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Assessing content and bias in South African Permo-Triassic Karoo tetrapod fossil collections

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A standardized taxonomic database as well as a Geographical Information System (GIS) database of all fossil tetrapods collected from the Permo-Triassic Beaufort Group rocks of South Africa has been compiled from a number of South African museum catalogues. The data capture required rigorous evaluation of the accuracy of the original records and the degree of collecting bias. The outcome of this evaluation endorsed the accuracy of the two databases and showed no significant degree of collecting bias. This standardized database, now linked to a new GIS-based database, will be a valuable resource to scientists researching Permo-Triassic biodiversity and faunal distribution patterns.

Keywords: digitized data, fossil database, Beaufort Group.

INTRODUCTION

The rocks of the Beaufort Group (Adelaide and Tarkastad subgroups) of the Karoo Supergroup cover a large proportion of the surface of South Africa (Smith 1990) and comprise an approximately 3000 m thick sequence of predominantly sedimentary rocks which are internationally renowned for their wealth of tetrapod fossils. These fossil-bearing strata represent one of the most complete and best preserved palaeo-ecological records of pre-mammalian terrestrial vertebrates in the world (Keyser & Smith 1979) and are pivotal in evolutionary studies because during this period the stem lineages to both mammals and dinosaurs arose (Broom 1932; SACS 1980).

The absolute age of the Beaufort Group is not yet well constrained, with current dates based mainly on faunal correlations. The oldest stratigraphic units are considered Middle Permian (Kazanian) (Rubidge 1995a), and the uppermost strata as Middle Triassic (Anisian) (Ochev & Shishkin 1989; Hancox *et al.* 1995; Hancox & Rubidge 1996; Hancox 1998). Because of the extensive and largely unbroken temporal record of sediment deposition, coupled with the abundance of fossils, the succession is held by many to be the global biostratigraphic standard for the non-marine Permo-Triassic (e.g. Shishkin *et al.* 1995; Lucas 1998).

For more than a century large collections of vertebrate fossils from the Beaufort Group of South Africa have been amassed (Fig. 1) and although these are now housed in institutions around the world, by far the largest and most representative collections are in museums in South Africa. These are: Albany Museum, Grahamstown; Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; Council for Geoscience, Tshwane; Iziko South African Museum, Cape Town; National Museum, Bloemfontein; Rubidge Collection, Wellwood, Graaff-Reinet; and the Northern Flagship Institution (Transvaal Museum), Tshwane.

As part of a project to assess Permo-Triassic tetrapod biodiversity patterns and for use in biostratigraphy and basin modelling, the catalogues of these South African collections have been amalgamated onto a single standardized dataset (Beaufort Group database) as well as a Geographical Information System (GIS) of vertebrate fossil data for the Beaufort Group (Nicolas 2007). This is the first time that such datasets have been compiled for mid-Permian–mid-Triassic continental vertebrate faunas and the resource (Nicolas 2007) serves as a research tool providing standardized taxonomic, stratigraphic and locality data for all specimens.

Digital acquisition, integration and application of biological collections data is increasingly viewed as fundamental to biodiversity research (Beaman *et al.* 2004). In setting up the database the quality of fossil data from contributing collections had to be evaluated and categorized to determine the degree of compliance with digital information requirements. A summary of general spatial data quality standards (as required for optimum delivery of GIS-based data) is provided in Nicolas (2007). This assessment determined and evaluated the percentage of records that could potentially be used for spatial mapping. In addition records were analysed and categorized depending on their degree of taxonomic and locality resolution, a process which further refined the quality of the data eventually utilized in the spatial map of the Beaufort Group (Nicolas 2007). This evaluation was a necessary precursor for the establishment of the GIS fossil database. The above procedure has been adopted to ensure compliance with other international natural history collection database projects such as the Global Biodiversity Facility, the Biological Collection Access Service for Europe and the European Natural History Specimen Information Network.

METHOD AND RESULTS

Primary analysis of original data from contributing collections

The original datasets provide 26 837 specimens that are theoretically usable for spatial mapping (Table 1). This figure is the sum of the original, unaltered records of each

