A note on Plio-Pleistocene insect cocoons from Prospekteerkop, Rietfontein, Northern Namibia

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Abstract :- Cocoons of invertebrates are rarely preserved as fossils, only a few reports existing in the literature. Yet many insect species produce cocoons as part of their life histories. We here report the discovery of what appear to be fossilised cocoons from Plio-Pleistocene cave breccia at Prospekteerkop, on farm Rietfontein in the Otavi Mountainland and try to identify them by comparing them to modern analogues among Lepidoptera (butterflies and moths) and Coleoptera (beetles). The specimens are most likely to have been made by a species of beetle.

Key words :- Plio-Pleistocene, Otavi Mountainland, fossilised cocoons.

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Introduction

The Otavi Mountainland (OML) is located in the north-central part of Namibia and as early as the late 19th century it received much attention on account of its base metal reserves which include copper, lead, zinc and vanadium, (Cairncross, 1997; Gebhard, 1999; Schwellnus, 1946). The OML is composed predominantly of Neoproterozoic carbonate rocks that have been modified by extensive chemical weathering processes that resulted in a rough karstic terrain endowed with many caves and fissures in which sediments and breccias accumulated. The spelean sediments of the OML have yielded abundant fossils of Middle Miocene to Recent age (Pickford & Senut, 2010).

At diverse sites in the OML, Pickford & Senut (2002, 2010) identified fossil remains among which micromammals predominated. The following groups were listed : Myriapoda (centipedes), Gastropoda (terrestrial snails - *Xerocerastus*), Amphibia, Squamata (lizards and snakes), Aves, Carnivora, Primates (Galagidae (bush babies), Hominoidea, Cercopithecidae), Tenrecidae, Macroscelididae (elephant shrews), Hyracoidea, Proboscidea, Chiroptera, Chrysochloridae (golden moles), Soricidae (shrews), Rodentia (Sciuridae, Gerbillinae, Gliridae, Muridae, Bathyergidae, Thryonomyidae, Pedetidae), Leporidae (hares), and Ruminantia (Giraffidae, Bovidae).

The mammalian fauna from the Prospekteerkop breccias, the existence of which was first mentioned by Schwellnus (1946), comprises two species of soricids (crocidurines), a macroscelidid (elephant shrew), three species of bat (two rhinolophoids and one vespertili-onid), a hare (*Pronolagus humpatensis*), a high diversity of rodents (*Graphiurus*, *Mystromys*, *Mastomys*, *Petromus*, *Steatomys*, *Malacothrix*, *Petromyscus*, *Tatera*, *Gerbillurus*, *Otomys*, *Rhabdomys*, *Zelotomys*, *Mus*, *Praomys*), a leopard (*Panthera pardus*), a dassie (*Procavia capensis*), two bovids (*Oryx*, *Antidorcas*) and a baboon (*Papio*) (Pickford & Senut, 2010; Mein, 2015). This fauna indicates correlation to the Plio-Pleistocene.

In 2022 and 2023 members of the Namibia Palaeontology Expedition discovered small ovoid fossils amongst the microfauna in the breccia occurrence at Prospekteerkop on Farm Rietfontein. Preliminary research indicates that they represent cocoons of an invertebrate, most probably of a species of coleopteran.

Stehr (2009) described a cocoon as a protective covering made of silk within which caterpillars of most moths, a few butterfly species, and several other insect orders such as Siphonaptera (fleas), Hymenoptera (ants, bees and wasps), Neuroptera (lacewings and antlions), and Trichoptera (caddis flies) pupate. Lea (1925) and Veatch (2020) reported on fossilised cocoons of the Australian weevil *Leptopius duponti* (Coleoptera) from Pleistocene localities in Australia.

According to Brasier *et al.* (2017) endogenous materials associated with pupation, such as cocoons, are not common in the fossil record. Therefore, these fossilised cocoons from Rietfontein are important and they may yield information about the environment of the area during the Plio-Pleistocene and the animals that lived here.

Moths, together with butterflies, comprise part of the order Lepidoptera. Today there are 481 genera and 890 species of Lepidoptera in Namibia (Kopij, 2017). However, according to the Namibia Biodiversity Database Web Site (Irish, 2023) 1,789 lepidopteran species currently live in Namibia and there are currently 4,058 species of Coleoptera in the country.

