

Multivariate analyses of Cenozoic mammalian faunas from Riversleigh, northwestern Queensland

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Mammalian faunal lists of Riversleigh fossil sites were compared using several techniques to assess the age relationships between 75 Riversleigh sites and the central Australian Ngama, Kutjamarpu and the Northern Territory Bullock Creek Local Faunas. Presence/absence data of the sites' mammalian faunas were compared in terms of faunal similarity using cluster analysis, ordination, seriation and cladistics (the latter method has not previously been used to compare such data). The analysis was repeated using only sites with eight mammal taxa or more. The analyses also tested and supported the Riversleigh System concept introduced by Archer *et al.* (1989). The analyses confirmed the placement of several sites previously assigned (Creaser 1997, Arena 2004) to a System based on their geology and topography. However, the analyses could not confirm the assignment of sites with less than eight taxa. Sites with eight mammal taxa or more were used as diagnostic sites for a preliminary description of the "Systems" or "Faunal Zones" (*sensu* Arena 2004).

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VERTEBRATE FOSSIL DEPOSITS in the Riversleigh World Heritage Area, located in Lawn Hill National Park, northwestern Queensland, have been excavated since the late 1970s. Over 300 sites have been recorded, spanning the late Oligocene to the Holocene. The faunal composition from each site has been collected, processed and interpreted to represent a unique local fauna (LF), assemblage or local palaeocommunity (Archer *et al.* 1997). Archer *et al.* (1989) also introduced the term "System" to define three sequential combinations of rock/faunal assemblages interpreted to span the late Oligocene to late Miocene sediments of Riversleigh. System A was interpreted as late Oligocene, System B as early Miocene and System C as middle to early late Miocene. This informal use of the term 'System' differs from the more traditional geological term 'System' which is a rock-specific term (i.e. 'a major chrono-

stratigraphic unit of worldwide significance' or 'the rocks formed during a *period* of geological time': Bates & Jackson 1984). Megirian (1994) challenged the Systems of Archer *et al.* (1989) by pointing out that it involves a combination of geological and faunal concepts rather than just one or the other. Moreover, Archer *et al.* (1997) used both geological and faunal data in their biocorrelation of the Riversleigh assemblages.

Radiometric dating of Riversleigh sites, using U/Pb isotopes recovered from calcite samples, is in progress (Elizabeth Price, pers. comm. 2006). In the interim and to date, biocorrelation (comparison of fossil taxa in undated deposits with others in securely-dated deposits) and stage of evolution have been the principle tools used to estimate the relative ages of Riversleigh fossil faunas (Archer *et al.* 1995, Archer *et al.* 1997, Murray & Megirian 2000, Myers & Archer 1997, Woodburne *et al.* 1994). The Kutjamarpu LF (South Australia), the Ngama

LF (South Australia) and the Bullock Creek LF (Northern Territory) are the principle sources of the correlation. The Riversleigh System A LFs have been demonstrated to correlate with the Ngama LF (late Oligocene, magnetostratigraphically dated at about 24–26 Ma), System B LFs with the Kutjamarpu LF (early Miocene) and System C with the Bullock Creek LF (middle Miocene) (Archer *et al.* 1995, Archer *et al.* 1997, Archer *et al.* 1999, Murray & Megirian 2000, Myers & Archer 1997, Woodburne *et al.* 1994). Topographic and stratigraphic data have been very useful in assessing the relative ages of the sites based primarily on demonstrated or inferred superposition (Creaser 1997, Arena 2004).

Statistical techniques such as cluster analysis and ordination have been used to interpret similarities of individual local faunas (LFs) at specific taxonomic levels (de Bonis *et al.* 1992, Shi 1993, Bennington & Bambach 1996, Bonuso *et al.* 2002, Elewa, 2004, Fenerci-Masse *et al.*, 2004, Myers 2002, Palombo *et al.* 2002, Peláez-Campomanes *et al.* 2003). Although the statistical method used by different authors may be slightly different worldwide (i.e. using different similarity indices or different types of ordination), fundamentally it is a well established method. Rich *et al.* (1991), for example, used cluster analysis (Simpson's Coefficient) at the generic level to assess the taxic similarity of Australian Cainozoic fossil vertebrate sites including a number from Riversleigh. In the appendix of Murray *et al.* (2000), Rich also performed a cluster analysis on *Neohelos* populations to extract taxonomic and biochronological meaning from the data. Similarly, Megirian *et al.* (2004) used a cluster analysis to compare the faunal similarity of Riversleigh sites. Their results are somewhat different from ours and are compared to our results and thoroughly reviewed in the Discussion.

In this study we test four main hypotheses:

1. Riversleigh sites accumulated fossils at different periods of time;
2. Riversleigh sites accumulated fossils during three main rock/taxa intervals

characterisable as Systems A, B and C;

3. Systems A, B and C are sequential in time with A being the oldest and C being the youngest; and

4. Specific LFs, groups of LFs or Systems at Riversleigh accumulated at periods of time that correlate with the Bullock Creek, Kutjamarpu and Ngama LFs.

In addition, research carried out in this study enables tests of current hypotheses about the relationships of individual assemblages (e.g. whether Keith's Chocky Block Site is referable to System B or C [Morrell 2002]). We also compare the results given by different analyses and by different similarity indices and assess the approach most suitable for data of this kind.

Materials and Methods

Data compilation

The data examined consist of the lists of land mammals identified to species level only from 75 Riversleigh sites and from three non-Riversleigh Australian sites, Kutjamarpu, Ngama and Bullock Creek, compiled from published and unpublished sources. Bats were excluded from the analysis because there is evidence that they may skew the results due to potential taphonomic biases (Hernández Fernández & Peláez-Campomanes 2003). The Riversleigh sites used are listed in Table 1. The raw data were extracted from the updated species list compiled by Archer *et al.* (2006) for the Riversleigh faunas. The species lists used for Kutjamarpu, Ngama and Bullock Creek are listed in the Appendix. The compiled data consists of all mammalian taxa identified before August 2005. A total of 215 mammal species (280 species from Riversleigh and 37 from the non-Riversleigh sites) were included as presence/absence data (0 indicates absence; 1 indicates presence). Although abundance data are usually found to be more descriptive of the fauna in palaeontological studies than presence/absence data (Johnson & McCormick 1999), it is

Table 1. List of sites with abbreviations ordered by Systems (as found in the literature).

System A sites

AL – AL Site₂
 BO – Burnt Offering Site₁
 Boles – Boles' Bonanza Site₁
 BR – Bone Reef Site₃
 D – D Site₁
 Dun – Dunsinane Site₂
 G – G Site₂
 GG – Gillespie's Gully Site₁
 H – Hiatus Site₁
 HS – Hiatus South Site₂
 JA – Jeannette's Amphitheatre Site₃
 JJJ – Judy's Jumping Joint₁
 LL – Rackham's Low Lion Site₁
 LSO – LSO Site₁
 MIM – MIM Site₁
 QL – Quantum Leap Site₁
 SB – Sticky Beak Site₁
 UBO – Upper Burnt Offering Site₁
 VIP – VIP Site₁
 WH – White Hunter Site₁

System B sites

Bite – Bitesantenary Site₁
 Boid – Boid Site₁
 BSE – Boid Site East₁
 CR – Creaser's Ramparts Site₂
 CS – Camel Sputum Site₁
 DT – Dirk's Towers Site₂
 Hel – Helicopter Site₁
 Ina – Inabeyance Site₁
 JH – Judith's Horizontalis Site₂
 MM – Mike's Menagerie Site₁
 MPP – Mike's Potato Patch Site₁
 NG – Neville's Garden Site₁
 Out – Outa Site₁
 PIR – Price Is Right Site₄
 RSO – RSO Site₁
 RV – Rat Vomit Site₁
 TB – Ten Bags Site₁
 U – Upper Site₁
 VD – View Delight Site₁
 WW – Wayne's Wok Site₂

₁ Creaser, 1997.₂ Arena, 2004.₃ Archer *et al.*, 1997.₄ Roberts, 2004.**System C sites**

AL90 – AL90 Site₂
 Bob – Bob's Boulders Site₁
 CK – Cadbury's Kingdom Site₂
 COA – Cleft of Ages Site₂
 Dome – Dome Site₂
 En – Encore Site₂
 FF – Fireside Favourites Site₁
 Gag – Gag Site₁
 GC – Gotham City Site₁
 GOH – Gone Over Here Site₁
 HH – Henk's Hollow₁
 JC – Jim's Carousel Site₂
 JJ – Jaw Junction Site₁
 JJS – Jim's Jaw Site₁
 KCB – Keith's Chocky Block Site₂
 KJ – Kangaroo Jaw Site₂
 LD94 – LD94 Site₁
 LM – Last Minute Site₁
 Main – Main Site₁
 Pha – Phalanger Site₁
 QQ – Quentin's Quarry Site₁
 Ring – Ringtail Site₁
 SD – Sue's Diprotodontid Site₁
 TT – Two Trees Site₁
 Wang – Wang Site₂

Sites of unknown age

300BR – 300BR Site
 AR – Arachnea Ridge Site
 FT – Fig Tree Site
 Mesa – Mesa 3 Site
 RRR – Rick's Rusty Rocks Site
 Roo – Roo site

Other sites

BC – Bullock Creek Local Fauna (Middle Miocene)₃
 CC – Carrington's Cave (Recent)
 Kut – Kutjamarpu Local Fauna (Early Miocene)₃
 MSC – Message Stick Cave
 Nga – Ngama Local Fauna (Late Oligocene)₃
 RR – Rackham's Roost Site (Pliocene)₃
 Ter – Terrace Site (Pleistocene)₃

very difficult to collect abundance data from the Riversleigh material. Aside from being time-consuming (with over 30,000 Riversleigh specimens now registered), this process involves assignment of all specimens to taxonomic groups. The majority of postcranial fossils from Riversleigh have not been assigned to a taxon because most of the specimens are disassociated and isolated postcranials are generally not diagnostic at the species level.

Data analysis

The data were first entered in an Excel spreadsheet and then transferred to the appropriate program for the analysis. There are several methods to measure sample size (e.g. NIS, number of identified specimens) and determine whether fossil sites are a representative sample of the original community. However, as outlined above in the data compilation section, determining NIS values for each site is problematic. For this reason, the size of sample (total number of species) for each site was compared using a bar graph. This can be used to gauge how much confidence may be placed in the results (small size of sample = low confidence). Four types of analyses were conducted: cluster analysis, ordination, seriation and cladistics. The four analyses approached the data in different ways. Ordination, cluster and cladistic analyses examined the taxonomic similarity of individual sites and grouped them according to their similarity. Seriation ordered each site in a sequence, showing a direction in time. Each analysis was performed twice with two different sets of data. The first set of data contained all the sites shown in Table 1 (78 sites in total). The second set of data contained only sites that had 8 mammal taxa or more (24 sites in total). We arbitrarily selected 8 taxa as the minimum for the second set of data after examining the results of the first set. The results of the two sets of analyses were compared to explore the effect of low sample size.

Cluster analysis

Cluster analysis is one of the most widely used techniques for comparing assemblages using

taxonomic similarity (de Bonis *et al.* 1992, Shi 1993, Bennington & Bambach 1996, Bonuso *et al.* 2002, Elewa 2004, Palombo *et al.* 2002, Peláez-Campomanes *et al.* 2003). Cluster analysis was performed at the species level only, using the unweighted pair group method in the software PAST. In the unweighted pair group method, a number of similarity indices can be used. According to Hammer (2002) and Hammer & Harper (2006), Dice's, Jaccard's, Simpson's and Raup-Crick's similarity indices are the most suitable indices to use for presence/absence data. Each of these indices is used for the clusters.

