Introduction to the tetrapod biozonation of the Karoo Supergroup

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Introduction

The main Karoo Basin of South Africa contains the most abundant, diverse, and time expansive record of terrestrial vertebrates around the Palaeozoic-Mesozoic transition. This 10 km thick sedimentary succession accumulated in a large intracratonic, retro-arc, foreland basin (Johnson 1991; Catuneanu et al. 2005) in front of the rising Cape Fold Belt portion of the Gondwanide Mountain range that fringed the southern margin of Gondwana. Today, rocks of the Karoo Supergroup have a spatial distribution of some 300 000 km^2 (Smith 1990), which is more than one-half the land surface of South Africa. They were deposited under environments ranging from glacial through intracontinental shallow marine, fluvio-lacustrine, fluvial, and aeolian providing an almost continuous 110-My record of continental sedimentation from the Late Carboniferous (300 Ma) to the Early Jurassic (190 Ma).

Abundant plant and animal fossils occur in most rock units of the Karoo Supergroup, providing insights into continental biodiversity from the Guadalupian to the Early Jurassic. This record has been crucial to studies of the late Guadalupian, end-Permian, and end-Triassic mass extinction events. The temporal framework for the Karoo record comprises tetrapod assemblage zones, representing associations of tetrapod (mostly therapsid) genera.

Although early geologists in South Africa used reptilian fossils to identify what would become the Beaufort Group (e.g. Bain 1845), biozones based on an assemblage of tetrapod forms was first suggested by Seeley (1892). This concept was expanded by Broom (1906a, 1906b, 1907, 1909), who proposed a six-fold biostratigraphic zonation for the Beaufort Group based on genera that, with slight modification (Hotton and Kitching 1963), was accepted by most for the next sixty years (Von Huene 1925; Du Toit 1954). Subsequent collecting in the Karoo Basin allowed for further revision of the Beaufort biostratigraphy (Kitching 1970, 1977, Keyser and Smith 1979; Keyser 1979; SACS 1980) and included the Elliot and Clarens formations of the upper Stormberg Group (Kitching and Raath 1984). In 1995, BSR edited a multi-authoured volume commissioned by the South African Commission for Stratigraphy that formalised the Beaufort Group biozones as assemblage zones defined by the co-occurrence of three or more index taxa, but for simplicity named after only one (Rubidge 1995).

Recent research has demonstrated the importance of Karoo fossils for global stratigraphic correlation and for the conceptualization of basin development models (e.g., Catuneanu, Hancox, and Rubidge 1998; Hancox 1998; Neveling 2002; Rubidge 2005). The discovery of datable ash beds that can be linked to biozone-defining fossils has considerably enhanced research possibilities by providing high-resolution radiometric ages for the Permian biozones (Rubidge et al. 2013; Day et al. 2015; Gastaldo et al. 2015, 2020), and thus opening up a way to ascertain rates of evolution in fossil tetrapod lineages (Roopnarine et al. 2017) , as well as the timing and duration of extinction events (e.g. Botha et al. 2020). The recent development of a geographic information system-based database of all the Karoo fossil tetrapods housed in South African national collections has facilitated research on tetrapod biodiversity and biogeographic changes during the Permian and Triassic (Nicolas 2007; Nicolas and Rubidge 2009).

This volume is an updated, refined, and extended version of Rubidge (1995), known to many as the 'purple book', and incorporates findings from the vast amount of new data collected over the past 25 years. This volume expands on its predecessor in that it presents, for the first time, a formal biozonation scheme for the Stormberg Group. Thus, the Beaufort and Stormberg groups can now be divided into nine tetrapod assemblage zones, many of which can be constrained by radiometric ages (Table 1). We also formalize the subdivision of four assemblage zones into subzones, including the long-established (and utilized) subzones of the Triassic *Cynognathus* Assemblage Zone, as concurrent range zones defined by the co-occurrence of only two tetrapod index taxa. The resulting increase in biostratigraphic resolution should facilitate more precise correlation of these strata with equivalent sequences elsewhere in the world, which in turn will provide more precise temporal constraints on tetrapod evolution.

We also present an updated map showing the geographic distribution of the assemblage zones in outcrop (Figure 1), as well as a composite stratigraphic section showing the ranges of all taxa mentioned in the descriptions of each assemblage zone (Figure 2).

Table 1. Lithostratigraphy, vertebrate biostratigraphy and geochronology of the Beaufort and Stormberg groups (Karoo Supergroup) in the Main Karoo Basin, South Africa. Radiometric age determinations from; (**A**) Duncan et al. (1997), (**B**) Bordy et al. (2020), (**C**) Botha et al. (2020), (**D**) Gastaldo et al. (2015), (**E**) Rubidge et al. (2013), (**F**) Day et al. (2015), (**G**) Gastaldo et al. (2020). Dates prefaced by < are maximum depositional ages based on detrital zircon analyses. Wavy lines represent unconformities. Gp=Group, Subgp=Subgroup, Fm=Formation, M=Member.

