Naukluft Park. Localities that yield fossil eggs of *Struthio camelus* have been omitted (image modified from Google Earth).

Geochronology and Palaeobiogeography

Pickford & Senut (1999) summarised the biochronology of the Neogene and Quaternary struthious eggs of Namibia. The succession of egg types is based on superposition of the strata from which they were collected. Calibration of the succession was based on fossil mammals that occur in the same strata as some of the eggs, but because some levels failed to yield mammals, then there is residual doubt about the age determinations of some of the taxa. For the latter taxa estimates of the age were made by interpolation.

Since then, fossil struthious eggs have been reported from Malawi (Stidham, 2004), Tanzania (Harrison & Msuya, 2005), Kenya (Harris & Leakey, 2003) and the United Arab Emirates (Bibi *et al.*, 2006) all of which are associated with fossil mammals and in the case of Tanzania and Kenya, with radio-isotopic age determinations on superjacent volcanic rocks.

Perhaps the most interesting assemblage from the point of view of its diversity is that from Lothagam, Kenya, where eggshells attributed to *Struthio* sp. by Harris & Leakey (2003) belong to *Diamantornis laini* and *Struthio* cf *karingarabensis* (or *daberasensis*). These fossils come from the Lower Nawata (7.4 – 6.5 Ma), Upper Nawata (6.5 – 5 Ma) and Apak Member (5 – 4.2 Ma) respectively. The Lothagam succession also yielded eggs with aepyornithoid morphology.

On the basis of the Lothagam eggshells, Stidham (2004) suggested that the age determinations of the Namibian egg types may need revision upwards by about a million years. Since biochronology based on mammals often has error margins of the order of half a million years, this suggestion may be valid, but before accepting it some aspects of the evidence need to be considered. According to Stidham (2004) the Lower Nawata levels yielded eggshell of *D. wardi* but Harrison & Msuya (2005) considered that the specimens concerned belong to

Figure 12: Eggshell fragment from Laetoli, Tanzania, housed in the NHM London, originally identified as *Struthio daberasensis* (Pickford & Senut, 1999). The eggshell is 3.2 mm thick which is substantially thicker than the range of variation in *S. daberasensis* (range 1.7 – 2.5 mm) and supports its re-identification as *Struthio kakesiensis*, even though its pore complexes are comparable to those of *S. daberasensis* (scale – 10 mm).

D. laini, which would resolve the apparent biochronologic problem. The thickness (2.2 – 3.4 mm, mean 3.7 mm) reported by Harrison & Msuya (2005) for their rendering of the Lothagam *D. laini* sample (i.e. a combination of specimens attributed to *D. wardi* and *D. laini* by Stidham, 2004) is similar to that of *D. laini*. Further study is required.

Diamantornis laini eggs occur in the Late Miocene of the United Arab Emirates (ca 7 Ma). The Malawi eggs attributed to *Struthio daberasensis* are associated with a Pliocene fauna (ca 3.9 - 3.5 Ma) (Stidham, 2004). The Kakesio, Tanzania eggs (Harrison & Msuya, 2005; Kingston & Harrison, 2005) were initially attributed to *Struthio daberasensis* by Pickford & Senut (1999) (Fig. 12), a determination accepted by Stidham (2004), but Harrison & Msuya (2005), on the basis of much enlarged samples, created a new species *Struthio kakesiensis* for eggs from the Lower Laetoli Beds (ca 4.2 - 3.7 Ma) and from the Upper Laetoli Beds beneath Tuff 3. The same type of eggshell occurs at Kanapoi, Kenya (4.2 – 4.1 Ma) (Harrison & Msuya, 2005). Above Tuff 3 at Laetoli, Harrison & Msuya (2005) recognised eggshells of *Struthio camelus* only, although some of the specimens are appreciably thicker than eggs of extant samples of ostrich from Namibia and Tanzania.

Overall, the sequence and timing of Namibian egg types has withstood the test of discoveries in other African countries and the Arabian Peninsula, although refinement of the biochronology is undoubtedly possible.

It should be noted however, that other kinds of eggshells have been found in Africa and Europe which do not fit into the above scheme. Harris & Leakey (2003) reported the presence of eggshells with aepyornithoid morphology in the Lower Nawata Member at Lothagam, Kenya. The Late Miocene of Spain (including the Canary Islands) has yielded similar eggs (Mein & Dauphin, 1995; Sauer & Roth, 1972) as has Turkey (Sauer, 1976). Eggs attributed to *Psammornis* have been reported from Algeria (Andrews, 1911). Eggshells from the Early Pliocene of Wadi Natrun, Egypt, possibly belong to this genus (Pickford *et al.*, in press).