Ordination

Ordination is also a very widely used technique for comparing assemblages using taxonomic similarity (de Bonis *et al.* 1992, Shi 1993, Bonuso *et al.* 2002, Myers 2002, Elewa 2004, Fenerci-Masse *et al.* 2004). Hammer (2002) and Hammer & Harper (2006) showed that ordination is most effective when it is compared with cluster analysis. There are a number of ordination methods that can be used. For presence/absence data, Hammer (2002) and Hammer & Harper (2006) recommend Principal Coordinate analysis (PCO) as one of the most suitable. Although it is usually used for abundance data, Principal Component Analysis (PCA) is also recommended by Brenchley & Harper (1998) because it works just as well for presence/absence data. PCA and PCO were both performed on the dataset.

Seriation

Seriation is an ordination often used on stratigraphic data which rearranges data in the form of a range chart with species in columns and samples (or sites) in rows. This is achieved by minimizing the range zones of taxa, which places similar samples in adjacent rows (Brower & Burroughs 1982). This is done by performing a series of iterations that includes the following steps: calculation of mean position of presences in rows, followed by ordering rows according to these means; then calculation of mean position of presences in columns, followed by ordering columns according to these means. There are

two types of seriations: constrained and unconstrained. In the constrained seriation, samples have a known order (i.e. stratigraphic position) and therefore only taxa are rearranged. The unconstrained version of seriation is used in this analysis because it rearranges both taxa and samples. The seriation was performed using the software PAST. To accommodate the software, sites were moved to columns and taxa to rows.

Cladistics

Although primarily used to analyse the relationships of taxa, cladistics has been used for other purposes. For example, O'Brien & Lyman (2003) explored the application of cladistics to archaeology by considering artefacts as human phenotypic characters. It has not been used previously to cluster fossil sites, which is why its potential value to do this was explored in the present study. Cladistics is typically used to group taxa on the basis of their shared derived characteristics. Usually, features unique to one taxon (autapomorphies) and characters common to all taxa (symplesiomorphies) are excluded from the phylogenetic analyses because they are uninformative. Only derived features shared by one or more taxa (synapomorphies) are used in the analysis. In this study, the taxon presence/absence replaces the derived/primitive character state and site names replace taxon names. Using the cladistic concept of autapomorphy, all taxa unique to a single assemblage were removed from the data set. "Symplesiomorphic" taxa do not occur in this data set because no taxa are present in all sites.

The analysis was performed using PAUP, version 4.0b10, for Windows, and the perl script PerlRat.pl (the perl script is available from Olaf Bininda-Emonds' website, <http://www2.uni-jena.de/%7Eb6biol2/>). The parsimony ratchet (Nixon 1999) was used to analyse the data. The ratchet settings used were 50 batches of 200 replicates, with 25% of the characters randomly upweighted by a factor of two in each replicate. This was then followed by a heuristic search

within the shortest trees already obtained, but without increasing the number of trees saved.

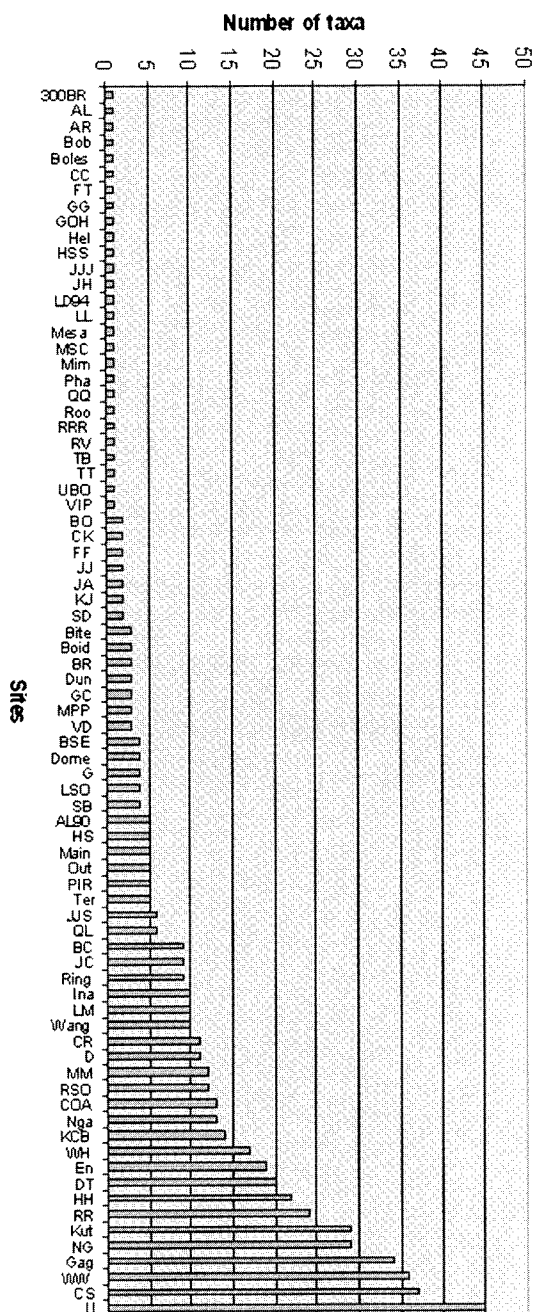


Fig. 1. Number of mammalian taxa identified in each of the Riversleigh site assemblages, and the Bullock Creek, Kutjamarpu and Ngama Local Faunas.

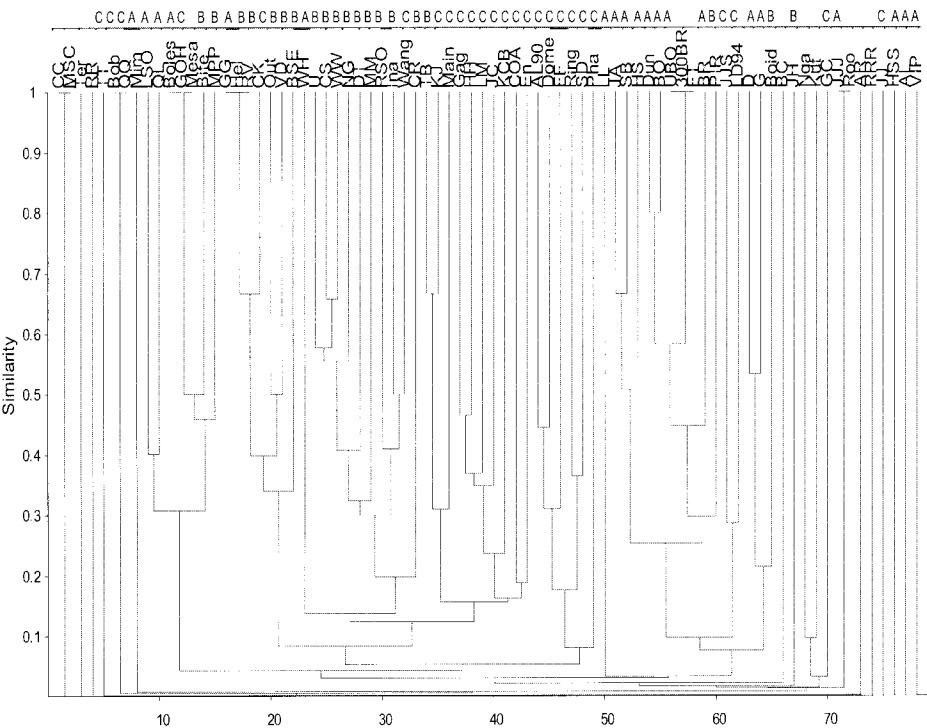


Fig. 2. Cluster Analysis on presence/absence data at the species level, using Dice's similarity index on all sites (corresponding Systems are shown above sites).

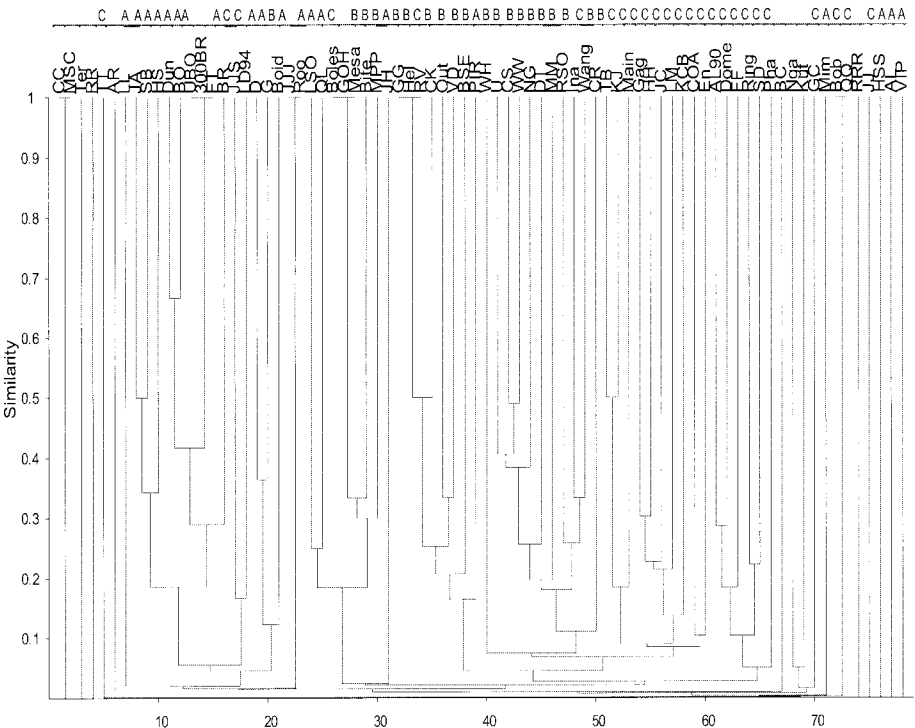


Fig. 3. Cluster Analysis on presence/absence data at the species level, using Jaccard's similarity index on all sites (corresponding Systems are shown above sites).

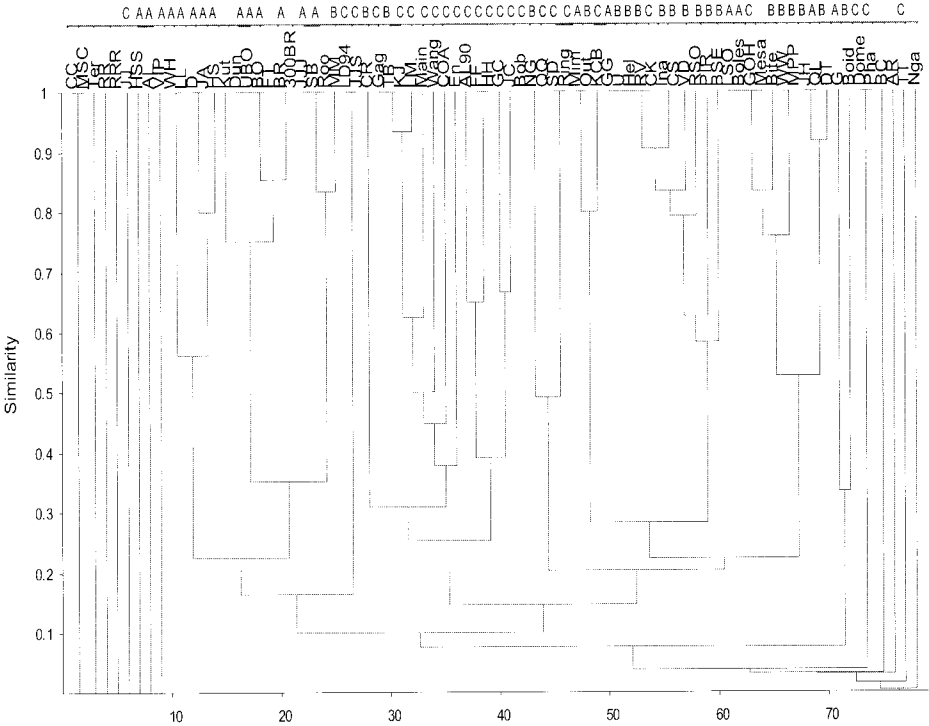


Fig. 4. Cluster Analysis on presence/absence data at the species level, using Simpson's similarity index on all sites (corresponding Systems are shown above sites).

