

1 Cold Feet: trackways and burrows in ice-marginal strata of the
2 end-Ordovician glaciation (Table Mountain Group, South
3 Africa)

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11

12 **ABSTRACT**

13 New observations from an outcrop of Upper Ordovician Table Mountain Group strata
14 (Matjiesgoedkloof, Western Cape Province, South Africa) have revealed an unexpected
15 ichnofauna, hosted within diamictites and sandstones that were deposited by a retreating low-
16 latitude (c. 30°S) ice sheet during the Hirnantian glaciation. The locality provides a rare window
17 onto animal-sediment interactions in an early Paleozoic ice-marginal shallow marine
18 environment and contains a trace fossil community with a surprising ichnodiversity and
19 ichnodisparity of burrows, trackways and trails (*Archaeonassa*, *Diplichnites*, *Heimdallia*,
20 *Metaichna*, *?Multina*, *Planolites*, *Protovirgularia*, *Skolithos*). Exceptional phenomena preserved
21 in the strata include evidence for direct colonization of glacial diamictites by deep-burrowing
22 *Heimdallia* infauna, and interactions between trackways and dropstones on substrates.

23 Observations from the newly-recognized outcrop dramatically expand our understanding of deep
24 time glacial habitats, demonstrating that deglaciating ice-margins had already been colonized by
25 the latest Ordovician. The freshwater influx that would have been associated with such settings
26 implies that faunal associations which were tolerant of brackish water were also established by
27 that time. The locality has further significance because it records the activity of a nearshore
28 animal community contemporaneous with the fauna of the nearby Soom Shale *lagerstatte*.
29 Combined, these reveal a paleoecological transect of the diverse marine life that inhabited cold-
30 climate, low-latitude shallow seas around the time of the end-Ordovician deglaciation.

31 **ICHOLOGY OF GLACIAL ENVIRONMENTS**

32 Compared to other sedimentary systems, there is a less complete understanding of the
33 ichnology of ancient glacial environments (Buatois and Mangano, 2011; Netto et al., 2012;
34 Schatz et al., 2013); in part because glacial sedimentary formations are relatively uncommon,
35 and restricted in their stratigraphic distribution to a few ice-age intervals. Deep time case studies
36 imply that ancient glacial ichnofaunas were low diversity assemblages of diminutive, simple
37 trace fossils (e.g., Buatois et al., 2006; Jackson et al., 2016); explained with reference to
38 environmental stresses such as freshwater and sediment influx from melting glaciers, or frozen
39 substrates impeding infaunal burrowing (Buatois and Mangano, 2011; Netto et al., 2012;
40 Hasiotis et al., 2015). However, these characteristics contrast with the ichnological signatures of
41 modern near-glacial settings (Schatz et al., 2013), and it is possible that existing perspectives
42 have been skewed by paleoenvironmental and stratigraphic biases, and a limited suite of
43 Phanerozoic case studies. For example, ancient glacial ichnofaunas are chiefly reported from
44 fine-grained glacio-lacustrine rhythmites and fjord deposits (e.g., Buatois et al., 2006; Netto et
45 al., 2012), rather than ice-marginal diamictites or sandstones. Likewise, while there are multiple

46 case studies from Carboniferous and younger glaciogenic strata (see Netto et al., 2012), isolated
47 reports of end-Ordovician ichnofaunas are limited to periglacial facies (Kumpulainen et al.,
48 2006; Le Heron, 2010).

49 Here we shed light on animal-sediment interactions in one of Earth's earliest glacial
50 habitats; using new field evidence from an outcrop of the Late Ordovician Table Mountain
51 Group, Western Cape Province, South Africa.