From this evidence it appears that Africa was populated by at least two taxa of ratites for much of the Miocene and Pliocene, but that their geographic ranges barely overlapped. Only one locality (Lower Nawata, Kenya) is reported to have yielded struthious and aepyornithoid eggs in the same stratigraphic unit.

As far as ratite eggshells are concerned, the presence of the same succession of species of *Diamantornis* and *Struthio* in Namibia, Kenya and the Arabian Peninsula, indicates that diffusion between these regions was likely relatively easy and could therefore take place rapidly, hence their utility for biochronology. This biogeographic pattern indicates the presence of an arid corridor between southwestern Africa and northeastern Afro-Arabia from about 12 Ma (if not earlier) to the Present.

Palaeoclimatic considerations

The new fossil eggshells from the Tsondab succession are from aeolian deposits indicative of arid to hyper-arid palaeoclimatic conditions. However, the aeolianites are heavily affected by bioturbation represented by rhizoliths, animal burrows and bioconstructions. The relatively high frequency of burrows and hives attributed to *Hodotermes*, the harvester termite, suggests that the bioturbation occurred under a summer rainfall regime and that grass was an important food resource. Some of the rhizoliths are large enough to indicate the presence of trees. Traces left by the sand termite, *Psammotermes*, are rare in the Tsondab area, whereas they are extremely common at Rooilepel and other parts of the Sperrgebiet in Southern Namibia. This suggests that during the Early Miocene, the northern part of the proto-Namib Desert enjoyed a summer rainfall regime whereas the southern part lay within a winter rainfall zone.

