PLEISTOCENE GREY KANGAROOS FROM THE FOSSIL CHAMBER OF VICTORIA FOSSIL CAVE, NARACOORTE, SOUTH AUSTRALIA.

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Summary

Craniodental characteristics of Pleistocene grey kangaroos from the Fossil Chamber deposit in the Victoria Fossil Cave (VFC-FC), Naracoorte are herein described and compared with South Australian samples of the two extant species, Macropus giganteus Shaw and M. fuliginosus (Desmarest), as well as Pleistocene Macropus material from Tight Entrance Cave in Western Australia. The VFC-FC fossil kangaroos are significantly larger than modern South Australian material in all craniodental attributes, but do not differ significantly in size from Tight Entrance Cave Macropus. Characteristics previously used to identify the extinct megafaunal species M. titan in VFC-FC are here deemed unreliable as diagnostic tools. It is suggested that M. titan is not represented in VFC-FC and that only one species is present. This species more closely resembles extant M. fuliginosus than M. giganteus.

KEY WORDS: Pleistocene, Macropus titan, Macropus fuliginosus, Macropus giganteus, Naracoorte Caves World Heritage Area.

Introduction

Considerable diversity of opinions exists regarding the taxonomy and temporal relationships of fossil grey kangaroos (Macropus (Macropus)), (Bartholomai 1975; Flannery 1981; Dawson & Flannery 1985). The relatively recent evolution within the genus has resulted in a group of closely related and morphologically similar taxa (Kirsch & Poole 1972; Poole et al. 1990). This paper investigates the taxonomy of Pleistocene grey kangaroos excavated from the Fossil Chamber of Victoria Fossil Cave (VFC-FC), Naracoorte Caves World Heritage Area. The principal aim is to verify, through analysis of craniodental attributes, how many and which species are present in the sample. Prior to 1998, VFC-FC grey kangaroos were catalogued as M. giganteus or M. titan based on cursory assessments of relative size or other arbitrary means. In general, smaller specimens were registered as M. giganteus, while larger forms were registered as M. titan. M. titan, the megafaunal representative, had the anatomical characteristics of extant grey kangaroos but in larger proportions (Owen 1858). The relationship between M. giganteus and M. titan has received much attention and the latter’s specific distinction has been questioned (eg Anderson 1929; Tedford 1967; Bartholomai 1971; Marshall & Corruccini 1978; Flannery 1981). This paper considers both size-related and morphological attributes, with specific emphasis on the presence/absence of craniodental attributes that have been suggested as diagnostic of M. titan (Tedford 1967; Marcus 1976; Davis 1996).

Materials and Methods

Dental nomenclature and species identification

Serial designation of the cheek teeth follows Flower (1867), Wilson & Hill (1897), and Luckett (1993). Deciduous teeth are designated dP3, the permanent premolar is P3, and the molars are M1 through M4. Dental cusp terminology follows Ride (1993). The taxonomic arrangement of species within the genus Macropus, accepted by Dawson & Flannery (1985), have been followed in this study.

A reference database of the craniodental characteristics of modern grey kangaroos was created from the material registered at the South Australian Museum (SAM). A total of 60 possible craniodental measurements and morphological characters, based on those described by Poole et al.
(1990) were taken from the 280 grey kangaroo crania in the SAM collection. The collection consisted of 28 *M. giganteus*, 27 *M. fuliginosus fuliginosus*, 184 *M. f. melanops* and one *M. f. ocydromus* specimens. A further 41 were labelled *M. fuliginosus/giganteus*, as they were collected pre-1972, before the taxonomic separation of the two extant species by Kirsch & Poole (1972). The reference database summarised means, standard deviations and overall size ranges, and the occurrence of specific craniodental morphologies of SAM grey kangaroos. Craniodental morphologies were noted to investigate characteristics previously used to identify *M. titan*. The three main characters investigated in this study were the hypolophid ornamentation of the lower molars, the incidence of a buccal cuspule on the metacone of dP3, and the occurrence of infra-orbital canals with double foramina (see Davis 1996). Note that the P3, a character often used to identify Macropodidae, was not used due to the paucity of P3’s within the VFC-FC deposit. Characters measured and noted in the reference database followed those used by Poole *et al.* (1980). An additional database summarised means, standard deviations, overall size ranges, and the occurrence of specific craniodental morphologies of each individual extant species/subspecies. These databases were used to establish the comparative size range of the VFC-FC grey kangaroo material to modern populations. They were also used to note the occurrence of craniodental morphologies present on VFC-FC material, relative to extant populations. A small amount of fossil *Macropus* material from Tight Entrance Cave in Western Australia was also available for comparisons.