Age	Gp		West of 24° E		East of 24° E		Free State / KwaZulu-Natal		Vertebrate Assemblage Zones	Vertebrate Subzones	Radiometric dates
JURASSIC					Drakensberg Gp		Drakensberg Gp				183.0 Ma (A)
JURASSIC	STORMBERG				Clarens Fm		Clarens Fm		*Massospondylus*		<187.5 Ma (B); <191.9 Ma (B)
JURASSIC	STORMBERG				upper Elliot Fm		upper Elliot Fm		*Massospondylus*		<199.9 Ma (B)
TRIASSIC	STORMBERG				lower Elliot Fm		lower Elliot Fm		*Scalenodontoides*		<204 Ma (B); <219 Ma (B)
TRIASSIC	STORMBERG				Molteno Fm		Molteno Fm				
TRIASSIC	BEAUFORT	Tarkastad Subgp			Burgersdorp Fm		Driekoppen Fm		*Cynognathus*	*Cricodon-Ufudocyclops*	
TRIASSIC	BEAUFORT	Tarkastad Subgp			Burgersdorp Fm		Driekoppen Fm		*Cynognathus*	*Trirachodon-Kannemeyeria*	
TRIASSIC	BEAUFORT	Tarkastad Subgp			Burgersdorp Fm		Driekoppen Fm		*Cynognathus*	*Langbergia-Gargainia*	
TRIASSIC	BEAUFORT	Tarkastad Subgp			Katberg Fm		Verkykerskop Fm		*Lystrosaurus declivis*		252.24 Ma (G)
TRIASSIC	BEAUFORT	Adelaide Subgp			Balfour Fm	Palingkloof M.	Verkykerskop Fm		*Lystrosaurus declivis*		251.7 Ma (C)
PERMIAN	BEAUFORT	Adelaide Subgp			Balfour Fm	Elandsberg M.	Normandien Fm	Harrismith M.	*Daptocephalus*	*Lystrosaurus maccaigi-Moschorhinus*	253.02 Ma (D)
PERMIAN	BEAUFORT	Adelaide Subgp			Balfour Fm	Elandsberg M.	Normandien Fm	Schoondraai M.	*Daptocephalus*	*Lystrosaurus maccaigi-Moschorhinus*	
PERMIAN	BEAUFORT	Adelaide Subgp			Balfour Fm	Ripplemead M.	Normandien Fm		*Daptocephalus*	*Dicynodon-Theriognathus*	
PERMIAN	BEAUFORT	Adelaide Subgp	Teekloof Fm	Steenkampsvlakte M.	Balfour Fm	Daggaboersnek M.	Normandien Fm	Rooinekke M.	*Daptocephalus*	*Dicynodon-Theriognathus*	
PERMIAN	BEAUFORT	Adelaide Subgp	Teekloof Fm	Steenkampsvlakte M.	Balfour Fm	Daggaboersnek M.	Normandien Fm	Frankfort M.	*Daptocephalus*	*Dicynodon-Theriognathus*	255.2 Ma (E)
PERMIAN	BEAUFORT	Adelaide Subgp	Teekloof Fm	Oukloof M.	Balfour Fm	Oudeberg M.	Volksrust Fm		*Cistecephalus*		256.247 Ma (E)
PERMIAN	BEAUFORT	Adelaide Subgp	Teekloof Fm	Hoedemaker M.	Middleton Fm		Volksrust Fm		*Endothiodon*	*Tropidostoma-Gorgonops*	
PERMIAN	BEAUFORT	Adelaide Subgp	Teekloof Fm	Poortjie M.	Middleton Fm		Volksrust Fm		*Endothiodon*	*Lycosuchus-Eunotosaurus*	259.262 Ma (E)
PERMIAN	BEAUFORT	Adelaide Subgp	Abrahamskraal Fm		Koonap Fm		Volksrust Fm		*Tapinocephalus*	*Diictodon-Styracocephalus*	260.259 Ma (F); 260.407 Ma (E)
PERMIAN	BEAUFORT	Adelaide Subgp	Abrahamskraal Fm		Koonap Fm		Volksrust Fm		*Tapinocephalus*	*Eosimops-Glanosuchus*	261.241 Ma (E)
PERMIAN	BEAUFORT	Adelaide Subgp	Abrahamskraal Fm		Koonap Fm		Volksrust Fm		*Eodicynodon*		
PERMIAN	ECCA		Waterford Fm		Waterford Fm		Volksrust Fm				
PERMIAN	ECCA		Tierberg/Fort Brown		Fort Brown		Volksrust Fm				

