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Coombs Hill: A Late Devonian fossil locality in the Witpoort Formation (Witteberg Group, South Africa)

Coombs Hill, a new fossil locality in the Witpoort Formation (Witteberg Group) of South Africa, preserves a record of Famennian (Late Devonian) life in Gondwana. Fossil plants collected at Coombs Hill are preliminarily assigned to several classes. Shelly invertebrates include a variety of bivalve mollusc forms, some of which appear to be preserved in life position. Biodiversity at Coombs Hill is comparable to that of the well-known Waterloo Farm *lagerstätte* in ordinal diversity, but exhibits differences in species composition. Ongoing taxonomic analysis will provide a rare window into the ecology of high-latitude environments during this pivotal stage of Earth history, which immediately preceded the end-Devonian extinction. Sandstone dominated sedimentary facies at Coombs Hill suggest a high-energy coastal marine setting, with brackish back-barrier estuarine/lagoonally derived fossiliferous mudstones. Exact stratigraphic placement within the Witpoort Formation is hampered by structural deformation, and precise age comparisons with Waterloo Farm are currently tenuous.

Significance:

- A new fossil locality at Coombs Hill comprises the second known site with a suite of well-preserved continental and marginal marine fossils from the Witpoort Formation, providing an exceptionally rare example of high-latitude life during the critical latest Devonian Famennian age.
- Several new plant taxa will be diagnosed from this locality, which also gives important insights into the morphology of *Archaeopteris notosaria*, South Africa's earliest known tree.
- Discovery of a second palaeontologically significant site in the Witpoort Formation provides impetus for further structural and sedimentary facies analyses to align the unit with datable global eustatic events, and to clarify its internal chronology.

Introduction

Coombs Hill (33°17'51.86"S 26°45'28.70"E) is situated within the predominantly quartzitic Witpoort Formation (mid Witteberg Group, Cape Supergroup) east of Makhanda (Figure 1). The Witteberg Group accumulated in a shallow marine setting along the southern coastline of Gondwana, between the Givetian (Middle Devonian) and Visean (Early Carboniferous), with the Witpoort Formation being of Famennian age^{1,2} – a time in which the region was within the Antarctic Circle³ (Figure 1).

Strata of the Witpoort Formation, along with the rest of the Cape Supergroup, crop out for more than 1000 km along South Africa's southern and western coastlines, having been tectonically deformed during the formation of the late Palaeozoic Cape Fold Belt.⁴

The Witpoort Formation has, in recent decades, provided evidence for high-latitude latest Devonian life, although exclusively from a single *lagerstätte* at Waterloo Farm (Figure 1), which comprises the only known high-latitude marginal marine ecosystem from the Famennian. The 23 plant and animal taxa as yet diagnosed include the only known high-latitude Devonian tetrapods, the earliest known lampreys and Gondwana's only Devonian terrestrial invertebrates.^{3,5,6} Here, we report the discovery of a new locality at Coombs Hill, 21 km to the east of Waterloo Farm.

The Late Devonian records the end of the Siluro-Devonian hothouse climate, with the appearance of continental glaciers and increasingly dramatic sea-level (eustatic) fluctuations⁷ associated with a series of major biotic crises⁸. Cooling is considered by many authors to have resulted from drawdown of CO₂ associated with widespread vegetation of land.^{9,10} Abundant vegetation at Coombs Hill and Waterloo Farm provides the only evidence for high-latitude forestation during the Late Devonian biocrisis.

Structural geology

The precise stratigraphic position of the Coombs Hill site in the Witpoort Formation is uncertain, as there is no continuous lithological section to formational contacts, and strata exhibit duplications of stratigraphic sequences at outcrop. This results from structural deformation characteristic of the eastern Cape Fold Belt¹¹ and is evident in a 350-m-long road cutting (Figure 2a), wherein indicators of younging direction reveal that most of the strata are overturned about a synclinal fold (Figure 2b). Strata are continuous around the fold hinge as is demonstrated by two distinct mudrock horizons, resulting in stratigraphic duplication of much of the overturned succession. Some minor faulting and brecciation occurs within the section, associated with kinking along the overturned limb, but it is insufficient to displace marker horizons.