52 **GLACIOGENIC STRATA AT MATJIESGOEDKLOOF**

53 The c. 4 km-thick lower Paleozoic Table Mountain Group, crops out throughout the Cape
54 Basin, and yields a number of direct and indirect signatures attesting to glacial influence (Figure
55 1) (Thamm and Johnson, 2006; Young et al., 2004; Turner et al., 2011). Most prominent
56 amongst the glacially-influenced units is the Pakhuis Formation: a succession of diamictites,
57 sandstones and rare mudrocks that reaches a maximum thickness of c. 80 meters in the basin
58 center, where it overlies glaciotectonically-deformed sandstones of the Peninsula Formation, and
59 thins northwards towards the basin margin, where it rests directly on glacially-carved pre-Cape
60 basement rocks (Blignault and Theron, 2010) (Figure 1C). The unit records glacio-marine
61 deposition by piedmont glaciers that descended southeastwards from a Gondwanan ice sheet
62 (Fig. 2), located at a paleolatitude of c. 30°S and isolated from the major south-polar end-
63 Ordovician ice sheet (Young et al., 2004; Blignault and Theron, 2010; Le Heron et al., 2018).

64 This study has recognized an outcrop of 11 meters of sandstones and glaciogenic
65 diamictites within the Table Mountain Group at the Matjiesgoedkloof farm (31° 38' 21" S; 18°
66 58' 51" E), close to the northern limit of the Pakhuis Formation's outcrop belt (Fig. 1A).
67 Although these strata have previously been mapped as belonging to the uppermost Peninsula
68 Formation (Council for Geoscience, 2001), multiple lines of stratigraphic and sedimentologic

69 evidence suggest that it may be more informative to consider them as constituent to the Pakhuis
70 Formation (Fig. 2B): 1) the strata rest directly on glacially-scoured pre-Cape basement of the late
71 Precambrian Vanrhynsdorp Group; 2) the strata directly underlie muddy diamictites (the “Kobe
72 Member”: Rust and Theron, 1964), grading into siltstones of the Cedarberg Formation; and 3)
73 the strata contain multiple glacial sedimentary signatures (see further discussion in
74 Supplementary Information).

75 Evidence that the strata were directly deposited by glaciers (Fig. 2) include an
76 erosionally-fluted bedrock base to the succession, overlain by a 0.1-1.2 meter-thick, clast-
77 supported diamictite. Constituent clasts are striated, and consist of regional basement lithologies:
78 dominantly quartz, chert, banded ironstone, granodiorite and schist. The diamictite is overlain by
79 c. 10 meters of medium- to coarse-grained sandstones with pebble lags and long-axis-vertical,
80 sand-draped lonestones (dropstones). The sandstone is mostly flat-bedded but becomes trough
81 cross-bedded upwards. There is lateral variation within the outcrop: discontinuous thin (< 50 cm)
82 packages of reworked diamictite occur near the top of the succession.

83 Although end-Ordovician glaciogenic strata are frequently sandy (Le Heron et al., 2018),
84 the high sandstone content at this locality is unusual because overlying and adjacent Pakhuis
85 Formation strata in the vicinity of Matjiesgoedkloof consist of clay-rich tillite (Rust and Theron,
86 1964; Rust, 1981; Blignault and Theron, 2010). As the sandy facies 1) is of local extent only; 2)
87 directly overlies clast-supported diamictite (implying till deposits were not reworked by waves or
88 slumping); and 3) contains dropstones (indicating subaqueous deposition); a plausible
89 explanation is that it records deposition as a sub-glacially-sourced ice-contact fan, adjacent to a
90 tidewater glacier (e.g., Powell, 1981; Fig. 2C). Yet irrespective of precise depositional setting (or
91 regional stratigraphy), the unequivocal evidence that the strata were deposited by glaciers is

92 significant, because the diverse and disparate ichnofauna at multiple horizons within the outcrop
93 (Figs. 1B, 2C) is exceptional for an early Paleozoic glacial ichnofauna (Netto et al., 2012).