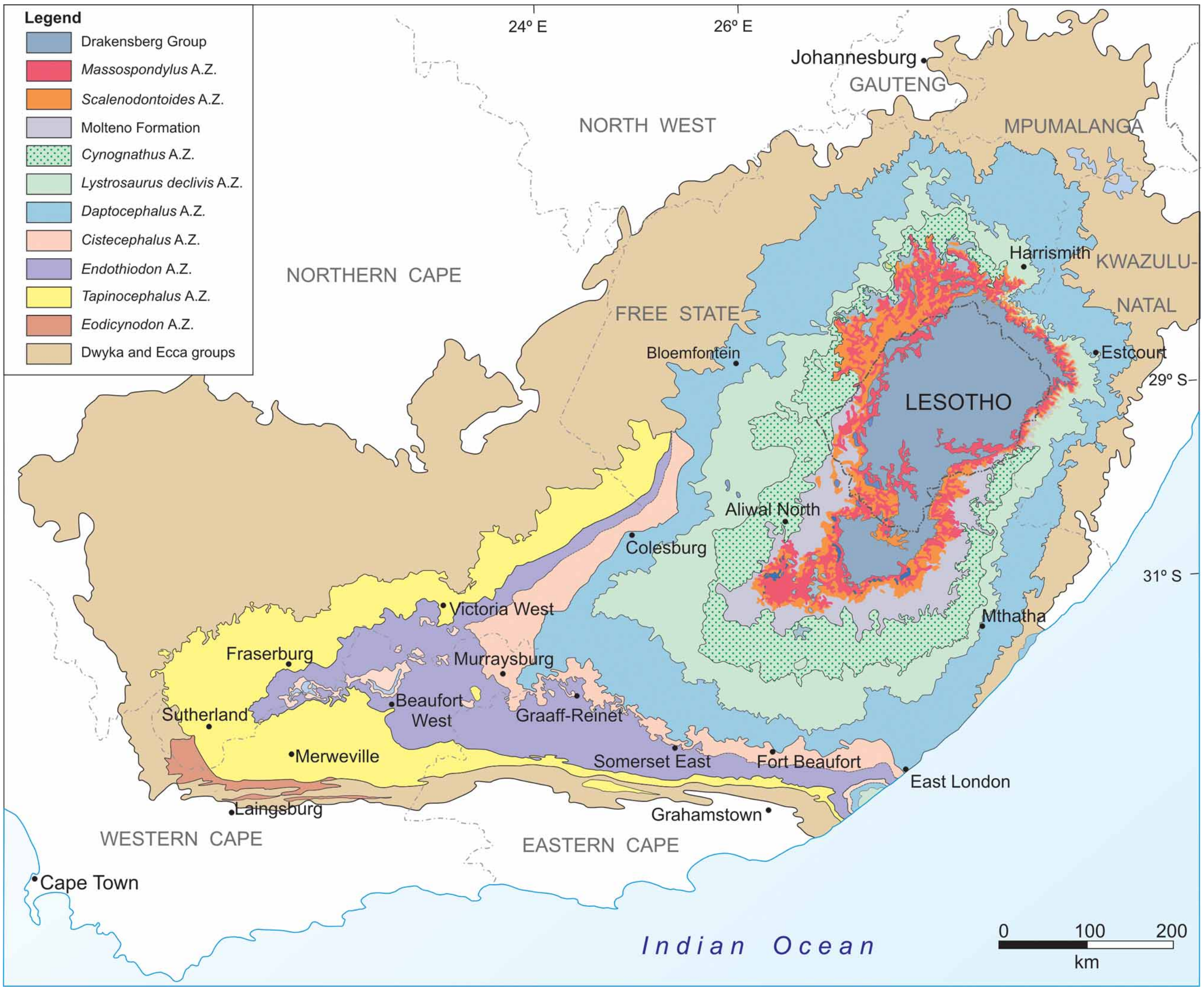

Figure 1. *Distribution of vertebrate biozones in the Main Karoo Basin of South Africa. AZ=Assemblage Zone.*

The biostratigraphic framework we present here is the state of affairs as of 2020; research and field collecting efforts in the Karoo remain active and new data is likely to provide further refinements in the near future, particularly regarding the *Cistecephalus* and *Tapinocephalus* assemblage zones. Some areas remain contentious, particularly surrounding the position of the Permian/Triassic boundary and the age of the *Cynognathus* Assemblage Zone. It nevertheless represents a major step forward.

The following articles in this volume are formal descriptions of the nine Karoo tetrapod biozones presented in ascending chronological order. Each was written as a separate publication by the recognised South African researchers who have done the most recent work on the relevant biozone. The manuscripts were subsequently reviewed independently by national and international experts in the field.