Out of the 4,593 lepidopteran fossil specimens described worldwide, 92.8% are body fossils and 7.2% are trace fossils. According to Sohn *et al*. (2015) only about 7% of these fossils have been formally named, and of the 145 lepidopteran fossil localities listed, 31 are Miocene, 23 are Pleistocene and Holocene, 22 are middle and late Eocene and 15 are early Oligocene.

Geological setting

The Prospekteerkop fossil site is located in the Otavi Mountainland on Farm Rietfontein (19°41’36"S 17°52’38"E) (Fig. 1, 2). It is close to the foot of a kopje which lies approximately 10 km north-north-east of the farmhouse. The fossiliferous breccia blocks lie next to and inside an old prospecting trench that is ca 2 metres wide, approximately 8 m long and 1.5 m deep (Fig. 3, 4). The trench exposes flowstone remnants (speleothems) in its southern end and the host rock surrounding the breccias is dolomite.

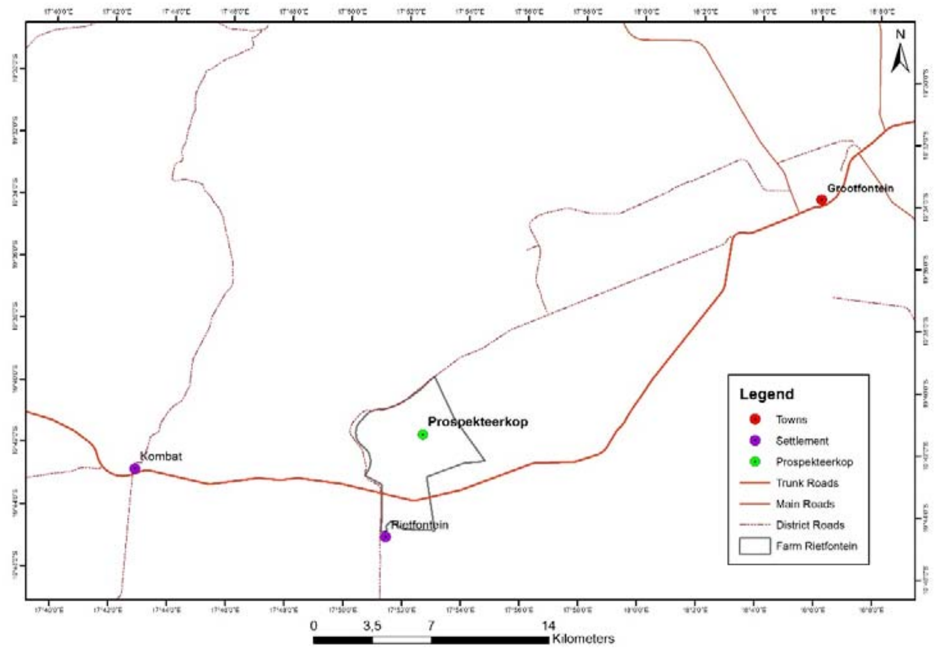

Figure 1. Prospekteerkop fossil locality on Farm Rietfontein in the Otavi Mountainland (map produced by Freddy Muyamba).

