# Fossil ratite eggshells: A useful tool for Cainozoic biostratigraphy in Namibia

# **Brigitte Senut**

Laboratoire de Paleontologie du Museum National d'Histoire Naturelle et UMR 8569 CNRS, 8, rue Buffon, 75005 Paris, France e-mail: bsenut@mnhn.ft

Fossil dunes are widespread in the Namib Desert, especially in the Sperrgebiet and the Namib-Naukluft Park where frag¬ments offossil "ostrich" eggshells have been known for a long time. But it was only in the 70's and 80's that they were collected for scientific purposes (Ward and Corbett, 1990). Recent fieldwork by the Namibia Palaeontology Expedition in the same areas led to the collection of a diverse series of fossil struthious eggshells associated with mammals at several localities. We have identified more than a hundred fossiliferous sites where 8 different types of eggshells occur which differ in their pore complexes and pore density. Three genera of eggshells have been identified: *Namornis, Diamantornis*, and *Struthio*. No two eggshell types occur together in the same stratigraphic level and when several types of eggshells are found in superposition, they always occur in the same order. In older levels (Lower Miocene), aepyornithoid eggshells have also been recorded. Eggshells are thus proving to be extremely useful for biostratigraphy and for correlating strata in the Namib and elsewhere in the Old World (South Africa, Tanzania, Arabian Peninsula). Having been calibrated by associated mammal faunas, the Namib egg sequence can now be used for geochronological purposes and the Namib Desert is suggested to have originated ca. 16 Ma.

#### Introduction

The first scientific report of large fossil struthious eggshells in Namibia was published in the late 60's by E.G.F. Sauer who erected a new species of a giant struthious bird, "Struthio oshanai", based on eggshells which had been collected from a borehole at Beisebvlakte at Etosha Pan, northern Namibia (Sauer, 1966). However, large struthious eggshells have been known to occur for a long time in the Namib Sand Sea but systematic collections for study were made only in the 80's and subsequent years by geologists and ecologists (Ward and Corbett, 1990). J. Ward collected eggshells of "Struthio oshanai" in the Tsondab Sandstone at Elim Gullies from the base of an aeolianite succession; W. Shaw reported some more eggshells from Schmidtfeld, north Lüderitz, I. Corbett at Kolmanskop and Grillental, south Lüderitz, M. Seely at Kalahari and Narabeb (in the Gobabeb area), J. Teller and J. Ward at Nutab and West Pan (near Gobabeb and 50 km west of Rooibank), J. Ward at Tjirundo (near Omaruru), and finally I. Corbett and J. Ward at Rooilepel in the Oranjemund area. The morphology of the eggshells being different from those of modem ostriches (Corbett, 1989), it was clear that a detailed study of the morphology and structure would be of interest. It also appeared that the eggshells were found throughout the Namib Sand Sea and that a systematic search of the area would yield more evidence.

In 1993, Pickford and Dauphin published the genus *Diamantornis* for these giant struthious eggshells based on a specimen collected by J. Ward and I. Corbett at Rooilepel. Since 1993, the Namibia Palaeontology Expedition has been carrying out fieldwork in the Namib Sand Sea in two major areas: the Sperrgebiet and the Namib-Naukluft Park. These surveys resulted in the discovery of more than a hundred fossiliferous sites (see Senut and Pickford, (1995) for an exhaustive list) that yielded diverse fossilized struthious eggshells which formed the basis for a biostratigraphic scale first established on the aeolianite succession at Rooilepel in the

Sperrgebiet (Senut *et al.*, 1994; Pickford *et al.*, 1995). It was refined later on the basis of the aeolianite succession at Awasib in the Namib Naukluft Park (Senut *et al.*, 1995). Recently, a more complete succession was found at Karingarab in the southern Sperrgebiet (Senut, 1998; Senut *et al.*, 1998) in which eight different levels with eight distinct types of large struthious eggshells have been identified. In lower Miocene fluviatile deposits at Langental, Grillental and Elisabethfeld, some aepyornithoid eggshells have been found (Senut *et al.*, 1995) and they were recorded later at Kamberg (Pickford and Senut, 1999).

