AUTHORS:
Robert W. Gess[1,2]
Caitlin Reddy[2]

AFFILIATIONS:
[1]Albany Museum, Rhodes University, Makhanda, South Africa
[2]Geology Department, Rhodes University, Makhanda, South Africa

CORRESPONDENCE TO:
Robert Gess

EMAIL:
robg@imaginet.co.za

HOW TO CITE:
Gess RW, Reddy C. South Africa's oldest ophiuroid fossils provide rare insights into the origination of the Malvinoxhosan Realm. S Afr J Sci. 2024;120(11/12), Art. #18896. https://doi.org/10.17159/sajs.2024/18896

ARTICLE INCLUDES:
☐ Peer review
☐ Supplementary material

KEYWORDS:
ophiuroid, Devonian, Malvinoxhosan, Baviaanskloof formation, Gondwana

FUNDING:
South African Millennium Trust, GENUS, South African Department of Science and Innovation, South African National Research Foundation

PUBLISHED:
04 December 2024

South Africa's oldest ophiuroid fossils provide rare insights into the origination of the Malvinoxhosan Realm

Significance:

Recent description of the oldest recorded brittle stars (ophiuroids) from the southern hemisphere revealed two distinct taxa of early Pragian age (approximately 410 million years old). Whereas one of the brittle stars belonged to a species previously described from younger strata, the others represent an unusually spiny taxon formerly unknown to science. Recovered from the 'upper member' of the Baviaanskloof Formation (the uppermost unit of the Table Mountain Group), they offer insights into the earliest recorded phase of the endemic Malvinoxhosan Realm, deposited in polar regions of the ancient supercontinent of Gondwana, and better known from the overlying Bokkeveld Group.

Palaeontology gives us windows into the past and is our only source of direct evidence for the history of life on earth, together with the evolution of the biosphere. It elucidates the increasing complexity of life systems and their response to changing continental configurations, resultant ocean currents, climatic shifts and extinction events. Some of the latter, including the End Devonian Extinction Event, are widely believed to, in turn, result from the evolution of novel biota.[1]

Our view of the past is, however, extremely patchy, often consisting of disconnected glimpses of life in different places at different times. It relies not only on the burial of organisms within suitable sediments, but also on the ultimate burial of those sediments in the earth's crust and their re-exposure at the surface during the brief tenure of current academia.

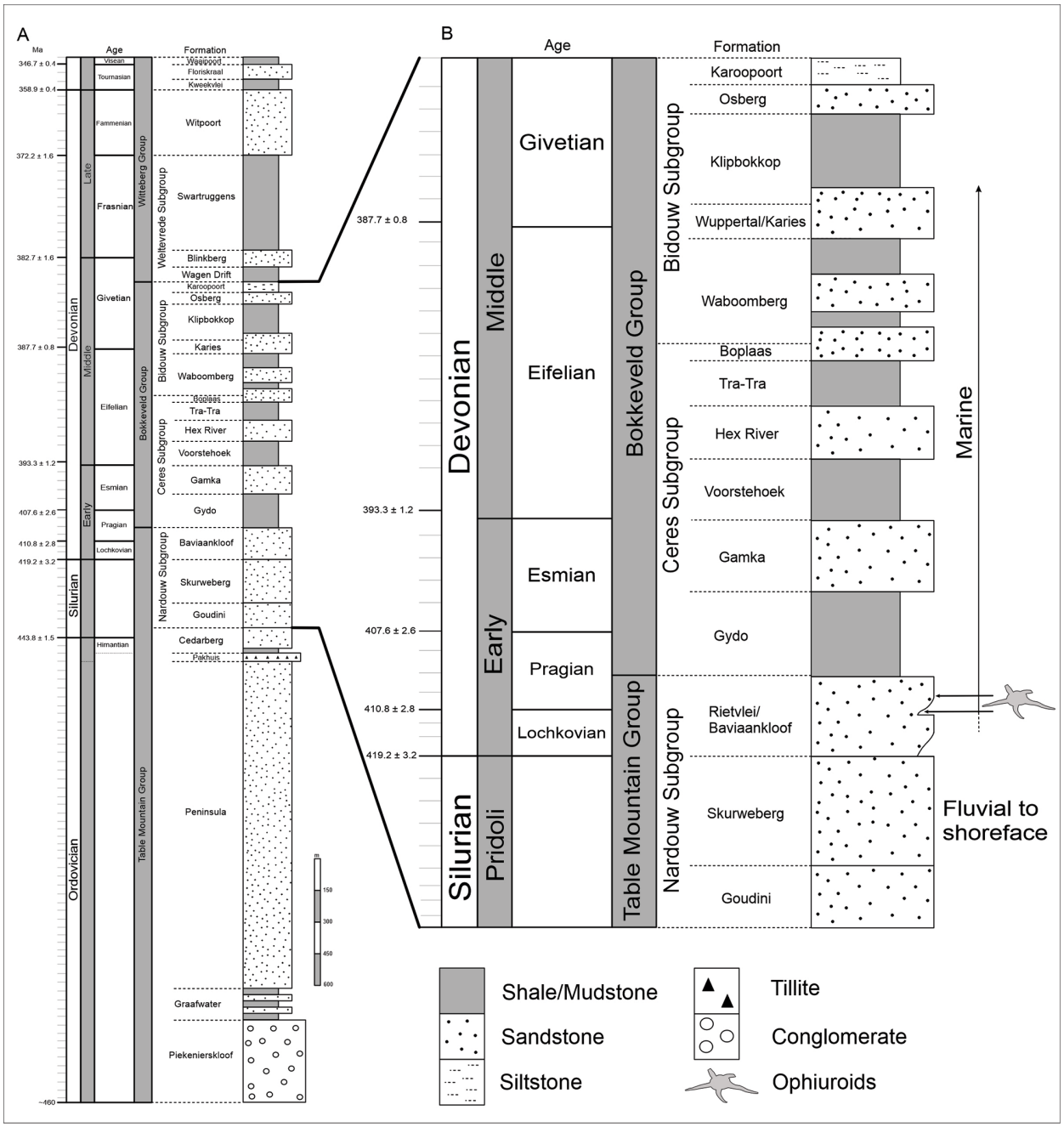
The evidence that we rely on therefore consists of patches of knowability within a matrix of temporal and spacial unknowns. As palaeontologists, we strive to expand the scope of what we know and drive back the boundaries of the unknown.