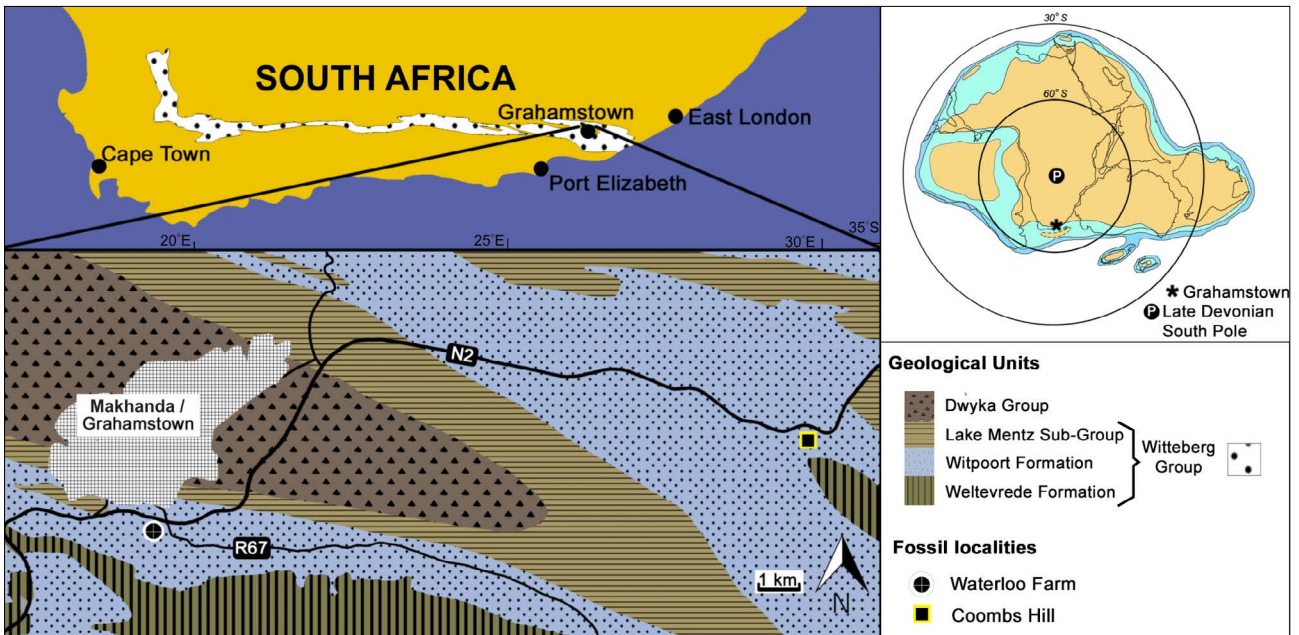


Figure 1: Geological map of the Makhandanda (Grahamstown) region (based on Council for Geoscience, Grahamstown sheet 3326 (1995)), showing the locations of fossil localities at Waterloo Farm and Coombs Hill. A key to stratigraphic units is provided at the bottom right. Palaeogeographic reconstruction of Late Devonian Gondwana (top right) modified from Gess and Ahlberg³.