94 **TRACE FOSSILS OF THE GLACIOGENIC STRATA**

95 Trace fossils have previously been reported from the Matjiesgoedkloof locality (Rust,
96 1967; Anderson, 1975; Braddy and Almond, 1999; Braddy, 2001; Buatois and Mángano, 2011),
97 but the existing census of ichnofauna is incomplete and the glaciogenic nature of the trace-
98 bearing strata has not been recognized. We have identified 7 different ichnogenera at the
99 Matjiesgoedkloof outcrop, and 8 from the Pakhuis Formation in total. The ichnofauna includes
100 dense concentrations of *Heimdallia* and *Planolites*, in addition to isolated instances of the large
101 plug-shaped burrow *Metaichna*, *Skolithos* and a branching burrow system (?*Multina*). Multiple
102 examples of the arthropod trackway *Diplichnites* are present, in addition to two instances of the
103 trail *Archaeonassa*. A newly-identified specimen of *Protovirgularia*, previously collected from
104 the Pakhuis Formation, has been recognized by the present authors in the collections of the
105 Council for Geoscience (expanding the known trace fossils of the unit, though not directly
106 witnessed at the locality). Additionally, sedimentary features that may potentially record
107 microbial colonization of the glacial substrates are associated with the trace fossils and include
108 blister marks (Fig. 3A) and putative petee structures (see Appendix).

109 Three characteristics of this early glacial ichnoassemblage are significant:

110 1) The ichnodisparity is high relative to the ichnodiversity. The number of architectural designs
111 of trace fossils (Buatois et al., 2017) is equal to the number of ichnogenera in the succession
112 (Fig. 2C).

113 2) Multiple different organisms occupied the ice margin environment. The size differential
114 between the trace fossils at this location suggests multiple unique trace-maker organisms: for

115 example, the witnessed diameter of *Planolites* (< 2 mm) contrasts with that of *Metaichna* (up to
116 230 mm).

117 3) Organisms interacted with glaciogenic substrates. There is indisputable evidence that trace-
118 makers were directly occupying glaciogenic sediments very shortly after deposition (Fig. 3): the
119 largest *Metaichna* burrows can be seen within 20 cm vertically of the basal diamictite;
120 *Diplichnites* trackways divert around dropstone obstacles on the substrate; and *Heimdallia*
121 burrows can be seen penetrating to depths of 15 cm in the sandiest patches of the basal
122 diamictite.

123 **DISCUSSION: LIFE AT THE ICE MARGIN DURING THE LATE ORDOVICIAN**

124 The ichnological complexity of this 11-meter-thick outcrop is exceptional amongst
125 known early Paleozoic glaciogenic successions; yet significantly, it bears strong similarities with
126 the neoichnological character of modern ice margin settings (Schatz et al., 2013). Additionally,
127 whilst phenomena such as burrowed diamictites are extremely rare in the global glacial record,
128 they are not wholly without precedent: two other instances are known from the Pleistocene of
129 Alaska (Eyles et al., 1992) and Carboniferous of Argentina (Schatz et al., 2011). Given that there
130 are parallels with aspects of much younger and modern sediments, the Matjiesgoedkloof
131 succession should not be considered a paleoenvironmentally-exceptional glacial ichnofauna. The
132 simplest explanation is rather that it is a fortuitously-identified/preserved instance of a mundane,
133 low-latitude, near-glacial habitat during the Late Ordovician (its lack of precedence being an
134 artefact of a relatively low outcrop volume of similar strata globally).

135 Salinity dilution of marine waters through glacial melting has previously been considered
136 to be an environmental stress that resulted in low diversity or diminutive ichnofaunas in late
137 Paleozoic strata (Buatois et al., 2006; Jackson et al., 2016). However, the Matjiesgoedkloof

138 ichnofauna differs from expectations as it is similar to non-glacial shallow marine strata
139 elsewhere in the Table Mountain Group (Rust, 1967; Braddy and Almond, 1999), and some of its
140 most prominent ichnotaxa are archetypal constituents of other lower Paleozoic Gondwanan
141 sandy littoral environments in non-glacial settings (e.g., *Heimdallia* and *Diplichnites*: Shillito
142 and Davies, 2020). The similarities between the glacial Matjiesgoedkloof ichnofauna and its non-
143 glacial contemporaries resembles trends observed in modern settings, where comparable
144 ichnofauna occur in both arctic and temperate littoral settings and its position on the high-low
145 tidewater transect that chiefly controls specific ichnoassemblages (Aitken et al., 1988).