South Africa's earliest rocks from the Phanerozoic Eon, debatably ranging from the Middle Ordovician Period (around 460 million years ago) until the Early Devonian Period (around 410 million years ago), constitute the Table Mountain Group, the oldest of three major subdivisions comprising the Cape Supergroup (Figure 1).[2] Sediments were deposited in a number of rift generated sedimentary basins, largely by river systems, with occasional marine incursions.[2] Most important of these basins was the Agulhas Basin, which would persist until late in the Carboniferous Period, accumulating a near continuous sedimentary sequence, which also includes the overlying Bokkeveld and Witteberg groups of the Cape Supergroup (Figure 1).[3] These strata, extending parallel to the coast from the Cederberg in the Western Cape to Fish River in the Eastern Cape, preserve an unparalleled record of early Palaeozoic life from the southern polar region of what was then Gondwana (a supercontinent which much later split into Africa, South America, Antarctica, Australia and India). The sandstone dominated Table Mountain Group, represents the Cape Supergroup's initial primarily fluvial stage.[2] As very little continental life existed during these time periods, this interval contains very few fossils. Trace fossils, in the form of invertebrate movement and feeding traces, do occur at various horizons, often associated with episodic marine incursions. The early Late Ordovician Graafwater Formation (beautifully exposed along Chapman's Peak drive in the Western Cape) exhibits a wide range of such ichnotaxa, as do sparse localities within the overlying Peninsula and Pakhuis formations.[2] A single body fossil containing formation within this time interval comprises the Late Ordovician Cedarberg Formation.[2] Cedarberg Formation fossils are largely concentrated within the Soom Shale Lagerstätte, a fine-grained clay horizon deposited during brief flooding of the Agulhas Basin in the immediate aftermath of the Hirnantian glaciation. Characterised by exceptional preservation of their soft tissues in clay minerals, the fossils represent a low-diversity cold-water community including giant conodonts, unarmoured jawless fish, lobopods, brachiopods, orthoconic nautiloids and trilobites.[4] Associated plant spores provide southern Africa's first evidence for terrestrial plants.[5] Low diversity plant spores are also recovered from the more sparsely fossiliferous overlying Disa Member of the Cedarberg Formation, tentatively assigned to an earliest Silurian age on the basis of brachiopod fauna.[6]

A far more substantial fossil record characterises the overlying Bokkeveld and Witteberg Groups (Figure 1), deposited after subsidence and extensive marine flooding of the basin initiated during the early Devonian period. Although first evidenced in the Baviaanskloof Formation (and western equivalent Rietvlei Formation) of the uppermost Table Mountain Group[7,8], this flooding resulted in a fully marine depositional setting for the mudstone dominated Ceres Subgroup (lower Bokkeveld Group), estimated to range in age from the mid-Pragian (approximately 409 million years ago) to late in the Eifelian (approximately 388 million years ago).[9]