#### The main sites

In the Namib Desert, the bulk of the aeolianites (fossil dunes) form the Tsondab Sandstone Formation which comprises eight biochronologic units deposited at different times during the Cenozoic. It is overlain by mobile sands of the Namib Sand Sea (the Sossus Sand Formation)(Ward, 1988). The sites are scattered over an area of more than a 10 000 km<sup>2</sup> (Figs. 1 and 2).

#### The Rooilepei Depression

The succession at Rooilepel consists of a thickness of 120 m of fossiliferous aeolianites. They crop out in a cliff 6 km long facing northwest. Five major units were recognized which served as a basis for the first biostratigraphy of the aeolianites (Senut *et al.*, 1994).

A lowermost level, 0.30 m thick, lies on the basement complex of the Proterozoic Gariep Group. Not identified in Senut *et al.*, 1994, it was subsequently found to contain eggshells of *Namornis oshanai* and abundant gastropods *Trigonephrus*.

The Lower acolianite lies on the basement on most of its exposure. Up to 30 m thick, the level is poorly fossiliferous. It yielded *Diamantornis corbetti*, a Pedetidae (sp. 1), *Bathyergoides neotertiarius*, a Macroscelidea, enamel of a Gomphotheriidae and many trace fossils made by *Psammotermes* and the gastropod



Figure 1: Locality map of fossil eggshell sites in the Namib Desert.

# Trigonephrus.

The upper surface of the aeolianite was eroded and covered by two waterlain silts 0.5 to 1.5 m thick which contain white nodules (probably a pan deposit in an interdune setting). These two levels are isolated from each other by sands. This erosional unconformity corresponds to the "super-bounding surfaces" defined by Lancaster (1989). The silts are overlain by a massive aeolianite, the **Middle aeolianite**, 70 m thick, which contains grey nodules and a rich fauna; trace fossils made by *Psammotermes*, the gastropod *Trigonephrus*, frogs, lizards, snakes, tortoises, eggshells of *Diamantornis wardi*, rodents such as Pedetidae sp. 2, *Bathyergoides neotertiarius*, another Bathyergidae, Macroscelidea, enamel fragments of a Gomphotheriidae and a Bovidae.

The Upper aeolianite, 40 to 50 m thick is poorly fos-

siliferous. It yielded Pedetidae, a giraffid, and *Diaman-tornis laini*.

At the top of the sequence the upper surface of the aeolianite underwent an important diagenetic change which led to the formation of a thin layer of calcrete (Pickford and Senut, 1999) which contains abundant shells of the gastropod *Trigonephrus* and eggshells of *Struthio camelus*, the modem ostrich, the preservation of which suggests a Pleistocene to Holocene age. The succession is overlain by widespread shifting modem sands containing *Trigonephrus* and *Struthio camelus* eggshells.

#### Daberas

In 1994, two outcrops of aeolianites in the Daberas Dune northeast of Oranjemund were surveyed. They



Figure 2: Fossil eggshell sites in the Sperrgebiet and South Africa.

contain the following fossils: a few gastropods (*Trigo-nephrus, Xerocerastus*), frogs, snakes, rodents (*Petro-myscus, Gerbillus*, Gerbillidae, *Otomys*), insectivores (Macroscelididae), lagomorphs (*Lepus capensis*), Proboscidea (*Loxodonta*) and Bovidae (*Oryx gazella*). The surface of the aeolianite is littered with Acheulean stone tools, which suggest that the sandstone was formed prior' to the Middle Stone Age. In the same level were found struthious eggshells which exhibit a morphology of the pores slightly different from that of the modem ostrich, and they have been assigned to *Struthio daberasensis*.

#### Awasib Region

The aeolianites in the Awasib region were first mapped as Tertiary consolidated dunes by Hoal (1990). They crop out in a cliff, 120 m high, 10km wide and in 13 main indurated horizons separated by almost horizontal surfaces which correspond to "super-bounding surfaces" of Lancaster (1989). These are erosional, but not sedimentary, surfaces. The sequence of eggshells is rather complete as we found in direct superposition from the lowermost levels up to the uppermost levels, *Namornis oshanai, Diamantornis corbetti, D. wardi, D. laini, Struthio daberasensis* and *S. camelus* (Senut *et al.*, 1995).