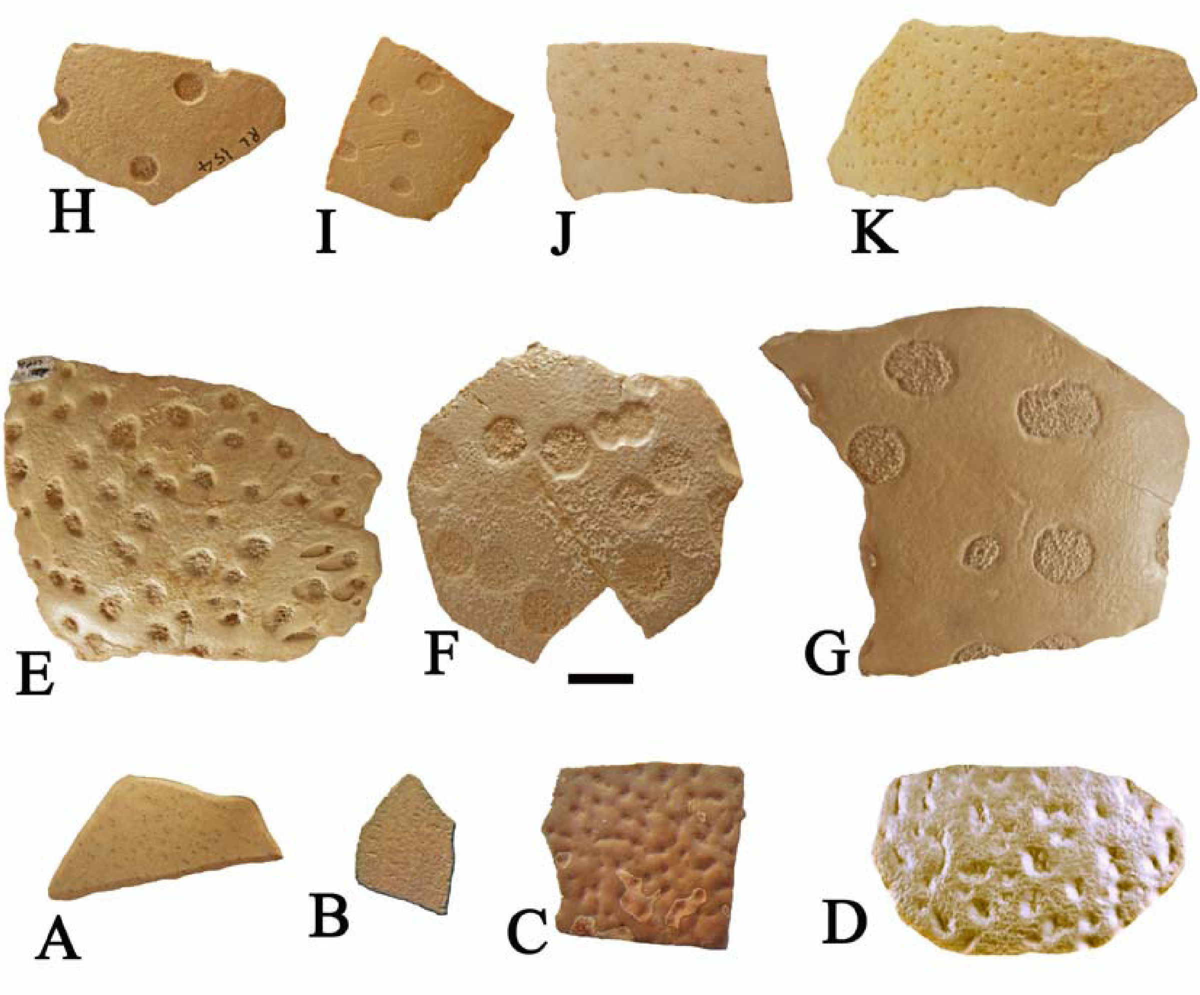

Figure 13: Succession of fossil eggshell types from the Namib Desert (A oldest to K youngest). A) *Tsondabornis minor*, B) *Tsondabornis psammoides*, C) *Namornis elimensis*, D) *Namornis oshanai*, E) *Diamantornis corbetti*, F) *Diamantornis spaggiarii*, G) *Diamantornis wardi*, H) *Diamantornis laini*, I) *Struthio karingarabensis*, J) *Struthio daberasensis*, K) *Struthio camelus* (scale – 10 mm).

