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# The genetic structure of the *Badumna candida* group of species (Araneae, Amaurobioidea)

**D. J. Colgan** and **M. R. Gray**
The Australian Museum,
P.O. Box A285, Sydney South,
Australia 2000

## Summary

Electrophoretic investigations were performed to assess genetic relationships within the *Badumna candida* species group, with particular attention being paid to *B. candida* itself, whose putative distribution covers nearly the whole of continental Australia. The results show that *B. candida* does indeed have a remarkably wide range. Its evolutionary history has been structured by a barrier to gene flow between two regions in Western Australia and by a trend to increasing genetic distance with an increase in geographic distance. This has resulted in the differentiation, from the main lineages of the species, of two taxa in the South-East which could be regarded as subspecies of *B. candida* despite their morphological similarity. Further, there are two populations in remote arid zone regions which electrophoresis and subsequent morphological examinations have shown to be so distinct that they warrant recognition as true species. Another unexpected result was the finding that *B. vandiemeni* occurs on the mainland as well as in Tasmania, where, indeed, its populations may include two cryptic species characterised by a fixed allozymic difference for 6-phosphogluconate dehydrogenase.

## Introduction

The *Badumna candida* species complex is a group of usually semi-communal spiders widely distributed throughout continental Australia and Tasmania in habitats ranging from open temperate and tropical forests to arid grasslands and shrublands (Main, 1981; Gray, 1983). Five species have been described from members of the group (Simon, 1908; Gray, 1983). Three of these, *Badumna candida* (L. Koch), *B. gausapata* (Simon) and *B. vandiemeni* Gray, are currently recognised. However, the status of *B. gausapata* is in doubt. Delayed dispersal is especially characteristic of *B. candida* populations. The juveniles remain together in a communal nest from which most appear to disperse before, or soon after, maturation. Extensive genetic mixing within south-western populations reported by D. J. Ayre (1977, unpubl. Hons. thesis, University of Western Australia) suggests that mating occurs primarily after dispersal. In *B. vandiemeni*, by contrast, spiderlings disperse soon after emergence and "colonial nests" do not occur.

Despite some variability in individuals from different areas, it is clear that all of the *candida* group taxa are morphologically very similar. It is well known that such morphological similarity does not always imply close genetic affinities between taxa — see Rowell (1990) for an example in spiders. Hence, it would not be unexpected if the large geographic distances between populations were found to be associated with significant genetic divergence. This is particularly the case for *B. candida* which has a distribution covering nearly all of continental Australia. The extreme South-East is occupied by *B. gausapata* according to Gray (1983). However, in this study the range of *B. candida* will be considered to include that of *B. gausapata* in anticipation of the synonymy noted above. Hence *B. candida* can be regarded as having a truly continental distribution. Such a range makes it one of the most widespread Australian arachnids (Main, 1981) and indeed there are few terrestrial animals, either invertebrate or vertebrate, apart from birds, with such an extensive distribution. Comparable ranges are only found for the legless lizard *Lialis burtonis* (Cogger, 1986), the echidna *Tachyglossus aculeatus*, and the bats *Nyctophilus geoffroyi* and *Chalinolobus gouldii* (Strahan, 1983), none of which has been the subject of genetic surveys of taxonomic or population structure. It would be remarkable if such a range as that of *B. candida* were not fragmented to at least some extent by partial barriers to gene exchange or by actual splits into distinct species. The purpose of the present paper is to investigate the genetic structure of the *Badumna candida* group of species with especial attention being paid to *B. candida* itself. Questions of the number of species in the group and of the interrelationships of populations within distinguishable taxa are of particular interest.

## Materials and methods

Spiders from the *B. candida* group of species and from *Badumna insignis* (L. Koch) and *B. socialis* (Rainbow)

| Number | Population name | Sample | Latitude S | Longitude E |
|---|---|---|---|---|
| 1 | Port Arthur | a | 43° 09′ | 147° 51′ |
| 2 | Taranna | a | 43° 04′ | 147° 51′ |
| 3 | Murdunna | a | 42° 57′ | 147° 52′ |
| 4 | Eaglehawk Neck | s | 43° 02′ | 147° 53′ |
| 5 | Copping | s | 42° 49′ | 147° 45′ |
| 6 | Sorell | a | 42° 47′ | 147° 34′ |
| 7 | Triabunna | a | 42° 30′ | 147° 55′ |
| 8 | Wilson's Promontory (Tidal R.) | a | 39° 02′ | 146° 20′ |
| 9 | Rushworth | a | 36° 35′ | 145° 01′ |
| 10 | Black Mountain | a | 35° 16′ | 149° 06′ |
| 11 | Neville | a | 33° 45′ | 149° 12′ |
| 12 | Goonoo State Forest | a | 32° 03′ | 148° 55′ |
| 13 | Gunbar | a | 34° 04′ | 145° 25′ |
| 14 | Dareton | a | 34° 11′ | 142° 06′ |
| 15 | Lake Munmorah | a | 33° 13′ | 151° 34′ |
| 16 | Mildura | a | 34° 14′ | 141° 58′ |
| 17 | Iron Knob | a | 32° 07′ | 136° 50′ |
| 18 | Roaches Rest | a | 31° 32′ | 127° 18′ |
| 19 | Cape Range | s | 21° 57′ | 114° 02′ |
| 20 | South Hedland | s | 20° 26′ | 118° 36′ |
| 21 | Pardoo Station | s | 20° 07′ | 119° 35′ |
| 22 | Canning Stock Route (Mellinjerie Well) | s | 21° 00′ | 123° 20′ |
| 23 | Canning Stock Route Miscellany | s | | |
| | Lake Gulì | | 21° 16′ | 125° 55′ |
| | Well 45 | | 20° 35′ | 126° 25′ |
| | Kidson Creek | | 21° 58′ | 123° 45′ |
| | Mellingerie Well sample 2 | | 21° 00′ | 123° 20′ |
| 24 | Anna Plains | s | 19° 15′ | 121° 29′ |
| 25 | Windy Corner | s | 23° 34′ | 125° 11′ |
| 26 | Carson Escarpment | s | 15° 21′ | 126° 37′ |
| 27 | Cape Bernier | s | 14° 00′ | 127° 28′ |
| 28 | Townsville | a | 19° 16′ | 146° 49′ |
| 29 | *Badumna insignis* Penrith | a | 33° 45′ | 150° 42′ |
| 30 | *B. socialis* Abercrombie Caves | a | 33° 55′ | 149° 19′ |

Table 1: Collection site data for all *Badumna* populations. Population numbers used in the text, tables and figures are indicated in the first column. The life-cycle stage of the individuals used for electrophoresis is also given, "a" indicating adults and "s" spiderlings.