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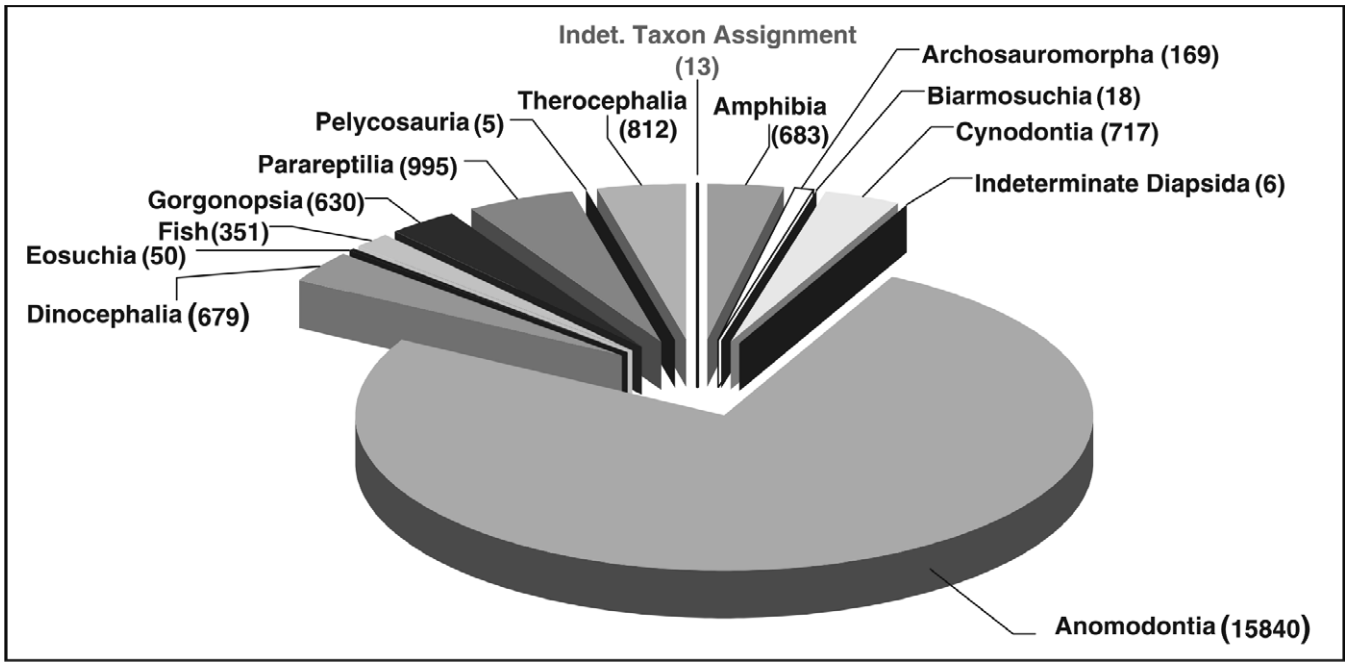

Figure 1. Relative numbers of fossils of taxa that have been recovered from the rocks of the Beaufort Group. Values in brackets reflect numbers of individuals. In the databases there are 13 taxon assignments for the Beaufort Group: Amphibia; Anomodontia; Archosauromorpha; Eosuchia, Biarmosuchia; Cynodontia; Diapsida; Dinocephalia; Fish; Gorgonopsia; Parareptilia; Pelycosauria and Therocephalia. Diapsida was subdivided into Archosauromorpha, Eosuchia and unidentified Diapsida for this study. The grouping of Diapsida is still retained to accommodate five errant specimens from the National Museum. In addition there is a final grouping of 13 fossils with unknown taxon assignment.

contributing museum. After careful investigation of the data from each museum catalogue, criteria for the elimination of unreliable data were established (Table 2). These included the removal of data pertaining to fossils not from the Beaufort Group, specimens that are not vertebrate, and records that had no identification and locality data. After this initial round of data elimination, the actual number of potentially useful vertebrate fossils from the Beaufort Group amounted to 20 968 (Table 1).

Primary analysis of the quality of Beaufort Group data

All recorded specimens from the Beaufort Group were categorized according to whether they had: locality data; no locality data; biozone data. This was necessary to assess the accuracy of locality information and is an exercise in quantifying the degree of compliance with digital information requirements. For this analysis no distinction was made for different methods of recording locality data (e.g. GPS coordinates or Farm Name data). However, such distinctions in locality data resolution were utilized in the establishment of the GIS database (Nicolas 2007). For accuracy it was necessary to update outdated biozone data in accordance with Rubidge (1995b), the currently accepted biozonation scheme of the Beaufort Group. The updating methodology (detailed in Nicolas (2007)) did not reconstruct biozone data for specimens with locality data. The majority of locality data from the contributing museum databases had written descriptions rather than geographic coordinates of localities. The difficulty in using these textual references to locate the provenance of specimens is problematic (Nicolas 2007) so it was decided to utilize the biozone assigned to each specimen in order to interpret biodiversity trends. The rationale for this action is that the portion of records with biozone data

Table 1. Useable data after initial elimination from original records. The original datasets from the seven contributing museum collections (Column 1) provide a *theoretical potential* of 26 837 (Column 2). The *theoretical potential* of 26 837 is the sum of the original, unaltered records of each contributing museum. Unreliable records were eliminated (see Table 2). After data elimination, the *actual potential of exploitable vertebrate specimens* in the Beaufort Group amounted to 20968 (Column 3). This table shows the number of records per museum collection remaining after elimination. These values are expressed as a percentage (column 4) of the records which can be utilized when compared to the original records.

Database	Total records	Record (after initial elimination)	% Potential viable data
Albany Museum	588	468	79.59
Bernard Price Institute	4780	4483	93.79
Council for Geoscience	7579	5322	70.22
National Museum	3520	3171	90.09
Rubidge Collection	854	850	99.53
Iziko South African Museum	6797	5424	79.80
Transvaal Museum	2719	1250	45.97
	Theoretical total	Potentially usable total	% Potential viable total
	26837	20968	78.13

would be capable of presenting broad biodiversity trends across and within the assemblage zones of the Beaufort Group. On completion of the GIS-initiative, all records will have been geo-referenced and so a fuller and more refined picture will result (Nicolas 2007).

