Biostratigraphy of the *Massospondylus* Assemblage Zone (Stormberg Group, Karoo Supergroup), South Africa

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Abstract

The *Massospondylus* Assemblage Zone is the youngest tetrapod biozone in the Karoo Basin (upper Stormberg Group, Karoo Supergroup) and records one of the oldest dinosaur dominated ecosystems in southern Gondwana. Recent qualitative and quantitative investigations into the biostratigraphy of the lower and upper Elliot formations (lEF, uEF) and Clarens Formation in the main Karoo Basin resulted in the first biostratigraphic review of this stratigraphic interval in nearly four decades, allowing us to introduce a new biostratigraphic scheme, the *Massospondylus* Assemblage Zone (MAZ). The MAZ expands upon the *Massospondylus* Range Zone by including the crocodylomorph *Protosuchus haughtoni* and the ornithischian *Lesothosaurus diagnosticus* as two co-occurring index taxa alongside the main index taxon, the sauropodomorph *Massospondylus carinatus*. With a maximum thickness of ~320 m in the southeastern portion of the basin, our new biozone is contained within the uEF and Clarens formations (upper Stormberg Group), however, based on vertebrate ichnofossils evidence, it may potentially extend into the sedimentary units of the lowermost Drakensberg Group. We do not propose any further subdivisions, and do not consider the *Tritylodon* Acme Zone (TAZ) as a temporal biostratigraphic marker within the MAZ. The MAZ is currently accepted to range in age between the Hettangian and Pliensbachian, however a faunal turnover, which observes an increase in the diversity of dinosaur clades, crocodylomorph, and mammaliaform taxa in the lower uEF, could reflect effects of the end-Triassic extinction event (ETE).

Name

Massospondylus Assemblage Zone (MAZ).

Proposer of name

Kitching and Raath (1984) proposed a *Massospondylus* biozone (originally the "*Massospondylus* Range Zone") in their landmark study on the biozonation of the Upper Triassic to Lower Jurassic of South Africa and Lesotho. The *Massospondylus* Assemblage Zone (MAZ) is defined for the first time in this contribution.

Stratigraphic position

Biostratigraphic position

The MAZ overlies the *Scalenodontoides* Assemblage Zone (SAZ) and represents the uppermost vertebrate assemblage zone of the Karoo Supergroup within the main Karoo Basin of South Africa and Lesotho.

Lithostratigraphic position

The MAZ extends across the upper Elliot and Clarens formations (Stormberg Group, Karoo Supergroup). It commences in the upper Elliot Formation (Hettangian–Sinemurian) and extends into the Clarens Formation (Pliensbachian), which together form the uppermost part of the Stormberg Group (Karoo Supergroup). Initially, the Elliot Formation was subdivided into informal lower, middle and upper units by Kitching and Raath (1984). Subsequently, the lithostratigraphy of the formation was redefined to contain only two informal units: the lower Elliot Formation (lEF) and the unconformably overlying upper Elliot Formation (uEF; Bordy et al., 2004a, b and c; Bordy and Eriksson, 2015). The uEF incorporates the middle and upper Elliot formations of Kitching and Raath (1984) and encompasses the lower boundary of the MAZ. The upper boundary of the MAZ lies at the contact of the Clarens Formation with the conformably overlying Drakensberg Group (e.g., Kitching and Raath, 1984; Bordy and Head, 2018).

Derivation of name

Named after the distinctive, abundant and field-identifiable sauropodomorph dinosaur *Massospondylus carinatus*, which co-occurs with the ornithischian dinosaur *Lesothosaurus diagnosticus* and the crocodylomorph *Protosuchus haughtoni* (Figure 1).

Historical background

Wyley, Huxley and Dunn first named the units of the "Stormberg formation" (reviewed in Rogers and Du Toit, 1909), but it was Du Toit (1903, 1905) who laid the foundation for the stratigraphic work on this uppermost Karoo succession. This would later influence Haughton's (1924) first attempt to subdivide the "Stormberg Series" into biozones documenting the upper Karoo fossils. During the 1950s and 1960s, Ellenberger and colleagues made further revisions however, their focus was primarily on the vertebrate ichnofossil assemblages in the upper Karoo of Lesotho (Ellenberger et al., 1964; Ellenberger, 1970). While Cooper (1982) briefly summarized the pre-1980 Karoo biostratigraphy, the first widely accepted biostratigraphic range zones for the Elliot and Clarens formations were proposed by Kitching and Raath (1984), and based upon the distributions of two sauropodomorph taxa: '*Euskelosaurus browni*' and *Massospondylus carinatus*. Although the taxonomic basis for the lower '*Euskelosaurus*' Range Zone has been questioned (e.g., Yates, 2003, 2007a; Yates and Kitching, 2003; Yates et al., 2004; McPhee et al., 2017; Viglietti et al., this volume), the validity of the *Massospondylus* Range Zone has been undisputed since its initial proposal (Kitching and Raath, 1984; Smith and Kitching, 1997; Knoll, 2005; Barrett et al., 2019). Using these findings, and new biostratigraphic data collected by McPhee et al. (2017), and during recent work conducted on the Karoo Collections Database, we recommend minor changes to the definition of this biozone. Our revisions make it an assemblage zone, by defining the MAZ as the first appearance of *Massospondylus*