146 A prominent characteristic of the Matjiesgoedkloof ichnofauna is its significant
147 ichnodisparity. This could indicate that it represents an early example of a community with
148 brackish water tolerance, as elevated ichnodisparity, relative to ichnodiversity, can be associated
149 with the initial colonization of new environments (Buatois et al., 2017). The variety of
150 architectural designs of trace fossils could reflect exploitation of locally-novel ecospace at the
151 outlet of a melting ice-sheet, but can also be seen in light of global evolutionary trends, as the
152 animal colonization of the land – and thus brackish and freshwater habitats – progressed through
153 the Ordovician and Silurian (Buatois et al., 2005; Shillito and Davies, 2019, 2020), with early
154 bursts of architectural diversification in trace fossils as new environmental niches were occupied
155 (Minter et al., 2017).

156 The Matjiesgoedkloof ichnofauna is also significant because of its relationship to the
157 Soom Shale lagerstätte (lower Cedarberg Formation: Fig. 1C). The Soom Shale Member
158 preserves skeletonized and soft-bodied fauna within very fine clastic outwash sediments
159 (containing occasional dropstones), deposited during a diachronous post-glacial marine
160 transgression as the Pakhuis ice-sheet receded northwards (e.g., Aldridge et al., 2001; Gabbott et

161 al., 2016). As the principal fossil site in the Soom Shale Member is at Keurbos farm (Gabbott et
162 al., 2016), 30 km south of Matjiesgoedkloof, deposition at the two sites was likely near-
163 contemporaneous (Fig. 2A). Together they provide a window onto a nearshore-offshore
164 paleoecological transect in a low-latitude, cold-water setting. The Soom Shale is unbioturbated,
165 due to dominantly anoxic and sometimes euxinic conditions, but yields an open-marine fauna of
166 vertebrates, arthropods, annelids, molluscs, brachiopods, algae, plankton, and problematica
167 (Gabbott et al., 2016). Moving closer to shore, the Matjiesgoedkloof ichnofauna indicates that
168 marine life also thrived where infaunal activity was not limited by anoxic or euxinic bottom
169 conditions. Speculatively, in the ice-contact fan setting, these may even have benefitted from a
170 localized ‘life support bubble’ in the form of well-oxygenated subglacial fluids (e.g., see Lechte
171 and Wallace, 2016). Here, in close proximity to the ice margin, diverse trace-makers likely
172 consisting of arthropods (e.g., *Diplichnites*), gastropods (e.g., *Archaeonassa*), vermiform
173 organisms (e.g., *Skolithos*) and bivalves (e.g., *Protovirgularia*) colonized and interacted with
174 glacial substrates.

175 **CONCLUSIONS**

176 Evidence from the Matjiesgoedkloof outcrop suggests that communities that could
177 tolerate ice-margin habitats, similar to those that exist today, had already evolved by the time of
178 the Hirnantian glaciation; the first significant ice-age to post-date the evolution of animal
179 motility. The ichnofauna demonstrates that ancient glacial ichnofaunas can exhibit high diversity
180 and disparity, despite perceived environmental stresses. Together with fossil-bearing strata
181 elsewhere in the Cape Basin (Soom Shale), the Matjiesgoedkloof ichnofauna provides an
182 unmatched window onto marine paleocommunities during the latest Ordovician glaciation:

183 demonstrating that preserved fossil and trace fossil diversity can be significant at basin- or
184 outcrop-scale, even against a global back-drop of major climate change and mass extinction.