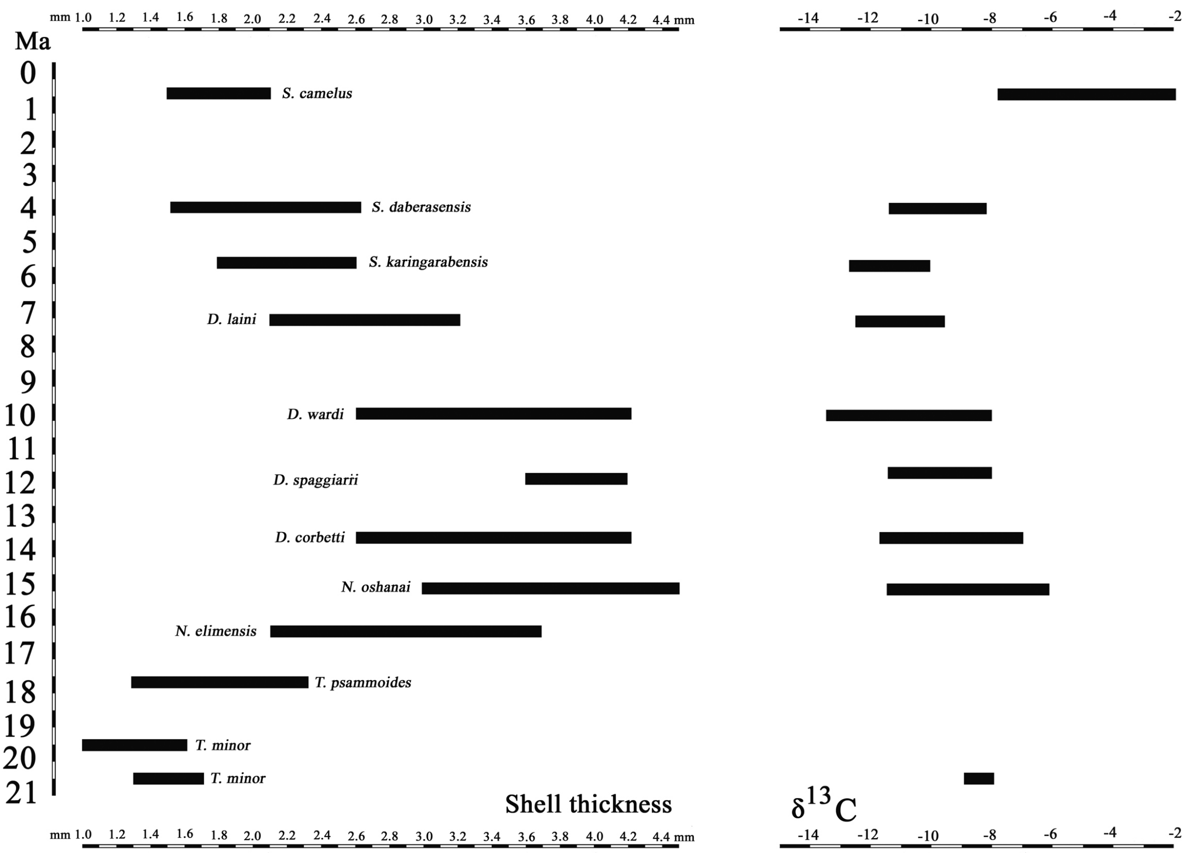

Figure 14: Variation in eggshell thickness and $\delta^{13}C$ values of fossil eggshells from the Miocene of Namibia. There appears to be an inverse correlation between the two trends, with thicker eggshells tending to have lower $\delta^{13}C$ values than thin eggs ($\delta^{13}C$ values from Ségalen *et al*., 2002).

Eggshell thickness in the Namib succession shows a trend of increase through the Early Miocene to the base of the Middle Miocene, followed by a slow decrease during the rest of the Miocene, speeding up during the Plio-Pleistocene (Fig. 14). Examination of the $d^{13}C$ values through the same succession of egg types reveals an inverse trend, with high values corresponding with thin eggshells, and lower values corresponding with thicker eggshells (Fig. 14). Ségalen *et al*., (2002) showed a correlation between the $d^{13}C$ values of the Namibian eggshells and the pCO_2 values in the atmosphere during the Miocene in the southern hemisphere (Pagani *et al*., 1999), with lower $d^{13}C$ values corresponding to higher values of pCO_2. The correlation between eggshell thickness and pCO_2 values noted herein, suggests that eggshell thickness in ratites is due not just to changes in the dimensions of the eggs (it has long been known that larger eggs have thicker shells), but may also be related to the concentration of CO_2 in the atmosphere where the birds were living.

Palaeoecology

Birds have a range of reproductive strategies correlated to clutch size. K-strategy birds lay few eggs and parental investment in the hatched young tends to be energy expensive and often prolonged. In contrast, r-strategy birds lay large clutches of eggs and the young tend to become relatively independent soon after hatching. Present day ostriches are r-strategy birds, several females usually laying several dozen eggs in the same nest and the young are able to walk and forage soon after hatching.

It is clear from the mapped fossil occurrences that *Diamantornis wardi*, *Diamantornis laini* and *Struthio daberasensis* laid many eggs in the same nest, as eggshell fragments of these species often occur in large concentrations indicating the former presence of many eggs in the same next. In contrast, the eggshell fragments of some species including *Namornis elimensis*, *Tsondabornis minor* and *Tsondabornis psammoides* tend to occur in small patches containing few fragments, suggesting that only one or two eggs were laid at each site. However, it cannot be ruled out that the occurrences of eggs of these species found so far represent "scatter" eggs (Sauer, 1968) in the same way that extant ostriches often lay an isolated egg away from the nest, immediately abandoning it. The possible exception is *Tsondabornis psammoides*, as one locality (Zebra Hill) yields many shell fragments in the surface deflation deposits. However, at all the other sites which yielded eggs of this taxon, shell fragments tended to be scarce, suggesting the former presence at each site of only one or two eggs.

Phylogeny

The transition from the basically aepyornithoid eggshell pattern of pores in slits and isolated dagger point pits in *Tsondabornis psammoides* to the more complex clustering of pores that occurs in *Namornis elimensis*, but with some arranged in sub-parallel slits, suggests that the struthious pattern was derived from the aepyornithoid pattern, as postulated by Sauer (1966) (see also Bibi *et al*., 2006). During the same period, the basically smooth external surface of eggshells in *Tsondabornis minor* became weakly undulating in *Tsondabornis psammoides*, culminating in the strongly undulating surface in eggs of *Namornis elimensis* a trend continued in *Namornis oshanai* (Sauer, 1966). Eggs attributed to subsequent species of *Diamantornis* generally possess smooth shell between the pore complexes, morphology carried over into the eggs of *Struthio*.