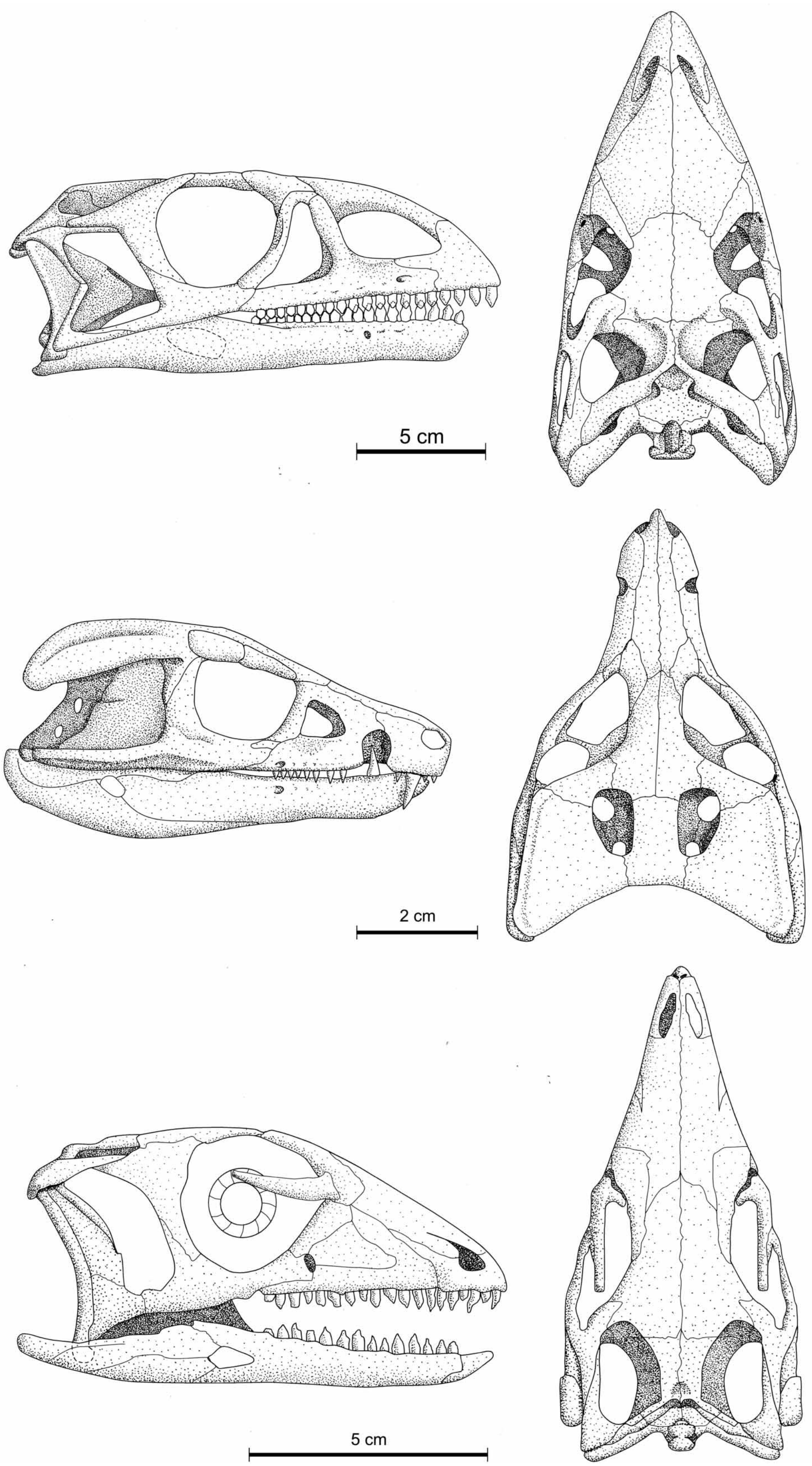

***Figure 1**. Lateral and dorsal skull views of the biozone defining fossils of the* Massospondylus *Assemblage Zone. (Top),* Massospondylus carinatus *(modified after Chapelle and Choiniere, 2018) (Middle),* Protosuchus haughtoni *(Modified after Gow, 2000). (Bottom),* Lesothosaurus diagnosticus *(Knoll et al., 2010).*

carinatus in co-occurrence with two other index taxa: *Lesothosaurus diagnosticus* and *Protosuchus haughtoni*. Diagnostic features for each of these taxa can be found in the following publications: *M. carinatus* (Chapelle and Choiniere, 2018; Barrett et al., 2019); *Lesothosaurus* (Knoll and Battail, 2001; Knoll, 2002a and b, 2008; Knoll et al., 2010; Butler, 2005; Sciscio et al., 2016; Baron et al., 2017); and *Protosuchus* (Busby and Gow, 1984; Gow, 2000).

A subdivision of the *Massospondylus* Range Zone, the *Tritylodon* Acme Zone (TAZ), was also proposed by Kitching and Raath (1984) based on the abundance of *Tritylodon longaevus,* an advanced cynodont, apparently found within a narrow interval of distinctive rubble-weathering matrix-supported nodule conglomerate in the lower uEF on Bramleyshoek farm in the northeastern Free State Province. The TAZ was identified within the MAZ, approximately ~1 to 3 m above a large nodule horizon that Kitching and Raath (1984) considered the boundary of their uppermost middle Elliot Formation. Smith and Kitching (1997) later concluded that the TAZ be retained purely to describe fossil occurrences and that its single intraformationally-derived glaebule and bone conglomerate represented one event of denudation and reworking of uEF palaeosols in the north of the basin, resulting in a concentration of *Tritylodon* fossils that over-represents true abundance. Subsequent regional stratigraphic work in the Clocolan-Ficksburg area (Free State Province – e.g., Moodley, 2015; Bordy et al., 2016) also showed that the TAZ as one laterally persistent abundance zone with one conglomerate layer is questionable, because multiple, laterally restricted carbonate nodule conglomerate layers occur, with or without *Tritylodon*, across the entire MAZ interval in this region (see the Subdivision section for details).

Palaeontology

Description of biozone

An assemblage zone characterised by the co-occurrence of *Massospondylus carinatus*, *Lesothosaurus diagnosticus* and *Protosuchus haughtoni*.