**Statistical analyses**

Means, standard deviations, overall size ranges and confidence levels for the means were tallied for all numerical parameters. Data were log_{10} transformed to counter for possible non-randomness and non-equal variances in the collections (Zar 1999). Coefficients of variation (CV = 100 sd/µ) were calculated to assess the degree of natural variation within all populations and thus to assess the homogeneity of the fossil population.

The most desirable statistical tools to analyse these data would be Principal Components Analysis (PCA) or Discriminant Analysis (Zar 1999). These test whether differences between the sample means are attributed to chance or whether there are real differences between the means of populations. They also identify suites of characters responsible for any differences. PCA and Discriminant Analysis utilise a subset of characters common to all groups. With *Macropus* data, however, four additional factors need to be taken into consideration when selecting these characters; (1) **Age:** Grey kangaroos grow continuously throughout life; that is, they never reach an ultimate “adult” size. Thus a representative age, based on some dental characteristics must be selected. For example, Poole *et al.* (1984) defined age categories based on the eruption status of the molar teeth. (2) **Molar progression:** Grey kangaroo dentition is never stable. The molars move forwards throughout life, avulsing the most anterior cheek tooth. This occurs with adult premolars and molars as well as the deciduous teeth. (3) **Sexual dimorphism:** With grey kangaroos, the adult males are significantly larger than the adult females. (4) **Tooth wear:** Molar teeth erode, especially in terms of length, with age.

These factors are compounded when investigating fossil material. Firstly a complete row of molar teeth is needed to identify the age. Often only a fragment of a molar row or no molars at all are present. Secondly, it is virtually impossible to tell whether a fossil specimen is male or female. The only character that is most likely to be present across the whole data set is the M2. Preliminary inspection of the SAM data in this study suggested that the M2 proportions were unreliable as discriminators of grey kangaroo species. Also by only analysing material with M2 present, 58% of available fossil material and characters would have been discarded.

For the purpose of this investigation, it was decided to use as many of the data as possible thus reverting back to basic Student’s t-tests to test the significant differences between means of all
possible characters. The reliability of these results was tested using the Holm’s Test adjustment of P<0.05 at the family-wise significance level (Holm 1979; Aickin & Gensler 1996).

Molar teeth made up the largest sample size of craniodental characters available for statistical analyses in both SAM and fossil groups. As well as the paucity of fossil cranial material available, the four factors noted previously needed to be addressed. Dividing material into age groups reduced the sample size of cranial material even further. Assessing the sex of the individual fossil material was impossible. Teeth are less likely to be affected by age and sexual dimorphism. Thus statistical analyses in this study focused on molar teeth. Descriptive statistics only were calculated for the cranial material.

Results

Size

Table 1 shows the means and overall size ranges of the molar widths and lengths of the SAM grey kangaroos, the VFC-FC grey kangaroos, and the Tight Entrance Cave Macropus. Mean molar lengths and widths of the VFC-FC material and the fossil Macropus material from WA were consistently higher than the SAM material. However confidence levels (CL) for the means showed molar widths of fossil kangaroos were generally within the range of the SAM material.

Table 1a. Number (N), means, standard deviations (sd), overall size ranges, and 95% confidence levels (CL) for the means, for lower molar lengths, and anterior widths (aw), for SAM modern grey kangaroos (M. giganteus and M. fuliginosus combined), VFC-FC fossil Macropus and WA fossil Macropus. Measurements are in mm.