Records with no locality and no biozone information cannot be used for either spatial mapping or biodiversity analysis. Those records with both biozone and locality data (with varying degrees of resolution) and those with only locality data may be used for spatial mapping. In so far as digital information is concerned, the optimum would be a 100% recording of fossil finds with locality information refined to thousandths of a degree, WGS datum coordinates. As it currently stands, 51% of the records from the Beaufort Group have locality information, but no biozone information; 44% have locality and biozone information; and 5% have neither locality nor biozone information.

Of the 9144 Beaufort Group specimens with biozone information, 57% (5193) are identified to genus level and the remaining 43% (3951) are unidentified (Fig. 2). The 9144 records with biozone information represent 44% of the total number of records for the Beaufort Group. This means that 25% of all records from the Beaufort Group are classified to genus level and have biozone information and 19% of records are unidentified, but have biozone information.

The unidentified specimens with biozone allocation (3951) (Fig. 2) were subdivided into their relative alliance to the eight biozones of the Beaufort Group. The *Eodicynodon* Assemblage Zone has 31 unidentified specimens, the *Tapinocephalus* Assemblage Zone has 140 unidentified specimens (1% of the total Beaufort Group population), the *Pristerognathus* Assemblage Zone lists five unidentified specimens, the *Tropoidostoma* Assemblage Zone lists 549 unidentified specimens (3% of the total Beaufort Group population), the *Cistecephalus* Assemblage Zone lists 2109 unidentified specimens (10% of the total Beaufort Group population), making it the biozone with the greatest amount of unidentified specimens, the *Dicynodon* Assemblage Zone lists 368 unidentified specimens (2% of the total Beaufort Group population), the *Lystrosaurus* Assemblage Zone lists 172 unidentified specimens (1% of the total Beaufort Group population) and the *Cynognathus* Assemblage Zone lists 259 unidentified specimens (1% of the total Beaufort Group population). The remaining 318 unidentified specimens that have biozone information are relegated to various transitional zones (Nicolas 2007).

Only 71% of all the 20 968 fossil vertebrates collected from the Beaufort Group have been identified to family, and of these only 5193 (25%) are identified to genus level and have biozone data. The *Eodicynodon* Assemblage Zone lists 51 specimens identified to genus level. The *Tapinocephalus* Assemblage Zone lists 183 specimens belonging to various genera (this comprises 1% of the total Beaufort Group vertebrate fossils), the *Pristerognathus* Assemblage Zone lists 34 specimens belonging to various genera, the *Tropidostoma* Assemblage Zone lists 361 specimens assigned to various genera (2% of the total Beaufort Group vertebrate fossils), the *Cistecephalus* Assemblage

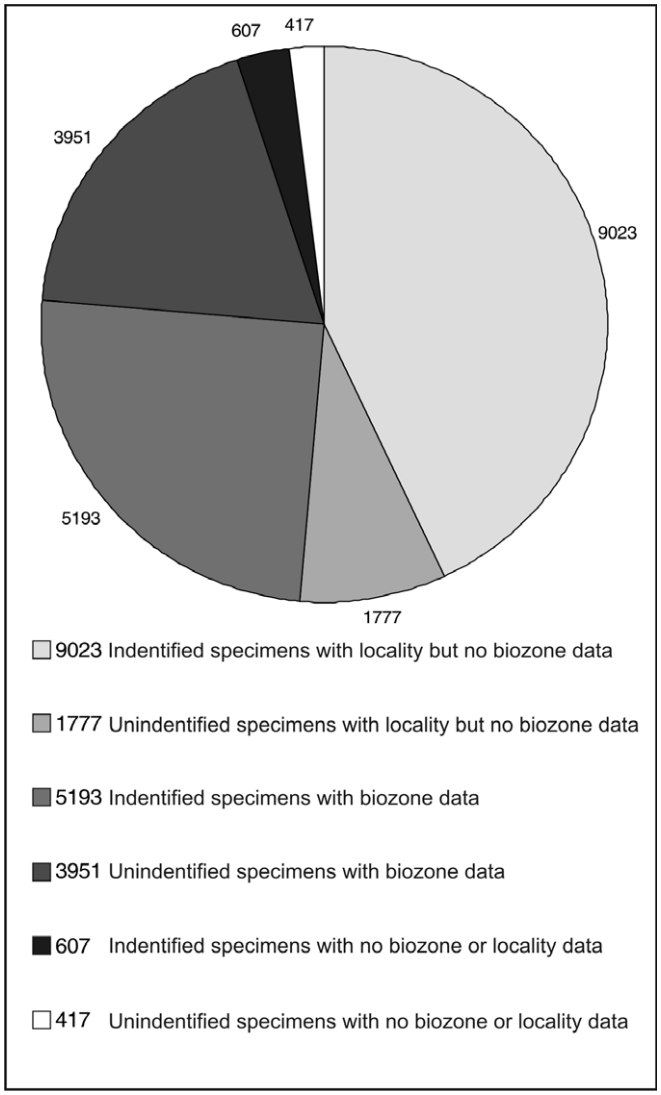

Figure 2. Analysis of Beaufort Group data, showing the subdivision of records into those identified to genus level or those as yet unidentified.