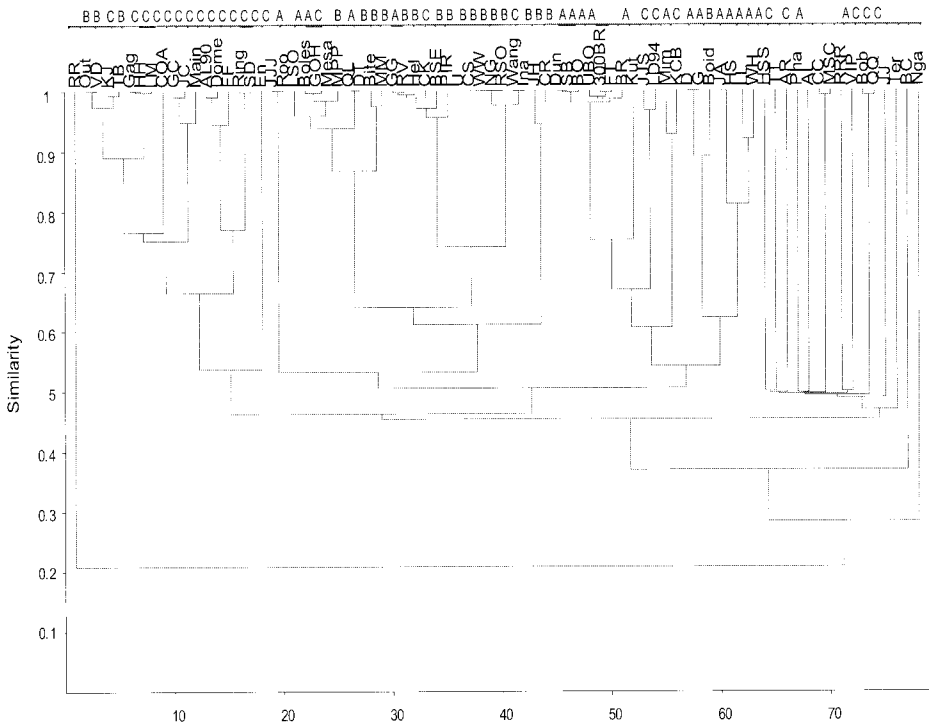


Fig. 5. Cluster Analysis on presence/absence data at the species level, using Raup-Crick's similarity index on all sites (corresponding Systems are shown above sites).

The results are summarised in the 50% majority-rule consensus tree. The heuristic method was used on the basis that it is more suitable for a large data set because it does not conduct an exhaustive search (Forey *et al.* 1992). As for all binary characters, characters (or taxa) were unordered in the analysis because there are no evolutionary sequences in presence/absence data. Similarly, the trees are unrooted to prevent any bias in finding the “ancestral” site. To measure the fitness of the data, the consistency index (CI) and retention index (RI) were calculated. Bootstrap and jack-knife analyses were used to estimate confidence intervals for the trees.

Results and Discussion

The total number of mammal taxa present in each site is shown in Fig. 1. Most sites have a very small sample size, with more than 50% of sites having less than 10 taxa. It is difficult to identify the minimum number of species required to be confident in the results, but the smaller the sample the higher chance of error. Results are discussed in relation to the current understanding of Systems nomenclature and included sites (Table 1).

Cluster analysis

Cluster analyses performed on all sites at the species level using Dice's, Jaccard's, Simpson's and Raup-Crick's similarity indices are shown in Figs 2, 3, 4 and 5, respectively. The clusters produced by Dice's (Fig. 2) and Jaccard's (Fig. 3) indices are almost identical, despite a few inversions of branches and that the cluster branches are slightly shorter using Dice. This was expected because Dice's index is less sensitive than Jaccard's index to differences in sample size (Hammer & Harper 2006). Most sites of the same System cluster together (e.g. Gag, HH, LM, JC, KCB, COA, En). However, some sites do not cluster with sites of the same System (e.g. Wang is interpreted as a System C site, but clusters with System B sites in the analysis). Cluster analysis performed using Simpson's index (Fig. 4) gives similar but slightly more resolved clusters. It is probably better

suited to this kind of data than the first two indices because, unlike Jaccard and Dice indices, it is totally insensitive to the size of the larger sample (Hammer & Harper 2006). The results found using Raup-Crick's index (Fig. 5) are somewhat different. Raup-Crick uses a randomisation method to cluster similar sites (Hammer & Harper 2006) and therefore all sites are placed in a cluster regardless of similarity. It explains why sites that the other indices left unresolved (e.g. Ter, RRR, JJ...) due to lack of similarity are clustered together in the Raup-Crick cluster. However, the three main clusters representing the three Systems are more clearly resolved with Raup-Crick's index, although some sites do not cluster with their putative System.

Results of the cluster analyses performed on sites with eight mammal taxa or more using Dice's, Jaccard's, Simpson's and Raup-Crick's indices are shown in Figs 6, 7, 8 and 9. The results found by each index is very similar, finding the same main clusters. WH and D, the only two System A sites always cluster together. JC, HH, Gag, KCB, COA and En, putative System C sites, also cluster together in each analysis. However, CS, WW, NG, U, RSO, Ina, DT, MM, and CR (putative System B sites) always cluster together with Wang and Ring. Non-Riversleigh sites (BC, Kut and Nga) cluster outside of the Systems, and RR (Pliocene) remains unresolved outside of the clusters.

Ordination

The Principal Components Analysis (PCA) performed on all sites (Fig. 10) shows some separation between the majority of sites of Systems A, B and C. However, sites with a smaller sample size tend to clutter near the (0, 0) coordinates. Sites with larger sample sizes (U, CS, WW, NG, Gag, HH) fall further to the right of (0; 0) coordinates. This means that the first eigenvector, which accounts for 19.5% of the variation, contains most of the species present in those sites. The second eigenvector only accounts for 8.3% of the variation but it is the most useful to distinguish the Systems.

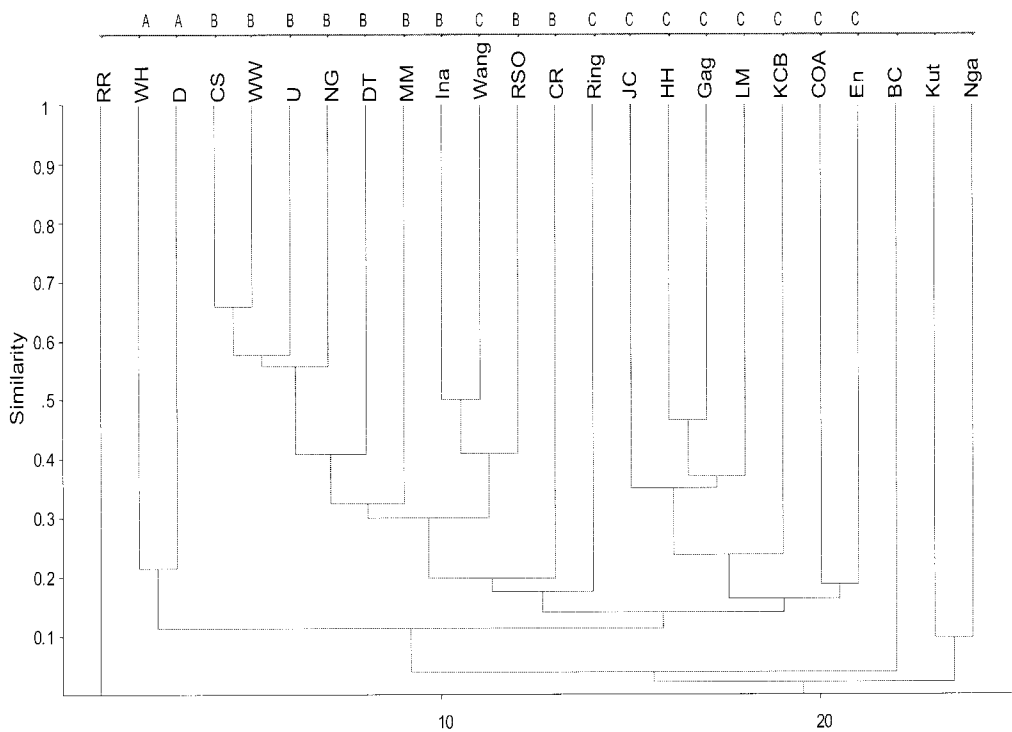


Fig. 6. Cluster Analysis on presence/absence data at the species level, using Dice's similarity index on sites with 8 mammal taxa or more (corresponding Systems are shown above sites).

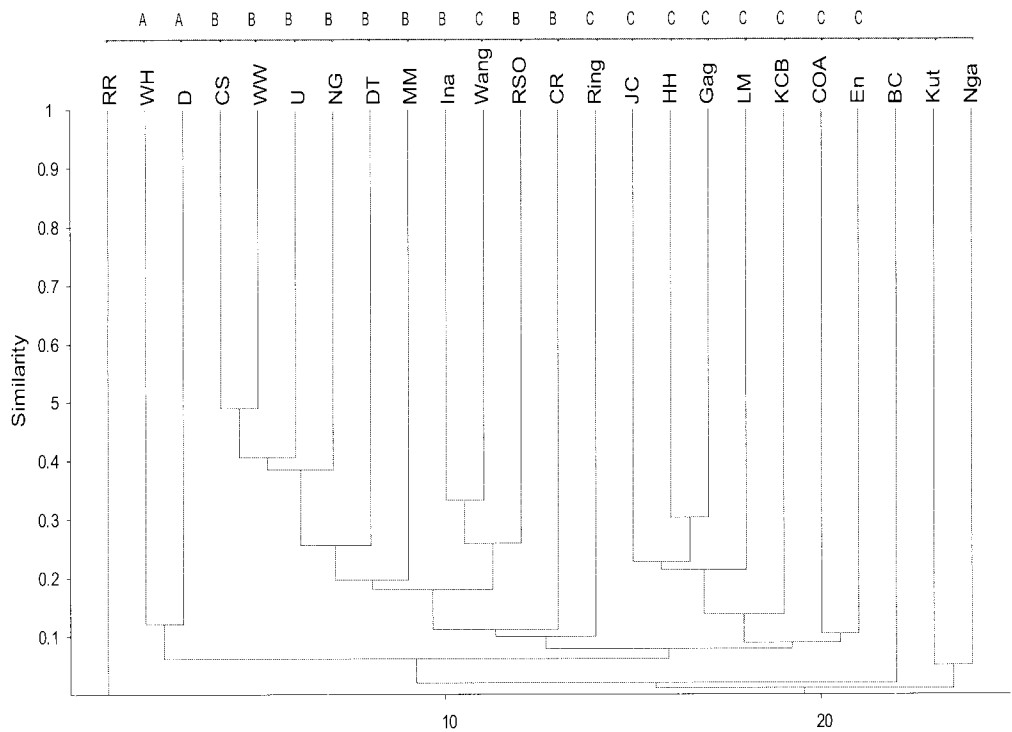


Fig. 7. Cluster Analysis on presence/absence data at the species level, using Jaccard's similarity index on sites with 8 mammal taxa or more (corresponding Systems are shown above sites).