|                  | SAM grey kangaroos | VFC-FC grey kangaroos | WA fossil Macropus |
|------------------|--------------------|-----------------------|-------------------|
|                  | N  | Mean (sd) | Range (95% CL) | N  | Mean (sd) | Range (95% CL) | N  | Mean (sd) | Range (95% CL) |
| M1 aw            | 15 | 6.6 (±0.45) | 6 – 7 (0.25) | 115 | 7.5 (±0.72) | 6 - 10 (0.13) | 23 | 7.6 (±0.13) | 6 – 9 (0.35) |
|                  | 15 | 10.0 (±0.7) | 8 - 11 (0.39) | 116 | 11.6 (±0.97) | 7 - 14 (0.18) | 24 | 11.9 (±0.85) | 10 - 13 (0.36) |
| M2 aw            | 9  | 7.7 (±0.54) | 6 – 8 (0.42) | 115 | 8.8 (±0.74) | 7 - 12 (0.14) | 23 | 8.7 (±0.48) | 7 – 9 (0.21) |
|                  | 10 | 11.8 (±1.02) | 10 - 13 (0.73) | 116 | 13.3 (±1.3) | 7 - 16 (0.24) | 23 | 13.2 (±0.81) | 11 - 14 (0.35) |
| M3 aw            | 12 | 8.2 (±0.38) | 7 – 9 (0.24) | 93  | 9.3 (±0.7) | 7 - 11 (0.14) | 13 | 9.7 (±1.33) | 8 - 13 (0.81) |
|                  | 12 | 12.5 (±0.94) | 11 – 14 (0.60) | 89  | 14.2 (±1.2) | 8 - 16 (0.25) | 11 | 14.2 (±1.32) | 11 - 15 (0.89) |
| M4 aw            | 11 | 14.2 (±1.32) | 11 - 15 (0.89) | 44  | 9.4 (±0.62) | 8 - 10 (0.19) | 5  | 9.5 (±0.91) | 8 - 10 (1.13) |
|                  | 8  | 12.8 (±14.02) | 11 – 14 (0.80) | 40  | 14.6 (±1.05) | 13 - 17 (0.34) | 5  | 16.5 (±1.15) | 14 - 18 (1.88) |
| dP3 aw           | 1  | 4.6 (±0.6) | 128 | 5.8 (±0.3) | 5 – 9 (0.1) | 12 | 6.3 (±0.49) | 5 – 7 (0.31) |
|                  | 1  | 8.0 (±0.86) | 130 | 9.5 (±0.15) | 5 - 11 (0.13) | 13 | 9.9 (±0.56) | 9 - 10 (0.33) |
Table 1b. Number (N), means, standard deviations (sd), overall size ranges and 95% confidence intervals for the means (CL) of upper molar anterior widths (aw) and lengths for SAM grey kangaroos (M. giganteus and M. fuliginosus combined), VFC-FC fossil Macropus and WA fossil Macropus. Measurements are in mm.

|                | SAM grey kangaroos | VFC-FC grey kangaroos | WA fossil Macropus |
|----------------|--------------------|-----------------------|-------------------|
|                | N                  | Mean (sd)             | Range (95% CL)    | N                  | Mean (sd)             | Range (95% CL)    | N                  | Mean (sd)             | Range |
| M1 aw          | 220                | 8.6 (±0.8)            | 6 – 11 (0.11)     | 112                | 9.0 (±1.13)           | 6 – 11 (0.20)      | 13                 | 9.2 (±0.52)           | 8 - 10 |
| M1 length      | 223                | 10.1 (±0.55)          | 7 - 12 (0.10)     | 114                | 11.5 (±0.9)           | 8 - 13 (0.17)      | 13                 | 12.0 (±1.12)          | 10 - 13 |
| M2 aw          | 216                | 9.7 (±1.02)           | 6 - 12 (0.14)     | 96                 | 10.3 (±0.11)          | 7 - 13 (1.5)       | 9                  | 10.3 (±0.69)          | 9 - 11  |
| M2 length      | 216                | 11.5 (±0.92)          | 8 - 14 (0.12)     | 100                | 13.2 (±0.87)          | 11 - 15 (0.17)     | 9                  | 13.3 (±0.96)          | 12 - 15 |
| M3 aw          | 138                | 10.3 (±1.28)          | 6 - 14 (0.22)     | 79                 | 11.1 (±1.06)          | 8 - 13 (0.24)      | 13                 | 10.8 (±0.27)          | 9 - 13  |
| M3 length      | 138                | 12.6 (±1.01)          | 10 - 15 (0.17)    | 78                 | 14.6 (±0.82)          | 12 - 16 (0.19)     | 13                 | 14.2 (±0.92)          | 12 - 15 |
| M4 aw          | 80                 | 10.23 (±1.21)         | 6 - 14 (0.27)     | 60                 | 10.8 (±1.02)          | 7 - 12 (0.27)      | 1                  | 12.5                 |        |
| M4 length      | 81                 | 13.2 (±1.07)          | 10 - 16 (0.24)    | 58                 | 15.3 (±0.87)          | 13 - 17 (0.23)     | 1                  | 15.59                |        |
| dP3 aw         | 47                 | 7.4 (±0.78)           | 6 - 9 (0.23)      | 102                | 7.4 (±1.0)            | 5 - 10 (0.2)       | 10                 | 7.4 (±0.65)           | 6 - 8   |
| dP3 length     | 44                 | 8.6 (±0.55)           | 7 - 10 (0.17)     | 106                | 9.9 (±0.78)           | 7 - 12 (0.15)      | 10                 | 9.9 (±0.43)           | 9 - 10  |