| Enzyme | Abbreviation | E.C. No. | Buffer | Loci |
|---|---|---|---|---|
| Glucosephosphate isomerase | GPI | 5.3.1.9 | TEM 50 | 1 |
| Phosphoglucomutase | PGM | 5.4.2.2 | TEM 50 | 1 |
| Malate dehydrogenase | MDH | 1.1.1.37 | TEM 50 | 2 |
| 6-Phosphogluconate dehydrogenase | 6-PGDH | 1.1.1.44 | TEM 50 | 1 |
| Fructose diphosphatase | FDP | 3.1.3.11 | TEM 50 | 1 |
| Pyruvate kinase | PK | 2.7.1.40 | TEM 50 | 2 |
| α-Glycerophosphate dehydrogenase | GPD | 1.1.1.8 | TEM 50 | 1 |
| Isocitrate dehydrogenase | IDH | 1.1.1.42 | TEM 50 | 2 |
| Acid phosphatase | AP | 3.1.3.2 | TEM 50 | 2 |
| Fumarate hydratase | FUM | 4.2.1.2 | TEM 50 | 1 |
| Mannosephosphate isomerase | MPI | 5.3.1.8 | TEM 50 | 1 |
| Hexokinase | HK | 2.7.1.1 | TEM 50 | 1 |
| Aldolase | ALD | 4.1.2.13 | TEM 50 | 1 |
| Aspartate aminotransferase | GOT | 2.6.1.1 | TC 100 | 2 |
| Lactate dehydrogenase | LDH | 1.1.1.27 | TC 100 | 2 |
| Glyceraldehyde phosphate dehydrogenase | GA-3-PDH | 1.2.1.12 | TEM 50 | 1 |
| Triosephosphate isomerase | TPI | 5.3.1.1 | TEM 50 | 1 |

Table 2: Electrophoretic methods for enzymes scored in this study. Enzyme abbreviations, E.C. number, buffer used and number of presumptive genetic loci are indicated in the second to fifth columns respectively. Buffer recipes are given in Colgan (1986).

were collected by M. R. G. from various sites throughout Australia (Table 1, Fig. 1) or were made available by other collectors. Samples are identified in this paper by the population numbers shown in Table 1. Hereinafter, numbers in parentheses refer to these localities. Some specimens in each sample were retained as vouchers for morphological examination. The remainder were frozen in liquid nitrogen or at −80°C until required for electrophoresis. Collections were made from *B. insignis* and *B. socialis* because these were considered to be potential outgroups.

Electrophoresis was performed on Titan III cellulose acetate plates following standard procedures, except as specified below. All gels were run for a period of 60 min

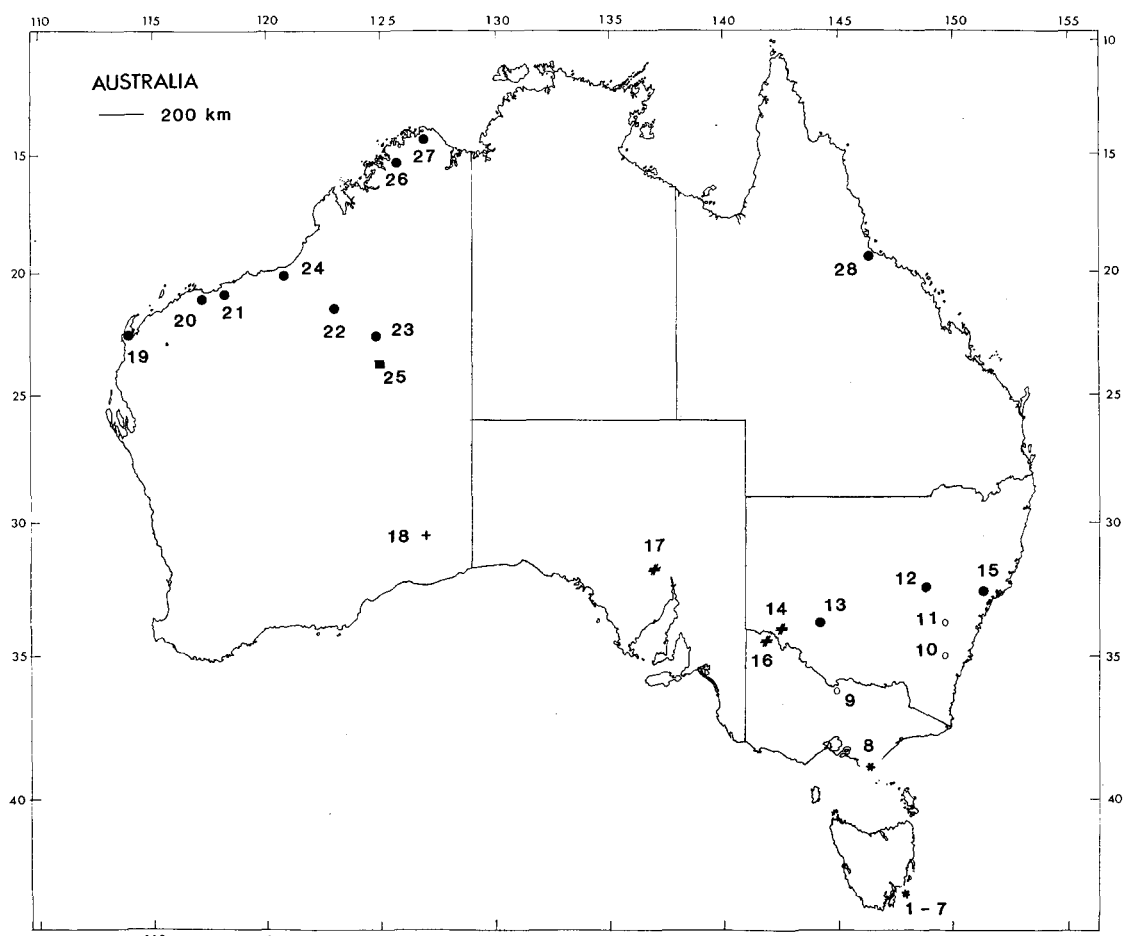


Fig. 1: Sample locations of studied populations of the *Badumna candida* group of species. Numbers besides sample points refer to designations given in Table 1. *B. vandiemeni* samples are indicated by * (1 to 7 are within 50 km of each other); the Southern Group (populations 9, 10 and 11) by ○; the Mallee Group (14, 16 and 17) by ⁂; (18) by +; (25) by ■; and other *B. candida* samples by ● (populations 19–24 comprise the Pilbara Group).

