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2016-09
Academy of Science of South Africa (ASSAf)
http://hdl.handle.net/10539/21287
Randolph-Quinney, P.S. et al. 2016. Response to Thackeray (2016) - the possibility of lichen growth on bones of Homo naledi: Were they exposed to light? South African Journal of Science 112(9/10):a0177

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Response to Thackeray (2016) – The possibility of lichen growth on bones of *Homo naledi*: Were they exposed to light?

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KEYWORDS:
Rising Star Cave; mineral staining; taphonomy; sedimentology

HOW TO CITE:
Randolph-Quinney PS, Backwell LR, Berger LR, Hawks J, Dirks PHGM, Roberts EM, et al. Response to Thackeray (2016) – The possibility of lichen growth on bones of *Homo naledi*: Were they exposed to light? S Afr J Sci. 2016;112(9/10), Art. #a0177, 5 pages. http://dx.doi.org/10.17159/sajs.2016/a0177

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Thackeray[1] questions the hypothesis of deliberate body disposal in the Rising Star Cave by *Homo naledi,* as proposed by Dirks and colleagues[2]. Thackeray proposes that lichens produced mineral staining on the skeletal remains of *H. naledi*. As lichens require some exposure to light, in Thackeray's opinion, the presence of mineral staining necessitates either a direct entrance deep into the Rising Star Cave that once admitted light into the Dinaledi Chamber, or relocation of mineral-stained bones from a location exposed to light. Here we consider multiple lines of evidence that reject Thackeray's hypothesis that lichens deposited mineral staining upon the surface of these skeletal remains. We welcome the opportunity to address the inferences presented by Thackeray, and further hope that this response may dispel misinterpretations of our research[2], and of other areas of the scientific literature that bear upon site formation processes at work within the Rising Star Cave system.

Briefly, we review Thackeray's[1] chain of inference: (1) lichens can be found today growing as colonies on the surface of chert, dolomite and sub-aerially exposed bones found within the Cradle of Humankind; (2) some colonies of lichen on extant rocks overlie deposits of black manganese oxy-hydroxide on the rock surfaces; (3) some manganese (Mn) mineral deposits appear as diffuse spots, which have some resemblance to the shape and surface patterning of some lichen colonies; (4) small dots or spots of Mn present on the surface of the bones of *H. naledi* may, therefore, have been produced as a consequence of lichen growth; (5) the growth of lichen colonies requires light, either in the open environment or within the light zone of caves; (6) by extension, the growth of lichen on the bones of *H. naledi* required the presence of subdued, but essential lighting; (7) the presence of such lighting indicates the existence of a second entrance into the Dinaledi Chamber; therefore (8) a re-assessment of the deliberate body disposal hypothesis is required.

We must state from the outset that we have no disagreement with conditions (1) to (3) above, which comport with our own first-hand observations from geological outcrops within the Cradle of Humankind. Lichens do indeed grow on chert, dolomite and bone; they do sometimes overlie Mn deposits; and there is often a diffuse spot pattern in their surface distribution. But available evidence is not consistent with the rest of this line of reasoning. We here combine previously published taphonomic and geological data from the Dinaledi Chamber[2], together with a fuller review of the literature and re-interpretation of photographic evidence presented by Thackeray[1].

Abundant actualistic research documents mechanisms of Mn deposition on bone that have nothing to do with lichens.[3] Mn and iron (Fe) deposition on bone in dark, wet, alkaline cave contexts like that found in the Dinaledi Chamber is normally a result of diagenetic recrystallisation of bone, incorporating trace elements from surrounding sediment and water via a diffusion–absorption process.[4] In dolomitic caves, which have relatively high pH and oxidising redox, the alkali metals sodium and potassium and the alkaline earth metals calcium and magnesium are the most abundant soluble cations, while the transition metals copper, Fe and Mn are the least abundant, and the alkaline earth metals strontium and barium, and the transition metal zinc are of intermediate availability.[5] Under these cave conditions, the stable forms of Fe and of Mn are hydrates and manganese oxide compounds, respectively. Precipitation of these highly insoluble hydrates and oxides varies with pH and tends to form crusts and coatings.[6] Mn is mainly located on the surface and crack edges of fossil bones, whereas Fe shows deeper penetration into the bone matrix.[7,8] Mn, which naturally occurs in groundwater, enters the bone environment as mobile Mn^{2+}. In the presence of free O_2, the oxidation of Mn^{2+} to Mn^{3+} and ultimately to insoluble Mn^{4+} is thermodynamically favourable, but proceeds extremely slowly unless mediated by microbial action, which is chemotrophic and does not require light.[9,10] Oxidised Mn precipitates as a number of manganese oxides and hydroxides.[11] Similarly, under the same conditions, mobile ferrous iron (Fe^{2+}) approaching the bone may be oxidised to ferric iron (Fe^{3+}) which rapidly precipitates as limonite ($FeOOH.nH_2O$), which later usually undergoes transformation to goethite (FeOOH). Alternatively, pyrite (FeS_2) is formed instead of haematite via precipitation of iron sulfide as decaying collagen releases sulfide ions into solution.[12] Black or dark brown colour of fossil bones is a result of high levels of pyrite and manganese and iron oxide and hydroxide coatings. To summarise, processes that do not involve lichens are sufficient to explain the presence of Mn stains on fossil bone in contexts like that found within the Dinaledi Chamber today.