Student’s t-tests analysed differences in means between the groups. Table 2 shows the significant differences of the means, and P-values where relevant. The means of the SAM and the VFC-FC grey kangaroos were significantly different (P<0.05; Holm’s Test adjusted for multiple testing) for all lengths and widths except the M¹ posterior widths and the dP³ widths. Lengths of molars were also significantly different between the SAM grey kangaroos and the WA fossil Macropus. No significant differences were noted between the molar lengths and widths of the two fossil sites except in M¹ and M² posterior widths, M₄ length, and dP³ widths. Fig. 1 shows the relative differences in size range between the SAM, VFC-FC, and WA fossil material in molar tooth proportions of M¹-³ and dP³.

Table 3 shows means, standard deviations (sd), and overall size ranges of the “adult” cranial and mandibular material. “Adult” was classified as specimens with M₂ fully erupted and correlates to individuals of greater than four years old (Poole et al. 1984). As the amount of cranial material available from the VFC-FC deposit was minimal (<12 specimens per character), statistical tests on differences between means were not performed. In general, the means of VFC-FC cranial material tended to be higher than the corresponding SAM material, although the overall size range suggested that most individuals were within the size range of the SAM grey kangaroos. Some fossil mandibular material was larger than SAM species in length and width. Larger mandibles in some of the VFC-FC individuals were also suggested by the longer lower diastema lengths of some specimens. Unfortunately only one cranium from the VFC-FC material was available where rostral lengths could be measured, and this one cranium was well within the size range of the SAM modern Macropus material.
Table 4 shows CVs of molar teeth widths and lengths of the SAM and VFC-FC. Within the VFC-FC material the size range of all characters was attributable to normal variation within a sexual dimorphic population except the M$^1$ and dP$^3$ aw and pw, and the pw of M$^3$ and M$^4$. Within the SAM grey kangaroos, all of the lower dentition had CVs attributable to normal variation within a population. However, while the lengths of the upper molars of the SAM material were all within the size range of normal variation, the widths were generally >10.

Having established that the VFC-FC material was larger than the SAM material, the percentage difference between the two groups was calculated. The means of all characters measured in each of the two groups were pooled and summed. The sum of the means of the VFC-FC material was then divided by the sum of the means of the SAM material. Based on these calculations, the VFC-FC fossil material was 17% larger than extant species. Note that *M. titan* from the Late Pleistocene was up to 30% larger (see Marshall & Corrucini 1978; Dawson & Flannery 1985).
Table 2. Holm’s Test adjusted family-wise significance levels of molar anterior widths (aw), posterior widths (pw), and lengths between extinct grey kangaroos (SAM), VFC-FC grey kangaroos and fossil *Macropus* from Tight Entrance Cave (WA). NS signifies that differences between means were not significantly different.

