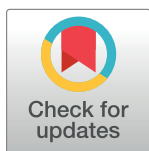


RESEARCH ARTICLE

A possible later stone age painting of a dicynodont (Synapsida) from the South African Karoo

Julien Benoit *

Evolutionary Studies Institute and School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa

* Julien.benoit@wits.ac.za

Abstract

The Horned Serpent panel at La Belle France (Free State Province, South Africa) was painted by the San at least two hundred years ago. It pictures, among many other elements, a tusked animal with a head that resembles that of a dicynodont, the fossils of which are abundant and conspicuous in the Karoo Basin. This picture also seemingly relates to a local San myth about large animals that once roamed southern Africa and are now extinct. This suggests the existence of a San geomyth about dicynodonts. Here, the La Belle France site has been visited, the existence of the painted tusked animal is confirmed, and the presence of tetrapod fossils in its immediate vicinity is supported. Altogether, they suggest a case of indigenous palaeontology. The painting is dated between 1821 and 1835, or older, making it at least ten years older than the formal scientific description of the first dicynodont, *Dicynodon lacerticeps*, in 1845. The painting of a dicynodont by the San would also suggest that they integrated (at least some) fossils into their belief system.

OPEN ACCESS

Citation: Benoit J (2024) A possible later stone age painting of a dicynodont (Synapsida) from the South African Karoo. PLoS ONE 19(9): e0309908. <https://doi.org/10.1371/journal.pone.0309908>

Editor: Dawid Surmik, University of Silesia, POLAND

Received: July 23, 2024

Accepted: August 20, 2024

Published: September 18, 2024

Copyright: © 2024 Julien Benoit. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the manuscript and its Supporting Information files.

Funding: This research was financially supported by the DSI-NRF African Origins Platform (AOP210218587003; UID: 136505). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Introduction

A crucial, yet outstanding question about the history of palaeosciences is that of palaeontological indigenous knowledge in the South African Karoo. The almost continuous Permo-Jurassic fossil record of the South African Karoo chronicles the rise, diversification, and fall of the Therapsida, as well as the evolutionary origins of mammals, turtles, dinosaurs, and lizards, providing many intermediate species each documented by dozens of specimens [1–4]. The abundance of tetrapod fossils in the Karoo and their quality of preservation both make it a konzentrat and konservat lagerstatten [1,5,6]. Given the wealth of fossils that the Main Karoo Basin and other Karoo-aged basins have delivered, and the long human occupation of this part of the African continent, the existence of a long-standing indigenous knowledge of fossils is very likely [7,8]. Yet, the study of African indigenous palaeontology is still fairly young [7,9–12], and the evidence remains accordingly sparse and debatable, especially given the scarcity of written accounts. Although patchy, a growing record of geomyths, place names, written accounts, and archaeological evidence supports that many southern African cultures knew and, in some cases, inquired about the fossils around them [7,8].

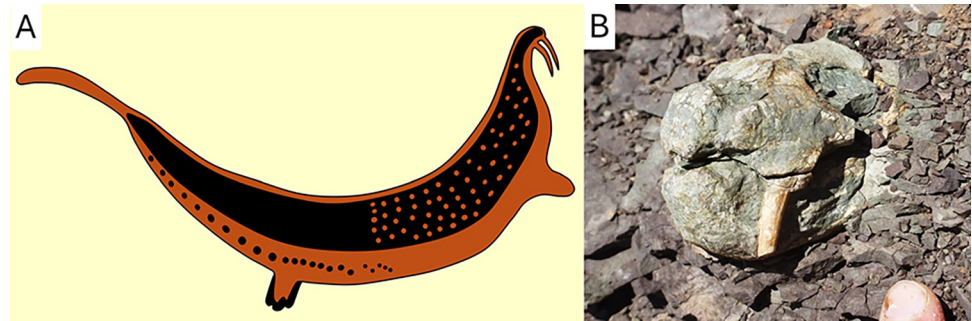


Fig 1. The tusked animal of the Horned Serpent panel compared to the skull of a dicynodont. A, the tusked animal of the Horned Serpent panel redrawn from Stow and Bleek [13]. B, skull of a *Diictodon feliceps* (BP/1/8140, Jansfontein, Victoria West District) photographed by the author in situ at the moment of its discovery, before excavation, and unprepared.

<https://doi.org/10.1371/journal.pone.0309908.g001>

The Horned Serpent panel, in the Koesberg mountains, gorgeously depicts elements of the San culture and was partly figured and described by Stow and Bleek [13] in plates 36–39. The rock art was made at an unknown date by the “Bushmen of the East” [14], now referred to as the /Xam speaking San [15]. One of these elements is an unidentified animal that bears two enlarged tusks, making it superficially look like a walrus (Fig 1A). This walrus-like figure has been the object of much speculation regarding its identity, because no representative of the Odobenidae lives or has ever lived nearby sub-saharan African coasts [16–18]. Tusked creatures (more or less imaginary and composite) are not rare in San rock art, including tusked lion, snake, antelopes, and people; but in those cases, the tusks are always curved upwards, like they do in warthogs and bushpigs [19–21], not downwards as in the tusked animal from La Belle France (Fig 1A).

The question of the identity of this animal has been dismissed because it is seemingly a rain-animal from the San “spirit-realm” [13], which is spiritual by essence and does not have to be realistic [18]; however, this does not address the question of what inspired this figure in the first place. Even the most fantastic elements of San art, such as therianthropes and rain-animals, are based on actual animals and phenomena [13,21–25]. The San spiritual pantheon is directly inspired from their real-life environment and the fantastic beings they painted are thus always an amalgamation of different existing animals [13,14,21–23,25–27]. As such, whether fantastic or not, the question of what inspired this tusked animal remains open.

The /Xam speaking San, who made the Horned Serpent painting, occupied the Karoo area [15], a landscape in which the fossil-richness is mostly due to the overly abundant and often well-preserved dicynodonts, a group of tusked therapsids [1,2,5,28,29]. In many cases, their skulls are naturally exposed by erosion in spectacular ways (Fig 1B), making them easy to find and collect, and their tusks are so conspicuous that their anatomy is not difficult to interpret, even to the untrained eyes. The downturned tusks of dicynodonts resemble those of the tusked animal of the Horned Serpent Panel (Fig 1).