Table 3: Allozymic frequencies in all *Badumna* populations. Rows led by "(N)" indicate the number of individuals scored for each enzyme in a population. Numbers identifying populations are explained in Table 1.

| | Population | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Locus** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **23** | **24** | **25** | **26** | **27** | **28** | **29** | **30** |
| **GPI** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 7 | 3 | 6 | 9 | 12 | 6 | 7 | 2 | 4 | 18 | 13 | 18 | 18 | 2 | 10 | 11 | 12 | 10 | 10 | 10 | 10 | 14 | 6 | 2 | 2 | 8 | 10 | 8 | 8 | 6 |
| 1 | | | | | | | | | | | | | | | | | | 0.15 | | | | | | | | 0.06 | | | | |
| 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1.00 |
| 3 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.94 | |
| 4 | 1.00 | 1.00 | 1.00 | 1.00 | 0.88 | 1.00 | 1.00 | | 0.25 | 0.94 | 0.92 | 0.94 | 0.14 | | 0.95 | 0.14 | 1.00 | 0.85 | 0.90 | 1.00 | 0.85 | 0.93 | 1.00 | 1.00 | 1.00 | 0.94 | 1.00 | 1.00 | | |
| 5 | | | | | | | | 1.00 | 0.75 | | | | | 1.00 | | 0.86 | | | | | | | | | | | | | 0.06 | |
| 6 | | | | | 0.12 | | | | | 0.06 | 0.08 | 0.06 | 0.86 | | 0.05 | | | | 0.10 | | 0.15 | 0.07 | | | | | | | | |
| **PGM** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 6 | 9 | 12 | 6 | 8 | 4 | 4 | 18 | 13 | 17 | 11 | 4 | 11 | 13 | 12 | 10 | 10 | 9 | 9 | 14 | 5 | 2 | 2 | 8 | 9 | 8 | 8 | 6 |
| 1 | | | | | | | | | | | | | | | | | 0.25 | | | | | | | | | | | | | |
| 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.25 | 1.00 |
| 3 | | | | | | | | | | | | | | | | | | | | | 0.22 | 0.36 | 0.10 | 0.50 | | | | | | |
| 4 | | | | | | | | | | | | 0.09 | 0.73 | 1.00 | 0.73 | 1.00 | 0.75 | 0.30 | 1.00 | | 0.17 | | 0.10 | | | 0.06 | | 0.31 | 0.75 | |
| 5 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | | | | | | | | | | | | | | | | | | | | | |
| 6 | | | | | | | | | 1.00 | 1.00 | 1.00 | 0.91 | 0.27 | | 0.27 | | | 0.45 | | 1.00 | 0.55 | 0.64 | 0.80 | 0.50 | 1.00 | 0.94 | 1.00 | 0.69 | | |
| 7 | | | | | | | | | | | | | | | | | | | | | 0.06 | | | | | | | | | |
| 8 | | | | | | | | | | | | | | | | | | 0.25 | | | | | | | | | | | | |
| **MDH-1** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 7 | 9 | 12 | 7 | 8 | 4 | 4 | 18 | 13 | 17 | 11 | 4 | 12 | 13 | 11 | 10 | 10 | 10 | 10 | 14 | 6 | 2 | 2 | 8 | 9 | 8 | 8 | 6 |
| 1 | | | | | 0.04 | | | | | | | | | | | | | | | | | | | | | | | | | |
| 2 | | | | | | | | | | | | 0.06 | | | | | | | | | | | | | | 0.06 | | | | |
| 3 | 1.00 | 1.00 | 1.00 | 1.00 | 0.92 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.94 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.94 | 1.00 | 1.00 | 1.00 | 1.00 |
| 4 | | | | | 0.04 | | | | | | | | | | | | | | | | | | | | | | | | | |
| **MDH-2** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 7 | 7 | 12 | 7 | 8 | 4 | 4 | 18 | 13 | 17 | 11 | 4 | 12 | 13 | 11 | 10 | 10 | 10 | 10 | 14 | 6 | 2 | 2 | 8 | 9 | 8 | 8 | 6 |
| 1 | | | | | 0.04 | | | | | | | | | | | | | | | | | | | | | | | | | |
| 2 | 1.00 | 1.00 | 1.00 | 1.00 | 0.96 | 1.00 | 0.87 | 1.00 | 1.00 | 1.00 | 1.00 | 0.97 | 0.96 | 1.00 | 1.00 | 0.92 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.62 | 0.92 |
| 3 | | | | | | | 0.13 | | | | | 0.03 | 0.04 | | | 0.08 | | | | | | | | | | | | | | |
| 4 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.38 | 0.08 |
| **6-PGDH** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 7 | 3 | 8 | 7 | 8 | 4 | 4 | 17 | 13 | 13 | 11 | 4 | 12 | 7 | 8 | 6 | 8 | 10 | 8 | 12 | 6 | 2 | 2 | 6 | 8 | 8 | 8 | 6 |
| 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.33 |
| 2 | | | | | | | | | | 0.12 | | 0.15 | 0.36 | | | | 0.56 | 0.08 | | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | | | 0.19 | | 0.17 |
| 3 | 0.75 | 0.25 | 0.29 | | 0.62 | 0.86 | 0.38 | 0.87 | 0.87 | 0.65 | 0.73 | 0.85 | 0.64 | 1.00 | 0.96 | 1.00 | 0.44 | 0.75 | 1.00 | | | | | | | 1.00 | 1.00 | | 0.31 | 0.50 |
| 4 | 0.25 | 0.75 | 0.71 | 1.00 | 0.38 | 0.14 | 0.62 | 0.13 | 0.13 | 0.23 | 0.27 | | | | 0.04 | | | 0.17 | | | | | | | | | | 0.81 | 0.69 | |
| 5 | | | | | | | | | | | | | | | | | | | | | | | | | 1.00 | | | | | |
| **FDP** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 6 | 4 | 6 | 8 | 12 | 6 | 6 | 4 | 2 | 14 | 8 | 15 | 11 | 4 | 12 | 12 | 10 | 10 | 8 | 8 | 9 | 11 | 6 | 2 | 2 | 6 | 10 | 6 | 8 | 4 |