185 **APPENDIX**

186 Further details and images showing the sedimentary and stratigraphic context of the trace fossils.

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279 **FIGURE CAPTIONS**

280 Figure 1. Geological context of trace-fossil-bearing strata at Matjiesgoedkloof. A: Location
281 relative to other outcrop of the Pakhuis Formation and Table Mountain Group in Western Cape
282 Province. B: Sedimentary log through the strata at Matjiesgoedkloof (KOB/SOOM—Overlying
283 Kobe Mb and Soom Shale Mb; VRD GP—Underlying Vanrhynsdorp Gp). C: Cross-section
284 through Cape Basin along line A-A' (in A) showing regional stratigraphic relationships within
285 the Table Mountain Group; modified after Rust (1973). PIE—Piekenierskloof Fm; GFW—
286 Graafwater Fm; PEN—Peninsula Fm; CED—Cedarberg Fm (SS—Soom Shale Mb; DM—Disa
287 Mb); NAR—Nardouw Subgroup.

288 Figure 2. Paleoenvironmental reconstructions showing context of the ichnofaunal community. A:
289 Regional reconstruction as the South African ice sheet receded northwards. Matjiesgoedkloof
290 witnesses diamictite and sandstone deposition from the melting of sea-level piedmont glaciers at
291 the northern edge of the Cape Basin. Contemporaneously, marine siltstones (the Soom Shale) are
292 being deposited offshore to the south – including at fossil lägerstätte localities such as Keurbos.

293 B: Reconstruction of deposition of the strata at Matjiesgoedkloof, showing paleoenvironmental
294 context of sedimentary-stratigraphic phenomena witnessed at outcrop. C: Trace-fossils of the ice-
295 marginal sediments seen in B, showing architectural design (after Buatois et al., 2017),
296 commonness and preference for pro-glacial sandstone or diamictite substrates. *Protovirgularia*
297 was identified within a sample of Pakhuis Formation (locality unknown) in the collections of the
298 Council for Geoscience, Bellville Office.

299 Figure 3. Trace fossils within indisputably glaciogenic strata at Matjiesgoedkloof. A: *Skolithos*
300 and *Diplichnites* within pro-glacial sandstones, containing dropstones. *Diplichnites* (arthropod
301 walking trail) can be seen to divert around dropstone obstacle. B: Dense patches of *Heimdallia*
302 burrows internal to matrix-dominated parts of the basal polymict glacial diamictite that rests
303 directly on the glacially-scoured contact with the Ediacaran Vanrhynsdorp Group. C: Large (23-
304 cm-diameter) plug-shaped *Metaichna* burrow, 20 cm above the top of the basal diamictite,
305 penetrating a wave-rippled sand substrate (lack of crestline deflection implies *Metaichna* post-
306 dates ripple marks). Scale bar in all images is 20 cm.

307 ¹GSA Data Repository item 202Xxxx, further geological context and high resolution images of
308 the Matjiesgoedkloof ichnofauna, is available online at www.geosociety.org/pubs/ft20XX.htm,
309 or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140,
310 Boulder, CO 80301, USA.

