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The rise and fall of the Malvinoxhosan (Malvinokaffric) bioregion in South Africa: Evidence for Early-Middle Devonian biocrises at the South Pole

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ABSTRACT

Global reconstructions, inclusive of environments and ecosystems, and biodiversity counts for the Devonian Period are often done so at the expense of high latitude regions given a historical lack of data presented from these areas. This has bearing on the recognition of biocrises (events marked by extinctions and faunal turnovers) at high latitudes as well as their controls and potential correlation with global, regional, and local tempos. The appearance and disappearance of high-latitude endemic Malvinoxhosan (synonymous with the "Malvinokaffric Realm" which it supersedes) marine invertebrate faunas from West Gondwana are often overlooked, in part owing to difficulties in correlating fossil-bearing strata with global frameworks given the absence and rarity of several key index taxa as well as detailed biostratigraphic appraisals in which to draw regional interbasinal correlations and comparisons. The Early to Middle Devonian Series of South Africa (upper Table Mountain, Bokkeveld and lower Witteberg groups) are a classic Malvinoxhosan-bearing section recording the rise of these endemic faunas, as well as their decline and replacement by cosmopolitan faunas. A detailed biostratigraphy of this interval was created following an assessment of fossil material curated at the Council for Geoscience and Iziko South African Museum, Cape Town as well as from literature. These data suggest that the Malvinoxhosan bioregion persisted as a cohesive unit during Rietvlei-Baviaanskloof to Waboomberg deposition (Pragian/Emsian-early Givetian) given that many representative taxa are found in these strata, however showing a trend of decreasing diversity with little origination through time. Above this interval, few representative taxa are known to continue into the upper Bokkeveld and Witteberg groups, disappearing entirely by the deposition of the Blinkberg Formation. The few fossils that are known in these strata and those succeeding it (e.g., the Swartruggens Formation) are entirely cosmopolitan in identity. Using novel multivariate statistical methods (non-metric multidimensional scaling and cluster analysis) in conjunction with network analysis (NA), the data were interrogated to indicate potential groupings of strata according to their fossil content as well as to track faunal changes through time. These analyses suggest the presence of at least seven to eight interval assemblage biozones housed within at least three larger faunal complexes (Eo-Malvinoxhosan, Malvinoxhosan and Post-Malvinoxhosan) based on their constituent faunal makeup. A closer inspection of these faunal complexes and interval assemblage biozones show a stepped decline in biodiversity with little to no origination and recovery through time that may be correlated with local base-level change at varying orders of magnitude. Declines in biodiversity show selectivity for taxa with epifaunal and semi-infaunal habits with respect to infaunal, deep infaunal and nektonic taxa. Environmental conditions associated with the collapse of the Malvinoxhosan bioregion are thought to have been catastrophic as few new (often short-ranging) immigrants are registered in Post-Malvinoxhosan strata. Further to this, those faunas that are prevalent in Post-Malvinoxhosan strata (e.g., *Tropidoleptus*) those with known high environmental tolerance and were already present in the region prior to the collapse of the Malvinoxhosan bioregion. Lastly, the observed biodiversity changes in South Africa with respect to local base-level show remarkable similarities with several time equivalent locales in South America suggesting that the decline and extinction of the Malvinoxhosan biota was regional and that the biostratigraphy presented herein has regional application. Here, it is thought regional tectonic controls are suggested to have brought on

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sea-level changes and entrained warmer waters into higher latitudes against the backdrop of overall rising temperatures from the late Givetian onwards. Whilst the decline of the Malvinoxhosan bioregion might associated with global Middle Devonian biocrises (e.g., Kačák; Taghanic) insufficient age constraints for these strata are available at present to make direct comparisons. Furthermore, an adequate driver for global sea-level change during the Devonian Period, needs to be established to tease out global and local signals in constructed local sea-level curves to establish if these changes (and their effects in changes in biodiversity) are truly global in extent.

1. Introduction

1.1. Biocrises of the Early-Middle Devonian

The Devonian Period is punctuated by at least twenty-eight biocrises of varying intensity, especially within the marine realm (Signor and Brett, 1984; House, 1985, 2002; Brett and Baird, 1995; Brett et al., 1996, 2009, 2020; Walliser, 1996; Sepkoski, 1996; Bambach et al., 2004; Bambach, 2006; Becker et al., 2016a, 2016b, 2020; Marshall et al., 2020). These biocrises are typified by periods of extinction, faunal turnover, sudden migrations, and radiations in addition to complete restructuring of benthic communities (Brett and Baird, 1995; Brett et al., 1996, 2009, 2020; McGhee Jr et al., 2013; Becker et al., 2020). Several of these biocrises are demonstrably extensive globally, being typically associated with hypoxic or anoxic events, as evidenced by the deposition of black shales, as well as positive $\delta\,^{13}$C excursions (House, 1985, 2002; Walliser, 1996; Becker et al., 2016a, 2020; Brett et al., 2020). The mechanisms for these phenomena are not entirely understood but they do seem to be short-term coincident with widespread and abrupt transgressions that may be correlated globally (House, 1985, 2002; Walliser, 1996; Becker et al., 2016a, 2020; Brett et al., 2020). Whilst biocrises from the Late Devonian Frasnian-Famennian (e.g., Frasnes and Lower and Upper Kellwasser and Hangenberg biocrises) are perhaps better understood given their great intensity and inclusion within the classical "Big Five" extinctions of the Phanerozoic (extinction of ~50 % marine genera), those from the Early and Middle Devonian have received comparatively less attention. Curiously, when marine biodiversity curves for the Palaeozoic (Sepkoski, 1996; Walliser, 1996; Brett and Baird, 1997; Bambach et al., 2004; Alroy et al., 2008; Fan et al., 2020) are considered, these suggest that Late Devonian biocrisis is perhaps the culmination of declining biodiversity that began in the Middle Devonian and thus are worthy of further detailed study. Pre Frasnian biocrises of importance are the Early Devonian Zlíchov (early Emsian), and Daleje (middle-early late Emsian) biocrises, and the Middle Devonian Choteč (early Eifelian), Kačák (Eifelian-Givetian boundary), and Taghanic (middle Givetian) biocrises (House, 1996, 2002; Walliser, 1996, 2000; Sepkoski, 1996; Becker et al., 2016a, 2020; Brett et al., 2020). An assessment of these biocrises, both in terms of their taxonomic severity (Sepkoski, 1996; Bambach et al., 2004; Bambach, 2006; McGhee Jr et al., 2013) and their ecological effects (McGhee Jr et al., 2013; Becker et al., 2016a, 2016b), suggest that some of these biocrises, in particular those of the Middle Devonian rank within the largest 10 extinction events of the Phanerozoic. These are namely, the terminal Eifelian (extinction of ~ 32% of marine genera) and middle Givetian (extinction of ~ 36% of marine genera) biocrises which are the focus of this study. Both biocrises are associated with third-order palaeoecological changes (McGhee Jr et al., 2013) which are associated with community-level changes within established ecosystems. According to Droser et al. (2000), such effects are associated with the appearance or disappearance of community types, a change in the tiering complexity as well as filling-in or thinning out of Bambachian megaguilds signalling changes within established ecosystems.

The Eifelian biocrisis comprises two distinct, but temporally closely spaced extinction events, namely the "Lower Kačák Event" (or "*otomari* Event"), and "Upper Kačák Event" (House, 1996, 2002; Walliser, 1996, 2000; McGhee Jr et al., 2013; Becker et al., 2016a, 2020; Brett et al., 2020) occurring at the Eifelian-Givetian boundary. The Givetian biocrisis comprises the middle Givetian "Taghanic" (or "*Pharciceras* Event") and is followed by the "Frasnes Event" (synonymous with the "*Manticoceras*", "Ense" and "Givetian-Frasnian Boundary" events) at the Givetian-Frasnian boundary (Johnson, 1970; House, 1996, 2002; Walliser, 1996, 2000; Bambach, 2006; McGhee Jr et al., 2013; Becker et al., 2016a, 2020; Brett et al., 2020). Ecologically, both biocrises are similar in that both appear to have been selective in nature, preferentially affecting benthic faunas occupying sessile epifaunal suspension feeder (e.g., brachiopods, corals, and stalked echinoderms) as well as mobile epifaunal detritivore (trilobites) and carnivore (phyllocarid crustaceans) megaguilds (House, 2002; McGhee Jr et al., 2013). The two biocrises differ, however, in that the Givetian biocrisis was more intense than the Eifelian biocrisis as well as having greater net extinctions among pelagic faunas within suspension (e.g., conodonts) and carnivorous (e.g., goniatite ammonoids) feeding guilds (House, 2002; McGhee Jr et al., 2013).

Perhaps the most concerning facet of the Eifelian and Givetian biocrises is their association with the collapse of endemic bioregions. During the Devonian Period, the global scale development of bioregion endemicity appears to have peaked during the Early Devonian and was followed by an overall collapse with the contraction and disappearance of some bioregions and the expansion of others during the Middle Devonian, eventually leading to a more cosmopolitan global condition by the Late Devonian (Dowding and Ebach, 2018, 2019; Dowding et al., 2021). Beginning in the Lochkovian and peaking in the Pragian-Emsian marine invertebrate faunas with marked levels of endemism and differences in community structure, occupied three broad bioregions, each latitudinally constrained. These are namely the Old World (30° N-30° S), Eastern Americas (30° S-60° S) and Malvinoxhosan (60° S-90° S) realms (Boucot et al., 1969; Boucot, 1971, 1975, 1985, 1988; Boucot and Gray, 1983; Penn-Clarke, 2019; Penn-Clarke and Harper, 2021). The establishment of these bioregions appear coincides with a period of short-term global cooling (within an overall trend of global warming: The Silurian-Devonian Hothouse) that is thought to have created allopatric barriers for speciation (e.g., geographic barriers brought on by lower sea-level as well as thermal boundaries) during the Pragian-Givetian (Early-Middle Devonian) (Penn-Clarke and Harper, 2021). The collapse of these bioregions from the Givetian into the Late Devonian and a shift to a more cosmopolitan global condition is conversely associated with warming that is thought to have set feedback loops in motion causing changes to ocean chemistry, anoxia and rises in sea level (Copper, 1977; Boucot and Gray, 1983; Joachimski et al., 2009; Cocks, 2011; Troth et al., 2011; Penn-Clarke and Harper, 2021; Suttner et al., 2021). This event, the "Great Devonian Interchange", *sensu* McGhee Jr (1997) saw the progressive invasion of warmer water taxa (e.g., *Tropidoleptus* alongside other Old World taxa) into cooler higher latitude regions, resulting in the extinction and replacement of endemics (Isaacson, 1974, 1977a, 1993; Isaacson and Perry, 1977; Isaacson and Sablock, 1990; McGhee Jr, 1997; Harper et al., 2010; Penn-Clarke, 2019; Penn-Clarke and Harper, 2021). In a focused study focused on lower latitude Old World and Eastern Americas realm brachiopods and bivalves, Rode and Lieberman (2004) suggest that the Great Devonian Interchange was gradual in nature with pulses of invasion and replacement being correlated with changes in base-level. It is plausible to assume that the Great Devonian Interchange was complex, involving both changes in base-level against the backdrop of rising global temperatures from the late Givetian onwards. Whilst it is evident that these controls operated at lower latitudes, the mechanisms behind the collapse of endemic regions and biocrises at higher latitudes (e.g., the Malvinoxhosan bioregion) is not as clear. Although attempts have been made in recent years by workers active in South America (e.g., Troth et al., 2011; Bosetti et al., 2011, 2012; Grahn et al., 2013, 2017; Horodyski et al., 2014; Marshall, 2016; Carbonaro et al., 2018; Sedorko et al., 2018a, 2018b, 2019, 2021) to correlate the collapse of the Malvinoxhosan bioregion with global biocrises, most notably the Kačák Event, all have been hampered to some degree primarily by poor biostratigraphic age constraints (owning to the highly endemic nature of these faunas) that have influence over the calibration and correlation of local changes in depositional trends with global or regional sea-level curves. The global reach and effects of Devonian biocrises, especially at high latitudes, is thus open for detailed study and is pertinent to understand given that these regions are environmentally sensitive in our present icehouse world. Using the Early to Middle Devonian of South Africa (present at palaeolatitudes higher than 70° S during this period) as a proxy for high latitude regions this research investigates the long-term faunal and ecological changes of the Malvinoxhosan bioregion in the wake of the Pragian-Givetian cold period by using detailed environmental and sequence stratigraphic calibrated biostratigraphy.

1.2. *The Malvinoxhosan bioregion*

The Malvinoxhosan bioregion was a high (~ 70-90° S) latitude marine palaeobiogeographic region that persisted during the Pragian-Eifelian, extending into the Givetian (Early-Middle Devonian) and equates largely with the "Malvinokaffric Realm" that it supersedes (Penn-Clarke and Harper, 2021) (Fig. 1). As outlined by Penn-Clarke (2019) and Penn-Clarke and Harper (2021), the change in nomenclature from "Malvinokaffric" to "Malvinoxhosan" stems from the racially insensitive connotations of the "-kaffric" suffix especially in a South African context. This restricted bioregion of southwestern Gondwana was associated with cool water, storm- and wave-dominated siliciclastic marine environments and extended across present day subequatorial South America, South Africa, West Antarctica, and the Falkland (Malvinas) Islands (Boucot et al., 1969; Johnson and Boucot, 1973; Barrett and Isaacson, 1988; Isaacson and Sablock, 1988, 1990; Meyerhoff et al., 1996; Penn-Clarke et al., 2018b; Penn-Clarke, 2019; de Vargas et al., 2020; Penn-Clarke and Harper, 2021). Recent detailed reviews on the composition of the Malvinoxhosan bioregion by Penn-Clarke et al. (2018a), Penn-Clarke (2019), and Penn-Clarke and Harper (2021) suggest that, with respect to adjacent bioregions, it is typified by its overall low diversity with endemism largely focused on only a handful of trilobite and brachiopod taxa that are unique to the area; commingling with more cosmopolitan taxa from adjacent bioregions. Those taxa that are unique to the area moreover show some similarity to those from the adjacent Eastern Americas bioregion with which it borders, suggesting a shared origin. Among trilobites, phacopides and proetides show the highest degree of endemism in the region. In phacopides, diversity is primarily focused on calmoniids (entirely endemic) as well as a few species-specific phacopids, dalmanitids and homalonotids. In proetides, a few genus- and species-specific endemic proetids and aulacopleurids are known from the Malvinoxhosan bioregion. Brachiopod endemism is focused mainly among rhynchonelliform brachiopods and include several endemic rhynchonellate (terebratulides, spiriferides, athyridides, and a probable rhynchonellides e.g., *Australocoelia, Antelocoelia, Tanerhynchia*) and strophomenate (productides and orthotetides) genera in addition to a few species endemic nonarticulate discinoids. Overall molluscs and echinoderms are cosmopolitan showing affinities with those from the adjacent Eastern Americas and Old World bioregions with few endemic taxa in comparison to brachiopod and trilobite taxa. In addition to the low diversity of the Malvinoxhosan bioregion is the absence and rarity of certain groups that were globally common at the time. Here, conodonts, graptolites and stromatoporoid sponges are notably absent as well as atrypide and pentameride brachiopods whilst goniatite ammonoids and lower trophic level thermophilic reef-building organisms (e.g., bryozoans and corals) and are exceptionally rare. Lastly, a key defining indicator for the Malvinoxhosan bioregion is the overall abundance of conulariids, tentaculitids, and hyolithids, some taxa of which might be entirely endemic to the area.

Investigations on the distributions of biota across the Malvinoxhosan bioregion as well as greater West Gondwana, specifically of trilobites (Wolfart, 1968; Baldis, 1979; Eldredge and Ormiston, 1979; Lieberman et al., 1991; Lieberman, 1993; Abe and Lieberman, 2009, 2012; Rustán, 2016; Carbonaro et al., 2018) and, more recently, brachiopods (Penn-Clarke and Harper, 2021) suggest that not all these taxa occur evenly throughout the region both in space and in time (Dowding and Ebach, 2018, 2019; Dowding et al., 2021). A general two-fold division of the Malvinoxhosan bioregion has been suggested in these studies with major centres of diversity focused on the broad Andean (Bolivia-Argentina) and South African regions with the Paraná of Brazil being noticeably less diverse. According to Penn-Clarke and Harper (2021), the Andean and South African regions, located at the peripheral of the Malvinoxhosan bioregion (~70°-80° S) show greater admixture of endemic taxa with adjacent lower latitude bioregions whilst the Paraná (~80°-90° S) is comprised of a more distinctly Malvinoxhosan faunule. These differences across the bioregion have been attributed variably to sea-level assisted vicariance and dispersal (e.g., Lieberman et al., 1991; Lieberman, 1993; Abe and Lieberman, 2009, 2012; Rustán, 2016; Carbonaro et al., 2018) or by latitude-induced climatic and oceanic forcing (Copper, 1977; Boucot and Gray, 1983; Boucot, 1988; Troth et al., 2011; Penn-Clarke and Harper, 2021).

The distribution of ichnofossils and body fossils associated with the Malvinoxhosan biota suggest that these organisms had a strong preference for habitation in lower shoreface, offshore transition zone, and offshore environments below wave-base where they exploited an array of infaunal and epifaunal based ethologies (Boucot, 1971, 1975; Hiller and Theron, 1988; Gaillard and Racheboeuf, 2006; Horodyski et al., 2014, 2018; Reid et al., 2015, 2019a; Penn-Clarke, 2019; Penn-Clarke et al., 2018b, 2019; Sedorko et al., 2018a, 2018b, 2019, 2021). The preservation of fossils in these environments, however, might be attributed to taphonomic biases accentuated by storm and wave reworking expected to affect organisms and communities in more proximal upper shoreface-foreshore environments that are above wave base.

A consensus on the diversity within the Malvinoxhosan bioregion across southwestern Gondwana suggests that it was perhaps at its acme during the latest Pragian-early Emsian followed by a stepped decline in diversity beginning possibly as early as the middle-late Emsian; eventually collapsing as a cohesive grouping during the late Eifelian; with few surviving taxa ranging into the Givetian (Boucot et al., 1969; Johnson and Boucot, 1973; Boucot, 1985, 1988; Boucot and Racheboeuf, 1993; Melo, 1988; Isaacson, 1977a, 1977b, 1993; Bosetti et al., 2011, 2012; Troth et al., 2011; Horodyski et al., 2014; Marshall, 2016; Grahn et al., 2017; Penn-Clarke, 2019; Penn-Clarke et al., 2018a; Penn-Clarke and Harper, 2021; Sedorko et al., 2018a, 2018b, 2021). The closure of the Malvinoxhosan bioregion in the late Eifelian to Givetian is associated with the regional appearance and dominance of supposed warm-water associated "trans-Atlantic" brachiopods, specifically the opportunistic *Tropidoleptus* and terebratulid *Rhipidothyris* in shelly assemblages as well as an abundance of the acritarch *Evittia sommeri* (Boucot et al., 1969, 1983; Isaacson, 1974, 1993; Copper, 1977; Boucot, 1985, 1988; Fonseca and Melo, 1987; Boucot and Theron, 2001; Troth et al., 2011; Grahn et al., 2017; Marshall, 2016; Penn-Clarke, 2019). In Bolivia, this is further preceded by the arrival of extra-basinal goniatite ammonoids into the Chaco Basin (Troth et al., 2011). In the Givetian "post-Malvinoxhosan" assemblages few macroinvertebrate taxa are known other than *Tropidoleptus* and *Rhipidothyris*. Here, rare occurrences of the Malvinoxhosan brachiopods *Australocoelia*, *Australospirifer,* and *Derbyina* as well as the calmoniids *Metacryphaeus* and *Pennaia* are known to coexist with extra-Malvinoxhosan bivalve and gastropod taxa as well

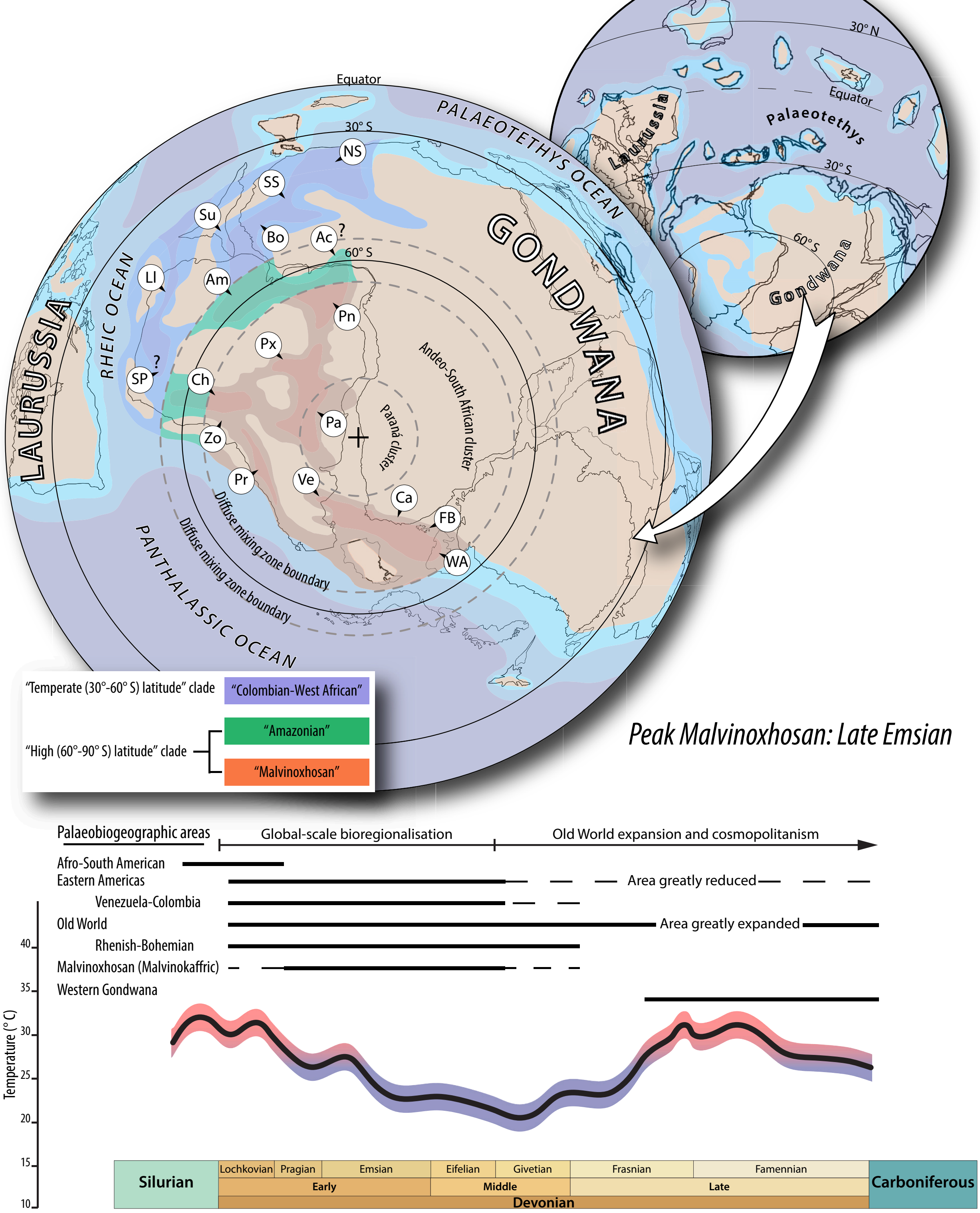

Fig. 1. Palaeobiogeography of West Gondwana during the Early Devonian (Late Emsian) showing peak extent of the Malvinoxhosan bioregion at high latitudes in the vicinity of the South Pole (70°-90° S) after Penn-Clarke and Harper (2021). Bordering the Malvinoxhosan bioregion are the Amazonian and Colombian-West African bioregions that largely equate with the Eastern Americas and Old-World Realms. These distinct bioregions persisted during a period of protracted cooling during the Pragian-Givetian, collapsing and resulting in a more cosmopolitan regime from the late Givetian onwards with rising global temperatures, after Joachimski et al. (2009). Abbreviations: Ac- Accraian (Ghana), Am- Amazonas (Brazil), Bo- Bové (Guinea, Guinea-Bissau, Senegal), Ca- Cape (South Africa), Ch- Chaco/Central Andean (Bolivia), FB- Fox Bay (Falkland Islands), Ll- Llanos (Colombia and Venezuela), NS- "North Saharan" (Tindouf, Ghadamis, Polignac, Murzuq basins), Pa- Paraná (Brazil, Paraguay, Uruguay), Px- Parecis (Brazil), Pr- Precordillera (western Argentina), Pn- Parnaíba (Brazil), SP- southern Peru, SS- "South Saharan" (Tamesna and Taoudeni basins and Adrar, Hodh regions), Su- Suwannee (Florida, Georgia, United States), Ve- Ventana (eastern Argentina), WA- West Antarctica ("Ellsworth-Whitmore Mountains"), Zo- Zorritas (northern Chile).

as scant occurrences of tentaculitids, conulariids, corals and crinoids (Isaacson, 1974, 1977b, 1993; Isaacson and Perry, 1977; Boucot et al., 1983; Hiller, 1990; Feist, 1991; Melo, 1988; Sedorko et al., 2021) that are known from the Paraná (Brazil) and Cape (South Africa) basins.