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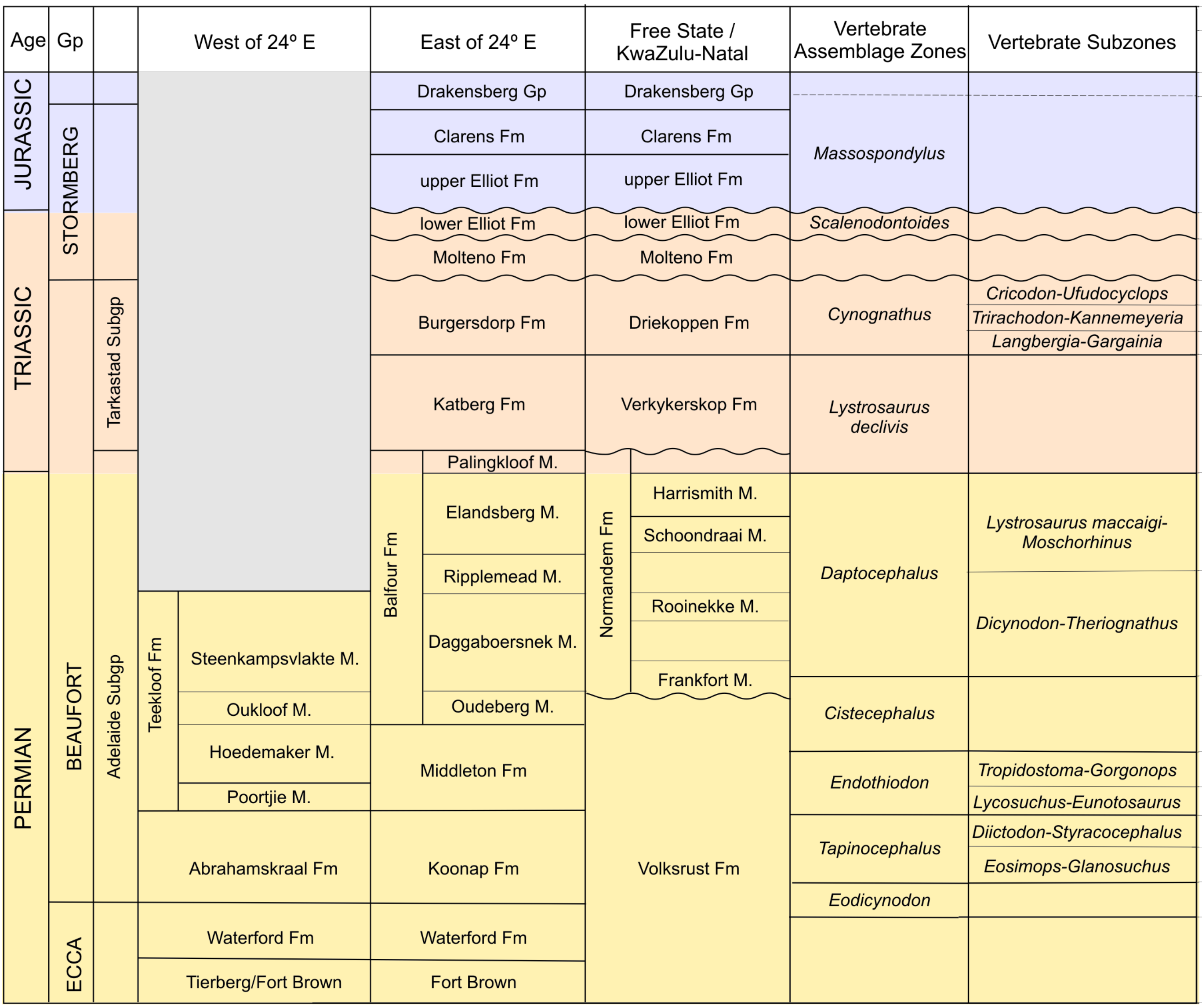


Figure 2. *Vertebrate biozonation range chart for the Main Karoo Basin of South Africa. Solid lines indicate known ranges, dotted lines indicate suspected but not confirmed ranges, single dot represents the stratigraphic position of taxa that have only been recovered from a single bed. Wavy lines indicate unconformities. PLYCSR=Pelycosauria and MAMMFMES=Mammaliaformes. Gp=Group, Subgp=Subgroup, Fm=Formation, M=Member.*

(The range chart is available as a single contiguous figure from the SAJG data repository. Click on the link to access and download. (https://doi.org/10.25131/sajg.123.0009.sup-mat))