Zone lists 1037 specimens classified to various genera (5% of the total Beaufort Group vertebrate fossils), the *Dicynodon* Assemblage Zone lists 268 specimens belonging to various genera (1% of the total Beaufort Group vertebrate fossils), the *Lystrosaurus* Assemblage Zone lists 2559 specimens classified to various genera (12% of the total Beaufort Group vertebrate fossils), the highest count of identified specimens in the Beaufort Group, and the *Cynognathus* Assemblage Zone lists 562 specimens belonging to various genera (3% of the total Beaufort Group vertebrate fossils). The remaining 143 specimens identified to genus level are catalogued as being from various transition zones. The low numbers of specimens listed above are minimum values as only those records with assemblage zone data were utilized. There are 9023 specimens identified to genus level without a biozone allocated, but they do have locality data (Fig. 2). These will be allocated a biozone once the GIS database is completed.

Comparative analysis of contributing museum collections

A comparative analysis of different museum collections was performed by focusing on the specimen totals in each

Table 2. Elimination of non-viable data. After investigation of the content of each museum collection, criteria for the elimination of certain records were established. This table shows those records per museum collection requiring elimination. Bold font in column 2 refers to a specific datafield within a collection.

Collection name	Data Eliminated (Spreadsheet Rows)
Rubidge Collection	**Locality**: Unlisted farm locality & district information; Keetmanshoop; Lady Frere. Taxon: Mesosaurus; Sysphinctostoma
BPI Collection	**Biozone**: Equivalent of L. Cistecephalus Z. **Geology**: ?Stormberg; Equivalent of Beaufort. **District/Country**: Ficksburg (FS); Namaqualand (NC); Fouriesberg (FS); Clocolan (FS); Ceres (WC); Worcester (WC); Calvinia (NC); Prieska (NC); Marquard; Ladybrand; Ladygrey; Zambia. **Genus**: Tritylodon; Amniota; Dinosauria; Plants; Taxon Indet.; Squamata? ?Diapsida; Reptilia; Indet.; Tetrapoda; Trace Fossil; Worm Burrows; Indet. Amniote; Indet. Dinosaur; Indet. Reptile; Indet. Tetrapod Burrow Cast; Unidentified Bone in Lag. **Locality**: Unlisted Locality Information; Locality Unknown; Various Localities.
National Museum Collection	**Taxon**: Unidentified Taxon & Current Identification; Aetonyx; Saurischia; Dinosauria; Anchisaurus; Baroqueosuchus; ?; Basutodon (Large Thecodont); Bothriolepis; Invertebrata; Conchostracans; Elpistostege; Euskelosaurus; Roccosaurus; Fabrosaurus; Footprints (Bradysaurus?); Unlisted Information; Gryponyx; Herrerasaurus; Holopthychius; Hout; Footprint (Ichnitis); Massospondylus; Melanosaurus; Mesosaurus; Orthosuchus; Mollusca (Palecypoda); Pedeticosaurus; Plant; Rauisuchid; Reptile; Riojasaurus (Prosaurosushia); Saurischia; Scaumenacia; Sysphinctostoma; Thecodontosaurus; Tritylodon; Unidentified; Unknown; Various; Worms; Dinosauria; Invertebrata; Lacertilia; Ornithischia. **Country/Locality**: Unlisted district/farm; Unlisted province; Quebec (Canada); Barkley East; Bethlehem; Clarens; Golden Gate; Clocolan; Elliot; Essex (England); Ficksburg; Fouriesburg; Gumtree; Herschel; Hopetown; Jamestown; Lady Frere; Ladybrand; Leribe; Marquard; Mafeteng; Maseru; Rosendal; Slabberts; Zastron; Wes Duitsland (Holzmaden). **Geology**: Non-applicable Biozone; Elliot; Clarens; Molteno; Ecca; Stormberg; Waterford; Whitehill. Zone: Euskelosaurus; Massospondylus; Trityledon Acme Zone
Iziko South African Museum Collection	**Geology/Age/Biozone**: Ecca; Stormberg; Dwyka; Witteberg; Carboniferous; Bokkeveld; Devonian; Late Jurassic; Early Cretaceous; Cretaceous; Eocene; Middle Pennsylvanian; Upper Dwyka; Sakemena; Adolphspoort; Blue Lias; Carbondale; Elliot; Great Oolite; Green River Shale; Greensand; Irati; Kirkwood; Kupferschiefer; Lower Chalk; Lower Elliot; Lower Greensand; Lower Sakemena; Rio Bonito; Serra Alba; Whitehill; Early Triassic; Earliest Triassic; Early Carboniferous; Early Devonian; Early Jurassic; Early Permian; Jurassic; Kimmeridgian; Late Cretaceous; Late Jurassic/Early Cretaceous; Late Triassic; Lower Devonian; Lower Permian; Middle Devonian; Oligocene; *Euskelosaurus*; Reptile