Archaeological evidence directly supports that the San did find and transport fossils over long distances [7,8], and could interpret them in surprisingly accurate ways [11,12]. If the San could identify the fossilised skulls of dicynodonts as belonging to once alive animals, it is possible that their tusked faces could have contributed to their rock art. In this respect, it is noteworthy that, to the San of the Koesberg, the animals depicted on the Horned Serpent panel were real and used to live among them: “The Bushmen of the east [. . .] declare that there were at one time a number of animals living in the country in the days of their forefathers, which are now extinct and nowhere to be found in Southern Africa. Some of these are described as

great monstrous brutes, exceeding the elephant or hippopotamus in bulk.” (p. 131 in [14]). In the next page of the same book, the tusked animal is described as an entity distinct from the rain-animal (referred to as ‘Kou-teign-Koo-rou’) and the Serpent (referred to as ‘Koo-be-eng’) [14]. In addition to its tusks, the extraordinary size of the animal evokes the heavily mineralised bones and disproportionately enlarged skulls of some dicynodonts found in abundance in the Main Karoo Basin, such as *Kannemeyeria*, *Lystrosaurus*, and *Daptocephalus* [2,6,28,30].

If the La Belle France painting pictures a dicynodont, it would have been made independently from, and perhaps before, the discovery of *Dicynodon lacerticeps*, the first dicynodont described in the western scientific literature [31]. This could be the oldest depiction of a dicynodont ever made. This possibility is intriguing and warrants scrutiny.

In this contribution, the Horned Serpent panel was re-examined to address its accuracy and determine its age. The accuracy of Stow and Bleek’s [13] reproductions has been questioned, which may alter significantly the interpretation of the depicted scenes [32], and as such, first hand photographs of the paintings were made. The palaeontology and geology of La Belle France were also explored to assess the fossil richness of the area and its potential for supporting a geomyth.

Material and methods

The paintings were located thanks to the help of Mr. and Mrs. Swanepoel, the landowners, and Mr. and Mrs. Kruger, to whom the author is infinitely grateful. The paintings were photographed using a regular camera. Fig 2A shows what the photographs look like without enhancement, but the closeups in Figs 2B–2E and 3A are slightly enhanced for readability (contrast, temperature, and saturation).

Stow and Bleek [13] locate the “Brakfontein Cave” on farm La Belle France (plot La Belle France 458), which is misleading because the paintings are neither on La Belle France 458 nor Brakfontein 83, but on plot Alpha 872. All three farm plots belong to the same landowner and access to Alpha 872 is through La Belle France 458, so to avoid confusion and ensure continuity with Stow and Bleek [13], the locality will be referred to simply as La Belle France throughout this work.

La Belle France was prospected by the author for one day to address the presence of fossils in the immediate vicinity of the paintings. Fossils were photographed in situ, positioned using a handheld GPS, and consolidated with Paraloid B72 glue. Given their possible association with the nearby rock art, the fossils were not collected. No permits were required for the described study, which complied with all relevant regulations.

Abbreviation: BP, Evolutionary Studies Institute of the University of the Witwatersrand, Johannesburg, South Africa.

Results

Paintings

The Horned Serpent panel is located at GPS coordinates S30° 15.776’ E26° 54.002’. The panel is well preserved (Fig 2A–2C), except for the drawings made with black pigment, but still depicts most of the elements redrawn by Stow and Bleek [13]. The locality is classically known as the “Brakfontein Cave”, but it is rather a rock shelter under a small sandstone overhang. This overhang and the site are located on the western side of a north-south ridge, a few kilometres west of the main Koesberg mountains. The paintings are made on a five-metres-thick exposed section of the Molteno sandstone (see the Geology and Palaeontology section below).

The complete panel is about 1.20 m long (Fig 2A) and is part of a larger mural that is about 10 m long (see The African Rock Art Digital Archive: <http://www.sarada.co.za>). Consequently,