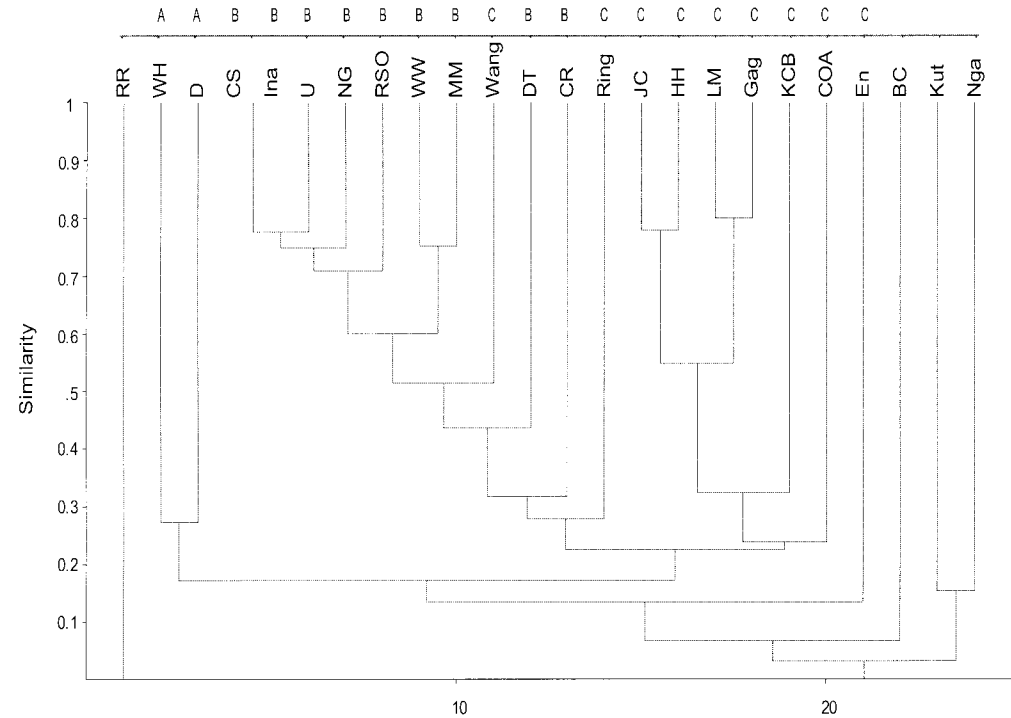


Fig. 8. Cluster Analysis on presence/absence data at the species level, using Simpson's similarity index on sites with 8 mammal taxa or more (corresponding Systems are shown above sites).

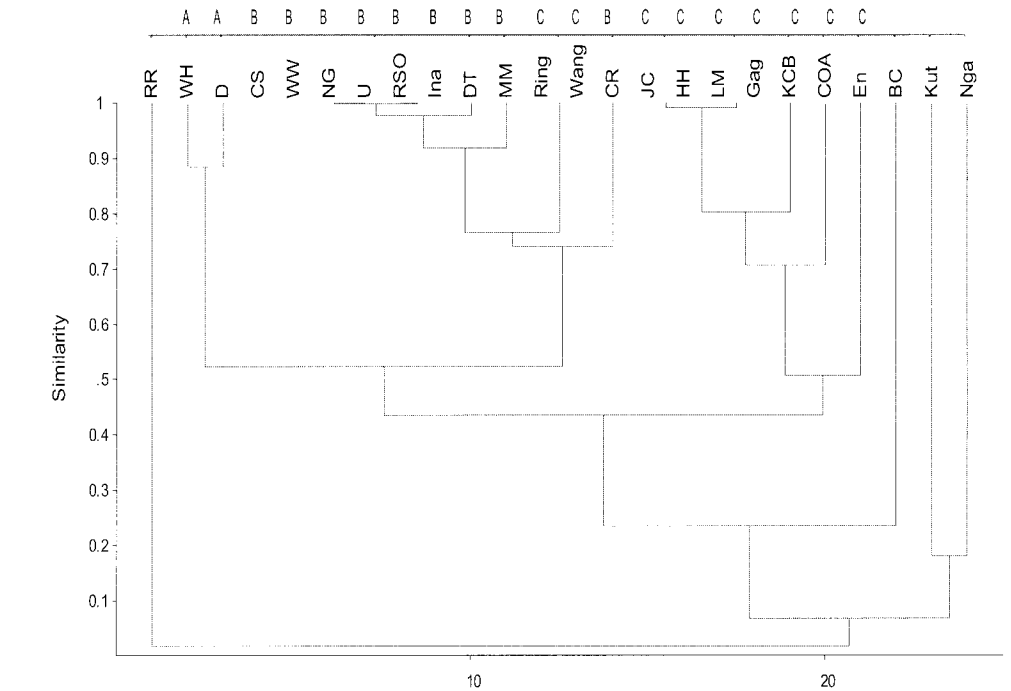


Fig. 9. Cluster Analysis on presence/absence data at the species level, using Raup-Crick's similarity index on sites with 8 mammal taxa or more (corresponding Systems are shown above sites).

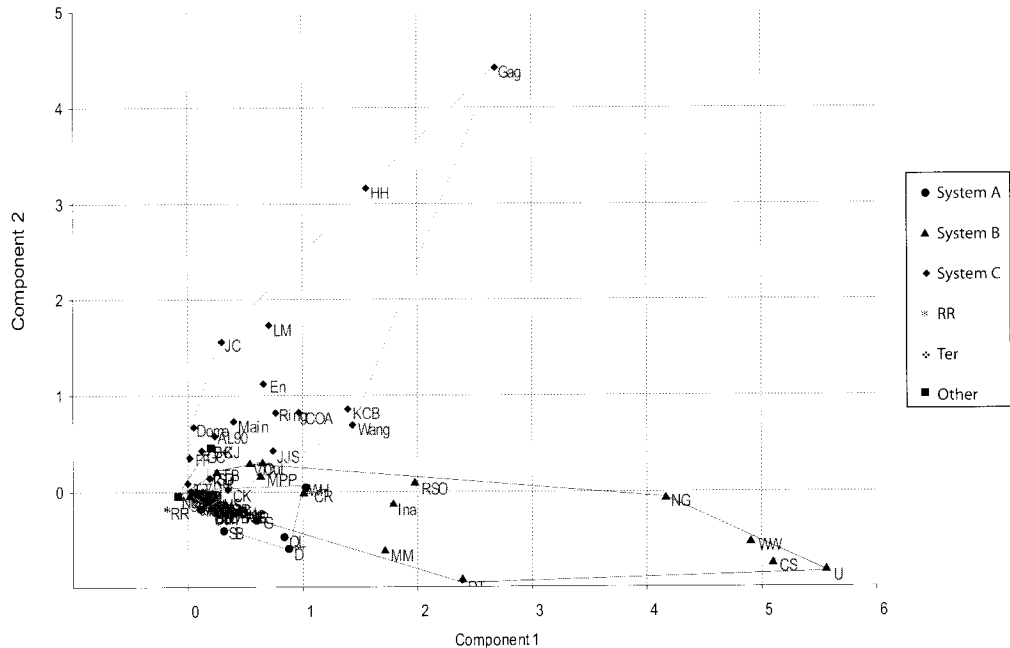


Fig. 10. Principal Components Analysis on presence/absence data at the species level on all sites (with convex hulls).

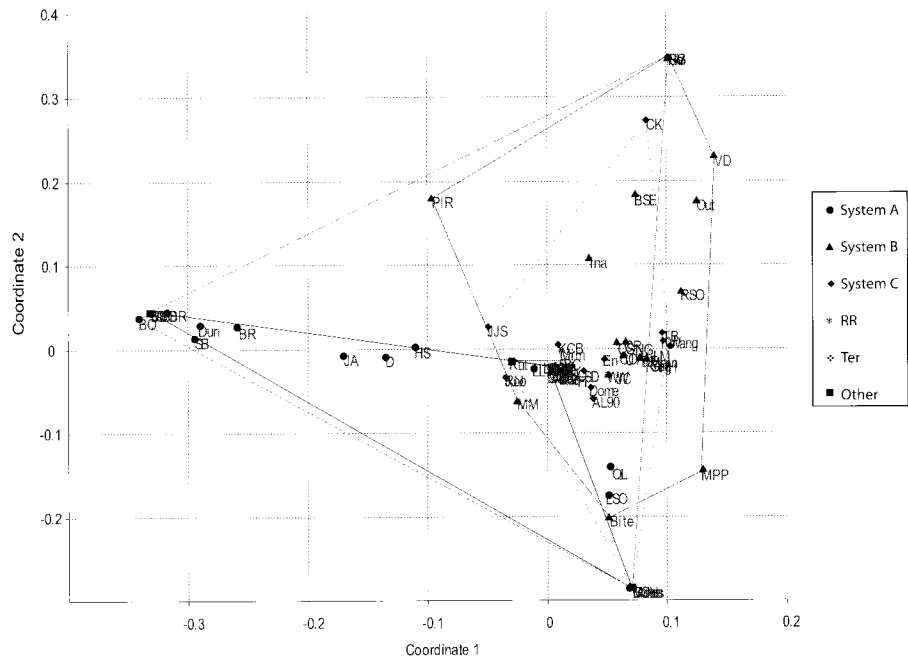


Fig. 11. Principal Coordinates Analysis on presence/absence data at the species level, using Dice's similarity index on all sites (with convex hulls).

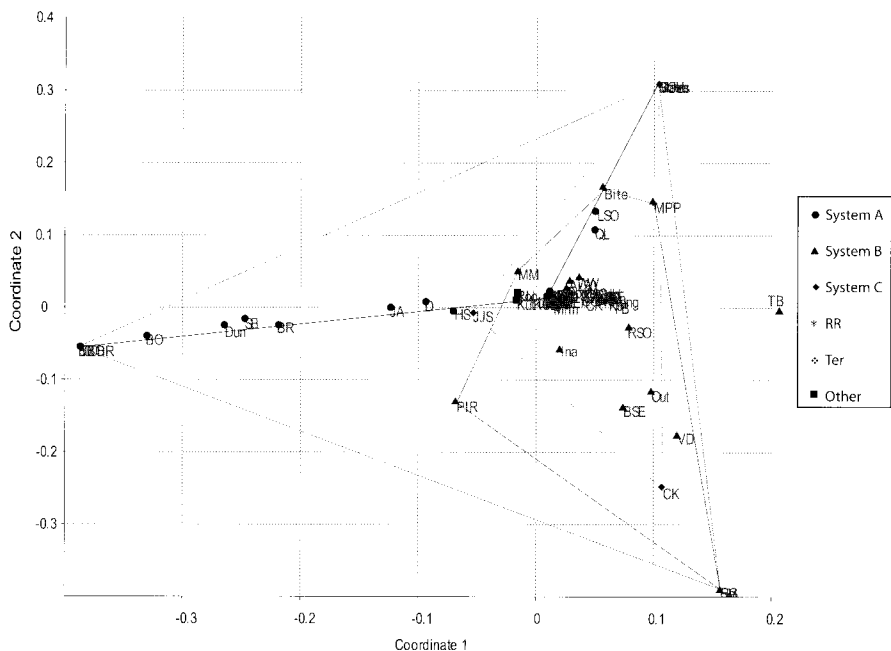


Fig. 12. Principal Coordinates Analysis on presence/absence data at the species level, using Jaccard's similarity index on all sites (with convex hulls).