Beds. **Country**: Scotland; USA; Tanzania; Madagascar; Zambia; Namaqualand; Angola; Australia; Brazil; England; France; Germany; Great Britain; Ireland; Lebanon; Lesotho; Malawi; Mozambique; Namibia; North America; Wales; Zimbabwe; Unlisted locality (district/farm). **Province**: Caithness; Cambridge; Dumfries; Illinois; Mocamedes; New South Wales; Parana. District: Barkley East; Boputhatswana; Calvinia; Britstown; Ceres; Clocolan; Carnarvon; Dorset; Elliot; Fouriesburg; Hay; Herbert; Herschel; Hopetown; Kirkwood; Jansenville; Lady Grey; Ladybrand; Luangwa; Maclear; Mafeteng; Messina; Mokerong; Not Known; Outshoorn; Port Elizabeth; Port Shepstone; Prieska; Swellendam; Ranohira; Quacha's Nek; Quthing; Sebungwe; Uitenhage; Underberg; Utrecht; Will County; Williston; Wodehouse; Worcester. **Genus**: Beetle; Mammal; Osteolepis; Acanthodes; Acanthodian; Acanthopterygid; *Acrodus*; *Adroichthys*; *Aestuarichthys*; *Aetonyx*; *Astrodon*; Camarasauridae; *Opisthias*; *Pleurocoelus*; *Algoasaurus*; *Alopias*; *Anaethalion*; Anchisaurid; *Anoxypristis*; Anura; Arthrodire; *Asteracanthus*. **Class/Subclass**: Aves; Insect; Insecta; Mammalia; Placodermi; Vertebrata incertae sedis; Holocephali; Lepospondyli; Neornithes; Prototheria; Testundinata; Theria; Insectifora; Antiarchi; Anura; Arthrodira; Batoidea; Chelonia; Crocodylia; Cyprinodontiformes; Ellimmichthyformes; Elopiformes; Gadiformes; Galeomorpha; Ichthyopterygia; Lepisosteiformes; Mesosauria; Ornithischia; Sauropodamorpha; Lebias; Diplomystus; Elopoidei; Dastilbe; Anaethalion; Palaeomolva; Lamna; Carcharodon; Squalicorax; Isurus; Alopias; Heterodontus; Campylodon; Communis; Leptolepiformes; Pachycormiformes; Paleospondyliformes; Pelecaniformes; Perciformes; Salmoniformes; Saurischia; Triconodonta
Council for Geoscience Collection	**Genus**: Indet.(No identification listed); Anura; Anomodontia; Lower Jaw; Nodules; Padda; Stromatolite; Therapsida; Theriodont; Vertebrata; Indet. Anomodontida. **Locality**: Unlisted locality information
Albany Museum Collection	Plants, Unlisted Acc. No., **Geology**: Buntsandstein, Lower Triassic; Elgin Sandstone; Gravel Banks; Cave Sandstone; Red Beds; Elliot Formation; Dwyka; Kirkwood Formation; Uitenhage Group (Kirkwood Formation); Upper Dwyka Shales; Shale. **Country and Locality**: England (Shale); Lyas (Switzerland). **District**: Barkley East; Scotland; Farm Rietfontein; Barkley Pass; Lyme Regis, England; Bolotive; Bunter Landstein, Switzerland; Farm Glencoe (Barkley East); Ibid.; Kirkwood Cliffs, Sunday's River; Lady Frere, Glen Gray; Mafeteng District, Lesotho; Moirosi's Mount, Lesotho; N. Luangwa Valley, N. Malawi; Near Alice; Penhoek, Stormberg; Riechen, Switzerland; Skietnek, Kirkwood Village; Thaba-Chau (Tsueu, Chu, Cho); Unknown. **Taxon**: Unknown; Small Reptile; Unidentified; Massopondylus; Chelonia; Unidentified; Sauropod Dinosaur; Dinosaur Prosauropod; Anomodont; Fossil Wood – Podocarpus; Dinosaur-like Styracosaurus; Hortalotarsus; Large Prosauropod? *Euskelosaurus*; *Mesosaurus*; Saurischia – Prosauropod Dinosaur; Saurischia (perhaps *Plateosaurus*); Saurischia (Dinosaur); Saurischia (Euskelosaurus); Small Reptile; Thecodontia – Pseudosuchian; Therapsid; Therapsid – Unidentified; Theropod – *Nqebasaurus*; Unidentified; Unidentified Small Reptile; Unidentified Small Dinosaur; Unknown; Unlisted Taxon Information
Transvaal Museum Collection	**Genus**: Unidentified; Undescribed Anomodont; Bivalve Shells; Boks 140; *Aristosaurus*; *Eozostrodon*; Fossil Bone with Matrix; Fossil Reptile; *Gangomopteris* (a plant); *Gigantoscelus*; Large Anomodont; Large Mammal; *Massopondylus*; Reptile; Small Anomodont; Therapsid?; Theriodontia?; Theropoda; Unident.; Unlisted Genera. **Biozone**: Cave Sandstone; Red Beds; Rhaetic (Late Triassic). Locality: Tunnels; 'Tunnels' Donga; Senekal; Jame's Donga; Provenance Unknown; St. Fort (Setsoanastad) Bethelehem District; Witjies Hoek; Milius Donga; Unlisted locality information; Letjiesbosch; Klipbank; Karoo Site; Arcadia Donga; Commander Jone's House; Apparently East of Fossil Valley; 'Diamond Diggings'. **Province**: Unlisted locality information. **Country**: Unlisted locality information; England

Table 3. Total numbers of specimens per collection.