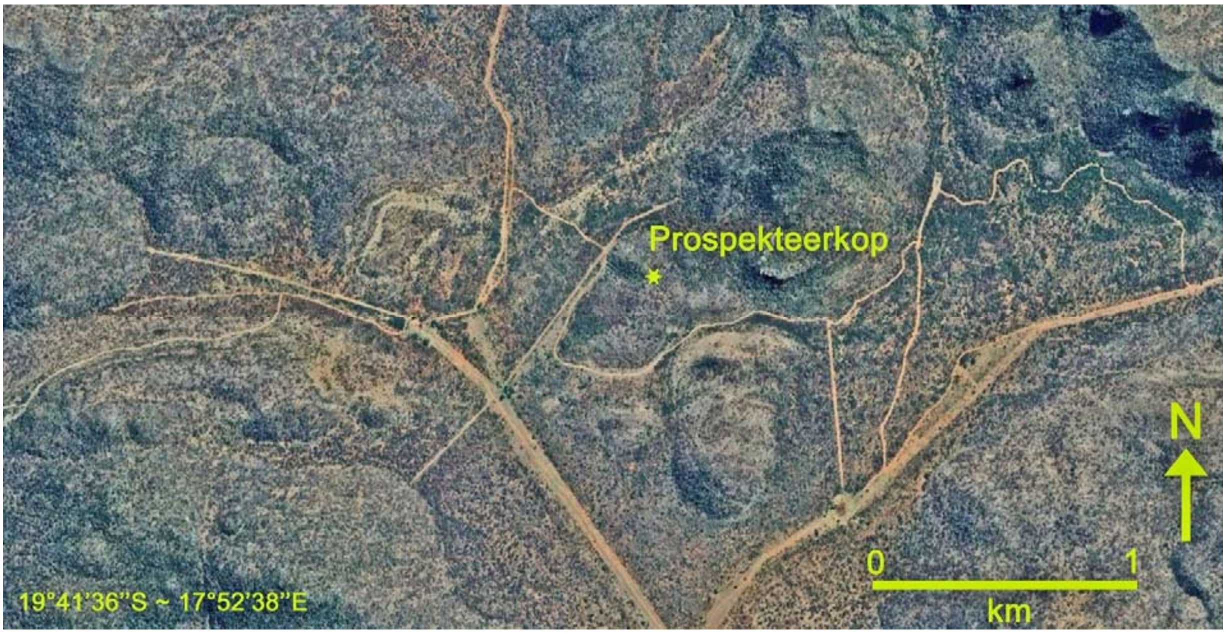

Figure 2. Position of the Prospekteerkop breccia dumps on Farm Rietfontein, Otavi Mountainland, Namibia. Map modified from Google Earth.

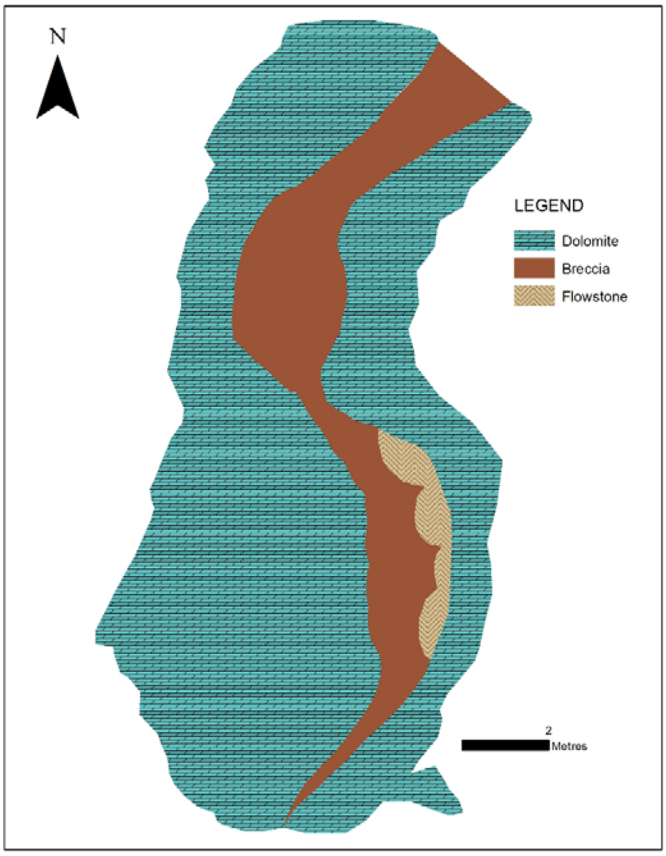

Figure 3. Prospekteerkop fossil site layout (figure prepared by Anna Upindi).

Figure 4. View of the old prospecting trench at the foot of Prospekteerkop (in the background). Grey blocks are dolomite, red ones are cave breccia.

Materials and Methods

In 2022 and 2023, palaeontological field surveys were carried out on Farm Rietfontein in the Otjozondjupa region, Grootfontein District.

Blocks of breccia containing fossilised micro- and macrofauna were collected for scientific analysis at the National Earth Science Museum of the Geological Survey of Namibia. Among the material collected were several insect cocoons.