Taphonomic notes on fossil occurrences

Well-preserved fossils, usually found as isolated specimens, occur especially in the fine-grained sedimentary rocks of the uEF, which are often associated with *in situ* carbonate nodules and other pedogenic alteration features (see Geological description, below). These rocks contain specimens of 'protosuchian' crocodylomorphs (e.g., *Protosuchus haughtoni*), eucynodontians (e.g., *Tritylodon longaevus*) and, less commonly, mammaliaforms (e.g., *Diarthrognathus broomi*, *Pachygenelus monus*, *Megazostrodon rudnerae*) in association with abundant dinosaur material (e.g., *Lesothosaurus diagnosticus*, *Megapnosaurus rhodesiensis*, *Massospondylus carinatus*) that range from isolated fragments to complete articulated skeletons. Fine-grained sandstones with variable intraformational rip-up clast content (i.e., facies Sc of Bordy et al., 2004b, 2005, 2016) locally preserve bonebed accumulations of ornithischian dinosaurs such as *Heterodontosaurus tucki* and *Lesothosaurus*. Partial articulation or associated disarticulated elements are the most common modes of skeleton preservation. Skull material is less common than postcranial material, which is the opposite of the fossil preservation trend in the Beaufort Group, likely due to the differences in skull construction between synapsids (firmly-sutured, robust bone) and archosaurs (lightly built and poorly fused). Fossils encased in carbonate nodules are commonly well preserved, whereas others show evidence of distortion and weathering, with "sun-cracked" fractures and haematite coatings (up to ~10 mm in thickness) as described in Kitching and Raath (1984). Carbonate nodule conglomerates, which are diagnostic facies in the uEF, often preserve reworked, isolated vertebrate remains. Rocks in the uEF and Clarens formations are commonly contact metamorphosed by dolerite intrusions, which can alter the properties (e.g., colour, texture, competence) of the rocks and enclosed fossils, and enhance preservation.

List of fossils

Figure 2 delineates ranges of vertebrate genera, which are shown in the range chart as relative position (% of overall stratigraphic height) rather than as meter notation in the generalized and simplified lithological section of the uEF and Clarens Formation. This information on the relative positions is necessary because of the extreme thickness variation of the MAZ across the main Karoo Basin. The taxa listed below are derived from: Owen (1854, 1884); Broom (1904, 1911, 1912); Watson (1913); Haughton (1915, 1924); Van Hoepen (1915); Crompton (1958, 1964); Brink (1959); Crompton and Charig (1962); Fourie (1963); Crompton and Jenkins (1968); Nash (1968); Plumstead (1969); Raath (1969); Ellenberger (1970, 1972); van Eeden and Keyser (1971); Forey and Gardiner (1973); Jubb (1973); Thulborn (1974); Hopson (1975); Kitching (1977); van Dijk (1978); Cooper (1981); Tasch (1984); Kitching and Raath (1984); Gow et al. (1990); Gaffney and Kitching (1994); Sues and Reisz (1995); Warren and Damiani (1999); Clark et al. (2000); Yates and Kitching (2003); Bamford (2004); Bordy and Catuneanu (2002); Clark and Sues (2002); Bordy (2008); Bordy et al. (2009, 2010, 2016); Bristow and Raath (2004); Weishampel et al. (2004); Galton and Upchurch (2004); Knoll (2005); Butler (2005); Raath and Yates (2005); Steyer and Damiani (2005); Butler et al. (2007); Yates (2007a and b); Barrett (2009); Smith et al. (2009); Knoll et al. (2010); Reisz et al. (2010); Yates et al. (2010); McPhee et al. (2015, 2017, 2018); Rubidge et al. (2016); Sciscio et al. (2016, 2017a and b); Abrahams et al. (2017); Baron et al. (2017); Dollman et al. (2017, 2019); Haupt (2018), Chapelle and Choiniere (2018); Chapelle et al. (2019).

There have been several taxonomic and stratigraphical revisions that affect uppermost Stormberg Group vertebrate taxa. *Geranosaurus capensis* (Broom 1911; Weishampel and Witmer, 1990), *Gryponyx africanus* (Broom, 1911, Galton and Upchurch, 2004), *Gyposaurus capensis* (Broom, 1911), *Stormbergia dangershoeki* (Butler, 2005; Baron et al., 2017), *Erythrochampsa longipes* (Broom, 1904; Haughton 1924, Whetstone and Whybrow, 1983), *Clarencia gracilis* (Brink, 1959; Clark et al., 2000), and *Pedeticosaurus leviseuri* (Van Hoepen, 1915; Clark and Sues, 2002), *Likhoelia ellenbergeria* (Ginsberg, 1962; Master, 2019), and *Pattsia likhoelensis* (Lees and Mills, 1983) are no longer considered valid. *Antetonitrus ingenipes* (McPhee et al., 2017) and *Elliotherium kersteni* (Sidor and Hancox, 2006) are now regarded as uEF taxa, rather than lEF taxa (unpublished work and result of Karoo Collections Database research). NMQR 3314 is considered distinct from *Melanorosaurus readi* (McPhee et al., 2017; PMB and JNC in prep.) and is placed in the uEF. Newly described MAZ taxa include: *Pulanesaura eocollum*