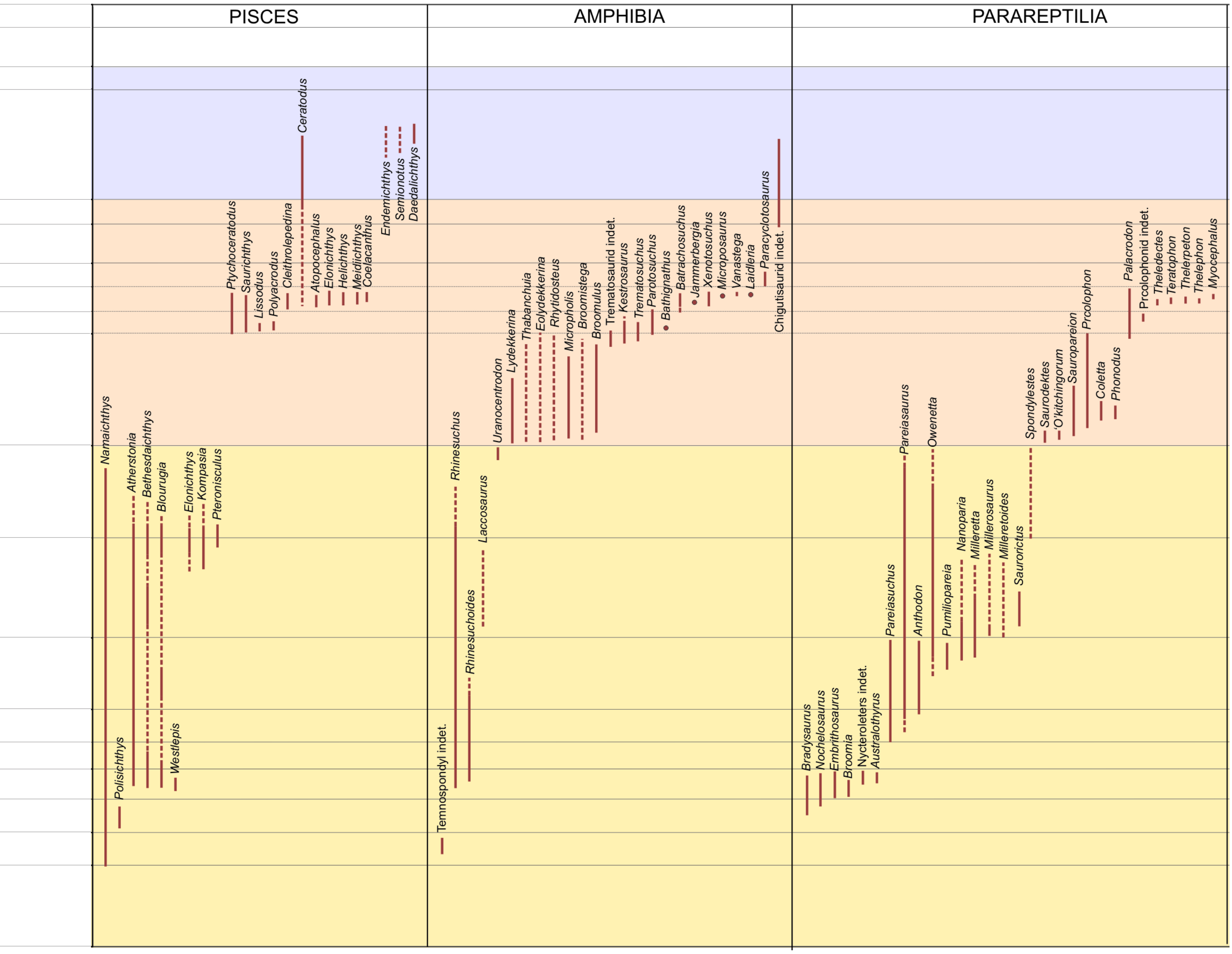
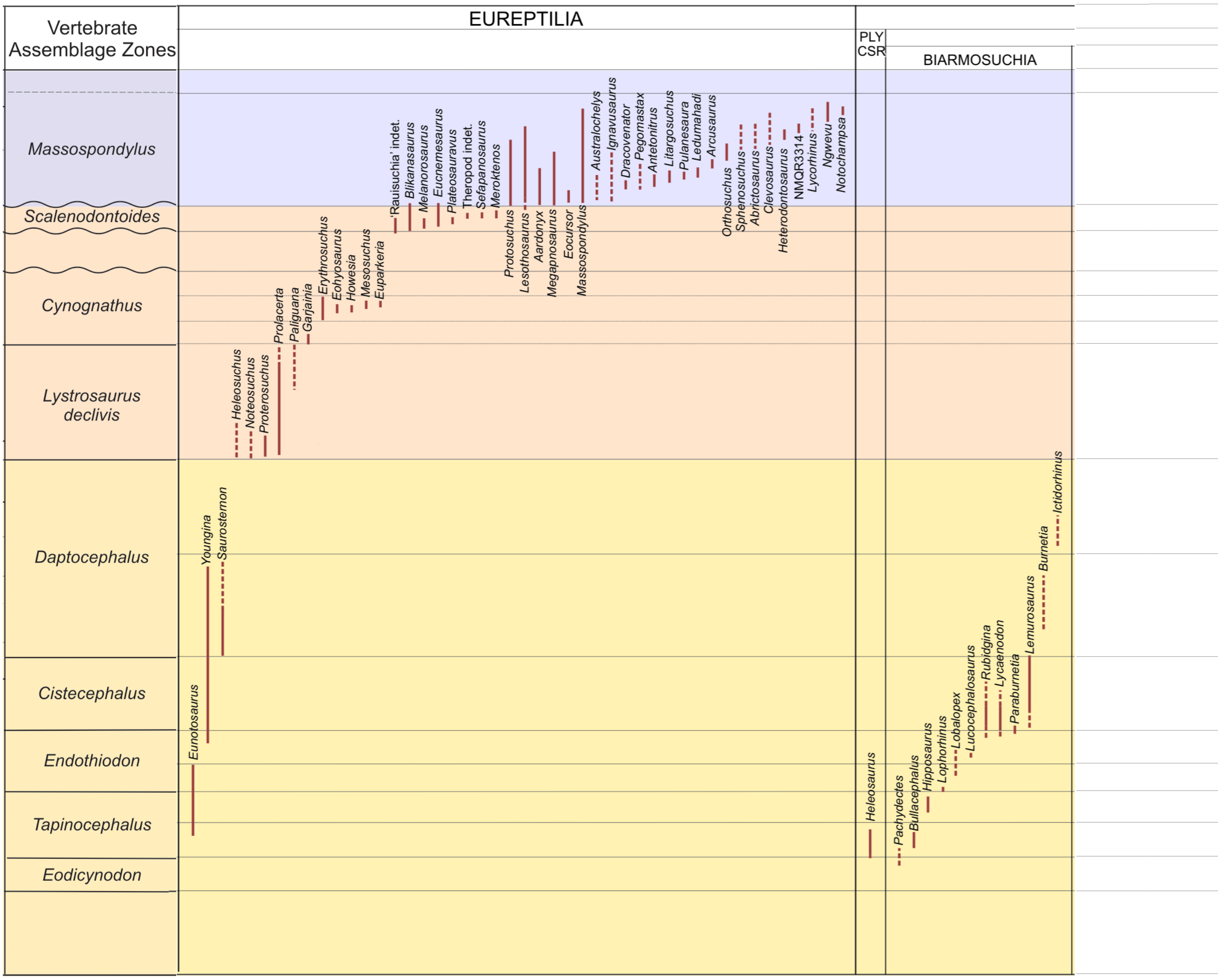