| Craniomaxillary region | SAM and VFC-FC | VFC-FC and WA | SAM and WA | SAM and VFC-FC | VFC-FC and WA | SAM and WA |
|-------------------------|----------------|----------------|-------------|----------------|----------------|-------------|
| M1 aw                   | P <0.0001      | NS             | P<0.0001    | P<0.0001       | NS             | P<0.0001    |
| M1 length               | P< 0.0001      | NS             | NS          | P<0.0001       | NS             | P<0.0001    |
| M2 aw                   | P<0.0001       | NS             | NS          | P<0.0001       | NS             | NS          |
| M2 length               | P<0.0001       | NS             | P<0.0001    | P<0.01         | NS             | P<0.0001    |
| M3 aw                   | P<0.0001       | NS             | NS          | P<0.0001       | NS             | P<0.0001    |
| M3 length               | P<0.0001       | NS             | P<0.0001    | NS             | P<0.0001       | NS          |
| M4 aw                   | P<0.001        | P<0.0001       | NS          | NS             | P<0.0001       | NS          |
| M4 length               | P<0.001        | P<0.0001       | P<0.001     | P<0.0001       | NS             | P<0.0001    |
| dP3 aw                  | NS             | NS             | NS          | NS             | P<0.0001       | P<0.0001    |
| dP3 length              | P<0.0001       | NS             | P<0.0001    | NS             | NS             | NS          |

Table 3a. Number (N), means, standard deviations (sd) and overall size range of cranial measurements of SAM grey kangaroos and the VFC-FC grey kangaroos. Measurements are in mm.

| Craniomaxillary region | SAM grey kangaroos | VFC-FC grey kangaroos |
|------------------------|--------------------|-----------------------|
|                        | N  | Mean (sd) | Range  | N  | Mean (sd) | Range  |
| Basilar length         | 174 | 163.2 (±13.8) | 132- 200 | 4  | 193.9 (±11.9) | 178- 207 |
| Occipitonasal length   | 174 | 142.3 (±11.3) | 115- 175 | 4  | 166.6 (±7.3) | 155- 171 |
| Palate length          | 177 | 112.3 (±12.1) | 75- 160  | 4  | 137.0 (±7.7) | 129- 147 |
| Palate width           | 175 | 31.6 (±3.7)   | 21 - 40  | 22 | 35.9 (±4.9)  | 30 - 53  |
| Nasal length           | 163 | 70.4 (±7.2)   | 53 - 91  | 2  | 83.64 (±3.0) | 81 - 85  |
| Nasal width            | 180 | 23.8 (±3.4)   | 12 - 33  | 7  | 27.4 (±2.5)  | 23 - 30  |
| Squamosal depth        | 180 | 29.7 (±2.8)   | 21 - 38  | 22 | 32.9 (±3.1)  | 23 - 37  |
| Interlacrimal width    | 180 | 47.6 (±4.5)   | 34 - 62  | 7  | 56.0 (±4.6)  | 49 - 63  |
| Zygomatic width        | 170 | 91.2 (±6.2)   | 75 - 107 | 12 | 102.9 (±7.3) | 88 - 112 |
| Postorbital width      | 174 | 24.4 (±4.5)   | 10 - 38  | 12 | 24.1 (±4.6)  | 17 - 34  |
| Rostral width          | 163 | 16.8 (±2.8)   | 10 - 33  | 1  | 18.2        |          |
| Supraoccipital depth   | 173 | 6.5 (±10.4)   | 25 - 85  | 25 | 40.1 (±14.7) | 26 - 83  |
| Paraoccipital depth    | 149 | 61.8 (±5.2)   | 56 - 8   | 3  | 57.6 (±12.2) | 43 - 65  |
| Incisive foramen length| 181 | 8.9 (±1.8)    | 4 - 15   | 2  | 9.0 (±3.0)   | 6 - 11   |
Table 3b. Number (N), means, standard deviations (sd) and overall size range of mandibular characters and diastema lengths of SAM grey kangaroos, VFC-FC grey kangaroos and fossil *Macropus* material from Tight Entrance Cave. Measurements are in mm.

|                  | SAM grey kangaroos | VFC-FC kangaroos | WA fossil *Macropus* |
|------------------|-------------------|------------------|----------------------|
|                  | N     | Mean (sd) | Range | N     | Mean (sd) | Range | N     | Mean (sd) | Range |
| **Mandible length** | 166   | 136.1 (±16.37) | 71-107 | 22   | 155.1 (±16.37) | 112-180 | 112   | 17.14 (±2.32) | 14-21 |
| **Mandible width**  | 170   | 14.6 (±1.52)  | 11-20  | 100  | 18.6 (±2.09)  | 11-24  | 13    | 25.2 (±3.26)  | 21-32 |
| **Mandible depth**  | 168   | 21.9 (±2.71)  | 16-40  | 106  | 26.0 (±3.22)  | 13-35  | 13    | 36.0 (±7.07)  | 21-34 |
| **Lower diastema length** | 79    | 43.2 (±6.45)  | 31-61  | 40   | 50.72 (±7.07) | 36-66  | 1     | 63.6  |  |