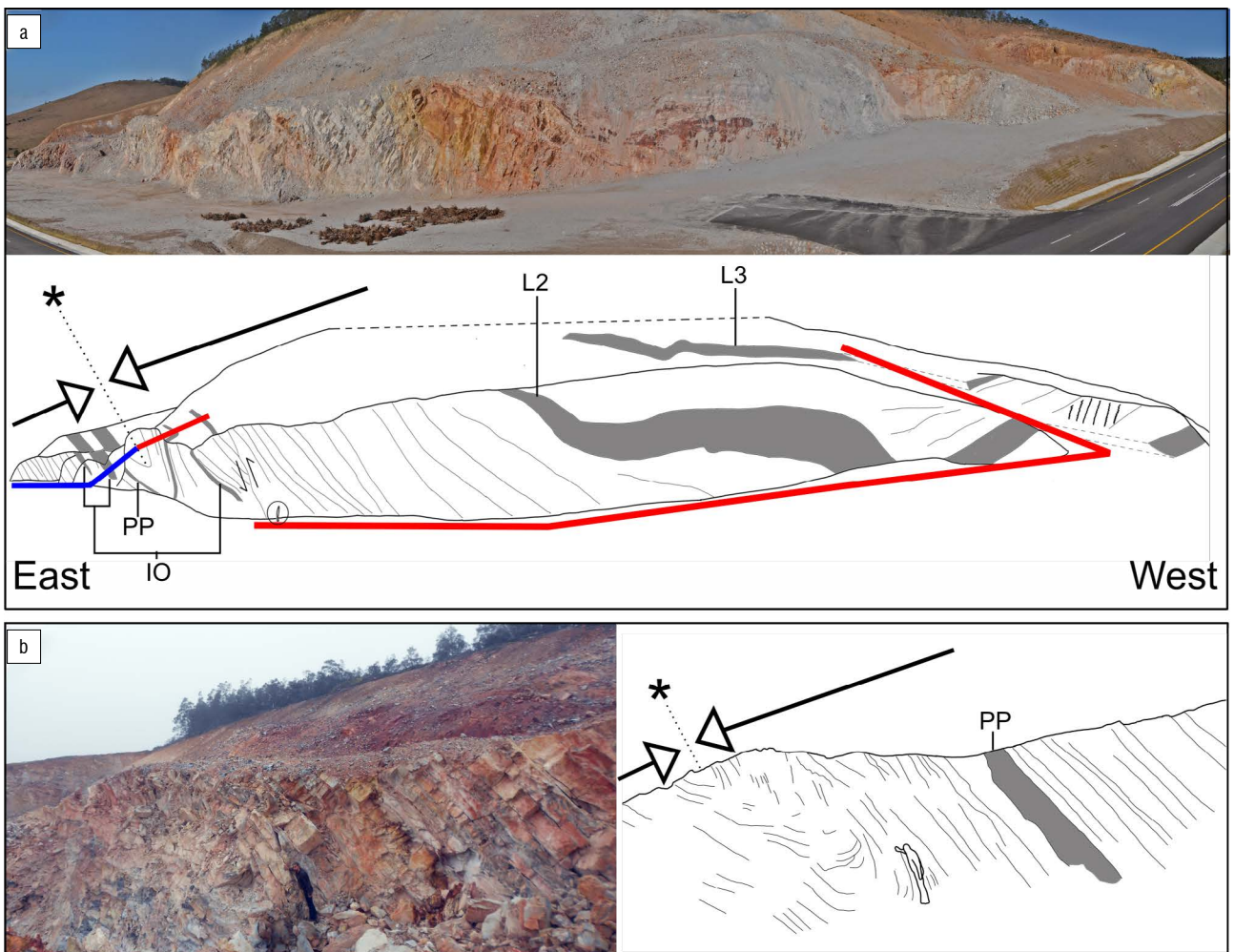


Figure 2: Geological structure of Coombs Hill. (a) Panoramic photograph of the road cutting with interpretive line drawing below. Arrows indicate younging direction of strata, which converge towards a fold axis (*); fossiliferous mudstone horizons are labelled (see Figure 3); the transect followed during systematic logging is indicated by a red line for the overturned strata and a blue line for the right-way-up strata; person for scale is circled. (b) Synclinal fold axis with interpretive line drawing to right, with arrows as in (a).

Stratigraphy and sedimentology

A stratigraphic log of exposures along the recent road cutting at Coombs Hill records roughly 80 m of stratigraphic sequence (Figure 3). The majority of the strata comprise clean blue-grey (when fresh; 5B 6/2–5B 7/1 (Munsell colour system)), medium-grained quartz arenites, which are stacked in a succession displaying only subtle lithological changes, and punctuated by discrete mudstone horizons, comprising ~10% of the succession. Many of the quartzitic strata superficially appear red to purple due to precipitation of minerals along joints. Weathered quartzites usually alter to light brown (5YR 5/6) or light grey (N8).

Quartzitic sedimentary facies include (1) planar cross-stratification (Figure 4a), (2) low-angle planar cross-stratification (Figure 4b), (3) trough cross-stratification (Figure 4d), (4) parabolic cross-stratification (Figure 4f), (5) low angle undulatory (c.f. swaley) cross-stratification (Figure 4c), (6) horizontal lamination, (7) ripple lamination and (8) internally structureless beds. Muddy facies include (9) horizontally laminated to structureless mudstone and (10) horizontally laminated

heterolithic greywacke. Mudstone horizons exhibit lateral variations in thickness and texture, and are commonly eroded at the contact with overlying arenaceous strata (Figure 4e).