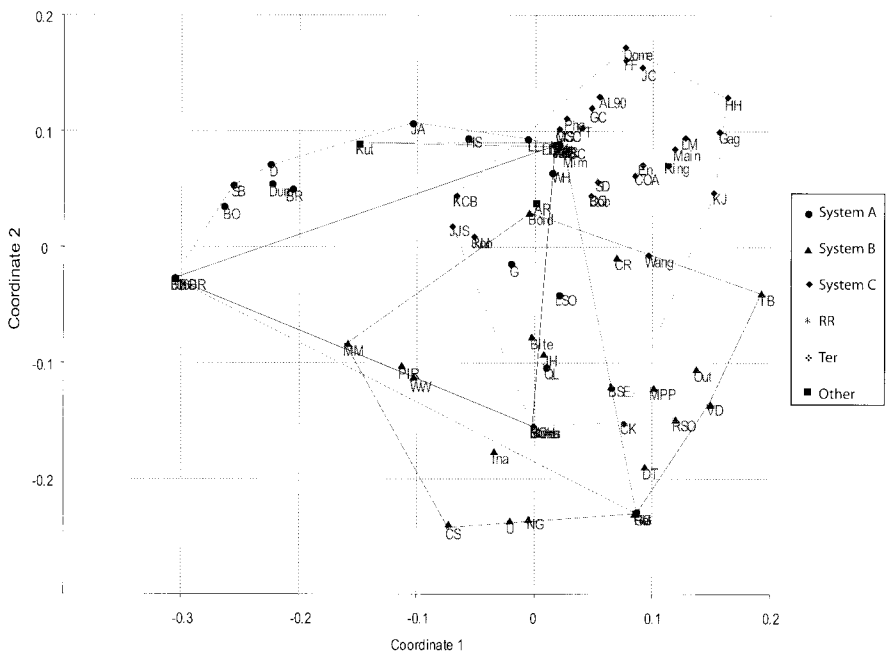


Fig. 13. Principal Coordinates Analysis on presence/absence data at the species level, using Simpson's similarity index on all sites (with convex hulls).

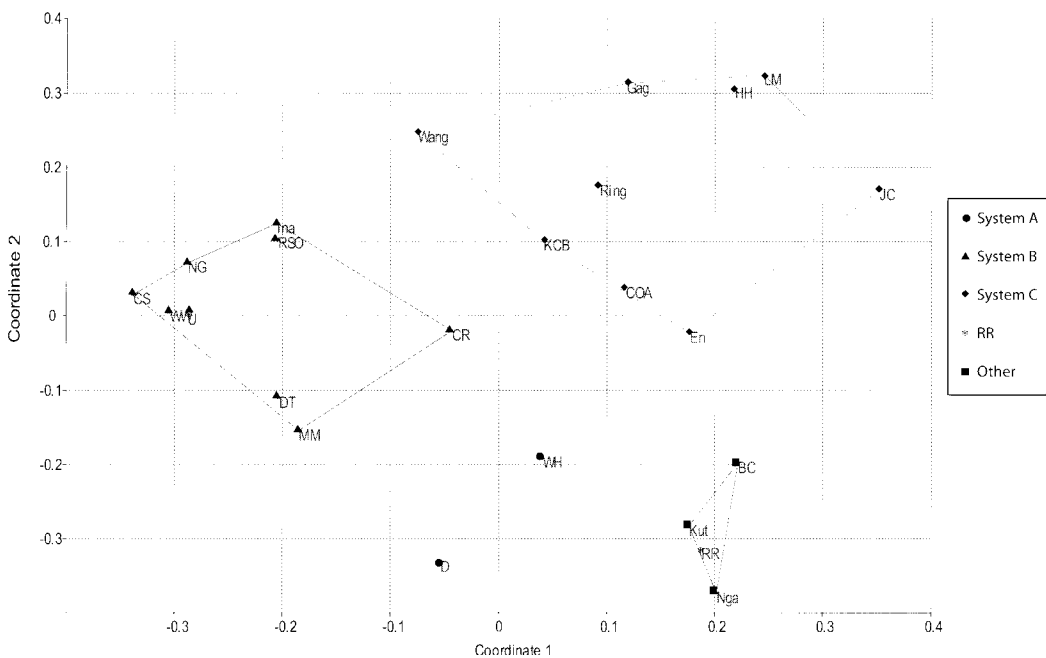


Fig. 16. Principal Coordinates Analysis on presence/absence data at the species level, using Dice's similarity index on sites with 8 mammal taxa or more (with convex hulls).

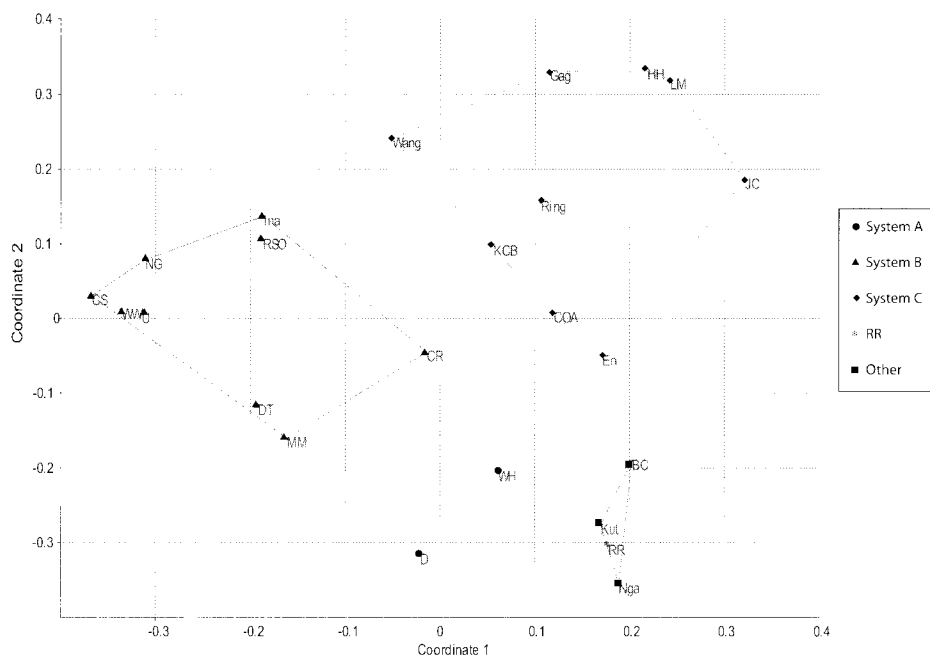


Fig. 17. Principal Coordinates Analysis on presence/absence data at the species level, using Jaccard's similarity index on sites with 8 mammal taxa or more (with convex hulls).

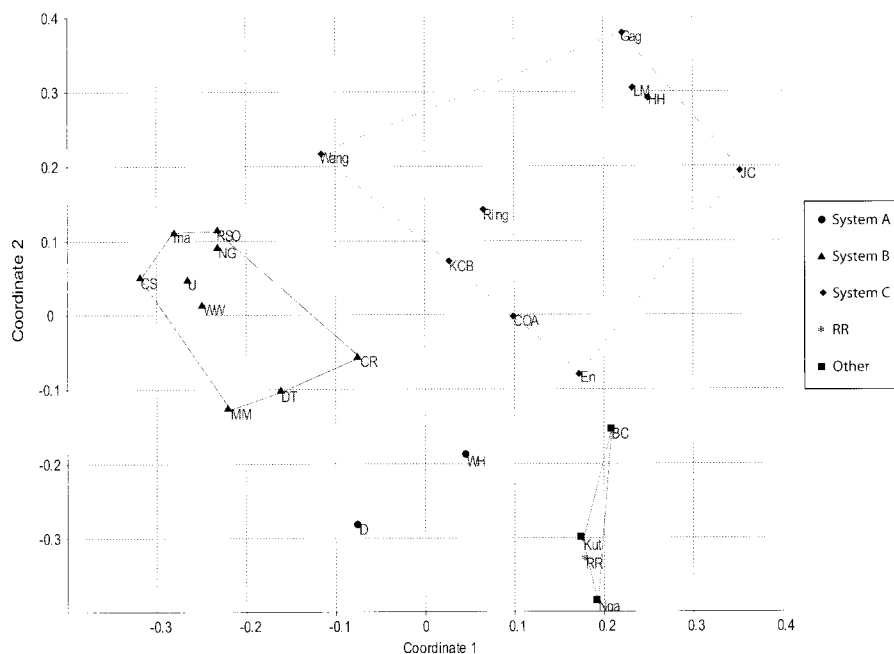


Fig. 18. Principal Coordinates Analysis on presence/absence data at the species level, using Simpson's similarity index on sites with 8 mammal taxa or more (with convex hulls).

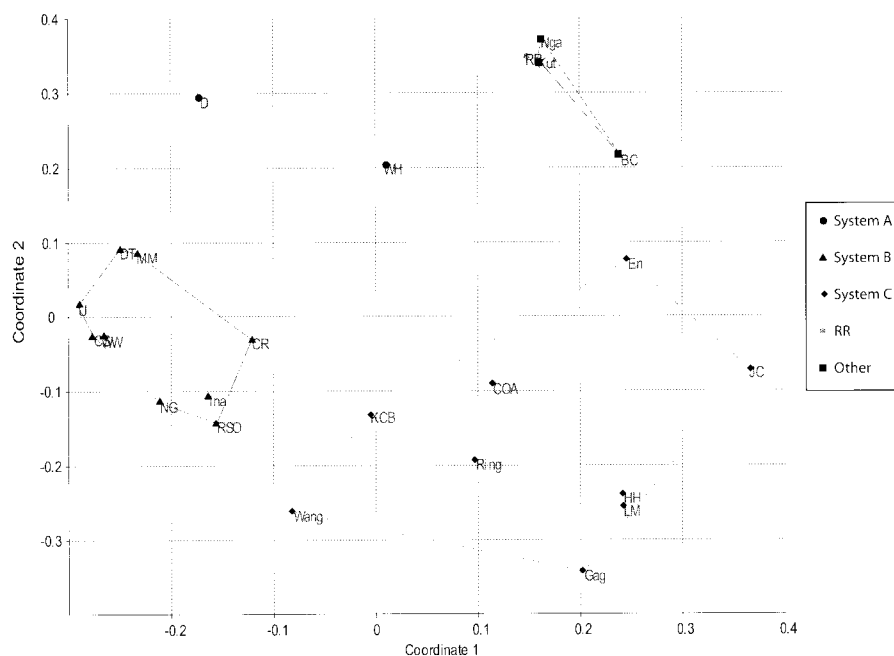


Fig. 19. Principal Coordinates Analysis on presence/absence data at the species level, using Raup-Crick's similarity index on sites with 8 mammal taxa or more (with convex hulls).