In addition to a large drop in diversity within the Malvinoxhosan bioregion, the appearance of *Tropidoleptus*-dominated shelly assemblages has been documented to coincide with other faunal and ecological effects in South America. In Bolivia, the appearance of *Tropidoleptus*-dominated shelly assemblages is documented to coincide with the appearance of goniatite ammonoids and Laurussian/Euramerican associated ambocoelid brachiopods (Isaacson, 1974, 1977a; Hünicken et al., 1980; Boucot and Racheboeuf, 1993; Troth et al., 2011). In the Paraná Basin, latest Eifelian and Givetian strata contain an impoverished Malvinoxhosan faunule that show an apparent miniaturisation ("Lilliput effect") in size prior to their complete disappearance. This is co-incident with the appearance of *Tropidoleptus*-dominated shelly assemblages (Bosetti et al., 2011; Horodyski et al., 2014; Grahn et al., 2017). Sedorko et al. (2019, 2021) have further shown a correlation between changes in macroinvertebrate fossil assemblages and ichnofossil assemblages in the Paraná Basin. In the Paraná Basin proximal lower shoreface to distal lower shoreface and offshore ichnofossil assemblages reach their greatest diversity with the establishment of the Malvinoxhosan bioregion in the late Pragian-early Emsian. These environments are respectively represented by proximal *Skolithos* and distal *Cruziana* ichnofacies assemblages characterised by *Asterosoma* and *Zoophycos* ichnoguilds, respectively. This is taken to represent optimum marine conditions. Following the first registered decline in biodiversity in the Paraná Basin in the late Emsian, and into the Eifelian, a shift towards more *Teichichnus* and *Planolites* ichnoguilds and *Skolithos* dominated ichnoguilds has been noted in distal offshore strata. Most noticeable is the apparent disappearance of *Zoophycos* in these strata (Sedorko et al., 2021). The overall composition of these ichnoguilds suggests a reduction in suspension- and detritus-feeding activities that has been interpreted to represent changes in basin organisation and a gradual influx of freshwater (Sedorko et al., 2019, 2021). At the Eifelian-Givetian boundary, a return to marine conditions is noted in the Paraná Basin following a regional transgression into the basin. In these deposits, proximal most facies are characterised by *Skolithos*, *Planolites* and *Asterosoma* ichnoguilds with distal most facies being represented by the *Phycosiphon* ichnoguild (Sedorko et al., 2021). Leading into the Frasnian, the *Asterosoma* ichnoguild disappears signalling an influx once more of freshwater into the Paraná Basin perhaps related to changes in tectonic configuration (Sedorko et al., 2021).

The exact causes for the decline, and eventual closure, of the Malvinoxhosan bioregion are uncertain, however, there is a correlation with interpreted changes in sea-level that may be linked to the knock-on effects of changing oceanic temperature and salinity. In Bolivia (Isaacson, 1974; Isaacson and Perry, 1977; Troth et al., 2011), Brazil (Copper, 1977; Melo, 1988; Bosetti et al., 2011, 2012; Grahn et al., 2013, 2017; Horodyski et al., 2014; Carbonaro et al., 2018; Sedorko et al., 2018a, 2018b, 2019, 2021) and the Falkland Islands (Marshall, 2016), the decline and collapse of the Malvinoxhosan bioregion is coincident with local changes in sea-level, most notably with transgressions. The timing of these local transgressive events suggests an apparent correlation with Laurussian/Euramerican (often assumed to be representative of "global" trends) third-order eustatic events if the limited palynological and chitinozoan biostratigraphic correlations from these areas are considered to be correct. It is well established that many, if not all, of the extinction events that took place during the Early-Middle Devonian appear to be correlated with first-order transgressive events, that are suspected to have been globally extensive, which lead to periods of dysoxia or anoxia, extinction and the deposition of black shales (Walliser, 1996, 2000; House, 1996, 2002; Brett et al., 2009; Suttner et al., 2021).

Whilst no convincing evidence has been reported for anoxia at the level of the Malvinoxhosan bioregion, there is tantalising evidence to suggest that observed stepped diversity declines in Brazil, Bolivia and the Falkland Islands may be correlated with at least three of these Early-Middle Devonian events. Here, the earliest middle-late Emsian diversity decline has been correlated with the Daleje Event in the Paraná Basin (Bosetti et al., 2012) whilst a decline in palynomorph diversity and arrival of extra-basinal goniatite ammonoids during the early Eifelian appears to be correlated with the Choteč Event, respectively, in the Falkland Islands and Bolivia (Troth et al., 2011; Marshall, 2016). The eventual closure (and collapse thereof) of the Malvinoxhosan bioregion in the late Eifelian to Givetian is suggested to correspond with the Kačák Event (House, 1996, 2002; Bosetti et al., 2011, 2012; Grahn et al., 2013, 2017; Horodyski et al., 2014; Marshall, 2016). When plotted against global palaeotemperature curves for the Devonian Period, the temporal range of the Malvinoxhosan bioregion (as with other distinct bioregions at this time) correlates with a period of moderate cooling (~ -10° C) during the Pragian-Eifelian and perhaps earliest Givetian (Copper, 1977; Boucot, 1988; Boucot and Gray, 1983; Boucot et al., 1997; 2013; Penn-Clarke and Harper, 2021).

The closure of the Malvinoxhosan bioregion appears to coincide with the collapse of other biogeographically distinct areas of endemism (e.g., Eastern Americas Realm, Old World Realm, etc.) that resulted in a more globally cosmopolitan condition beginning in the late Givetian, leading into the Late Devonian (see Dowding and Ebach, 2018, 2019; Dowding et al., 2021). The collapse of these distinct areas of faunal endemism further shows some correlation with an increase in global warming beginning in the Givetian (Penn-Clarke and Harper, 2021; Suttner et al., 2021). When the sum of evidence is considered, it is plausible that transgressions into West Gondwana could have drawn warmer water currents and faunas from lower latitudes into Devonian circumpolar regions against the backdrop of increasing global oceanic temperatures. Successive (and arguably "warmer") transgressions would have broken down inferred circumpolar currents whilst altering palaeogeographic boundaries and features, leading to the gradual breakdown of these allopatric barriers.

2. The Early-Middle Devonian of South Africa

2.1. Stratigraphy, sedimentology and palaeoenvironmental interpretations

In South Africa, Lower to Middle Devonian deposits crop out extensively throughout the Cape Fold Belt within both the Clanwilliam and Agulhas sub-basins of the Cape Supergroup (Fig. 2). Here the entire system is represented by a relatively thick (~1,500-2,000 m) siliciclastic succession that accumulated in a broadly marginal-shallow marine environment strongly influenced by storm- and wave-dominated conditions (Theron, 1970, 1972; Tankard and Barwis, 1982; Tankard et al., 1982; Theron and Loock, 1988; Hiller, 1990; Hiller and Taylor, 1992; Cotter, 2000; Penn-Clarke, 2017, 2019; Penn-Clarke and Theron, 2020; Penn-Clarke et al., 2018b, 2019) (Fig. 6). In the context of this study, fossil-bearing deposits from the Rietvlei and Baviaanskloof formations (Nardouw Subgroup, Table Mountain Group), Bokkeveld Group and the lower Weltevrede Subgroup (Witteberg Group) are considered given that these rocks contain fossils associated with the Malvinoxhosan bioregion. Relative biostratigraphic constraints for this interval based on macrofaunal fossils suggest that it possibly spans the Pragian-Givetian (Penn-Clarke et al., 2018a; Penn-Clarke, 2019), however, an earlier Lochkovian age cannot be excluded for the lowest strata.

2.1.1. Rietvlei and Baviaanskloof formations

The Lower Devonian (Lochkovian to Pragian) Rietvlei Formation (100-200m thick), and its distal equivalent the Baviaanskloof Formation (80-190 m thick) (Fig. 2), comprise the earliest occurrence of fossils associated with the Malvinoxhosan bioregion, let alone those of Devonian age, in South Africa (Penn-Clarke et al., 2018a; Penn-Clarke, 2019) in addition to recently described Early Devonian plants (Gess and Prestianni, 2021). Malvinoxhosan fossils (as well as accompanying bioturbation), however, are apparently exclusively known from the

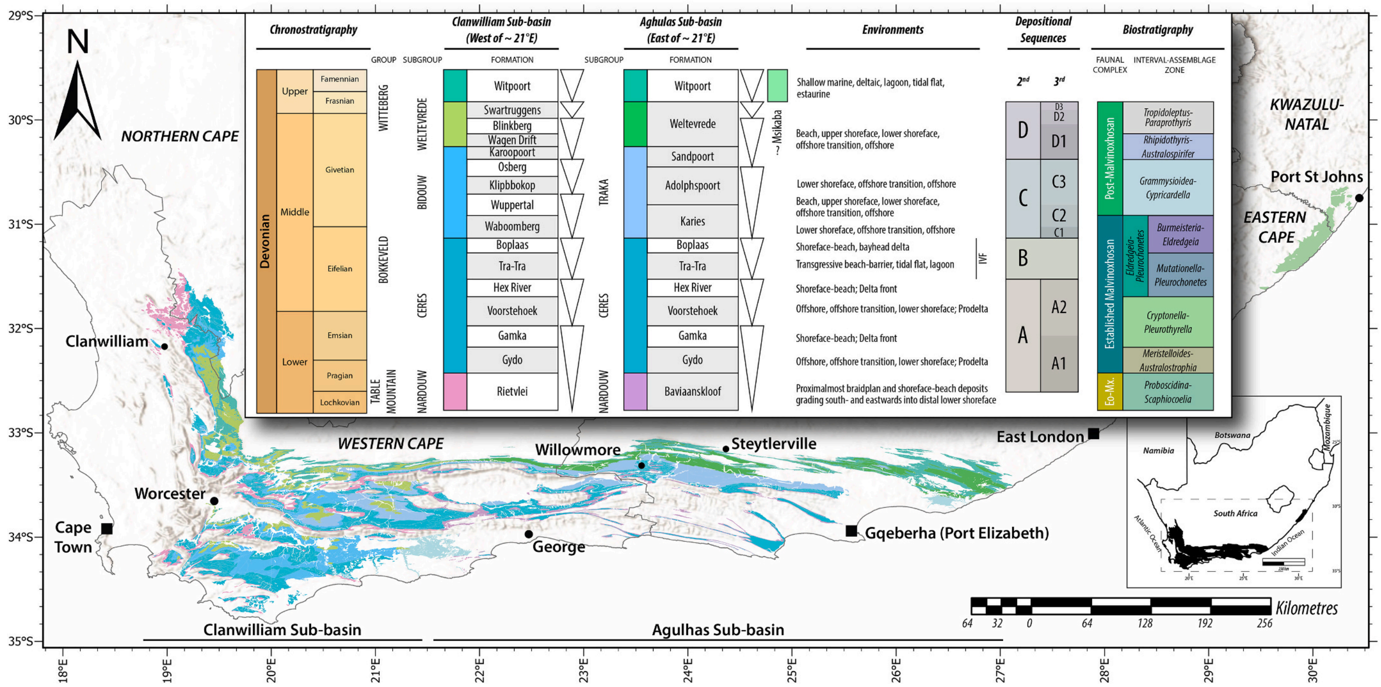

Fig. 2. Geological map of the Devonian System of South Africa. Stratigraphic ages, environmental interpretations depositional sequences and biostratigraphic frameworks presented herein (Map data after Council for Geoscience).

uppermost portion of both formations (Reed, 1906; Rossouw et al., 1964; Theron, 1972; Oosthuizen, 1984; Hiller and Theron, 1988; Boucot and Theron, 2004; Gess and Prestianni, 2021) from the so-called "passage beds" facies that directly underlie shales of the Gydo Formation.

The Rietvlei Formation occurs in the western and northern reaches of the Cape Fold Belt and is restricted largely to the Clanwilliam Sub-basin. It is characterised as a succession of medium- to thick-bedded quartz arenites and subarkoses with occasional conglomeratic stringers and finer-grained heterolithic-laminated and shale-rich interbeds (Thamm, 1984, 1987; Theron and Loock, 1988; Theron and Basson, 1989). Quartz arenites and subarkoses often manifest as trains of interbedded trough and tabular cross-bedded co-sets that are interspersed by laterally continuous upper plane-laminated sandstones. These are interpreted to be littoral shoreface-beach deposits. In certain exposures, as is most prevalent in the northernmost reaches of the Cape Fold Belt, well-amalgamated channel scour-and-fill features with conglomeratic lags are present (Thamm, 1984, 1987; Theron and Loock, 1988; Theron and Basson, 1989). These are interpreted to be proximal braidplain to beach deposits.

Within the lower third of the formation, especially in the southern and easternmost outcrop area, a succession of interbedded sandstones and mudstones (~ 15-50 m) is present which weather more recessively than the succeeding succession. This has been referred to informally as the "soft band" by Newton (1975) who first recognised it and later referred to as the "Verlorenvalley member" by Hartnady and Hay (2002) from groundwater studies. At this same stratigraphic level, the Verlorenvalley member has been shown in recent geological mapping to be present in the central-northern extent of the outcrop area in the Cederberg where it is represented as a succession of negatively weathering, very thin-bedded, fine-grained sandstones. Although the palaeoenvironmental genesis of this stratigraphic interval in the Rietvlei Formation is still to be deduced, it is assumed to perhaps be a distal shelf-offshore environment in the south, grading northwards into more proximal nearshore environments.

In the upper reaches of the Rietvlei Formation, the succession fines upwards into the "passage beds" facies (~ 3-15 m thick) that are characterised as being a succession of heterolithic-laminated sandstone and siltstone that is sharply interbedded with non-amalgamated fine-grained wave-ripple laminated and hummocky cross-stratified quartz wacke sandstones (Hiller and Theron, 1988; Theron and Basson, 1989; Penn-Clarke, 2017; Penn-Clarke et al., 2018b). These deposits bear resemblance to the Verlorenvalley member but still await detailed sedimentological study. The passage beds facies are interpreted to have accumulated in more distal offshore transition zone-lower shoreface environments (Hiller and Theron, 1988). Ichnologically, heterolithic intervals of the Rietvlei Formation (especially of the upper passage beds facies) contains a low diversity marine ichnoassemblage. Here this horizon comprises *Scolicia* group burrows in addition to vertical simple sandstone-infilled *Skolithos* and annulated *Monocraterion* burrows in addition to mud-lined burrows ascribed to *Palaeophycus*, and *Rosselia*, as well as occasional giant rusophycid type burrows (Almond, 1998, 2008). The passage beds facies conformably fine upwards into offshore shales and mudrocks of the Gydo Formation (basal Bokkeveld Group).

The Baviaanskloof formation, present in the southern and eastern reaches of the Cape Fold Belt, and is within the Agulhas Sub-basin, is markedly more argillaceous than the Rietvlei Formation. This succession comprises a basalmost heterolithic-laminated sandstone and siltstone that is interbedded with wave-ripple laminated, fine-grained quartz wacke sandstone which may fine upwards locally into rhythmites and mudrocks (Malan and Theron, 1989; Hill, 1991). Like the passage beds facies of the upper Rietvlei Formation, these are interpreted to perhaps be of a similar genesis. In the middle of this succession a prominent medium- to coarse grained package of cross-bedded and upper plane-laminated quartz arenites and subarkoses is present, the Kareedouw Member (Malan and Theron, 1989; Hill, 1991). Interspersed among these quartz arenites and subarkoses are conspicuous lenses of plant fossil-rich interbedded quartz wackes and black micaceous siltstones (Gess and Prestianni, 2021). Collectively, the facies of the Kareedouw Member bear resemblance to those akin to having been deposited in a mixed proximal beach-barrier and lagoon setting (Gess and Prestianni, 2021). The rhyniophytoid floral assemblage of the Kareedouw Member is interpreted to be at least Lochkovian in age (Gess and Prestianni, 2021). The Kareedouw Member fines upwards overall into a succession of heterolithic-laminated sandstone and siltstone that is sharply interbedded with fine grained wave-ripple laminated and hummocky cross-stratified quartz wacke sandstones that may locally contain a *Skolithos* ichnoassemblage (Malan and Theron, 1989; Theron et al., 1991; Hill, 1991) and is identical to the passage beds facies of the uppermost Rietvlei Formation and have thus accumulated in a distal offshore transition zone-lower shoreface environment. These deposits, in turn, conformably fine upwards into offshore shales and mudrocks of the overlying Gydo Formation (Malan and Theron, 1989; Hill, 1991).

Both the Rietvlei and Baviaanskloof formations overlie, with sharp contacts, thick- to very thick-bedded coarse-grained and conglomeratic quartz arenites and subarkoses of the Silurian Skurweberg Formation and are noticeably finer-grained overall. In the Rietvlei Formation, this surface is delineated by a thick-bedded conglomerate that fines upwards into medium-bedded fine-grained quartz arenites that are succeeded by interbedded shale and sandstone (Theron and Basson, 1989). In the Baviaanskloof Formation, this surface is indicated either by a sharp onlap of interbedded siltstones, shales and fine-grained quartz wackes, or by a fine-grained quartz wacke that fines upwards into a succession of interbedded quartz wackes, siltstones and shales (Hill, 1991).

2.1.2. Bokkeveld Group

The Lower to Middle Devonian (Pragian/Emsian to Givetian) Bokkeveld Group (700-3,500 m thick) is markedly more argillaceous with respect to the Table Mountain and Witteberg groups that bound it. In outcrop, the Bokkeveld Group is typically characterised by a series of alternating basin-wide argillaceous and arenaceous units that form the basis for formation level lithostratigraphic subdivision of the entire succession. At outcrop scale, and from sedimentological studies, these units may be arranged into five (Agulhas Sub-basin) to six (Clanwilliam Sub-basin) upward coarsening successions each comprising shales and mudstones that, ideally, coarsen upward into siltstones, quartz wackes and quartz arenites (Fig. 2) (Swart, 1950; Csaky, 1969; Csaky et al., 1969; Theron, 1970, 1972; Johnson, 1976; South African Committee for Stratigraphy (SACS), 1980; Tankard and Barwis, 1982; Tankard et al., 1982; Theron and Loock, 1988; Penn-Clarke, 2017; Penn-Clarke et al., 2018b, 2019; Penn-Clarke and Theron, 2020). The entire succession is overall more sandy towards its northern and western outcrop limits and is, conversely, more muddy towards the south and east (South African Committee for Stratigraphy (SACS), 1980; Theron and Johnson, 1991). This difference in gross sedimentology and stacking pattern is most evident in the upper stratigraphic interval of the Bokkeveld Group and is used as the basis to separate the western Bidouw Subgroup from the eastern Traka Subgroup, both of which conformably overlie the Ceres Subgroup (Theron and Johnson, 1991). Here, the second arenaceous stratigraphic unit in the Bidouw Subgroup (the Wuppertal Formation) is conspicuously absent in the Traka Subgroup and, in its place, a siltstone interval is present in the upper Karies Formation (the overall eastern equivalent of the Waboomberg Formation).

