The pre-eminence of the Karoo Basin in the knowledge of the Permo-Jurassic cynodonts: a historical synthesis and taxonomical quantification

Fernando Abdala[1,2*] §, Christophe Hendrickx[2], Sandra C. Jasinoski[1], Leandro C. Gaetano[1,3] & Jun Liu[4,5]

[1]*Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS, Johannesburg, 2050 South Africa*
[2]*Área de Paleontología, Unidad Ejecutora Lillo, CONICET, Fundación Miguel Lillo, Miguel Lillo 251, Tucumán, Argentina*
[3]*Instituto de Estudios Andinos "Don Pablo Groeber" (IDEAN, UBA-CONICET), C1428EGA Ciudad Autónoma de Buenos Aires, Argentina*
[4]*Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, People's Republic of China*
[5]*College of Earth and Planetary Sciences, University of Chinese Academy of Sciences, Beijing 100049, People's Republic of China*

Received 12 July 2023. Accepted 30 October 2023

The search for the ancestors of mammals is historically connected with the extensive Karoo Basin of South Africa. This is because the Karoo features some of the largest exposures of Permo-Jurassic terrestrial deposits in the world and fossil discoveries were made here early in the history of palaeontology. Among the mammal-like lineages that are well-represented in Karoo fossil assemblages are the cynodonts. Originally conceived as a group exclusively containing fossil taxa, Cynodontia was subsequently redefined to include living mammals, and its Permian and early Mesozoic members are now referred to as non-mammaliaform cynodonts. Here we present a historical account of the research programme on non-mammaliaform cynodonts in the Karoo Basin, which represent the most important record of this group in the world. It covers a time spanning from the first named species in 1859 until the present day, which we arbitrarily divided into three periods: the *Early Period* extending from 1859 until 1932, the *Second Period* from 1933 to 1982, and the *Current Period* from 1983 until now. In the context of the global record of named species, we present quantitative analyses documenting the total number of nominal non-mammaliaform cynodont species from the Karoo (including junior synonyms and homonyms) as well as numerical comparison with taxa currently considered valid. Lastly, we compare the record of non-mammaliaform cynodont species from South Africa with other places in the world, such as Argentina and Brazil, which also have a diverse record of this group.

Keywords: non-mammaliaform cynodonts, Karoo Basin, South Africa, species, taxonomic validation.

INTRODUCTION

The Karoo Basin of South Africa is emblematic for having the richest record globally of the Permo-Triassic transition in terrestrial environments, with its succession of vertebrate-defined assemblage zones (AZs) exemplifying faunal changes through this time (Kemp 1982; Rubidge 2013; Smith *et al*. 2020). Therapsida, the group that includes extant mammals and their stem lineages, is exceptionally well represented in the Karoo faunas. The abundance of therapsid fossil remains in the Karoo has led to their use as index fossils, with all of the AZs of the Beaufort Group (the main Permo-Triassic portion of the Carboniferous-Jurassic Karoo Supergroup) being named after characteristic therapsid taxa (Hancox & Rubidge 1997).

From the first discoveries of therapsids in the Karoo, it was evident that some fossil forms particularly resembled mammals, as the earliest names for these fossils clearly indicate. Cynodontia, coined in 1861 by the famous English palaeontologist Richard Owen (1804–1892), literally translates as 'dog teeth' from the ancient Greek, and the first described Triassic cynodont from South Africa, *Galesaurus* Owen, 1859 (Fig. 1A), means 'weasel lizard'. Owen (1860) discussed the dual condition of a mammal-like dentition and some cranial characters interpreted to be similar to crocodilians. The connection of these fossil forms with mammals, supported by Owen, Osborn, and Broom (the latter two in an explicitly evolutionary context), was firmly established by the beginning of the 20th century (Gregory 1910). For nearly 70 years after the discovery of *Galesaurus*, the fossil record of cynodonts (and therapsids generally) was mostly restricted to the Karoo Basin. This historical primacy in the collection of fossils, as well as the arid conditions and extensive outcrop of the Karoo, resulted in South Africa becoming the primary source of knowledge for this lineage, and it remains important and relevant to cynodont palaeontology today.

In this contribution, we present a succinct yet well-

*Author for correspondence. E-mail: nestor.abdala@wits.ac.za

Palaeontologia africana **56**: 213–227 — ISSN 2410-4418 [Palaeontol. afr.] Online only
Permanently archived on the15th of December at the University of the Witwatersrand, Johannesburg, South Africa
The article is permanently archived at: https://hdl.handle.net/10539/37136

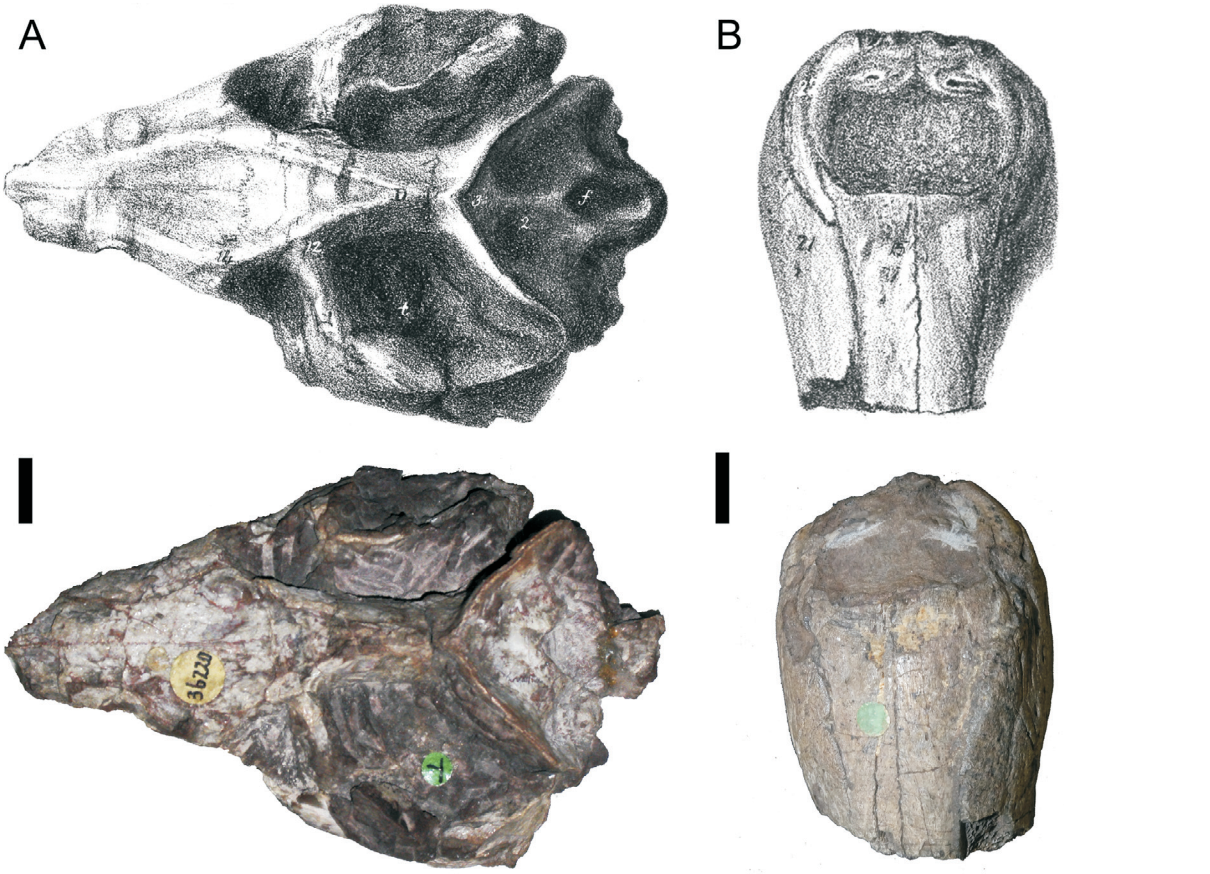

Figure 1. The first described non-mammaliaform cynodonts from the Karoo Basin. **A**, Holotype of *Galesaurus planiceps* in dorsal view, original illustration of Owen (1859) above and photograph of the specimen below. **B**, Holotype of *Cynochampsa laniarius* in dorsal view, original illustration of Owen (1859) above and photograph of the specimen below. Scale bars equal 1 cm.

sourced historical account of the development of the knowledge of non-mammaliaform cynodonts (henceforth abbreviated nmc) from the South African Karoo Basin. This study is complemented by a quantitative analysis of the Permo-Jurassic record of nmc from the Karoo as well as a brief comparison with the record of this group in other parts of the world. We also highlight some early discussions concerning the possible mammalian identity of Triassic remains and how the meanings of the terms Mammalia and Cynodontia shifted during the 1980s.

HISTORICAL REVIEW ON THE STUDY OF NON-MAMMALIAFORM CYNODONTS FROM SOUTH AFRICA

Three arbitrary periods, divided by the publications of two influential books on therapsids, are recognized in this historical review. The *Early Period* (a range of 73 years) spans from 1859, the year of the first published record of a nmc from the Karoo Basin, to 1932, the year of the publication of Broom's *The Mammal-like Reptiles of South Africa and the Origin of Mammals*. The *Second Period* (a range of 49 years) spans from 1933 to 1982, the year of the publication of Kemp's *Mammal-like Reptiles and the Origin of Mammals*. The *Current Period* spans from 1983 to the present day, and at the time of writing (2023) encompasses 40 years.

The Early Period (1859–1932)

> *The most interesting peculiarity in the skull is the well-marked definition from the other teeth, by a contrasted superiority of size, of an upper and lower canine tooth on each side, having the same position in the skull and relative position to each other as in the carnivorous mammals. In no other Saurian are incisors so divided from molars by a single canine; in none is such definition of the three kinds of teeth so plain and unequivocal.*
> Passage referring to *Galesaurus planiceps* from 'On Some Reptilian Fossils from South Africa' by Richard Owen (1860, p. 59).

The history of discoveries leading to the recognition of pre-Tertiary mammal-like forms started in 1764, when Christopher Sykes (1749–1801) obtained a lower jaw from the Jurassic Stonesfield Slate in Oxfordshire, England (Simpson 1928; Kermack & Kermack 1984). A few decades later, this and other specimens were identified as 'mammals' by William Buckland (1784–1856) when describing *Megalosaurus* (Buckland, 1824), and later referred to the triconodont mammaliaform taxa *Amphilestes* and *Phascolotherium* (Owen 1838, 1871; Osborn 1888). The report of 'mammals' in the Mesozoic Era generated heated debate (for summary, see Owen 1846, 1871; Goodrich 1894; Gregory 1910; Simpson 1928). The first report of a 'mammal' fossil now considered to be a non-mammaliaform cynodont was that of the tritylodontid *Stereognathus ooliticus*, also from the Stonesfield Slate (Charlesworth 1855; Panciroli *et al*. 2017). Only four years later, Owen (1859, 1860; Fig. 2) published the first Karoo cynodonts: *Galesaurus planiceps* (which is still considered valid) and *Cynochampsa laniarius* (a suppressed name synonymous with *Diademodon tetragonus*; ICZN 1985) (Fig. 1A,B). These specimens, housed in the Natural

Figure 2. Researchers who have worked on Karoo non-mammaliaform cynodonts. In all cases they are named from left to right. **First row**: Richard Owen; Harry Govier Seeley; Robert Broom; Ferdinand Broili; Joachim Schröder; Sidney Henry Haughton; **second row**: David Meredith Seares Watson; Francis Rex Parrington; Thomas Stainforth Kemp and Alfred Walter Crompton (students of F.R. Parrington); D.M.S. Watson and Alfred Sherwood Romer; James William Kitching in Antarctica; **third row**: Adrian Smuts Brink (student of D.M.S. Watson); Christiane Hélène Mendrez-Carroll; Frederick Edward Grine; Chris E. Gow; Bernard Battail; Steve Fourie; Roger Malcom Harris Smith; **fourth row**: Jun Liu, T.S. Kemp and James Allen Hopson; field trip photograph in the farm Renostervallei, Fraserburg, South Africa in February 2015 (researchers who work more intensively with non-mammaliaform cynodonts are indicated in bold): Sifelani Jirah, William Frederick de Klerk, **Leandro Carlos Gaetano**, Pia Viglietti, Michael Oliver Day, **Nestor Fernando Abdala**, Marc van den Brandt, Frank Schie, Armstrong Koso and **Julien Benoit**; Christian Alfred Sidor; Christian Farrell Kammerer, Adam Keith Huttenlocker and Bruce Sidney Rubidge; **fifth row**: Jennifer Botha and Johan Neveling; Vincent Fernandez; Luke Allan Norton; Sandra Christine Jasinoski, Anusuya Chinsamy-Turan; Christophe Hendrickx.