Museum collection	Total number of specimens	Unidentified specimens	Total number of identified specimens
Albany Museum	468	44	424
Bernard Price Institute	4 483	2 470	2 013
Council for Geoscience	5 322	58	5 264
National Museum	3 171	987	2 184
Rubidge Collection	850	509	341
Iziko South African Museum	5 424	1 629	3 795
Transvaal Museum	1 250	448	802
Totals	20 968	6 145	14 823

collection and the diversity of genera in each collection. This exercise identified the collections which curate the largest sample of any particular taxon and will thus facilitate future research. In addition it has highlighted problems in the fossil record and where future collecting should be undertaken. We have found that the content of the different collections is dependent on: geographic position of the museum; research focus of past and present palaeontologists employed by the museum; and diligence of the palaeontologists to pursue fieldwork. Because of these variables the numbers of specimens and taxonomic diversity of the individual collections varies greatly.

Specimen totals in each collection

The total number of specimens within each of the collections is recorded in Table 3. This total includes both unidentified specimens as well as specimens identified to genus level. Any record that had no taxonomic classification (e.g. 'Unknown' or 'Unidentified' or 'Indet.') or the taxonomic classification was too broad (e.g. 'Parareptile' or 'Synapsid') was relegated to the category 'Unidentified Specimens'. Because of the very large number of records spread between the seven contributing collections, it was considered beyond the scope of the project to verify each entry from each museum for correct identification. However, because of the accessibility of the BPI Palaeontology, the classification in the amphibian and anomodont categories were updated, verified and recorded in the synthesized records of the Bernard Price Institute for Palaeontological Research (Nicolas 2007). The remaining taxa were updated in so far as current taxonomy allowed. Flaws in the contributing datasets became apparent after completion of the standardization and 'clean-up' procedures (Nicolas 2007: appendix F). The contents of this Appendix F will be used as part of the data-cleaning component in Phase 1 of the GIS-initiative (Nicolas 2007) and will fast-track the taxonomic updating of all the museum collection records.

Diversity of genera in each collection

Iziko South African Museum has the greatest diversity of genera (163), followed by the Bernard Price Institute (124), the National Museum (88), the Rubidge Collection (85), the Transvaal Museum (73), the Council for Geoscience (63) and the Albany Museum (56) (Table 4)

Table 4. Diversity of genera within each collection. This table lists the diversity of genera within each collection, in order of decreasing diversity.

Museum collection	Diversity of genera
Iziko South African Museum	163
Bernard Price Institute	124
National Museum	88
Rubidge Collection	85
Transvaal Museum	73
Council for Geoscience	63
Albany Museum	56

Extent of collecting bias of fossils from the Beaufort Group

Once the amalgamated Beaufort Group dataset and the foundation GIS database of fossils from the Beaufort Group were established, it was essential to determine the 'validity' of the collection for biodiversity analyses by calculating the degree of collecting bias (this bias being the over-representation of fossils from a particular locality, biozone or of a specific taxon). The foundation GIS database was utilized only to determine the extent of collecting bias within the Beaufort Group (Karoo Supergroup) of South Africa caused by the specialist interest of a field collector/palaeontologist currently or in the past and is currently undergoing further refinement, with the end result that it will be an invaluable research tool. The methods and processes involved in setting up the foundation GIS-database are explained in Nicolas (2007).

Using geo-spatial data in the form of Neighbourhood and Gap Analysis to determine collecting bias

To test the reliability of the Beaufort Group data for analytical purposes it was necessary to determine 'evenness' in the geographic distribution of fossil localities in the Beaufort Group. If the distribution of fossil localities were found to be highly localized or biased to specific regions, this would impact negatively on the accuracy and significance of any current or future distribution or biodiversity study. Accordingly a 'Gap and Neighbourhood' Analysis was undertaken to determine if there was any geographic bias in the museum records.

Arcview 3.2 program with its spatial analysis extension were used to create a distance surface. The distance was calculated between the locations of all the specimen points. A contrast stretch was applied to the resultant surface to improve the visualization of the surface