Description of the Fossil Cocoons

The most complete fossil cocoon described herein is whitish, oval in shape and is preserved in a reddish-brown breccia. Its length is approximately 2.5 cm and its width is approximately 1.3 cm. It has a somewhat rough surface texture with several small cavities visible, which may be due to weathering, or possibly damage to the cocoon when it was still fresh. Small patches of sediment are stuck to the cocoon (Fig. 5).

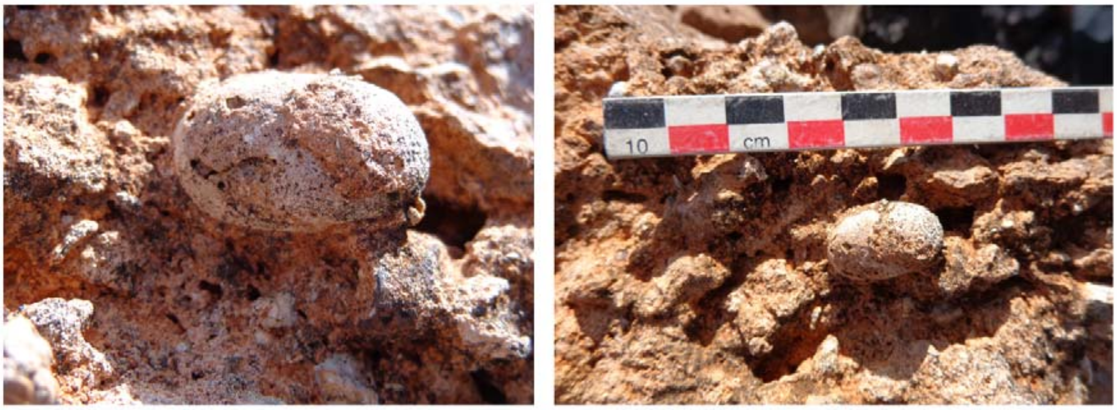

Figure 5. Fossilised cocoon from Prospekteerkop, Rietfontein.

Figure 6. Stereo images of a sectioned cocoon in cave breccia from Prospekteerkop, Otavi Mountains, Namibia. Note the greyish sediment 'halo' (in which there are fragments of petrified vegetation : yellow arrows) enclosing the cocoon for a thickness of ca 7 mm and which is partly coated by calcite crystals (blue arrows) (scale in cm).

A sectioned cocoon in breccia from Prospekteerkop is of interest on account of the fact that it is surrounded by a layer of greyish sediment ca 7 mm thick, that differs in colour from the surrounding redder sandy breccia (Fig. 6). This coating is itself covered by an irregular and incomplete layer of calcite crystals and the inner wall of the cocoon is lined with a similar layer of small crystals of calcite. The halo of sediment contains small angular fragments of petrified vegetation (Fig. 6). The length of the cocoon, as preserved, is 20.8 mm and the diameter in the middle is 12.5 mm. The surrounding halo of greyish sediment is 36.5 mm long x 22.8 mm in diameter, making for a coating that is ca 7 mm thick.

The way that the specimen is preserved suggests that it had a coating of organic matter, only parts of which were fossilised, but which persisted long enough for calcite to precipitate over parts of the surface. Most of the organic matter then rotted away slowly, leaving space for fine-grained sand to infill the void, much of the iron in the sand being reduced as it was replacing the organic matter. If this scenario is correct, then it suggests that the cocoon belonged to a beetle such as the garden fruit chafer (*Pachnoda*) that coats its cocoons in a relatively thick layer of organic debris (Fig. 12). These beetles typically construct their cocoons in compost-like debris in the soil profile.

Interpretation of the Cocoons

The entomological collections of the National Museum of Namibia were studied to determine whether any cocoons have been accessioned into the collections. The cocoons of the moths *Gonometa postica* and *Schausinna regia* were photographed and compared to the Rietfontein fossil cocoons. However, these were larger, more elongated and more irregularly shaped than the fossil ones.

Two entomologists who are experts on Namibian insects, Dr John Irish and Dr Rolf Oberprieler were consulted for advice on the identification of the fossil cocoons.