History Museum in London, were donated by the then-Governor of the Cape Colony, George Grey (1812–1898), together with most of the Karoo material collected by the Scottish geologist and road engineer Andrew Geddes Bain (1797–1864), a foundational fossil hunter in the history of South African palaeontology (Broom 1932; Dubow 2004). These Karoo records represented the only fossils of their kind known from southern Pangaea at the time, and established the paramount importance of South Africa in the search for 'mammal-like' vertebrate remains.

Another early nmc described by Owen, *Tritylodon longaevus*, generated heated debate lasting for decades. The type specimen of *Tritylodon* consists of a partial snout with a clear differentiation of incisors separated by a long diastema from multituberculated postcanines, resembling the dentitions of some rodents and marsupials (Owen 1884). This South African record and that of *Microlestes* (currently the haramiyid *Thomasia*) in Germany (Plieninger 1847) were interpreted as Triassic mammals by Owen (1884), although a post-Triassic age was also considered possible by William Thomas Blanford (1832–1905) in the discussion following Owen's presentation (p. 152), which has since proven to be the case for the levels of the upper Elliot Formation where *Tritylodon* is found (Bordy *et al*. 2020). Seeley (1894a) argued that *T. longaevus* was intermediate between theriodont 'reptiles' (i.e. therapsids) and mammals. Broom (1905, 1910) refuted Seeley's arguments, strongly affirming the mammalian nature of *Tritylodon*, a stance also held by Petronievics (1917) and Simpson (1928), who considered it to be the earliest representative of the extinct mammal lineage Multituberculata. However, the discovery of the new Chinese tritylodontid *Bienotherium* Young, 1940, documented by more complete remains, demonstrated the presence of postdentary bones in the lower jaw, establishing the current taxonomic status of tritylodontids as advanced nmc (Watson 1942).

Early discoveries such as *Galesaurus* and *Tritylodon* clearly stimulated a strong interest in the palaeontological circles of the United Kingdom, resulting in the immediate incursion by palaeontologists of that country in search of Karoo fossils (Dubow 2004). Although Owen described some other Karoo cynodont species (Owen 1876), he relied on material shipped to London and never visited South Africa himself. Instead, it was the contributions by English palaeontologist Harry Govier Seeley (1839–1909) (Fig. 2) in 1894–1895 that produced the first real glimpse of the enormous diversity of cynodonts in the Karoo (e.g. Seeley 1894b, 1895a,b). During these two years, Seeley described no fewer than 13 new cynodont species resulting from an 1889 expedition sponsored by the Royal Society of London (Lydekker 1909). Following his arrival in Cape Town in July of 1889, Seeley did fieldwork in the Karoo from early August to mid-September, visiting an array of important Permian and Triassic localities including Prince Albert, Beaufort West, Burgersdorp, and Aliwal North. The success of the trip was enhanced by the fossil hunting skills of Seeley's guide, the South African road engineer Thomas Charles John Bain (1830–1893), son of A.G. Bain (Broom 1932), which included discovering the holotype of the large carnivorous cynodont *Cynognathus crateronotus*, represented by a beautifully-preserved partial skeleton (Seeley 1895b). Seeley also benefitted from meeting with and examining the findings of other local collectors such as Alfred Brown (1834–1920), William Bisset Berry (1839–1922), and Daniel Rossouw Kannemeyer (1843–1925), which included the first specimens of *Trirachodon* (Seeley 1895a).

The large contribution of Seeley, however, paled in comparison to that of Robert Broom (1866–1951) (Fig. 2). This Scottish-born medical physician, who moved to South Africa in 1897 (Broom 1913; Wyllie 2003; Rubidge 2013), documented and named many taxa of early therapsids and other Permo-Triassic vertebrates from the Karoo, as well as South African Cenozoic mammals (notably including fossil hominids). Between 1903 and 1950, Broom described 38 new species of nmc, leading to a phenomenal increase in the documentation and knowledge of the group. The first named nmc from the Karoo by Robert Broom is *Karoomys browni* Broom, 1903, represented by the tiny partial mandible of a cynodont with a sectorial dentition, whereas his last named nmc is the gomphodont *Sysphinctostoma gracilis* Broom, 1950, now considered to be a junior synonym of *Diademodon tetragonus* (Hopson & Kitching 1972). Thus, Broom worked for almost fifty years describing and erecting new species of nmc, making him by far the most prolific researcher at this task.

Another fundamental figure researching Karoo fossils at this time was the English geologist Sidney Henry Haughton (1888–1982), who moved to work at the South African Museum in Cape Town (now the Iziko South African Museum) in 1911 and worked at several of the country's main palaeontological institutions over the course of his long career (Dunham 1983). Haughton described few new species of nmc (e.g. Haughton 1918, 1924), but made a major contribution to subsequent systematic work as co-author of 'A bibliographic list of Reptilia from the Karroo beds of Africa' in the second volume of *Palaeontologia africana* (Haughton & Brink 1954), which remains one of the main taxonomic compilations of Karoo fossils.

The English vertebrate palaeontologist David Meredith Seares Watson (1886–1973) travelled to South Africa in 1911, visiting fossil collections, meeting with Robert Broom, and spending ten months travelling throughout the Karoo collecting fossils (Parrington & Westoll 1974). Watson only named a few new cynodonts, but his contributions included great advancements in the knowledge of nmc anatomy (e.g. Watson 1920, 1921, 1953) and a major taxonomic review of the group with Alfred Sherwood Romer (1894–1973) (Fig. 2), 'A classification of therapsid reptiles' (Watson & Romer 1956). Watson's field work was followed, in the 1920s and early '30s, by field parties of scientists from the United Kingdom, Germany, and the United States who did extensive collecting in the Karoo (Broom 1935), although they were much more modest than Broom in coining new taxa.

The fossil collections of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany include a large number of Karoo specimens discovered by Joachim Schröder (1891–1976) (Fig. 2) in 1927–1928 and Georg Grossarth (1869–1953) in successive trips in 1931 and 1933 (Reich & Wörheide 2018). These findings were presented in a string of publications by Ferdinand Broili (1874–1946) (Fig. 2) in collaboration with Schröder, with some of them providing detailed descriptions of superbly preserved and well-prepared specimens of nmc (e.g. Broili & Schröder 1934a,b, 1935a,b,c).

In 1930, the English vertebrate palaeontologist Francis Rex Parrington (1905–1981) (Fig. 2) from the Museum of Zoology at Cambridge participated in a field trip led by personnel from the British Museum of Natural History (now the Natural History Museum, London), to the Tendaguru Beds (famous for their fossil-rich Jurassic–Cretaceous outcrops) of Tanganyika Territory (now Tanzania). Following this expedition, Parrington collected fossils in the Karoo for six months (Charig 1990). Three years later, Parrington undertook a six-month expedition to the Ruhuhu Valley in Tanzania, discovering an amazing number of Permian fossils, some of them very similar to those from the Karoo basin, but also Middle Triassic fossils not represented in the South African record (Charig 1990). Afterwards, Parrington went back to South Africa to continue collecting, but he became ill and had to cut the trip short. Like Watson, Parrington named very few new species of nmc, but made important contributions to the literature on cynodont anatomy and evolution (e.g. Parrington 1934, 1936, 1961). Notable among them is Parrington's very first publication (1933), which provided the first detailed description of the abundant South African nmc *Thrinaxodon*.

At the end of the *Early Period*, 65 nmc species had been named worldwide, of which 50 (77%) came from the Karoo. During this period, nmc were also known from a few specimens from the United Kingdom, Germany, the United States, and, towards the end of this period, Russia and Brazil. It took 69 years after the description of the first Karoo fossils before a nmc was published from a second southern Pangaean region, Brazil. Brazil is thus the only place in Gondwana other than South Africa with a species of nmc (*Gomphodontosuchus brasiliensis* Huene, 1928) named during the *Early Period*.

The Second Period (1933–1982)

> *The mammal-like reptiles of South Africa may be safely regarded at the most important fossil animals ever discovered, and their importance lies chiefly in the fact that there is little or no doubt that among them we have the ancestors of the mammals, and the remote ancestors of man.*
>
> Opening passage of *The Mammal-like Reptiles of South Africa and the Origin of Mammals* by Robert Broom (1932).

The beginning of the *Second Period* nearly coincided with an important development: the creation of the Rubidge Collection at Wellwood, Graaff-Reinet in 1934, following the deep interest in fossils developed by the local farmer Sidney Henry Rubidge (1887–1970) (Haughton 1965; Appendix 1). Since 1965, this collection was reorganized, catalogued, and maintained by the efforts of his son Richard Stephen Rubidge (1929–2018) and daughter-in-law Pamela Kate Rubidge (*nee* Nash) (1930–1984). Numerous Karoo fossils, including late Permian cynodonts, were also collected at this time by another local farmer, Cornelius John Mathew Kitching (1898–1943), and both Rubidge and Kitching's finds were eagerly studied by Robert Broom. This productive association initiated a new burst in the discovery and naming of nmc (e.g. Broom 1938a, 1940), including pivotal specimens for understanding the ancestral cynodont condition, such as cranial and postcranial material of the key late Permian nmc *Procynosuchus delaharpeae* (Broom 1937, 1948). This association had another important outcome: the arrival of the Kitching family on the palaeontological scene. C.J. Kitching was helped in the endeavour by his four sons (Haughton 1965), one of whom, James William Kitching (1922–2003) (Fig. 2) was to become perhaps the most important figure in the history of Karoo fossil collection. Due to his great skill (being known as 'the man with X-ray eyes'), he was also recruited to collect fossils in the initial vertebrate palaeontological expeditions to Antarctica in which he discovered the first nmc from that continent (Rubidge 1997; Raath & Rubidge 2005). J.W. Kitching was additionally the inception nucleus of the Bernard Price Institute (BPI) for Palaeontological Research (now known as the Evolutionary Studies Institute), founded in 1945 at the University of the Witwatersrand, Johannesburg (Dunham 1983; Rubidge 1997; Raath & Rubidge 2005). An intensive research collection programme overseen by him at the BPI resulted in one of the richest collections of Permo-Jurassic fossils from the southern hemisphere (Rubidge 1997; Rubidge & Raath 2003).

Broom remained active during part of the *Second Period*, coining no less than 19 new species of nmc, a few of them in collaboration with John Talbot Robinson (1923–2001). Broom was followed by Adrian Smuts Brink (1924–1991) (Fig. 2) as the next major source of new nmc species names. From 1950 to 1965, Brink contributed to erecting ten new Karoo nmc species, some of them in co-authorship with J.W. Kitching. Brink also co-authored an important, aforementioned taxonomic compilation of Karoo fossils (Haughton & Brink 1954). Near the beginning of the *Current Period* he published two extensive volumes of the *Illustrated Bibliographical Catalogue of the Synapsida*, which included information and illustrations of nmc of the world (Brink 1986).