Mn, Fe and other mineral deposition occurs on a large fraction of the skeletal material from the Dinaledi Chamber in a variety of depositional forms. Thackeray[1] chose to illustrate the pattern of Mn staining (specifically spotting) on only a single specimen. In his Figure 6 he provides a photograph of tibial specimen U.W. 101-996 (his figure caption misidentifies this specimen as U.W. 101-1070) with the figure legend:

> *Tibial shaft specimen U.W. 101-1070* [sic] H. naledi *from the Dinaledi Chamber, with dotted coatings of manganese oxy-hydroxide. It is suggested that the black dots result, at least in part, from the growth of lichen as a bacterial-algal-fungal symbiont that includes a photobiont. The growth of lichen on such bone surfaces, even for a limited time, may have occurred in subdued, but essential lighting. Note the* distribution [our emphasis] *of manganese oxy-hydroxide, extending from a continuous matt to more dotted occurrences; this pattern is* potentially analogous [our emphasis] *to the dispersal of lichen from a central thallus.*[1]

However, the distribution of Mn staining is not only on this one side of the specimen, but on all anatomical sides (anterior, posterior, medial and lateral), as shown in Figure 1. Such a distribution can also be seen on many specimens (for example, in Figure 2, specimen U.W. 101-1070, correctly attributed here). The distribution of Mn staining on the Dinaledi Chamber material is generally circumferential, occurring on multiple sides of bones. That distribution is not compatible with lichen growth in the present context, and there are significant reasons to reject the hypothesis that the Dinaledi Chamber is a secondary deposit.[2,13]



(a) Medial aspect; (b) lateral aspect; (c) close-up of anterior shaft; (d) mid shaft; (e) close-up of distal end seen in (a); (f) close-up of distal end seen in (b).

Figure 1: Patterns of mineral staining affecting tibia U.W. 101-996. Note the distribution of manganese (black) and iron (yellow-red) oxides around the circumference of the shaft.

Instead, we have abundant evidence for Mn formation which occurs at the interface between soil matrix and free air. Our published analysis of the mineral staining on the Dinaledi Chamber skeletal material demonstrates not only the presence of black spots as noted by Thackeray[1], but also tide marks of both Mn and Fe minerals on many of the specimens[2]. An example of these tide marks is shown in Figure 3. Lichens do not create such tide marks. These patterns form at the interface of soil and free air, and are a reflection of the function of the relative position of individual bones (or conjoin fragments) in the soil profile.[2] Such patterns of mineral deposition are most parsimoniously explained by bone to soil matrix contact[3,14] and are inconsistent with lichen growth.

So what evidence points Thackeray[1] toward lichens? Thackeray's citation for lichen involvement is his own technical note[15] in which he suggested a possible link between manganese dioxide staining and lichen growth on hominin crania from Sterkfontein and Swartkrans. This note, similar to his current contribution, posits merely that 'the spotty, discontinuous distribution of young lichen thalli appears to be analogous to the spotty distribution of MnO_2 on at least some hominid crania'[3(p.28)]. To support this hypothesis, it is incumbent upon Thackeray to quantify this resemblance in some way and show that it is unlikely to occur by chance. We have no opinion about whether lichen has deposited Mn on surface rocks such as those illustrated from Kromdraai (Figures 2 and 3 in Thackeray[1]). However, the lichen thalli illustrated in Thackeray's photographs do not have similar sizes to the Mn spots he has chosen to illustrate together with them. Nor do they have a similar density distribution. A very simple mode of quantification is to count the number of lichen thalli per square centimetre and the number of Mn spots; in the illustrated examples, these appear to be completely dissimilar. Further, Thackeray might have attempted to quantify the overall shape of lichen colonies and the overall shape of Mn staining. From his illustrations, we do not detect any such similarity except in the most general sense, in that they both have some dendritic portions, and thus any association with lichen may be a case of visual pareidolia.[16] As such, any possible causal link awaits empirical testing and validation. Thackeray admits this is the case, indicating that '…long-term experimental work on lichen on bone substrates in the Cradle of Humankind is planned for a 10-year period, in and around cave environments'[1(p.5)].