Dr Irish postulated that we may well be dealing with a cocoon, possibly of a Saturniidae moth, such as *Gonimbrasia* (Mopane moth), because its size and shape correspond well with the fossils from Rietfontein. However, he questioned what he saw as "*a possible longitudinal seam, especially visible along the left and bottom sides of the object*". We interpret this as an artefact of weathering.

Dr Oberprieler observed that the find is interesting, but that it may be difficult to propose a definite identification of the cocoon or cocoon-maker. He emphasised that there are many moth caterpillars that produce cocoons, but most of these cocoons look quite different from the Prospekteerkop cocoons. They tend to be more elongate, larger and less symmetrical. The smaller ones are soft, and as moth cocoons are made of silken fibre, they might not fossilise at all. According to the shape of the Rietfontein cocoons and the fact that they needed to be durable in order to be fossilised, he postulated that the most likely candidate, if indeed we are dealing with a moth cocoon, would be the slug moth, *Coenobasis amoena* of the family Limacodidae, which has also been recorded in Namibia. Its cocoon however is smaller, about 10 mm in length and it is attached to a tree branch. However, no fossil twigs have been observed at Prospekteerkop. Dr Oberprieler is currently studying weevils in Australia and alerted us that there are beetles whose larvae produce cocoons underground. Their cocoons become hard and can easily fossilise if the ground chemistry is suitable, especially if calcium is present. Articles about fossilised beetle cocoons, in particular weevils, have been published about Australian specimens, but so far little has been reported from Africa.

Figures 7-11 show various extant moth species from Namibia and their cocoons.

Figure 7. *Argema mimosa* moth and cocoon (images from Oberprieler, 1995b).

Figure 8. *Epiphora bauhiniae* moth and cocoon (images from Oberprieler, 1995a).

Figure 9. *Gonometa postica* moth and cocoon.

Figure 10. *Schausinna regia* moth and cocoons.

Figure 11. *Coenobasis amoena* moth, caterpillar and cocoon on a twig (images from Staude *et al*. 2023).

In contrast to moth cocoons, those of coleopterans, such as the garden fruit chafer, *Pachnoda sinuata*, have larger, rounder and more symmetrical cocoons that the beetle constructs in compost. The cocoon is approximately 2.5-3 cm in length and 2.5 cm in diameter. Plant matter is attached to the surface of the cocoon, as can be seen in Fig. 12.

Figure 12. *Pachnoda sinuata* A) adult beetle, B) cocoons coated in vegetable debris and C) larva inside broken cocoon (photo credits : Alexander Mocke).

Discussion

The literature on the fossil record of terrestrial arthropods from Africa is not extensive, but what has been described comprises body fossils (Leakey, 1952; Paulian, 1976; Morris, 1979; McKay & Rayner, 1986; Rayner & McKay, 1986; Rayner & Waters 1991; Rayner *et al*. 1991; Pickford & Senut, 2002; 2010) as well as bioconstructions made by insects (termite hives, termite mounds, ant nests, diverse cocoons) and spiders (spider webs) and other traces (foraging tunnels) (Coaton, 1981, 1973, 1975; Corbett, 1989; Crossley, 1986; Duringer *et al*. 2000; Harrison & Baker, 1997; Moore & Picker, 1991; Pickford, 2000, 2005, 2008; Ritchie, 1987; Sands, 1987; Seely & Mitchell, 1986; Tessier, 1959a, 1959b; Thackeray, 1994; Ward, 1988; Wilson & Taylor, 1964).

Among the body fossils described in the literature, beetles predominate (Paulian, 1976) whereas among the trace fossils, those attributed to termites are the most commonly described (Seely & Mitchell, 1986; Pickford, 2008). Soft tissue fossils are exceptionally rare in Africa but are known from Cretaceous crater infillings at Orapa, Botswana (Insects : Rayner & McKay, 1986) and from aeolianites of the Namib Desert (Spider webs : Pickford, 2000, 2005)

Kitching (1959) described a fossilised puparium from Plio-Pleistocene cave breccias at Makapansgat, South Africa, and the presence of insect cocoons has been listed at various Early Miocene localities in Kenya (Rusinga, Mfwanganu, Koru, Songhor, Kirimun : Pickford, 1982, 1986a, 1986b) and Uganda (Napak :

Musalizi *et al*. 2009; Pickford *et al*. 1986) but none of the material has been described in detail, although measurements of the Kirimun specimens were published (Pickford, 1982). For many years, East African fossil cocoons were misidentified as snake eggs (Musalizi *et al*. 2009).