Another influential South African palaeontologist, Lieuwe Dirk Boonstra (1905–1975), did intensive research on Karoo fossils at the South African Museum (Haughton 1974), but only had a single contribution focused on nmc (Boonstra 1935).

Following decades of proliferation in the nominal species of Karoo nmc (considered by some to be excessive 'splitting'), a counter-current 'lumping' movement started in the last years of this second period, particularly during the seventies. At this time, extensive work was done in synonymizing taxa that were represented by either fragmentary material, poorly described specimens, and/or taxa lacking diagnoses, most of which emanated from Broom's research. The contribution 'A revised classification of cynodonts (Reptilia; Therapsida)' by James Allen Hopson (Fig. 2) and J.W. Kitching remains as a classic work of this period. Prior to this work, Hopson and Kitching (1972, p. 71) counted the existence of approximately 125 named nmc species worldwide, a number that they reduced to ~49. These included particularly intense synonymies of the Karoo nmc fauna, such as recognizing 26 nominal cynodont species to be synonymous with *Procynosuchus delaharpeae* and 21 with *Diademodon tetragonus*. This contribution, as well as the work led by the palaeoanthropologist Frederick Edward Grine (Fig. 2) (e.g. Grine *et al*. 1978; Grine & Gow 1978), can be highlighted as major steps in the reduction of nmc species. Other works on nmc taxonomy of the era included a paper on *Procynosuchus* by John Malcolm Anderson (Anderson 1968), before starting his career as a noted South African palaeobotanist, and a few contributions by South African zoologist Jacques Van Heerden on the earliest cynodonts with complete secondary palates, *Thrinaxodon* and *Nanictosaurus* (e.g. Van Heerden 1972, 1976).

Concurrently, there was a strong research programme interested in understanding the biomechanics of mastication and the auditory system, dental replacement, evolution of the braincase, and postcranial functional anatomy. Notable in this programme were both the eldest and youngest students of F.R. Parrington: Alfred Walter Crompton and Thomas Stainforth Kemp (Fig. 2), with additional researchers of importance being Edgar F. Allin, Chris E. Gow (Fig. 2), and Farish Alston Jenkins Jr (1940–2012) (e.g. Allin 1975, 1986; Crompton 1963, 1972; Gow 1986; Jenkins 1971; Kemp 1969, 1980). Christiane Hélène Mendrez-Carroll (1937–1978) (Fig. 2) was the first woman palaeontologist to research nmc from the Karoo Basin. Although most actively involved in the study of therocephalians, this French researcher also contributed to the knowledge of basal South African nmc, with at least four papers on the group (e.g. Mendrez 1972a,b) before her tragic early death (Berta & Turner 2020).

During this period, a total of 99 new species of nmc were erected worldwide, 37 of them (37%) from the Karoo Basin. It is also during this period that nmc were first described from Tanzania, China, Argentina, Zambia, Namibia, and India. The most remarkable were the findings made in Argentina, especially in the 1960s and '70s (Abdala *et al*. 2020, 2022), which brought a completely new outlook to knowledge of nmc from southern Pangaea. Between 1943 and 1980, 21 new species of nmc from Argentina were named, most of them being represented by multiple specimens (Abdala *et al*. 2020). In northern Pangaea, the record of nmc from China started in 1940 with the publication on *Bienotherium*, which is represented by several specimens and was initially reported as a Triassic mammal (Young 1940). By the end of this period, ten species of nmc from China had been named.

The Current Period (1983–2023)

> *Due to a series of fortunate geological coincidences the fossil record of the mammal-like reptiles is more complete than that of any other group of terrestrial vertebrates, with the exception of Tertiary mammals. Moreover, their evolution spanned a huge morphological progression, from early forms of a very primitive reptilian grade through to others which are technically to be regarded as mammals. Therefore this is the one example known where the evolution of one class of vertebrates from another class is well documented by the fossil record.*
> Passage from the introduction of *Mammal-like Reptiles and the Origin of Mammals* of Thomas Stainforth Kemp (1982).

The *Current Period* is characterized by an absolute plateau in taxonomic naming up until 2001. Only nine new species have been coined from the South African Karoo during the *Current Period*, all of them after 2000 (Fig. 3). The recent history of species naming in the Karoo has been much more modest than during Broom's heyday, with publications by J.A. Hopson, Christian Alfred Sidor and Nestor Fernando Abdala (Fig. 2) and colleagues who erected two species each, plus the recognition of a couple of new species from previously described material and the revival of others by Christian Farrell Kammerer (e.g. Kammerer 2016, Tolchard *et al*. 2021; Pusch *et al.* 2023) (Fig. 2). In this period there is a marked increase in the participation of women in the research programme of nmc, with notable work on cynodont palaeobiology by Jennifer Botha, Anusuya Chinsamy-Turan (Fig. 2), Sandra Christine Jasinoski, and Sanghamitra Ray (e.g. Botha & Chinsamy 2000; Ray *et al*. 2004; Botha-Brink *et al*. 2012; Jasinoski & Chinsamy 2012; Abdala *et al*. 2013; Jasinoski *et al*. 2015; Jasinoski & Abdala 2017a,b). Contributions by women to nmc research have continued to steadily increase, recently including works by Elize Butler and Safiyyah Iqbal focusing on descriptive (Butler *et al*. 2019) and functional (Iqbal 2019) studies of the postcranium of basal nmc, respectively. At the time of this writing, the most recently published projects regarding the anatomy and taxonomy of Karoo nmc were both led by women: the naming of a new species (*Guttigomphus avilionis*) at the end of 2022 by Romy Rayner (Rayner *et al*. 2022) and the revival of *Nythosaurus larvatus*, a nmc originally described by Owen (1876), by Luisa Christina Pusch (Pusch *et al*. 2023).

The chronostratigraphically oldest nmc from the Karoo, and probably from the world (but see Ivakhnenkho 2012), were also found during the *Current Period*. A general tenet during previous work on the Karoo was that the oldest nmc came from the *Daptocephalus* AZ (Kitching 1977), representing the fauna at the end of the late Permian. However, small cynodonts characterized by marked differences in the skull and dentition from the upper *Endothiodon* AZ (former *Tropidostoma* AZ), at the base of the late Permian, were discovered in the 2000s and published by a team led by J. Botha (Botha *et al*. 2007; Botha-Brink & Abdala 2008; Kammerer 2016), indicating an even older, not yet known, origin of the lineage (Lukic-Walther et al. 2018; Abdala 2021).

This period could also be characterized as the age of cladistics, as the first manual cladistic analyses on nmc cynodonts were introduced (Kemp 1983; Hopson & Barghusen 1986; Battail 1991), followed by numerical cladistic (parsimony) analyses (Martinez *et al*. 1996; Hopson & Kitching 2001; Liu & Olsen 2010; see Abdala *et al*. 2020 for details on cladistic studies in this period), which continue to be the most common way of exploring relationships between nmc (e.g. Gaetano *et al*. 2022; Benoit *et al*. 2022; Kerber *et al*. 2022). It is also during the *Current*

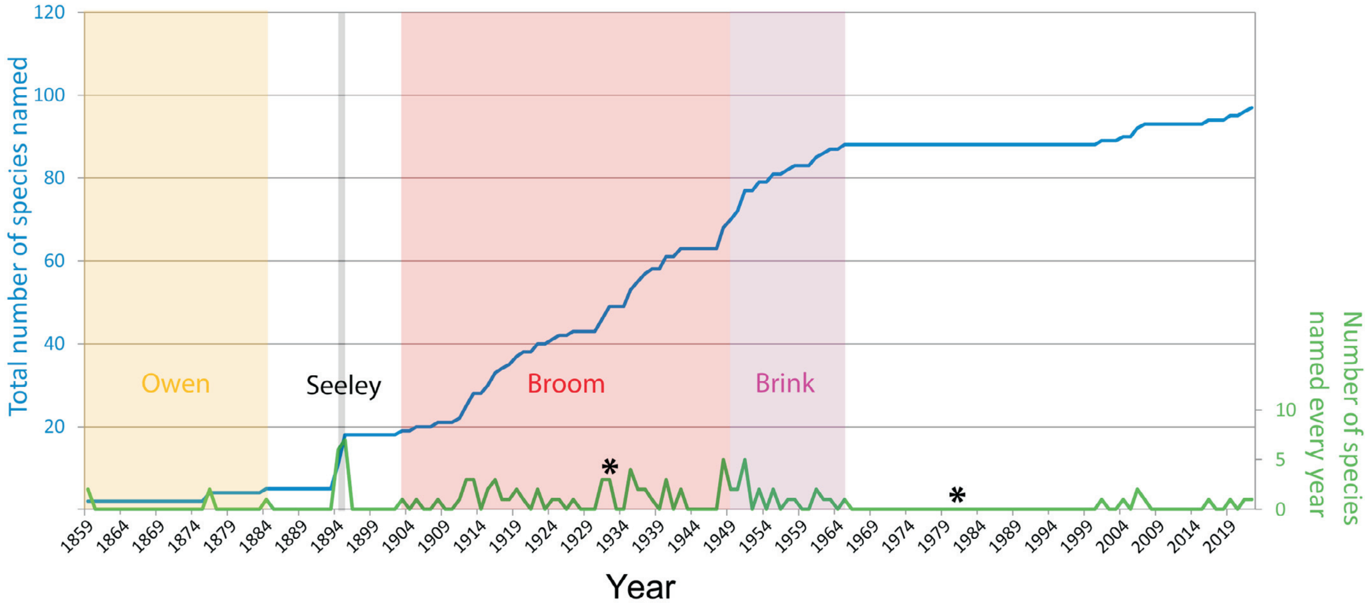

Figure 3. Non-mammaliaform cynodonts named from South Africa. Green line indicates number of nmc per year; blue line indicates the total number of nmc. Scale on the left indicates total number of species named and scale on the right is the number of species named every year to spot bursts of activity. Asterisks represent arbitrary points of division of the research history of non-mammaliaform cynodonts (1932 and 1982). The main researchers who named new cynodont species and their periods of peak activity are also indicated. Note the great plateau from 1966 to 2001.

Period that the exclusive use of the term Cynodontia was robbed from palaeontology. When originally coined by Owen (1861), cynodonts referred to a group of solely Triassic fossils. With the advent of cladistic analyses, the definition of Cynodontia expanded to include living mammals as well as their fossil ancestors (Rowe 1988; Wible 1991), and the original 'cynodonts' of Owen now corresponds to non-mammalian or non-mammaliaform cynodonts (i.e. identified by naming the group of which they are not members). The 1980s and '90s were also a period of enhancing the study of cranial anatomy and ontogeny in different Karoo nmc (e.g. Gow 1985, 1986; Allin & Hopson 1991; Luo & Crompton 1994), with a continuation in the functional studies already started in the previous period (e.g. Thomason & Russell 1986; Crompton & Hylander 1986). *Thrinaxodon liorhinus*, the iconic nmc first found in the Karoo and quite likely the most common taxon, became the first nmc to have a digital atlas of its skull published (Rowe *et al.* 1993).

The research programme of Karoo nmc in the 21st century, as is the case in most palaeontological research, is dominated by the advent of micro-computed tomographic (μCT) scanning techniques. This has allowed for important advancements in the knowledge of internal morphology, whereas in previous times this was only possible in species that were abundantly represented, because such studies were destructive (e.g. Broom 1938b; Fourie 1974; Benoit & Jasinoski 2016). Several pivotal studies using X-ray and neutron μCT data have now been published by S.C. Jasinoski (Jasinoski *et al.* 2015; Jasinoski & Abdala 2017a), Luke Allan Norton (Fig. 2) (e.g. Norton *et al.* 2020, 2021), and Julien Benoit (Fig. 2) (e.g. Benoit *et al.* 2017, 2020) on the cranial ontogeny, dental replacement, and the central nervous systems and sensory organs, respectively. CT-based investigations also led to the remarkable discovery of a complete skeleton of the nmc *Thrinaxodon* lying beside the temnospondyl amphibian *Broomistega*, without any mechanical preparation of the material (Fernandez *et al.* 2013), and have contributed to cranial studies of many Karoo species in great detail (e.g. Pusch *et al.* 2019). There has also been a marked advance in the knowledge of the postcranial anatomy of nmc in recent contributions (Gaetano *et al.* 2017; Butler *et al.* 2019; Benoit *et al.* 2022).