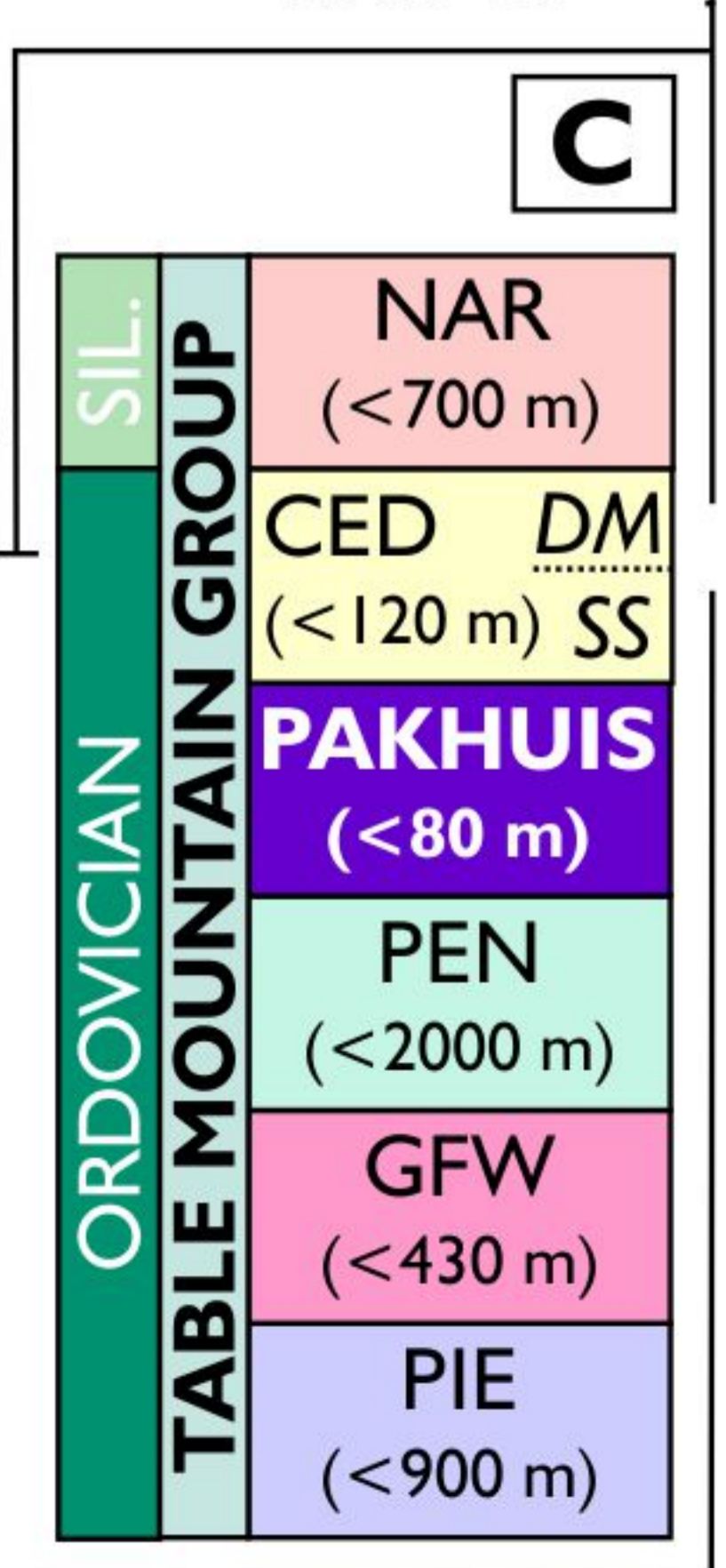