South of A wasib, an extensive exposure of aeolianites crops out south of Haiber Hill, a site which has yielded *Diamantornis wardi*, *Diamantornis laini* and *Struthio daberasensis*. The *Diamantornis wardi* level is rich in larval cases of Cerambicidae (longicorn beetles) and rodents such as *Ternania* but a few fragments of ruminants were also collected. Eighteen fossiliferous localities have been identified in the A wasib region and the 13 stratigraphic levels can be grouped into six major biostratigraphic units.

# Karingarab

Early in 1995, R. Spaggiari, a geologist with Namdeb, collected fragments of eggshells of *Diamantornis corbetti* and *Diamantornis laini*, as well as a few Pedetidae and tortoises at a new locality called Karingarab, 40km north of Oranjemund, Sperrgebiet. In June 1995, a further survey at the locality was undertaken by the NPE team and R. Spaggiari. We found classic eggshells of *Diamantornis* and *Struthio*, but also two new intermediate types of eggshells. The discovery of the two new eggshell types at Karingarab intermediate in structure between already known types permitted the refinement of the biostratigraphy in the palaeodunes (Senut *et al.*, 1998). Karingarab represents today the most complete known sequence of avian biostratigraphy and the best reference for local biostratigraphy.

# The coastal fluviatile deposits

In the northern part of the Sperrgebiet, at three different localities (Langental, Grillental and Elisabethfeld), fluviatile deposits have yielded a rich mammalian assemblage typical of the Lower Miocene. At Elisabethfeld, the sediments consist of red silts overlain by marly clays and coarse sands, which are covered by travertine levels. The fossils come from the red silts. At Grillental, the fossils have been discovered in gypsiferous green silt overlain by fluviatile sands. At Langental, the sediments consist of variegated marly silts with gypsum crystals and calcareous nodules (Pickford and Senut, 1999).

#### The eggshells

#### Materials

Hundreds of fragments of eggshells have been collected in stratigraphic context from more than 70 sites in the Namib Desert. Despite the scarcity of the fragments found at Karingarab, each level has yielded dozens of fragments, including in some cases complete or 90% complete eggshells. The sample size was thus quite adequate. We did not find any mixed assemblage in a stratigraphic unit.

#### Methodology

The eggshells have been identified on the basis of

pore macrostructure morphology and thickness of the eggshell. This paper will concentrate on the descriptions of the external surface of the shells which is the most useful feature for the geologist in the field. The microstructures of the eggshells have been discussed in detail by Dauphin *et al.* (1996) (Table 1). Large or small, rounded or slit-like shapes, all the pores show a ramified, complex structure. Diagenetic changes in the mineral and organic phases of fossil eggshells have been looked at. Despite good preservation of microstructural and mineralogical features, the organic matrices have been altered in quantity and quality. The soluble and insoluble matrices show different behaviour during diagenetic processes (Dauphin *et al.*, 1998).

Concerning the taxonomy of fossil eggshells, three main schools of thought exist: 1. Some authors prefer to use a parataxonomic approach using the suffix *olithes* for the genus but usual species names (cf. Hirsch, 1985); 2. Others use a strict parataxonomic nomenclature (the suffix *orum* is used for the genus name, and

the name *ovum* for the species name; cf. Schleich and Kastle, 1988); 3. Most authors employ a binomial system of genus and species (cf. Sauer, 1966). It is this last approach which has been used for the study of the eggshells of the Namib Desert. Three genera of fossil eggshells have been identified on the basis of pore macrostructure morphology and thickness of the eggshell: *Namornis, Diamantornis* and *Struthio*. Another type of eggshell, aepyornithoid, has been identified.

# Descriptions

#### Namornis oshanai

The pores are irregular, vermiform to roughly circular and occur in shallow depressions up to 4 mm long and 1.5 mm wide. The pores are often ramified producing small island-like structures. The thickness of the shell varies from 2.2 to 4.0 mm.