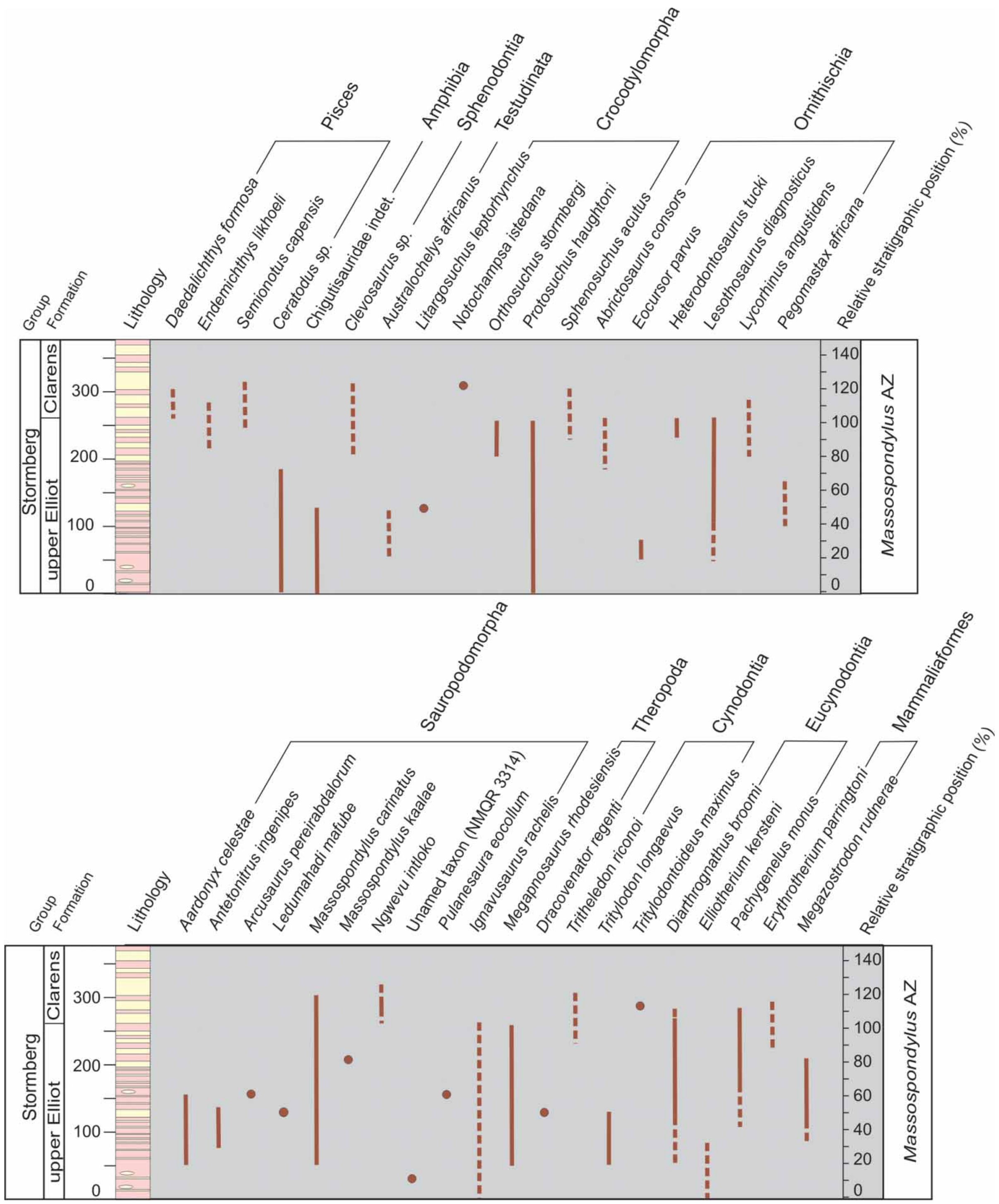

Figure 2. *Stratigraphic section showing the ranges of vertebrate taxa (relative position %) present in the* Massospondylus *Assemblage Zone. The generalized and simplified lithological section is based on the holostratotype of the upper Elliot Formation at Barkly Pass (Eastern Cape Province), and the lectostratotype of the Clarens Formation at Wonderkop (farm Gibraltar 346, Free State Province), and is modified from Bordy and Eriksson (2015), and Bordy and Head (2018), respectively.*

(McPhee et al., 2015), *Ledumahadi mafube* (McPhee et al., 2018), and *Ngwevu intloko* (Chapelle et al., 2019). Note that *Ngwevu* has been provenanced to the lower Clarens Formation as per Gow et al. (1990) rather than the uppermost uEF (Chapelle et al., 2019).

Vertebrates	
Pisces	*Daedalichthys formosa*
	Endemichthys likhoeli
	Semionotus capensis
	Ceratodus sp.
Amphibia	Chigutisauridae indet.
Amniota	
Eureptilia	
Lepidosauromorpha	*Clevosaurus* sp.
Archosauromorpha	*Australochelys africanus*
Pseudosuchia	*Litargosuchus leptorhynchus*
	Notochampsa istedana
	Orthosuchus stormbergi
	Protosuchus haughtoni
	Sphenosuchus acutus
Ornithodira	
Ornithischia	*Abrictosaurus consors*
	Eocursor parvus
	Heterodontosaurus tucki
	Lesothosaurus diagnosticus
	Lycorhinus angustidens
	Pegomastax africana
Sauropodomorpha	*Aardonyx celestae*
	Antetonitrus ingenipes
	Arcusaurus pereirabdalorum
	Ledumahadi mafube
	Massospondylus carinatus
	Massospondylus kaalae
	Ngwevu intloko
	Unnamed taxon (NMQR 3314)
	Pulanesaura eocollum
	Ignavusaurus rachelis
Theropoda	*Megapnosaurus rhodesiensis*
	Dracovenator regenti
Synapsida	
Therapsida	
Cynodontia	*Tritheledon riconoi*
	Tritylodon longaevus
	Tritylodontoideus maximus
Eucynodontia	*Diarthrognathus broomi*
	Elliotherium kersteni
	Pachygenelus monus
Mammaliaformes	*Erythrotherium parringtoni*
	Megazostrodon rudnerae
Invertebrates	
Insecta	
Apodidae	*Lepidurus stormbergensis*
Coleoptera	*Coleopterus* sp.
Plectoptera	*Phthartus africanus*
Orthoptera	*Striatotegmen africanum*
Gryllidae	*Archaegryllodes stormbergensis*
	Branchipoda ('Choncostraca') indet
	Notostraca indet.
	Ostracoda indet.
	Malacostraca indet.
Trace fossils	
Vertebrate	*Ameghinichnus* isp.
	Anomoepus isp.
	Batrachopus isp.
	Episcopopus isp.
	Eubrontes isp.
	Grallator isp.
	Kayentapus isp.
	Moyenisauropus isp.
	Trisauropodiscus isp.
	Burrow casts
Invertebrate	*Arthropodichnus* isp.
	Acropentapodiscus isp.
	Dipodiscus isp.
	Insectichnus isp.
	Naktodemasis isp.
	Homosiroidea meandrica
	Taenidium isp.
	Planolites isp.
	Diplichnites isp.
	Putative termite nests
Plants	
Sphenophytes	*Equisetites* sp.
	Equisetum sp.
	Equisetites nkoakhomoensis
Bennettitaleans	*Otozamites* sp.
Conifers	*Sphenolepidiurn* sp.
	Pinus sp.
Seed ferns	*Dicroidium* sp.
	Phoenicopsis sp.
Wood	*Agathoxylon* sp.
	Podocarpoxylon sp.
	Araucarioxylon arficanum
Pollen and spores	*Lacrimasporonites levis*
	Uvaesporites verrucosus
	Cyathidites minor
Algal mats	*Spirogyra* sp.