The accumulation of vast amounts of data on nmc, clarification of nmc alpha taxonomy and a relatively stable phylogeny have permitted a variety of broad-scale analyses of the group (e.g. Abdala & Ribeiro 2010; Ruta *et al.* 2013; Lukic-Walther *et al.* 2018), including studies on the impact of taxonomic practices on nmc diversity (Lukic-Walther *et al.* 2018) and the quality (completeness) of their fossil record (Varnham *et al.* 2021).

So far, during the *Current Period*, 93 species of nmc have been coined worldwide, and only nine of them (10%) are from South Africa. Non-mammaliaform cynodonts were reported in Luxembourg, Canada, Mexico, Belgium, France, Madagascar, Greenland, Italy, Japan, Mongolia and Poland for the first time.

QUANTITATIVE ASSESSMENT OF SOUTH AFRICAN NON-MAMMALIAFORM CYNODONTS

The first two species of Karoo nmc were reported in 1859, with Richard Owen, who established the first five species of nmc from the Karoo, being the sole scientist to provide a description of these new taxa (Fig. 3). This first burst of description was then followed by the contributions of Seeley, who described 13 new species in just two years (1894–1895). The period ranging from 1903 to 1950 saw the predominance of Broom in the description of new nmc, with 19 species erected up to 1932 (represented by an asterisk in Fig. 3). Besides Broom, only four other researchers with sporadic contributions coined new species of nmc, namely Watson (two species), Van Hoepen (four species), Haughton (three species), and Schmidt (one taxon). A small peak of new species erected by Broili & Schröder occurred in 1935 (the first peak in the green line after the asterisk in Fig. 3) and until 1950, all the subsequent peaks of published species by year (green line in Fig. 3) represent the contributions of Broom. During the following year, Brink, who is the fourth most influential researcher in this history, became active (Fig. 3), coining eleven species up through 1965, with an important peak of new species in 1951. During that time there were also contributions by Crompton (two species), Ginsburg (one species from Lesotho), and Fourie (two species). Only nine species were named in South Africa during the *Current Period*, all after 2000. Indeed, no new species from South Africa were coined between 1966 and 2001, here referred to as 'the great plateau' (Fig. 3).

Thus, at the end of this history a total of 97 nmc species from the Karoo Basin have been named, among which 28 were from the late Permian (29%), 62 from the Triassic (64%), and seven from the Jurassic (7%) (Appendix 2).

KAROO NON-MAMMALIAFORM CYNODONTS AND THE GLOBAL RECORD

There are currently 259 species of nominated nmc, among which 120 (46%) are currently considered as valid (Appendix 2). Of the 259 ever named species, 97 (37%) are from the Karoo Basin of South Africa and 25 are still valid (26% of the current valid species), the same number as in Brazil. However, the total number of named species from South Africa (97) hugely outnumbers that from Brazil (31).

South African nmc provided most of the known species globally for approximately 77 years, from 1855 to 1932 (Fig. 4). Since then, the records of named nmc from the Karoo and other parts of the world start to diverge. The peak of new species in 1936 (orange line, Fig. 4) results from the new species described from Brazil and Tanzania, whereas the strong peak differences between new species from the Karoo and those from the rest of the world during the 1960s and the beginning of the '70s is linked to the sustained discovery of new species in Argentina. In 1983, which marks the beginning of the *Current Period*, new species of nmc are recorded in China, India, and the United States, but none from the Karoo Basin (Appendix 2). Since then, the influence of 'the great plateau' in the Karoo produced important differences between the record of new species from the Karoo and the world at large, with a marked increase of new species described from Brazil in the last 20 years.

Comparing the palaeogeographical context between the north and the south of Pangaea (Fig. 5), it is clear that the record of nmc is significantly richer in southern Pangaea, with a rich taxonomic diversity in South Africa, Brazil, and Argentina. The most important records from northern Pangaea are those from China and the United States, but both have a much lower number of nmc than the countries from southern Pangaea (Fig. 5). It is also interesting to highlight the predominantly Triassic record of nmc in southern Pangaea, whereas nmc of northern Pangaea mainly come from the Jurassic and Cretaceous (Fig. 6; Appendix 2). In Figures 5 and 6 only the regions where new species of nmc were named are considered, which is why, for example, Antarctica is not represented despite *Thrinaxodon* being found there.

QUANTIFICATION OF NON-MAMMALIAFORM CYNODONTS IN PRIMARY SOUTHERN PANGAEAN FAUNAS

Three countries, all from southern Pangaea, include the largest number of nmc currently recognized: South Africa, Brazil, and Argentina. As is clear from the narrative

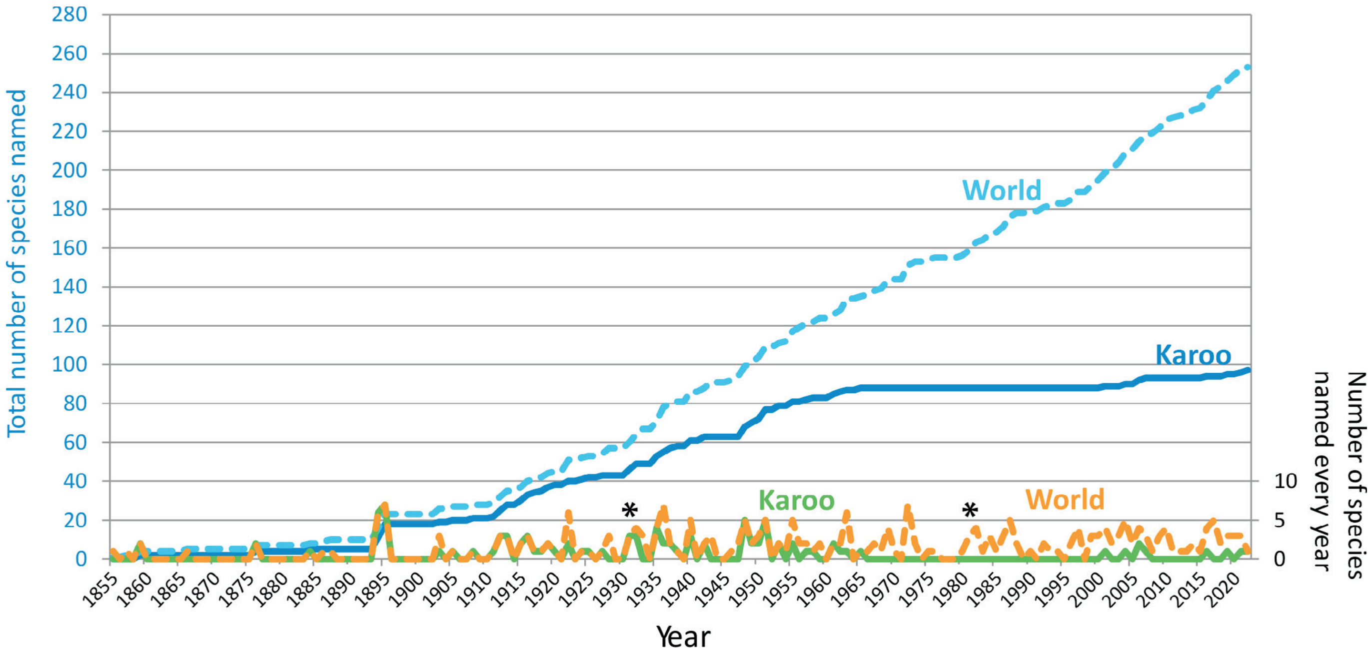

Figure 4. Non-mammaliaform cynodonts named from South Africa (solid lines) and from the world (dashed lines). Orange and green lines indicate number of nmc per year; blue lines indicate the total number of nmc. Scale on the left indicates total number of species named and scale on the right is the number of species named every year to spot bursts of activity. Asterisks represent arbitrary points of division of the research history of non-mammaliaform cynodonts (1932 and 1982).

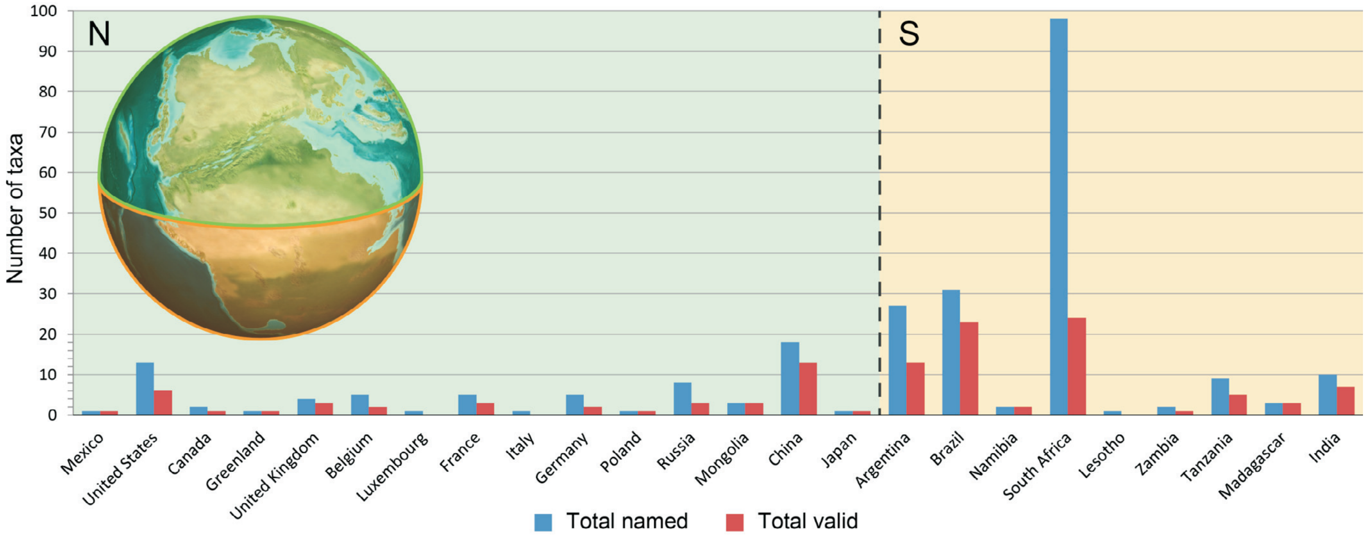

Figure 5. Non-mammaliaform cynodonts named and valid in the world. N, in green, is north Pangaea and S, in yellow, south Pangaea. Only places where species were nominated for the first time are presented.