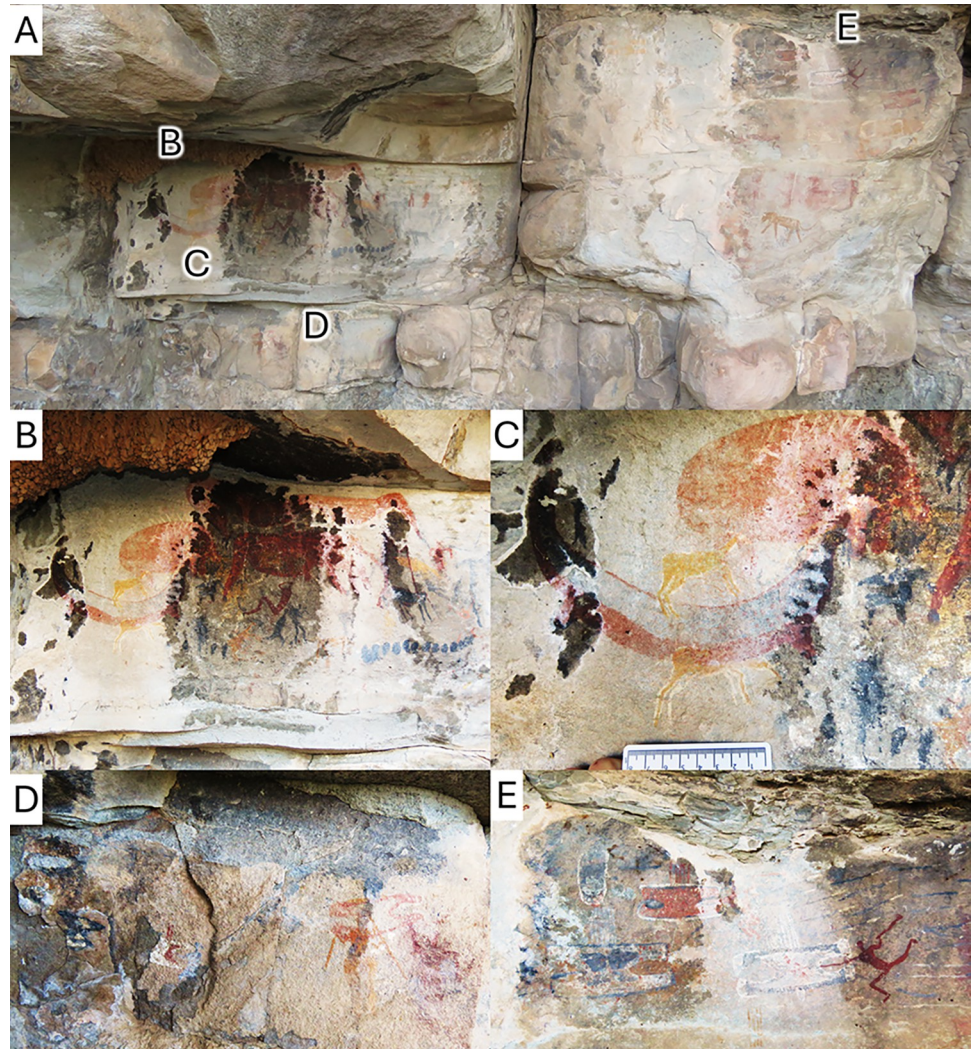


Fig 2. The Horned Serpent panel. A, general view of the Horned Serpent panel photographed in 2024 by the author. B, close up of the section figured in Stow and Bleek's [13] plate 39. C, close up of the tusked animal. D, close up of the warriors painted below the Horned Serpent panel. E, close up of the warriors painted to the right of the panel.

<https://doi.org/10.1371/journal.pone.0309908.g002>

Stow and Bleek [13] plates 36 to 39 illustrate only a small fraction of the paintings available at the site. These include, but are not limited to, unpublished paintings of a feline, aardvark, many eland and other antelope, and hunting and battle scenes, description and interpretation of which are beyond the scope of the current work.

The tusked animal itself has a slightly longer and more slender body than in Stow and Bleek's [13] reproduction (Figs 1 and 3A). The presence of tusk-like structures is verified. They are not an artifact of Stow and Bleek's [13] reproduction, and they do not appear to belong to another element of the painting. Stow and Bleek [13] figured the tusk-like structures as being the same red colour as the rest of the body (Fig 1), whereas tusks are usually depicted in a different, lighter colour in most San rock art [19–21]. This could have weakened the interpretation that they may indeed be tusks; however, the new observations made here show that the tusks were painted in a different, more greyish colour than the black head of the animal (Fig 3A and 3B). This conforms to the usual depiction of tusks in San art.