Geological description

Thickness

The thickness of the MAZ changes across the main Karoo Basin from ~320 m near Barkly Pass in the south to ~100 m west of Clarens in the north (Bordy et al., 2004; Bordy and Eriksson, 2015; Bordy and Head, 2018). These total thickness values include the combined variable thicknesses of the upper Elliot and Clarens formations. The upper Elliot Formation thins fairly uniformly from ~250 m in the south to <50 m in the north, whereas the Clarens Formation has highly variable thickness ranging randomly from 10 and 300 m within the main Karoo Basin (Bordy and Head, 2018).

Lithology

The MAZ is confined to the uEF and the conformably overlying Clarens Formation. The uEF comprises very fine to fine-grained, lesser medium-grained sandstones, pedogenically altered mudstones (mostly siltstones) and intraformational conglomerates consisting mostly of reworked pedogenic nodules and bone fragments (Bordy et al., 2004b). The latter facies, as well as the clast-rich, massive, silty, very fine-grained sandstone, are diagnostic in the MAZ (e.g., Bordy et al., 2004b: pp. 393, 395, 397; Bordy et al., 2016: pp. 366, 369). The uEF sandstones are tabular, sheet-like bodies with thickness ranges of <1 to 6 m and can extend laterally for several hundreds of metres. The uEF sandstones contain planar stratification (horizontal lamination), ripple cross-lamination and, less commonly, planar cross-bedding. Soft sediment deformation and bioturbation structures are common. In the uppermost uEF, sandstones are slightly coarser-grained and occur as lenticular, channel-shaped bodies that are up to 15 m in thickness, giving the uEF an overall upward-coarsening and upward-thickening character (Bordy et al., 2004b). The uEF mudstones are brick-red, maroon to light pink in colour, and regularly show evidence for pedogenic overprinting (e.g., desiccation cracks, *in situ* carbonate nodules, rootlets, colour mottling, bioturbation structures) in contrast to the lEF mudstones. Laminated mudstones are also present and, in the uppermost uEF, can be rich in organic matter (e.g., Sciscio et al., 2017c; Rampersadh et al., 2018).

The Clarens Formation comprises white, cream or pink, very fine to fine-grained, and less commonly medium-grained, poorly sorted, immature sandstone and silty sandstone beds (Beukes, 1970; Eriksson, 1981; Visser, 1984; Eriksson, 1986; Bordy and Head, 2018). The sandstones are thick- to very thickly bedded, and contain massive, and less commonly, large-scale cross-bedding, ripple marks, desiccation cracks, and clay-pellet conglomerates. Carbonate concretions also occur in the lower part of the formation, where mudstones are more common (e.g., Bordy and Head, 2018). Pre-1980, this unit was known as the 'Cave Sandstone' due to the common occurrence of shallow caves, extensive overhangs atop the weaker red beds of the uEF, and other unusual prominent landforms (Grab, 2015; Bordy and Head, 2018).

Depositional history

Sedimentological evidence indicates that during the Hettangian–Sinemurian the type area of the MAZ was prone to flash floods and drying in a low-energy depositional system that was characterized by shallow but wide watercourses, broad floodplains with abundant calcic palaeosols and shallow, mostly ephemeral lakes (Bordy et al., 2004b). During the Pliensbachian, new palaeoenvironments emerged and supported both wet and dry deserts with large, down-wind and eastward migrating sand dunes (e.g., Beukes, 1970; Bordy and Head, 2018).

Boundaries

Lower boundary

The base of the MAZ is defined by the earliest occurrence of *Massospondylus carinatus*, which, currently, does not coincide with the lower boundary of the uEF. The first confidently identified *M. carinatus* with high-precision provenance information occur approximately 20% of the way into the uEF (currently BP/1/7855, BP/5262, and SAM-PK-K1112). Kitching and Raath (1984) described occurrences of *M. carinatus* from the very base of the uEF, but these specimens have poor provenance information. Thus, we consider that the base of the MAZ is within approximately 20% of the stratigraphic height into the uEF and hypothesize that it may extend to the very base of the uEF, pending further investigations. The onset of the MAZ marks a pronounced faunal turnover that might reflect temporal separation between the lEF and the uEF due to an unconformity (Bordy et al., 2004a, b and c), or the effects of the end-Triassic Extinction event (ETE).

Although less fossiliferous than the rest of the uEF, fossils in the lowermost uEF have been documented by Ellenberger (1970) and Kitching and Raath (1984) in South Africa and Lesotho, respectively. Kitching and Raath (1984) also observed an increase in the relative abundance of fossils in the lower uEF, and noted that this interval (their "middle Elliot") is less accessible to collecting due to relatively dense plant cover and scree from the overlying beds.