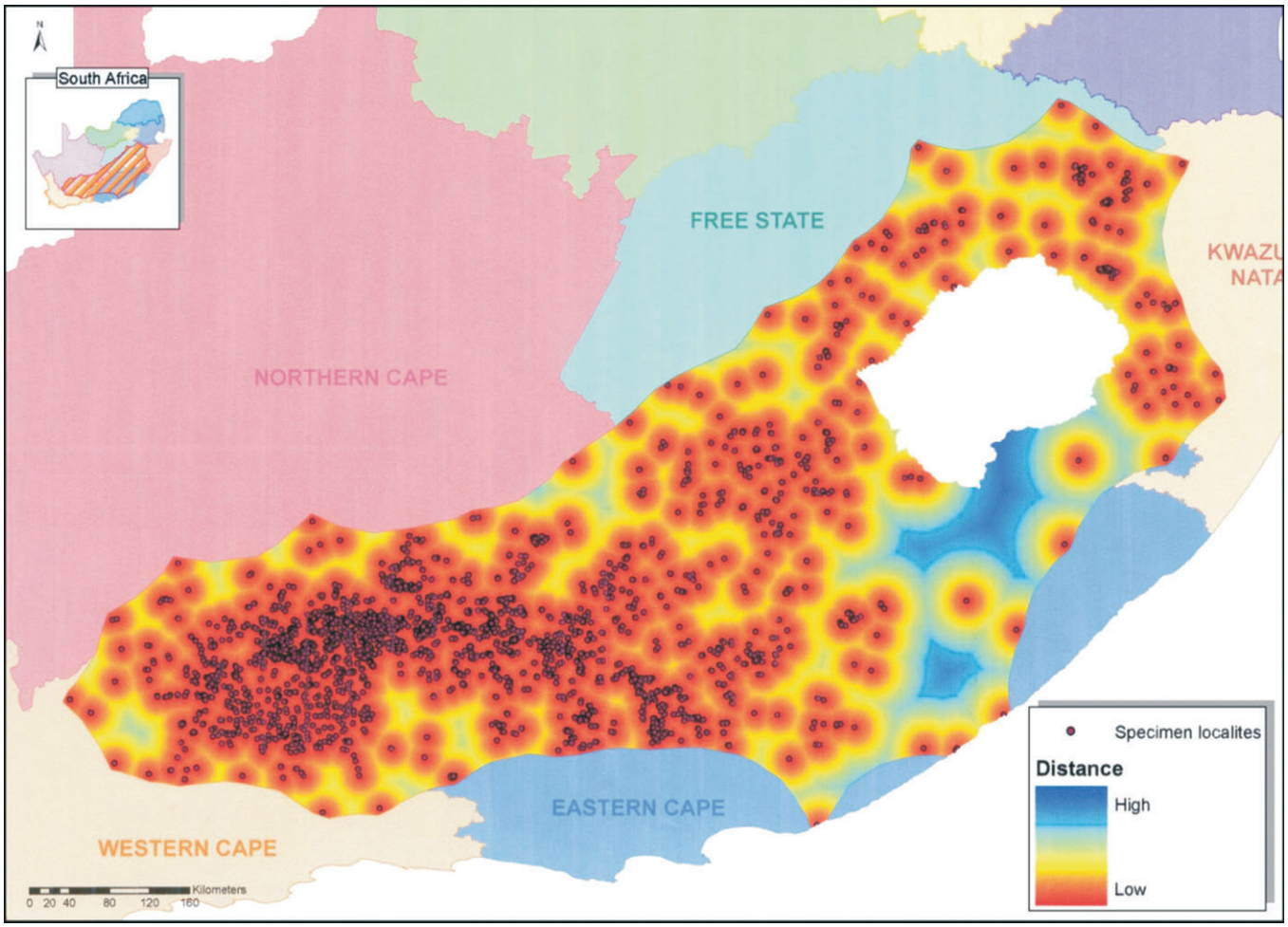

Figure 3. Gap analysis of tetrapod fossil localities in the Beaufort Group of South Africa.

(Cooper & Netterberg 2004). The surface was derived for an area larger than the extent of the Beaufort Group, and then masked to the extent of the sampling to remove edge effects.

Figure 3 indicates the sampling distribution of fossils in the Beaufort Group. Several factors could account for a lack of sampling in certain areas. These include absence of outcrop; lack of prospecting; or paucity of fossils. Blue shading indicates a substantial distance between fossil collecting sites, while a red–orange spatial pattern indicates a relative closeness of fossil sites to each other. The overwhelming dominance of orange–red (Fig. 3) indicates that the majority of fossil localities are in close proximity to each other with an *even* distribution and points to a lack of sampling bias. This implies that the sampling of the Karoo fossil fauna as represented by the fossils in the collections will provide an accurate interpretation of the reality of faunal distribution patterns and ecological representation for the Beaufort Group.

Once the equality of the distribution of fossil finds across the Beaufort Group was established, Neighbourhood Analysis Technique was applied to determine where the highest density of specimens was located (Fig. 4). The Neighbourhood Statistic used was the sum of all the points, with a circle neighbourhood within an 8-km radius (Cooper & Netterberg 2004). This was used to provide an indication of the number of specimens from a given locality. The resultant surface was 'smoothed out' to improve visual representation of the analysis (Cooper & Netterberg 2004).

The incidence of dark red shading represents those localities which have the highest density of specimens (Fig. 4). The obvious horizontal line of red/orange dots in Figure 4 highlights that it is most certainly a collecting bias caused by the superior vertical exposures of fossil bearing strata in the Sneeuberg and Neuweveld mountain ranges along the Great Escarpment. The strata most exposed in the escarpment belong to the *Tropidostoma, Cistecephalus* and *Dicynodon* biozones. Figures 3 & 4 clearly show the geographic collecting bias along the Great Escarpment. This means that these biozones may have been over-collected compared to other biozones.