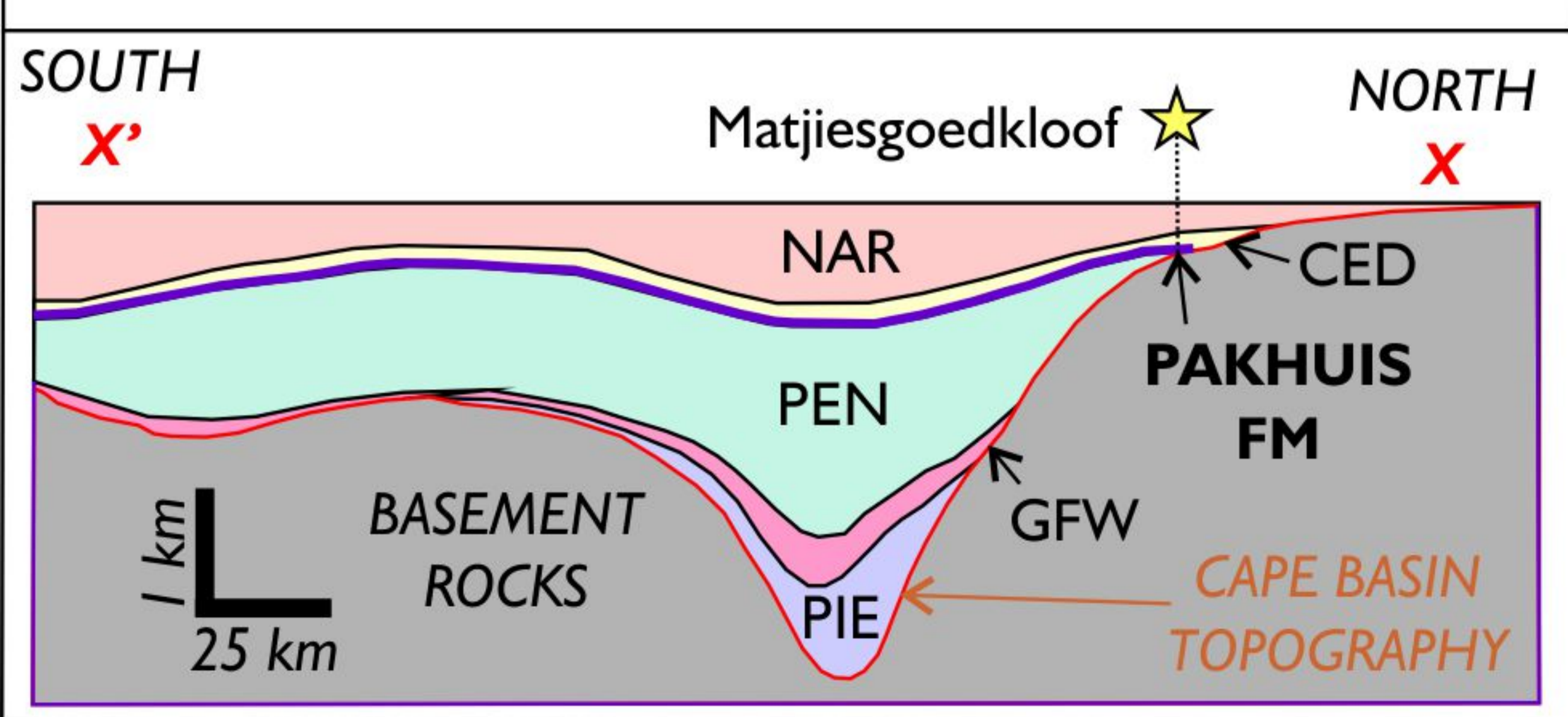
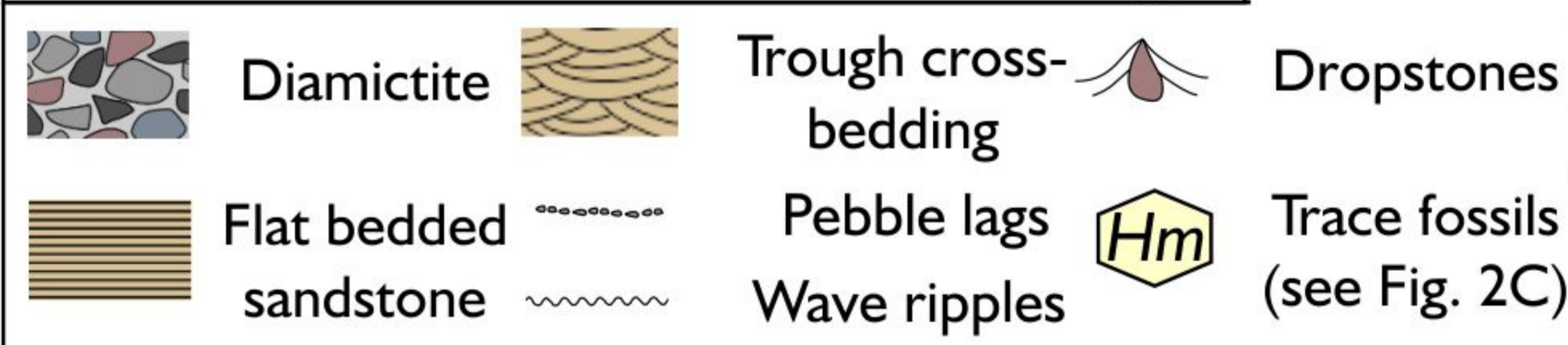