In most of the publications dealing with fossil arthropods and their traces, there were discussions about their palaeoenvironmental significance. For this reason, it is important to put on record the discovery of fossilised cocoons at Prospekteerkop, Namibia.

Conclusion

The fossil cocoons from Prospekteerkop, Rietfontein, in northern Namibia, are not attributed to a specific invertebrate maker, although the available evidence suggests that two of them may have been made by a beetle such as the fruit chafer. Nevertheless, the specimens do indicate that an organism was living in northern Namibia during the Plio-Pleistocene that needed a cocoon to protect the pupa against adverse environmental conditions (e.g. aridity, heat), parasites or predators.

Taking into account the size, shape and symmetry of the cocoons, the most plausible conclusion is that they may have been constructed by a beetle which deposited its resistant casing, coated in vegetable matter, in the soil so that the pupa could pupate safely.

To date, there is no evidence that the cocoons were attached longitudinally to twigs, which, had this been the case, would have indicated that the cocoons might belong to a species of moth that attached its cocoons to the branches or twigs of trees well above ground level.

Therefore, on the basis of the available information, especially the symmetry and dimensions of the specimens and the halo of greyish sediment containing angular fragments of petrified plant debris, and the calcite crystals that surrounds one of them, we conclude that the most likely maker of the Prospekteerkop fossil cocoons was a species of coleopteran that constructed its cocoon in compost in the soil profile, and that attached organic debris to the surface of the cocoon, as is done by fruit chafers. Until the maker of the cocoons is securely identified it will be difficult to base reconstructions of the palaeoenvironment upon them.

Other research methods such as X-ray Tomography may shed light on the possible contents and immediate surroundings of the cocoons. If so this could narrow down the identification of their maker.

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References

Brasier, A.T., Cotton, L.J., Garwood, R.J., Baker-Brian, J., Howlett, E. & Brasier, M.D. 2017. Earliest Cretaceous cocoons or plant seed structures from the Wealden Group, Hastings, UK. *In*: Brasier, A.T., McIlroy, D. & McLoughlin, N. (Eds) Earth System Evolution and Early Life: A Celebration of the Work of Martin Brasier. London, *Geological Society of*

London, Special Publications, **448**, 399-411. Doi:https://doi.org/10.1144/SP448.21.

Cairncross, B. 1997. The Otavi Mountain Land Cu-Pb-Zn-V Deposits. *The Mineralogical Record*, **28**, 109-157.

Coaton, W. 1981. Fossilised nests of Hodotermitidae (Isoptera) from the Clanwilliam District, Cape Province. *Journal of the Entomological Society of South Africa*, **44**, 79-81.

Coaton, W.G.H. & Sheasby, J.L. 1973. National survey of the Isoptera of southern Africa. 3. The genus *Psammotermes* Desneux. *Cimbebasia*, Series A, **3**, 19-28.

Coaton, W.G.H. & Sheasby, J.L. 1975. National survey of the Isoptera of southern Africa. 10. The genus *Hodotermes* Hagan (Hodotermitidae). *Cimbebasia*, Series A, **3**, 105-138.

Corbett, I.B. 1989. *The Sedimentology of Diamondiferous Deflation Deposits within the Sperrgebiet, Namibia*. PhD Thesis, University of Cape Town, 1-430.

Crossley, R. 1986. Sedimentation by termites in the Malawi Rift Valley. *In*: Frostick, L., Renaut, R., Reid, I. & Tiercelin, J. (Eds) Sedimentation in the African Rifts. *Geological Society Special Publication*, **25**, 191-199.

Duringer, P., Brunet, M., Cambefort, Y., Likius, A., Mackaye, H., Schuster, M. & Vignaud, P. 2000. First discovery of fossil dung beetle brood balls and nests in the Chadian Pliocene Australopithecine levels. *Lethaia*, **33**, 277-284.