Palaeocurrent trends derived from cross-strata ($n=47$) are polymodal, with modes towards the east, south-southwest, and a minor component to the northwest (Figure 3). These trends, relative to a roughly east–west trending shoreline^{12,13}, indicate both offshore and longshore sediment transport with a minor landward component, consistent with the fluctuations of current, wave and storm energy in shallow marine rather than fluvial settings^{14,15}.

Many of the facies associations formerly described in the Witpoort Formation around Makhanda¹³ are recognised at Coombs Hill, and three broad depositional environments are provisionally identified: (1) shoreface, (2) foreshore and (3) backshore (as illustrated in Figure 3). The new locality is similarly interpreted as representing a shallow to marginal-marine succession characterised by high wave energy and continual reworking of sediments.

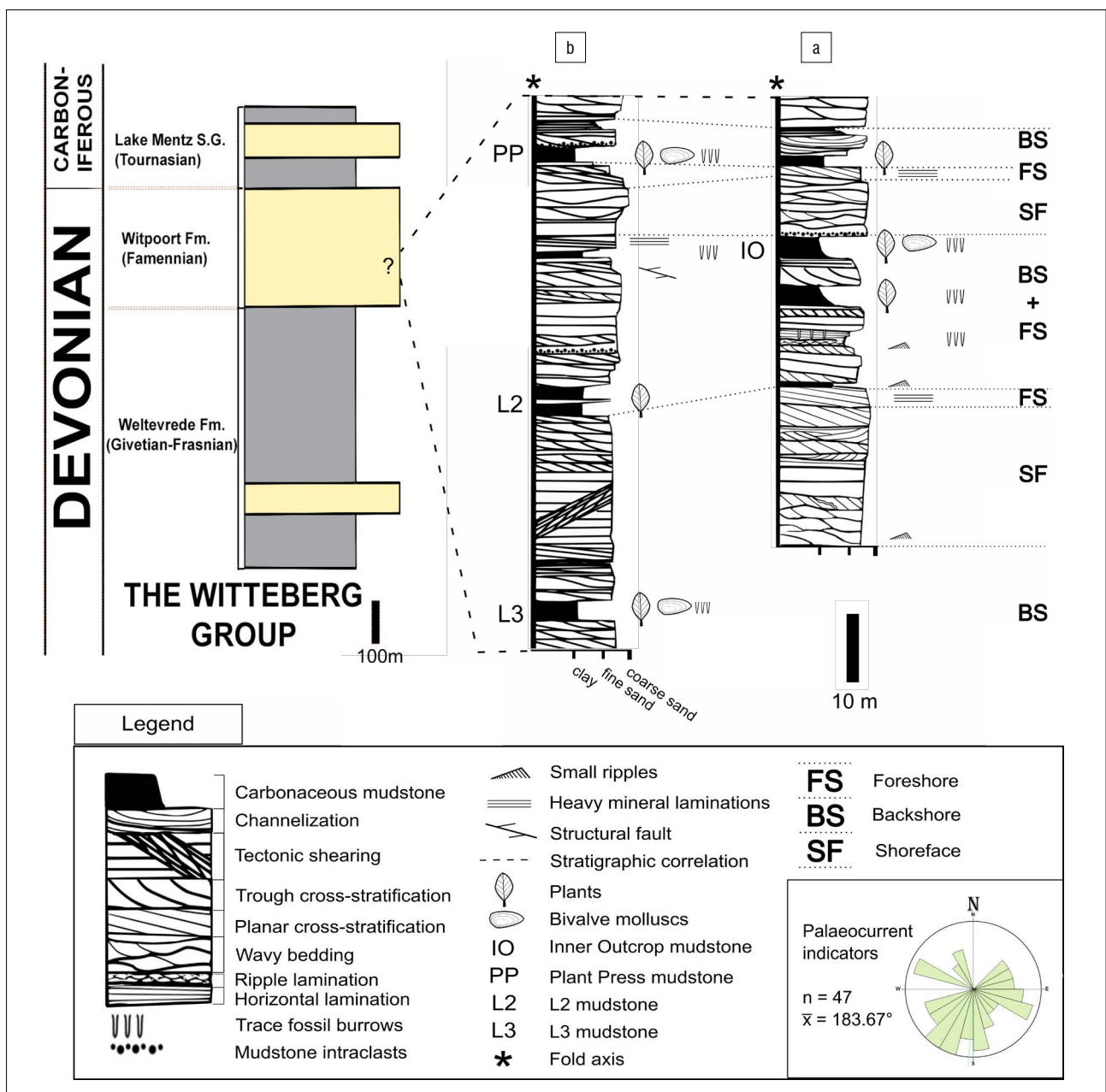


Figure 3: Stratigraphic log of the Coombs Hill road cutting showing (a) the right-way-up portion and (b) the overturned portion of the succession (refer to Figure 2). Cumulative palaeocurrent indicators for the whole succession are inset at the bottom right.