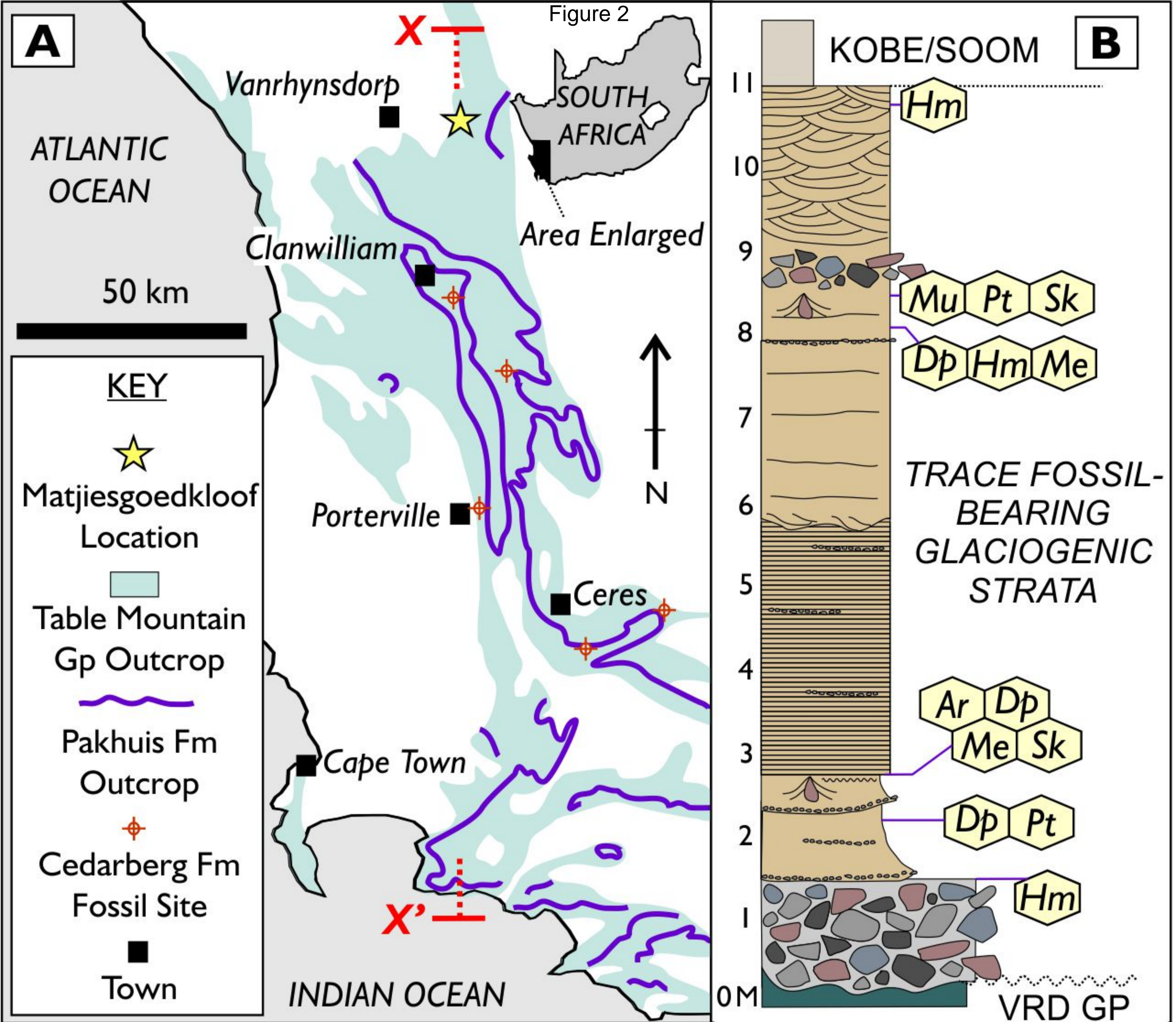


Figure 2