| 1 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.75 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | 1.00 | 1.00 | 1.00 | 0.38 | 0.50 |
| 2 | | | | | | | | | | | | | | | | | | | 0.25 | | | | | | 1.00 | | | | | |
| 3 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.62 | 0.50 |
| **PK-1** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 7 | 8 | 10 | 7 | 8 | 4 | 4 | 15 | 11 | 15 | 7 | 4 | 6 | 13 | 7 | 8 | 6 | 6 | 4 | 12 | 6 | | 1 | 4 | 6 | 4 | 2 | 2 |
| 1 | | | | | 0.05 | | | | | | 0.05 | | 0.14 | 0.13 | | | | | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | | | | | 0.75 | 1.00 |
| 2 | 0.94 | 0.87 | 0.86 | 0.87 | 0.80 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.95 | 1.00 | 0.86 | 0.50 | 0.75 | 0.92 | 1.00 | 1.00 | | | | | | | | 1.00 | 0.92 | 1.00 | 0.25 | |
| 3 | 0.06 | 0.13 | 0.14 | | 0.10 | | | | | | | | | 0.37 | 0.25 | 0.08 | | | | | | | | | 1.00 | | 0.08 | | | |
| 4 | | | | 0.13 | 0.05 | | | | | | | | | | | | | | | | | | | | | | | | | |
| **PK-2** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 6 | 4 | 5 | 7 | 10 | 5 | 6 | 2 | 4 | 8 | 5 | 7 | 7 | 4 | 6 | 11 | 8 | 8 | 5 | 6 | 5 | 12 | 6 | | 2 | 5 | 6 | 5 | 2 | |
| 1 | | | | 0.14 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 2 | | | | | | | | | | | | 0.14 | 0.07 | | | | | | 0.20 | 0.83 | 0.80 | 0.65 | | | | 0.80 | 0.17 | | | |
| 3 | 0.83 | 0.62 | 0.20 | 0.71 | 0.95 | 0.80 | 0.83 | 1.00 | 0.75 | 0.94 | 1.00 | 0.86 | 0.93 | 1.00 | 1.00 | 0.95 | 0.87 | | 0.80 | 0.17 | 0.20 | 0.35 | 1.00 | | | 0.20 | 0.83 | 1.00 | 1.00 | |
| 4 | 0.17 | 0.25 | 0.80 | 0.14 | 0.05 | 0.20 | 0.17 | | 0.25 | | | | | | | 0.05 | | | | | | | | | 1.00 | | | | | |
| 5 | | 0.13 | | | | | | | | 0.06 | | | | | | | 0.13 | 1.00 | | | | | | | | | | | | |
| **GPD** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 6 | 4 | 5 | 9 | 12 | 5 | 6 | 2 | 4 | 15 | 12 | 17 | 11 | 4 | 11 | 13 | 12 | 10 | 10 | 10 | 10 | 11 | 6 | 2 | 2 | 6 | 10 | 7 | 8 | 6 |
| 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.14 | | |
| 2 | | | | | | | | | | | | | | | | | | | | | | | | | | 1.00 | | | | |
| 3 | | | | | | | | | | | | | | | | | | | | | | | | | | | 1.00 | | | |
| 4 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | | 0.86 | 1.00 | 0.92 |
| 5 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.08 |
| **IDH-1** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 7 | 9 | 12 | 7 | 8 | 4 | 4 | 16 | 12 | 17 | 11 | 4 | 11 | 13 | 12 | 10 | 10 | 10 | 10 | 13 | 6 | 2 | 2 | 7 | 10 | 7 | 7 | 6 |
| 1 | 0.19 | 0.13 | 0.29 | | 0.08 | 0.21 | | | | 0.03 | 0.50 | 0.15 | 0.86 | | 1.00 | | | | | | | | | | | | | 0.07 | | |
| 2 | | | | | | | | | | | | | | | | | | | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | | | | | |
| 3 | | | | | | | | 0.75 | 0.13 | 0.03 | 0.08 | | | 1.00 | | 1.00 | 1.00 | | | | | | | | | | | | 0.43 | |
| 4 | 0.81 | 0.87 | 0.71 | 0.83 | 0.67 | 0.79 | 1.00 | 0.25 | 0.87 | 0.88 | 0.42 | 0.85 | 0.14 | | | | | 0.95 | | | | | | | 1.00 | 1.00 | 0.95 | 0.93 | 0.57 | 1.00 |
| 5 | | | | 0.17 | 0.25 | | | | | 0.06 | | | | | | | | 0.05 | | | | | | | | | | | | |
| 6 | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.05 | | | |
| **IDH-2** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 7 | 9 | 11 | 7 | 8 | 4 | 4 | 8 | 11 | 3 | 6 | 4 | 8 | 11 | 7 | 8 | 10 | 10 | 8 | 8 | 6 | | 2 | 4 | 7 | 5 | 4 | 4 |
| 1 | 1.00 | 0.75 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | | | | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| 2 | | 0.25 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 3 | | | | | | | | | 1.00 | 1.00 | 1.00 | 1.00 | | | | | | | | | | | | | | | | | | |
| **AP-2** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 7 | 3 | 6 | 6 | 8 | 4 | 4 | 7 | 7 | 5 | 9 | 4 | 8 | 3 | 6 | 5 | 2 | 10 | 5 | 7 | 6 | | 2 | 3 | 6 | 6 | 6 | 4 |
| 1 | | | | | | | | | | | | | | | | | | 1.00 | | | | | | | | | | | | |
| 2 | 0.87 | 0.62 | 0.79 | | 0.83 | 0.75 | 0.69 | 0.38 | | | | | | | | | | | | | | | | | | | | | | |
| 3 | 0.13 | 0.38 | 0.21 | | | 0.25 | 0.31 | 0.62 | 1.00 | 1.00 | 1.00 | 1.00 | | 1.00 | | 1.00 | 1.00 | | | | | | | | 1.00 | | | | | |
| 4 | | | | 1.00 | 0.17 | | | | | | | | 1.00 | | 1.00 | | | | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | | 1.00 | 1.00 | 1.00 | | |
| 5 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1.00 | 1.00 |