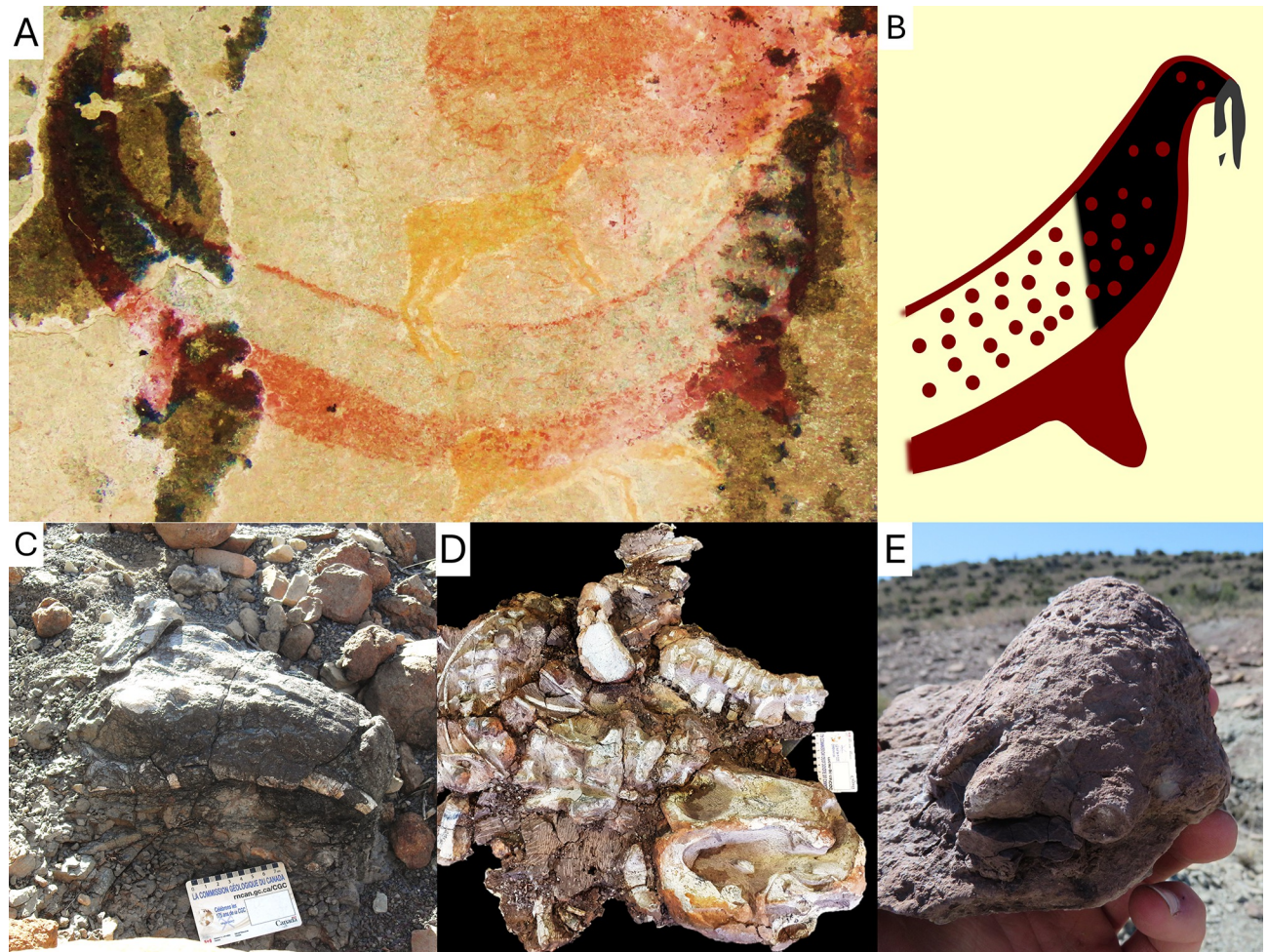


Fig 3. Interpretation of the tusked animal of the Horned Serpent panel and its dicynodont-like traits. A, Photo of the tusked animal of the Horned Serpent panel. B, interpretive drawing of its head. C, skull of a *Lystrosaurus* (14-03-2024, Oviston Nature Reserve) showing the prominent tusks, photographed in situ at the moment of its discovery, before excavation, and unprepared. D, complete skeleton of a *Lystrosaurus* (BP/1/9100, Oviston Nature Reserve) with its vertebral column curved into an opisthotonic "death pose", ex situ, prepared. E, the 'mummified' foot of a *Lystrosaurus* (28-08-2022, Fairydale, Bethulie District) showing the warty aspect of its preserved skin, ex situ, unprepared.

<https://doi.org/10.1371/journal.pone.0309908.g003>

Alternatively, these tusk-like structures may be interpreted as a fish or a snake being held in the mouth of a larger animal (such as a seal). Snakes are sometimes depicted as if they were held in the mouth of another animal (see plate 67A in [13]), but the inverted U shape formed by the tusk-like structures is far too short and featureless to conform to the usual depiction of snakes in San rock art [13,21–25]. The same applies to possible fish and eels. Another possibility is that the tusked animal could, in fact, be bleeding from its nose rather than sporting tusks, which is quite common in the San rock art [33,34]. This can also be safely excluded as nose-bleed are painted in red and usually displayed as exaggeratedly long and slender sprays in San rock art [25,33–35]. The tusk-like structures are finally too thick to be whiskers or rain-spitting [25]. Overall, they best match downward pointing teeth, consistent with dicynodont tusks (Fig 3A–3C). Their irregular shape compared to real tusks may be due to damage combined with the coarse grain and irregular surface of the sandstone, which made the drawing of this small element difficult.

Finally, the new observations show that the Horned Serpent panel is integrated in a larger scene that includes Sotho/Tswana and IsiZulu warriors, identifiable by their shields (Fig 2A, 2D and 2E). The San depiction of IsiZulu warriors battling with the Sotho/Tswana suggests that they were not made before the Mfecane, circa 1821–1828 [14,22]. As such, assuming that the warriors were painted at the same time as the tusked animal, the rock art at La Belle France may not be older than 1821. Most of the San retreated to the Maloti in 1835 and had completely abandoned the area by the 1850s [14,36,37], which gives the youngest possible age of the paintings. Consequently, the tusked animal was likely painted during this short interval, between 203 and 189 years ago, but could be older. Some paintings in the area have been dated to between 300 to 4000 years old [38–40], but previous records of the Horned Serpent panel (see The African Rock Art Digital Archive: <http://www.sarada.co.za>) demonstrate that the rock art at La Belle France is fading rapidly (especially the black pigment), so a younger age of about 200 years old is favoured here.

Geology and palaeontology

The La Belle France paintings are located on the western face of a north-south-running dolerite dike, west of which the Molteno Formation is exposed (Fig 4A). The exposures preserve at least three cycles of alternating conglomerate, sandstone and blue to green siltstone that likely represent the Indwe Sandstone Member of the Molteno Formation [41]. The paintings were made on the five-meter-thick section of the uppermost layer of sandstone, at the top of the ridge. Fossil bones are rare in the Molteno Formation [1,41], but, in the course of this work, abundant bone fragments were found in ex situ blocks of conglomerate. More importantly, in situ bone fragments were found in a gulley exposing blue to grey-green siltstone outcrops, some 50 m north of the paintings, at GPS coordinates S30°15.670' E26°53.960', S30°15.660' E26°53.951', and S30°15.596' E26°53.997' (Fig 4B–4D). They are not identifiable beyond tetrapod indet.

Discussion

The La Belle France animal is unique in San rock art. Its back is curved as a wide U, which is often found in paintings of fish and half-fish therianthropes [13,42,43]. This connection to water, coupled with its spotted skin and association with a horned snake are all consistent with its interpretation as a rain-animal [25,43]. As stated above, rain-animals are fantastic in nature, but they were arguably inspired by real-life elements [23,42].

The general outline of the La Belle France animal is evocative of a skink (such as *Mochlus* spp.). It has a small and rounded head, thick neck, long trunk and tail, short limbs, and a dark and spotted skin [44]; however, skinks are small, fossorial, and easily scared animals, and the ethnographic literature indicates they did not leave much impact on the San culture (unlike snakes and agamids, for instance; [13,14,26,45]). Moreover, unlike the La Belle France animal, lizards are always depicted in dorsal view in South African rock art, with all four legs visible, and the rare counterexamples are limited to therianthropes only [13,22,45,46]. So even though, at first glance, the body proportions may be consistent with skinks, this is not a parsimonious interpretation considering their inconspicuous nature and the ethnographic literature.

The animal depicted on the Horned Serpent panel bears two prominent structures, here best identified as tusks. They resemble those of the fossilised skull of a dicynodont (Fig 3A and 3B), consistent with the local San myth that designates this animal as an extinct species [14]. Its tusks point straight down, unlike in the San's depictions of other tusked animals (real or fantastic), in which the tusks always point upwards [19–22]. It also differs from an elephant by the absence of a trunk. Carnivorans, rock hyraxes, and hippopotami are usually depicted with