The Ceres Subgroup contains an abundant and diverse record of endemic cold-water marine invertebrate faunas, also characteristic of contemporary strata of South America, west Antarctica and the Falkland Islands. These are largely associated with sediments laid down in lower shoreface, offshore transition zone and offshore environments below wave base[9] and form a biotic realm that can be traced upwards as high as the Waboomberg Formation, lowermost formation of the upper Bokkeveld Bidou Subgroup of late Eifelian to earliest Givetian age.[9]

The well-known fauna characteristic of the lower Bokkeveld Ceres Subgroup (and Waboomberg Formation) is traditionally referred to as the Malvinokaffric Realm, in acknowledgement of its commonality with faunas recovered from the Falkland Islands (Malvinas), South America and west Antarctica, although a name change to Malvinoxhosan



Source: Created by Shawn Johnstone, reproduced under a Creative Commons Attribution 4.0 International Licence.

Figure 1: Stratigraphic column of (A) the Cape Supergroup and (B) upper Table Mountain Group and Bokkeveld Group, illustrating the stratigraphic context of the recently described high-latitude Brittle stars.[8,9–11]

bioregion has been introduced in response to sensibilities regarding the word 'Kaffraria'.[12] A huge diversity of marine invertebrate fossils are recorded from this realm, representing 142 genera, including 41 molluscs (of which 24 are bivalves, 8 are gastropods and 3 cephalopods), 34 brachiopods, 36 echinoderms (including 10 crinoids, 2 asteroids/starfish, 6 ophiuroids/brittle stars and 18 of other classes), 15 trilobite arthropods, 6 ostracod arthropods, 9 cnidarians (including 5 anthazoans/corals and 4 conularias), 1 poriferan (sponge), as well as a number of ostracods, hyolithids and tentaculitids.[9] Of these, 37 genera are entirely endemic to the Malvinoxhosan realm.[9] Changing depositional environments within the Agulhas Basin, combined with global changes in climate and oceanic currents, probably resulted in a collapse of the Malvinoxhosan realm during the Givetian, with subsequent faunas belonging to a post-Malvinoxhosan Realm, characterised by rapidly declining representation of endemic genera, an increased proportion of cosmopolitan taxa, and generally reduced diversity.[9]

The origination of the Malvinoxhosan Realm presents a tantalising research question. Fossil bearing marine sediments are largely absent from the South African geological sequence in the interval between strata hosting the distinctive Ordovician cold-water fauna of the Cedarberg Group (Table Mountain Group) and those hosting the early to mid-Devonian Malvinoxhosan faunas of the Early Devonian lower Bokkeveld Group (Figure 1A). Between these lies the Nardouw Subgroup of the Table Mountain Group. Its lowermost subdivision, the Goudini Formation, comprises sandstones of fluvial and nearshore origin, entirely lacking in known body fossils.[13] This is overlain by massive, entirely unfossiliferous fluvial to shoreface quartzites of the Skuweberg Formation which comprises the middle unit of the Nardouw Subgroup.[14] The uppermost unit of the Nardouw Subgroup (and of the Table Mountain Group), formerly known as the 'Passage Beds'[15] is the Baviaanskloof Formation and its western lateral equivalent, the Rietvlei Formation.[3] This Formation records the transition from the fluvially dominated Table Mountain Group

to the marine dominated Bokkeveld Group (Figure 1B). It is informally subdivided into a 'lower member', a middle Kareedouw Member and an 'upper member'. The Kareedouw Member preserves apparent paralic estuarine black mudstones rich in terrestrial plants, although no marine invertebrates. The diverse flora of this unit suggests a Lochkovian (earliest Devonian) age.[8]

However, the Baviaanskloof Formation's upper member contains thin storm deposits of nearshore brachiopods and a low diversity of other taxa. These include the earliest records of Malvinoxhosan indicator taxa, and the combined fauna of the unit has been defined as the 'Eo-Malvinoxhosan'.[9] Prior to the ophiuroids recently described from this unit, only 13 taxa of invertebrates had been recorded, including 1 taxon of bivalve, 1 gastropod, 9 brachiopods, an indeterminate sponge and crinoid remains. All but three of these are also known from the overlying 'Established Malvinokaffric Realm', with the majority being Malvinoxhosan endemics.[9] This suggests that much of the diversity seen in the overlying Bokkeveld Group may have a deeper history, 'off-stage' as it were, in deeper marine settings that are not recorded within our stratigraphic sequence.