In contrast, the Principle Coordinates analyses (PCO) using Dice's (Fig. 11) and Jaccard's (Fig. 12) indices shows no clear separation between Systems. The convex hulls (a set of points is the smallest convex set that includes the points) of each System are covering each other, showing no difference between the Systems. The first two eigenvalues account only for 6.9% and 5.8% of the variation, respectively for Dice, and 5.4% and 4.8% of the variation, respectively for Jaccard.

In the case of Simpson's (Fig. 13) and Raup-Crick's (Fig. 14) indices, the Systems separate more clearly, with still some overlap. Coordinates 1 (8.3% of the variation for Simpson and 9.3% for Raup-Crick) and 2 (7.6% of the variation for Simpson and 8.9 for Raup-Crick) are equally useful to determine the relationship between the Systems, and unlike PCA. As in cluster analysis, the Simpson and Raup-Crick indices are not as heavily influenced by sample size as Dice and Jaccard, explaining why there is less overlap.

The PCA (Fig. 15), and the PCO using Dice's (Fig. 16), Jaccard's (Fig. 17), Simpson's (Fig. 18) and Raup-Crick (Fig. 19) indices performed on sites with eight taxa or more all showed very similar results. Unlike cluster analysis, all the sites grouped with their own System without overlapping the convex hulls. The first and second eigenvalue accounts for 19.3 % and 8.4% of variation in the PCA respectively, 11.9% and 8.4% in the PCO with Dice, 9.2% and 6.7% in the PCO with Jaccard, 15.8% and 10.3% in the PCO with Simpson, and 21.1% and 13.5% in the PCO with Raup-Crick. BC, Kut, Nga and RR grouped away from the Systems.

Seriation

Seriation based on presence/absence data at the species level is given in Fig. 20 for all sites and Fig. 21 for sites with eight mammal taxa or more. Due to the large size of the seriation, Figs 20-21 have been reduced to fit the page. Taxon and site names are therefore unreadable. Site names are recapitulated below and the order of the sites is as shown in the seriation. Subscripts refer to putative System or age as follows: 1, System A; 2,

System B; 3, System C; 4, Pliocene; 5, Pleistocene; 6, Recent; 7, Unknown.

All sites (seriation criterion = 0.28):

VIP₁, AL₁, HSS₁, Nga, LL₁, JA₁, Boid₂, LSO₁, Dun₁, SB₁, HS₁, BO₁, Roo₇, JJJ₁, AR₇, Mesa₇, Boles₁, GOH₃, D₁, WH₁, G₁, QL₁, UBO₁, 300BR₇, FT₇, BR₁, DT₂, JH₂, MM₂, WW₂, BSE₂, U₂, CS₂, RSO₂, Bite₂, Ina₃, Hel₂, RV₂, GG₁, MPP₂, PIR₃, NG₂, CK₃, CR₂, Wang₃, VD₂, Out₂, QQ₃, Bob₃, JJS₃, COA₃, TB₂, KCB₃, MIM₃, Kut, Ring₃, SD₃, Gag₃, AL90₃, KJ₃, Main₃, HH₃, GC₃, LD94₃, LM₃, JC₃, BC, FF₃, En₃, Dome₃, TT₃, Pha₃, JJ₃, RRR₇, RR₄, Ter₆, CC₆, MSC₆

Sites with eight mammal taxa or more (seriation criterion = 0.55):

Nga, Kut, WH₁, D₁, CR₂, DT₂, WW₂, MM₂, CS₂, Ina₃, RSO₂, NG₂, U₂, Wang₃, KCB₃, COA₃, Ring₃, Gag₃, HH₃, LM₃, JC₃, En₃, BC, RR₄.

The seriation shows the chronological sequence in which System A sites are followed by System B sites, which are then followed by System C sites. In the seriation with all sites, only a few sites are grouped with a different System. Boid (B) and GOH (C) are grouped with System A sites, GG (A) is grouped with System B and TB (B) with System C sites. The sample size is quite low for these sites (Boid has 3 taxa, GOH, GG and TB have 1 taxon each) which might explain the error. CK (C) and Wang (C) group with System B sites, or CR (B), VD (B) and Out (B) group with System C sites. Nga, Kut and BS are placed among System A, B and C sites respectively. RR (Pliocene), Ter (Pleistocene) and recent sites (CC, MSC) follow at the end of the seriation.

In the seriation using sites with eight mammal taxa or more, sites followed the System A, B and C chronological order. In contrast to the seriation with all sites, Kut grouped with Nga before System A sites. The criterion in this seriation (0.55) is also much higher than in the seriation with all sites (0.28). This means that the seriation using sites with eight mammal taxa or more is much better resolved and more reliable.

Cladistics

The parsimony Ratchet analysis resulted in 10000 shortest trees using all sites and 156 shortest trees using sites with eight mammal taxa or more.

The trees are summarised below in the 50% majority-rule consensus trees (Figs 22-23). For all sites, 94 out of 215 characters were informative (i.e. 121 uninformative); for sites with eight taxa

or more, 83 out of 195 characters were informative (i.e. 112 uninformative). Sites containing uninformative characters (300BR to VIP in fig. 22) are left unresolved in the tree. Indices for the

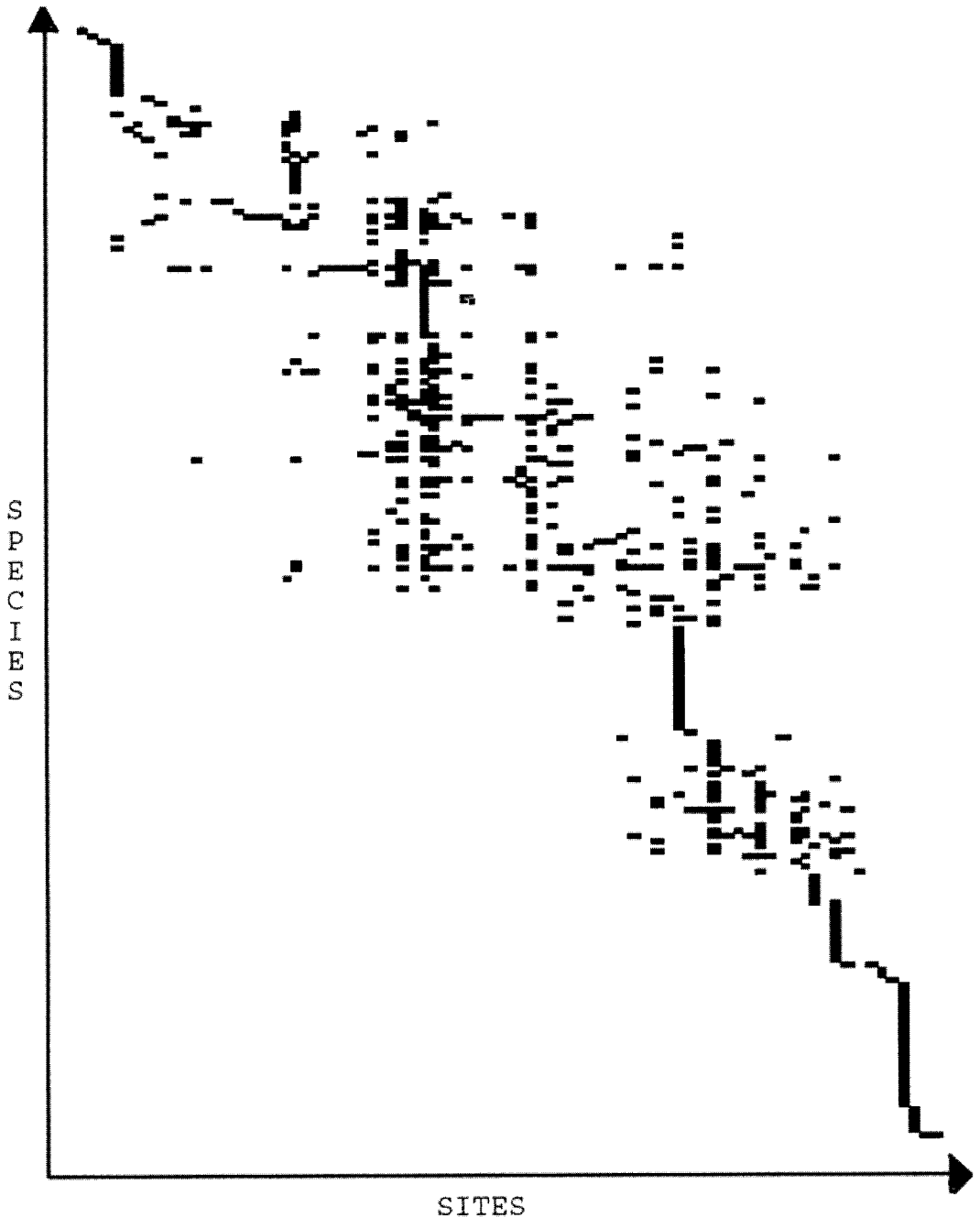
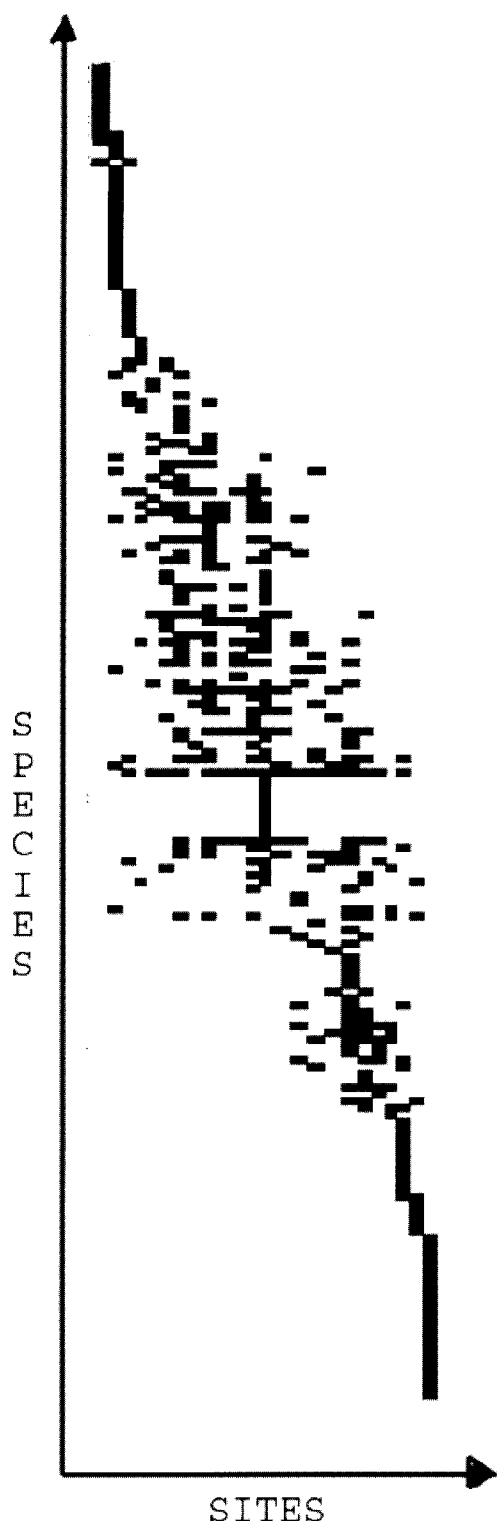


Fig. 20. Seriation of all sites based on presence/absence data at the species level.



majority rule consenses were as follows: All sites, $CI=0.5012$, $RI=0.4121$; sites with eight taxa or more, $CI=0.5821$, $RI=0.4400$. Both values are quite low, indicating that the tree describes the data set poorly. The two trees (all sites and sites with eight mammal taxa or more) resulting from the parsimony analysis are quite similar to results from the cluster analysis. However, the parsimony analysis left more sites unresolved than cluster analysis, due to the removal of uninformative characters. Bootstrap and jack-knife analyses were also performed to test the confidence of the branching. From the bootstrap and jack-knife analyses, there are four well-supported branches suggesting relationships between:

- CS, U, WW and NG (all sites and sites with eight mammal taxa or more);
- GAG and HH (all sites and sites with eight mammal taxa or more);
- Bob and QQ (all sites only); and
- Kut and Ng (sites with more than eight mammal taxa only)

Comparison of analyses and size of samples

The fauna of each site is a sample of a local community (or local fauna) that has then been compared with other sites. Sites with a small number of species have typically been less well sampled than sites with a large number of species. If the number of species in a site is low due to undersampling, there is a greater chance of error in the similarity comparison. With increasing numbers of species, there is increasing confidence in the results of the comparison. We performed the similarity analyses on all sites and on sites with eight mammal taxa or more to investigate that particular sampling problem. Interpreting the results and making conclusions based on the analyses using all sites could lead to severe error.