Fable	1	: Microstructure	of the	bird	eggshells	(after	Dauphin	et al.,	1996).	
-------	---	------------------	--------	------	-----------	--------	---------	---------	--------	--

TAXON	MICROSTRUCTURE			
Struthio camelus	<ul> <li>Mammilary internal layer clearly distinguishable</li> <li>Spongious level with chevron pattern well developed and regular units</li> <li>Third prismatic layer generally present</li> <li>External surface with small, rounded or slightly elongated pores</li> </ul>			
Struthio daberasensis	<ul> <li>Inner layer with spherolites composed of divergent fibers and numerous curved growth layers</li> <li>Outer layer with fishbone pattern, very thin linear horizontal growth lineation and vertical columns</li> <li>Irregular boundary between the two layers</li> </ul>			
Struthio karingarabensis	<ul> <li>Complex, ramified structure in funnel-shaped pore complexes</li> <li>Mammilary internal layer indistinct</li> </ul>			
Diamantornis laini	<ul> <li>Inner layer with only outer part of the spherolites preserved (large prisms and rare curved growth patterns)</li> <li>Distinct boundary between inner and outer layers</li> <li>Outer layer devoided of fishbone pattern, with thin growth lineation on the outer part</li> <li>A third prismatic outer layer is preserved</li> </ul>			
Diamantornis wardi	<ul> <li>Pores with funnel-shape</li> <li>Inner layer spherolitic developing a mammilary bed composed of divergent prisms in tabular position</li> <li>Boundary with second layer not gradual</li> <li>Outer columnar layer with chevron pattern well developed</li> </ul>			
Diamantornis spaggiarii	<ul> <li>Pores with divergent structure from the exteral to internal surface</li> <li>Inner layer with spherolites eroded, disjointed, recrystallised; thin divergent fibres recrystallised in large prisms</li> <li>Outer layer columnar recrystallised; locally, chevron structure preserved</li> </ul>			
Diamantornis corbetti	<ul> <li>Pores complex and irregular in shape</li> <li>Pores well defined in oval or rounded depressions</li> <li>Inner layer composed of different thin fibres without growth lines</li> <li>Outer layer devoid of growth lineation and fishbone pattern</li> <li>Some fishbone pattern at the boundary zone</li> </ul>			
Namornis oshanai	<ul> <li>Pores complex and ramified</li> <li>Inner surface with distinct spherolite</li> <li>Inner layer composed of large divergent prisms divided into thin fibres (curved growth layers)</li> <li>Outer layer with thin horizontal growth layers</li> <li>Fishbone pattern preserved at the boundary of the inner and outer layers</li> <li>Boundary between two layers progressive</li> </ul>			
Aepyomithoid eggshell	<ul> <li>The inner and outer layers are clearly identifiable</li> <li>Inner layer with classic divergent fibers with a few curved growth layers</li> <li>Spongious layer with chevron pattern</li> <li>External surface with numerous apertures, usually parallel or elongated pores; some apertures clearly more rounded</li> </ul>			

# The Diamantornis eggshells

All the *Diamantornis* eggshells are characterized by a system of more or less circular megapores or pore complexes with different patterns.

*Diamantornis corbetti*: the pores occur in oval to roughly circular depressions with a diameter between 0.9 to 2.7 mm. The pores are usually isolated from each other and the shell is 2.6 to 4.1 mm thick.

*Diamantornis spaggiarii*: the pores occur in circular depressions between 2.7 mm and 5 mm in diameter well separated from each other. The thickness of the eggshell varies from 3.5 to 4.2 mm.

*Diamantornis wardi*: the pores are large circular to subcircular shallow depressions 5 mm to 10 mm in diameter. The thickness of the shell varies from 2.5 mm to 2.9 mm.

*Diamantornis laini*: the pores appear in circular, generally shallow depressions of approximately equal diameter (5 mm). The thickness of the eggshell varies from 2.1 to 2.9mm.

#### Struthio

The pores are widely scattered at the surface of the shell which is generally thinner than in *Diamantornis*.

*Struthio karingarabensis*: The pores are irregular to oval ranging in diameter from 2.4 to 2.7 mm forming a shallow depression. The shell thickness varies from 2.9 to 3.2 mm being slightly thicker than in *Struthio camelus*.