Figure 2. (Continued)



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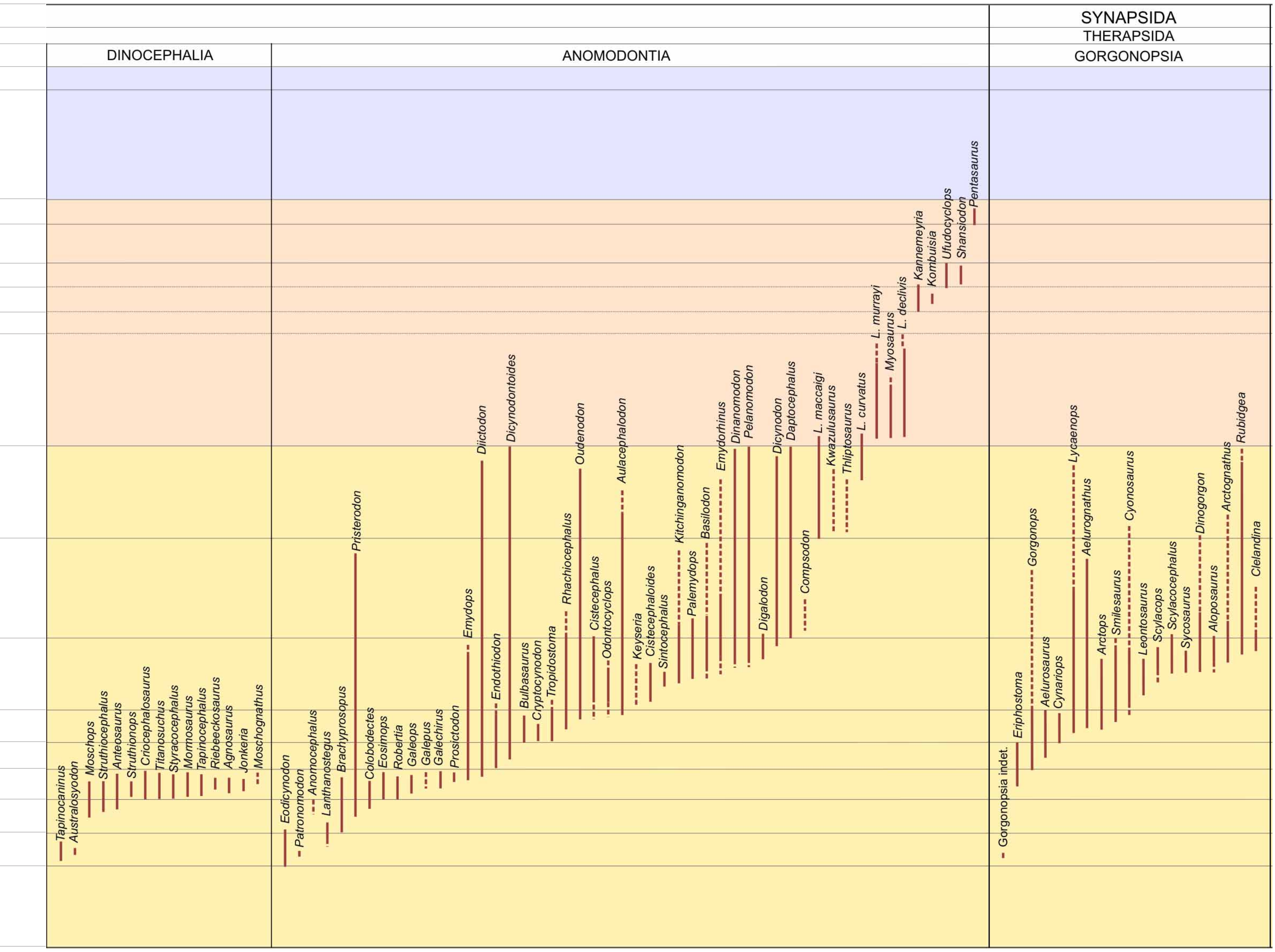