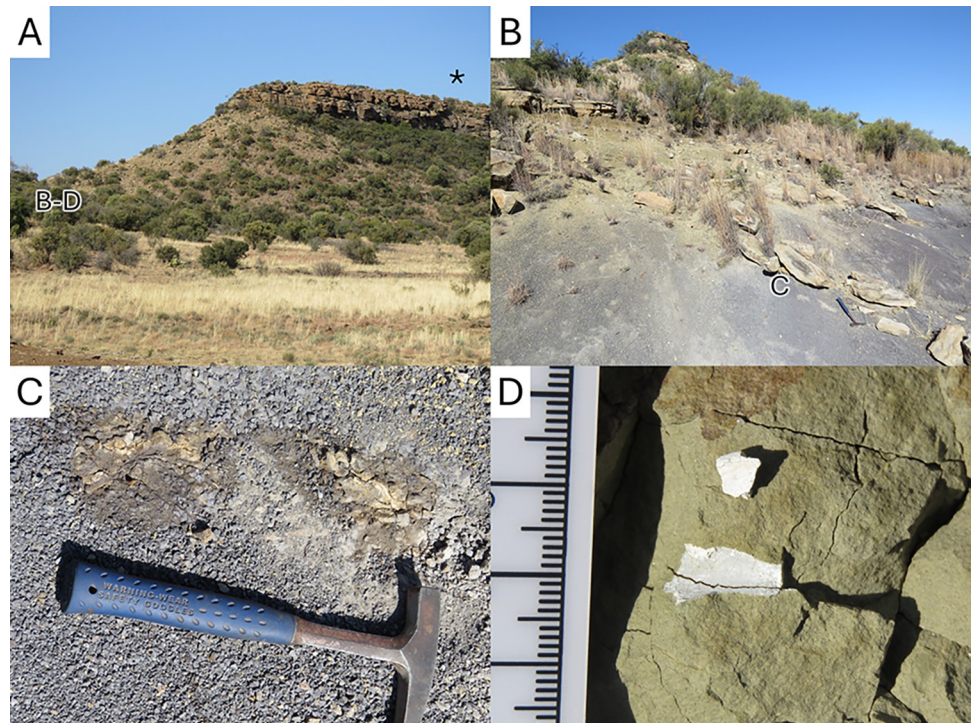


Fig 4. Pictures of the La Belle France locality. A, general view of the outcrops, from the west. The paintings are located below the * and the fossils were found where marked B-D. B, a siltstone outcrop. The position of the fossil in panel C is marked by a small C on the picture. C and D, close up views of some of the in-situ bone fragments discovered.

<https://doi.org/10.1371/journal.pone.0309908.g004>

their mouth closed in San rock art, but when they do show their teeth, both the upper and lower canines or tusks are clearly depicted [21–25]. The tusked animal of La Belle France has upper tusks only, like a dicynodont (Fig 3A–3C). It, thus, does not appear to be a living animal, or a creation based partly on an existing animal.

Moreover, the tusked animal assumes a pose with its back curved as a wide U (Fig 3A), which is unusual in San rock art (except for fish [13]). This is evocative of the opisthotonic “death pose” often displayed by fossilised skeletons in the area (Fig 3D) [47]. The skin of the tusked animal is dotted (Fig 3A and 3B), which is not unusual in San rock art, but is also consistent with the warty mummified skin preserved in some dicynodont fossils in the area (Fig 3E) [5]. The depiction of short limbs on the panel (Fig 3A) may be because, in the Karoo Basin, the limbs are often buried deeper than the rest of the body (if the animal sunk into the mud) or are the first to disarticulate from the rest of the body before fossilisation [5,47,48]. The discovery of partly buried or disarticulated skeletons coupled with the intrinsic spiritual nature of these long dead “great monstrous brutes” (as related in Stow and Theal [14]) may be responsible for the liberty taken in picturing the body proportions of the tusked animal. For instance, rain-animals are often pictured as aquatic beings [23–25], which may also account for the seal-like body of the tusked animal. All these elements are consistent with the hypothesis that the tusked animal may have been inspired, in part, by the discovery of dicynodont fossils.

As stated above, tetrapod fossil fragments are not rare in the immediate vicinity of the paintings (Fig 4C and 4D); but more importantly, La Belle France is located immediately near Rouxville and 60 km from Aliwal North, in an area where the Burgersdorp Formation of the

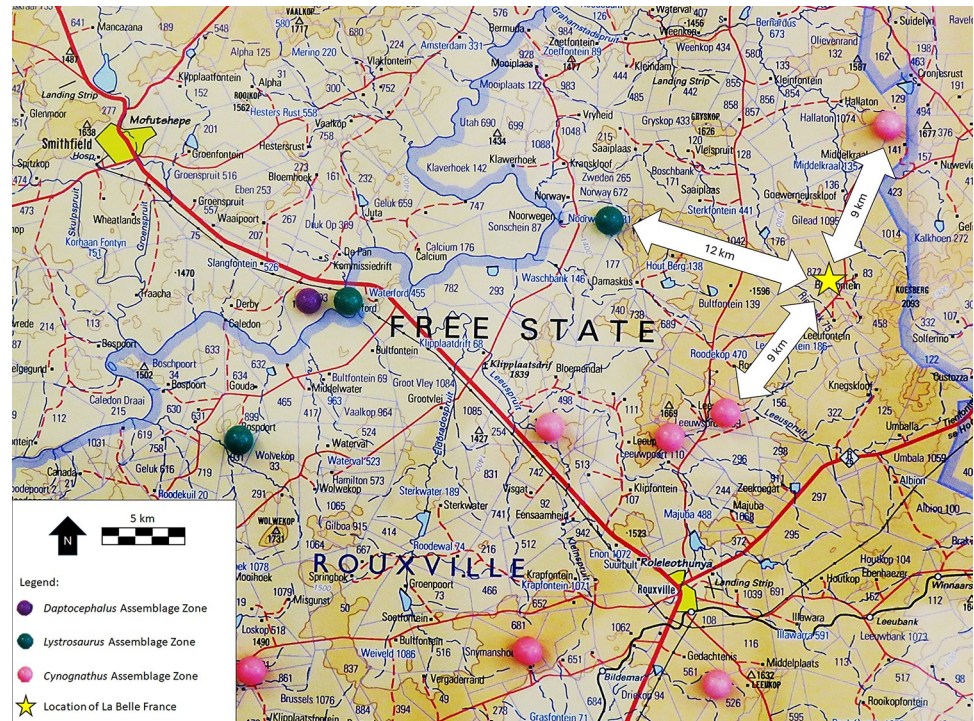


Fig 5. Excerpt of James Kitching's wall-sized compilation of 1:250 000 topocadastral maps made in 1972. The position of La Belle France is marked with a star. Outcrops are marked with coloured pins. The colours correspond to the Assemblage Zones as identified by Kitching [28] based on the fossil fauna.