*Struthio daberasensis*: The pores are irregular in morphology, oblong, ranging in size from 0.5 to 2.2 mm and produce almost no depression at the surface. The thickness of the shell varies from 1.7 to 2.6 mm.

*Struthio camelus*: the pinpoint pores are seen as abundant depressions scattered over the entire surface. The shell is 1.6 to 2 mm thick.

# The non-struthioniform eggshells

These eggshells differ strongly from the large struthious eggshell in several features which recall those seen in the giant bird from Madagascar, *Aepyornis*: the numerous pores occur in elongated depressions, almost parallel to each other and accompanied by a few comma-shaped pores. The eggshells are thinner (1.2 to 1.25 mm) and closer to those of *Struthio*. On the basis of the morphology of the pores, we have referred these eggshells to "aepyornithoid".

# Towards a biostratigraphy

The different types of struthioniform eggshells are easily identifiable with the naked eye. No two types of eggshells have ever been found together in the same level; they are always found in levels which are in superposition. In several levels, the eggshells are associated with mammalian microfauna or macrofauna which permits the calibration of the age of the deposits. Today, the oldest known levels are estimated to be ca. 16 million years (Fig. 3) and the entire sequence extends from 16 Million years up to the present. No characteristic fossils have been yet found in the lowermost level which overlies the basement. But for depositional reasons, the time span between the *Namornis oshanai* level and the *Diamantornis corbetti* level cannot have been long and was probably not more than a million years.

The aepyornithoid eggshells do not seem to be of interest for biostratigraphy as they occur throughout the sequence from the lower Miocene (at Elisabethfeld, Grillental and Langental) to more recent levels such as the Kamberg aeolianites. At Elisabethfeld, some bones of an extinct ostrich have been described as *Struthio coppensi* which might have laid aepyornithoid type eggs. This suggests that two struthionid lineages have inhabited Africa (Mourer-Chauviré *et al.*, 1996).

# Correlations

For a long time giant struthious eggshells have been recorded only in the Sperrgebiet and the Namib-Naukluft in Namibia. Recently, D. Roberts a geologist at the Council for Geoscience of South Africa reported some eggshells of Diamantornis wardi at Prospect Hill near Saldanha in South Africa. Diamantornis laini has been found from Abu Dhabi (palaeontology exhibition at the Natural History Museum in London) but there is no published record of this material. Struthious eggshells, have been reported at the Pliocene hominid site of Laetoli (Leakey and Hay, 1979) but have not been identified. Some specimens housed at the Natural History Museum in London belong to Struthio daberasensis as do specimens from the Pleistocene of Olduvai (Site MNK) in Tanzania (Pickford, pers. comm.). At Olduvai, some bird bones have been found and attributed to Struthio oldawayi (Lowe, 1933) but it is not clear if they belong to the eggshells reported later. At Langebaanweg in South Africa, some bird bones have been classified as Struthio sp. (Rich, 1980). Struthio camelus has been found in the uppermost deposits at Bosluis Pan in Namaqualand (South Africa)(Senut et al., 1996). Some other struthioniform eggshells have been found in Algeria attributed to the genus Psammornis by Andrews (1911) and reported from Arabia by Lowe (1933); these eggshells seem to be considerably larger than those of modem ostriches and are thicker (3.2 mm for the Algerian specimen and 3.0 mm for the Arabian one). Unfortunately, the author did not have the chance to see these materials and it will be difficult to correlate them with the Southern African species. However, from the present study, the eggshells seem to have had a wide distribution in Africa and in cases may be useful for intercontinental correlations. The age estimates established on the aeolianites of the Namib Desert are confirmed by the record of other Afro-Arabian sites