Studies on the sedimentology of the Bokkeveld Group suggest that it accumulated in an essentially paralic-shallow marine depositional setting and is a more distal expression of the Rietvlei and Baviaanskloof formations that it retrogrades from as well as the overlying Witteberg Group which it progrades into. The upward coarsening successions that typify the Bokkeveld Group have been reasoned to be allocyclic transgressive-regressive (T-R) cyclothems (Theron, 1970, 1972; Tankard and Barwis, 1982; Penn-Clarke, 2017; Penn-Clarke et al., 2018b, 2019). Older sedimentological studies on the Bokkeveld Group broadly suggested that each cyclothem accumulated in a series of laterally amalgamated, storm-and wave-dominated deltaic depositional systems (Csaky, 1969; Csaky et al., 1969; Theron, 1970, 1972; Tankard and Barwis, 1982; Theron and Loock, 1988; Theron, 1999, 2003; Basson et al., 1995; Theron et al., 1995a, 1995b). These rather simplistic studies further suggest that each cyclothem is identical in its succession of environments; each being deposited in a single T-R event and comprising basal prodelta-offshore deposits that grade upwards into progressively shallower delta-front/lower or middle shoreface deposits that in turn are capped by proximal distributary mouth bar, nearshore, shoreface, beach, bay or tidal-estuarine deposits (Csaky, 1969; Csaky et al., 1969; Theron, 1970, 1972; Tankard and Barwis, 1982; Theron and Loock, 1988).

More recent sedimentological studies of the Bokkeveld Group by Penn-Clarke et al. (2018b, 2019) and Penn-Clarke and Theron (2020) found little evidence for deltaic sedimentation, at least in the Clanwilliam Sub-basin where those studies took place. Their work suggested that deposition, by and large, occurred within storm- and wave-dominated shallow marine depositional systems. Individual allocycles comprise deposits akin to those in offshore, offshore transition zone to distal lower shoreface (OTZ-dLSF), proximal lower shoreface (pLSF) and upper shoreface-beach environments (USF-Beach). The succession of these environments (and their bounding surfaces) in outcrop and across the basin, suggests a complex control on cyclicity that can be explained at multiple scales, differing from previous studies. In addition to these deposits, their research also found evidence for sedimentation occurring in transgressive beach barrier lagoon and wave-influenced deltaic depositional systems within the Tra-Tra-Boplaas interval. Here, tidal flat, lagoon and lower shoreface reworked transgressive beach-barrier environments were recognised in the Tra-Tra Formation whilst prodelta, distal delta front and proximal delta front environments were recognised in the uppermost Tra-Tra and Boplaas formations (Penn-Clarke et al., 2018b; Penn-Clarke and Theron, 2020).

A paralic to shallow marine interpretation for the Bokkeveld Group is supported by its cosmopolitan array of at least 50 marine-associated ichnogenera ascribed to both *Cruziana* and *Skolithos* ichnofacies (Almond, 1998, 2008; Penn-Clarke, 2017; Penn-Clarke et al., 2018b, 2019; Penn-Clarke and Theron, 2020). Ichnofossils from the Bokkeveld Group are typically associated with OTZ-dLSF and pLSF deposits where they are preserved within pre- and post-storm hummocky cross-stratified and wave ripple-laminated tempestites. The abundance and diversity of ichnofossils in the Bokkeveld Group closely parallels that of body fossils in the succession. Here, ichnofossils are generally common and diverse (with high bioturbation indices) in OTZ-dLSF and pLSF deposits of the Ceres (Gydo, Voorstehoek and Tra-Tra formations) and the lower Bidouw (Waboomberg and Wuppertal formations) subgroups. Ichnofossils from these formations record a suite of domichnic, fodinichnic, pasichnic, repichnic, and cubichnic ethologies. Within the Ceres Subgroup, the diversity and abundance of ichnofossils is greatest in the Gydo and Voorstehoek formations while those present in the Tra-Tra Formation are markedly more restricted (Almond, 1998, 2008; Penn-Clarke, 2017; Penn-Clarke et al., 2018b; Penn-Clarke and Theron, 2020). This has been interpreted as a reflection of differences in environmental conditions with OTZ-dLSF and pLSF deposits in the Gydo and Voorstehoek formations having been accumulated under open marine conditions while those in the Tra-Tra Formation accumulated in more restricted paralic conditions (Almond, 1998, 2008; Penn-Clarke and Theron, 2020). In addition to ichnofaunas within the *Cruziana* and *Skolithos* ichnofacies, present in transgressive beach-barrier derived lower shoreface and tidal flat environments, the Tra-Tra Formation additionally comprises a suite of ichnofaunas associated with the *Psilonichnus* ichnofacies where parts of the original backshore portion of the beach-barrier are preserved (Penn-Clarke and Theron, 2020).

In the lower Bidouw Subgroup, the Waboomberg and Wuppertal formations comprise a rich and diverse ichnoassemblage that is associated with OTZ-dLSF and pLSF deposits often with high bioturbation indices (Penn-Clarke, 2017; Penn-Clarke et al., 2019), similar to that observed in the Gydo and Voorstehoek formations. Ichnofaunas are, however, exceedingly rare and disparate in the upper Bidouw Subgroup (Klipbokkop, Osberg and Karoopoort formations) (Almond, 1998, 2008; Penn-Clarke, 2017; Penn-Clarke et al., 2019). In the lower Klipbokkop Formation, a limited number of simple endichnic and epichnic *Skolithos* ichnofacies associated ichnotaxa (*Arenicolites*, *Bifungites/Diplocraterion*, *Cochlichnus*, *Psammichnites*, *Planolites*, *Rosselia*, *Skolithos*, *Thalassinoides*) are present in OTZ-dLSF and pLSF deposits displaying predominantly domichnic, pasichnic and fodinichnic ethologies. Ichnodiversity in OTZ-dLSF and pLSF deposits decreases further in the upper Klipbokkop Formation being solely represented by diminutive fodinichnia of *Spirophyton/Zoophycos* and *Lorenzinia* (Almond, 1998, 2008; Penn-Clarke, 2017; Penn-Clarke et al., 2019). A slight recovery in ichnodiversity is registered in OTZ-dLSF and pLSF deposits of the Osberg and Karoopoort formations, albeit still dominated by intensely bioturbated *Spirophyton/Zoophycos* rich beds. Here, an impoverished *Cruziana* ichnofacies is present, comprising domichnia and fodinichnia of *Arenicolites*, *Altichnus*, *Bergauria*, *Diplocraterion*, *Rosselia* and *Skolithos* are present alongside pasichnia of *Planolites* and *Psammichnites*, repichnia of *Cochlichnus* and *Cruziana* as well as rare *Rusophycos* cubichnia are present alongside *Spirophyton/Zoophycos* (Penn-Clarke, 2017; Penn-Clarke et al., 2019).

2.1.3. *Weltevrede Subgroup and Weltevrede Formation (Witteberg Group)*

Conformably overlying the rocks of the Bokkeveld Group are siliciclastic deposits of the Middle Devonian-Lower Carboniferous Witteberg Group. In the Clanwilliam Sub-basin this is represented by the rocks of the Middle to Upper Devonian (Givetian to Frasnian) Weltevrede Subgroup (~570 m thick) (comprising the Wagen Drift, Blinkberg and Swartruggens formations) and its eastern lateral equivalent in the Agulhas Sub-basin, the Weltevrede Formation (~ 800 m thick). The Weltevrede Subgroup is differentiated from the Weltevrede Formation in that regular mappable formation level subdivisions can be recognised in the former (South African Committee for Stratigraphy (SACS), 1980). Sedimentologically, both the Weltevrede Subgroup and Formation are similar to that of the Bokkeveld Group in that they comprise several alternating basin-wide argillaceous and arenaceous units organised into upward coarsening successions of varying scale but is, however, considerably sandier (South African Committee for Stratigraphy (SACS), 1980; Johnson et al., 2006). As in the Bokkeveld Group, the stratigraphic arrangement of these units forms the basis for lithostratigraphic subdivision into the lower, more argillaceous Wagen Drift Formation, the quartzitic Blinkberg Formation and the uppermost Swartruggens Formation that typically manifests as a series of alternating sandstones and shales (South African Committee for Stratigraphy (SACS), 1980). Stratigraphic work by Hiller and Dunlevey (1978) on the Bokkeveld-Witteberg contact suggest that the Wagen Drift Formation may be subdivided into two informally named members, namely the lower arenaceous "Nougaspoort" and the upper argillaceous "Byenest Krans" members. The Weltevrede Subgroup thickens eastward and is markedly muddier in the Agulhas Sub-basin where it is referred to as the Weltevrede Formation. Here, a similar lithological stacking pattern is observed, and a "sandier" succession is observed in the upper 2/3 of the succession. This sandier succession is informally referred to as the Blinkberg Member (South African Committee for Stratigraphy (SACS), 1980; Johnson et al., 2006). Both the Weltevrede Subgroup and Formation are, apparently, conformably but erosionally overlain by the Witpoort Formation (South African Committee for Stratigraphy (SACS), 1980; de Beer, 1990; Hiller, 1990; Hiller and Taylor, 1992; Cotter, 2000; Johnson et al., 2006).

With respect to the Bokkeveld Group and the succeeding Witpoort Formation, few detailed sedimentological studies have been conducted on the Weltevrede Subgroup and Formation, let alone that of the Devonian of the Witteberg Group, in recent years (Loock, 1967; Johnson, 1976; Hiller and Dunlevey, 1978; Tankard and Barwis, 1982; Tankard et al., 1982; Cole and Labuschagne, 1983; de Beer, 1990; Hiller, 1990; Hiller and Taylor, 1992; Cotter, 2000). Collectively, these studies suggest a broadly similar palaeoenvironmental genesis and depositional style for the Weltevrede Subgroup and Formation to that continued on from the Bokkeveld Group: both intervals comprising allocyclic T-R controlled storm- and wave-dominated marginal-shallow marine setting in deltas and shallow marine beach-shoreface depositional systems.

In the Weltevrede Subgroup, Tankard and Barwis (1982) suggested that the succession and identity of observed lithofacies in the Wagen Drift Formation were similar to that of the Bokkeveld Group, e.g., shales representative of shelf-prodelta deposits and increasingly arenaceous lithofacies representative of more proximal distributary mouth bar, tidal flat, interdistributary bay and beach-shoreface deposits. Overlying this succession, thickly bedded sandstones of the Blinkberg Formation were interpreted to be barrier sandstone deposits that formed in response to wave-reworking of delta front deposits (Tankard et al., 1982). The interbedded sandstones and mudstones of the overlying Swartruggens Formation have been interpreted to be the accumulation of tidal-flat deposits (Tankard et al., 1982; de Beer, 1990). More recent, and detailed, work by Cotter (2000) suggested that the deposition of the entire Weltevrede Subgroup may be explained within several upward coarsening and progradational cyclothems of varying scale. At the smallest scale (equivalent to a 'parasequence' *sensu* Cotter, 2000) an idealised cyclothem comprises basal weakly burrowed mudstones that may be interspersed with wave-rippled or hummocky cross-stratified (HCS) sandstones. These deposits grade upwards into compound wave-rippled, isotropic HCS and flat- and wavy-laminated very fine- to fine-grained sandstones. This arenaceous lithofacies in turn passes upward into fine- to coarse-grained cross-laminated, anisotropic HCS and compound wave-ripple laminated sandstones which cap the top of cyclothems. The identity of these lithofacies (and their succession) are similar to those presented for the Bokkeveld Group by Penn-Clarke (2017) and Penn-Clarke et al. (2018b, 2019) in their storm- and wave-dominated shallow marine depositional system model. As such, deposition for the Weltevrede Subgroup has been explained to have occurred within inner shelf, lower shoreface and middle to upper shoreface environments (Cotter, 2000).

The Weltevrede Formation is markedly more argillaceous in comparison with its western equivalent, the Weltevrede Subgroup. Here Cole and Labuschagne (1983), Hiller (1990) and Hiller and Taylor (1992) have noted a similarity in lithofacies and depositional style to that of the Bokkeveld Group (*sensu* Tankard and Barwis, 1982). Here the succession has been described as comprising multiple upward coarsening depocycles of basal heterolithic laminated shales, siltstones and fine-grained sandstones that coarsen upward first into non-amalgamated interbedded fine-sandstone and siltstone and then into more amalgamated thicker-bedded lithic arenites and fine sandstones that display cross bedding. These deposits are interpreted to have accumulated in a distal delta slope and proximal distributary mouth bar (delta front) environment (Hiller, 1990; Hiller and Taylor, 1992). In turn, these facies fine upward into heterolithic laminated shale, siltstone and thin sandstone beds that are arranged into thin fining- and coarsening upward units and are explained to have accumulated in tidal flats associated with delta platform (delta plain) environments (Hiller, 1990; Hiller and Taylor, 1992). Cole and Labuschagne (1983), however favour a storm-dominated shallow marine interpretation for the Weltevrede Formation based on cross bedding in sandstones resembling hummocky cross stratification. Here, they suggest that each upward coarsening depocycle is representative of successive prograding subtidal sandbars which formed under storm-surge activity.

2.2. *Sequence stratigraphic interpretation*

At the largest (local 1st order) outcrop scale, the Lower-Middle Devonian succession of South Africa has an overall retrogradational-progradational stacking pattern suggestive of overall highstand conditions following a large initial transgression into the Cape Basin. Here, the distinctive sharp onlap relationships of the basal Rietvlei and Baviaanskloof formations with underlying coarser grained sandstone deposits of the Skurweberg Formation is reasoned to have culminated during the earliest phases of transgression as the basin retrograded. These deposits, in turn, culminated into overall more distal marine deposits of the Bokkeveld Group chiefly represented by the Gydo-Waboomberg interval, gradually regressing to increasingly more proximal marine deposits of upper Bidouw Subgroup and the Weltevrede Subgroup and Formation with sustained highstand conditions.

Few attempts have been made in the past to contextualise the seemingly repetitive depositional patterns and trends observed in the South African Devonian (Cooper, 1986; Cotter, 2000). Cooper (1986) suggested that the overall repetitive outcrop scale upward coarsening cycles of sedimentation observed in the Devonian of South Africa are comparable to second- and third-order T-R cyclicity of the constructed Devonian sea-level curve of Euramerica (*sensu* Johnson et al., 1985). This sea-level curve was held as the standard for comparison at a global scale given that the Devonian Period was a time of global highstand and that, owing to the near ubiquity of conodont fossils their biostratigraphy could be used in most places across the globe to elucidate depositional trends. Although a sequence stratigraphic framework was not implicitly presented by Cooper (1986), his adapted framework for South Africa implies the use of thick marine shales to indicate depositional conditions akin to maximum flooding surfaces following peak transgression and a change over to early highstand conditions and were a prerequisite in determining individual second- and third-order T-R cycles. A subset of these marine shales, referred to by Cooper (1986) as “black shales” were used to determine the largest and most extensive of transgressions into the Cape Basin during the Devonian Period and were reasoned to have been laid down under oxygen-minimum conditions associated with base-level rises of this magnitude. Here, marine shales were used to delineate smaller third-order transgressions whilst “black shales” delineated larger second-order transgressions. Consequently, Cooper (1986) recognised “black shales” in the Gydo, Waboomberg and Wagen Drift formations, whilst marine shales occur in the Voorstehoek, Tra-Tra and Klipbokkop formations.

According to this framework, two large transgressions occurred in the Cape Basin during the Devonian that were equated with two global second-order highstands (T-R cycle I and II of Johnson et al., 1985) comprising smaller third-order T-R depocycles or ‘parasequences’. Here, Cooper considered that the T-R cycle I of Johnson et al. (1985) explained deposition within the uppermost Nardouw Subgroup-Bokkeveld Group interval. His model suggests that the Rietvlei and Baviaanskloof formations accumulated during the third-order T-R cycles Ia-Ib, whilst the Gydo-Gamka, Voorstehoek-Hex River and Tra-Tra-Boplaas intervals accumulated during T-R cycles Ic-Ie respectively whilst the entire Bidouw Subgroup accumulated during T-R cycle If. The Weltevrede Subgroup, Weltevrede Formation and the Witpoort Formation accumulated with a renewed global transgression explained by T-R cycle II. Here, the Wagen Drift-Blinkberg interval accumulated during T-R cycle Iia, whilst the Swartruggens Formation accumulated in response to the events of T-R cycle Iib-d and, lastly, T-R cycle Iie-f explained the deposition of the Witpoort Formation. More recent work on the sedimentology and sequence stratigraphy of the Weltevrede Subgroup by Cotter (2000) suggests a similar correlation of depositional trends during the Devonian of the Cape Basin with global second- and third-order eustatic trends. The framework presented by Cotter (2000), however, departs from Cooper (1986) in that he suggests that the Weltevrede Subgroup accumulated against the backdrop of T-R cycles Iia-c only. Here, similarly, the Wagen Drift-Blinkberg is explained to have accumulated under T-R cycle Iia which perhaps began with the initial transgression associated with the Karoopoort Formation whilst the Swartruggens Formation accumulated under T-R cycle Iib and c. In this same study, Cotter (2000) both suggested a recurrence of approximately 3 Ma for each third-order depocycle and that owing to the number and recurrence of intervening smaller fourth-order depocycles observed in the Weltevrede Subgroup that these may perhaps be equated with the expected periodicities (200-350 ka, quoted by Cotter) of Milankovitch cycles. Based on these time estimates, Cotter (2000) suggested a match with the mid-Givetian-Frasnian portion of the Johnson et al. (1985) Devonian sea-level curve for the Wagen Drift-Swartruggens interval.

In more recent years, Penn-Clarke (2017) and Penn-Clarke et al. (2018b, 2019) attempted to reconcile the observed depositional trends in the Bokkeveld Group within a sequence stratigraphic framework. Here, they have explained depositional trends in a T-R sequence framework comprising three-orders of magnitude (second-fourth) that are ranked according to observed changes in depositional stacking patterns, independent of global sea-level orders. Their second-order T-R sequences were described as being the largest fluctuations in shoreline shifts and were characterised by sharp changes in lithology and palaeoenvironment across the sequence boundary. They recognised at least four 2nd order T-R sequences (A-D) in the Bokkeveld Group. The marked difference in palaeoenvironment across the second-order sequence boundary, and its equivalent sequence stratigraphic surface, is often apparently unconformable (more correctly, diastemic) in nature. Here, the sequence stratigraphic surfaces manifest as a diastemic composite maximum regressive-transgressive ravinement surface (MRS-TRS) above which transgressive systems tract (TST) deposits occur. In their framework, T-R sequence A comprises the Rietvlei-Hex River interval, specifically from the base of the upper “passage beds” facies of the Rietvlei Formation to the uppermost regressive USF-Beach deposits of the Hex River Formation. T-R sequence B comprises the Tra-Tra-Boplaas interval, T-R sequence C comprises the Waboomberg-Osberg interval whilst T-R sequence D comprises the Karoopoort Formation and was thought to continue into the overlying Weltevrede Subgroup (Penn-Clarke, 2017; Penn-Clarke et al., 2018b, 2019). T-R sequence D was equated to include the third-order T-R cycles Iia (Karoopoort-Blinkberg interval), Iib and Iic (Swartuggens Formation) of Cotter (2000). Erroneously, Penn-Clarke (2017) and Penn-Clarke et al. (2019) suggested that the Blinkberg Formation represents a major forced regressive infill bounded by an unconformity which removed all of the Wagen Drift Formation. subsequent mapping and fieldwork in the Cederberg area where this initial claim was made has shown that the Wagen Drift Formation is present, however, it is perhaps represented only by the sandier Nougaspoort member (Penn-Clarke, 2020, 2022a, 2022b, 2023). Third- and fourth-order T-R sequences explained increasingly smaller fluctuations in base-level within larger second- and third-order T-R sequences and are bound by MRSs that show a conformable succession of environments within a base-level fall and rise (Penn-Clarke, 2017; Penn-Clarke et al., 2018b, 2019). No driver for T-R cyclicity was identified in these studies but it was assumed that local and regional Gondwanide tectonics was the most likely candidate.

Whilst these are significant attempts at explaining the observed depositional patterns and governing controls on deposition during the Early-Middle Devonian of South Africa, these frameworks are all constrained by the same issue: chronostratigraphic resolution. As mentioned previously, there are currently no known reliable “best-age” indicators known from the succession, including geochronological indicators (e.g., dated ash tuffs) and widely used biostratigraphic index taxa (e.g., conodonts, graptolites, palynomorphs, and goniatite ammonoids). Owing to the highly endemic nature of the Malvinoxhosan biota, there are few age diagnostic taxa that can be used to determine reliable comparative age constraints. This means that any attempt to reliably compare depositional trends from the Devonian of South Africa with time equivalents elsewhere, as well as the global eustatic curve for the Devonian, should be approached with caution unless firm stratigraphic correlations can be made.