We used four similarity indices to compare the results given by each of them. In the all site analysis, the results given by Dice's and Jaccard's indices were almost identical, although

Fig. 21. Seriation of sites with 8 mammal taxa or more based on presence/absence data at the species level.

Dice was slightly less sensitive to sample size. Simpson's and Raup-Crick's indices identified the Systems much better than the other two indices. This is in agreement with Hammer's (2002) and Hammer & Harper's (2006) recommendations: Simpson's and Raup-Crick's indices are more suitable when sampling is considered incomplete. In the analysis based on sites with eight mammal taxa or more, the results given by the four indices were almost identical, indicating that sampling error was reduced or perhaps even removed.

Ordination was one of the most useful methods for comparing faunal lists. The Systems were distinguished in both PCA and PCO, but they were more clearly separated by PCO. As Clarke and Warwick (1994) noted, PCO is more flexible in defining dissimilarity than PCA, but both suffer from poor distance preserving (the proximity between data points does not accurately reflect their similarities). This phenomenon is shown in our analysis by the grouping of RR with Kut, Nga and BC, although RR does not share any species with them.

Cluster analysis was not as successful as ordination in defining the Systems, with many sites remaining unassigned in the all sites analyses. Clarke and Warwick (1994) pointed out that cluster analysis was weak at working out relationships at higher levels and it is always recommended to use it in conjunction with ordination. This means that the higher branches of the cluster, which supposedly represent the Systems, are less reliable than the larger groupings in ordination. Ultimately, ordination should be used to identify groups (in our case Systems) and cluster analysis to identify similarities within those groups.

Seriation was very useful at identifying the chronological order of the Systems by placing sites in a sequence according to their similarities. System A becomes the oldest followed by System B and then by System C. Assuming that the seriation placed the site in the correct chronological order, the results of seriation could be used to make predictions about what species might be expected to be found in a site assuming

the appropriate palaeoenvironment.

The cladistics method was not particularly useful in identifying Systems. In the analysis using sites with eight mammal taxa or more, it clustered small groups such as En and COA, or CR and MM, outside the System branches. The removal of unique species (autapomorphies) from the data set may not be the best method for faunal comparison. In fact, it is recommended (Etter 1999) to include unique (rare) species because they may be highly important and even characteristic of some of the samples. For example, in the analyses En groups with System C. Myers *et al.* (2001) demonstrated that En (Encore Local Fauna) was younger than other System C sites. It contains taxa that are more derived than System C taxa and these taxa are unique to En (11 unique taxa out of 19 in total). In cladistics analysis, these taxa are treated as uninformative, resulting in grouping En with COA based on the eight remaining taxa in common with System C sites. In ordination, cluster analysis and seriation, En is placed between COA and BC, or JC and BC.

Bullock Creek, Kutjamarpu and Ngama Local Faunas

The Ngama Local Fauna (Ng) has been magnetostratigraphically dated at about 24–26 mya, in the late Oligocene (Woodburne *et al.* 1994). The biocorrelation of a taxon shared between Ngama and Riversleigh's System A White Hunter Site (*Kuterintja ngama*) indicated that they were of a similar age (Myers & Archer 1997, Archer *et al.* 1997). Murray & Megirian (1992) and Murray *et al.* (2000) demonstrated that Bullock Creek (BC) might be middle Miocene in age. BC shares a number of taxa with Riversleigh's System C sites (*Neohelos stirtoni* and *Propalorchestes novaculacephalus*) and the Encore Local Fauna (*Wakaleo vanderleueri*) suggesting that they are of a similar age. Woodburne *et al.* (1994) suggested that Kutjamarpu, like Ngama, was late Oligocene in age, but Archer *et al.* (1997) argued that it shares more taxa with Riversleigh's System B sites than System A, and hence is probably early Miocene.

In the analyses, Ngama and Kutjamarpu always group together either with System A sites or distantly from all Riversleigh sites. Ngama has more taxa in common with Kutjamarpu (two: *Bulungamaya* sp. A and *Peramelemorphian* sp. B) than Riversleigh (one: *Kuterintja ngama*) hence its position in the analyses. Kutjamarpu shares six of its taxa with Riversleigh sites: *Wakaleo oldfieldi* is known from KCB and COA (System C), *Wakiewakie lawsoni* from U (System B), *Litokoala kutjampensis* from Gag, GC, HH and JC (System C), *Marlu kutjampensis* from Gag, Ring and Wang (System C), *Rizosphascolonus crowcrofti* from BR, DT and COA (System A, B and C) and *Neohelos tirarensis* from 300BR, BR, BO, CS, D, Dun, FT, Ina, JJS, KCB, MM, NG, PIR, SB, U, UBO and WW (Systems A, B and C). These Kutjamarpu species occur in all three Riversleigh Systems, making biocorrelation problematic.

Comparison with the literature

Rich *et al.* (1991) compared the taxonomic composition of Australian Cenozoic terrestrial mammalian sites based on the number of genera shared in common between the sites using Simpson's coefficient. They found that Kutjamarpu and Ngama clustered together with all other South Australian Oligo-Miocene sites. All three Riversleigh Systems clustered together and were closely related to Bullock Creek. Performing a similarity analysis at the generic (or familial) level over a long time span, such as carried out by Rich *et al.* (1991), provides a good understanding of the major chronological groups. However, genera (and families) exist significantly longer than species, and have turnover times that can be too long to be of biocorrelative value for the Oligo-Miocene. Similarity analyses performed on shorter time spans require the use of species level taxa to distinguish smaller changes in time.

Megirian *et al.* (2004) performed two analyses using Riversleigh sites. In their first analysis (fig. 18 and table 8), the authors used a presence/absence matrix in a similarity cluster analysis to compare mid-Cenozoic formations. The variables used in the matrix are diverse in nature: presence of a sediment type, an aquatic plant, an aquatic vertebrate and the presence at different taxonomic levels (order, family, genus and species) of aquatic invertebrates, amphibious vertebrates, terrestrial invertebrates and terrestrial vertebrates. One of the assumptions of multivariate analyses is that each variable is given the same weight. This means that all variables should be equal and is why multivariate analyses are more conventionally used to compare morphometric measurements or to compare assemblages using taxa at the same taxonomical level (Etter 1999, Hammer 2002, Hammer & Harper 2006). The variables used in the analysis of Megirian *et al.* are unlikely to be of equal value and the results given are unsupported.

In the second analysis (Megirian *et al.* 2004, fig. 20), data are used from Murray & Megirian (2000) to cluster eight Riversleigh sites (D, WH, MM, NG, CS, Ina, Gag and HH). The sample size of the sites ranged from eight taxa (CS) to two taxa (MM). The size of sample is low because all unique species were removed from the data set. Etter (1999) recommends leaving rare species in the data set because these species may be characteristic of the sample. In Megirian *et al.* (2004), all the sites clustered according to Systems except MM (System B) which clustered with D and WH (System A). The authors concluded that the Riversleigh site assemblages might be diachronous and dismissed the utility of the Systems nomenclature. However, those authors did not consider the likelihood that their results could be undermined by low sample sizes. In our analysis, MM's 12 mammal taxa were included, six times more than in the Megirian *et al.* (2004) analysis, and MM always clusters with System B sites (in the eight mammal taxa or more analysis). Moreover, recent excavations at Riversleigh have demonstrated that that CS and MM sites are confluent and are almost certainly part of the same deposit.

Revision of the “Systems”

Archer *et al.* (1989) defined the “Systems” as regionally clustered sites that appear to be superpositionally-related and/or space-related. A “system” is also a stratigraphic analogue of the chronological term “period”. To avoid confusion, Arena (2004) proposed using two terms to describe Riversleigh sites rather than “System”: the faunal concept of System A, B and C would be replaced by “Faunal Zone” A, B and C and the geological concept by “Depositional Phase” A, B and C. Arena (2004, 2005) also found that Riversleigh deposits could be interpreted as having been formed and modified during successive stages of karst development divided into four phases. Encore Site is referred to by Arena (2004, 2005) as Faunal Zone D and Depositional Phase D.

The results of our analyses (using the data

from sites with eight mammal taxa or more) show at least three distinct groups (sometimes four with Encore separate) and therefore supports the hypotheses and concept of Faunal Zones. The diagnostic characters of each faunal zone have yet to be defined. As a preliminary description, sites with eight mammal taxa or more can be used as diagnostic sites for each Faunal Zone. D and WH are representatives of Faunal Zone A, CR, CS, DT, Ina, MM, NG, RSO, U and WW are representatives of Faunal Zone B, COA, Gag, HH, JC, KCB, LM, Ring and Wang are representatives of Faunal Zone C and En is representative of Faunal Zone D. Taxa unique to a Faunal Zone, and those found in two or more Faunal Zones are listed below. For single occurrences of taxa, sites names are given after the name of the taxon in brackets. Taxa that are not found in the diagnostic sites but are found in other sites are in parentheses.