Approx.Age Morphotypes of bird Ma eggshells		Species	Type Locality	Other localities	
0 - 2		Struthio camelus	Aucune	E-Bay Bosluis Pan	
2 - 5		Struthio daberasensis	Daberas Duine	Awasib (N <sup>x</sup> sup.) Karingarab (N <sup>x</sup> sup.) Fiskus, Laetoli Kolmanskop	
5 - 8		Struthio karingarabensis	Karingarab	Awasib (N <sup>x</sup> sup.)	
8 - 10	0	Dlamantornis laini	Target Pan	Rooilepel (N <sup>s</sup> sup.) Awasib (N <sup>s</sup> moyens) Tsaus Karingarab (N <sup>s</sup> moy.)	
10 - 12		Diamantornis wardi	Rooilepel (N <sup>x</sup> moy.)	Prospect Hill Schmidtfeld Awasib (N* inf.) Karingarab (N* inf.) Vreemdelingspoort Tsaus	
12 - 14	0.000	Diamantornis spaggiarii	Karingarab	GP Pan North	
14 - 15	Contraction of the second	Diamantornis corbetti	Rooilepel (N* inf.)	West Pan Rooilepel West Elim, Diep Rivier Awasib (N <sup>*</sup> inf.)	
15 - 16	and the second	Namornis oshanai	Etosha	Rooilepel (base) Karingarab (base) Awasib (base)	
16 - 20		Aepyomithoid	Aucune	Zebra Hill, Tsauchab Paradys Valley Langental, Grillental Elisabethfeld	

Figure 3: Avian biostratigraphy of the Namib Desert (eggshells about x0.95 except Aepyornithoid about x19)

where the biostratigraphy has been calibrated. The new age estimates suggest that the Namib Desert had already formed by about 16 million years ago, but is probably not as old as the Palaeogene or Cretaceous as previously suggested.

# Acknowledgements

I am particularly grateful to Dr. J. Ward for introducing me to Rooilepel and the Namib Desert, to Mr. R. Spaggiari for his time and efforts to introduce me and the NPE to Karingarab and to Dr. B. Hoal for help with the Awasib area. This paper could not have been written without input from members of the Namibia Palaeontology Expedition and especially Dr. M. Pickford co-leader of the expedition. Thanks are extended to the CDM (Pty Ltd)(today Namdeb), the Ministry of Environment and Tourism (especially Mr. P. Bridgeford), the National Monuments Council, the Geological Survey of Namibia (Dr. G. Schneider) for research permits in Namibia and for their help at different stages of this work. Sincere thanks are due to the personnel of the French Cooperation Mission in Windhoek for all the support that they provided throughout the expedition. This work was supported by URA 12, UMR 8569, GDR 983 of

the CNRS, the College de France (Chaire de Paleoanthropologie et de Prehistoire) and the Museum National d'Histoire Naturelle (Laboratoire de Paleontologie). The figures are due to the skill of Mrs F. Pilard and photographs are due to Dr. Y Dauphin.

#### References

- Andrews, C.W. 1911. Note on some fragments of the fossil egg-shell of a large Struthious bird from Southern Algeria with some remarks on some pieces of the eggshell of an ostrich from northern India. *Verh. Inter. Ornith. Kongress*, Berlin, V, 169-174.
- Corbett, I. 1989. *The sedimentology of diamondiferous deflation deposits within the Sperggebiet, Namibia.* Unpubl. PhD thesis, Univ. Cape Town, 430 pp.
- Dauphin, Y, Pickford, M. and Senut, B. 1996. Microstructures des coquilles d'oeufs d'oiseaux fossiles de Namibia. *Rev. Paleont.*, 15, 225-241.
- Dauphin, Y., Pickford, M. and Senut, B. 1998. Diagenetic changes in the mineral and organic phases of fossil avian eggshells from Namibia. *App. Geochem.*, 13, 243-256.
- Hirsch, K.F. 1985. Fossil crocodilian eggs from the Eocene of Colorado. *J. Palaeont.*, **59**, 531-542.
- Hoal, B. 1990. The geology and geochemistry of the Proterozoic Awasib Mountain Terrain, Southern Namibia. *Mem. geol. Surv. Namibia*, **11**, 163 pp.
- Lancaster, N. 1989. Eolian depositional patterns in time and space: evidence tram the Namib and Gran Desierto Sand Seas. *Pangea*, 15/16, 30.
- Leakey, M.D. and Hay, R.L. 1979. Pliocene footprints in the Laetolil Beds at Laetoli, northern Tanzania.

Nature, 278, 317-323.