Table 4. CVs of molar anterior widths (aw) and lengths within SAM and VFC-FC grey kangaroos.

|                  | Upper dentition | Lower Dentition |
|------------------|-----------------|-----------------|
|                  | SAM grey kangaroos | VFC-FC grey kangaroos | SAM grey kangaroos | VFC-FC grey kangaroos |
| M1 aw            | 9.3             | 12.5            | 6.8             | 9.6             |
| M1 length        | 5.4             | 7               | 7.0             | 8.4             |
| M2 aw            | 10.5            | 10              | 7.0             | 8.4             |
| M2 length        | 8               | 6.6             | 8.6             | 9.8             |
| M3 aw            | 12.4            | 9.5             | 4.6             | 7.5             |
| M3 length        | 8               | 5.6             | 7.6             | 8.4             |
| M4 aw            | 11.8            | 9.5             | 9.3             | 6.6             |
| M4 length        | 8               | 5.7             | 8.0             | 7.2             |
| dP3 aw           | 10.6            | 13.4            | 10.3            |                 |
| dP3 length       | 6.4             | 7.9             |                 |                 |

**Morphology**

Craniodental morphology was examined to investigate firstly, whether there were differences between extant *M. fuliginosus* and *M. giganteus* (see Poole *et al.* 1980, 1990), and secondly, to note the occurrence and frequency of morphological characters identified with *M. titan*. The three main morphological characters investigated in this study were the hypolophid ornamentation of the lower molars, the incidence of a buccal cuspule on the metacone of dP3, and the occurrence of infra-orbital foramen with double openings (see Davis 1996).
HYPOLOPHID ORNAMENTATION

Fig. 2 shows percentage of each hypolophid ornamentation noted within each group. Previous studies (Tedford 1967; Marcus 1976) suggested that the hypolophids of *M. giganteus* were more commonly ornamented by a vertical groove, *M. fuliginosus* by a pocket/fossa, while *M. titan* was characterized as having a deep fossa with inflated ridges. The “*M. giganteus* vertical groove” was the most common ornamentation, peaking at ~52% of the SAM *M. giganteus* molars. The “*M. fuliginosus* pocket/fossas” were more common in SAM *M. fuliginosus*, VFC-FC material and the WA *Macropus* material. Molar hypolophids with no ornamentation occurred in all groups but was less common in the fossil groups. VFC-FC material had more of the less common ornamentations; for example, “vertical grooves with inflated ridges” only occurred in the VFC-FC material. Only one specimen (from Naracoorte) showed the supposedly diagnostic *M. titan/M. ferragus* deep fossa with inflated ridges. Note that the largest specimen measured, (FU1640 registered as *M. titan*), had M₄ length of 17.9 mm, aw of 10.5 mm and pw of 9.2 mm, but was ornamented by only a very shallow posterior groove on the hypolophid.

dP³ BUCCAL CUSPULE

The occurrence of a buccal cuspule on the metacone of the dP³ in *M. titan* is a key diagnostic character of the species. The presence/absence of this cuspule on the SAM material was recorded. Of the SAM *M. giganteus* collection, only eight specimens had dP³ present and none had a cuspule on the metacone. Of the 130 specimens of SAM *M. fuliginosus* with dP³ still present, 5% had a buccal cuspule on the metacone. Eighty-four specimens from the VFC-FC had a dP³ present. Of these, 76% had a buccal cuspule on the metacone. Large molars were not necessarily associated with dP³ buccal cuspules.