In addition to lichen, Thackeray suggests[1(p.5)] that snails and beetles could indicate the presence of leaf litter (on which they feed), which would be found near the cave entrance and therefore in a situation with diffuse light. However, as noted by Dirks and colleagues[13], snails have been recognised to colonise dark caves to considerable depth[17], and are far from restricted in diet to just plant matter[18]. *Gulella* sp. and *Euonyma varia* (Connolly, 1910) occur in large numbers in the Rising Star Cave system, including in deep chambers in the dark zone, and may well be responsible for some of the bone surface modifications on the fossils. Subulinid snails (including *Euonyma*) are largely omnivorous and are thus not dependent on green plant material as a food source (Herbert D 2016, personal communication, January 28), while *Gullela* spp. are carnivorous and feed mostly on other snails.[18]



Figure 2: Patterns of mineral staining affecting tibia U.W. 101-1070. Note differential mineral staining patterns between conjoined fragments at the distal end.

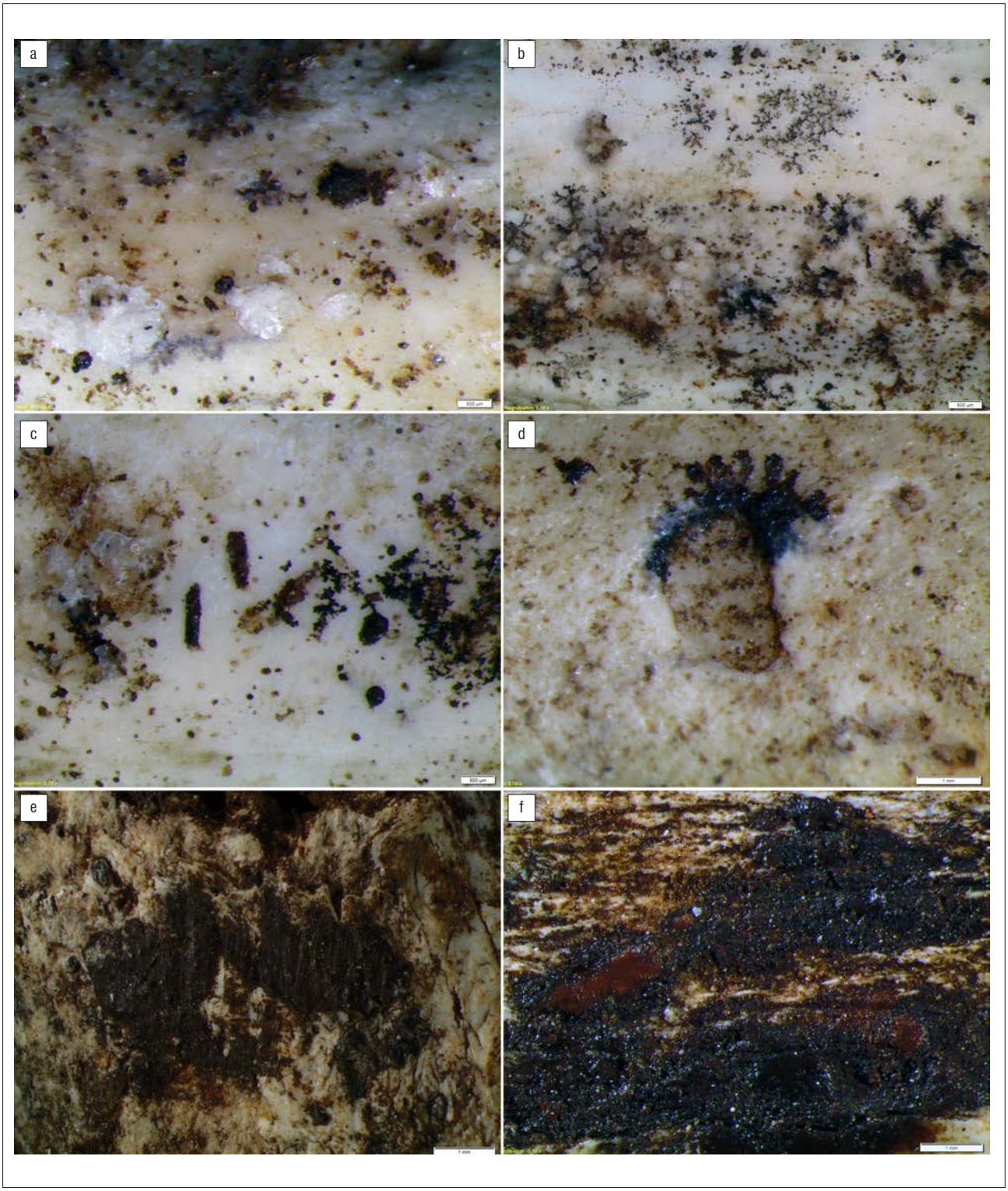


Figure 3: Specimen U.W. 101–419 Cranium A(1) displaying tide lines of mineral staining which extends across different vault fragments. Tide lines mark a contact boundary between the bone surface and surrounding sediment, and indicate the resting orientation of the bone during precipitation of the stains.