<https://doi.org/10.1371/journal.pone.0309908.g005>

Beaufort Group is well exposed [28,49,50]. This formation encompasses the *Trirachodon*-*Kannemeyeria* Subzone of the *Cynognathus* Assemblage Zone, which is famous for producing countless bones belonging to the dicynodont *Kannemeyeria* [49], a bull-sized animal which would match the description provided by the San of a “great monstrous brutes” [14]. The closest outcrops of the *Cynognathus* Assemblage Zone are located 12 km away (Fig 5). Other rich fossiliferous areas nearby include those where the underlying Katberg Formation of the Beaufort Group is exposed, and in which the dicynodont *Lystrosaurus* is found in great numbers [28,47,51]. The closest outcrops of the corresponding *Lystrosaurus* Assemblage Zone are less than 10 km from La Belle France (Fig 5), towards Smithfield [28,50]. One of the richest localities, Fairydale (Donald 207, Bethulie District) where hundreds of dicynodont bones and skulls were found, is located just a 100 km away [5,29]. The occurrence of stone tools alongside the fossils demonstrates the occupation of these palaeontological sites by the San, as has been documented since the pioneering work of D. R. Kannemeyer and A. Brown [52–54].

The ability of the San to observe and interpret their environment in an essentially scientific way is well-known [55–57]. Their tracking skills are famous for the accuracy of the data they can extract from footprints [27,55–57]. They also use the same names across different species to designate muscles and bones, which implies that they understand the notion of homology [27]. It is well-established that the San from the Karoo were aware of the geological items and fossils in their surroundings, as they sometimes collected and made paintings of the fossils they found [7,8,11]. The possible depictions of dinosaur footprints at Boesmankoppie (Northern Cape Province, South Africa) and the Mokhali Cave (Lesotho) exemplify how the San could integrate fossils into their rock art [11,12]. At Schaapplaats and Avondzon (Free State Province, South Africa), the paintings do not depict any fossil or extinct species, but the

painted surfaces are so close to conspicuous dinosaur footprints and bones, respectively, that the artists most likely noticed them [7]. Fossil awareness among the San was not limited to footprints, as the purported dinosaur bone of Bolahla (Lesotho), dated between the 12th and 18th century, demonstrates [58]. Ellenberger et al. [11] also noted the presence of a dinosaur skeleton on the path to the Mokhali Cave, 10 m from the site, that would have been noticed by the San. These examples are mostly concentrated in the Stormberg Group (in the Drakensberg), likely because rock art and archaeological sites are better preserved in the rock shelters and caves of the Clarens Formation, but they do suggest that the San were capable of finding fossils, including bones. As dicynodonts are very abundant in the underlying Beaufort Group but exceedingly rare in the Stormberg Group [28,30,59], the tusked animal on the Horned Serpent panel could be the first evidence of San palaeontology in the Beaufort part of the Karoo Basin.

Conclusion

The ethnographic, archaeological, and palaeontological evidence are consistent with the hypothesis that the Horned Serpent panel could possibly depict a dicynodont. This is supported by i) the downward orientation of the tusks on the La Belle France tusked animal (Fig 3A and 3B), which does not match that of any modern African animals, but does match the tusks of dicynodonts (Figs 1B and 3C), ii) the abundance of dicynodont fossils in the area (Fig 5), and iii) the local San belief into a long extinct, large animal [14]. This would imply that the San may have i) discovered dicynodont fossils, ii) interpreted them as long-extinct species, iii) made a painting of one of them at La Belle France, and iv) integrated them into their worldview. If so, this would evidence that Later Stone Age people were aware of dicynodont fossils at least a decade before their formal scientific description by western scientists [31], and made the first known reconstruction of one of them. Even if one considers that the Horned Serpent panel has a purely spiritual meaning, it does not invalidate the hypothesis that the tusked animal itself may have been imagined based on a dicynodont fossil. The spiritual and palaeontological interpretation of this painting are not mutually exclusive. Helm et al. [7] were the first to propose that some of the strangest animals in the San rock art may be interpreted as depictions of Permian reptiles, and the current contribution supports that perhaps there may be more dicynodont depictions to be found among some of the paintings and petroglyphs preserved in the Karoo [7,19–21,60,61].

Acknowledgments

To Mr. and Mrs. Swanepoel and Mr. and Mrs. Kruger for access to La Belle France and showing the location of the paintings. To Luyanda Gcaza, Nomatile Nombewu, the Eastern Cape Province Tourism Agency, and Eastern Cape Province Heritage Resources Agency for access to the Oviston Nature Reserve. To the two anonymous reviewers for their help towards improving this work.

Author Contributions

Conceptualization: Julien Benoit.

Data curation: Julien Benoit.

Formal analysis: Julien Benoit.

Funding acquisition: Julien Benoit.

Methodology: Julien Benoit.

Writing – original draft: Julien Benoit.

Writing – review & editing: Julien Benoit.