A combination of these existing sequence stratigraphic frameworks, as well as data from published lithostratigraphic and sedimentological appraisals of Lower-Middle Devonian aged strata have been used to create a consensus sequence stratigraphic framework for the Lower-Middle Devonian succession of South Africa. This consensus framework, further, only considers those strata with records of Malvinoxhosan biotas, as such, it excludes all beds older than the passage beds facies of the Rietvlei and Baviaanskloof formations as well as the Upper Devonian Witpoort Formation. The consensus sequence stratigraphy presented herein uses the existing nomenclature and framework of Penn-Clarke (2017), and Penn-Clarke et al. (2018b, 2019) to name and describe largest to smallest magnitude sequences but departs from using a T-R sequence approach (Fig. 3). As such, the maximum regressive surface (end of lowstand and of regression) has not been used as a sequence

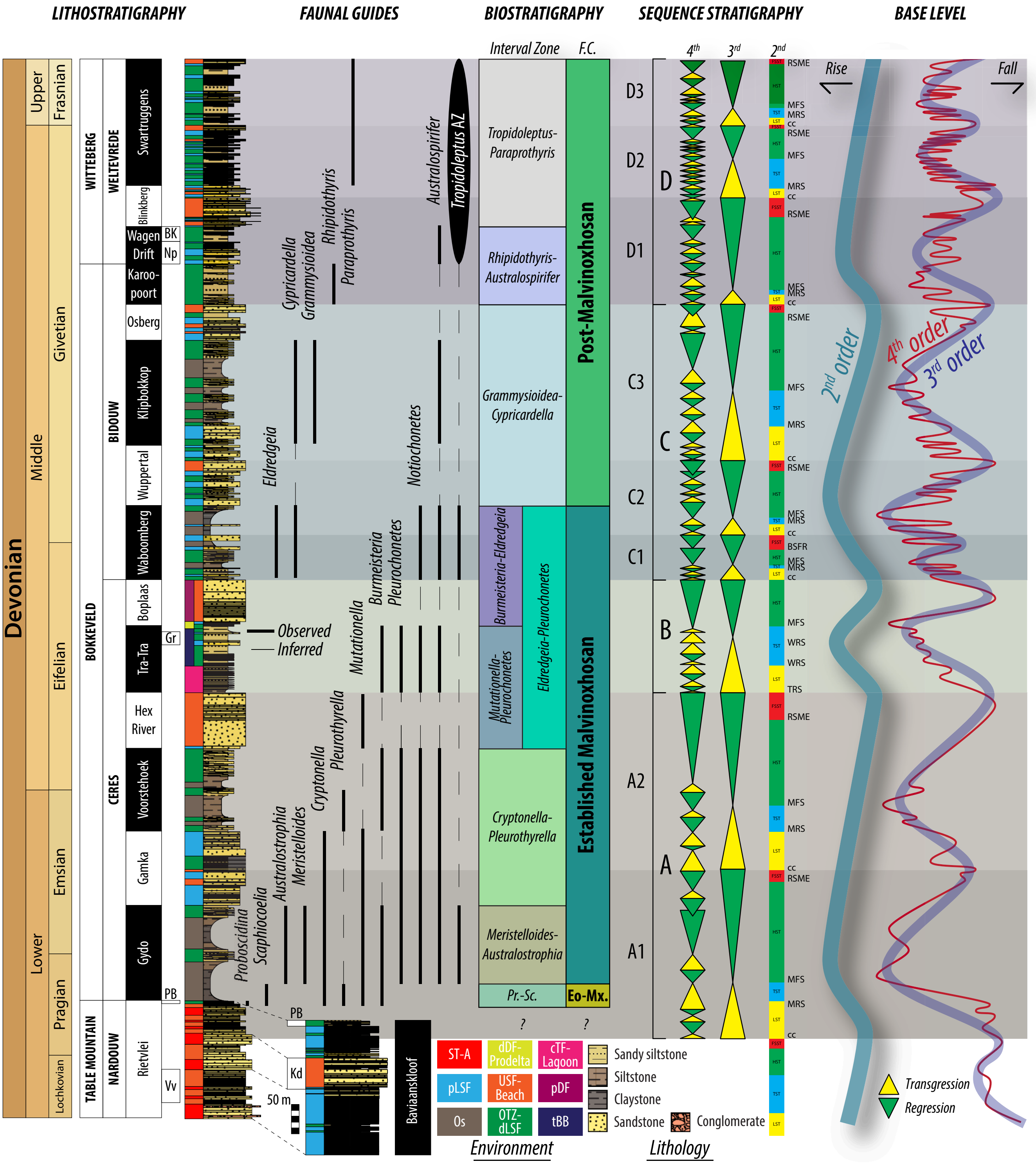

Fig. 3. Litho- and biostratigraphy of the Lower-Middle Devonian of South Africa with respect to sequence stratigraphy and inferences of changes in relative base-level through time. Lithostratigraphy and sequence stratigraphy in the Western Cape (Clanwilliam Sub-basin) after Hiller and Dunlevey (1978), Malan and Theron (1989), Theron and Basson (1989), Hill (1991), Cotter (2000), Penn-Clarke (2017), Penn-Clarke et al. (2018b, 2019). Select faunal guides and biostratigraphy are from data presented herein. Abbreviations: AZ – Abundance Zone, BK- 'Byenest Krans member' of the Wagen Drift Formation, BSFR- Basal surface of forced regression, cc- correlative conformity, cTF-Lagoon- Channelised tidal flat to lagoon, dDF-Prodelta- Distal delta front to prodelta, Eo-Mx.- Eo Malvinoxhosan faunal complex, F.C.- Faunal complex, FSST- Falling stage systems tract, Gr-Grootrivierhoogte Member of the Tra-Tra Formation, HST- Highstand systems tract, Kd- Kareedouw Member of the Baviaanskloof Formation, LST- Lowstand systems tract, MFS- Maximum flooding surface, MRS- Maximum regressive surface, Np-'Nougaspoort member' of the Wagen Drift Formation, Os- Offshore, OTZ-dLSF- Offshore transition zone to distal lower shoreface, PB- 'passage beds' of the Rietvlei-Baviaanskloof formations, Pr-Sc.- Proboscidina-Scaphiocoelia Zone, pDF- Proximal delta front, pLSF- Proximal lower shoreface, RSME- Regressive surface of marine erosion, ST-A- Supratidal beach to alluvial, tBB- Transgressive beach barrier, TST-Transgressive systems tract, USF-Beach- Upper shoreface to beach, WRS- Wave-ravinement surface, and Vv- 'Verlorenvalley member' of the Rietvlei Formation.

boundary. Instead, the correlative conformity, or subaerial unconformity, has been used as the sequence boundary. This surface delineates the end of forced regression, given the manifestation of lowstand deposits as 2nd order regressive successions beneath retrogradational deposits signifying overall transgressive settings. The advantage of using this scheme to explain strata as depositional sequences is that they can be more easily equated with local base-level curves with sequence boundaries that mark the initiation of the rising base-level. The correlative conformity and subaerial unconformity, however, represents a caveat in that it marks a hiatus in the depositional record and are expected to be diastemic (or even unconformable) in nature in a conformable succession. The exact amount of time missing at these surfaces is difficult to quantify given the limited chrono- and biostratigraphic resolution afforded for the South African record over this time interval at present. The sequence framework of Cotter (2000) for the Weltevrede Subgroup is similar to that of Penn-Clarke (2017), and Penn-Clarke et al. (2018b, 2019) in that it uses a T-R approach to delineate T-R sequences. Reconciliation of their T-R sequence framework with a depositional sequence framework was achieved by reviewing the stratigraphic profiles presented in Cotter (2000) and suggesting where depositional sequence tract boundaries were located to estimate where correlative conformities and subaerial unconformities were located.

According to this revised sequence stratigraphic framework, four 2nd order depositional sequences (Table 2.1) are recognised (A-D) that are superimposed by up to eight 3rd order (A1-A2, C1-C3; D1-D3) comprising at least fifty-eight 4th order depositional sequences (Fig. 3). These depositional sequences have been used to create relative base-level curves for the Early-Middle Devonian series of South Africa at different magnitudes.

2.3. Early-Middle Devonian marine invertebrate faunas

The Early-Middle Devonian marine invertebrate faunas of South Africa have been the subject of recent intensive review by Penn-Clarke et al. (2018a) and Penn-Clarke (2019). These reviews, as well as new data presented herein, suggest that the Malvinoxhosan bioregion is restricted to the Rietvlei-Baviaanskloof-Waboomberg interval, and is suspected to span Pragian-Eifelian time, possibly extending into the earliest Givetian. This interval, referred to as the 'Malvinokaffric Faunal Assemblage' by Penn-Clarke (2019), is represented by a diverse invertebrate fauna typified by Malvinoxhosan endemics which comingled with extra-Malvinoxhosan and cosmopolitan taxa (Table 2.2).

A closer inspection of the faunal characteristics of the Malvinokaffric Faunal Assemblage of Penn-Clarke (2019) suggest that it can be subdivided into an early low-diversity founding faunule (referred to herein as the 'Eo-Malvinoxhosan faunal complex') characterised by several distinct short-ranging large terebratuloid brachiopods restricted to the passage beds of the Rietvlei-Baviaanskloof and lowermost Gydo formations (Table 2.2; Fig. 4). This early faunal complex is succeeded by more diverse faunas in the overlying Gydo-Waboomberg interval as well as its eastern equivalents in the Gydo-Karies interval (referred herein as the 'Established Malvinoxhosan faunal complex') (Table 2.2; Fig. 4). Most Malvinoxhosan endemics and extra-Malvinoxhosan taxa went extinct by the end of Waboomberg-Karies Formation (Hiller and Theron, 1988; Penn-Clarke, 2019). An exception is the spiriferid *Australospirifer*, which continues into the Wagen Drift Formation (Hiller, 1990). Marine invertebrate faunas are rare in strata succeeding the Waboomberg Formation being known primarily from the Klipbokkop and Karoopoort (Boucot and Theron, 2001) formations of the Bokkeveld Group, as well as the Wagen Drift and Swartruggens formations (Weltevrede Subgroup) and their lateral equivalent, the Weltevrede formation of the Witteberg Group (Hiller and Dunlevey, 1978; Boucot et al., 1983; Hiller, 1990). This 'Post-Malvinoxhosan faunal complex' is represented by a handful of cosmopolitan and extra-Malvinoxhosan marine invertebrate taxa, many of which crossed over from the Waboomberg Formation with few new arrivals (Table 2.2; Fig. 4). These faunas are suspected to be Givetian in

Table 2.1
Summary of criteria used to delineate 2nd order T-R sequences in the Early-Middle Devonian of South Africa.

2nd order depositional sequence (after Penn-Clarke, 2017; Penn-Clarke et al., 2018b, 2019)	Stratigraphic interval	Description of bounding surfaces
D	Lowermost Karoopoort Formation-Swartruggens-Witpoort contact	Lower: Diastemic, sharp and planar onlap of LST OTZ deposits (Karoopoort Formation) above HST-FSST USF-Beach deposits (Osberg Formation) Upper: Diastemic, but more likely unconformable, sharp and planar onlap of LST tidally-derived deposits (Witpoort Formation) above HST-FSST paralic USF-Beach deposits (Swartruggens Formation)
C	Lowermost Waboomberg Formation-lowermost Karoopoort Formation	Lower: Diastemic, sharp and planar onlap of LST dLSF-pLSF deposits (Waboomberg Formation) above HST USF-Beach or pDF deposits (Boplaas Formation) Upper: Diastemic, sharp and planar onlap of LST OTZ deposits (Karoopoort Formation) above HST-FSST USF-Beach deposits (Osberg Formation)
B	Hex River-Tra-Tra contact-lowermost Waboomberg Formation	Lower: Diastemic, but more likely unconformable, sharp and planar onlap of LST tidally-derived deposits (Tra-Tra Formation) above FSST USF-Beach deposits (Hex River Formation) Upper: Diastemic, sharp and planar onlap of LST OTZ-dLSF deposits (Waboomberg Formation) above HST USF-Beach or pDF deposits (Boplaas Formation)
A	Uppermost Rietvlei and Baviaanskloof formations (inclusive of passage beds facies) – Hex River-Tra-Tra contact.	Lower: Diastemic, sharp and planar onlap of LST OTZ-dLSF deposits ('passage beds': upper Rietvlei-Baviaanskloof formations) above HST-FSST USF-Beach facies or pLSF deposits (Kareedouw Member in the Baviaanskloof Formation and its unnamed lateral equivalent in the Rietvlei Formation) Upper: Diastemic, but more likely unconformable, sharp and planar onlap of LST tidally-derived deposits (Tra-Tra Formation) above FSST USF-Beach deposits (Hex River Formation)

Table 2.2
Summary taxonomic table of the Lower-Middle Devonian of South Africa. * Denotes Malvinoxhosan endemic taxa.

Taxonomy				Faunal Complex		
Phylum	Class	Order	Genus	Eo-Malvinoxhosan (Pragian-early Emsian)	Established Malvinoxhosan (Emsian-early Givetian	Post-Malvinoxhosan (Givetian-Frasnian)
Mollusca	Bivalvia	Cardiida	*Leptodomus*		X	
			Cardiomorpha		X	
			Grammysia		X	X
			? Grammysioidea			X
			Sanguinolites		X	X
		Carditida	*Cypricardella*			X
		Lucinida	*? Paracyclas*			X
		Modiomorphida	*Goniomorpha*		X	
			Modiomorpha	X	X	X
			Glossites?		X	
			Sphenotomorpha		X	
		Orthonotida	*Orthonota*		X	
		Myalinida	*Myalina*		X	
		Nuculanida	*Phestia*		X	
			Nuculites		X	X
			Palaeoneilo		X	X
			Nuculana		X	
		Ostreida	*Actinopteria*		X	
			? Pterinea		X	
		Pectinida	*Pterinopecten*		X	
		Pholadomyida	*?Pholadella*		X	
			*Pleurodapis**		X	
			Prothyris (Paraprothyris)			X
		Praecardiidina	*? Panenka*		X	
			? Buchiola		X	
		Solemyida	*Solemya*		X	
			Ctenodonta		X	
			Janeia		X	X
	Cephalopoda	Orthoceratida	*Orthoceras*		X	X
		Bactritida	*? Cyrtobactrites*		X	
			? Bactrites		X	
	Gastropoda	Bellerophontida	*Tropidodiscus*		X	
			Bellerophon	X	X	
			Plectonotus		X	X
		Eumophalina	*Platyceras*		X	
			Holopea		X	
		Murchisoniina	*Loxonema*		X	
		Pleurotomariida	*Mourlonia*		X	
			Pleurotomaria		X	
	Rostroconcha	Conocardiida	*Conocardium*		X	
	Multiplacophora		*Hannestheronia*		X	
	Monoplacophora	Archinacellida	*Lepetopsis*		X	
Brachiopoda	Lingulata	Lingulida	*Lingula/Lingulida*		X	X
		Discinida	*Orbiculoidea*		X	X
			Gigadiscina		X	
	Craniata	Craniia	*? Petrocrania*		X	
	Rhynchonellata	Terebratulida	*Podolella*	X		
			*Proboscidina**	X		
			*Pleurothyrella**	X	X	
			*Scaphiocoelia**	X	X	
			Cryptonella	X	X	
			Mutationella	X	X	
			*Derbyina**	X	X	
			Centronella?		X	
			Rhipidothyris			X
		Rhynchonellida	*? Tanerhynchia**	X		
			*Australocoelia**	X	X	
		Spiriferida	*Acrospirifer*		X	
			*Australospirifer**		X	X
			Metaplasia		X	
			Plicoplasia		X	
			Pustulatia		X	
		Athyridida	*Meristella*		X	
			*Meristelloides**		X	
			Coelospira		X	
		Tropidoleptida	*Tropidoleptus*		X	X
	Strophomenata	Productida	*Kentronetes**	X	X	
			*Australostrophia**		X	
			? Eodevonaria		X	
			Anoplia		X	
			*Babina?**		X	

(*continued on next page*)

Table 2.2 (*continued*)

Taxonomy				Faunal Complex		
Phylum	Class	Order	Genus	Eo-Malvinoxhosan (Pragian-early Emsian)	Established Malvinoxhosan (Emsian-early Givetian	Post-Malvinoxhosan (Givetian-Frasnian)
			*Pleurochonetes**		X	
			*? Austronoplia**		X	
			*Notiochonetes**		X	
			*Aseptonetes**		X	
			Chonetid indet. *'Chonetes'*	X	X	X
		Orthotetida	*Schuchertella*		X	
			Schellwienella		X	
		Orthida	*? Salopina*		X	
		Strophomenida	*Stropheodonta*		X	
Echinodermata	Asteroidea		*Aulacolatiaster*		X	
			Ulrichaster		X	
	Ophiuroidea		*Marginix (Marginura)*		X	
			Hexuraster		X	
			Eugasterella		X	
			*Gamiroaster**		X	
			Ophiuroid arms indet. A.		X	
			Ophiuroid arms indet. B		X	
			Ophiuroid arms indet. C		X	
			Ophiuroid indet.	X		
			Encrinaster		X	
			Strataster		X	
	Stenuroidea		*Eophiura*		X	
			Haughtonaster		X	
	Crinoidea		*Arthroacantha*		X	
			Corocrinus		X	
			Kopficrinus		X	
			Mandelacrinus		X	
			Othozecrinus		X	
			Sacrinus		X	
			Eckidocrinus		X	
			Thalamocrinus		X	
			Ophiocrinus		X	
			Craedeocrinus		X	
			Crinoidea indet	X	X	
	Stylophora		*? Rutroclypeus*		X	
			*Bokkeveldia**		X	
			*Placocystella**		X	
			*Paranacystis**		X	
			Carpoid gen et sp. Indet		X	
	Blastoidea		*Brachyschisma*		X	
			*Pachyblastus**		X	
	Holothuroidea		*Holothuroidea gen et sp indet*		X	
Arthropoda	Trilobita	Proetida	*Maurotorion (Malvinotarion)**		X	
			*Ormistoniella**		X	
		Phacopida	*Francovichia**		X	
			*Gamonedaspis**		X	
			*Burmeisteria**	X	X	
			? Trimerus			X
			Deltacephalaspis		X	
			*Kozlowskiaspis**		X	
			*Oosthuizenella**		X	
			*Renniella**		X	
			*Typhloniscus**		X	
			*Bainella**		X	
			*Phacopina**		X	
			*Pennaia**		X	
			*Metacryphaeus**		X	
			*Eldredgeia**		X	
	Ostracoda		*? Pircawayra**		X	
			Gen. 2 sp. A		X	
			Gen. 7 sp. A		X	
			? Keslingiella		X	
			*Petrisigmoopsis**		X	
			Kloedenellacea		X	
Incertae sedis	Hyolitha	Hyolithida	*? Hyolithes*		X	
		Orthothecida	*? Orthotheca*		X	
	Tentaculita	Tentaculitida	*Tentaculites*		X	
			Styliolina		X	
Bryozoa			*? Trepostomata*		X	

(*continued on next page*)

Table 2.2 (*continued*)

Taxonomy				Faunal Complex		
Phylum	Class	Order	Genus	Eo-Malvinoxhosan (Pragian-early Emsian)	Established Malvinoxhosan (Emsian-early Givetian	Post-Malvinoxhosan (Givetian-Frasnian)
			Stenopora		X	
			Fenestella		X	
			Bryozoan indet.	X	X	X
Cnidaria	Anthozoa	Tabulata	*Michelinia*		X	
			Pleurodictyum		X	
			Favosites		X	
		Rugosa	*Zaphrentis*		X	
	Conulata	Conulariida	*Malvinoconularia**		X	
			Paraconularia		X	
			Reticonularia		X	
			Conularia		X	
Porifera			*Porifera indet.*		X	

age given the presence of *Rhipidothyris* in the Karoopoort Formation (Boucot and Theron, 2001) and abundance of *Tropidoleptus* in the overlying lower Witteberg Group (Boucot et al., 1983; Hiller, 1990).

2.3.1. *Eo-Malvinoxhosan Faunal Complex*

The earliest Early-Middle Devonian faunas are known from the Rietvlei and Baviaanskloof formations (uppermost Nardouw Subgroup: Table Mountain Group). Faunas of the Rietvlei-Baviaanskloof formations have received limited attention in the past with most work relegated to mere mentions of shelly material present in the uppermost passage beds facies just below the base of the Gydo Formation (Reed, 1906; Rossouw et al., 1964; Theron, 1972; Hiller and Theron, 1988; Theron and Basson, 1989; Hill, 1991; Oosthuizen, 1984; Boucot and Theron, 2004). An appraisal of those specimens that have been collected and described comprise a distinctive brachiopod-rich assemblage (Table 2.2; Fig. 4), characterised by a founding stock of the large Malvinoxhosan endemic terebratulide brachiopods *Proboscidina, Scaphiocoelia,* and *Pleurothyrella* that are present alongside smaller terebratulides, namely *Podolella, Cryptonella, Mutationella* and *Derbyina* and the rhynchonellides *Australocoelia* and *Tanerhynchia*. Other brachiopods present include large orbiculoids resembling *Gigadiscina* as well as *Orbiculoidea* and *'Lingula'* with rare occurrences of productids, most likely *Kentronetes*, as well as indeterminate chonetids (Appendix B). Molluscan faunas are restricted to a handful of cosmopolitan taxa, namely the bivalve *Modiomorpha* and gastropod *Bellerophon* whilst trilobites are solely represented by forms resembling *Burmeisteria*. Additional taxa include indeterminate bryozoans and echinoderms (crinoids and ophiuroids), the latter of which are the subject of ongoing research (Reddy, 2022).

The brachiopod fauna of the passage beds is of interest in that many of the taxa are short-ranged (Appendix B; Fig. 3) being restricted either to the passage beds facies themselves (*Podolella* and *Proboscidina*) or making their last appearances in the lowermost Gydo Formation (*Scaphiocoelia* and *Tanerhynchia*) with certain taxa extending into the Gamka (*Cryptonella*) and Voorstehoek (*Pleurothyrella* and *Kentronetes*) formations. Given the ranges of these taxa, it is suggested that the passage beds facies and lowermost Gydo Formation are most likely Pragian to earliest Emsian in age. This relative age constraint is derived from several palaeontological indicators. Rhyniophytoid fossil floras from the underlying Kareedouw Member of the Baviaanskloof Formation are interpreted to be at least Lochkovian (earliest Devonian) in age (Gess and Prestianni, 2021) whilst certain terebratulides have well-established Lochkovian (*Podolella*) to Lochkovian-Emsian (*Mutationella*) and Emsian-Givetian (*Cryptonella*) ages (Brice et al., 2000; Williams et al., 2006). The large and distinctly Malvinoxhosan terebratulides *Proboscidina, Pleurothyrella* and *Scaphiocoelia* are further thought to range from the Pragian to earliest Emsian (Boucot and Theron, 2004). The passage beds facies of the uppermost Rietvlei and Baviaanskloof formations, and by extension, the Eo-Malvinoxhosan faunal complex is thus interpreted to be Pragian-early Emsian in age.

2.3.2. *Established Malvinoxhosan Faunal Complex*

Fossils in the overlying Gydo-Waboomberg (Bokkeveld Group) interval characterise the Malvinoxhosan bioregion in South Africa as virtually all endemics make their first appearances (Appendix B; Table 2.2; Fig. 4) (Penn-Clarke, 2019; Penn-Clarke et al., 2018a) alongside a suite of cosmopolitan and extra-Malvinoxhosan taxa from adjacent bioregions (Penn-Clarke and Harper, 2021). Diversity is more or less even across the molluscans, brachiopods, echinoderms and arthropods with substantial representation of diversity among other smaller groups (corals, bryozoans, tentaculitids, conulariids, etc.) (Fig. 4). Much of this diversity, as well as virtually all first appearances in South Africa, are focused in the Gydo Formation with a trend of decreasing diversity through time (Theron, 1972; Cooper, 1982, 1986; Oosthuizen, 1984; Hiller and Theron, 1988; Jell and Theron, 1999; Penn-Clarke et al., 2018a; Penn-Clarke, 2019). Few new taxa appear to enter the Cape Basin following its initial colonisation during Gydo Formation sedimentation. Apparent new originations in post-Gydo Formation strata are limited to a handful of taxa that make their appearances mainly in the Voorstehoek Formation and to a lesser extent in the Waboomberg and Gamka formations. Echinoderms show perhaps the greatest apparent increase in diversity in post-Gydo Formation strata, with numerous ophiuroid and to a lesser extent asteroid, stenuroid, crinoid, blastoid, stylophoran and holothuroid genera making their first appearances in the Voorstehoek Formation and to a lesser extent in the Gamka and Waboomberg formations (Breimer and Macurda Jr., 1972; Macurda Jr., 1979; Ruta, 1997; Ruta and Theron, 1997; Jell and Theron, 1999; Reid et al., 2019b) (Appendix B). Among the molluscs, apparent originations are limited to the multiplacophoran *Hannestheronia* (Vinther et al., 2012), as well as bivalves resembling *Cypricardella* and *Pterinea* (Penn-Clarke, *pers obs.*) in the Waboomberg Formation whilst the trilobites *Gamonedaspis* and *Eldredgeia* make their first appearances in the Gamka and Waboomberg formations, respectively (Cooper, 1986) (Appendix B).