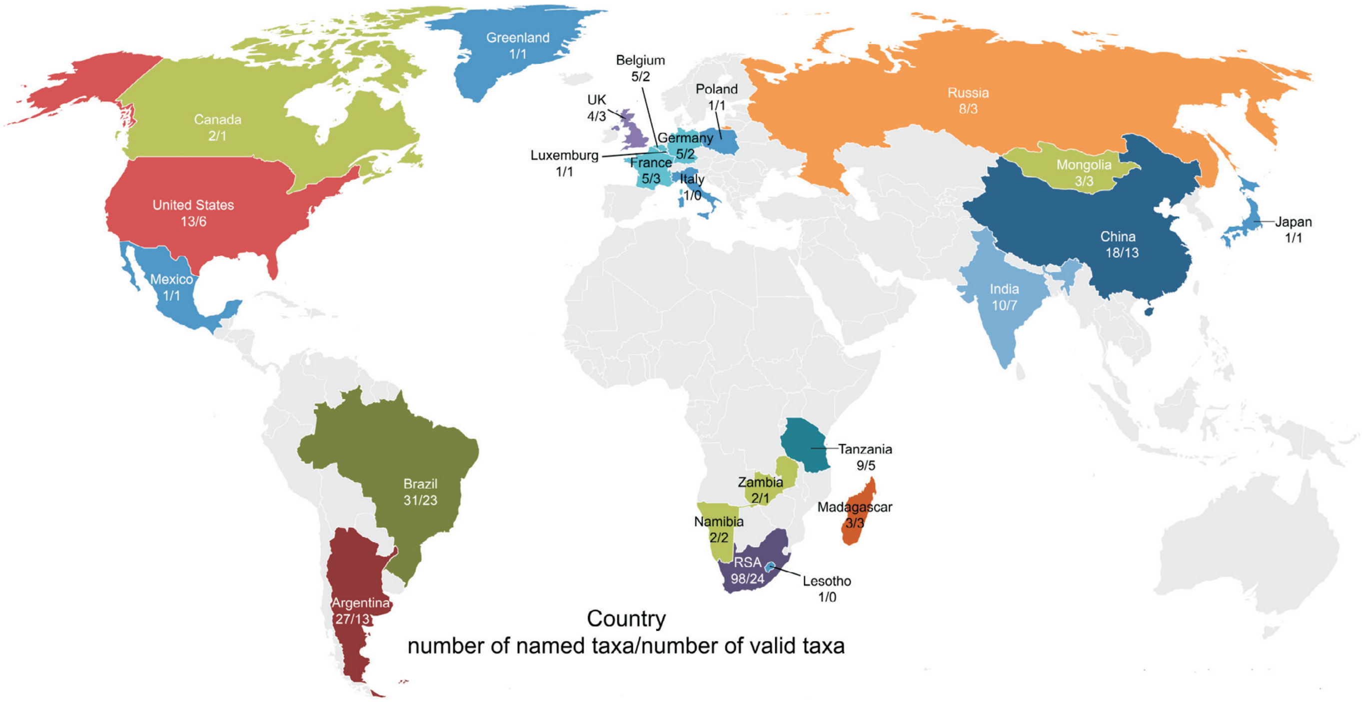

Figure 6. World map showing number of non-mammaliaform cynodonts named and number of valid taxa. Only places where species were nominated for the first time are presented.

presented above, the very early palaeontological exploration of the rich, fossiliferous levels of the Karoo Basin has led to the initial marked dominance of South African nmc (Fig. 4). During the *Early Period*, 50 of the total species of nmc in the Karoo were named, whereas a peak in nmc named occurred in the *Second Period* in Argentina (21 species coined), and during the *Current Period*, at the beginning of the 21st century, in Brazil (23 species named; Fig. 7A).

With the re-evaluation of the taxonomic status of the species, there was a marked reduction in the number of valid species, particularly in the Karoo (Fig. 7B). For the rejection ratio (i.e. the percentage of species names that were discarded), 74% of the nominated species of nmc of the South African Karoo are recognized as junior synonyms and therefore only 26% remain valid today; whereas 48% and 77% of those named nmc taxa from Argentina and Brazil (respectively) are still considered valid (Appendix 2).

The rejection ratio is not constant among the considered stages. As expected, the number of rejected species always drops during the third and most recent period, principally due to the intersubjectivity agreement of researchers working at the moment. The rejection ratio is 17% in Argentina and Brazil and 0% (i.e. no species rejected since 1983 onwards) in South Africa (Fig. 7C). In the latter country, the rejection ratio is very high for the first two periods (78% and 86%, respectively), whereas the values for the *Second Period* are 43% in Brazil and 62% in Argentina (Fig. 7C).

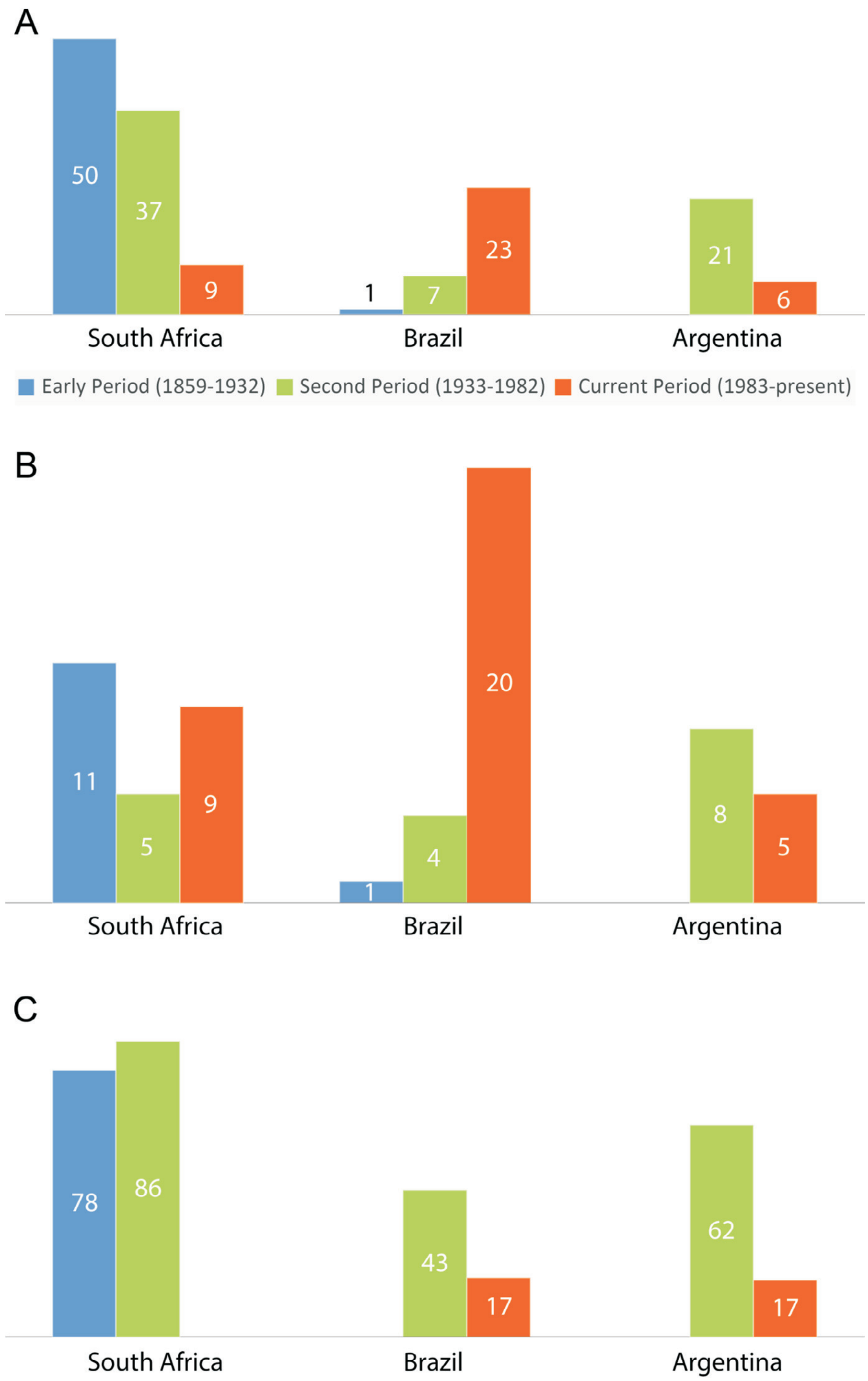

Figure 7. Non-mammaliaform cynodonts species in primary southern Pangaean faunas. **A**, Named species. **B**, Valid species. **C**, Rejection ratio (percentage).

RESEARCH ON NON-MAMMALIAFORM CYNODONTS IN THE 21ST CENTURY

We will close this contribution by highlighting the power of research centres undertaking research on nmc in the Karoo and in the rest of the world in what is now nearly the close of the first quarter of the 21st century. In South Africa, five main institutions had an important role in the actual research programme on nmc, with ten researchers in the Evolutionary Studies Institute in Johannesburg, one researcher from the Iziko South African Museum, two from the University of Cape Town, three researchers from the National Museum in Bloemfontein, and one researcher from the Council for Geoscience. In addition, several researchers from different countries are also actively using the knowledge of Karoo Basin cynodonts in their studies. In Appendix 3, we include researchers that have had recent contributions on nmc studies worldwide and in Appendix 2 a list of publications (which is not considered exhaustive) on Karoo Basin nmc or with use of information of these nmc in a more global context. We counted 120 research items from 2000 to 2023, which is *circa* 32% of the total publications since the beginning of the nmc history, which clearly indicates a burst of research on the lineage. Although taxonomic issues are not the primary concern in the robust current research programme of nmc, new findings and reinterpretations of the taxonomy always will have a strong influence on our understanding of the record and evolution of the group.

It is a pleasure to dedicate this research on the history of the study of mammalian ancestors in the Karoo Basin to Bruce Rubidge. Most of the authors of this contribution have been conducting research with Bruce during the first years of the current century. We salute his deep involvement with fossils from the Karoo and his continued efforts for at least 40 years in a programme of research that allowed a massive increase of the knowledge of the Permo-Triassic terrestrial fauna of South Africa. We are also glad to present this work in *Palaeontologia africana*, an African journal with a strong tradition of publications devoted to Karoo palaeontology. We are grateful to Tom Kemp, Luke Norton, Bruce Rubidge, Christian Sidor, Hans-Dieter Sues and Jean-Sébastien Steyer for sending photographs to illustrate Fig. 2 and to Arnaud Brignon, Jocelyn Falconet, James Hopson, Adam Huttenlocker, Robert Reisz, Bruce Rubidge, Jean-Sébastien Steyer, and Susan Turner for kindly providing information. Comments of an anonymous reviewer and, especially, from Christian Kammerer are greatly appreciated. Appendix 1 was prepared after a film by Pia Viglietti. This research is part of the PICT-2020-01498 of the ANPCyT, Argentina to FA, CH, LCG and JL; Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000) and International Partnership Program of the Chinese Academy of Sciences (132311KYSB20190010) to JL. FA and CH were supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and CH by the Agencia Nacional de Promoción Científica y Tecnológica, Argentina (Beca Pos-doctoral CONICET Legajo 181417). This is L.C.G.'s R-469 contribution to the IDEAN.

[§]ORCID iDs

F. Abdala: orcid.org/0000-0001-9838-2497
C. Hendrickx: orcid.org/0000-0002-8500-2405
L.C. Gaetano: orcid.org/0000-0001-5436-8060
J. Liu: orcid.org/0000-0003-2205-9671

REFERENCES

ABDALA, F. 2021. *Permo-Jurassic cynodonts: the early road to mammalness. Reference Module in Earth Systems and Environmental Sciences.* Elsevier.
DOI: 10.1016/B978-0-12-409548-9.12020-2

ABDALA, F., GAETANO, L.C., MARTINELLI, A.G., SOARES, M.B., HANCOX, P.H. & RUBIDGE, B.S. 2020. Non-mammaliaform cynodonts from western Gondwana and the significance of Argentinean forms in enhancing understanding of the group. *Journal of South American Earth Sciences*, **104**, 102884

ABDALA, F., JASINOSKI, S.C. & FERNANDEZ, V. 2013. Ontogeny of the Early Triassic cynodont *Thrinaxodon liorhinus* (Therapsida): dental morphology and replacement. *Journal of Vertebrate Paleontology* **33**, 1408–1431.