Gebhard, G. 1999. *Tsumeb II*. GG Publishing, Grossenseifen, Germany, 328 pp.

Harrison, T. & Baker, E. 1997. Paleontology and biochronology of fossil localities in the Manonga Valley, Tanzania. *In*: Harrison, T. (Ed.) Neogene Paleontology of the Manonga Valley, Tanzania. *Topics in Geobiology,* **14**, 362-393, Plenum, New York.

Irish, J. 2023. *Namibia Biodiversity Database Web Site. Page: Order Lepidoptera in Namibia. Interpretive collation based on the combined published sources for all included taxa, as listed*. URL: https://biodiversity.org.na/taxondisplay.php?nr=3727, accessed at: 2023-11-07T11:40:07+02:00.

Kitching, J.W. 1959. Note on a fossil puparium from the Limeworks Quarry, Makapansgat, Potgietersrus. *South African Journal of Science*, **55**, 280-281.

Kopij, G. 2017. *Invertebrate Fauna of Namibia, Biodiversity and Bibliography*. Department of Integrated Environmental Sciences, University of Namibia, Oshakati, Ogongo Campus, Namibia, 120 pp.

Lea, A.M. 1925. Notes on some calcareous insect puparia. *Records of the South Australian Museum*, **3**, 35-36.

Leakey, L.S.B. 1952. Lower Miocene invertebrates from Kenya. *Nature*, **169**, 624-625.

McKay, I.J. & Rayner, R.J. 1986. Cretaceous fossil insects from Orapa, Botswana. *Journal of the Entomological Society of South Africa*, **49**, 7-17.

Mein, P. 2015. *African Micromammal Palaeontology Archives of Pierre Mein*, Unpublished compilation by M. Pickford. PDF copies in author's personal library and at the Geological Survey of Namibia. 1,636 pp.

Moore, J.M. & Picker, M.D. 1991. Heuweltjies (earth mounds) in the Clanwilliam District, Cape Province, South Africa: 4,000 year old termite nests. *Oecologia,* **86**, 424-432.

Morris, S. 1979. A new fossil terrestrial isopod with implications for the East African Miocene landform. *Bulletin of the British Museum of Natural History (Geology)*, **32**, 71-75.

Musalizi, S., Senut, B., Pickford, M. & Musiime, E. 2009. Geological and palaeontological archives relating to Early Miocene localities of Uganda, 1957-1969. *Geo-Pal Uganda*, **1**, 2-96.

Oberprieler, R. 1995a. *Epiphora bauhiniae* (Guérin-Méneville). *In*: Oberprieler, R. *The Emperor Moths of Namibia*. Ekogilde, Hartbeespoort, South Africa, pp. 32-33.

Oberprieler, R. 1995b. *Argema mimosae* (Boisduval). *In*: Oberprieler, R. *The Emperor Moths of Namibia*. Ekogilde, Hartbeespoort, South Africa, pp. 34-35.

Paulian, R. 1976. Three fossil dung beetles (Coleoptera, Scarabeidae) from the Kenya Miocene. *Journal of the East African Natural History Society and National Museum*, **31** (**158**), 1-4.

Pickford, M. 1982. Report on invertebrates from Kirimun. *In*: Ishida H. & Ishida S. (Eds) *Study of Tertiary Hominoids and their Palaeoenvironments in East Africa*. **1**, 140-145. Osaka, Osaka University Press.

Pickford, M. 1986a. Sedimentation and fossil preservation in the Nyanza Rift System, Kenya. *In*: Frostick L. *et al* (Eds) Sedimentation in the African Rifts. *Geological Society Special Publication*, **25**, 345-362.

Pickford, M. 1986b. Cainozoic palaeontological sites of Western Kenya. *Münchner Geowissenschafliche Abhandlungen*, **A 8**, 1-151.

Pickford, M. 2000. Fossil spider's webs from the Namib Desert and the antiquity of *Seothyra* (Araneae, Eresidae). *Annales de Paléontologie*, **86**, 147-155.

Pickford, M. 2005. The Namib's amazing fossil spider webs. *Quest,* Johannesburg, South Africa, **1**(**4**), 30-32.