Upper boundary

The last appearance of *M. carinatus* is currently in the lower 45 m of the Clarens Formation (currently SAM-PK-K1858) and fossil discoveries are sparse above this level. The absence of fossils from higher levels might be due to the difficulty in accessing the formation above this point, which is often exposed in vertical cliffs. Dinosaurs and other vertebrates as well as plants were unquestionably present during the deposition of the entire Clarens Formation as vertebrate tracks and plant fossils are found throughout this unit (e.g., Ellenberger, 1970; Knoll, 2005). In addition, the stratigraphically highest vertebrate fossil in the main Karoo Basin is currently the holotype (and only known specimen) of *Notochampsa istedana* (SAM-PK-004013), which we provenanced to 65 m above the base of the Clarens Formation on Funnystone Farm (Free State Province). Given that biozones are not defined by the last appearances of index taxa, we consider that the upper boundary of the MAZ terminates with the disappearance of all vertebrate fossils. Currently, we only tentatively hypothesize that this boundary is at the top of the Clarens Formation, because the conformably overlying Drakensberg Group has not yet yielded relevant body fossils, although trackways of quadrupedal and bipedal dinosaurs, crocodylomorphs and mammaliaforms were documented from the lower part of this Pliensbachian–Toarcian unit by Ellenberger (1970) and Bordy et al. (2020a). In some locations in central Lesotho, this may extend vertebrate occurrences some 450 m above the base of the volcano-sedimentary succession (Ellenberger, 1970), opening the possibility of either extending the MAZ or creating another assemblage zone should more diagnostic vertebrate material be recovered.

Lateral boundaries

The MAZ has no lateral transitions in the main Karoo Basin, where its outcrop area is between 28 to 31º south and 26 to 28º east as defined by post-Karoo erosion.

Subdivisions

No formal subdivision has been proposed, but Kitching and Raath's (1984) *Massospondylus* Range Zone also contained the *Tritylodon* Acme Zone (TAZ). While the TAZ was implemented to document an interval with abundant remains of *Tritylodon longaevus* (Kitching and Raath, 1984), subsequently Smith and Kitching (1997) regarded it as a taphonomic concentration zone rather than an acme zone of true abundance. Moreover, Smith and Kitching (1997) associated this taphonomic concentration zone with a single regional downwasting of the Elliot land surface in the northern half of the basin. Also found in this interval are fossils of *Massospondylus carinatus*, *Megapnosaurus rhodesiensis* and *Lesothosaurus diagnosticus* and, in single occurrences, specimens of the primitive testudinate *Australochelys africanus* (Gaffney and Kitching, 1994), and the advanced cynodont *Diarthrognathus broomi* (Gow, 1994). Our primary field data and work on the Karoo Collections Database also question the biostratigraphic utility of the TAZ. Firstly, with the exception of a few *Tritylodon* specimens from central Lesotho (e.g., SAM-PK-K00405-408), all other *Tritylodon* are from the northeastern Free State (as originally defined by Kitching and Raath, 1984). Secondly, these fossils cluster in at least two distinct stratigraphic levels and in various sedimentary facies (e.g., conglomerates, pedogenically altered mudstones) in the MAZ. We consider these results to be *prima facie* evidence that *Tritylodon* fossils in the MAZ are currently regionally restricted to the northern half of the basin but stratigraphically recurring, rather than confined to a discrete stratigraphic level, a view in line with the work of others (e.g., Gow, 1994; Bordy et al., 2004c, 2016; Moodley, 2016). Therefore, we do not consider the TAZ as a temporal biostratigraphic marker within the MAZ.

Regional aspects

Geographic distribution

Outcrops within the MAZ occur in the main Karoo Basin in the Eastern Cape, Free State and western Kwa-Zulu Natal provinces in South Africa and in the western half of Lesotho. The best exposures can be seen in and around Clarens, Golden Gate National Park as well as Lady Grey in South Africa, Qacha's Nek, Quthing, and Mohale's Hoek in Lesotho (Figure 3). In addition, rocks containing MAZ fossils also crop out in other Karoo-aged basins in the northern region of South Africa (e.g., Tuli, Tshipise, Ellisras, Springbok Flats and Lebombo basins: see Bordy and Catuneanu, 2002; Catuneanu et al., 2005; Bordy et al., 2010; Bordy and Head, 2018).

Lateral and vertical variation

The faunal content in the MAZ shows no lateral variation. The host uEF and Clarens formations are also devoid of regional facies changes (Bordy and Head, 2018), although lateral thickness reduction is documented in the uEF from south to north (Bordy et al., 2004a; Bordy and Eriksson, 2015).

Correlation

Global stratigraphic correlation of the MAZ is difficult based on occurrences of vertebrate fossils alone. Most species and genera within the *Massospondylus* Assemblage Zone are basinal endemics. Therefore, correlations with other units in southern Africa, outside of the main Karoo Basin, are based on occurrences of closely-related taxa (Bond, 1973). We regard them as potentially falsifiable either by more detailed taxonomic study or by future geochronological work that could change the temporal relationships of these sedimentary basins. Karoo-aged basin correlations have been made with Namibia (Waterberg Basin; Smith et al., 1993), Botswana (Kalahari Karoo Basin; Bordy et al., 2010), Zambia (Luangwa Basin; Drysdall and Kitching, 1962; Choiniere and Barrett, 2015) and the lower Forest Sandstone in Zimbabwe (Mana Pools and Mid-Zambezi basins; Johnson, 1996; Catuneanu et al., 2005; Viglietti et al., 2018). However, these correlations are based mainly on lithostratigraphical similarities rather than shared index fossils. For example, *Massospondylus carinatus* does not occur outside of southern Africa, and whereas it may be a useful index fossil for the regional correlation of Karoo-aged basins (e.g., between the main Karoo Basin and the Tuli and Mid-Zambezi Basins of Zimbabwe), it still remains to be verified whether the material from these other non-South African basins is definitely referable to this species (Cooper, 1981; Rogers et al., 2004; Barrett et al., 2019).