Relative age constraints within the Established Malvinoxhosan faunal complex are difficult to deduce, especially since the Emsian-Eifelian boundary is poorly constrained. It is suggested that this boundary is possibly present in strata of the Voorstehoek Formation. This age estimation is based on the last appearances of several Pragian-Emsian brachiopods, namely *Pleurothyrella*, *Acrospirifer*, *Metaplasia,* as well as *Anoplia* and *Kentronetes* (Brice et al., 2000; Boucot and Theron, 2004; Williams et al., 2000, 2006) in the Voorstehoek Formation that entirely, or partially, overlap with Eifelian-ranging taxa (e.g., *Aseptonetes, Coelospira*, *Pleurochonetes, Notiochonetes*) that continue into the Tra-Tra, Boplaas and Waboomberg formations (Appendix B; Fig. 3). Although present as low down as the Gydo Formation (Oosthuizen, 1984; Appendix A; B), *Tropidoleptus* is present in the Established Malvinoxhosan Faunal Complex, but is exceedingly rare in shelly

Fig. 4. Summary of the taxonomic diversity of faunal complexes in the Lower-Middle Devonian of South Africa.

assemblages in the Ceres Subgroup. In the Waboomberg Formation, however, *Tropidoleptus* becomes more common in shelly assemblages and is frequently encountered alongside the few Malvinoxhosan brachiopod endemics inherited from the lower Eifelian strata that precede it. Above the Waboomberg Formation virtually all Malvinoxhosan endemics are unknown except *Australospirifer* (Appendix A; Hiller, 1990). The Eifelian-Givetian boundary is suspected to be located in the Waboomberg Formation and is thought to be coincident with the rise of *Tropidoleptus* dominated shelly assemblages and the termination of the Malvinoxhosan bioregion as virtually all endemic taxa disappear around this boundary here and elsewhere in South America where few surviving taxa linger into the early Givetian (Bosetti et al., 2011, 2012; Troth et al., 2011; Horodyski et al., 2014; Marshall, 2016; Grahn et al., 2017; Penn-Clarke, 2019; Penn-Clarke et al., 2018a; Penn-Clarke and Harper, 2021; Sedorko et al., 2018a, 2018b, 2021). An Emsian-early Givetian age is thus inferred for the Established Malvinoxhosan faunal complex.

2.3.3. Post-Malvinoxhosan Faunal Complex

Shelly fossil assemblages in post-Waboomberg formation strata are exceedingly rare and are characterised by their poor diversity (Table 2.2; Fig. 4; Appendix B). The Post-Malvinoxhosan faunal complex is characterised by its complete lack of echinoderms and few (if any) trilobites. Diversity is focused more within molluscs in comparison with other phyla, especially brachiopods (Fig. 4). Those fossils that are present typically comprise a handful of cosmopolitan bivalves (*Modiomorpha, Nuculites, Palaeoneilo,* and *Janeia*) and gastropods (*Plectonotus*), as well as lingulate brachiopods (*'Lingula'* and *Orbiculoidea*) that range through the Klipbokkop-Weltevrede interval (Appendix B). Some "Established Malvinoxhosan hold-over" taxa, however, characterise the early Post-Malvinoxhosan faunal complex. There are the bivalves, *Grammysia* and *Cypricardella* that make their last appearances alongside immigrant bivalves resembling *Grammysioidea* and the enigmatic *Paracyclas* (Appendix B; Penn-Clarke, *pers obs*). *Australospirifer* is the only Malvinoxhosan taxon present in post-Waboomberg Formation strata, albeit quite rare and known only from the Klipbokkop-Adolphspoort (upper Bokkeveld Group) formations; disappearing in the Wagen Drift Formation (lowermost Witteberg Group) (Appendix B; Hiller, 1990). Alongside *Australospirifer*, last occurrences of possible nautiloids ascribed to '*Orthoceras*', indeterminate chonetids, and bryozoans have been reported (Appendix B; Theron, 1962; Hiller, 1990) in the Wagen Drift Formation. The Old World trans-Atlantic brachiopods *Rhipidothyris* and *Tropidoleptus* are perhaps the most important components of the Post-Malvinoxhosan faunal complex as these taxa both indicate a Givetian-Frasnian age for the faunal complex as well as a breakdown of faunal endemism in South Africa, let alone that of the Malvinoxhosan bioregion in West Gondwana (Penn-Clarke, 2019; Penn-Clarke and Harper, 2021). *Rhipidothyris* is short-lived in South Africa being present only Karoopoort Formation (Boucot and Theron, 2001) whilst *Tropidoleptus* dominates shelly assemblages in the Wagen Drift-Swartruggens interval and Weltevrede Formation (Appendix B; Boucot et al., 1983; Hiller, 1990) and could possibly constitute an informal "*Tropidoleptus* abundance zone" (Fig. 3). Other than the appearances of these brachiopods to the Cape Basin, the last immigrants before the close of the Middle Devonian, include the bivalve *Prothyris* (*Paraprothyris*) and trilobites ascribed to *Trimerus* present in the uppermost Weltevrede Formation (Appendix B; Hiller, 1990). The suspected Frasnian upper age limit of *Tropidoleptus* (Harper et al., 2010) however means that an early Late Devonian age for at least the uppermost Swartruggens and Weltevrede formations and indeed the Post-Malvinoxhosan faunal complex cannot be excluded.

3. Methodology

The stratigraphic interval considered in this study only includes those strata from South Africa with known fossils that are of Early-Middle Devonian age. As such, only the Lochkovian-Pragian Rietvlei and Baviaanskloof formations (Nardouw Subgroup: uppermost Table Mountain Group), Pragian/Emsian-Givetian Bokkeveld Group and Givetian-Frasnian Weltevrede Subgroup and Formation (Witteberg Group) are considered. Their naming conventions and stratigraphy are after that approved by the South African Committee for Stratigraphy (SACS). Data from the Rietvlei and Baviaanskloof formations were pooled together as these are known lateral equivalents. Similarly, data from the Weltevrede Formation were equated with its western lateral equivalent, the Weltevrede Subgroup in accordance to its stratigraphy. Here data from the lower, middle, and upper Weltevrede Formation were equated with western equivalents in the Weltevrede Subgroup, respectively the Wagen Drift, Blinkberg and Swartruggens formations. Owing to differences in the stratigraphy of the upper Bokkeveld Group (namely the western Bidouw Subgroup and eastern Traka Subgroup) certain units were equated as being lateral equivalents. Here the Waboomberg-Wuppertal interval was equated with the Karies Formation whilst the Klipbokkop-Osberg interval was equated with the Adolphspoort Formation. Further to this the Karoopoort and Sandpoort formations were considered as potential west-east lateral equivalents. A composite stratigraphic profile for the Early-Middle Devonian was created from all known published sedimentological and stratigraphic literature.

An extensive biostratigraphic database (with references) of all known fossil genera from the Early-Middle Devonian of South Africa has been amassed from the literature (see in depth reviews with cited articles by Penn-Clarke et al., 2018a and Penn-Clarke, 2019) in addition to data from meticulously collected reference biostratigraphic collections housed at the Council for Geoscience (CGS) and Iziko South African Museum, Cape Town (SAM) (Appendix A; B). Collection subsets from these repositories that were used in this study include the PRV, and Theron and Almond collections at the CGS and the Oosthuizen collection. Much of the material from these collections has good stratigraphic and locality data associated with it; however, their taxonomic identities required revision which was done using the most relevant and up-to-date literature. Further to these collections, data from smaller, but significant, collections housed at the Albany Museum, Grahamstown (Makanda) (AM), Kwa Zulu-Natal Museum, Pietermaritzburg (NM), Sedgwick Museum, Cambridge University (SMC), Evolutionary Studies Institute, University of the Witwatersrand (BP), and Geology Department, Stellenbosch University (SU) were consulted.

Palaeontological data were used to create a presence-absence matrix for the Early-Middle Devonian according to their stratigraphic occurrence (Appendix A). This data matrix was condensed from an excess of 15,000-25,000 known individual data points. Supporting this data matrix is a database of the full taxonomic considerations of the fauna in question as well as their relative ages and their inferred ecological niches from the Treatise on Invertebrate Palaeontology, the Paleobiology Database and other published literature for analyses. Calculations of taxonomic counts and rate measures (after Foote and Miller, 2009) were calculated and included in the database from revised relative age constraints of the taxa from literature. Data pertaining to the inferred proportional rates of extinction and origination per million years are referred to in text to provide additional contextual support to observed biotic trends through time. These collective data were used to both display and perform several analyses presented in this study.

Presence-absence data were used to create a biostratigraphy for the stratigraphic interval under consideration. This framework includes known ranges in addition to inferred ranges where fossils are expected to be found between known stratigraphic strata. The presence-absence matrix was further used to perform a cluster analysis (CA) of fossil occurrences according to their stratigraphy. This method was used to elucidate if any natural biostratigraphic groupings exist and how those groupings are related since CA focuses on creating a hierarchical structure to the dataset. Of interest in this study is to test whether the identified Eo-Malvinoxhosan, Established Malvinoxhosan and Post-Malvinoxhosan faunal complexes create tangible biostratigraphic groupings and if there are any smaller biostratigraphic groupings therein. A bootstrapped ($n= 100$) CA was performed using the Jaccard similarity coefficient with an unweighted pair group method, using the arithmetic mean (UPGMA) neighbour joining algorithm to construct a hierarchical cluster dendrogram. Data from the Rietvlei and Baviaanskloof formations formed a natural outgroup to the CA given that it comprises the earliest and least diverse assemblage of fossils. Linked to the CA, a nonmetric multidimensional scaling (NMDS) analysis of the biostratigraphic data was performed to plot an ordination of similar groupings that was superimposed on a minimum spanning tree (MST) to elucidate the distances and relationships among the groupings supporting traditional CA methods. A Shepard plot with stress value was included in this analysis to indicate "goodness of fit" of the data as well as an ordination of distances against similarities.

In addition to multivariate analyses, stacked charts were created to display taxonomic and ecological considerations from the palaeontological data according to stratigraphy. These charts were used to highlight changes in taxonomy and ecology through stratigraphy. Included on these charts are curves showing calculated proportional extinction and origination rates per million years after Foote and Miller (2009) based on best age estimates for the succession. These calculations and curves were used to highlight where extinction and origination events occurred throughout the studied interval.

All multivariate analyses were conducted, and charts made using PAST v. 4.10 (see Hammer et al., 2001). Lastly, a bipartite network analysis (NA) of the data was performed using Gephi v. 0.9.7. The resulting analysis was displayed using the ForceAtlas 2 layout and with a modularity algorithm (after Blondel et al., 2008) with a resolution limit of 1.0 to separate any natural forming biostratigraphic groupings in the data. The biostratigraphic frameworks of the NA, CA and NMDS were compared using an alluvial diagram to reconcile any differences or

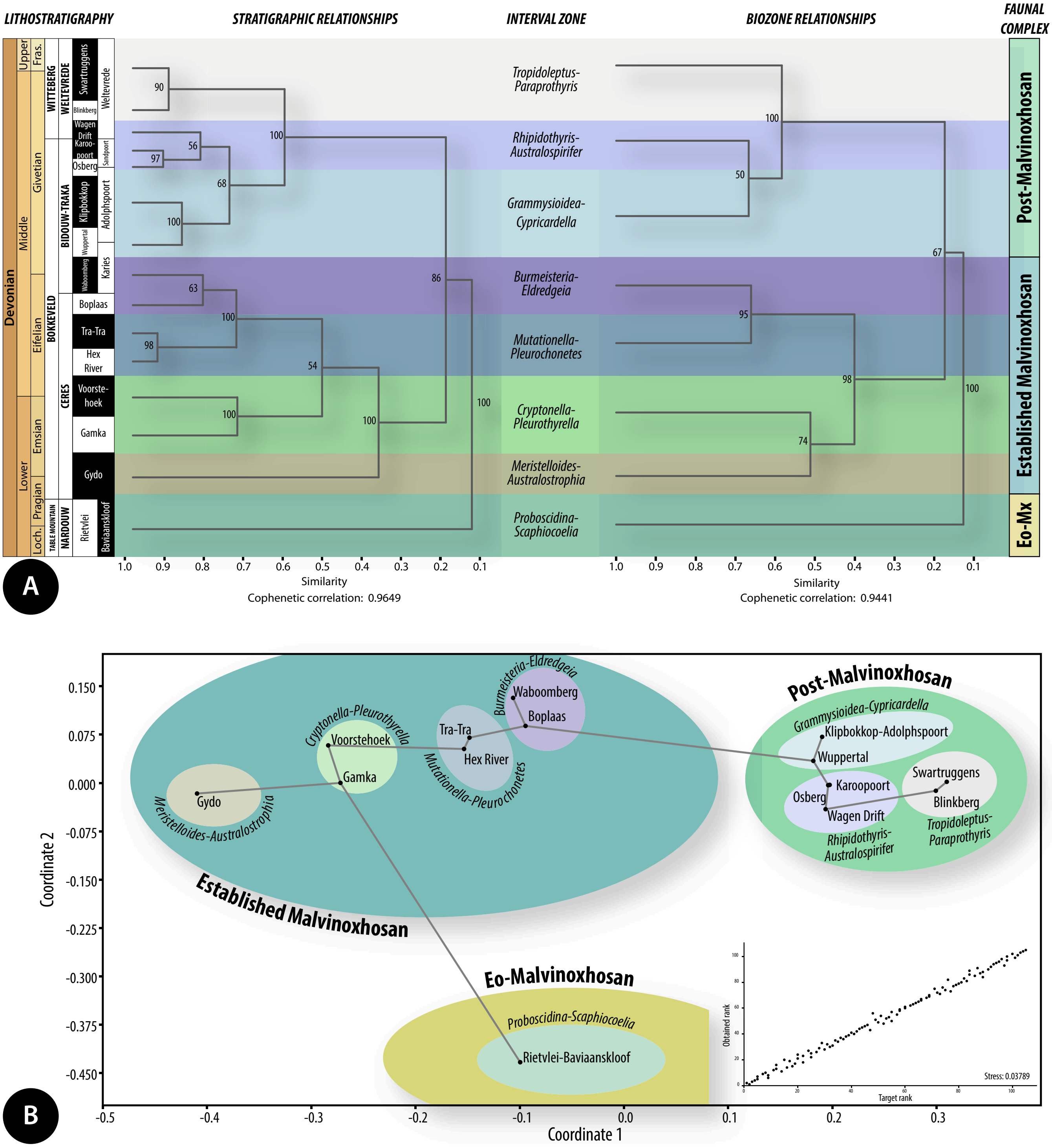

Fig. 5. Results of multivariate analyses of Early-Middle Devonian invertebrate taxa from South Africa and their potential stratigraphic groupings according to 1st order faunal complexes and 2nd order biozones. A – Bootstrapped (n = 100) cluster analysis comparing the stratigraphic relationships of taxa (left) and relationships among their constructed biozones (right). Abbreviations: Eo-Mx – Eo-Malvinoxhosan, Fras.- Frasnian, Loch.- Lochkovian, B – Nonmetric multidimensional scaling analysis with superimposed minimum spanning tree. Inset is a Shepard plot showing stress value and goodness of fit of data.

similarities in their resultant frameworks. Similar procedures have been used recently by Viglietti et al. (2022) with much success to compare and reconcile biostratigraphic frameworks for the Permian-Triassic of South Africa.

The constructed biostratigraphic groupings as well as stacked charts were compared against the constructed sequence stratigraphic framework and relative base-level curve for the Devonian of South Africa (see Fig 3) to highlight any potential basinal correlations and controls.

4. Results

4.1. Biozonation

The results of the cluster (Fig. 5 A) and nonmetric multidimensional scaling (Fig. 5 B) analyses of the data show similarities in the construction potential biostratigraphic groupings of taxa at different observable orders during the Early-Middle Devonian of South Africa. Three 1st order biostratigraphic groupings can be identified based on the preponderance of their contained Malvinoxhosan endemic versus extra-Malvinoxhosan and cosmopolitan taxa. The stratigraphic ranges of these biostratigraphic groupings further show great overlap with 1st order faunal complexes identified from literature (Figs. 3; 4) and as such are referred to as the Eo-Malvinoxhosan (Rietvlei-Baviaanskloof formations), Established Malvinoxhosan (Gydo-Waboomberg interval) and Post-Malvinoxhosan (Wuppertal-Swartruggens interval) faunal complexes. These faunal complexes manifest as major nodes in the CA (Fig. 5 A) that may be reconciled as distantly related groupings in the NMDS (Fig. 5 B). Broadly similar 1st order faunal complexes may be recognised in the NA based on the distribution of, and identical clustering of stratigraphic units based on their palaeontological content (Fig. 6). All analyses suggest that the Eo-Malvinoxhosan faunal complex forms a natural outgroup to the dataset but is most closely related to the Established Malvinoxhosan faunal complex (Figs. 5; 6). Similarly, the Post-Malvinoxhosan faunal complex is a distinct entity that shares numerous faunal ties and similarities with the Malvinoxhosan faunal complex (Figs. 5; 6).

The cluster analysis and nonmetric multidimensional scaling further reveal smaller 2nd order biostratigraphic divisions contained within the Established Malvinoxhosan and Post-Malvinoxhosan faunal complexes. These have been equated to represent biozones and are named herein according to overlapping partial ranges of particular taxa as well as the first and last appearance data of particular taxa and may thus be equated as interval-assemblage biozones. These 2nd order biozone groupings correspond with large-scale upward fining cycles in the Lower-Middle Devonian of South Africa (Fig. 3) where each comprises a basal arenaceous lithostratigraphic unit that is overlain by a progressively argillaceous lithostratigraphic unit(s). The exceptions to this are the Gydo and Rietvlei-Baviaanskloof formations that form distinct populations restricted to these units. As such, the Eo-Malvinoxhosan faunal complex is entirely comprised of the *Proboscidina-Scaphiocoelia* biozone, whilst the Established Malvinoxhosan faunal complex comprises the *Meristelloides-Australostrophia* (Gydo Formation), *Cryptonella-Pleurothyrella* (Gamka-Voorstehoek interval), *Mutationella-Pleurochonetes* (Tra-Tra-Hex River interval), and *Burmeisteria-Eldredgeia* (Boplaas-Waboomberg interval) biozones. Three potential biozones are recognised in the Post-Malvinoxhosan faunal complex, namely the *Grammysioidea-Cypricardella* (Wuppertal-Klipbokkop interval), *Rhipidothyris-Australospirifer* (Osberg-Wagen Drift interval) and *Tropidoleptus-Paraprothyris* (Blinkberg-Swartruggens interval) biozones. Similar biozones can be recognised in the NA (Fig. 6) with minor differences (Fig. 7).

Notably, the NA could not reconcile the *Mutationella-Pleurochonetes* and *Burmeisteria-Eldredgeia* biozones as distinct biozones but instead has grouped these as a larger cluster, referred to here as the '*Eldredgeia-Pleurochonetes'* biozone (Figs. 6; 7). The NA was further unable to note any appreciable stratigraphic differences among the biota in the Wuppertal-Swartruggens interval but was able to reconcile this interval with the Post-Malvinoxhosan faunal complex as a distinct 1st order biostratigraphic grouping as in the CA and NMDS (Figs. 6; 7). Lastly, the CA, NMDS, and NA collectively show a similar pattern of shared stratigraphic linkages of successive biozones through time. This suggests an inheritance of depleted or shared stocks through time.

4.2. Biotic diversity trends

The Lower to Middle Devonian of South Africa is characterised by early accelerating and high proportional origination rates (PO) during the Pragian to Emsian followed by a stepped decline in diversity marked by increasing proportional extinction rates (PE) from the Emsian onwards (Appendix B; Fig. 8). High PO's are associated with the establishment of the Malvinoxhosan bioregion in South Africa beginning with the deposition of the Rietvlei-Baviaanskloof Formation (Eo-Malvinoxhosan faunal complex: *Proboscidina-Scaphiocoelia* biozone) (PO = 1), culminating into the Gydo Formation (Established Malvinoxhosan faunal complex: *Meristelloides-Australostrophia* biozone) (PO = 0.86) (Table 4.1; Fig. 8).

In the Eo-Malvinoxhosan faunal complex, the *Proboscidina-Scaphiocoelia* biozone comprises a low-diversity population of early founding Malvinoxhosan stocks (Appendix B), namely *Australocoelia*, *Burmeisteria*, *Derbyina, Gigadiscina, Kentronetes, Pleurothyrella, Scaphiocoelia,* and *Tanerhynchia* that are shared with the overlying Gydo Formation. *Proboscidina* is an additional Malvinoxhosan taxon that is present but is restricted to the Eo-Malvinoxhosan faunal complex. Alongside these endemics are extra-Malvinoxhosan taxa, namely the brachiopods *Cryptonella* and *Mutationella* in addition to cosmopolitan molluscs (*Modiomorpha* and *Plectonotus*) as well as lingulid and orbiculoid brachiopods. *Podolella* is a long-ranging Silurian-Devonian brachiopod that is distinctly restricted to the Eo-Malvinoxhosan faunal complex in South Africa.

Diversity gains continued into the overlying Gydo Formation, reaching their zenith in the *Meristelloides-Australostrophia* biozone (Table 4.1; Figs. 8; 9). Here, virtually all taxa from all representative marine invertebrate groups present in the Lower-Middle Devonian of South Africa (Appendix B) make their first appearances in South Africa, as well as the Malvinoxhosan faunal complex being firmly established. Most Eo-Malvinoxhosan taxa are present in the *Meristelloides-Australostrophia* biozone, except for the brachiopods *Podolella* and *Proboscidina*. *Scaphiocoelia*, and *Tanerhynchia* most likely, have only been reported from the basalmost Gydo Formation (Penn-Clarke, 2019). The disappearance of these early founding stocks perhaps marks the first recorded decline in diversity during the Early-Middle Devonian in South Africa.