References

1. MacRae CS. Life Etched in Stone: Fossils of South Africa. Pretoria: Geological Society of South Africa; 1999.
2. Rubidge BS, Sidor CA. Evolutionary Patterns Among Permo-Triassic Therapsids. *Annu Rev Ecol Evol Syst.* 2001; 32: 449–480. <https://doi.org/10.1146/annurev.ecolsys.32.081501.114113>
3. Bever GS, Lyson TR, Field DJ, Bhullar B-AS. Evolutionary origin of the turtle skull. *Nature.* 2015; 525: 239–242. <https://doi.org/10.1038/nature14900> PMID: 26331544
4. McPhee BW, Benson RBJ, Botha-Brink J, Bordy EM, Choiniere JN. A Giant Dinosaur from the Earliest Jurassic of South Africa and the Transition to Quadrupedality in Early Sauropodomorphs. *Curr Biol.* 2018; 28: 3143–3151.e7. <https://doi.org/10.1016/j.cub.2018.07.063> PMID: 30270189
5. Smith RMH, Botha J, Viglietti PA. Taphonomy of drought afflicted tetrapods in the Early Triassic Karoo Basin, South Africa. *Palaeogeogr Palaeoclimatol Palaeoecol.* 2022; 604: 111207. <https://doi.org/10.1016/j.palaeo.2022.111207>
6. Bordy EM, Smith RMH, Choiniere JN, Rubidge BS. Selected Karoo geoheritage sites of palaeontological significance in South Africa and Lesotho. *Geol Soc Spec Publ.* 2024; 543: 431–446. <https://doi.org/10.1144/SP543-2022-202>
7. Helm CW, Benoit J, Mayor A, Cawthra HC, Penn-Clarke CR, Rust R. Interest in geological and palaeontological curiosities by southern African non-western societies: A review and perspectives for future study. *Proc Geol Assoc.* 2019; 130: 541–558. <https://doi.org/10.1016/j.pgeola.2019.01.001>
8. Benoit J, Penn-Clarke CR, Rust R, Groenewald DP, Vickers-Rich P, Helm CW. Indigenous knowledge of palaeontology in Africa. *Geol Soc Spec Publ.* 2024; 543: 357–370. <https://doi.org/10.1144/SP543-2022-236>
9. Mayor A. The First Fossil Hunters: Paleontology in Greek and Roman Times. Princeton, New Jersey: Princeton University Press; 2000.
10. Mayor A. The First Fossil Hunters: Dinosaurs, Mammoths, and Myth in Greek and Roman Times. Princeton, New Jersey: Princeton University Press; 2011.
11. Ellenberger P, Mossman DJ, Mossman AD, Lockley MG. Bushmen Cave Paintings of Ornithopod Dinosaurs: Paleolithic Trackers Interpret Early Jurassic Footprints. *Ichnos.* 2005; 12: 223–226. <https://doi.org/10.1080/10420940591008971>
12. Helm C, Crause K, Mccrea R. Mokhali Cave revisited—dinosaur rock art in Lesotho. *The Digging Stick.* 2012; 29: 6–9.
13. Stow GW (George W, Bleek DF (Dorothea F. Rock paintings in South Africa from parts of the Eastern Province and Orange Free State. London: Methuen; 1930.
14. Stow GW (George W, Theal GM. The native races of South Africa: a history of the intrusion of the Hottentots and Bantu into the hunting grounds of the Bushmen, the aborigines of the country, with numerous illustrations. London: Swan Sonnenschein & Co., limited; New York: The Macmillan Co.; 1905.
15. Barnard A. Bushmen: Kalahari Hunter-Gatherers and Their Descendants. Cambridge: Cambridge University Press; 2019.
16. Berta A., Overview. In: Perrin WF, Würsig B, Thewissen JGM, editors. *Encyclopedia of Marine Mammals* (Second Edition). London: Academic Press; 2009. pp. 878–885. <https://doi.org/10.1016/B978-0-12-373553-9.00202-9>
17. Heuvelmans B. Les Derniers Dragons d'Afrique. Paris, France: Librairie Plon; 1978.
18. Naish D. Speculative Zoology. *Fort Times.* 2014; 316: 52–53.
19. Woodhouse HC. Creatures with tusks in the rock paintings of Southern Africa. *S Afr J Cult Hist.* 1987; 2: 40–46. https://doi.org/10.10520/AJA02583542_5
20. Blundell G, Ferreira A. Tusk and transformation in southern African San rock art: an iconographic analysis of WAR2. *Azania Archaeol Res Africa.* 2018; 53: 341–368. <https://doi.org/10.1080/0067270X.2018.1513239>
21. Lewis-Williams JD, Dowson TA. Images of Power: Understanding San Rock Art. Johannesburg: Southern Book Publishers; 1989.
22. Vinnicombe P. People of the Eland: Rock Paintings of the Drakensberg Bushmen as a Reflection of Their Life and Thought. Pietermaritzburg: University of Natal Press; 1976.