Potential global correlations have been proposed based on occurrences of '*Massospondylus*-like' taxa or members of Massospondylidae from Lower Jurassic deposits in Argentina (e.g., *Adeopapposaurus mognai*, *Leyesaurus marayensis*; Martinéz, 2009; Apaldetti et al., 2011), China (*Lufengosaurus hueni*; *Xingxiulong chengi* Lower Lufeng Formation; Hettangian–Sinemurian; Xing et al., 2014; Wang et al., 2017), North America (*Sarahsaurus aurifontanalis*; Kayenta Formation; Sinemurian–Pliensbachian; Attridge et al., 1985; Rowe et al., 2011) and Antarctica (*Glacialisaurus hammeri*; Hanson Formation; Early Jurassic; Smith and Pol, 2007). *Protosuchus haughtoni* is potentially more useful for correlation as this genus has been reported from the Moenave Formation (Hettangian) of Arizona, USA (Clark and Fastovsky, 1986), the McCoy Brook Formation (Hettangian) of Nova Scotia, Canada (Shubin et al., 1994), and the Przysucha Formation (Hettangian) of Poland (Gierlinksi and Potemska, 1987). *Clevosaurus* sp. also has a wide geographic distribution and is known from the Norian of Brazil (e.g., Hsiou et al., 2015, 2019), the Rhaetian of Luxembourg and Belgium (e.g., Godefroit and Sigogneau-Russell, 1995), the Rhaetian–Hettangian of the United Kingdom (e.g., Fraser, 1988; Evans and Kermack, 1994), the McCoy Brook Formation (Hettangian) of Nova Scotia, Canada (Shubin et al., 1994) and the Lower Lufeng Formation (Hettangian–Sinemurian) of China (Luo and Wu, 1994).

Age

On the basis of the age of the overlying Drakensberg Group, the MAZ has been estimated to range in age between the Hettangian–Pliensbachian: Hettangian–Sinemurian for the uEF and Sinemurian-Pliensbachian for the Clarens Formation (e.g., Kitching and Raath, 1984; Olsen and Galton, 1984; Smith and Kitching, 1997; Lucas and Hancox, 2001; Knoll, 2005; Bordy and Head, 2018). To some degree, these age assessments were also centered on a small number of faunal correlations with other Lower Jurassic strata around the world, and to a lesser extent on magnetostratigraphic evidence from the uEF, which allows for correlations with the Newark-Hartford astronomically tuned geomagnetic polarity timescale, the Moenave Formation of the Glen Canyon Group (USA) and the St Audrie's Bay/East Quantoxhead composite of the United Kingdom (Sciscio et al., 2017a). Nevertheless, recent geochronological assessment for the maximum depositional age of the upper Stormberg Group confirms a Hettangian–Pliensbachian age for the MAZ, by assigning a Hettangian-Sinemurian age for the uEF and a Pliensbachian age for the Clarens Formation (Bordy et al., 2020b).

Based on these new age assessments, time-equivalent stratigraphic units of the MAZ (though usually lacking shared index taxa) could include: McCoy Brook Formation and Newark Basin, Canada (Fedak et al., 2015); Portland Formation, Hartford Rift Basin (Hubert et al., 1992) and the Moenave and Kayenta formations in the Colorado Plateau (Suarez et al., 2017), USA; Trossingen Formation, Germany (Rhaeto-Liassic); La Boca Formation (Huizachal Canyon), Mexico; Upper Evergreen Formation, Australia; Upper Maleri (Pranhita-Godavari Basin) and Upper Dharamaram formations (Pranhita-Godavari Valley), India; and the Victoria and Ferrar Groups (Hanson Formation) of Antarctica (Rubidge, 2005; Smith et al., 2007, 2012; Bomfleur et al., 2011; Sciscio et al., 2017a).