Conclusions

Palaeontological field work in the Tsondab Vlei and Tsondab Flats to the west has resulted in the recognition of two new kinds of extinct bird eggs. The older of the two, on the basis of superposition of strata is *Tsondabornis psammoides* nov. gen. nov. sp., the eggs of which are somewhat thicker than those of the extant ostrich *Struthio camelus*. This species was followed by a bird which laid much thicker eggs, *Namornis elimensis* nov. sp., the eggs of which were about twice as thick as those of the extant ostrich but thinner than those of the type species *Namornis oshanai*. In other parts of the Namib-Naukluft Park, eggs of younger species of bird have been found, including those of *Namornis oshanai*, *Diamantornis corbetti*, *Diamantornis wardi*, and *Diamantornis laini*, all of Miocene age, whereas in Pleistocene to Recent levels, eggs of *Struthio camelus* are common.

The main interest of this work concerns the downwards extension of the biostratigraphic scheme based on gigantic avian eggs from the Sperrgebiet and the southern sector of the Namib-Naukluft Park (Dauphin *et al*., 1998; Pickford & Senut, 1999). As such the two new oo-species fill a gap that used to exist between the so-called "aepyornithoid" eggs from the Early Miocene fluvio-paludal deposits of the Sperrgebiet (Elisabethfeld, Grillental, Fiskus, Langental) (Senut *et al*., 1995) and *Namornis oshanai* from the basal Middle Miocene levels at Rooilepel, Karingarab and Awasib (Pickford *et al*., 1995) and by inference to Beisebvlakte, near Etosha (Sauer, 1966). The large morphometric gap that used to separate the aepyornithoid eggshells from those of *Namornis oshanai* is now reduced by the presence of two intermediate kinds. This indicates the likelihood of autochthonous evolution rather than extinction of the aepyornithoid type followed by immigration of *Namornis*. It also reduces the punctuated aspect of the evolution of Namibian fossil eggs, and suggests instead a gradual, albeit quite rapid, evolutionary process within the country (continent).

Fossil eggs hold tremendous potential for unravelling the history of sandstone deposition in the Central Namib Desert, something that traditional mapping techniques have thus far failed to reveal. The distribution of fossil eggs in the Tsondab Formation indicates a complex history of interplay between aeolian deflation and deposition spanning the entire Miocene and Pliocene, resulting in sand bodies which are separated from each other by super-bounding and erosional surfaces (not necessarily horizontally disposed), a process that continues to the present day with the Sossus Sand Sea, much of the sand of which is derived by reworking from the Tsondab Formation.

The aeolianites that have yielded the eggs of *Tsondabornis psammoides* are younger than the Early Miocene fluvio-paludal sites in the Sperrgebiet (21-19 Ma) which yield eggs of *Tsondabornis minor* and bones of *Struthio coppensi*. However, it is stressed that there is a great deal of aeolianite beneath the levels that yielded the oldest eggs found in the Namib-Naukluft Park, so there remains the possibility that the onset of aeolianite deposition could have been earlier than previously thought, perhaps as early as 19 Ma (Fig. 14) (Ségalen *et al*., 2004a). Further south in the Sperrgebiet the onset of aeolianite deposition coincided in time with eggshells of *Namornis oshanai*, which are younger than those of *Namornis elimensis*, indicating a later start of sand deposition in the south (ca 16 Ma) than in the north (Pickford & Senut, 1999) although arid conditions could have existed for some time prior to the first deposition of aeolianite.

The fact that struthious oo-species defined in Namibia have been recognised as far afield as Tanzania, Kenya and the Arabian Peninsula indicates that the birds producing them were able to diffuse widely and rapidly between Southwestern Africa, Eastern Africa and Arabia, which in turn suggests that an arid corridor existed between these regions for a considerable period of time.

Finally, in the succession of Namibian fossil eggs, there appears to be a correlation between eggshell thickness and the concentration of carbon dioxide (pCO_2) in the atmosphere.

Acknowledgements

Authorisation to carry out the 2010 palaeontology survey in the Namib-Naukluft Park was provided by Nature Conservation of Namibia (Mr T. Iita, Mr A. Engelbrecht) kindly organised by the Geological Survey of Namibia (Dr G. Schneider, Mrs E. Grobler). Authorisation to carry out palaeontological research in the country was accorded by the National Monuments Council of Namibia (Mrs E. Ndalekokule). Thanks to the Geological Survey of Namibia and the French Embassy in Windhoek. Funding for the survey was provided by the French CNRS and the Muséum National d'Histoire Naturelle de Paris. I would like to thank Terry Harrison for measurements of individual eggshells from Lothagam, Kenya.

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