- Lowe, P.R. 1933. On some Struthious remains: 1. Description of some pelvic remains from a large fossil ostrich, *Struthio oldawayi*, sp. n., from the Lower Pleistocene of Oldaway (Tanganyika Territory); 2. Egg shell fragments referable to *Psammornis* and other Struthiones collected by Mr. St. John Philby in Southern Arabia. *Ibis*, **13**, 652-658.
- Mourer-Chauviré, C., Senut, B., Pickford, M., Mein P. and Dauphin, Y. 1996. Ostrich legs, eggs and phylogenies. S. Afr. J. Sci., 92, 492-494.
- Pether, J. 1994. *The sedimentology, palaeontology and stratigraphy of coastal-plain deposits at Hondeklip Bay, Namaqualand, South Africa.* Unpubl. MSc thesis, Univ. Cape Town.
- Pickford, M. and Dauphin, Y. 1993. *Diamantornis wardi* novo gen. novo sp. giant extinct bird from Rooilepel, Lower Miocene, Namibia. C. R. Acad. Sci. Paris, **316**, II, 1643-1650.
- Pickford, M. and Senut, B. 1999. Geology and Palaeobiology of the Namib Desert, Southwestern Africa. *Mem. geol. Surv. Namibia*, 18, 155 pp.
- Pickford, M., Senut, B. and Dauphin, Y. 1995. Biostratigraphy of the Tsondab Sandstone (Namibia) based on gigantic avian eggshells. *Geobios*, 28, 85-98.
- Rich, P.V. 1980. Preliminary report on the fossil avian remains from late Tertiary sediments at Langebaanweg (Cape Province), South Africa. S. Afr. J. Sci., 76, 166-170.
- Sauer, E.G.F. 1966. Fossil eggshell fragments of a giant struthious bird (*Struthio oshanai*, sp. nov.) from Etosha Pan, South West Africa. *Cimbebasia*, 14, 1-51.
- Schleich, H.H. and Kastle, W. 1988. *Reptile egg-shells* SEM atlas. Gustav Fischer Verlag, Stuttgart, 119 pp.
- Senut, B. 1998. Karingarab : a deflation basin in the Rooilepel aeolianites containing a complete succession of struthious egg types. *Abs. Palaeont. Soc. southern Afr., Windhoek*, 1998, 25.
- Senut, B., Dauphin, Y. and Pickford, M. 1998. Nouveaux restes aviens du Néogène de la Sperrgebiet (Namibie): complément à la biostratigraphie avienne des éolianites du désert de Namib. C. r. A cad. Sci. Paris, **327**, IIa, 639-644.
- Senut, B. and Pickford, M. 1995. Fossil eggs and Cenozoic continental biostratigraphy of Namibia. *Palae*ont. afr., **32**, 33-37.
- Senut, B., Pickford, M. and Dauphin, Y. 1995. Découverte d'oeufs de type "Aepyornithoïde" dans Ie Miocène infèrieur de Namibie. *C. r. Acad. Sci. Paris*, 320, IIa, 71-76.
- Senut, B., Pickford, M. and Mein, P. 1995. Les falaises d'Awasib : une coupe-type pour le Cénozoïque continental de Namibie. C. r. Acad. Sci. Paris, **321**, Ila, 775–780.
- Senut, B., Pickford, M. and Ward, 1. 1994. Biostrati-

graphie des éolianites néogènes du sud de la Sperrgebiet (Désert de Namib, Namibie). *C. r. Acad. Sci. Paris*, **318**, IIa, 1001-1007.

- Senut, B., Pickford, M., Ward, J., De Wit, M., Spaggiari, R. and Morales, J. 1996. Biochronology of the Cainozoic sediments at Bosluis Pan, Northern Cape Province, South Africa. S. Afr. J. Sci., 92, 249-251.
- Ward, J. 1988. Eolian, fluvial and pan (playa) facies of the Tertiary Tsondab Sandstone Formation in the Central Namib Desert, Namibia. Sed. Geol., 55, 143-162.
- Ward, J. and Corbett, I. 1990. Towards an age for the Namib. *Monogr. Transv. Mus.*, 7, 17-26.