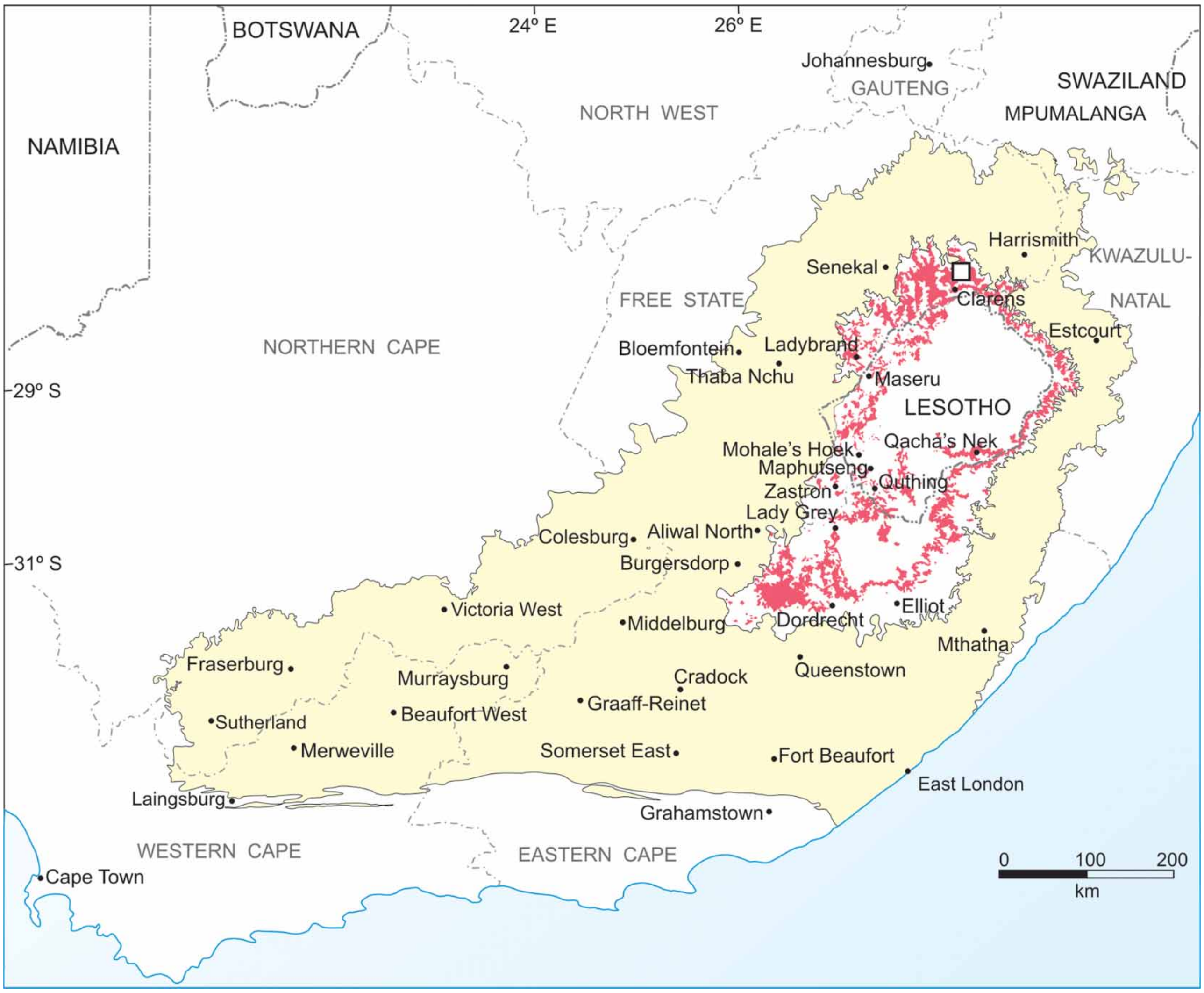

Figure 3. *Distribution map of the* Massospondylus *Assemblage Zone (MAZ) within South Africa and Lesotho with position of the type locality for the MAZ indicated with open square. Light yellow shading=Beaufort Group, white area within the yellow shading =Stormberg and Drakensberg groups.*

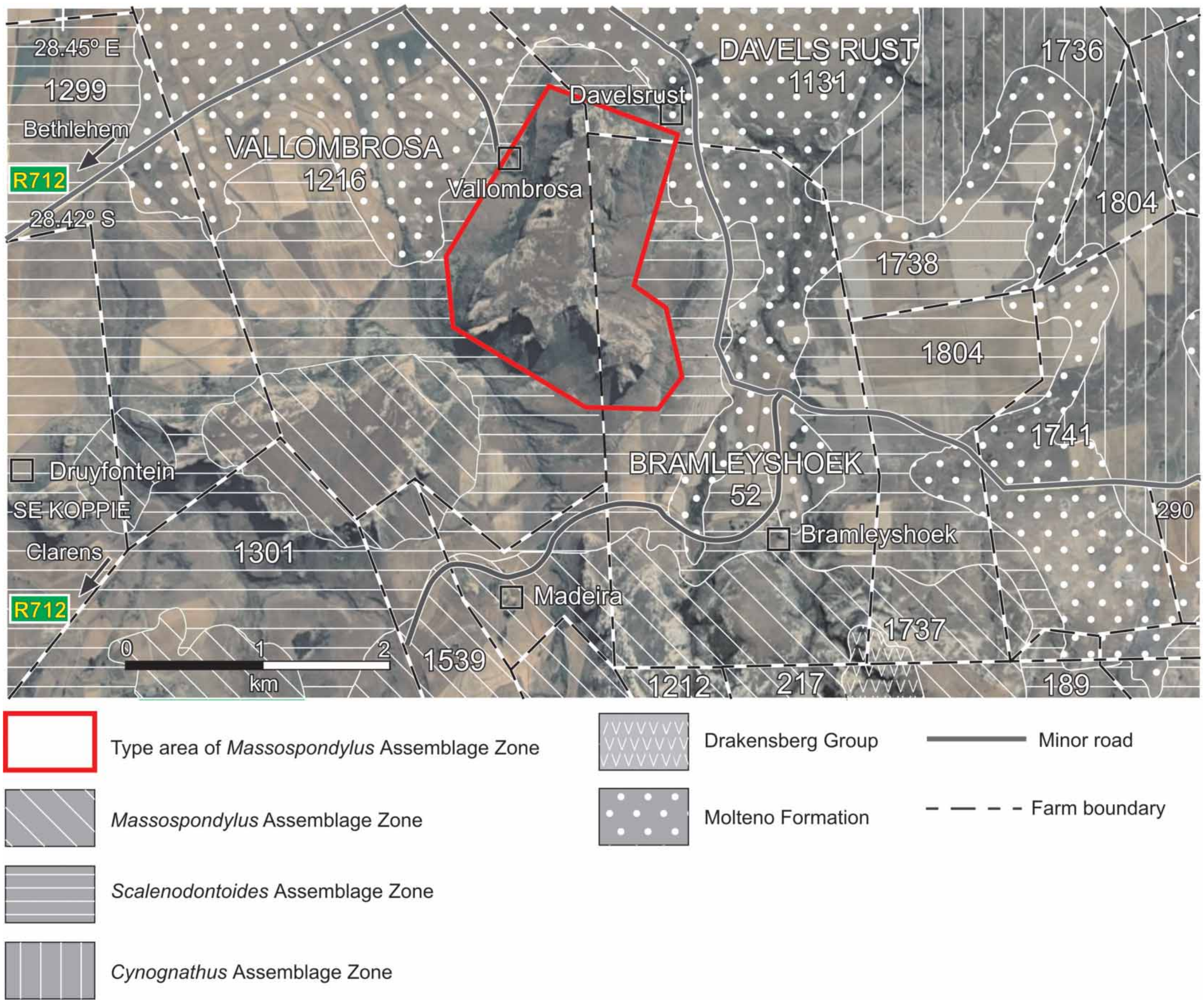

Figure 4. *Type locality of the* Massospondylus *Assemblage Zone on farm Bramleyshoek 52, in the Free State Province, South Africa.*

Type locality

The MAZ type locality is on the farm Bramleyshoek 52 (-28.428780S, 28.507664E), near Clarens, northeastern Free State Province (Figure 4). The holostratotype of the uEF is in the Barkly Pass (Eastern Cape Province, -31.256389S, 27.829167E; see Bordy and Eriksson, 2015), whereas the lectostratotype of the Clarens Formation is on Wonderkop (farm Gibraltar 346, Free State Province, -28.671972S, 27.698822E; Bordy and Head, 2018).

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