INFRA-ORBITAL FORAMEN

Davis (1996) noted the occurrence of double infra-orbital foramina on fossil *Macropus* material in the Monaro Fauna, NSW. This cranial characteristic had not been recorded in previous papers on fossil *Macropus*. The occurrence of the double foramina was investigated in this study. While two *M. fuliginosus* specimens from SAM had the double infra-orbital foramina, no SAM *M. giganteus* did. Seventy-two VFC-FC specimens had infra-orbital foramen present. Of these 40% had double infra-orbital foramina present on both sides of the maxilla. Two specimens had a single foramen on one side and double foramina on the other.

Figure 2. Hypolophid ornamentation variation between modern grey kangaroos (SAM), VFC-FC fossil grey kangaroos, and the fossil grey kangaroos from Tight Entrance Cave, WA. “Normal” ornamentation denotes that commonly found on the lower molars of modern populations of *M. giganteus*. “Smooth” denotes no ornamentation on the lower molar hypolophid. “Fossa” and “Pocket” are two variations commonly found in modern *M. fuliginosus*. 
OTHER MORPHOLOGY

Other morphological characters have been used to identify *M. titan* (see Davis 1996; Tedford 1967). These include accessory links and spurs on molars, weak or absent forelinks on M1, highly variable P3, and narrow and shorter molar anterior cingula. Accessory links and spurs on molars were noted for four fossil specimens but much of the dental material was coated with sediment and hardener, and details such as accessory links and spurs were hard to detect. Weak or absent forelinks on M1 were only observed on one *M. fuliginosus* from SAM (M1863). Narrow and shorter molar anterior cingula were not investigated in this study. Cingula are primary abrasion areas and are thus often hard to observe. The highly variable P3 needs to be further investigated in extant populations before basing any description of *Macropus* species identification on its characteristics (Marcus 1976).

Discussion

The primary aim of this study was to establish whether the size range of fossil grey kangaroo material from the VFC-FC was comparable to the size range of modern grey kangaroos. If not, four further questions could be addressed. Was the VFC-FC material larger than modern species? Was there evidence for two distinct species within the VFC-FC deposit? Is *M. titan* present in the VFC-FC deposit? Were there any morphological characters that could give clues to the identity of the species of *Macropus* in VFC-FC?

Was the VFC-FC material larger than modern species? The overall size range of the VFC-FC material was different to the overall size range of the SAM modern material. Addressing the question of comparative size based on dental characteristics, the mean size of the VFC-FC population was 17% larger than the SAM modern grey kangaroo material. Some VFC-FC individuals had longer muzzles as evident from the longer molar lengths, longer lower diastemas, and longer and wider mandibles. However, in no instances were any VFC-FC individuals larger in every craniodental measurement than SAM species. Some had larger cranial proportions but had dental proportions within the size range of SAM modern grey kangaroos. For example one specimen (P25041) had large cranial proportions and exceptionally long nasal and maxillary bones (although a narrow intra-orbital region), but had dental proportions within the size range of SAM modern grey kangaroos. Other VFC-FC individuals had large molars but had cranial proportions within the size range of the SAM modern species. The fossil *Macropus* material from Tight Entrance Cave was similarly sized to the VFC-FC material, with means not significantly different for 89% of the dental characteristics measured, suggesting an analogous population.

Was there evidence for two distinct species within the VFC-FC deposit? The CVs suggested a homogeneous fossil population, albeit with substantial sexual dimorphism. While some of the CVs were in excess of 10, (the highest value for homogeneity), high CVs for molar size were also calculated for the SAM modern material, indicating that within grey kangaroos, variation exceeds that usually encountered in mammal species. This evidence is supported by Tedford (1967) who noted high CVs in M3 and M4 lengths (12.3 mm and 12.8 mm respectively) in the Lake Menindee fossil grey kangaroo fauna. He also noted CVs >10 for *M. fuliginosus* M2, M3 and M4 lengths, and M4 pw from sites “pan-Australia”. They were explained as the consequence of pooling of populations from different regions (ie not accounting for geographic clines).
Is M. titan represented in the VFC-FC deposit? The relationship between M. titan and M. giganteus has been alluded to by most researchers studying fossil Macropus. While some argued that M. giganteus is a dwarfed version of M. titan (eg Dawson & Flannery 1985), others argued that the two co-existed as separate, albeit closely related species (eg Marshall & Corruccini 1978). There is general agreement that there were Pleistocene grey kangaroo species/subspecies of up to 30% larger size than modern species. What is not agreed upon is whether all of these larger forms are M. titan. If M. titan sensu stricto were the 30% larger form (see Owen 1858), results of this study suggest that M. titan does not occur in the VFC-FC deposit.