As indicated by the yellow shading in Fig. 4 most fossil sites yield an average of 1–60 specimens. Localized bias on the yield of fossils at specific sites is the result of differing resolutions of locality information (i.e. GPS, Farm Name, and District) and well as the result of superior exposures. Localized biases become inconsequential when viewed across the scale of the entire Beaufort Group because the finer details of locality data specifics are blurred in the light of the larger low resolution picture of the Beaufort Group. We are satisfied that the concentration of collecting in the Great Escarpment is the result of superior and extensive exposures of clean rock faces and that the Gap and Neighbourhood analyses generally reflect a lack of collecting bias as regards individual taxonomic specializa-

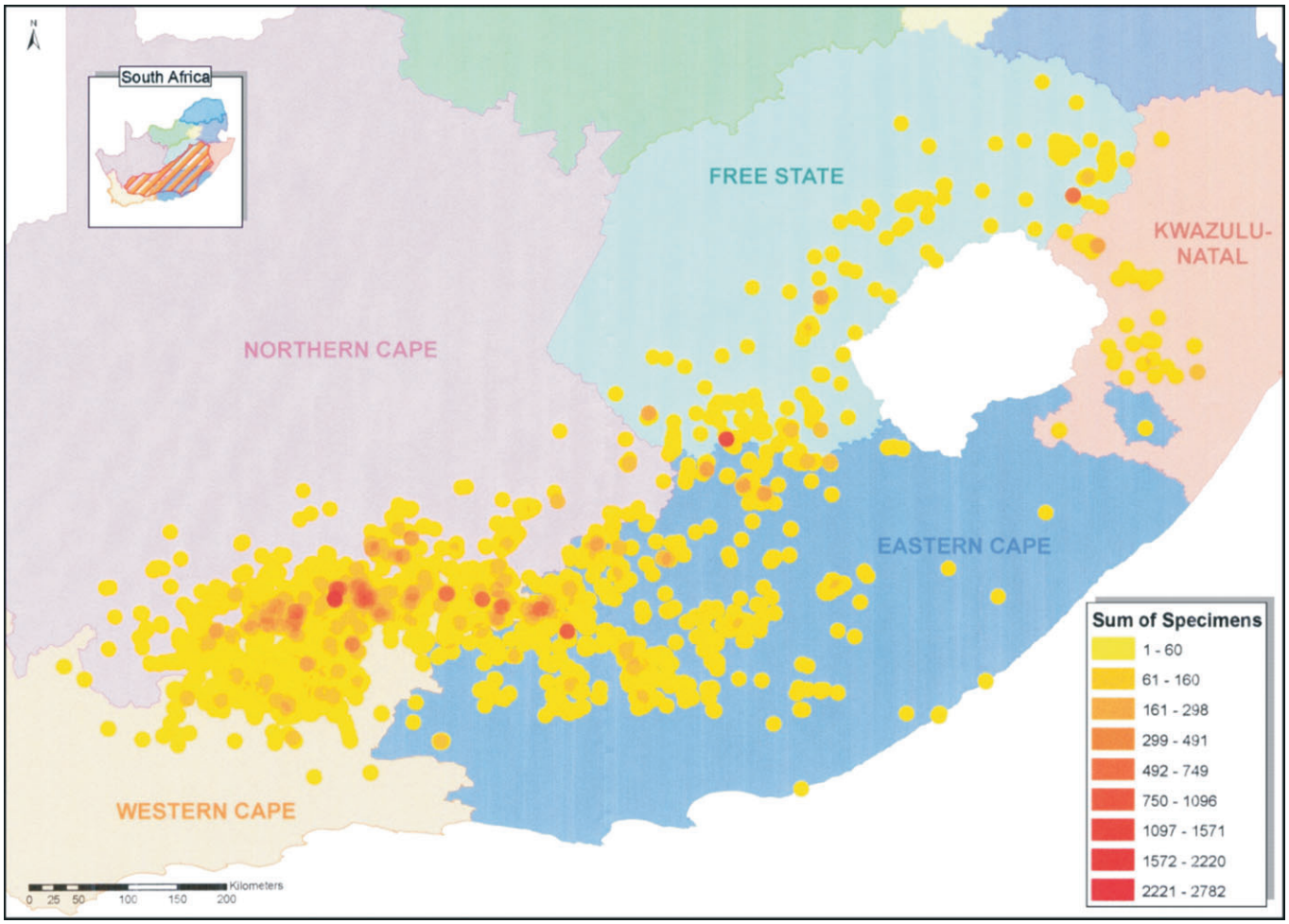

Figure 4. Neighbourhood analysis of fossil finds in the Beaufort Group of South Africa.

tions, or localized over-representation. Such a resultant allows researchers to confidently analyse the faunal distribution assemblage as well as biodiversity patterns of the Beaufort Group (Karoo Supergroup) of South Africa.

CONCLUSION

For the first time an amalgamated, standardized database (Beaufort Group database) as well as a GIS database incorporating all tetrapod fossils from the rocks of the Beaufort Group has been established. They are stored on a dedicated computer at the Bernard Price Institute for Palaeontological Research and are available to scientists to be utilized as a research tool. As the Beaufort Group succession preserves the most complete record of Middle Permian to Middle Triassic continental tetrapod biodiversity, this database is of great importance for an understanding of biodiversity changes and for biostratigraphic input to basin modelling over this extended period.

The databases reflect the diversity of tetrapod genera and the collections where they are curated, including numbers of specimens of each genus and their respective locality and/or biozone data. This unique dataset provides accurate numbers of specimens of the various taxa which have been collected. In addition the database will facilitate future taxonomic research as it is now possible for researchers to identify museums which curate the largest sample of any particular taxon. Finally, future researchers can be assured of the reliability of their results pertaining to biodiversity within the Beaufort Group because we have found no taxonomic bias due to selective collecting of particular taxa by specialist palaeontologists.

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