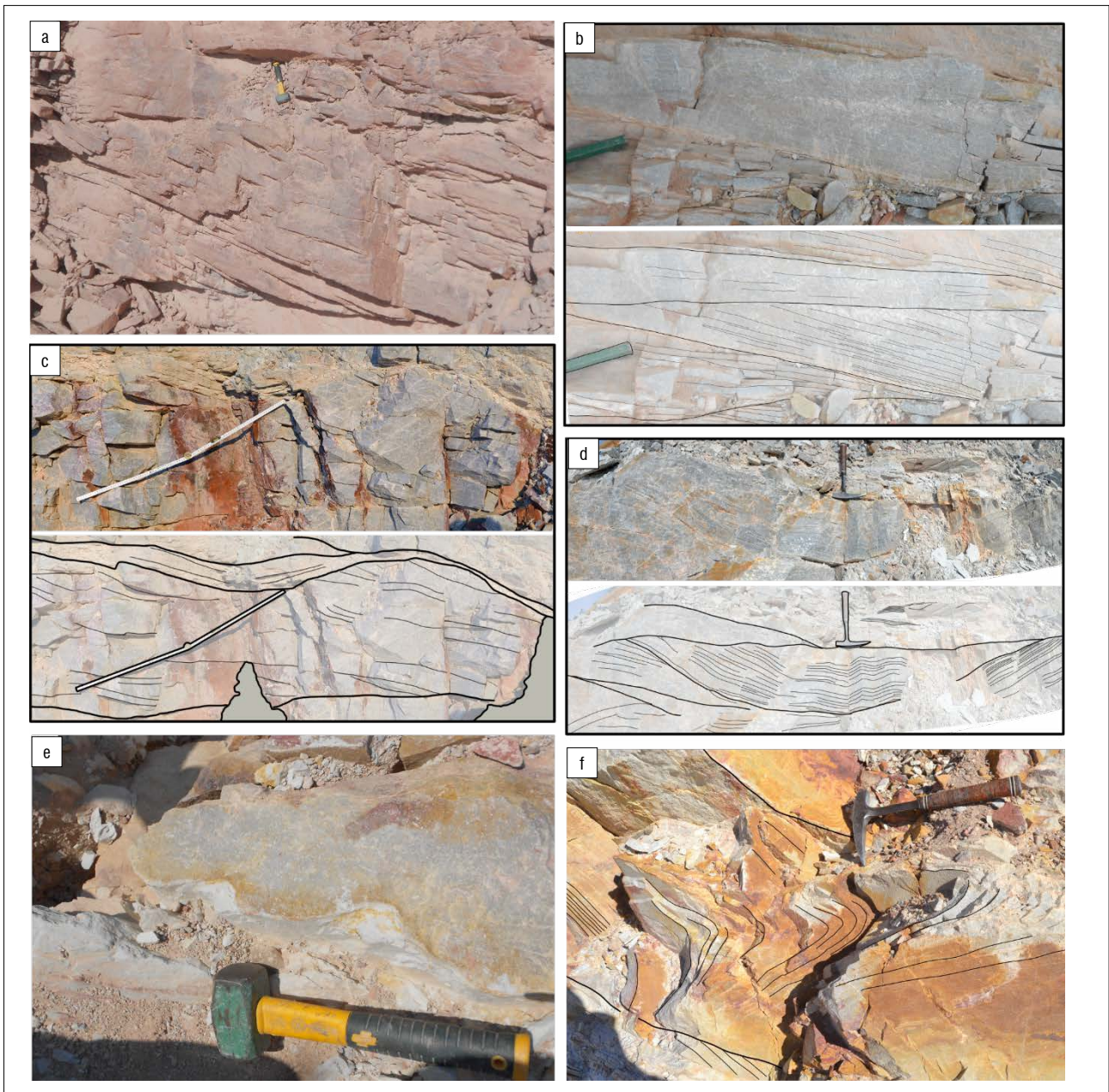


Figure 4: Sedimentary facies at Coombs Hill. (a) Thickly bedded planar cross-stratification (4-lb hammer for scale). (b) Low-angle planar cross-stratification (handle of chisel is approximately 2 cm wide). (c) Swaley cross-stratification (scale is 1 m). (d) Channelised trough cross-stratification (geological pick for scale). (e) Stepped channel bank eroded into mudstone (4-lb hammer for scale). (f) Parabolic cross-stratification (younging direction towards the bottom of the photograph, geological pick for scale). (b,c,d,f.) Interpretive line drawings showing erosive set bounding surfaces (thicker lines) and bedding planes (thinner lines).

The alternation between shoreface and backshore is the result of transgressive-regressive cycles, the chronology and driving mechanisms of which are not clearly understood. Further detailed facies studies are required to test the postulated depositional environments.

Fossil biota

Excavations by R.W.G. and C.H. in 2015 and 2016 produced a representative sample of the biotic remains preserved in the mudstones, including more than 200 specimens of relatively well-preserved plants and shelly invertebrates which are curated at the Albany Museum.

Mudstones preserve an association of putative marine algae, abundant terrestrial plant matter and bivalve remains. This evidence is in line with existing hypotheses which propose stagnant brackish-water lagoonal¹³

or estuarine¹⁶ depositional environments for the genesis of fossiliferous mudstone in the Witpoort Formation around Makhanda.

Fossil plants include remains provisionally ascribed to Cladoxylopsida, Progymnospermopsida (*Archaeopteris notosaria* Anderson et al. 1995), Lycopsida, Zosterophyllopsida, Gymnospermopsida and form taxa *Palaeostigma* Kräusel and Dolianti 1957, '*Dutoitia*' *alfreda* Plumstead 1967 and '*Dutoitia*' *maraisia* Plumstead 1967.¹⁷

Archaeopteris notosaria, hitherto only known from Waterloo Farm, provides the earliest evidence for trees at high palaeolatitudes.¹⁸ Exquisite vegetative and fertile remains from Coombs Hill contribute significantly to taxonomic understanding of this species (Figure 5a, b). Lycopod remains comprise at least three new taxa, none of which is known to occur at Waterloo Farm.¹⁷