Pledge (1990) noted that the grey kangaroo material from Henschke's Cave fossil deposit, also in the Naracoorte area, was 20% larger than modern populations. He suggested that this group represented an intermediate form between M. titan and modern M. giganteus, with tooth dimensions that were smaller than M. titan, with the characteristic fossa on the lower molar hypolophid reduced. These intermediate forms have been noted from many Pleistocene sites including the Monaro fauna (Davis 1996) and the Lake Menindee fauna (Tedford 1967), and are generally 17% larger than modern species based on dental measurements (Dawson & Flannery 1985). Tedford (1967) named the Lake Menindee group M. birdselli.

Would there be any morphological characters that could give clues to the identity of the species of the VFC-FC grey kangaroos? Morphological characters (as well as size differences) supposedly separate M. giganteus and M. fuliginosus from M. titan. This study investigated the reliability of the presence of buccal cuspules on dP3's, lower molar hypolophid ornamentation, and double infra-orbital foramen, as identification tools for M. titan, by examining their occurrence in SAM modern, and VFC-FC fossil material. The observations were inconclusive. The presence of the dP3 buccal cuspule was noted on 76% of all VFC-FC material with a dP3 present, and also on several SAM modern M. fuliginosus, but no M. giganteus did. The hypolophid ornamentation was extremely variable in both SAM modern and the VFC-FC fossil material. Some fossil material had no hypolophid ornamentation. Only one specimen carried the supposedly diagnostic M. titan hypolophid character, but molars of this specimen were not outside the size range of SAM modern species. These results support previous studies (eg Tedford 1967; Marcus 1976; Davis 1996), which suggested that while some hypolophid ornamentations were more likely to occur on some species, no particular ornamentation distinguished any of the groups from another. The double infra-orbital foramina were present on many fossil specimens. Two SAM modern M. fuliginosus also had this character.

Are the VFC-FC fossil Macropus, M. giganteus or M. fuliginosus? M. fuliginosus is more common than M. giganteus in the Naracoorte area at the present time. Is the material from VFC-FC registered as M. giganteus in fact M. fuliginosus, albeit a population that was larger in size, and more variability in craniodental morphology than the modern species? M. giganteus and M. fuliginosus are difficult to separate when presented with craniodental material only. Wood Jones (1968) separated M. giganteus from M. fuliginosus by the dental ornamentation on the I1, and by the relative positions of sutures of the anterior palate. Poole et al. (1990) attempted to separate M. giganteus and M. fuliginosus using craniodental measurements. They noted that M1 and M2 were important discriminators and that there were differences in the structure of molar teeth, but did not state what the differences were. Currently, modern grey kangaroo species are separated by serological and reproductive characteristics, and by pelt colour (Kirsch & Poole 1972).

Preliminary measurements taken for this study from the SAM modern grey kangaroo material suggested that M. fuliginosus molar teeth were wider than M. giganteus. M. fuliginosus also had dental morphologies (eg some incidence of dP3 buccal cuspules, comparable hypolophid ornamentation) which were also common with the VFC-FC fossil material. The 17% larger VFC-FC population with the frequent occurrence of the dP3 buccal cuspule (also found on M. fuliginosus) and the high number of double infra-orbital foramina (also noted on M. fuliginosus), suggests that it is more closely related to M. fuliginosus than to M. giganteus. That is, a relationship of the VFC-FC fossil population to modern M. fuliginosus is supported by the
occurrence of modern *M. fuliginosus* with the retention of the ancestral dental morphology. Tedford (1967) also advocated this view. However the sample size of modern *M. giganteus* at SAM was much smaller than the *M. fuliginosus* sample size, and a larger sample size of *M. giganteus* is needed to support this observation.

These results were part of a larger study on the *Macropus* species found in the VFC-FC (Turner 1999). Results of the wallaby species have been published elsewhere (Easton 2004). It is hoped that these results will be useful as comparative data for other researchers who are working with the problematical tasks of identification and taxonomic relationships of fossil *Macropus* species, and those investigating megafaunal lineages or evolutionary dwarfism (nanism).

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