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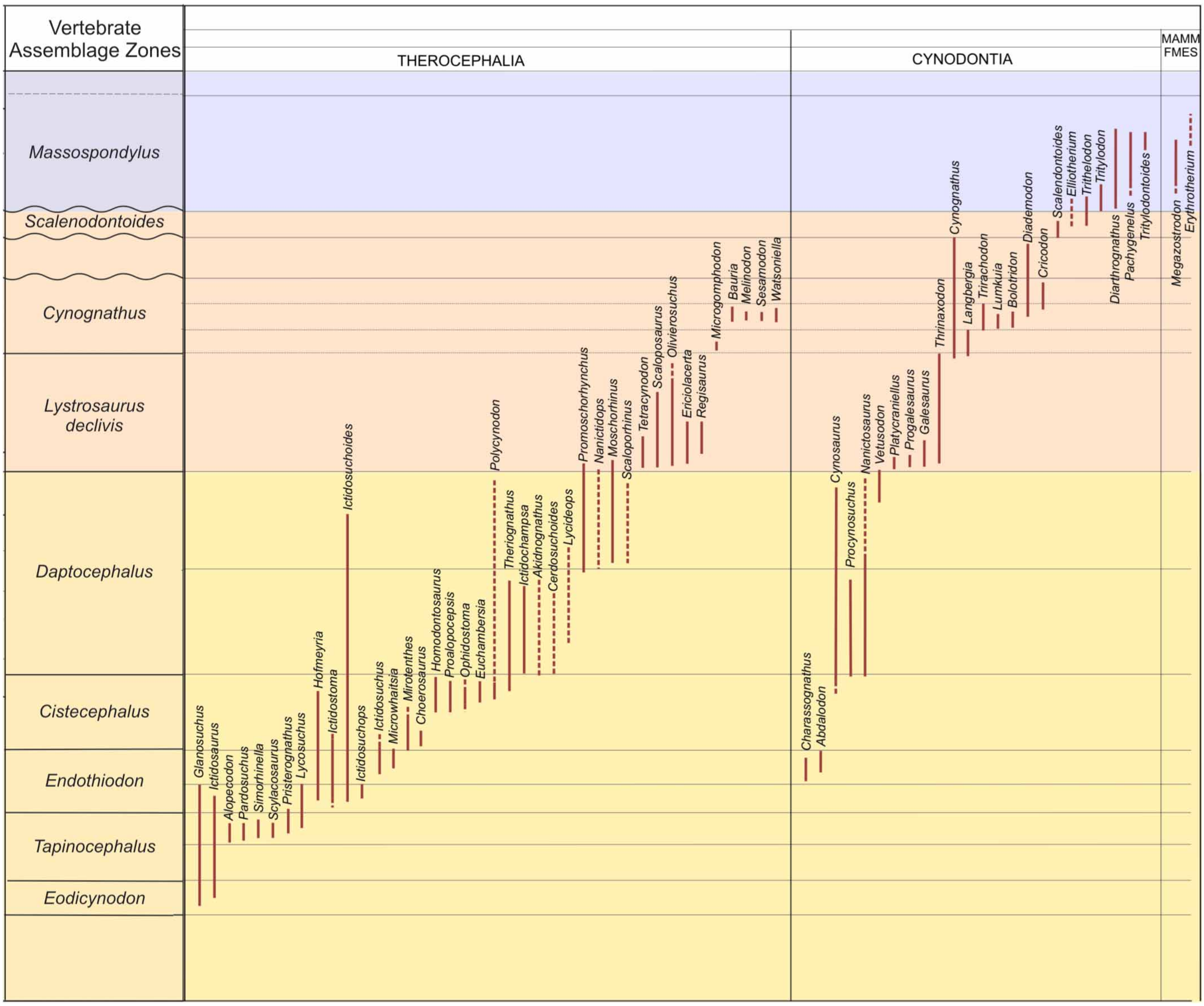