Table 3: *Continued.*

| Locus | Population 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **FUM** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 7 | 9 | 12 | 7 | 8 | 4 | 4 | 18 | 13 | 17 | 11 | 4 | 10 | 13 | 12 | 9 | 10 | 10 | 10 | 13 | 6 | 2 | 2 | 8 | 10 | 8 | 8 | 1 |
| 1 | 0.50 | 0.50 | 0.07 | | | 0.29 | 0.06 | 0.25 | | | | | | | | | | | | | | | | | | | | | | |
| 2 | 0.50 | 0.50 | 0.93 | 1.00 | 1.00 | 0.71 | 0.94 | 0.75 | | | | 0.06 | | | | | | 0.06 | | | | | | | | | | | | |
| 3 | | | | | | | | | 0.50 | 1.00 | 1.00 | 0.94 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.94 | 0.40 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | |
| 4 | | | | | | | | | 0.50 | | | | | | | | | | 0.60 | | | | | | | | | | | |
| 5 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1.00 |
| 6 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1.00 | |
| **MPI** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 7 | 8 | 12 | 7 | 8 | 4 | 4 | 16 | 11 | 15 | 8 | 4 | 10 | 11 | 10 | 10 | 10 | 10 | 9 | 14 | 6 | 2 | 2 | 6 | 9 | 6 | 2 | 2 |
| 1 | | | | | | | | | | | | | | | 1.00 | | | | | | | | | | | | | | 0.25 | 0.25 |
| 2 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.90 | 1.00 | | | | 1.00 | 0.10 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.75 | 0.75 |
| 3 | | | | | | | | | | | | 0.10 | | 1.00 | | 1.00 | | 0.90 | | | | | | | | | | | | |
| **HK** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 7 | 9 | 12 | 7 | 8 | 4 | 4 | 15 | 13 | 16 | 11 | 4 | 12 | 13 | 12 | 10 | 10 | 10 | 10 | 14 | 6 | 2 | 2 | 6 | 9 | 7 | 7 | 4 |
| 1 | 0.31 | 0.50 | 0.21 | 0.22 | 0.08 | 0.07 | 0.25 | | | | | | | 0.13 | | | | | | | | | | | | | | | | |
| 2 | 0.69 | 0.50 | 0.79 | 0.78 | 0.92 | 0.93 | 0.75 | 1.00 | 1.00 | 0.97 | 0.96 | 1.00 | 1.00 | 0.87 | 1.00 | 1.00 | 1.00 | 1.00 | 0.95 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| 3 | | | | | | | | | | 0.03 | 0.04 | | | | | | | | 0.05 | | | | | | | | | | | |
| **ALD** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 4 | 4 | 4 | 9 | 11 | 4 | 4 | 2 | 2 | 14 | 12 | 16 | 11 | 4 | 11 | 12 | 12 | 10 | 10 | 10 | 10 | 14 | 6 | 2 | 1 | 8 | 10 | 7 | 7 | 5 |
| 1 | 1.00 | 1.00 | 1.00 | 1.00 | 0.91 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | 1.00 | 1.00 | 1.00 | 0.93 | 1.00 | 1.00 |
| 2 | | | | | 0.09 | | | | | | | | | | | | | | | | | | | 1.00 | | | | 0.07 | | |
| **GOT-1** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 7 | 4 | 6 | 7 | 8 | 4 | 4 | 9 | 5 | 4 | 5 | 4 | 4 | 9 | 6 | 8 | 7 | 7 | 8 | 11 | 6 | 2 | 2 | 6 | 10 | 2 | 2 | |
| 1 | | | | | | | | | | 0.72 | 1.00 | | | | | | | | | | | | | | | | | | | |
| 2 | | | | | | | | | | | | | | | | | | | | | | | | | | 1.00 | | | | |
| 3 | | | | | | 0.14 | | | | 0.28 | | | | | | 1.00 | 1.00 | | 1.00 | 1.00 | | 1.00 | 1.00 | 1.00 | | | 1.00 | | | |
| 4 | 0.13 | | | | | | 0.13 | | | | | 1.00 | | | | | | | | | | | | | | | | | | |
| 5 | | | | 0.13 | | | | | | | | | 1.00 | 1.00 | 1.00 | | | | | | 1.00 | | | | 1.00 | | | | | |
| 6 | 0.87 | 1.00 | 1.00 | 0.87 | 1.00 | 0.86 | 0.87 | 1.00 | 1.00 | | | | | | | | | | | | | | | | | | | | 1.00 | |
| 7 | | | | | | | | | | | | | | | | | | 1.00 | | | | | | | | | | | | |
| 8 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1.00 | | |
| **GOT-2** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 7 | 4 | 8 | 7 | 8 | 4 | 4 | 6 | 5 | 7 | 3 | 4 | 3 | 9 | 4 | 4 | 7 | 5 | 9 | 7 | 6 | 2 | 2 | 4 | 7 | 2 | | |
| 1 | 1.00 | 1.00 | 1.00 | 0.50 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | |
| 2 | | | | 0.50 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **LDH-2** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 5 | 2 | 3 | 6 | 12 | 4 | 3 | 4 | 1 | 7 | 4 | 14 | 10 | 2 | 7 | 7 | 7 | 10 | 4 | 8 | 9 | 4 | | 2 | | 6 | 8 | 5 | 6 | 2 |
| 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.17 | |
| 2 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.50 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | 1.00 | | 1.00 | 1.00 | 1.00 | 0.75 | 1.00 |
| 3 | | | | | | | | | | | 0.50 | | | | | | | | | | | | | | | | | | 0.08 | |
| **GA-3-PDH** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 8 | 4 | 7 | 7 | 12 | 7 | 8 | 4 | 4 | 17 | 11 | 18 | 11 | 4 | 10 | 11 | 12 | 10 | 8 | 10 | 10 | 13 | 6 | 2 | 2 | 8 | 8 | 8 | 6 | 4 |
| 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1.00 | | | | | |
| 2 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | 1.00 | 1.00 | 0.94 | 1.00 | 1.00 |
| 3 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0.06 | | |
| **TPI** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (N) | 7 | 3 | 6 | 7 | 8 | 6 | 7 | 2 | 2 | 11 | 9 | 8 | 9 | 2 | 10 | 8 | 12 | 10 | 8 | 10 | 10 | 14 | 6 | 2 | 2 | 8 | 10 | 6 | 6 | 4 |
| 1 | | | | 0.71 | 0.13 | | | | | | | 0.25 | | | | | | | | | | | | | | | | | 1.00 | 0.87 |
| 2 | 1.00 | 1.00 | 1.00 | | 0.75 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.62 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | 1.00 | 1.00 | 0.83 | | 0.13 |
| 3 | | | | 0.29 | 0.12 | | | | | | | 0.13 | | | | | | | | | | | | | 1.00 | | | 0.17 | | |
| 4 | | | | | | | | | | | | | | | | | | 1.00 | | | | | | | | | | | | |

with a constant potential drop of 200 V between electrodes. Gels were incubated at 37°C during staining. The enzymes stained, E.C. numbers, abbreviations, buffers used and number of presumptive genetic loci are shown in Table 2. Individual spiders were ground (1:1 volume of tissue:volume of buffer) in homogenising buffer (Colgan, 1986). The whole body of both spiderlings and adults was ground. The stages available for analysis are indicated in Table 1. Generally, there was no effect of stage on isozyme expression. The exception to this was glucose-6-phosphate dehydrogenase which was scorable in juveniles but which had a low level of activity in adults. Staining recipes usually follow those in Richardson *et al.* (1986). Method A given in Richardson *et al.* (1986) was used for ALD and FUM, and method B for AP. Most recipes require little modification for use with the agarose overlays in which Titan III stains are applied. The overlays were made up by rapidly mixing 2 ml of stain solution with 2 ml of 2.5% molten agarose (held at 65°C in a water bath) in soda glass vials and pouring this over the gel surface. The agar was removed after staining by allowing it to stick to blotting paper and then removing both from the gel. Fluorescent stains (AP) were placed in the stain mixture without agarose for 5 min, and then blotted before incubation. Positive stained gels were photocopied and AP was photographed using a Polaroid Quickshooter Photosystem and transmitted 312 nm UV light.

Allozymes are designated numerically in order of their relative anodal mobility, as were multiple loci encoding the same enzyme. Where computer assistance was required, data were analysed using the BIOSYS-1 and Hennig 86 packages and a BASIC program written to convert the output of the former to input for the latter. Characters in cladistic analyses were defined by individual alloxymes. States were determined as "1" if an allozyme were present at any frequency in a sample and as "0" otherwise. In an alternative approach states were determined as "1" if the allozyme were present in more than a specified frequency (usually 0.05) and as "0" if it were absent or present in less than this frequency. Some analyses were conducted with the locus assumed to be the character, with its states determined by the most common allozyme in a sample. Series of runs were made assuming that the states were additive (i.e. that transitions were

only possible between numerically sequential allozymes) or that they were not (i.e. changes between any pair of allozymes could be made in one step).