23. Lewis-Williams JD. Images of Mystery: Rock Art of the Drakensberg. Cape Town: Double Storey Books; 2003.
24. Lewis-Williams JD. San Rock Art. Johannesburg: Jacana Media; 2011.
25. Lewis-Williams D, Challis S. Deciphering Ancient Minds: The Mystery of San Bushmen Rock Art. London: Thames & Hudson; 2011.
26. Hollmann J. Customs and Beliefs of the |Xam. New York: New York University Press; 2022.
27. Bieseke M. The Bushmen: San Hunters and Herders of Southern Africa. Cape Town and Pretoria: Human & Rousseau; 1978.
28. Kitching JW. The Distribution of the Karoo Vertebrate Fauna: With Special Reference to Certain Genera and the Bearing of this Distribution on the Zoning of the Beaufort Beds. Johannesburg: Bernard Price Institute for Palaeontological Research, University of the Witwatersrand; 1977.
29. Viglietti PA, Smith RMH, Compton JS. Origin and palaeoenvironmental significance of *Lystrosaurus* bonebeds in the earliest Triassic Karoo Basin, South Africa. *Palaeogeogr Palaeoclimatol Palaeoecol*. 2013; 392: 9–21. <https://doi.org/10.1016/j.palaeo.2013.08.015>
30. Smith RMH, Rubidge BS, Day MO, Botha J. Introduction to the tetrapod biozonation of the Karoo Supergroup. *S Afr J Geol*. 2020; 123: 131–140. <https://doi.org/10.25131/sajg.123.0009>
31. Owen R. Report on the Reptilian Fossils of South Africa: PART I.—Description of certain Fossil Crania, discovered by A G Bain, Esq, in Sandstone Rocks at the South-eastern extremity of Africa, referable to different species of an Extinct genus of Reptilia (*Dicynodon*), and indicative of a new Tribe or Sub-order of Sauria. *Trans Geol Soc London*. 1845; 7: 59–84.
32. Dowson T, Ouzman S, Blundell G, Holliday A. A Stow site revisited: Zaaron District, Eastern Orange Free State. In: Dowson T, Lewis-Williams D, editors. Contested images: diversity in southern African rock art research. Johannesburg: Witwatersrand University Press; 1994. pp. 177–188.
33. Butler FG. Nose-bleed in shamans and Eland. *S Afr Field Archaeol*. 1987; 6: 82–87.
34. Butler FG, Cannan C. Nose-bleed in zebra rock paintings, Zimbabwe. *S Afr Field Archaeol*. 1998; 7: 82–89.
35. Challis S, Skinner A. Art and Influence, Presence and Navigation in Southern African Forager Landscapes. *Religions*. 2021; 12: 1099. <https://doi.org/10.3390/rel12121099>
36. Ellenberger V. La fin tragique des Bushmen: les derniers hommes vivants de l'âge de la pierre. Paris, France: Amiot-Dumont; 1953.
37. Wright JB. Bushman Raiders of the Drakensberg, 1840–1870: A Study of Their Conflict with Stock-keeping Peoples in Natal. Pietermaritzburg: University of Natal Press; 1971.
38. Bonneau A, Pearce D, Mitchell P, Staff R, Arthur C, Mallen L, et al. The earliest directly dated rock paintings from southern Africa: new AMS radiocarbon dates. *Antiquity*. 2017; 91: 322–333. <https://doi.org/10.15184/aqy.2016.271>
39. Bonneau A, Staff RA, Higham T, Brock F, Pearce DG, Mitchell PJ. Successfully Dating Rock Art in Southern Africa Using Improved Sampling Methods and New Characterization and Pretreatment Protocols. *Radiocarbon*. 2017; 59: 659–677. <https://doi.org/10.1017/RDC.2016.69>
40. Bonneau A, Pearce DG, Mitchell PJ, Didier L, Eoin LN, Higham TFG, et al. Characterization and dating of San rock art in the Metolong catchment, Lesotho: A preliminary investigation of technological and stylistic changes. *Quat Int*. 2022; 611–612: 177–189. <https://doi.org/10.1016/j.quaint.2021.03.014>
41. Bordy EM, Hancox PJ, Rubidge BS. The contact of the Molteno and Elliot formations through the main Karoo Basin, South Africa: a second-order sequence boundary. *S Afr J Geol*. 2005; 108: 351–364. <https://doi.org/10.2113/108.3.351>
42. Willcox AR. The Rock Art of South Africa. London: Nelson; 1963.
43. Lewis-Williams JD. Discovering Southern African Rock Art. Cape Town and Johannesburg: David Philip; 1990.
44. Broadley DG. A review of the *Riopa sundevalli* group (Sauria: Scincidae) in southern Africa. *Arnoldia* (Rhodesia). 1966; 34: 1–7.
45. Bleek WHI, Lloyd L, Theal GM. Specimens of Bushman Folklore. London: G. Allen, Limited; 1911.
46. Rudner J. The hunter and his art. Cape Town: C. Struik.; 1970.
47. Smith RMH, Botha-Brink J. Anatomy of a mass extinction: Sedimentological and taphonomic evidence for drought-induced die-offs at the Permo-Triassic boundary in the main Karoo Basin, South Africa. *Palaeogeogr Palaeoclimatol Palaeoecol*. 2014; 396: 99–118. <https://doi.org/10.1016/j.palaeo.2014.01.002>
48. Boonstra LD. The fauna of the *Tapinocephalus* zone (Beaufort beds of the Karoo). *Ann S Afr Mus*. 1969; 56: 1–73.

49. Hancox PJ, Neveling J, Rubidge BS. Biostratigraphy of the *Cynognathus* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. *S Afr J Geol*. 2020; 123: 217–238. <https://doi.org/10.25131/sajg.123.0016>
50. Neveling J, Hancox J, Rubidge B. Biostratigraphy of the lower Burgersdorp Formation (Beaufort Group; Karoo Supergroup) of South Africa—implications for the stratigraphic ranges of early Triassic tetrapods. *Palaeontol Afr*. 2005; 41: 81–88.
51. Botha J, Smith RMH. Biostratigraphy of the *Lystrosaurus declivis* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. *S Afr J Geol*. 2020; 123: 207–216. <https://doi.org/10.25131/sajg.123.0015>
52. Hoffman AC, Esterhuysen DJ. Preliminary report on Archaeological, Palaeontological and Anthropological field expeditions in the Orange River area. *Navors nas Mus Bloemfontein*. 1965; 2: 23–27. https://doi.org/10.10520/AJA00679208_100
53. Goodwin AJH, Van Riet Lowe C. The Stone Age Cultures of South Africa. *Ann S Afr Mus*. 1929; 27: 1–289.
54. Drennan MR. Gogga Brown: The Life Story of Alfred Brown. Cape Town: Maskew Miller Limited; 1938.
55. Liebenberg L. The Art of Tracking: The Origin of Science. Cape Town: D. Philip; 1990.
56. Pastoors A, Lenssen-Erz T, Ciqae T, Kxunta U, Thao T, Bégouën R, et al. Tracking in Caves: Experience Based Reading of Pleistocene Human Footprints in French Caves. *Camb Archaeol J*. 2015; 25: 551–564. <https://doi.org/10.1017/S0959774315000050>
57. Lenssen-Erz T, Pastoors A, Uthmeier T, Ciqae T, Kxunta U, Thao T. Animal tracks and human footprints in prehistoric hunter-gatherer rock art of the Doro! nawas mountains (Namibia), analysed by present-day indigenous tracking experts. *PLOS ONE*. 2023; 18: e0289560. <https://doi.org/10.1371/journal.pone.0289560> PMID: 37703266
58. Plug I. Late Pleistocene and Holocene Hunter–Gatherers in the Eastern Highlands of South Africa and Lesotho: A Faunal Interpretation. *J Archaeol Sci*. 1997; 24: 715–727. <https://doi.org/10.1006/jasc.1996.0153>
59. Kammerer CF. The first skeletal evidence of a dicynodont from the lower Elliot Formation of South Africa. *Palaeontol Afr*. 2018; 52: 102–123.
60. Rusch N, Parkington J. San Rock Engravings: Marking the Karoo Landscape. Cape Town: Struik Travel & Heritage; 2010.
61. Parkington J, Morris D, Rusch N. Karoo Rock Engravings: Follow The San. Cape Town: Living Landscape Project; 2008.