Figure 2. *(Continued)*

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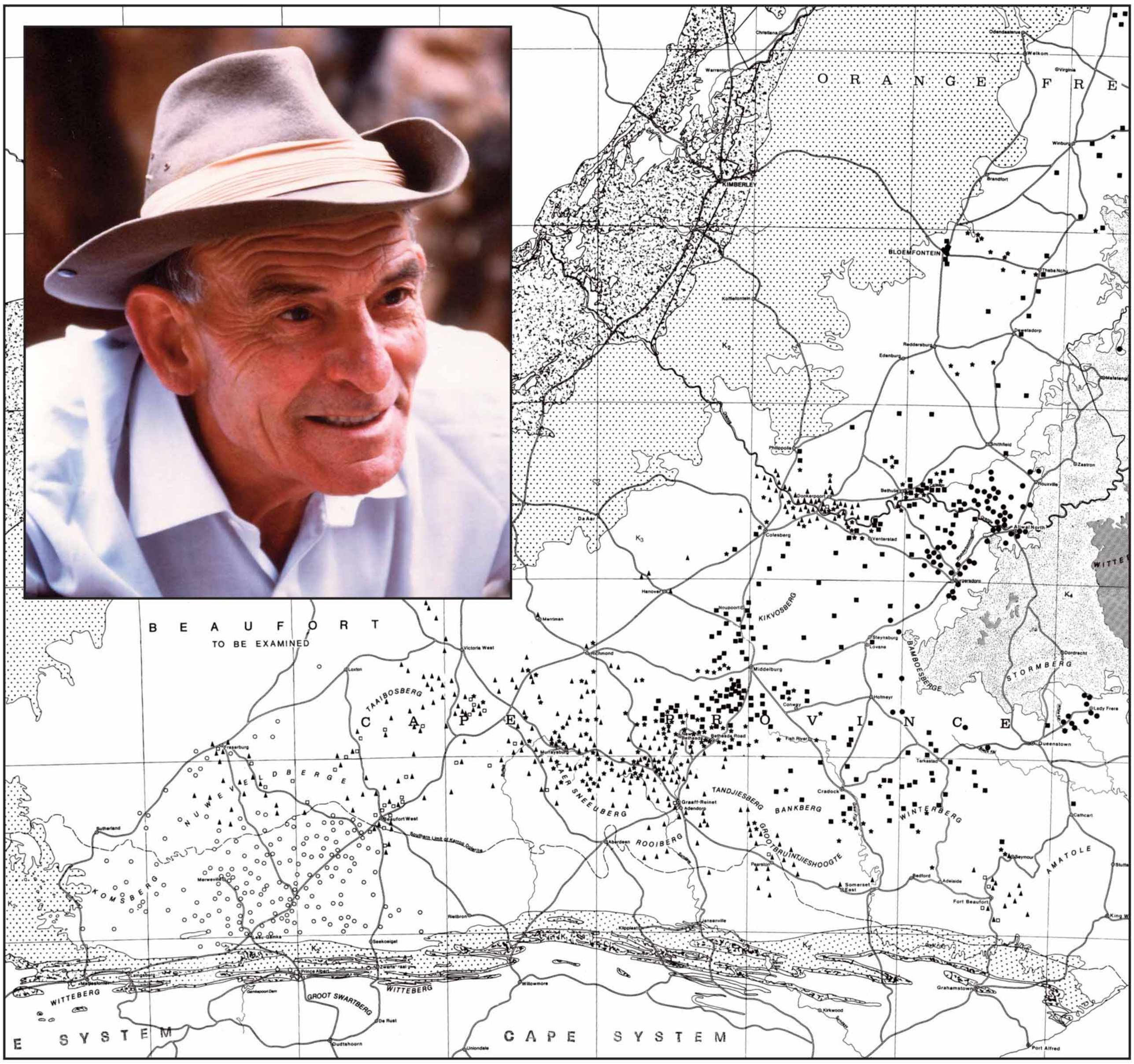

JAMES WILLIAM KITCHING

1922 TO 2003

James Kitching was a world-renowned fossil-finder and the doyen of Karoo palaeontology. Throughout his working career (1945 to 1990) he was employed at the Bernard Price Institute for Palaeontological Research (now Evolutionary Studies Institute) at the University of the Witwatersrand, and has the distinction of having been the first member of staff hired by the institute as a fossil-finder and ending his career as the director. This volume is a tribute to his lifelong interest in Karoo fossils, and his passion for fieldwork. There is no doubt that he laid the foundation for the latest biozonation scheme presented here, and his efforts are gratefully acknowledged by every author.