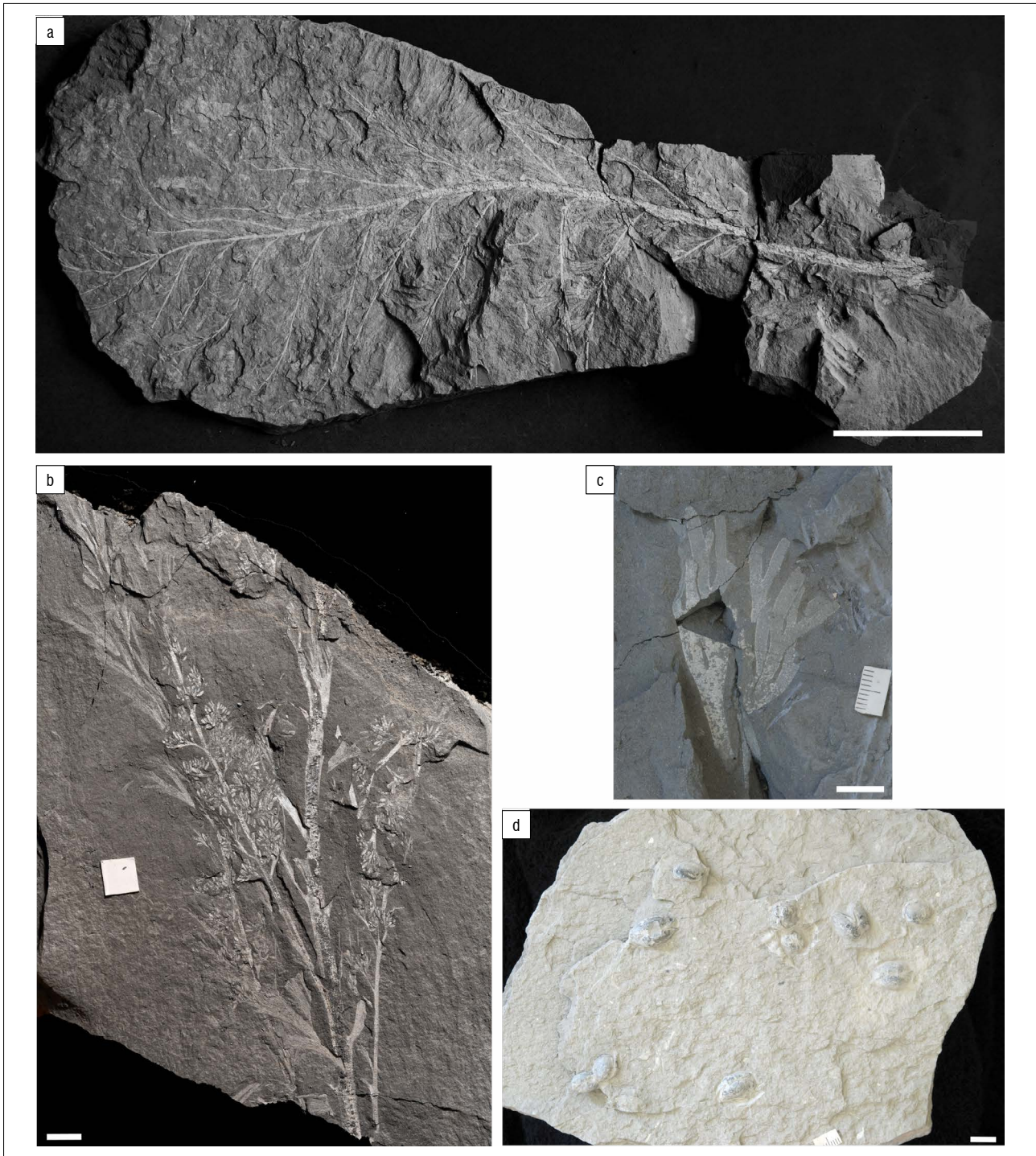


Figure 5: Fossil remains from Coombs Hill. (a) A near-complete lateral branch system of *Archaeopteris notosaria*, AM 7710a (scale bar = 10 cm). (b) Fertile branch of *A. notosaria*, AM 7714a (scale bar = 1 cm). (c) Putative marine alga, AM 7717 (cf. *Hungerfordia fionae*) (scale bar = 1 cm). (d) Articulated bivalve shells on a bedding plane, AM 7718a (scale bar = 1 cm).

Algal thalli, similar to *Hungerfordia fionae* Hiller and Gess 1995, are relatively common at Coombs Hill (Figure 5c), although they are more elongate and less bilaterally symmetrical, probably representing a new species.

Invertebrates are solely represented by abundant articulated bivalves consistently preserved with the umbo upwards (in apparent life position), usually in mudstones but sometimes in underlying sandstones (Figure 5d). These likely comprise several euryhaline genera, and their dominance of the muddy substrate suggests a brackish setting.¹⁹

Future research

The palaeontology of Coombs Hill is the subject of a series of taxonomic papers allowing palaeoecological comparisons with Waterloo Farm. Structural analysis will facilitate finer stratigraphic resolution of these localities and improved understanding of their relative ages. Detailed reconstructions of the depositional environments form part of a broader study on the Witpoort Formation and are important in understanding the relative influence of autocyclic (i.e. subsidence and sediment supply) and allocyclic (eustatic) processes on environmental change that could elucidate major bioevents in the Late Devonian.



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Competing interests

We declare that there are no competing interests.

Authors' contributions

C.H.: Conceptualisation, data collection, data analysis, writing – the initial draft, writing – revisions. R.W.G.: Conceptualisation, methodology, data collection, writing – revisions, student supervision. C.R.P.C.: Methodology, data collection, writing – revisions, student supervision. B.S.R.: Methodology, writing – revisions, project management, funding acquisition, student supervision.