## Results

Allozymic frequencies are summarised in Table 3. With one notable series of exceptions, populations are generally in Hardy-Weinberg equilibrium for all loci. The exceptions are for 6-PGDH in the Tasmanian samples (1–7) and Black Mountain (10). Heterozygote deficits are not found at this locus in other mainland populations. The deficit is significant for populations 1, 3, 5, 7 and 10 (using the LEVENE, EXACTP options for the HDYWBG program in BIOSYS-1). Indeed, there is a complete absence of heterozygotes in Tasmania. This suggests that two cryptic species coexist on the island. This suggestion would be strongly supported if there were another locus exhibiting significant heterozygous deficits which was in linkage disequilibrium with 6-PGDH. No such locus was found in the present study. Neither cladistic nor phenetic analyses were at all successful in associating sub-populations from different localities when the samples were divided according to whether individuals had 3/3 or 4/4 6-PGDH genotypes. (The 6-PGDH data themselves were ignored in these analyses.) However, the genetic distances between these sub-populations are small, being due to allozymic frequency, rather than fixed, differences. And, whilst a variety of causes of heterozygous deficit have been postulated (Colgan, 1981; Zouros & Foltz, 1984), none is likely to lead to a total absence of the genotype. It seems then most probable that two closely-related, morphologically-cryptic species are included in the Tasmanian samples.

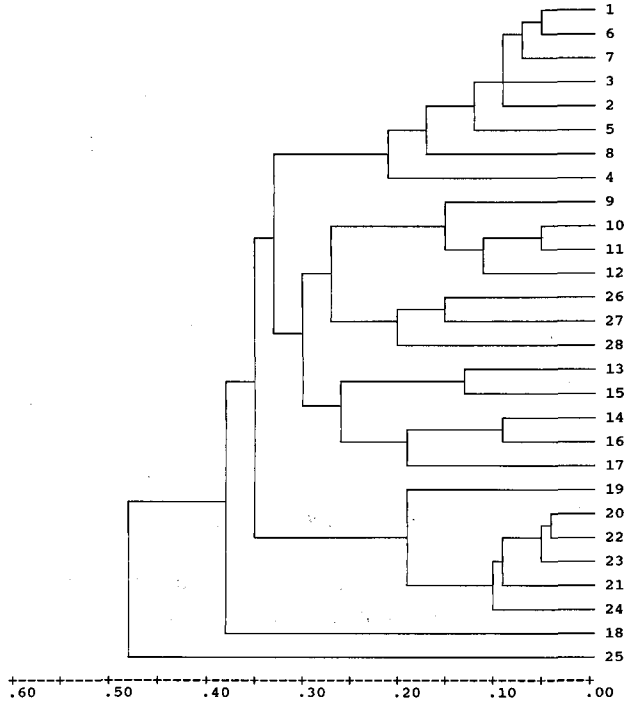


Fig. 2: Phenogram of relatedness of all *Badumna* populations based on Wright's modification of Rogers' genetic distance. Distances are based on all loci except LDH-2. It is assumed that (24) is fixed for the most common allozyme at (20) for the PK-1, PK-2, IDH-2 and AP-2 loci which were not scored in the former sample.

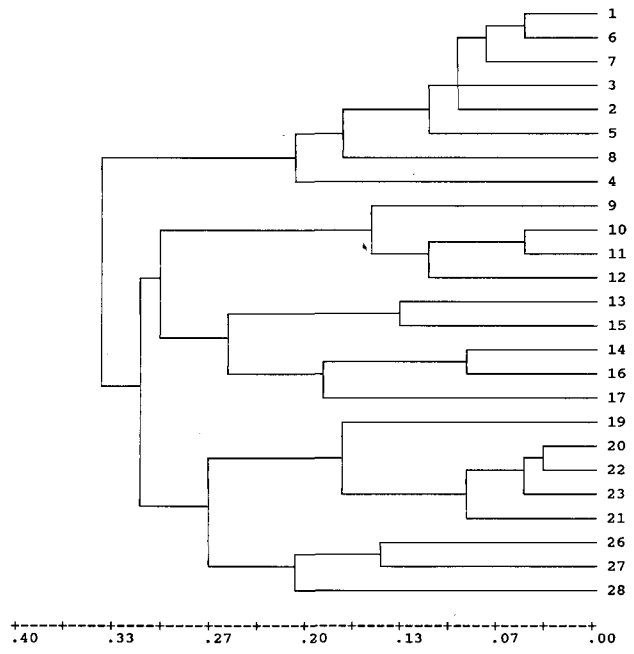


Fig. 3: Phenogram of relatedness of *Badumna* populations excepting (18) and (25) based on Wright's modification of Rogers' genetic distance. Calculations are explained in the legend to Fig. 2.

Phenograms of the *B. candida* populations are shown in Figs. 2 to 4. Figures 2 and 3 are based on Wright's (1978) modification of Rogers' genetic distance and Fig. 4 on Nei's unbiased genetic distance. Genetic distance data are shown in Table 4. To accommodate missing values, (29) and (30) were not included and the LDH-2 locus was ignored for this reason. Further, population (24) was assumed to be fixed, for those loci which were not scored, for the most common allozyme at the nearby (20). A parallel series of phenograms without (24) showed that this procedure had little effect on overall tree topology.

Some features of the phenograms are robust against the changes in genetic distance metric used in these examples and in the variety of other analyses which were performed. Firstly, the mainland populations at (18) and (25) exhibit high distances from all others in all analyses. Specimens from both of these localities have now been examined morphologically and both differ from *B. candida* to such an extent that they must be supposed to be distinct species (Gray, in prep.). It is interesting to note that whilst (18) is geographically very distant from other samples, (25) is not, being 200 km or less from the sub-samples comprising (23).

In all analyses, the Tasmanian localities and (8) form a discrete cluster. There is some variability in the linkage of this cluster to other large groups near the bases of the phenograms and there is some variation in its internal structure (which may be due to the possible existence of cryptic species on the island, as mentioned above). Yet it appears that the Tasmanian plus (8) grouping reflects a true biological division. Some further support for Gray's (1983) recognition of the morphological distinctiveness of these populations is to be found in the comparison of (8) with its nearest neighbour at (9). These two localities are separated by a significant geographical distance (about 200 km). But this would not seem large enough, without an additional barrier to gene flow, to account for their

large genetic distance. They have fixed differences at 3 loci and a large frequency difference at another.

The situation in the remainder of the populations, here referred to *B. candida*, is more complex. There is strong support for the suggestion that populations 9, 10 and 11 (here designated the Southern Group) are closely related. These are always found in the same cluster in phenetic analyses and in the same clade in cladograms. Generally, however, in phenograms they are joined in a cluster with (12). Whilst inspection of the data suggests that (12) is close to the Southern Group populations, the sharing of a unique allozyme at the IDH-2 locus is primarily responsible for their tight association. The linkage breaks down in analyses where this locus is ignored. Then (12) clusters with more northerly areas. It remains possible that either the IDH-2 3 allozyme has been independently evolved in the Southern Group and (12) or that this grouping is a result of near evolutionary relationships. Interestingly, the PGM 6 allozyme is the most common in (12) and in each of the Southern Group samples but does not attain this condition in any other South-Eastern population.