In the Eastern Cape, the upper member largely represents shoreface and foreshore deposits[16] containing fairly monotaxic, well-sorted, storm deposits of shallow water *Proboscidina* brachiopods (personal observations of R.W.G.), that, although endemic, are not found in the Bokkeveld Group[9]. Small, highly informative windows into greater diversity are occasionally encountered. A silty to muddy interval, indicative of greater transgression, occurs just above the base of the upper member in the Mpofu Dam section (near Humansdorp). This reveals a bed of shells of *Australocoelia*, a classic and near ubiquitous endemic taxon of the 'Established Malvinoxhosan Realm' – indicating their generally unrecorded proximity in adjacent, slightly deeper water, marine habitats. Approximately 50 cm above this horizon, evidently buried whilst sheltering in a thin storm deposit of *Proboscidina* shells, a single entire ophiuroid was discovered during fieldwork by R.W.G. (Figure 2). Taxonomic work published in Reddy et al.[16] establishes it to be *Hexuraster weitzi* (Spencer, 1950)[17,18], a taxon previously described from the Gydo Formation. This provides the earliest record of an ophiuroid in the southern hemisphere, and again suggests a temporally deeper origination of classic Malvinoxhosan taxa than is normally recorded from our sedimentary record.

Approximately 3.5 kilometres to the southeast of the Mpofu Dam section, at a slightly higher stratigraphic horizon within the upper member of the Baviaanskloof Formation, fieldwork (by R.W.G.) revealed a relatively thick (approximately 10 cm) tempestite lens of *Proboscidina* shells. This deposit, only a few metres across, contained remains of a small population of ophiuroids representing both adults and juveniles. Preserved in life positions, twined amongst the shells (Figure 3), they undoubtedly inhabited the sheltered environment prior to being smothered by a pulse of mud washed out of a nearby river mouth. Bearing thorn-like spines on their dorsal disc and running the length of their arms, they were revealed to be an entirely new genus and species, *Krommaster spinosus* (Reddy et al., 2023)[16], now known only from this single lens of rock.

These windows into the pre-Bokkeveld Malvinoxhosan Realm suggest that the marine faunas typical of the lower Bokkeveld Group were already present during deposition of the uppermost Table Mountain Group, though at slightly deeper water depth than normally recorded in the sedimentary sequence. Furthermore, the discovery of a unique taxon in a single serendipitously preserved lens demonstrates that much of the early, shallow water diversity of the Malvinoxhosan Realm may yet await discovery. The low diversity of marine invertebrates so far described from the Eo-Malvinoxhosan may be ascribed to a number of factors. Firstly, preservation is far rarer than in the fossil-rich shallow marine muds of the lower Bokkeveld Group, including only occasional glimpses of life beyond the low diversity foreshore and shoreface environment. Secondly, exposure of fossil sites is less frequent, the resistant hosting sandstones tending to form weathered hilly country in which softer fossiliferous lenses are destroyed near the surface by weathering. In this regard, it is also worth considering that the fossil-rich mudstones of the lower Bokkeveld Group are a preferred source of soft aggregate for surfacing untarred roads – leading to frequent exposure of fresh material in borrow pits and quarries, from which much of the historically collected material originates. Clearly, more targeted fieldwork

Photo: Robert Gess

Figure 2: Photo of an approximately 10 cm diameter specimen of *Hexuraster weitzi* (Spencer, 1950)[17,18] in situ in strata of the Upper Member of the Baviaanskloof Formation (Table Mountain Group).

Photo: Caitlyn Reddy

Figure 3: Photo of an approximately 10 cm diameter specimen of *Krommaster spinosus spinosus*[16] recovered in life position from a brachiopod lag deposit in the Upper Member of the Baviaanskloof Formation (Table Mountain Group).

within the Baviaanskloof and Rietvlei Formations is required to locate and study the rare palaeoecological windows that they present, in order to better understand the emergence of the Malvinoxhosan Realm.

Acknowledgements

We thank Shawn Johnstone for drafting Figure 1.

Funding

This research forms part of the work of the Devonian Ecosystems Project, which is funded by Millennium Trust, South Africa, GENUS (DSI-NRF Centre of Excellence in Palaeosciences) and the National Research Foundation of South Africa.

Declarations

We have no competing interests. We have no AI or LLM use to declare. Both authors read and approved the final manuscript.