Thus the notion that snails are light-dwelling, leaf-litter feeders is incorrect, and bone surface modification by snails cannot be used to imply a close entrance to the surface or redeposition of the hominin fossil material from a location near light. Furthermore, much of the radula damage observed on the bones of *H. naledi* occurs *after* they were mineralised – therefore most invertebrate damage was probably produced inside the dark Dinaledi Chamber on bones already covered in coatings of manganese and iron oxide deposits (Figure 4).

Our work on the taphonomy and geology of the Dinaledi Chamber has been multidisciplinary, and we re-emphasise (as in Dirks et al.[2]) that any hypothesis must be consistent with all lines of evidence including geological, geochemical and taphonomic data. Thackeray proposes that an alternative opening to the Dinaledi Chamber, capable of transmitting diffuse light from the surface to this location more than 30 m underground, may have existed at the time the fossils were deposited. He cites the commentary of Val[19], who likewise suggested that the fossils were once close to the surface in an environment with some light. Neither critic considers the strong geological or sedimentological evidence against such a scenario.[13] As detailed in Dirks and colleagues[2], the basic stratigraphic development of the Dinaledi Chamber comprises two facies subdivided into three stratigraphic units. Of these, hominin remains are found in Unit 2 remnants, with the bulk of the assemblage derived from Unit 3 – which accumulated along the floor of the chamber and is composed of largely unconsolidated sediment derived from weathering and erosion of Units 1 and 2.[2] Sedimentological analyses indicate that the clay-rich sediments making up these units were derived from in-situ weathering, and from exogenous clays and silts, which entered the chamber through fractures that prevented passage of coarser-grained materials. Thus the infill of the Dinaledi Chamber is the end product of a series of filters or traps, which winnowed out all large-grained sediments or clastic material, en route to final deposition within the chamber. The sediment inside these fossil-bearing units of the Dinaledi Chamber is significantly different in particle size and composition[2] from the neighbouring Dragon's Back Chamber, which is presently the only route from the Dinaledi Chamber toward the surface. If the fossils had been deposited at a time when there existed a larger opening into the Dinaledi Chamber, a secondary opening, or any substantially more open route to the surface, the sediment would not have these properties. Further, if the entrance to the Dinaledi Chamber had been illuminated and, therefore, accessible to surface fauna, or if there had not been special selection for only hominins, the bones of non-hominin fauna should be evident within the assemblage, in addition to other taphonomic markers of sub-aerial exposure, which are absent.[2,13]

In summary, we find that Thackeray's hypothesis of lichen deposition of Mn upon *H. naledi* fossil material is inconsistent with available evidence. Published evidence indicates that access to the Dinaledi Chamber was restricted to a single species of large-bodied animal, deposited over time, to the exclusion of all other animal forms during the period of the *H. naledi* depositional event.[2] Any alternative model must allow fleshed and articulated remains to enter the chamber, including articulated hands and feet[20,21], which are areas of anatomy that in articulation are unlikely to survive even short transport unless held together by soft tissues at the time of transport[22,23]. Furthermore, any other model must be restrictive enough that very limited externally derived sediments or organic material entered the chamber. Given these facts, we see nothing presented by Thackeray[1], or other commentators[19], that disproves the deliberate body disposal hypothesis we have put forward[2].



Scales in (a) and (b) = 500 µm; (c)–(f) = 1 mm.

Figure 4: (a) Black manganese deposits above and below petals of calcium carbonate on the bone surface (U.W. 101-40b). Dendrites penetrate bone and tooth surfaces, sometimes staining them grey. (b) Black manganese and orange iron oxide deposits on specimen U.W. 101-35. Note the dendritic pattern and tiny balls of calcium carbonate and manganese on the lower half of the bone. (c) Iron oxide deposit associated with balls of manganese oxide and modern frass in the centre of specimen U.W. 101-40c. The occurrence of iron and manganese dendrites suggest a microbial origin for the pattern of deposition. (d) Manganese deposit presenting as an amorphous ink-like stain on U.W. 101-965, which appears to have been partially removed by a gastropod. (e) Thick manganese coating on top of an iron oxide deposit on specimen U.W. 101-711. (f) Second-generation iron oxide deposit on a manganese coating that overlies an iron oxide one on specimen U.W. 101-312.

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