Pickford, M. 2008. Arthropod bioconstructions from the Miocene of Namibia and their palaeoclimatic implications. *Memoir of the Geological Survey of Namibia*, **20**, 53-64.

Pickford, M. & Senut, B. 2002. *The Fossil Record of Namibia*. Ministry of Mines and Energy, Geological Survey of Namibia, Windhoek, Namibia, 39 pp.

Pickford, M. & Senut, B. 2010. Karst geology and palaeobiology of northern Namibia. *Communications of the Geological Survey of Namibia*, **21**, 1-74.

Pickford, M., Senut, B., Hadoto, D., Musisi, J. & Kariira, C. 1986. Nouvelles découvertes dans le Miocène inférieur de Napak, Ouganda Oriental. *Comptes Rendus de l'Académie des Sciences, Paris,* **302**, 47-52.

Rayner, R.J. & McKay, I.J. 1986. The treasure chest of the Orapa diamond mine. *Botswana Notes and Records,* **18**, 55-61.

Rayner, R.J. & Waters, S.B. 1991. Floral sex and the fossil insect. *Naturwissenschaften*, **78**, 280-282.

Rayner, R.J., Waters, S.B., McKay, I.J., Dobbs, P.N. & Shaw, A.L. 1991. The mid-Cretaceous palaeoenvironment of central Southern Africa (Orapa, Botswana). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **88**, 147-156.

Ritchie, J.M. 1987. Trace fossils of burrowing Hymenoptera from Laetoli. *In*: Leakey, M.D. & Harris, J. (Eds) *Laetoli: A Pliocene Site in Northern Tanzania*, pp. 433-450. Oxford, Clarendon.

Sands, W.A. 1987. Ichnocoenoses of probable termite origin from Laetoli. *In*: Leakey, M.D. & Harris, J. (Eds) *Laetoli: A Pliocene Site in Northern Tanzania*, pp. 409-433. Oxford, Clarendon.

Seely, M. & Mitchell, D. 1986. Termite casts in Tsondab Sandstone? *Palaeoecology of Africa*, **17**, 109-112.

Schwellnus, C.M. 1946. Vanadium deposits in the Otavi Mountains, South-West Africa. *Transactions of the Geological Society of South Africa*, **48**, 49-73.

Sohn, J-C., Labandeira, C.C. & Davis, D.R. 2015. The fossil record and taphonomy of butterflies and moths (Insecta, Lepidoptera): implications for evolutionary diversity and divergence-time estimates. *BMC Evolutionary Biology*, **15**, 1-15.

Staude, H.S., Picker, M. & Griffiths, C. 2023. *Southern African Moths and their Caterpillars*. Struik Nature, ISBN 978 1 77584 795 3, 464 pp.

Stehr, F.W. 2009. Cocoon. *In*: Resh, V.H. & Cardé, R.T. (Eds), *Encyclopedia of Insects*, Second Edition, Elsevier/Academic Press, 1,132 pp.

Tessier, F. 1959a. La latérite du cap Manuel à Dakar et ses termitières fossiles. *Comptes Rendus de l'Académie des Sciences, Paris,* **248**, 3320-3322.

Tessier, F. 1959b. Termitières fossiles dans la latérite de Dakar (Sénégal): Remarques sur les structures latéritiques. *Annales de la Faculté des Sciences, Université de Dakar,* **4**, 91-132.

Thackeray, G.D. 1994. Fossil nests of sweat bees (Halictinae) from a Miocene palaeosol, Rusinga Island, western Kenya. *Journal of Paleontology.* **68**, 795-800.

Ward, J.D. 1988. Eolian, fluvial and pan (playa) facies of the Tertiary Tsondab Sandstone Formation in the Central Namib Desert, Namibia. *Sedimentary Geology*, **55**, 143-162.

Veatch, S.W. 2020. *Ancient weevil pupal cases: Trace fossils from Australia's Pleistocene*. https://depositsmag.com/2020/07/12/ ancient-weevil-pupal-cases-trace-fossils-from-australias-pleistocene/, accessed on: 2023-11-20.

Wilson, E.O. & Taylor, R.W. 1964. A fossil ant colony: new evidence of social antiquity. *Psyche*, **71**, 93-103.