References

1. Algeo TJ, Scheckler E, Maynard JB. Effects of the middle to late Devonian spread of vascular land plants on weathering regimes, marine biotas, and global climate. In: Gensel PG, Edwards D, editors. Plants invade the land: Evolutionary and environmental perspectives. New York: Columbia University Press; 2001. p. 213–236. https://doi.org/10.7312/gens11160-013
2. Penn-Clarke CR, Browning C, Harper DAT. The Ordovician system of South Africa: A review. Geol Soc Spec Publ. 2023;533:175–197. https://doi.org/10.1144/SP533-2022-23
3. Thamm AG, Johnson MR. The Cape supergroup. In: Johnson MR, Anhaeusser CR, Thomas RJ, editors. The geology of South Africa. Johannesburg: Geological Society of South Africa; 2006. p. 443–459.
4. Gabbott SE, Browning C, Theron JN, Whittle RJ. The late Ordovician Soom Shale Lagerstätte: An extraordinary post-glacial fossil and sedimentary record. J Geol Soc. 2016;174:1–9. https://doi.org/10.1144/jgs2016-076
5. Gray J, Theron JN, Boucot AJ. Age of the Cedarberg formation, South Africa and early land plant evolution. Geol Mag. 1986;123:445–454. https://doi.org/10.1017/S0016756800033537
6. Wellman CH, Penn-Clarke CR, Browning C. Early land plant remains from the uppermost Ordovician-?lowermost Silurian Cedarberg Formation of South Africa. Est J Earth Sci. 2023;72(1):164. https://doi.org/10.3176/earth.2023.03
7. Cooper MR. Facies shifts, sea-level changes and event stratigraphy in the Devonian of South Africa. S Afr J Sci. 1986;82(5):255.
8. Gess RW, Prestianni C. An early Devonian flora from the Baviaanskloof Formation (Table Mountain group) of South Africa. Sci Rep. 2021;11(1), Art. #11859. https://doi.org/10.1038/s41598-021-90180-z
9. Penn-Clarke CR, Harper DAT. The rise and fall of the Malvinoxhosan (Malvinokaffric) bioregion in South Africa: Evidence for early-middle Devonian biocrises at the South Pole. Earth-Sci Rev. 2023;246, Art. #104595. https://doi.org/10.1016/j.earscirev.2023.104595
10. Theron JN, Thamm AG. Stratigraphy and sedimentology of the Cape Supergroup in the Western Cape. In: Guidebook, Geocongress '90. Johannesburg: Geological Society of South Africa, PR2; 1990. p. 1–64.
11. Cotter E. Depositional setting and cyclic development of the lower part of the Witteberg Group (Mid- to Upper Devonian), Cape Supergroup, Western Cape, South Africa. S Afr J Geol. 2000;103(1):1–14. https://doi.org/10.2113/103.1.1
12. Penn-Clarke CR, Harper DAT. Early Middle Devonian brachiopod provincialism and bioregionalization at high latitudes: A case study from southwestern Gondwana. Geol Soc Am Bull. 2021;33:819–836. https://doi.org/10.1130/B35670.1
13. Malan JA, Theron JN, Hill RS. Lithostratigraphy of the Goudini formation (Table Mountain group). Lithostratigraphic Series, No. 2. Pretoria: Council for Geoscience, South African Committee for Stratigraphy; 1989. p. 5.
14. Theron JN, Malan JA, HILL RS. Lithostratigraphy of the Skurweberg formation (Table Mountain group). Lithostratigraphic Series, No. 3. Pretoria: Council for Geosciences, South African Committee for Stratigraphy; 1989. p. 6.
15. Rossouw PJ, Meyer EI, Mulder MP, Stocken CG. Die geologie van die Swartberge, die Kangovallei en die omgewing van Prins Albert [The geology of the Swartberg, the Cango Valley and the vicinity of Prince Albert], K.P. Exploration Sheets 3321 B (Gamkapoort) and 3322 A (Prince Albert). Port Elizabeth: Geological Survey of South Africa; 1964. Afrikaans.
16. Reddy C, Thuy B, Reid M, Gess R. Earliest known ophiuroids from high palaeolatitude, southern Gondwana, recovered from the Pragian to earliest Emsian Baviaanskloof formation (Table Mountain group, Cape supergroup) South Africa. PLoS ONE. 2023;18(10), e0292636. https://doi.org/10.1371/journal.pone.0292636
17. Spencer WA. Monograph of the British Palæozoic Asterozoa. Part IX. Palaeontogr Soc Monogr. 1934;87(394):437–494. https://doi.org/10.1080/02693445.1934.12035629
18. Jell P, Theron J. Early Devonian echinoderms from South Africa. Mem-Qld Mus. 1999;43(1):115–200.