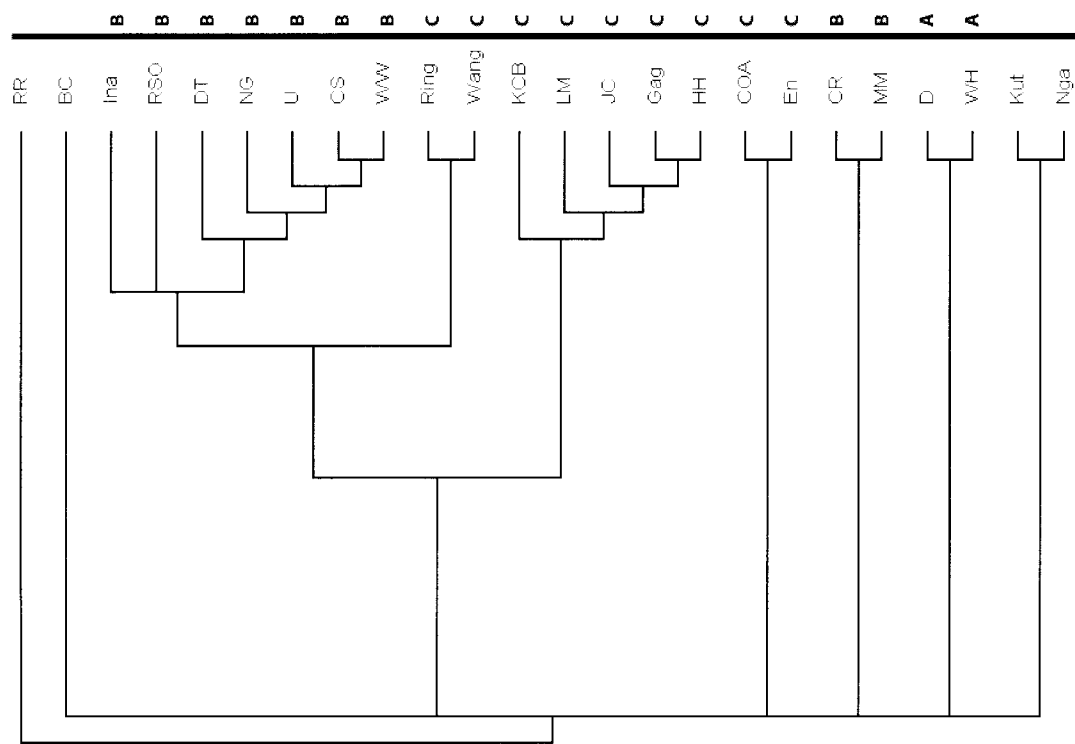


Fig. 23. 50% majority-rule consensus of 156 trees of the unordered analysis of sites with 8 mammal taxa or more (corresponding Systems are shown next to sites).

Taxa found in Faunal Zone A only:

Badjicinus turnbulli (WH), *Kuterintja ngama* (WH), (*Namilamadeta* sp. cf. *N. albivenator*), (*Ngapakaldia* sp.), (*Silvabestius michaelbirti*), (*Silvabestius johnnilandi*), *Silvabestius* sp. (D), (*Marada arcanum*), *Ganawamaya aediculis* (WH), *Balbaroo* sp. 3 (WH), *Galanarla tessellata*, *Wururoo dayamayi* (WH), *Nambaroo couperi* (WH), *Nambaroo* sp. 8, *Nowidgee* sp. 2 (WH), *Gumardee pascuali* (D)

Taxa found in Faunal Zone B only:

Wabulacinus ridei (CS), *Ngamalacinus timmulvaneyi*, Dasyuridae genus indet. sp. 1 (U), Dasyuridae genus indet. sp. 2 (U), Dasyuridae genus indet. sp. 3 (U), Dasyuridae genus indet. sp. 4 (U), Notoryctidae new genus new sp., Peramelemorphia new genus 2 sp. 2, Peramelemorphia new genus 2 sp. 3, Peramelemorphia new genus 5 sp. 2 (U), (*Litokoala garyjohnstoni*), Phascolarctidae new genus new sp., Thylacoleonidae new genus new sp. (NG), Vombatidae genus 1 sp. 1, *Namilamadeta* sp. (U), *Paljara maxbourkei* (CS), *Paljara tirarensae* (WW), *Gawinga aranaea*, ?*Djilgaringa* sp. (U), *Wyulda asherjoeli*, Phalangeridae new genus 1 sp. 3, *Ektopodon* sp. cf. *E. serratus*, *Chunia* sp., Ektopodontidae new genus new sp., *Durudawiri inusitatus*, *Durudawiri anfractus*, *Ganawamaya ornate* (WW), *Ganawamaya acris*, *Ganawamaya* sp. 4 (CR), (*Wururoo* sp. 3), *Nambaroo* sp. 2, *Nambaroo* sp. 4 (WW), *Nambaroo* sp. 6, *Nambaroo* sp. 7 (U), (*Bulungamaya* sp. cf. *B. delicata*), (*Ganguroo* sp. cf. *G. bilamina*), *Wakiewakie lawsoni* (U), *Yingabalanara richardsoni*

Taxa found in Faunal Zone C only:

Maximucinus muirheadae (Ring), *Muribacinus gadiyuli*, Thylacinidae cf. *Mutpuracinus archibaldi* (JJ), *Joculusium muizoni* (Gag), Dasyuromorphia new genus new sp. (Gag), Peramelemorphia new genus 5 sp. 1, *Litokoala kutjampensis*, (*Litokoala* new sp. 1), *Wakaleo oldfieldi*, *Nimbadoron lavarackorum*, *Neohelos* sp. A (COA), *Neohelos stirtoni*, (*Neohelos* sp.

C), *Pseudochirops* sp. 1 (and En), *Pseudochirops* sp. 2 (HH), *Paljara* sp. 1 (Gag), *Marlu kutjampensis*, *Marlu* sp. 2 (JC), *Marlu* cf. sp. 3, *Marlu* sp. 4, *Pildra* sp. 1, *Pildra* sp. 3 (Gag), *Pildra* sp. 4 (LM), Pseudocheiridae new genus 2 sp. 2 (Gag), “*Strigocuscus*” *reidi*, “*Trichosurus*” *dicksoni*, Phalangeridae new genus 1 sp. 2 (KCB), (Phalangeridae new genus 3 sp. 1), *Balbaroo* sp. 4, *Ekaltadeta jamiemulvaneyi* (and En), *Bettongia moyesii*, *Ganguroo* sp. 2, *Wanburoo hilarus*, *Wanburoo* sp. 2, *Yalkaparidon jonesi*

Taxa found in Faunal Zone D (En) only:

Thylacinus sp. cf. *T. macknessi*, *Ganbulanyi djadjinguli*, *Mayigriphus orbus*, *Phascolarctos* sp., *Wakaleo vanderleueri*, *Warendja* sp. 1, *Palorchestes annulus*, *Neohelos* sp., *Trichosurus* sp., *Ganguroo* new sp., *Rhizosthenurus flanneryi*, Marsupialia new genus sp. 2

Taxa found in Faunal Zones A and B:

Wakaleo new sp. 1, *Namilamadeta albivenator*, *Namilamadeta crassirostrum*, *Ngapakaldia bonythoni*, *Marlu* sp. 1, *Balbaroo gregoriensis*, *Nambaroo* sp. 3, *Nambaroo* sp. 5, *Wabularoo naughtoni*, *Yalkaparidon coheni*

Taxa found in Faunal Zones B and C:

Obdurodon dicksoni, *Thylacinus macknessi*, *Barinya wangala*, Peramelemorphia new genus 1 sp. 1, Peramelemorphia new genus 2 sp. 1, Peramelemorphia new genus 3 sp. 1, Peramelemorphia new genus 4 sp. 1, Peramelemorphia new genus 4 sp. 2, *Yarala burchfieldi*, *Priscileo roskellyae*, Vombatidae genus 2 sp. 1, *Propalorchestes novacula-cephalus*, *Cercartetus* new sp., *Paljara nancyhaywardae*, *Marlu* sp. 3, *Pildra* sp. 2, *Djaludjangi yadjana*, *Djilgaringa gillespieae*, Phalangeridae new genus 1 sp. 1, Phalangeridae new genus 2 sp. 2, *Wururoo* sp. 2, *Hypsi-prymnodon bartholomaii*, *Hypsi-prymnodon* new sp., *Ganguroo bilamina*

Taxa found in Faunal Zones A, B and C:

Nimbacinus dicksoni, *Nimiokoala greystanesi*, *Rhizophascolonus crowcrofti*, *Neohelos tirarensis*, Pseudocheiridae new genus 2 sp. 1, Phalangeridae new genus 2 sp. 1, *Balbaroo fangaroo*, *Nowidgee matrix*, *Bulungamaya delicata*

Taxa found in Faunal Zones A, B, C and D:
Burrarnys brutyi, *Ekaltadeta ima*

Conclusions

The four hypotheses tested were supported in this study, indicating that Riversleigh sites accumulated fossils at different periods of time and during four main faunal intervals characterisable as Faunal Zones (*sensu* Arena 2004, 2005) A (oldest), B, C and D (youngest), which are sequential in time. Faunal Zone A correlates with Ngama LF and Faunal Zone C correlates with Bullock Creek LF. The biostratigraphic position of Kutjamarpu LF remains ambiguous based on current data.

The small sample size for most sites was a limitation for all techniques and a possible source of error in assessing site similarity. Using sites with eight mammal taxa or more in the analysis reduced or possibly even removed this limitation and error. The latter sites were used to produce a preliminary description of each Faunal Zone.

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APPENDIX

Bullock Creek Local Fauna:

- ⁵*Nimbacinus richi*
- ⁵*Mutpuracinus archibaldi*
- ⁷*Nimbador whitelawi*
- ⁸*Neohelos stirtoni*
- ¹*Propalorchestes novaculacephalus*
- ¹*Wakaleo vanderleueri*
- ¹*Balbaroo campfieldensis*
- ⁴*Nambaroo bullockensis*

Kutjamarpu Local Fauna:

- ¹*Ankotarinja* sp. A
- ¹*Ankotarinja* sp. B
- ¹*Keeuna* sp. A
- ³*Wakamatha tasselli*
- ³Dasyuridae genus A sp. B
- ³Peramelemorphian sp. A
- ³Peramelemorphian sp. B
- ³Peramelemorphian sp. C
- ³Peramelemorphian sp. D
- ³Peramelemorphian sp. E
- ¹*Litokoala kutjampensis*
- ¹*Neohelos tirarensis*
- ¹*Wakaleo oldfieldi*
- ¹*Rhizophascolonus crowcrofti*
- ¹Burramyid sp. A
- ¹Burramyid sp. B
- ¹*Paljara tirarensae*
- ¹*Marlu kutjampensis*
- ¹*Pildra tertius*
- ¹*Ektopodon serratus*
- ⁶*Ektopodon litolophus*
- ¹*Balbaroo* sp. A
- ¹*Balbaroo* sp. B
- ³*Nambaroo* sp. D
- ¹*Bulungamaya* sp. A
- ¹*Bulungamaya* sp. B
- ¹*Wakiewakie lawsoni*
- ¹*Pinaroo* sp. C
- ¹Macropodine genus W sp. A

Ngama Local Fauna:

- ²*Obdurodon* sp. cf. *O. insignis*
- ²*Dasyurina kokuminola*

2	Peramelemorphian sp. B	
1	<i>Litokoala</i> sp. cf. <i>L. kutjampensis</i> (previously named <i>kanunkaensis</i>)	
1	<i>Kuterintja ngama</i>	1 Rich <i>et al.</i> 1991
1	<i>Burramys wakefieldi</i>	2 Pledge pers. comm. 2005
1	<i>Marlu</i> sp. cf. <i>M. kutjampensis</i>	3 Woodburne <i>et al.</i> 1994
1	<i>Pildra magnus</i>	4 Schwartz & Megirian 2004
1	<i>Ektopodon stirtoni</i>	5 Murray & Megirian 2000
1	<i>Nambaroo</i> sp. B	6 Long <i>et al.</i> 2002
2	<i>Bulungamaya</i> sp. A	7 Hand <i>et al.</i> 1993
1	<i>Pinaroo</i> sp. B	8 Murray <i>et al.</i> 2000
1	<i>Purtia</i> sp. A	