ABDALA, F., MARTINELLI, A.G. & GONZALEZ, F.R. 2022. La Paleoherpetología en el Instituto Miguel Lillo de la Universidad Nacional de Tucumán, Argentina. **In**: Gasparini, Z., Salgado, L., Desojo, J.B. (eds), Paleoherpetología en la Argentina: 150 años de historia. *Publicación Electrónica de la Asociación Paleontológica Argentina*, **22**, 67–87.
DOI: 10.5710/PEAPA.16.05.2021.360

ABDALA, F. & RIBEIRO, A.M. 2010. Distribution and diversity patterns of Triassic cynodonts (Therapsida: Cynodontia) in Gondwana. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* **286**, 202–217.

ALLIN, E.F. 1975. Evolution of the mammalian middle ear. *Journal of Morphology*, **147**: 403–437.
DOI: 10.1002/jmor.1051470404

ALLIN, E.F. 1986. The auditory apparatus of advanced mammal-like reptiles and early mammals. **In**: Hotton N., MacLean P.D., Roth J.J. & Roth E.C. (eds), *The Ecology and Biology of Mammal-like Reptiles*. Washington, Smithsonian Institutional Press. 283–294.

ALLIN, E.F. & HOPSON, J.A. 1992. Evolution of the auditory system in Synapsida ("mammal-like reptiles" and primitive mammals) as seen in the fossil record, **In**: Webster D.B., Fay R.R. & Popper A.N. (eds), *The Evolutionary Biology of Hearing*, 587–614. New York, Springer-Verlag.

ANDERSON, J.M. 1968. The confused state of classification within the family Procynosuchidae. *Palaeontologia africana*, **11**, 77–84.

BATTAIL, B. 1991. Les cynodontes (Reptilia, Therapsida): une phylogénie. *Bulletin du Museum Nationale d'Histoire Naturalle d'Paris* **13**, 17–105.

BENOIT, J., ABDALA, F., VAN DEN BRANDT, M., MANGER, P.R. & RUBIDGE, B.S. 2015. Physiological implications of the abnormal absence of the parietal foramen in a Late Permian cynodont (Therapsida). *The Science of Nature* **102**, 69.
DOI: 10.1007/s00114-015-1321-4

BENOIT, J. & JASINOSKI, S.C. 2016. Picking up the pieces: the digital reconstruction of a destroyed holotype from its serial section drawings. *Palaeontologia Electronica* **19.3.3T**, 1–16.

BENOIT J., JASINOSKI S.C., FERNANDEZ V. & ABDALA, F. 2017. The mystery of a missing bone: revealing the orbitosphenoid in basal Epicynodontia (Cynodontia, Therapsida) through computed tomography. *The Science of Nature* **104**,66.

BENOIT, J., NXUMALO, M., NORTON, L.A., FERNANDEZ, V., GAETANO, L.C., RUBIDGE, B.S. & ABDALA, F. 2022. Synchrotron scanning sheds new light on *Lumkuia fuzzi* (Therapsida, Cynodontia) from the Middle Triassic of South Africa and its phylogenetic placement. *Journal of African Earth Sciences* **196**, 104689

BENOIT, J., RUF, I., MIYAMAE, J.A., FERNANDEZ, V., RODRIGUES, P.G. & RUBIDGE B.S. 2020. The evolution of the maxillary canal in Probainognathia (Cynodontia, Synapsida): reassessment of the homology of the infraorbital foramen in mammalian ancestors. *Journal of Mammalian Evolution***27**, 329–348.

BERTA, A. & TURNER, S. 2020. *Rebels, Scholars, Explorers – Women in Vertebrate Paleontology*. Johns Hopkins University Press. 352 pp.

BOONSTRA, L.D. 1935. A note on the cynodont *Glochinodontoides gracilis* Haughton. *American Museum Novitates*, **782**, 1–6.

BORDY, E.M., ABRAHAMS, M., SHARMAN, G.R., VIGLIETTI, P.A., BENSON, R.B.J., McPHEE, B.W., BARRETT, P.M., SCISCIO, L., CONDON, D., MUNDIL, R., RADEMAN, Z., JINNAH, Z., CLARK, J.M., SUAREZ, C.A., CHAPELLE, K.E.J. & CHOINIERE, J.N. 2020. A chronostratigraphic framework for the upper Stormberg Group: implications for the Triassic-Jurassic boundary in southern Africa. *Earth-Science Reviews* **203**, 103120.
DOI: 10.1016/j.earscirev.2020.103120

BOTHA, J. & CHINSAMY, A. 2000. Growth patterns deduced from the bone histology of the cynodonts *Diademodon* and *Cynognathus*. *Journal of Vertebrate Paleontology* **20**, 705–711.

BOTHA, J., ABDALA, F. & SMITH, R. 2007. The oldest cynodont: new clues on the origin and diversification of the Cynodontia. *Zoological Journal of the Linnean Society* **149**, 477–492.

BOTHA-BRINK, J. & ABDALA, F. 2008. A new cynodont record from the *Tropidostoma* Assemblage Zone of Beaufort Group: implications for the early evolution of cynodonts in South Africa. *Palaeontologia africana* **43**, 1–6.

BOTHA-BRINK, J., ABDALA, F. & CHINSAMY, A. 2012. Bone histology and radiation of Permo-Jurassic non-mammaliaform cynodonts. **In**: Chinsamy, A. (ed.), *The Forerunners of Mammals: Radiation. Biology. Histology*, 223–246. Bloomington, Indiana University Press. ISBN 978-0-253-35697-0.

BRINK, A. S. 1986. *Illustrated Bibliographic Catalogue of the Synapsida*. Parts 1 and 2. *Handbook* **10**. Pretoria, Department of Mineral and Energy Affairs. 540 pp.

BROILI, F & SCHRÖDER, J. 1934a. Zur Osteologie des Kopfes von *Cynognathus*. *Sitzungsberichte der Bayerischen Akademie der Wissenchaften*, *Mathematisch-Naturwissenschaftliche*, *Abteilung* **1934**: 95–128.

BROILI, F. & SCHRÖDER, J. 1934b. Beobachtungen an Wirbeltieren der Karrooformation. II. Über den Cynodontier *Tribolodon frerensis* Seeley. *Sitzungsberichte der Bayerischen Akademie der Wissenchaften*, *Mathematisch-Naturwissenschaftliche*, *Abteilung* **1934**: 163–177.

BROILI, F & SCHRÖDER, J. 1935a. Beobachtungen an Wirbeltieren der Karrooformation. X. Über die Bezahnung von *Trirachodon* Seeley. *Sitzungsberichte der Bayerischen Akademie der Wissenchaften*, *Mathematisch-Naturwissenschaftliche*, *Abteilung* **1935**: 189–198.

BROILI, F & SCHRÖDER, J. 1935b. Beobachtungen an Wirbeltieren der Karrooformation. XI. Über den Schädel von *Cynidiognathus* Haughton. *Sitzungsberichte der Bayerischen Akademie der Wissenchaften*, *Mathematisch-Naturwissenschaftliche*, *Abteilung* **1935**: 199–222.

BROILI, F & SCHRÖDER, J. 1935c. Beobachtungen an Wirbeltieren der Karrooformation. IX Über den Schädel von *Gomphognathus* Seeley. *Sitzungsberichte der bayerischen Akademie der Wissenchaften*, *Mathematisch-Naturwissenschaftliche*, *Abteilung* **1935**: 115–182.

BROOM, R. 1903. On the lower jaw of a small mammal from the Karroo Beds of Aliwal North, South Africa. *Geological Magazine* **10**, 345.

BROOM, R. 1905. On the affinities of *Tritylodon*. *Transactions of the South African Philosophical Society*, **16**, 73–77.

BROOM, R. 1910. On *Tritylodon* and on the relationships of the Multituberculata. *Proceedings of the Zoological Society of London*, 760–768.

BROOM, R. 1913. South African fossil reptiles. *The American Museum Journal* **13**, 334–346.

BROOM, R. 1932. *The Mammal-like Reptiles of South Africa and the Origin of Mammals*. London, Witherby. 376 pp.