This early peak in diversity is followed by a stepwise decline beginning with the deposition of the Gamka and Voorstehoek formations (*Cryptonella-Pleurothyrella* biozone), leading up to the eventual collapse of the Malvinoxhosan faunal complex and bioregion where most endemics and other taxa went extinct near the Waboomberg-Wuppertal formational boundary (terminal *Eldredgeia-Pleurochonetes* biozone) (Fig. 8). Constructed biozones in this interval are marked by successively increasing proportional extinction rates (0.4-0.67) and near negligible origination rates (0-0.2) (Table 4.1). Although diversity trends suggest that all invertebrate groups were affected during these successive extinction events, the collapse of the Malvinoxhosan bioregion was most detrimental to echinoderms, trilobites, tentaculitids, and hyolithids that were previously important contributors to the overall diversity of the Malvinoxhosan bioregion in South Africa along with smaller groups: ostracods, conulariids, corals and sponges.

A closer interrogation of the relative biomass contribution within biozones associated with the Malvinoxhosan bioregion in South Africa suggests that the early phase establishment, the Eo-Malvinoxhosan faunal complex, is associated with higher diversity contributions among brachiopods (lingulates, rhynchonellates, strophomenates) followed by molluscs (bivalves and gastropods) whilst echinoderms (crinoids) and trilobites (phacopides) comprise a smaller contribution

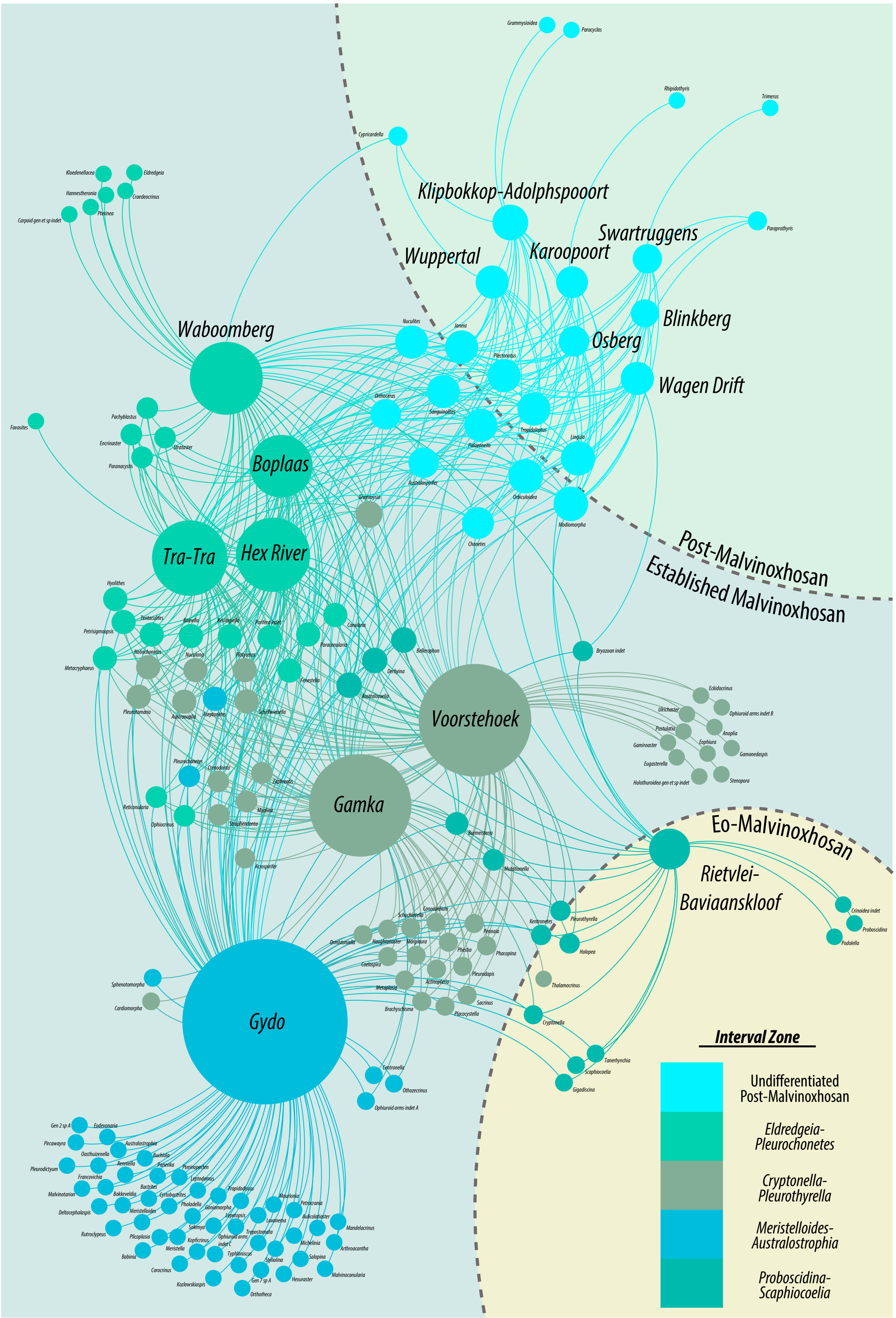

Fig. 6. Bipartite network analysis of Early-Middle Devonian invertebrate fauna with a modularity algorithm revealing the presence of at least five biozones (interval zones) which may loosely cluster within larger faunal complexes recognised in multivariate statistical analyses.

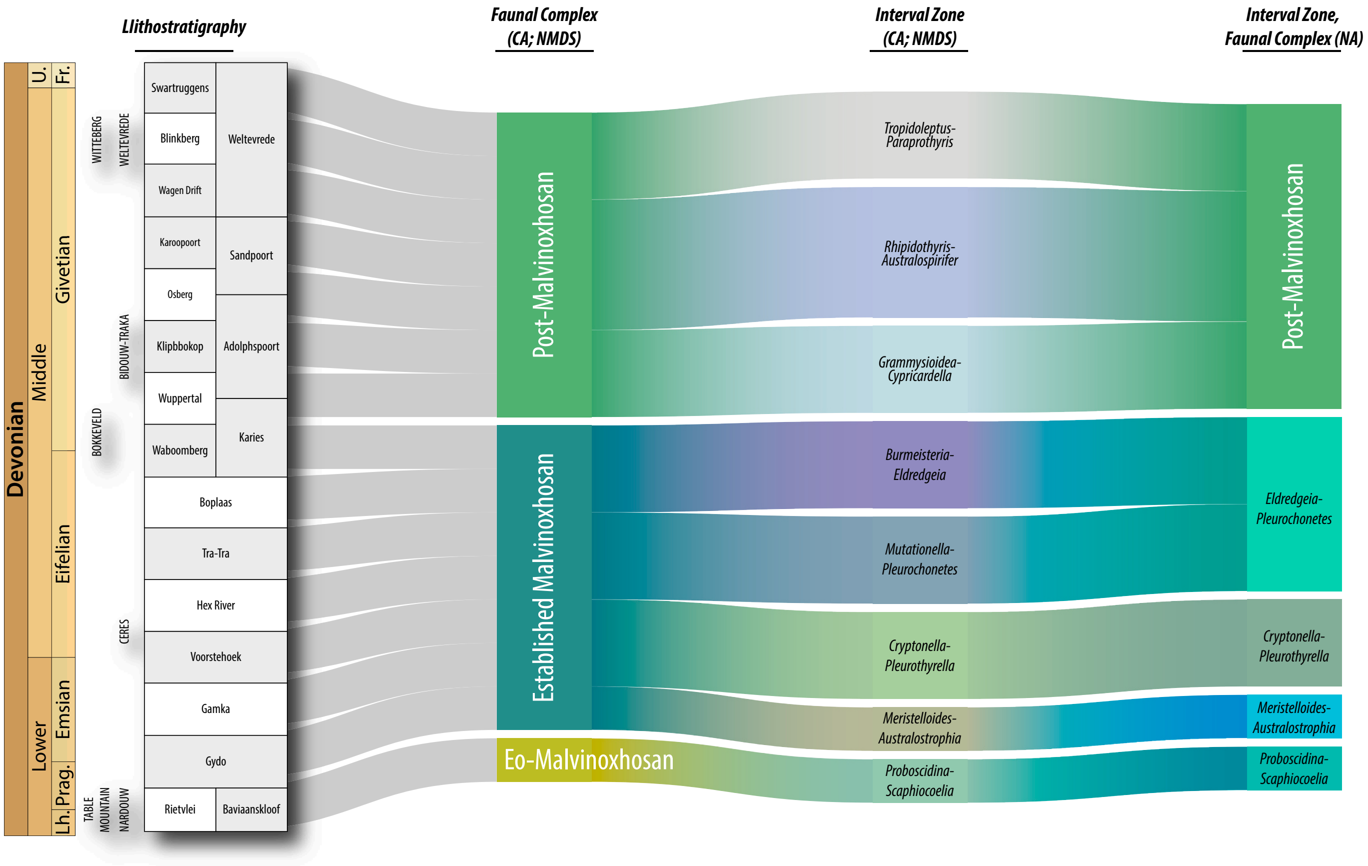

Fig. 7. Alluvial diagram showing comparison and similarity of biostratigraphic frameworks for the Lower-Middle Devonian of South Africa generated using cluster analysis (CA), nonmetric multi-dimensional scaling (NMDS) and network analysis (NA). Abbreviations: Fr.- Frasnian, Lh.- Lochkovian, Prag.- Pragian, U.- Upper.

(Appendix B; Fig. 9). Diversity is greatest in the Established Malvinoxhosan faunal complex among all representative taxa (Appendix B; Fig. 9); however, certain trends are observed. The relative diversity contribution between mollusc and brachiopod groups are more or less equitable throughout the Established Malvinoxhosan faunal complex, contributing ~30-33% each to the overall diversity at each successive biozone (Fig. 9). Echinoderms and trilobites both display a trend of declining diversity through time respectively contributing each ~15 to 10 % to the overall diversity at the initiation of the Established Malvinoxhosan faunal complex and decreasing to ~10 and 5% at its closure (Fig. 9). In the wake of decreasing successive biodiversity contributions among echinoderms and trilobites, smaller groups namely, ostracods, bryozoans, and conulariids show slight increases in their biodiversity contributions of between 4-7 % through the duration of the Established Malvinoxhosan faunal complex. The contribution of hyoliths, tentaculitids, corals and sponges were more or less constant, never exceeding more than 3-4% of the overall diversity of the Established Malvinoxhosan faunal complex through time.

The faunal make-up of the Post-Malvinoxhosan faunal complex is markedly less diverse than the preceding Malvinoxhosan faunal complex but is distinctly cosmopolitan in nature (Appendix B; Figs. 8; 9). As with the preceding Established Malvinoxhosan and Eo-Malvinoxhosan complexes, the Post-Malvinoxhosan faunal complex is characterised by low PO's (0.06-0.13) and successively high PE's (0.23-1) (Table 4.1; Fig. 8) and shows a stepped decline in diversity through time. An analysis of the overall biodiversity of the Post-Malvinoxhosan faunal complex suggests that although diversity was low overall, it was focused mainly among molluscs (Fig. 9). Whereas previously mollusc and brachiopod diversity was equitable in the Established Malvinoxhosan faunal complex, molluscs contribute between ~55-70% and brachiopods ~30-45% of diversity in the Post-Malvinoxhosan faunal complex with smaller contributions (< 10 %) from other groups (e.g., bryozoans and trilobites) (Appendix B; Fig. 9). Mainstays of Post-Malvinoxhosan shelly assemblages typically comprise a handful of cosmopolitan bivalves (*Modiomorpha, Nuculites, Palaeoneilo,* and *Janeia*) and gastropods (*Plectonotus*) as well as lingulate brachiopods (*'Lingula'* and *Orbiculoidea*) that were established over the course of Klipbokkop-Weltevrede time deposition (Appendix B; Fig. 8). Malvinoxhosan endemics are completely absent, save for rare reports of *Australospirifer* being present in parts of the Klipbokkop-Adolphspoort (upper Bokkeveld Group) formations and disappearing by the Wagen Drift Formation (lowermost Witteberg Group) (Appendix B; Hiller, 1990). Further to this, the trans-Atlantic brachiopod *Tropidoleptus* becomes an increasingly important contributor to shelly assemblages, dominating assemblages in the uppermost *Rhipidothyris-Australosprifer* and *Tropidoleptus-Paraprothyris* biozones (Appendix B; Boucot et al., 1983; Hiller, 1990).

There are slight variations in diversity, however, within the Post-Malvinoxhosan faunal complex as several new taxa make their appearance. In the lower *Grammysioidea-Cypricardella* biozone (Klipbokkop-Adolphspoort formation) bivalves resembling *Grammysioidea* and *Paracyclas* are present alongside last appearing "Malvinoxhosan hold-overs" bivalves, namely *Grammysia* and *Cypricardella* (Appendix B). These taxa, however, collectively make their last appearance by the end of Klipbokkop-Adolphspoort deposition. Overlying this biozone, the *Rhipidothyris-Australospirifer* biozone (Osberg-Wagen Drift interval) the trans-Atlantic brachiopod *Rhipidothyris* makes its short-lived appearance in the Karoopoort Formation (Boucot and Theron, 2001). In the upper *Rhipidothyris-Australospirifer* biozone (Wagen Drift Formation), last occurrences of possible nautiloids ascribed to '*Orthoceras*', indeterminate chonetids, bryozoans and *Australospirifer* have been reported (Appendix B; Theron, 1962; Hiller, 1990). The *Tropidoleptus-Paraprothyris* biozone heralds the end of the Middle Devonian in South Africa with the

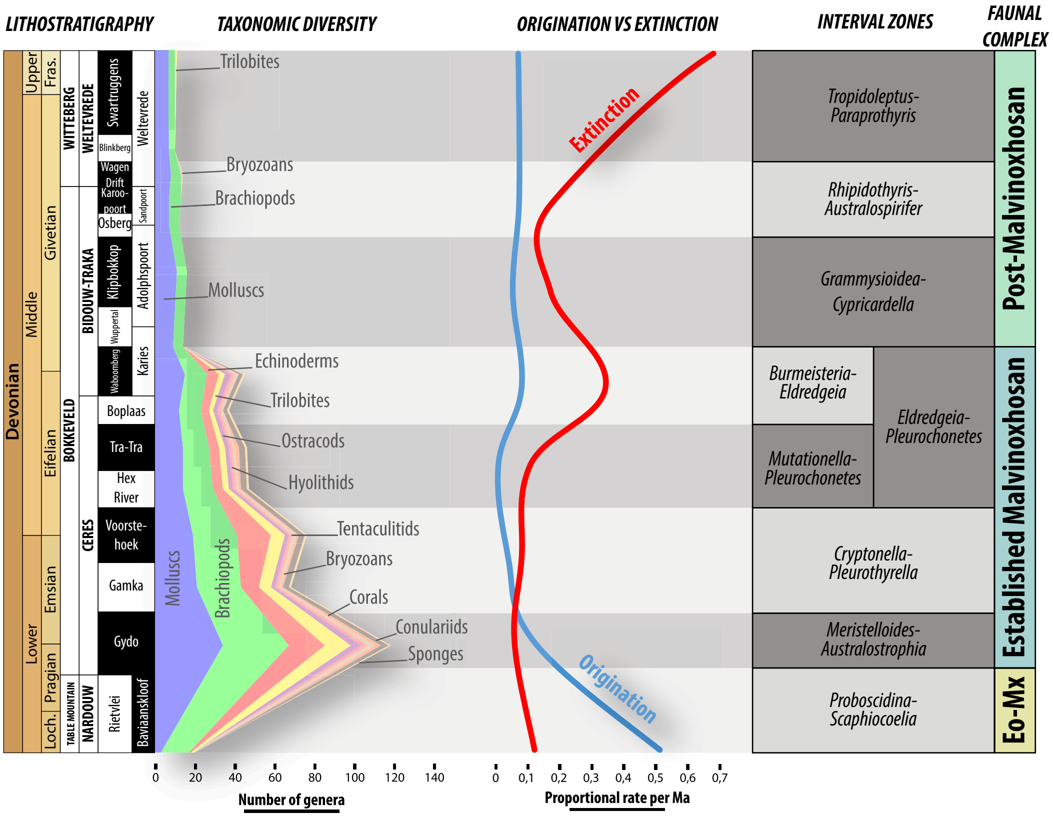

Fig. 8. Taxonomic diversity of Early-Middle Devonian invertebrate groups of South Africa. Abbreviations: Eo-Mx.- Eo-Malvinoxhosan, Fras.- Frasnian, Loch.- Lochkovian.

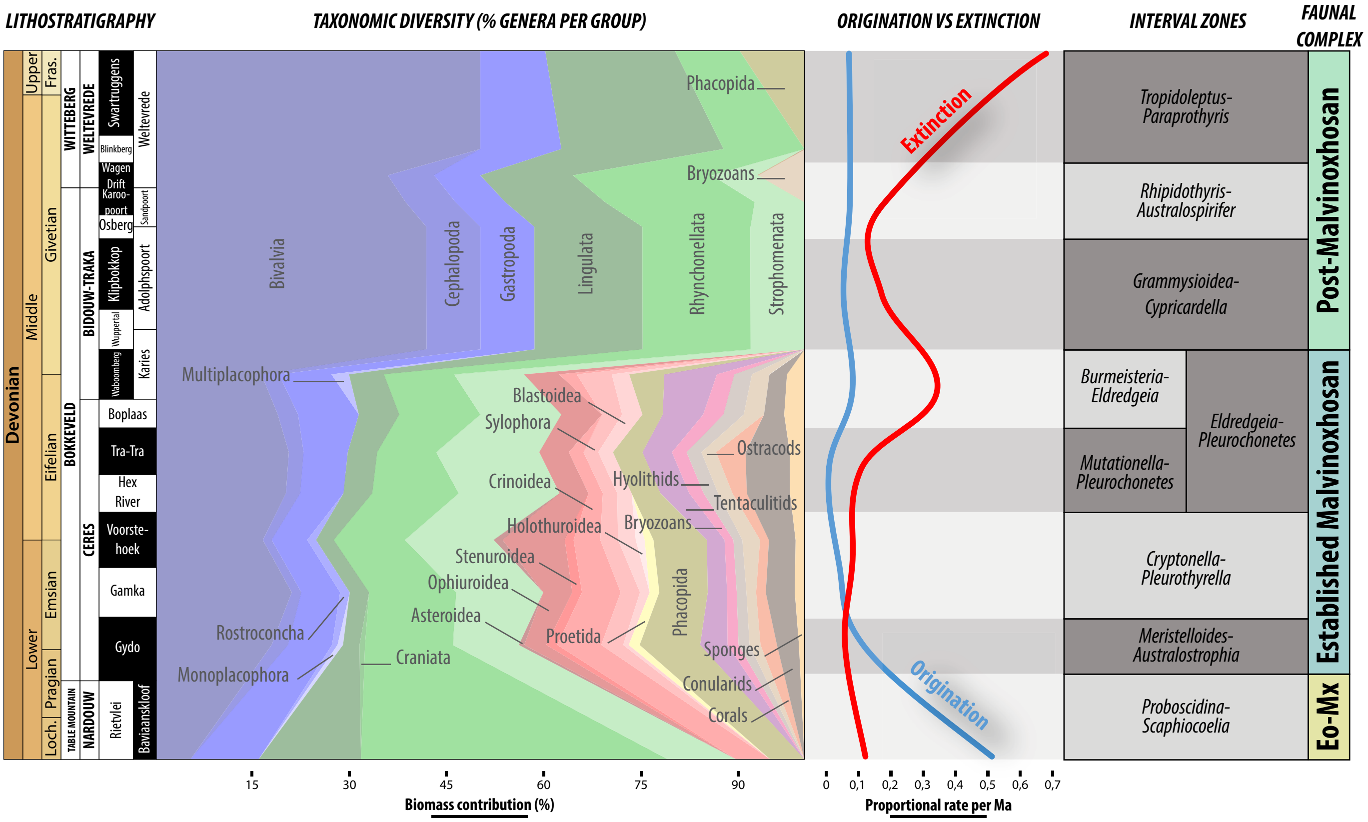

Fig. 9. Taxonomic diversity within Early-Middle Devonian invertebrate groups of South Africa. Abbreviations: Eo-Mx.- Eo-Malvinoxhosan, Fras.- Frasnian, Loch.- Lochkovian.

Table 4.1
Taxonomic counts and rate measures for biozones recognised in the Early-Middle Devonian of South Africa

Formation	*Faunal Complex*	*Interval Biozone*		Total genera in interval	Number of first appearances	Number of last appearances	Proportional origination rate	Proportional extinction rate
Swartruggens Blinkberg	*Post-Malvinoxhosan*	*Tropidoleptus-Paraprothyris*		11	1	11	0.09	1
Wagen Drift Karoopoort Osberg		*Rhipidothyris-Australospirifer*		15	2	5	0.13	0.3
Klipbokkop Wuppertal		*Grammysioidea-Cypricardella*		17	1	4	0.06	0.23
Waboomberg Boplaas	*Established Malvinoxhosan*	*Eldredgeia-Pleurochonetes*	*Burmeisteria-Eldredgeia*	46	7	31	0.15	0.67
Tra-Tra Hex River			*Mutationella-Pleurochonetes*	46	0	9	0	0.2
Voorstehoek Gamka		*Cryptonella-Pleurothyrella*		82	16	36	0.20	0.44
Gydo		*Meristelloides-Australostrophia*		118	102	47	0.86	0.4
Rietvlei-Baviaanskloof	*Eo-Malvinoxhosan*	*Proboscidina-Scaphiocoelia*		18	18	4	1	0.2

Givetian-Frasnian boundary thought to be drawn somewhere within the upper Swartruggens Formation. This biozone has the lowest diversity (11 genera) of all biozones considered in this study. Shelly assemblages in this interval are dominated by *Tropidoleptus* and lingulid brachiopods that co-mingle alongside the bivalves *Modiomorpha, Nuculites, Palaeoneilo, Janeia and Prothyris (Paraprothyris)* as well as the gastropod *Plectonotus* with reports of homalonotid trilobites possibly resembling *Trimerus* (Appendix B; Hiller, 1990).