Four clusters other than the Southern Group (populations 9, 10 and 11) can be seen in Figs. 2 to 4. These are not disrupted during any phenetic analysis. They are:

(1) Populations (13) and (15);
(2) Populations (26), (27) and (28);
(3) Populations (14), (16) and (17) — this will be designated the Mallee Group;
(4) Populations (19–24) — the Pilbara Group.

There are differences between metrics in the grouping of these four clusters with each other and the Southern Group. The Pilbara Group is always included in the grouping most distant from the Southern Group. The Mallee Group tends to be more closely affiliated to the Southern Group and always lies within the same branch of the primary dichotomy in the Southern Group/*B. candida* portion of the phenograms. Using the Nei distance (Fig. 4), the Mallee and Southern Groups cluster with the Tasmanian samples rather than the other mainland populations. The positions of clusters 1 and 2 (defined above) are variable (Figs. 2–4) so that phenetic approaches do not clarify their relationships. It may be emphasised, however, that the tight clustering of (26) and (27) with (28) is in spite of great geographical separation and the relative proximity of other Western Australian populations.

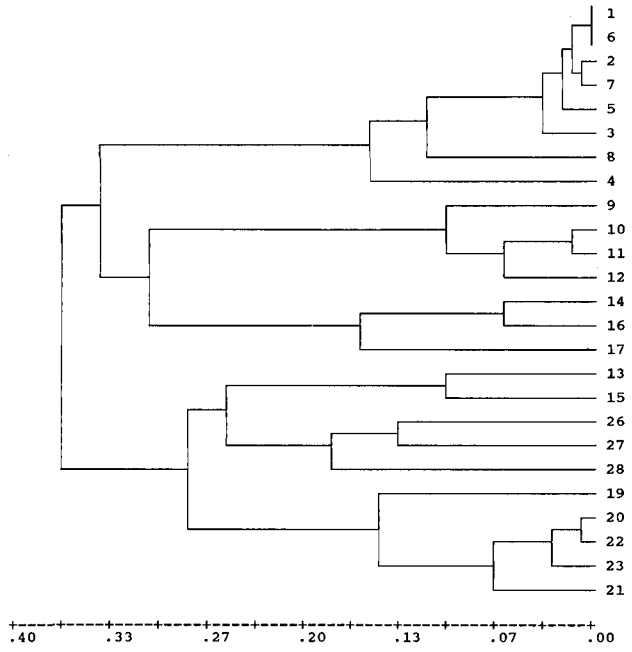


Fig. 4: Phenogram of relatedness of *Badumna* populations excepting (18) and (25) based on Nei's unbiased genetic distance. Calculations are explained in the legend to Fig. 2.