References

1. Cooper MR. Facies shifts, sea-level changes and event stratigraphy in the Devonian of South Africa. *S Afr J Sci.* 1986;82(5):255.
2. Gess RW. Vertebrate biostratigraphy of the Witteberg Group and the Devonian-Carboniferous Boundary in South Africa. In: Linol B, De Wit MJ, editors. *Origin and evolution of the Cape Mountains and Karoo Basin*. Cham: Springer; 2016. p. 131–140. https://doi.org/10.1007/978-3-319-40859-0_13
3. Gess R, Ahlberg PE. A tetrapod fauna from within the Devonian Antarctic Circle. *Science.* 2018;360(6393):1120–1124. <https://doi.org/10.1126/science.aag1645>
4. Shone RW, Booth PWK. The Cape Basin, South Africa: A review. *J Afr Earth Sci.* 2005;43(1–3):196–210. <https://doi.org/10.1016/j.jafrearsci.2005.07.013>
5. Gess RW, Coates MI, Rubidge BS. A lamprey from the Devonian period of South Africa. *Nature.* 2006;443(7114):981–984. <https://doi.org/10.1038/nature05150>
6. Gess RW. The earliest record of terrestrial animals in Gondwana: A scorpion from the Famennian (Late Devonian) Witpoort Formation of South Africa. *Afr Invertebr.* 2013;54(2):373–379. <https://doi.org/10.5733/afin.054.0206>
7. Eriksson KA, McClung WS, Simpson EL. Sequence stratigraphic expression of greenhouse, transitional and icehouse conditions in siliciclastic successions: Paleozoic examples from the central appalachian basin, USA. *Earth-Sci Rev.* 2019;188:176–189. <https://doi.org/10.1016/j.earscirev.2018.11.010>
8. Bond DP, Wignall PB. The role of sea-level change and marine anoxia in the Frasnian–Famennian (Late Devonian) mass extinction. *Palaeogeogr Palaeoclimatol Palaeoecol.* 2008;263(3–4):107–118. <https://doi.org/10.1016/j.palaeo.2008.02.015>
9. Algeo TJ, Scheckler SE, Maynard JB. Effects of the Middle to Late Devonian spread of vascular land plants on weathering regimes, marine biotas, and global climate. In: Gensel P, 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>
10. Kenrick P, Wellman CH, Schneider H, Edgecombe GD. A timeline for terrestrialization: Consequences for the carbon cycle in the Palaeozoic. *Philos Trans R Soc Lond B Biol Sci.* 2012;367(1588):519–536. <https://doi.org/10.1098/rstb.2011.0271>
11. Booth PWK, Munro AJ, Shone RW. Lithological and structural characteristics of Cape Supergroup rocks at Port Alfred, Eastern Cape, South Africa. *S Afr J Geol.* 1999;102(4):391–404.
12. Theron JN, Looock JC. Devonian deltas of the Cape Supergroup, South Africa. In: *Proceedings of the Second International Symposium on the Devonian System*; Calgary, Canada. CSPG Special Publications; 1988.
13. Hiller N, Taylor FF. Late Devonian shoreline changes: An analysis of Witteberg Group stratigraphy in the Grahamstown area. *S Afr J Geol.* 1992;95(5–6):203–214.
14. Clifton HE. A reexamination of facies models for clastic shorelines. In: Posamentier HW, Walker RG, editors. *Facies models revisited*. Special Publication no. 84. Tulsa, OK: Society for Sedimentary Geology; 2006. p. 293–337.
15. Plint AG. Wave- and storm-dominated shoreline and shallow-marine systems. *Facies Models.* 2010;4:167–200.
16. Gess RW, Whitfield AK. Estuarine fish and tetrapod evolution: Insights from a Late Devonian (Famennian) Gondwanan estuarine lake and a southern African Holocene equivalent. *Biol Rev.* 2020;95(4):865–888. <https://doi.org/10.1111/brv.12590>
17. Harris C. Exploring biodiversity patterns among southern Gondwana's primeval forests [MSc dissertation]. Johannesburg: University of the Witwatersrand; 2019.
18. Anderson HM, Hiller N, Gess RW. *Archaeopteris* (Progymnospermopsida) from the Devonian of southern Africa. *Bot J Linn Soc.* 1995;117(4):305–320. <https://doi.org/10.1111/j.1095-8339.1995.tb02593.x>
19. Dalrymple RW, Choi K. Morphologic and facies trends through the fluvial-marine transition in tide-dominated depositional systems: A schematic framework for environmental and sequence-stratigraphic interpretation. *Earth-Sci Rev.* 2007;81(3–4):135–174. <https://doi.org/10.1016/j.earscirev.2006.10.002>