BROOM R. 1935. Review of some recent work on South African fossil reptiles. *Annals of the Transvaal Museum* **18**, 397–413.
BROOM, R. 1937. A further contribution to our knowledge of the fossil reptiles of the Karroo. *Proceedings of the Zoological Society of London B***107**, 299–318.
BROOM, R. 1938a. The origin of the cynodonts. *Annals of the Transvaal Museum* **19**, 279–288.
BROOM, R. 1938b. On the structure of the skull of the cynodont, *Thrinaxodon liorhinus*, Seeley. *Annals of the Transvaal Museum* **19**, 263–269.
BROOM, R. 1940. On some new genera and species of fossil reptiles from the Karroo beds of Graaff-Reinet. *Annals of the Transvaal Museum* **20**, 157–192.
BROOM, R. 1948. A contribution to our knowledge of the vertebrates of the Karroo Beds of South Africa. *Transactions of the Royal Society of Edinburgh* **61**, 577–629.
BROOM, R. 1950. Some fossil reptiles from the Karoo Beds of Lady Frere. *South African Journal of Science* **47**, 86–88.
BUCKLAND, W. 1824. Notice on *Megalosaurus*. *Transactions of the Geological Society of London* **1**, 390–396.
BUTLER, E., ABDALA, F. & BOTHA-BRINK, J. 2019. Postcranial anatomy of the Early Triassic non-mammaliaform cynodont *Galesaurus planiceps* (Owen, 1859) from the Karoo Basin, South Africa. *Papers in Palaeontology* **5**, 1–32.
DOI: 10.1002/spp2.1220
CHARIG, A.J. 1990. Francis Rex Parrington. 20 February 1905 – 17 April 1981. *Biographical Memoirs of Fellows of the Royal Society* **36**, 360–378.
CHARLESWORTH, E. 1855. Notice on new vertebrate fossils. *Report of the British Association for the Advancement of Science* **1854**, 80.
CROMPTON, A.W. 1963. On the lower jaw of *Diarthrognathus* and the origin of the mammalian lower jaw. *Proceedings of the Zoological Society of London* **140**, 697–753.
CROMPTON, A.W. 1972a. The evolution of the jaw articulation in cynodonts. **In**: Joysey, K.A. & Kemp, T.S. (eds), *Studies in Vertebrate Evolution*, 231–251. Edinburgh, Oliver and Boyd.
CROMPTON, A.W. 1972b. Postcanine occlusion in cynodonts and tritylodontids. *Bulletin of the British Museum (Natural History) Geology* **21**, 29–71.
CROMPTON, A.W. & HYLANDER, W.L. 1986. Changes in mandibular function following the acquisition of a dentary-squamosal jaw articulation. **In**: Hotton, N., MacLean, P.D., Roth, J.J. & Roth, E.C. (eds), *The Ecology and Biology of Mammal-like Reptiles,* 263–282. Washington, Smithsonian Institution Press.
DUBOW, S. 2004. Earth history, natural history, and prehistory at the Cape, 1860–1875. *Comparative Studies in Society and History* **46**, 107–133.
DUNHAM, K. 1983. Sidney Henry Haughton. 7 May 1888 – 24 May 1982. *Biographical Memoirs of Fellows of the Royal Society*, **29**, 245–267.
FERNANDEZ, V., ABDALA, F., CARLSON, K., COLLINS COOK, D., RUBIDGE, B.S., YATES, A. & TAFFOREAU, P. 2013. Synchrotron reveals Early Triassic odd couple: injured amphibian and aestivating therapsid share burrow. *PLOS ONE* **8(6)**, e64978.
DOI: 10.1371/journal.pone.0064978
FOURIE, S. 1974. The cranial morphology of *Thrinaxodon liorhinus* Seeley. *Annals of the South African Museum* **65**, 337–400
GAETANO, L., ABDALA, F. & GOVENDER, R. 2017. The postcranium of *Tritylodon longaevus* from the Karoo Basin of South Africa. *Ameghiniana* **54**, 1–35.
DOI: 10.5710/AMGH.11.09.2016.3011
GAETANO, L.C., ABDALA, F., SEOANE, F.D. TARTAGLIONE, A., SCHULZ, M., OTERO, A., LEARDI, J.M., APALDETTI, C., KRAPOVICAS, V. & STEINBACH, E. 2022. A new cynodont from the Late Triassic Los Colorados Formation (Argentina, South America) reveals a novel paleobiogeographic context for mammalian ancestors. *Scientific Reports*, **12**, 6451.
DOI: 10.1038/s41598-022-10486-4
GOODRICH, E.S. 1894. On the fossil Mammalia from the Stonesfield Slate. *Quarterly Journal of Microscopical Sciences* **35**, 407–432.
GOW, C.E. 1985. Dentitions of juvenile *Thrinaxodon* (Reptilia: Cynodontia) and the origin of mammalian diphyodonty. *Annals of the Geological Survey of South Africa* **19**, 1–17.
GOW, C.E. 1986. The side wall of the braincase in cynodont therapsids, and a note on the homology of the mammalian promontorium. *South African Journal of Zoology* **21**, 136–148.
GREGORY, W.K. 1910. The orders of mammals. *Bulletin of the American Museum of Natural History* **27**, 1–524.
GRINE, F.E. & GOW, C.E. 1978. Aspects of relative growth and variability in *Didemodon* (Reptilia; Therapsida). *South African Journal of Science* **74**, 50–58.
GRINE, F.E., HAHN, B.D. & GOW, C.E. 1978. Allometric growth in the Diademodontinae (Reptilia; Therapsida): a preliminary report. *Palaeontologia africana* **21**, 161–166.
HANCOX, P.J. & RUBIDGE, B.S. 1997. The role of fossils in interpreting the development of the Karoo Basin. *Palaeontologia africana* **33**, 41–54.
HAUGHTON, S.H. 1918. Investigations in South African fossil reptiles and Amphibia (Part 11). Some new carnivorous Therapsida, with notes upon the brain-case in certain species. *Annals of the South African Museum* **12**, 196–215.
HAUGHTON, S.H. 1924. On Cynodontia from the middle Beaufort beds of Harrismith, Orange Free State. *Annals of the Transvaal Museum* **11**, 74–92.
HAUGHTON, S.H. 1965. The Rubidge collection of fossil Karroo vertebrates. *Palaeontologia africana* **9**, 1–17.
HAUGHTON, S.H. 1974. In reminiscent vein. *Annals of the South African Museum* **64**, 7–9.
HAUGHTON, S.H. & BRINK, A.S. 1954. A bibliographic list of Reptilia from the Karroo beds of Africa. *Palaeontologia africana* **2**, 1–171.
HOPSON, J.A. & BARGHUSEN, H.R. 1986. An analysis of therapsid relationships. **In**: Hotton, N., MacLean, P.D., Roth, J.J. & Roth, E.C. (eds), *The Ecology and Biology of Mammal-like Reptiles*, 83–106. Washington, Smithsonian Institution Press.
HOPSON, J.A. & KITCHING, J.W. 1972. A revised classification of cynodonts (Reptilia; Therapsida). *Palaeontologia africana* 14, 71–85.
HOPSON, J.A. & KITCHING, J.W. 2001. A probainognathian cynodont from South Africa and the phylogeny of nonmammalian cynodonts. *Bulletin of the Museum of Comparative Zoology* **156**, 5–35.
HUENE, F. VON. 1928. Ein Cynodontier aus der Trias Brasiliens. *Zentralblatt für Mineralogie*, *Geologie und Paläontologie* **1928**, 251–270.
IQBAL, S. 2019. *Limb loading of* Thrinaxodon liorhinus: *postural inference of non-mammaliaform cynodonts*. Ph.D. thesis, University of the Witwatersrand, Johannesburg. 118 pp.
INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (ICZN). 1985. Opinion 1324. *Diademodon* Seeley, 1894, and *Diademodon tetragonus* Seeley, 1894, conserved by suppression of *Cynochampsa* Owen, 1859, and *Cynochampsa laniaria* Owen, 1859 (Reptilia, Therapsida). *Bulletin of Zoological Nomenclature* **42**, 185–187.
IVAKHNENKHO, M.F. 2012. Permian Cynodontia (Theromorpha) of eastern Europe. *Palaeontological Journal* **46**, 199–207.
JASINOSKI, S.C. & ABDALA, F. 2017a. Cranial ontogeny of the early Triassic basal cynodont *Galesaurus planiceps*. *Anatomical Record* **300**, 353–381.
JASINOSKI, S.C. & ABDALA, F. 2017b. Aggregations and parental care in the Early Triassic basal cynodonts *Galesaurus planiceps* and *Thrinaxodon liorhinus*. *PeerJ* **5**, e2875
DOI: 10.7717/peerj.2875
JASINOSKI, S.C., ABDALA, F. & FERNANDEZ, V. 2015. Ontogeny of the Early Triassic cynodont *Thrinaxodon liorhinus* (Therapsida): cranial morphology. *Anatomical Record* **298**,1440–1464.
DOI: 10.1002/ar.23116
JASINOSKI, S.C. & CHINSAMY, A. 2012. Mandibular histology and growth of the nonmammaliaform cynodont *Tritylodon*. *Journal of Anatomy* **220**, 564–579.
DOI: 10.1111/j.1469-7580.2012.01494.x
JENKINS, F.A., Jr. 1971. The postcranial skeleton of African cynodonts. *Peabody Museum of Natural History Bulletin* **36**, 1–216.
KAMMERER, C.F. 2016. A new taxon of cynodont from the *Tropidostoma* Assemblage Zone (upper Permian) of South Africa, and the early evolution of Cynodontia. *Papers in Palaeontology* **2**, 387–397.
KEMP, T.S. 1969. The atlas-axis complex of the mammal-like reptiles. *Journal of Zoology* **159**, 223–248.
KEMP, T.S. 1980. The primitive cynodont *Procynosuchus*: structure, function and evolution of the postcranial skeleton. *Proceedings of the Royal Society B* **288**, 217–258.
KEMP, T.S., 1982. *Mammal-like Reptiles and the Origin of Mammals*. London, Academic Press. 363 pp.
KEMP, T.S. 1983. The interrelationships of mammals. *Zoological Journal of the Linnean Society* **77**, 353–384.
KERBER, L., MARTINELLI, A.G., MÜLLER, R.T. & PRETTO, F.A. 2022. A new specimen provides insights into the anatomy of *Irajatherium hernandezi*, a poorly known probainognathian cynodont from the Late Triassic of southern Brazil. *Anatomical Record* **305**, 3113–3132.
KERMACK, D.M. & KERMACK, K.A. 1984. *The Evolution of Mammalian Characters*. Kent, Croom Helm. 149 pp.
KITCHING, J.W. 1977. *The Distribution of the Karroo Vertebrate Fauna*. *Memoir*, **1**, 1–131. Johannesburg, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand.
LIU, J. & OLSEN, P. 2010. The phylogenetic relationships of Eucynodontia (Amniota: Synapsida). *Journal of Mammalian Evolution* **17**, 151–176.

LUKIC-WALTHER, M., BROCKLEHURST, N., KAMMERER, C.F. & FRÖBISCH, J. 2019. Diversity patterns of non-mammalian cynodonts (Synapsida, Therapsida) and the impact of taxonomic practice and research history on diversity estimates. *Paleobiology* **45**, 56–69.

LUO, Z. 1994. Sister-group relationships of mammals and transformations of diagnostic mammalian characters. **In**: Fraser, N.C. & Sues, H-D. (eds), *In the Shadow of the Dinosaurs,* 98–128. Cambridge, Cambridge University Press.

LUO, Z. & CROMPTON, A.W. 1994. Transformation of the quadrate (incus) through the transition from nonmammalian cynodonts to mammals. *Journal of Vertebrate Paleontology* **14**, 341–374.

LYDDEKER, R. 1909. Prof. H.G. Seeley, F.R.S. *Nature* **79**, 314–315.

MARTINELLI, A.G., KAMMERER, C.F., MELO, T.P., PAES NETO, V.D., RIBEIRO, A.M., DA-ROSA, A.A.S., SCHULTZ, C.L. & SOARES, M.B. 2017. The African cynodont *Aleodon* (Cynodontia, Probainognathia) in the Triassic of southern Brazil and its biostratigraphic significance. *PLOS ONE* **12**, e0177948.

MARTÍNEZ, R.N., MAY, C.L. & FORSTER, C.A., 1996. A new carnivorous cynodonts from the Ischigualasto Formation (Late Triassic, Argentina), with comment on eucynodont phylogeny. *Journal of Vertebrate Paleontology* **16**, 271–284.

MENDREZ, C.H. 1972a. On *Cyrbasiodon boycei*, Broom 1931, (Cyndontia: Procynosucidae), from South Africa. *Palaeontologia africana* **14**, 51–69.

MENDREZ, C.H. 1972b. Revision du genre *Protocynodon* Broom 1949 et discussion de sa position taxonomique. *Palaeontologia africana* **14**, 19–50.

NORTON, L., ABDALA, F., RUBIDGE, B.S. & BOTHA, J. 2020. Tooth replacement patterns in the Early Triassic epicynodont *Galesaurus planiceps* (Therapsida, Cynodontia). *PLOS ONE* **15**, e0243985. DOI: 10.1371/journal.pone.0243985

NORTON, L., ABDALA, F., RUBIDGE, B.S. & BOTHA, J. 2021. Tooth replacement patterns in the Early Triassic epicynodont *Cynosaurus suppostus* (Therapsida, Cynodontia). *Journal of Vertebrate Paleontology* **41**, e2001650. DOI: 10.1080/02724634.2021.2001650

OSBORN, H.F. 1888. On the structure and classification of the Mesozoic Mammalia. *Journal of the Academy of Natural Sciences*, *Philadelphia* **1888**, 292–301.

OWEN, R. 1838. On the jaws of the *Thylacotherium prevostii* (Valenciennes) from Stonesfield. *Proceedings of the Geological Society of London* **3**, 5–9.

OWEN, R. 1846. *History of British Fossil Mammals and Birds*. London, John Van Voorst. 560 pp.

OWEN, R. 1859. On some reptilian remains from South Africa. *The Edinburgh New Philosophical Journal* **10**, 289–291.

OWEN, R. 1860. On some reptilian fossils from South Africa. *Quarterly Journal of the Geological Society* **16**, 49–63.

OWEN, R. 1861. *Palaeontology, or a Systematic Summary of Extinct Animals and their Geological Relations* (2nd edn). Edinburgh, Adam and Black. 163 pp.

OWEN, R. 1871. Monograph of the fossil Mammalia of the Mesozoic formations. *Monograph of the Palaeontological Society* **33**, 1–115.

OWEN, R. 1876. *Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa in the Collection of the British Museum*. London, Order of the Trustees. 88 pp.

OWEN, R. 1884. On the skull and dentition of a Triassic mammal (*Tritylodon longaevus*) from South Africa. *Quarterly Journal of the Geological Society of London* **40**, 146–152.

PANCIROLI, E., WALSH, S., FRASER, N.C., BRUSATTE S. L. & CORFE, I. 2017. A reassessment of the postcanine dentition and systematics of the tritylodontid *Stereognathus* (Cynodontia, Tritylodontidae, Mammaliamorpha), from the Middle Jurassic of the United Kingdom. *Journal of Vertebrate Paleontology* **37**, e1351448.

PARRINGTON, F.R. 1933. On the cynodont reptile *Thrinaxodon liorhinus* Seeley. *Annals and Magazine of Natural History* **11**, 16–24.

PARRINGTON, F.R. 1934. On the cynodont genus *Galesaurus*, with a note on the functional significance of the changes in the evolution of the theriodont skull. *Annals and Magazine of Natural History* **13**, 38–67.