4.3. Palaeoecology

All South African Early to Middle Devonian invertebrate taxa (except for cephalopod molluscs) show a strong tendency towards benthic lifestyles with exploitation of an array of deep-infaunal, infaunal, semi-infaunal and epifaunal niches (Fig. 10). Key differences are, however, evident through time. Faunas in the Eo-Malvinoxhosan and Established Malvinoxhosan faunal complexes are dominated by epifaunal (>75-90 %) taxa and reflect the diversity registered among brachiopods, trilobites, echinoderms, and to a lesser extent bryozoans, conulariids, tentaculitids as well as epifaunal gastropods and bivalves among others (Appendix B; Figs. 9; 10). This great diversity is reflected in the many feeding strategies and ethologies occupied by these organisms during the duration of these faunal complexes (Fig. 10). Infaunal lifestyles (mainly among burrowing bivalves) show a steadily increasing trend

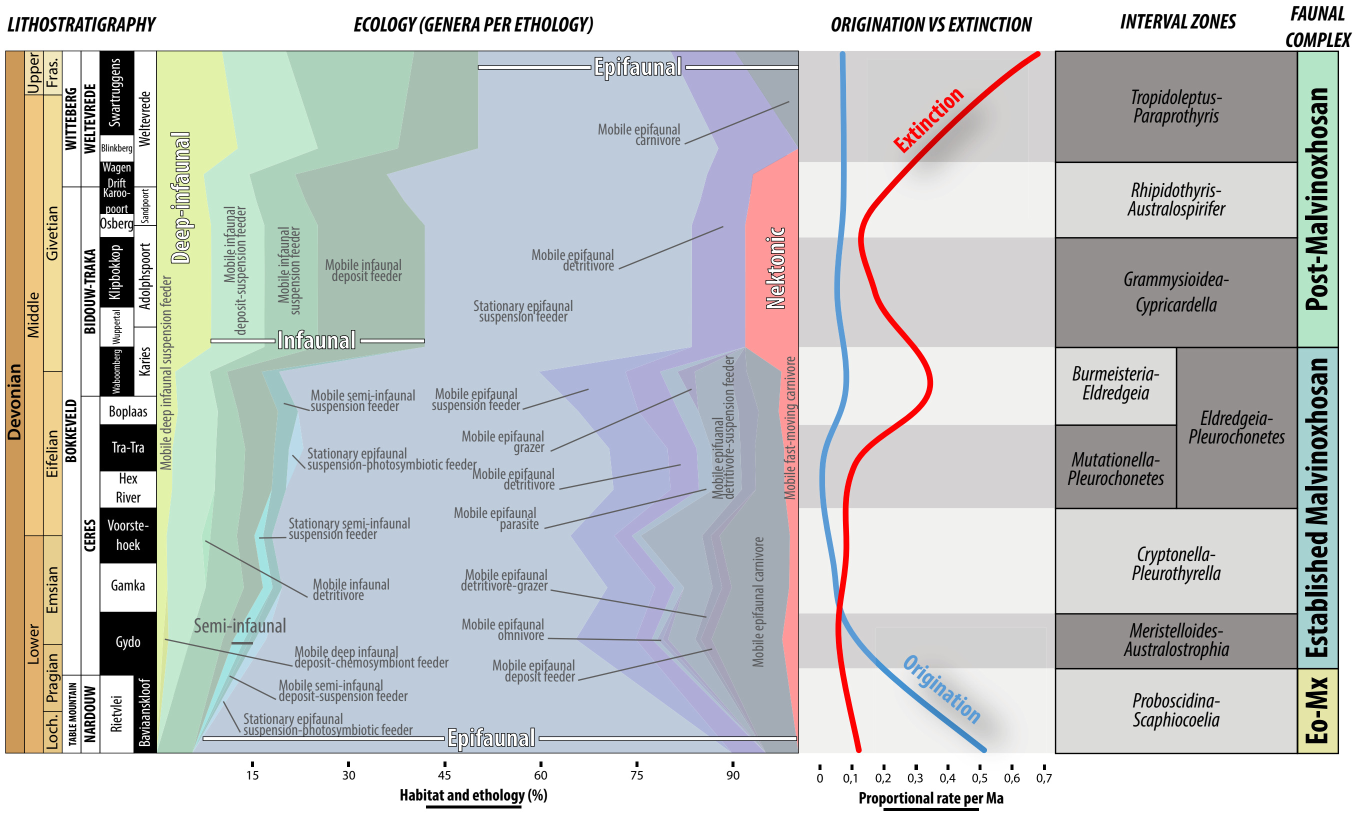

Fig. 10. Palaeoecology of Early-Middle Devonian invertebrate groups of South Africa through time. Abbreviations: Eo-Mx.- Eo-Malvinoxhosan, Fras.- Frasnian, Loch.- Lochkovian.

through from ~5 to 15% by the close of the Established Malvinoxhosan faunal complex, whilst nektonic, semi-infaunal and deep-infaunal ethologies never amount to more than 5% throughout its duration.

As discussed previously, observations on the bulk diversity and collapse of the Established Malvinoxhosan faunal complex suggest that it was stepped, terminating somewhere close to the Waboomberg-Wuppertal formational contact. An analysis of the habitat and feeding strategies of these organisms suggests that epifaunal and semi-infaunal organisms were preferentially impacted through time. Here, those epifaunal and semi-infaunal organisms with grazing, detritivorous (gastropods and some asterozoans), suspension (inclusive of mixed deposit-suspension, photosymbiotic-suspension, and detritivore-suspension e.g., brachiopods, crinoids, corals, and conulariids, inclusive of a few bivalves and gastropods) and carnivorous (trilobites and some asterozoans) feeding strategies were severely affected through time. Infaunal and deep-infaunal deposit feeders, mainly bivalves (inclusive of those with mixed feeding strategies e.g., deposit-chemosymbiotic) and nektonic carnivores (cephalopods, although not diverse) only experienced minor losses through time. These losses are evident when considering the diversity of ethologies and feeding strategies in the Post-Malvinoxhosan faunal complex (Fig. 10). Although epifaunal taxa still comprise the largest portion of the fauna in the Post-Malvinoxhosan faunal complex, they are drastically reduced and relatively equivalent to slightly lower in numbers (~40-50%) than other deep-infaunal, infaunal and nektonic lifestyles (~50-60% combined). Deep-infaunal and infaunal taxa both show a trend of increasing dominance through the Post-Malvinoxhosan faunal complex, increasing from approximately 5 to 10% and 30 to 50% respectively (Fig. 10). Further to this, the representation of nektonic faunas (based entirely on rare reports of *'Orthoceras'*) in the upper Bokkeveld and lower Witteberg

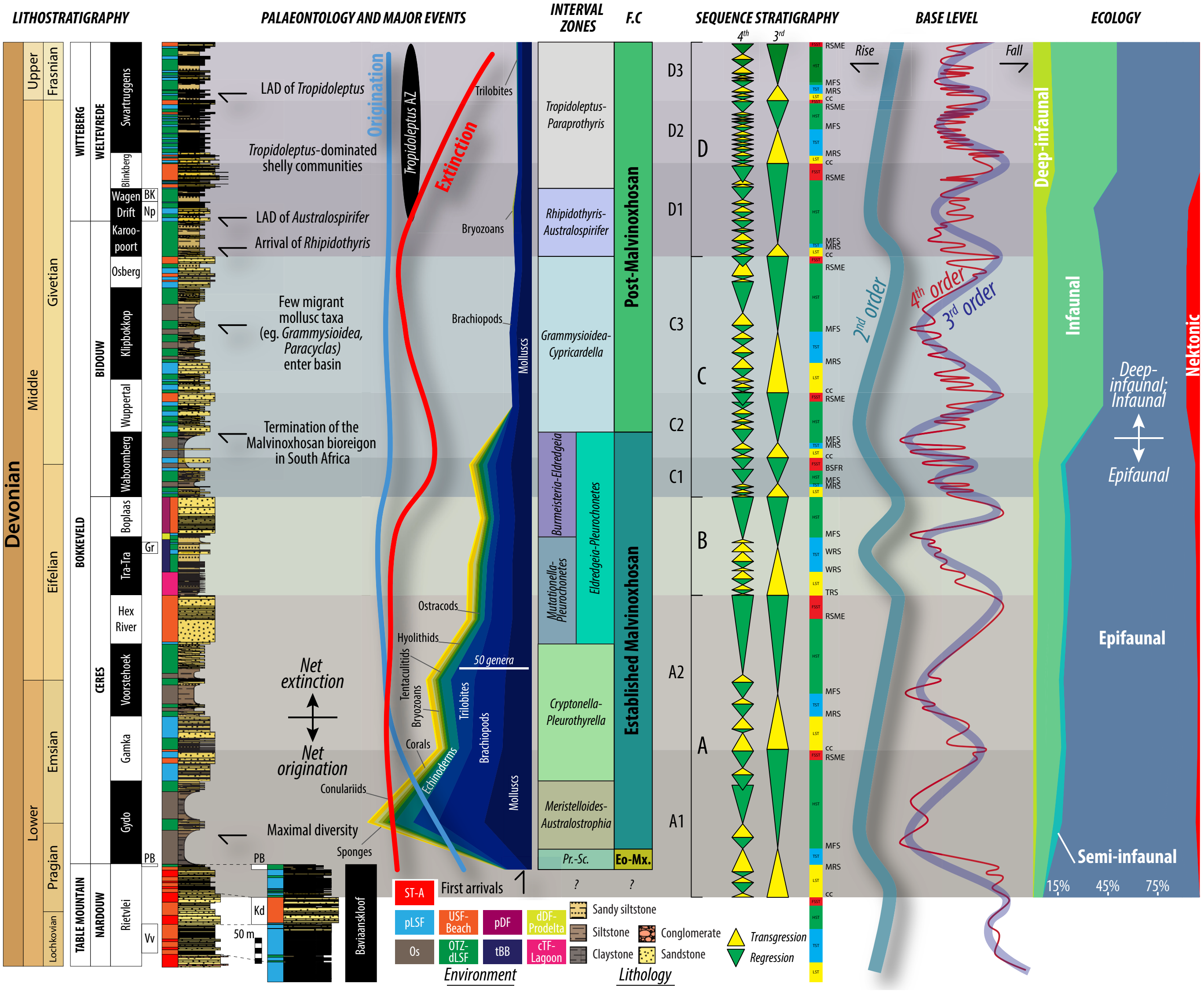

Fig. 11. Comparison of diversity and ecological changes in South Africa through the Early-Middle Devonian with respect to constructed local base-level curves and sequence stratigraphy. Abbreviations: AZ – Abundance Zone, BK- 'Byenest Krans member' of the Wagen Drift Formation, BSFR- Basal surface of forced regression, cc-correlative conformity, cTF-Lagoon- Channelised tidal flat to lagoon, dDF-Prodelta- Distal delta front to prodelta, Eo-Mx.- Eo Malvinoxhosan faunal complex, F.C.- Faunal complex, FSST- Falling stage systems tract, Gr-Grootrivierhoogte Member of the Tra-Tra Formation, HST- Highstand systems tract, Kd- Kareedouw Member of the Baviaanskloof Formation, LAD- Last appearance datum, LST- Lowstand systems tract, MFS- Maximum flooding surface, MRS- Maximum regressive surface, Np- 'Nougaspoort member' of the Wagen Drift Formation, Os- Offshore, OTZ-dLSF- Offshore transition zone to distal lower shoreface, PB- 'passage beds' of the Rietvlei-Baviaanskloof formations, Pr.-Sc.- Proboscidina-Scaphiocoelia Zone, pDF- Proximal delta front, pLSF- Proximal lower shoreface, RSME- Regressive surface of marine erosion, ST-A- Supratidal beach to alluvial, tBB- Transgressive beach barrier, TST-Transgressive systems tract, USF-Beach- Upper shoreface to beach, WRS- Wave-ravinement surface, and Vv- 'Verlorenvalley member' of the Rietvlei Formation.

groups, suggest a slight recovery in representation (Fig. 10). These increasing trends are marked against the backdrop of declining presence of epifaunal organisms over the same interval.

5. Discussion: Sea-level change, temperature, or both as a control on biotic turnover?

A comparison of diversity and ecological changes with estimations of depositional trends during the Early to Middle Devonian of South Africa suggest a correlation with changes in local base-level, in particular 2nd and 3rd order base-level changes (Fig. 11). Here, declines in diversity from the Gydo Formation onwards, correspond with falling base-levels that are related to smaller, though stratigraphically significant, 3rd order regressions. Conversely, 3rd order transgressions are associated with recoveries in diversity with the arrival of new taxa. This pattern appears to hold true for most of the South African record, barring the transgression associated with the deposition of the Tra-Tra Formation, which itself, is a 2nd order transgression (Sequence B) (Fig. 11). Correspondingly, the identified biozones, presented in Figs. 5-7, are located between sequences with upper and lower boundaries approximating with late highstands.

The arrival and first appearance of the Malvinoxhosan biota in South Africa corresponds with a 2nd order transgression (Sequence A) into the Cape Basin. With reference to the contained 3rd order Sequence A1, the earliest (and most diverse) Early to Middle Devonian biotas are present in the passage beds of the Rietvlei-Baviaanskloof formations and marine shales of the Gydo Formation. As previously mentioned, the passage beds mark the uppermost 3rd order lowstand deposits of Sequence A1 and are interpreted to have accumulated during early accelerating base-level rise. The overlying offshore marine shales of the Gydo Formation represent decelerating transgressive to early highstand conditions once flooding in the basin had peaked. In Sequence A1, early low diversity pioneer taxa belonging to the Eo-Malvinoxhosan faunal complex and *Proboscidina-Scaphiocoelia* Zone (present in the passage beds and basal most Gydo Formation) are entirely restricted to the lowstand systems tract deposits, whilst the transgressive to early highstand systems tract contains the more diverse, Established Malvinoxhosan faunal complex in addition to the *Meristelloides-Australostrophia* Zone. If this sequence framework holds true, it is thought that future fossil discoveries belonging to the Eo-Malvinoxhosan faunal complex as well as the *Proboscidina-Scaphiocoelia* Zone might be made in lowstand deposits preceding the passage beds.

The *Proboscidina-Scaphiocoelia* Zone of South Africa shows great similarities with the *Scaphiocoelia* Zone of Bolivia, especially in terms of its brachiopod fauna, as described by Isaacson (1977a) and later by Eldredge and Branisa (1980), itself a revision of earlier proposals by Branisa (1960a, 1960b). In Bolivia, as in South Africa, the *Scaphiocoelia* Zone is found at the base of the major Malxinoxhosan-bearing Devonian successions, namely the Lower Belen Member of the Belen Formation and Lower Shale Member of the Icla Formation where it is in contact with the underlying Vila Vila and Santa Rosa formations (Isaacson, 1977a, 1993). In Bolivia, the fauna of the *Scaphiocoelia* Zone is similar to the *Proboscidina-Scaphiocoelia* Zone in that it is typified by *Scaphiocoelia* alongside other short-ranged (and typically large) mutationellid terebratuloids, *Podolella, Proboscidina, Cryptonella*, *Pleurothyrella* and *Mutationella* with ranges that overlap with *Australocoelia, Australospirifer, Derbyina, Plicoplasia, Meristelloides, "Schuchertella", Notiochonetes, Pleurochonetes, Protoleptrostrophia*, and *Australostrophia*.

Coincidently, the *Scaphiocoelia* Zone of Bolivia is found within a succession that is lithologically similar to that of the passage beds in the Rietvlei-Baviaanskloof Formation. The *Scaphiocoelia* Zone has been described by Isaacson (1977a) as being sandier than the overlying and more argillaceous parts of the succession (Upper Belen and Upper Shale members of the Belen and Icla formations respectively) where it occurs. He interprets the entire package to be retrogradational with the *Scaphiocoelia* Zone facies representative of intertidal deposits and the overlying Malvinoxhosan-diverse Upper Belen and Upper Shale members being transgressive subtidal, deeper-water deposits. This retrogradational stacking pattern mirrors that seen in South Africa with the only difference being that the passage beds are interpreted to have accumulated in a distal lower shoreface setting. It is possible that, upon closer and more detailed examination of the Bolivian *Scaphiocoelia* Zone beds that these might be lower shoreface in origin given the bulk similarities (heterolithic lamination with fine grained sandstone interbeds) between these deposits with details that might be overlooked. Other than in Bolivia, similar short-ranging shelly fossil assemblages comprising *Scaphiocoelia* and, or, several other mutationellid terebratuloids (*Podolella, Proboscidina, Cryptonella*, and *Pleurothyrella*) akin to that of the *Scaphiocoelia* Zone and *Proboscidina-Scaphiocoelia* Zone are known from the very basal more sandy horizons of retrogradationally stacked Malvinoxhosan bearing successions in several well-studied West Gondwanan sites. Importantly, the appearance of these characteristic shelly assemblages always precedes the climax of diversity in their respective depocentres. Examples include the Lolén Formation, Ventana, Argentina (Borrello, 1962; Andreis, 1964; Siccardi, 2012, 2015), Talacasto Formation, Precordillera, Argentina (Levy and Nullo, 1970; Herrera, 1991, 1993; Herrera and Racheboeuf, 1997), as well as at, or near to, the Furnas-Ponta Grossa contact, Paraná Basin, Brazil (Boucot and Caster, 1984; Melo, 1988; Scheffler et al., 2020). It is suspected that these near-identical faunal and depositional similarities point to a shared first-order driver and transgression across West Gondwana that was associated with the arrival of the Malvinoxhosan biota. This also shows support for continuity among West Gondwanan depocentres during this time period as postulated by Penn-Clarke and Harper (2021).

Diversity reached its zenith with peak transgression of Sequence A (and by extension, its contained Sequence A1) represented by offshore deposits of the Gydo Formation (Pragian-early Emsian), representative of the *Meristelloides-Australostrophia* Zone (Fig. 11). The first appearances of several other Malvinoxhosan endemic taxa in the *Meristelloides-Australostrophia* Zone heralds the firm establishment of the Malvinoxhosan bioregion in South Africa. These new appearances are, however, associated with the disappearances of *Scaphiocoelia*, *Podolella, Proboscidina* and *Tanerhynchia*. Following this peak in diversity in the *Meristelloides-Australostrophia* Zone is a drop in diversity (PE = 0.4) that is coincident with the onset of regression at the end of Sequence A1, which resulted in the deposition of the lower Gamka Formation (Fig. 11). Similar to what is observed in the transgressive systems tract of Sequence A1, there is some (although minor) recovery in diversity with the first apparent appearances of a handful of taxa in the *Cryptonella-Pleurothyrella* Zone associated with the onset of transgression of the 3rd order Sequence A2 present in the Gamka-Voorstehoek interval (Fig. 11). With the regression of Sequence A2 (shared in part with Sequence A itself), there is a substantial drop in diversity (PE = 0.44). In fact, by the close of Sequence A more than ~60% of diversity was lost; many of these were Malvinoxhosan endemics with epifaunal organisms that were preferentially affected (Fig. 10). The disappearances of several well-established Lochkovian to Pragian-Emsian brachiopods at the end of the *Cryptonella-Pleurothyrella* Zone (e.g., *Anoplia, Acrospirifer, Australostrophia, Pleurothyrella, Cryptonella, Kentronetes, and Plicoplasia*) suggests that Emsian-Eifelian boundary lies somewhere either within the Voorstehoek Formation or at the Voorstehoek-Hex River Formation contact. This is important in establishing a Pragian-Emsian to possible earliest Eifelian age for Sequence A.

The handful of taxa that cross over into the upper Eifelian-Givetian belong to the *Eldredgeia-Pleurochonetes* Zone (Hex River-Waboomberg interval) (Fig. 11). This assemblage spans the regressive (late highstand-falling stage systems tracts) component of Sequence A2 in addition to the entirety Sequence B and C1, ending in the late highstand of Sequence C2. The contained *Mutationella-Pleurochonetes* (Hex River-Tra-Tra interval) and *Burmeisteria-Eldredgeia* (Boplaas-Waboomberg) subzones reflect minor diversity changes across the transgressive phases of their respective sequences B and C1 and C2 (Fig. 11). Here key differences across both subzones include the last appearances of both *Mutationella* (Hex River Formation) and *Pleurochonetes* (Tra-Tra Formation) in the *Mutationella-Pleurochonetes* subzone whilst the *Burmeisteria-Eldredgeia* subzone is marked by the apparent first appearances of a handful of short-ranging taxa (e.g., *Cypricardella, Eldredgeia, Pterinea,* and *Craedeocrinus*) (Appendix B). The *Eldredgeia-Pleurochonetes* Zone is significant in that it marks the last appearances of all Malvinoxhosan endemics, except *Australospirifer* (Appendix B; Figs 7, 11) in addition to multiple extra-Malvinoxhosan taxa. Here, the termination of the Malvinoxhosan is suspected to take place during the regression (late highstand-falling stage) of Sequence C2. Losses were particularly significant among epifaunal organisms, particularly among echinoderms and trilobites that went completely extinct by the end of the *Burmeisteria-Eldredgeia* subzone as well as virtually all rhynchonellate and strophomenate brachiopods and epifaunal and semi-infaunal bivalves.

Few new taxa entered the basin with subsequent transgressions into the Cape Basin leading into the Late Devonian with the overall pattern suggestive of net extinction during successive regressions (Fig. 11). All new taxa encountered in the Cape Basin are short-ranged being restricted to their contained 3rd order sequences. New taxa include the bivalves *Grammysioidea* and *Paracyclas* in Sequence C3, the trans-Atlantic brachiopod, *Rhipidothyris* in Sequence D1 (Karoopoort Formation) and the bivalve *Paraprothyris* alongside the trilobite *Trimerus* in Sequence D2, or D3 (upper Weltevrede Formation and Swartruggens Formation) (Appendix B; Fig. 11; Hiller, 1990; Boucot and Theron, 2001). *Australospirifer* further makes its last appearance in South Africa by the end of Sequence D1 (lower Weltevrede Formation and Wagen Drift Formation) (Appendix B; Fig 11; Hiller, 1990). The second-order Sequence D (*Rhipidothyris-Australospirifer* and *Tropidoleptus-Paraprothyris* zones: Karoopoort-Swartruggens interval) is perhaps of particular interest in that it is typified by an overall abundance of *Tropidoleptus* in shelly assemblages where it is found alongside other cosmopolitan taxa with wide environmental and ecological tolerances such as lingulids (eg *'Lingula'*, and *Orbiculoidea*), bivalves (*Sanguinolites, Modiomorpha, Nuculites, Palaeoneilo, Paraprothyris,* and *Janeia*) and gastropods (*Plectonotus*) as well as the trilobite *Trimerus* (Appendix B; Fig 11; Hiller, 1990; Boucot et al., 1983). *Tropidoleptus* is a long-ranging (Lochkovian-Frasnian) morphologically conservative brachiopod known primarily from circum-Atlantic continents and typified by a single species *Tropidoleptus carinatus* (Conrad) (Boucot, 1975; Isaacson and Perry, 1977; Harper et al., 2010). Its near-global extent and presence in a wide-range of environments suggest that it was eurythermal and perhaps opportunistic. The presence of these non-diverse cosmopolitan shelly assemblages in South Africa suggests when Sequence D was initiated conditions were unfavourable to support the Malvinoxhosan biota. It is apparent that these effects were compounded through time leading up to Sequence D in South Africa, given the stepped disappearance of taxa with preceding transgressive-regressive cycles (Fig. 11).

Similar biodiversity trends and turnover related to base-level change have been observed in the Ponta Grossa Formation, Paraná Basin, Brazil, as well as the Devonian of the Central Andean Basin, Bolivia over the Pragian-earliest Eifelian (Isaacson, 1977a, 1977b, 1993; Racheboeuf et al., 1993; Bosetti et al., 2011, 2012; Horodyski et al., 2014; Sedorko et al., 2019, 2021; Dalenz Farjat et al., 2022). Similarities of changes in faunal content have been observed to be coincident with local 3rd order base-level changes in Brazil as they are in South Africa. Direct comparisons can be observed between Sequence A1 and A2 of this study respectively with "Sequence B" and "Sequence C" of Grahn et al. (2013) that overlap with the "Siluro-Devonian" and "Devonian I" sequences of Sedorko et al. (2018b) with additional datasets presented by Bosetti et al. (2011, 2012), Horodyski (2014), Sedorko et al. (2021). According to Grahn et al. (2013), Sequence B spans the late Pragian-early Emsian and Sequence C, the late Emsian-early Eifelian, whilst the Siluro-Devonian sequence of Sedorko et al. (2018b) spans the Pridoli-middle Emsian and the Devonian I sequence, the late Emsian-middle Eifelian. Sequence B and C recognised in this study, further show close respective parallels with "Sequence D" and "Sequence E" of Grahn et al. (2013) that overlap with "Devonian II" of Sedorko et al. (2018b).

To highlight a few of these shared similarities between the Ponta Grossa Formation, the Bokkeveld Group, and the Devonian of Bolivia, among brachiopods, virtually all rhynchonellates do not cross into the upper Eifelian- lower Givetian, except for *Australocoelia, Australospirifer*, and *Derbyina* and large orbiculoids, namely *Gigadiscina*, are absent. The survivorship of molluscs into the upper Eifelian- lower Givetian across all depocentres are also similar. Among bivalves, infaunal and semi-infaunal dominated assemblages comprising *Prothyris (Paraprothyris), Janeia, Palaeoneilo, Nuculana,* and *Nuculites* are present as well as the gastropods *Pleurotomaria* and *Platyceras*. This too is mirrored in Bolivia as not only are most of these taxa present but other infaunal and semi-infaunal taxa such as *Grammysioidea, Grammysia, Modiomorpha, Paracyclas,* and *Sanguinolites* are shared with South Africa during the Eifelian-Givetian (Dalenz Farjat et al., 2022).

In South Africa, nautiloids are present in the Eifelian and Givetian and are known to occur in the Waboomberg and Wagen Drift formations (Appendix B) but are unknown from the Ponta Grossa Formation at that time. Other similarities across both the Paraná and Cape basins, include the presence of both *Paraconularia* and *Conularia* as Eifelian and Givetian stage crossers. Although there are indeed many similarities across both depocentres, there are some differences. In the Cape Basin, a few strophomenate brachiopods cross over into the Eifelian and Givetian, namely *Austronoplia, Aseptonetes, Notiochonetes, Pleurochonetes,* and *Schellwienella* are present whereas in the Ponta Grossa Formation only *Schuchertella* is present and in Bolivia only *Austronoplia* and perhaps *Notochonetes* extend into the Eifelian. In Brazil and Bolivia, as in South Africa, *Tropidoleptus* dominates shelly assemblages during the Givetian (Fonseca and Melo, 1987; Melo, 1988) and is commonly associated with *Rhipidothyris* in Bolivia (Isaacson, 1974, 1977a, 1993; Isaacson and Perry, 1977; Isaacson and Sablock, 1990). Among trilobites *Metacryphaeus* is a shared upper Eifelian and Givetian stage crosser, however, there are slight differences. In the Bokkeveld Group, *Burmeisteria* crosses over into the Tra-Tra Formation but disappears soon thereafter whilst *Bainella* is suspected to be present in the Eifelian as it is known from the probable upper Eifelian- lower Givetian Waboomberg Formation. In the Ponta Grossa Formation, *Pennaia* is present in the Eifelian and Givetian. Echinoderms are difficult to compare as very few taxa are shared across both basins, however, what is striking is the near complete reduction in diversity in the Eifelian-Givetian of both depocentres. These similarities, as well as those observed between the Bolivian *Scaphiocoelia* Zone and the South African *Proboscidina-Scaphiocoelia* Zone and other pre Malvinoxhosan climax biotas in South America, suggest a continuity among West Gondwanan depocentres as well as an overarching control on cyclicity which in turn affected biodiversity change. The remarkable similarities in biodiversity change across West Gondwana suggest that the biozones identified in this study might have future application in aiding regional correlations. If the biodiversity contained within these biozones can further be shown to be bound by sequence boundaries of the same age and type, then these intervals could signify periods of regional community-level stability across West Gondwana. If this can be demonstrated on a regional scale, then the faunal complexes and biozones identified in this study might be equated with ecological-evolutionary units (EEU) (Boucot, 1983, 1990; Sheehan, 1996), and smaller ecological-evolutionary subunits (EESU) (*sensu* Brett and Baird, 1995; Brett et al., 2009) respectively depending on their duration and order of their sequence boundaries.

The narrow range of taxa within the biota with no real increase in origination both in South Africa and in South America, suggests a complete ecological collapse in the wake of the extinction of the Malvinoxhosan biota. Cyclical changes in base-level at third- and second-order are an obvious smoking gun responsible for biotic turnover in the Early-Middle Devonian of South Africa. Given that epifaunal and semi-infaunal taxa were preferentially impacted by changes in base-level the kill-mechanism must have been located at the sediment-water interface. It is possible to assume that regressions might have resulted in excess sediment supply into the basin. The effect of additional sediment input to the basin might have had a role in smothering organisms living at the sediment-water interface, or increasing the turbidity of the water column and, in doing so, affecting the feeding strategies of the benthos. If this were the prime cause, it would be reasonable to assume that both endemic and cosmopolitan taxa would have been affected equally. It is, however, observed both in South Africa and South America that the Malvinoxhosan biotas were preferentially impacted by changes in base-level whilst most cosmopolitan faunas appeared to be hardly affected.

In Bolivia, Brazil, and the Falklands, the stepped decline in biodiversity and collapse of the Malvinoxhosan bioregion is suspected (based on sparse palynological and chitinozoan records) to correlate with globally extensive, extinction events during the Early-Middle Devonian of which the Daleje (middle-early late Emsian) events, and the Middle Devonian Choteč (early Eifelian), and Kačák (late Eifelian) appear to prime candidates (Isaacson, 1974; Copper, 1977; Isaacson and Perry, 1977; Melo, 1988; Troth et al., 2011; Bosetti et al., 2011, 2012; Grahn et al., 2013, 2017; Horodyski et al., 2014; Marshall, 2016; Carbonaro et al., 2018; Sedorko et al., 2018a, 2018b, 2019, 2021). These events (and the local base-level changes associated with them) have often been linked to global first-order transgressive events. In Laurussian/Euramerican regions, these events usually are marked by dysoxia or anoxia, die off and deposition of black shales (Walliser, 1996, 2000; House, 1996, 2002; Suttner et al., 2021). Other than precise age constraints, the correlation of observed biotic turnover events in West Gondwana during the Early-Middle Devonian with global events elsewhere is problematic for several reasons. Other than organic-rich shales (e.g., Baby et al., 1995; Iñigo et al., 2012) in parts of the Devonian System of Bolivia and northern Argentina, there is little compelling evidence to link black deep marine shales to having high organic carbon content as well as having formed under dysoxic or anoxic conditions with transgression. In South Africa, at least, these shales appear to be black due to the crystallisation of illite and is associated with diagenetic alteration and metamorphism as opposed to an organic origin (Esquevin, 1968; Boltenhagen, 1969; Rowsell and de Swardt, 1976).

What is perhaps most problematic for the correlation of these events at high latitudes is the comparison of local depositional trends with the “global” sea-level curve for the Devonian. The global sea-level curve for the Devonian itself is strongly biased to low-latitude equatorial regions (e.g., Laurussia/Euramerica) after Johnson et al. (1985). As commented on by Becker et al. (2020), the Johnson et al. (1985) sea-level curve is problematic in that it is not based on sequence stratigraphy and that it focused on the correlation of imprecisely dated transgressive events across different parts of Euramerica that themselves are now known to not be correlative at all. This means that the definitions for depophases presented by Johnson et al. (1985), i.e., sequence boundaries and other sequence stratigraphic surfaces are poorly defined and are difficult to correlate. In recent times, however, refinements to the Devonian Euramerican sea-level curve and accompanying sequence stratigraphy have been made by Brett et al. (2011) that have improved its applicability in correlating depophases both locally and globally. Although the South African and Euramerican sea-level curves for the Devonian do show great similarities (e.g., both record overall highstand conditions with few oscillations during the Early Devonian and frequent oscillations in the Middle Devonian), the near total lack of globally biostratigraphic important taxa in the Malvinoxhosan bioregion (e.g., ammonoids, conodonts, graptolites), especially in South Africa, makes any correlation of local base-level trends with regional trends tenuous at best. Lastly, what is perhaps most problematic about the global sea-level curve for the Devonian Period as presented by Johnson et al. (1985) and Brett et al. (2011) is the identification of what the driver(s) for global eustasy is. It is often thought that for most of the Devonian, Earth was characterised by warm conditions with global highstands and ice-free. Palaeoclimatic reconstructions, variably from conodont apatite and brachiopod calcite oxygen isotopes do suggest a trend of decreasing mean temperatures through time (van Geldern et al., 2006; Elrick et al., 2009; Joachimski et al., 2009; Brugger et al., 2019) with distinct cooling trends present in the Pragian-Givetian and late Famennian Global cooling during the Pragian-Givetian was more pronounced than that of the late Famennian (van Geldern et al., 2006; Joachimski et al., 2009; Brugger et al., 2019) but did not result in the formation of ice-sheets. Evidence for glaciation, especially at southern high latitude polar regions where the only major landmass was located, only manifests during the very latest Devonian (Famennian) with the onset of Carboniferous-Permian glaciation of Gondwana as evidenced from localised glacial deposits from Bolivia, Brazil and possibly South Africa (Caputo, 1985; Caputo and Crowell, 1985; Díaz-Martínez and Isaacson, 1994; Isaacson et al., 1999, 2008; Streel et al., 2000; Almond et al., 2002). In light of this evidence, numerical climate modelling for the Devonian Period presented by Elrick et al. (2009), Elrick and Witzke (2016); Brugger et al. (2019) alludes to the possibility of continental ice-sheets elsewhere, or sea ice at the palaeo-North Pole as a proxy for the regulation of global climate for the period. If palaeoclimatic reconstructions for the Devonian Period, especially during the Early to Middle Devonian, did have a global eustatic effect (either through the growth of icesheets or some thermal expansion and contraction of ocean water) it somewhat stands in contradiction with observed base-level trends, both in South Africa and Euramerica, that is high sea-levels during periods of cooling. That being said, the apparent similarities of base-level fluctuations between both regions are compelling and an overarching regional control, climatic or otherwise, might exist but the mechanisms for which are still yet to be understood.Given the problems of correlating Devonian West Gondwanan events with global events, our interpretation for the collapse of the Malvinoxhosan bioregion in South Africa favours mechanisms that are intrinsic to West Gondwana itself but were influenced by global climate shifts at the time. Penn-Clarke and Harper (2021) noted that the collapse of the Malvinoxhosan bioregion during the Givetian is associated with an increase in global temperature and further suspected that a breakdown of circumpolar currents brought about the demise of these cool water specialists. Further to this, Isaacson and Perry (1977) and Isaacson and Sablock (1990) demonstrated the gradual appearance and dominance of extra-Malvinokaffric faunas (e.g., *Rhipidothyris*) alongside *Tropidoleptus* across West Gondwana from the late Eifelian- early Givetian onwards. Isaacson and Sablock (1990) present a model suggesting that these extra-Malvinoxhosan taxa and warmer water currents from lower latitudes entered West Gondwana from North Africa, North America and Colombia and into southern Peru and Bolivia via the Amazonas Basin following the breakdown of an allopatric barrier, the Purus Arch with transgression during the Middle Devonian. The Purus Arch is suspected to have acted as an isthmus between the Amazonas and Central Andean Basin separating Eastern American and Malvinoxhosan bioregions and providing limited communication between both basins. The presence of *Tropidoleptus* as early as the Emsian in South Africa (Appendix A; Oosthuizen, 1984), albeit rare, and perhaps similarly in Bolivia and Brazil (Isaacson, 1977a; Melo, 1988) suggest that this taxon was always present in the Malvinoxhosan bioregion. It's increasing dominance in Eifelian-Givetian shelly assemblages coincides with the demise of the Malvinoxhosan bioregion by the end of the Givetian, suggesting that environmental conditions must have deteriorated to the point that only the opportunistic *Tropidoleptus* (in addition to a handful of cosmopolitan molluscs) could survive. Its proliferation to the point of dominating shelly assemblages in Givetian-aged strata suggest that it was a disaster taxon that thrived due to lack of competition. Given the striking similarities in biodiversity change and its links to base-level change across both in South Africa and South America during the Early-Middle Devonian, it is postulated that the combined effects of regional base-level change and a warming climate provide the probable cause for the collapse of the Malvinoxhosan bioregion. In this scenario, it is postulated that a similar regional driver for base-level change existed across West Gondwana. It is suspected that this driver is probably tectonic in origin and is related to events that took place along the Famatinian Belt and Patagonia during the Ordovician-Devonian. As has been documented by Ariza et al. (2018), Astini et al. (1995), Milani and De Wit (2008), Ramos (1988), Ramos (2004, 2009, 2018), Ramos et al. (1998, 2020), Pankhurst et al. (2003, 2006), Tankard et al. (1995), Tankard et al. (2012), Uriz et al. (2011), de Vargas et al. (2020) and Vorster et al. (2021) that 1st order intervals of subsidence, depophases and stratigraphy are similar across West Gondwana during the Ordovician-Devonian and that their chronology appears to mirror magmatic and metamorphic events of the Famatinian Belt and in Patagonia. It is thus probable to assume that observed smaller 3rd to 4th order depophases across West Gondwana are also allocyclic and regional in nature and related to the activity in the Famatinian Belt and Patagonia.

With a regional tectonic driver for cyclicity established, during transgressive events, warmer oceanic waters from lower latitudes entered higher latitude West Gondwanan depocentres with the breakdown of allopatric barriers such as the Purus Arch. Since global temperatures are suspected to have increased from the late Givetian onwards it is thought that successive transgressions into higher latitudes would have entrained increasingly warmer waters as well as causing the gradual amelioration of circumpolar currents leading to an increase in oceanic temperatures around the South Pole. With the breakdown of these allopatric barriers, eurythermal and warmer water extra-Malvinoxhosan taxa such as *Tropidoleptus* and *Rhipidothyris* were both able to enter and proliferate in higher latitude depocentres replacing the relict Malvinoxhosan biota by the end of the Givetian. Since the Malvinoxhosan biotas were cool-water specialists, the effects of increasing water temperatures were detrimental to their survival, leading to their eventual demise. Given that increasing temperatures for the Devonian Period are only thought to have occurred from the late Givetian onwards but that there are observable declines in biodiversity linked to base-level changes across the Malvinoxhosan bioregion from the Pragian it is hypothesised that even these early transgressive events brought in warmer waters from lower latitudes. Since similar taxa appear consistently to have restricted ranges both in South Africa and South America (e.g., the Eo-Malvinoxhosan *Proboscidina-Scaphiocoelia* and *Scaphiocoelia* Zone taxa) it is probable to assume that these taxa had specific temperature-related thresholds to ensure their survival. Oceanic temperatures at high latitudes probably reached a critical threshold from the late Givetian onwards which might have been too great for the Malvinoxhosan biota to handle, leading to a complete and permanent collapse of these high-latitude benthic ecosystems as no real biodiversity boom is observable both in South Africa and South America. Further to the complete lack of biodiversity, the Givetian aged post-Malvinoxhosan 'Lilliput faunas' from Brazil would support this notion that conditions were stressful in the wake of the collapse of the Malvinoxhosan bioregion (Bosetti et al., 2011). Some taxa, particularly cosmopolitan infaunal to semi-infaunal bivalves (e.g., *Modiomorpha, Nuculites, Palaeoneilo,* and *Sanguinolites*) appear to have been unaffected by changes in base-level and inferred temperature and perhaps speak to a higher tolerance by these forms (Dalenz Farjat et al., 2022).

6. Conclusions

Observed biodiversity changes during the Early-Middle Devonian of South Africa allude to the presence of three large faunal complexes, namely: the Eo-Malvinoxhosan (Pragian-early Emsian), Established Malvinoxhosan (Emsian-early Givetian) and Post-Malvinoxhosan (Givetian-Frasnian) faunas that were verified by using a combination of novel multivariate statistical methods in conjunction with network analysis. These methods allowed for further subdivision of faunal complexes into smaller biostratigraphic units that have been equated with interval assemblage zones. These are namely the *Proboscidina-Scaphiocoelia* biozone (Eo-Malvinoxhosan faunal complex), the *Meristelloides-Australostrophia* (Gydo Formation), *Cryptonella-Pleurothyrella* (Gamka-Voorstehoek interval), *Mutationella-Pleurochonetes* (Tra-Tra-Hex River interval), and *Burmeisteria-Eldredgeia* (Boplaas-Waboomberg interval) biozones (Established Malvinoxhosan faunal complex) and the *Grammysioidea-Cypricardella* (Wuppertal-Klipbokkop interval), *Rhipidothyris-Australospirifer* (Osberg-Wagen Drift interval) and *Tropidoleptus-Paraprothyris* (Blinkberg-Swartruggens interval) biozones of the Post-Malvinoxhosan faunal complex.

Eo-Malvinoxhosan faunas are present in the 'passage beds' of the Rietvlei-Baviaanskloof and lowermost Gydo formations and are typified by a low-diversity founding faunule of short-ranging (and typically large) terebratulides and orbiculoids as well as a handful of chonetids, rhynchonellides, echinoderms, bryozoans, bivalves, gastropods, and trilobites. Malvinoxhosan faunas present in the Gydo-Waboomberg interval show greater diversity spanning a suite of endemic brachiopods and trilobites in addition to molluscs, echinoderms and other groups (e.g., bryozoans, corals, conulariids, hyolithids etc.). Collectively these faunas comprise the Established Mavinoxhosan faunal complex. At least three to four declines in biodiversity are observed throughout the temporal range of the Established Malvinoxhosan faunal complex, with few new originations, that correspond with identified interval assemblage zones. The Established Malvinoxhosan faunal complex is suspected to have lasted at least 8-10 Ma based on relative age estimates. Virtually all Malvinoxhosan endemics are unknown in post Waboomberg Formation strata, signalling their extinction in South Africa at some point during the late Eifelian to early Givetian. Epifaunal and semi-infaunal taxa appear to have been preferentially targeted with respect to infaunal, deep infaunal and nektonic taxa. Post-Malvinoxhosan faunas present in the Wuppertal-Swartruggens interval are characteristically depauperate in terms of biodiversity being typified by a handful of survivor cosmopolitan invertebrate taxa with *Australospirifer* being the only Malvinoxhosan endemic for part of the faunal complex. Shelly Post-Malvinoxhosan assemblages are almost always dominated by the trans-Atlantic and opportunistic brachiopod, *Tropidoleptus* as well as other eurythermal taxa. Similar to the Established Malvinoxhosan faunal complex, recognised interval assemblage biozones are associated with declining biodiversity through time with little in terms of new originations. This has been taken to suggest that environmental changes and their resulting biocrises during the Early-Middle Devonian impacted high latitude regions to such a degree that these ecosystems could never recover from.

A comparison of observed faunal complexes and their contained interval assemblage biozones with local sea-level curves constructed from sequence stratigraphy suggest a correlation with second and third order changes in sea-level. It is suspected that transgressions into the Cape Basin during the Early-Middle Devonian entrained increasingly warmer waters from lower latitudes along with extra-Malvinoxhosan immigrant taxa that gradually replaced the cool-water specialist Malvinoxhosan faunas leading to their eventual extinction. Strikingly similar sea-level controlled biostratigraphic trends have been observed in several South American locales suggesting that the mechanisms involved in the decline and eventual extinction of the Malvinoxhosan faunas are of a regional nature. While it is tempting to correlate these with known global Devonian biocrises during the Early-Middle Devonian (namely the Eifelian and Givetian biocrises) more research is required to provide better relative biostratigraphic and chronostratigraphic constraints for these deposits. Further research is also required to flesh-out global and regional signals from locally constructed sea-level curves especially given that the drivers for sea-level change during the Devonian are not well established and that high latitude regions are especially sensitive to any changes in sea-level. In high latitude polar regions even the very slightest of changes in sea-level at the global scale could manifest as major signals. Lastly, the biostratigraphic framework presented herein shows some promise and applicability as the beginnings of a standard for West Gondwanan Devonian biostratigraphy to aid both intra- and interbasinal correlations across South America and South Africa. Given the remarkable similarities of sea-level controlled biodiversity changes between South Africa and South America (seemingly at the same time) this framework might rather indicate evolutionary-ecological units and subunits signifying shared periods of regional stability across West Gondwana between biodiversity turnover events.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data used in this research is available in the supplemental material

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