PARRINGTON, F.R. 1936. On the tooth-replacement in theriodont reptiles. *Philosophical Transactions of the Royal Society of London Series B*, *Biological Sciences* **226**, 121–142.

PARRINGTON, F.R. 1961. The evolution of the mammalian femur. *Proceedings of the Zoological Society of London* **137**, 285–298.

PARRINGTON, F.R. & WESTOLL T.S. 1974. David Meredith Seares Watson. 1886–1973. *Biographical Memoirs of Fellows of the Royal Society* **20**, 482–504.

PETRONIEVICS, B. 1917. On the skull of *Tritylodon longaevus*, Owen. *Annals and Magazine of Natural History*, *Series 8*, **20**, 283–289.

PLIENINGER, W.H. 1847. Zähnen aus der oberen Grenzbreccie des Keupers bei Degerloch und Steinenbronn. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, 164–167.

PUSCH L.C., KAMMERER, C.F. & FRÖBISCH, J. 2019. Cranial anatomy of the early cynodont *Galesaurus planiceps* and the origin of mammalian endocranial characters. *Journal of Anatomy* **234**, 592–621.

PUSCH L.C., KAMMERER, C.F., FERNANDEZ, V. & FRÖBISCH, J. 2023. Cranial anatomy of *Nythosaurus larvatus* Owen, 1876, an Early Triassic cynodont preserving a natural endocast. *Journal of Vertebrate Paleontology*, e2174441.

RAATH, M.A. & RUBIDGE, B.S. 2005. James William Kitching (1922–2003): a tribute. *Palaeontologia africana* **41**, 1–5.

RAY, S., BOTHA, J. & CHINSAMY, A. 2004. Bone histology and growth patterns of some nonmammalian therapsids. *Journal of Vertebrate Paleontology* **24**, 634–648.

REICH, M. & WÖRHEIDE, G. 2018. München: the fossil collections of the Bavarian State Collections at Munich. **In**: Beck, L. & Joger, U. (eds) *Paleontological Collections of Germany, Austria and Switzerland*. Natural History Collections, 427–443. Cham, Springer. DOI: 10.1007/978-3-319-77401-5_43

ROWE, T. 1988. Definition, diagnosis, and origin of Mammalia. *Journal of Vertebrate Paleontology* **8**, 241–264.

ROWE, T., CARLSON, W. & BOTTORFF, W. 1993. *Thrinaxodon*: digital atlas of the skull. CD-ROM. Austin, Texas, University of Texas Press.

RUBIDGE, B.S. 1997. The BPI – 50 years of palaeontological activity. *Palaeontologia africana* **33**, 1–9.

RUBIDGE, B.S. 2013. The roots of early mammals lie in the Karoo: Robert Broom's foundation and subsequent research progress. *Transactions of the Royal Society of South Africa* **68**, 41–52,

RUBIDGE, B.S. & RAATH, M.A. 2003. James William Kitching FRSSAf 1922–2003. *Transactions of the Royal Society of South Africa* **58**(1), 95–97.

RUTA, M., BOTHA-BRINK, J., MITCHELL, S.A. & BENTON, M.J. 2013. The radiation of cynodonts and the ground plan of mammalian morphological diversity. *Proceedings of the Royal Society B* **280**, 2013.1865.

SEELEY, H.G. 1894a. Researches on the structure, organization, and classification of the fossil Reptilia. Part IX., Section 2. The reputed mammals from the Karroo Formation of Cape Colony. *Philosophical Transactions of the Royal Society of London B* **185**, 1019–1028.

SEELEY, H.G. 1894b. Research on the structure, organization, and classification of the fossil Reptilia. Pt. 9, Section 3. On *Diademodon*. *Philosophical Transaction of the Royal Society of London B* **185**, 1029–1041.

SEELEY, H.G. 1895a. Research on the structure, organization, and classification of the fossil Reptilia. Pt. 9, Section 4. On the Gomphodontia. *Philosophical Transaction of the Royal Society of London B* **186**, 1–57.

SEELEY, H.G. 1895b. Research on the structure, organization, and classification of the fossil Reptilia. Pt. 9, Section 5. On the skeleton in new Cynodontia from the Karroo rocks. *Philosophical Transaction of the Royal Society of London B* **186**, 59–148.

SIMPSON, G.G. 1928. *A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum*. London, Trustees of the British Museum. 215 pp.

SMITH, R.M.H., RUBIDGE, B.S., DAY, M.O. & BOTHA, J. 2020. Introduction to the tetrapod biozonation of the Karoo Supergroup. *South African Journal of Geology* **123**, 131–140.

THOMASON, J.J. & RUSSELL, A.P. 1986. Mechanical factors in the evolution of the mammalian secondary palate: a theoretical analysis. *Journal of Morphology* **189**, 199–213.

TOLCHARD, F., KAMMERER, C.F., BUTLER, R.J., HENDRICKX, C., BENOIT, J., ABDALA, F. & CHOINIERE, J.N. 2021. A new large gomphodont from the Triassic of South Africa and its implications for Gondwanan biostratigraphy. *Journal of Vertebrate Paleontology* **41**, e1929265.

VAN HEERDEN, J. 1972. Intraspecific variations and growth changes in the cynodont reptile *Thrinaxodon liorhinus*. *Researches of the National Museum* **2**, 307–347.

VAN HEERDEN, J.1976. The cranial anatomy of *Nanictosaurus rubidgei* Broom and the classification of the Cynodontia (Reptilia: Therapsida). *Navorsinge van die Nasionale Museum* **3**, 141–164.

VARNHAM, G.L., MANNION, P.D. & KAMMERER, C.F. 2021. Spatiotemporal variation in completeness of the early cynodont fossil record and its implications for mammalian evolutionary history. *Palaeontology* **64**, 307–333.

WATSON, D.M.S. 1920. On the Cynodontia. *Annals and Magazine of Natural History* (9)**6**, 506–524.

WATSON, D.M.S. 1921. The bases of classification of the Theriodontia. *Proceedings of the Geological Society of London* **1921**, 35–98.

WATSON, D.M.S. 1942. On Permian and Triassic tetrapods. *Geological Magazine* **49**, 81–116.

WATSON, D.M.S. 1953. The evolution of the mammalian ear. *Evolution* **7**, 159–177.
WATSON, D.M.S. & ROMER, A.S. 1956. A classification of therapsid reptiles. *Bulletin of the Museum of Comparative Zoology* **114**, 38–89.
WIBLE, J.R. 1991. Origin of Mammalia: the craniodental evidence reexamined. *Journal of Vertebrate Paleontology* **11**, 1–28.
WYLLIE, A. 2003. A review of Robert Broom's therapsid holotypes: have they survived the test of time? *Palaeontologia africana* **39**, 1–19.
YOUNG, C.C. 1940. Preliminary notes on the Mesozoic mammals of Lufeng, Yunnan, China. *Bulletin of the Geological Society of China* **20**, 93–111.

Appendix 1

Video recording (MP4) — Rubidge collection – *by Bruce Rubidge*

Click here to view attachment, then double-click on attachment

Appendix 2

Historical information/data (Excel spreadsheets)

Click here to view attachment, then double-click on attachment

Appendix 3

Current research power in non-mammaliaform cynodonts in the world

The Evolutionary Studies Institute (ESI) in Johannesburg had the involvement of several researchers: F. Abdala (now at the Unidad Ejecutora Lillo, Argentina), J. Benoit, Kristian J. Carlson (now at the University of Southern California), Jonah Nathaniel Choiniere, Vincent Fernandez (now at the European Synchrotron Radiation Facility, France), John Philip Hancox, Christophe Hendrickx (now at the Unidad Ejecutora Lillo, Argentina), S.C. Jasinoski, S. Iqbal, L.A. Norton, Bruce Sidney Rubidge, Frederick Tolchard and Marc van den Brandt; the Iziko, South African Museum and the University of Cape Town in Cape Town: Emese Marie Bordy, A. Chinsamy-Turan and Roger Malcom Harris Smith (now at the ESI); the National Museum in Bloemfontein: J. Botha (now at the ESI), E. Butler and Johann Welman (now at University of Limpopo); and the Council for Geosciences in Tshwane with Johann Neveling. Contributions on nmc from the Karoo Basin by researchers based outside South Africa include the works of Bernard Battail, Richard James Butler, Jörg Fröbisch, J.A. Hopson, Leandro Carlos Gaetano, C.F. Kammerer, Jun Liu, L.C. Pusch, R. Rayner and C.A. Sidor. As can be grasped by the number of actors, the nmc research programme in South Africa is very active.

Sustained collective efforts were also developed in Zambia and Tanzania and most recent contributions on nmc are from J.A. Hopson, Adam Keith Huttenlocker, C.A. Sidor and Brenen Wynd. In Namibia, new contributions in nmc were developed by F. Abdala, L.C. Gaetano, C. Hendrickx, Helke Brigitte Mocke and R.M.H. Smith. Starting with the discovery of Triassic nmc in Madagascar in the 21st century, contributions by John Joseph Flynn, C.F. Kammerer, Lovasoa Ranivoharimanana and André R. Wyss. Continuing in southern Pangaea, India shows a few contributions from Mohd Shafi Bhat, Pradipendra Mohan Datta and Sanghamitra Ray. In Argentina, the research panorama on nmc was quite active in general but relatively quiet in relation to taxonomic changes with contributions by F. Abdala, Jose Fernando Bonaparte (1928–2019), Guillermo Cassini, Eliana Fernandez, Florencia Soledad Filippini, L.C. Gaetano, T.S. Kemp, J. Liu, Agustin Guillermo Martinelli, Ricardo Nestor Martinez, Jaime Eduardo Powell (1953–2016), Timothy Rowe, Rachel Veronica Simon Wallace and B. Wynd. In Brazil, research on nmc is excelling, which is demonstrated by the dominance of new species proposed over the first 20 years of the 21st century. Several researchers have been and are doing intensive research on nmc of southern Brazil such as F. Abdala, Mario Costa Barberena (1934–2013), J.F. Bonaparte, J. Botha, Sergio Furtado Cabreira, Ian Corfe, Sergio Dias-da-Silva, José Eduardo Figueiredo Dornelles, Jorge Ferigolo, Pamela G. Gill, Morgan Lionel Guignard, C.F. Kammerer, Leonardo Kerber, J. Liu, A.G. Martinelli, Tomas Panceri Melo, Ane Elise Branco Pavanatto, Emily Jane Rayfield, Miriam Reichel, Téo Veiga de Oliveira, Ana Maria Ribeiro, Martha Richter, Pablo Gusmão Rodrigues, Arymathéia Santos Franco, Mauricio R. Schmitt, Cesar Leandro Schultz, Marina Bento Soares and Micheli Stefanello.

Taxonomic research on nmc has been relatively quiet in northern Pangaea at the beginning of the 21st century. In Canada, contributions by Tim Fedak, Paul E. Olsen and Hans-Dieter Sues; in the United States J.A. Hopson, Ben T. Kligman, J. Liu, Adam Douglas Marsh, C.A. Sidor and H-D. Sues; in Greenland, F.A. Jenkins Jr and Michael D. Shapiro; in Germany, J.A. Hopson and H-D. Sues; in Poland Tomasz Sulej; in United Kingdom, Elsa Panciroli and I.J. Corfe; in China, Richard Carr Fox, Ke-Qin Gao, J. Liu, Lu Liu, Michael W. Maisch, Fang-Yuan Mao, Jin Meng and Corwin Sullivan; in Russia, Alexander Averianov, Mikhail Feodosievich Ivakhnenko (1947–2015), Alexey Vladimirovich Lopatin, Thomas Martin and Leonid Petrovich Tatarinov (1926–2011); in Mongolia, Paul M. Velazco, Mahito Watabe and Michael J. Novacek; in Japan, I.J. Corfe and Hiroshige Matsuoka.