| Population | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | | 0.15 | 0.21 | 0.38 | 0.16 | 0.09 | 0.15 | 0.31 | 0.45 | 0.47 | 0.48 | 0.47 | 0.49 | 0.57 | 0.51 | 0.56 | 0.47 | 0.55 | 0.52 | 0.58 | 0.57 | 0.56 | 0.55 | 0.63 | 0.67 | 0.51 | 0.49 | 0.45 | 0.59 | 0.66 |
| 2 | 0.01 | | 0.18 | 0.34 | 0.22 | 0.19 | 0.15 | 0.35 | 0.44 | 0.47 | 0.49 | 0.49 | 0.52 | 0.59 | 0.55 | 0.58 | 0.48 | 0.56 | 0.55 | 0.59 | 0.57 | 0.57 | 0.56 | 0.63 | 0.66 | 0.54 | 0.52 | 0.44 | 0.59 | 0.67 |
| 3 | 0.04 | 0.02 | | 0.35 | 0.21 | 0.20 | 0.17 | 0.37 | 0.48 | 0.51 | 0.52 | 0.53 | 0.53 | 0.62 | 0.56 | 0.60 | 0.51 | 0.57 | 0.56 | 0.59 | 0.58 | 0.57 | 0.58 | 0.63 | 0.64 | 0.55 | 0.54 | 0.47 | 0.61 | 0.67 |
| 4 | 0.16 | 0.13 | 0.14 | | 0.31 | 0.37 | 0.32 | 0.46 | 0.56 | 0.57 | 0.58 | 0.56 | 0.54 | 0.67 | 0.57 | 0.66 | 0.57 | 0.58 | 0.57 | 0.60 | 0.58 | 0.58 | 0.58 | 0.64 | 0.68 | 0.57 | 0.55 | 0.43 | 0.55 | 0.65 |
| 5 | 0.02 | 0.04 | 0.04 | 0.11 | | 0.14 | 0.14 | 0.30 | 0.47 | 0.49 | 0.51 | 0.50 | 0.49 | 0.58 | 0.52 | 0.57 | 0.49 | 0.55 | 0.51 | 0.58 | 0.56 | 0.55 | 0.54 | 0.62 | 0.67 | 0.53 | 0.50 | 0.44 | 0.57 | 0.66 |
| 6 | 0.00 | 0.02 | 0.04 | 0.16 | 0.01 | | 0.14 | 0.29 | 0.43 | 0.45 | 0.47 | 0.46 | 0.48 | 0.56 | 0.50 | 0.53 | 0.45 | 0.54 | 0.50 | 0.58 | 0.57 | 0.55 | 0.54 | 0.62 | 0.67 | 0.50 | 0.47 | 0.45 | 0.59 | 0.66 |
| 7 | 0.01 | 0.01 | 0.02 | 0.11 | 0.01 | 0.01 | | 0.32 | 0.45 | 0.47 | 0.49 | 0.48 | 0.52 | 0.59 | 0.54 | 0.57 | 0.48 | 0.55 | 0.54 | 0.59 | 0.58 | 0.57 | 0.56 | 0.63 | 0.67 | 0.53 | 0.51 | 0.43 | 0.59 | 0.67 |
| 8 | 0.10 | 0.13 | 0.15 | 0.26 | 0.10 | 0.08 | 0.11 | | 0.40 | 0.51 | 0.51 | 0.52 | 0.50 | 0.46 | 0.56 | 0.45 | 0.45 | 0.61 | 0.56 | 0.63 | 0.61 | 0.60 | 0.59 | 0.67 | 0.71 | 0.58 | 0.55 | 0.53 | 0.58 | 0.68 |
| 9 | 0.24 | 0.23 | 0.28 | 0.41 | 0.27 | 0.22 | 0.24 | 0.18 | | 0.29 | 0.32 | 0.31 | 0.51 | 0.52 | 0.56 | 0.50 | 0.48 | 0.57 | 0.57 | 0.60 | 0.60 | 0.59 | 0.58 | 0.66 | 0.64 | 0.51 | 0.49 | 0.48 | 0.63 | 0.69 |
| 10 | 0.27 | 0.26 | 0.33 | 0.43 | 0.31 | 0.25 | 0.27 | 0.32 | 0.09 | | 0.12 | 0.22 | 0.48 | 0.54 | 0.51 | 0.51 | 0.41 | 0.54 | 0.54 | 0.54 | 0.55 | 0.52 | 0.51 | 0.60 | 0.61 | 0.47 | 0.43 | 0.41 | 0.67 | 0.68 |
| 11 | 0.29 | 0.29 | 0.35 | 0.46 | 0.33 | 0.27 | 0.30 | 0.32 | 0.11 | 0.01 | | 0.26 | 0.47 | 0.54 | 0.49 | 0.52 | 0.43 | 0.56 | 0.55 | 0.55 | 0.56 | 0.54 | 0.52 | 0.62 | 0.64 | 0.50 | 0.47 | 0.44 | 0.68 | 0.69 |
| 12 | 0.28 | 0.30 | 0.36 | 0.43 | 0.32 | 0.26 | 0.29 | 0.34 | 0.10 | 0.05 | 0.07 | | 0.49 | 0.54 | 0.51 | 0.52 | 0.44 | 0.52 | 0.56 | 0.56 | 0.56 | 0.55 | 0.54 | 0.62 | 0.61 | 0.48 | 0.46 | 0.44 | 0.66 | 0.69 |
| 13 | 0.30 | 0.36 | 0.37 | 0.39 | 0.30 | 0.29 | 0.34 | 0.31 | 0.33 | 0.29 | 0.27 | 0.30 | | 0.45 | 0.30 | 0.49 | 0.43 | 0.56 | 0.44 | 0.49 | 0.40 | 0.46 | 0.45 | 0.55 | 0.64 | 0.48 | 0.45 | 0.40 | 0.62 | 0.69 |
| 14 | 0.43 | 0.47 | 0.52 | 0.65 | 0.46 | 0.41 | 0.46 | 0.25 | 0.33 | 0.37 | 0.36 | 0.37 | 0.24 | | 0.45 | 0.24 | 0.42 | 0.57 | 0.55 | 0.64 | 0.58 | 0.62 | 0.60 | 0.68 | 0.68 | 0.62 | 0.60 | 0.57 | 0.65 | 0.73 |
| 15 | 0.33 | 0.39 | 0.40 | 0.43 | 0.34 | 0.31 | 0.38 | 0.39 | 0.40 | 0.33 | 0.29 | 0.33 | 0.10 | 0.24 | | 0.49 | 0.47 | 0.55 | 0.47 | 0.55 | 0.48 | 0.52 | 0.51 | 0.60 | 0.67 | 0.51 | 0.48 | 0.44 | 0.66 | 0.72 |
| 16 | 0.40 | 0.45 | 0.48 | 0.62 | 0.43 | 0.36 | 0.42 | 0.23 | 0.31 | 0.31 | 0.33 | 0.33 | 0.29 | 0.06 | 0.29 | | 0.33 | 0.55 | 0.50 | 0.61 | 0.62 | 0.58 | 0.56 | 0.65 | 0.72 | 0.60 | 0.53 | 0.55 | 0.65 | 0.73 |
| 17 | 0.27 | 0.29 | 0.33 | 0.43 | 0.30 | 0.24 | 0.28 | 0.24 | 0.28 | 0.20 | 0.22 | 0.23 | 0.22 | 0.21 | 0.26 | 0.18 | | 0.55 | 0.44 | 0.48 | 0.51 | 0.45 | 0.43 | 0.53 | 0.65 | 0.53 | 0.45 | 0.44 | 0.63 | 0.70 |
| 18 | 0.40 | 0.42 | 0.43 | 0.47 | 0.42 | 0.38 | 0.41 | 0.50 | 0.43 | 0.37 | 0.41 | 0.35 | 0.42 | 0.42 | 0.39 | 0.38 | 0.38 | | 0.61 | 0.62 | 0.61 | 0.61 | 0.62 | 0.66 | 0.67 | 0.54 | 0.55 | 0.51 | 0.68 | 0.69 |
| 19 | 0.34 | 0.40 | 0.42 | 0.45 | 0.34 | 0.32 | 0.39 | 0.40 | 0.43 | 0.38 | 0.40 | 0.41 | 0.23 | 0.37 | 0.26 | 0.31 | 0.22 | 0.51 | | 0.38 | 0.41 | 0.34 | 0.33 | 0.44 | 0.70 | 0.53 | 0.46 | 0.49 | 0.61 | 0.70 |
| 20 | 0.45 | 0.46 | 0.45 | 0.48 | 0.45 | 0.43 | 0.46 | 0.53 | 0.46 | 0.36 | 0.38 | 0.39 | 0.29 | 0.55 | 0.37 | 0.47 | 0.27 | 0.50 | 0.16 | | 0.24 | 0.10 | 0.19 | 0.25 | 0.67 | 0.50 | 0.46 | 0.47 | 0.69 | 0.72 |
| 21 | 0.43 | 0.44 | 0.44 | 0.46 | 0.43 | 0.42 | 0.45 | 0.50 | 0.48 | 0.40 | 0.40 | 0.41 | 0.19 | 0.42 | 0.28 | 0.51 | 0.31 | 0.50 | 0.19 | 0.06 | | 0.23 | 0.29 | 0.32 | 0.63 | 0.51 | 0.52 | 0.47 | 0.67 | 0.71 |
| 22 | 0.41 | 0.43 | 0.43 | 0.45 | 0.41 | 0.39 | 0.43 | 0.48 | 0.45 | 0.35 | 0.37 | 0.39 | 0.26 | 0.50 | 0.34 | 0.43 | 0.24 | 0.50 | 0.13 | 0.01 | 0.06 | | 0.13 | 0.25 | 0.67 | 0.51 | 0.45 | 0.45 | 0.67 | 0.71 |
| 23 | 0.39 | 0.41 | 0.44 | 0.43 | 0.38 | 0.37 | 0.41 | 0.45 | 0.42 | 0.31 | 0.33 | 0.36 | 0.23 | 0.46 | 0.30 | 0.39 | 0.22 | 0.51 | 0.12 | 0.04 | 0.09 | 0.01 | | 0.33 | 0.67 | 0.53 | 0.44 | 0.43 | 0.66 | 0.72 |
| 24 | 0.54 | 0.55 | 0.54 | 0.58 | 0.52 | 0.51 | 0.56 | 0.63 | 0.60 | 0.48 | 0.51 | 0.52 | 0.38 | 0.65 | 0.46 | 0.56 | 0.34 | 0.61 | 0.22 | 0.06 | 0.11 | 0.06 | 0.11 | | 0.72 | 0.56 | 0.54 | 0.53 | 0.73 | 0.75 |
| 25 | 0.65 | 0.62 | 0.58 | 0.67 | 0.67 | 0.63 | 0.63 | 0.76 | 0.55 | 0.50 | 0.54 | 0.50 | 0.56 | 0.63 | 0.63 | 0.75 | 0.58 | 0.63 | 0.71 | 0.60 | 0.53 | 0.62 | 0.62 | 0.74 | | 0.67 | 0.66 | 0.62 | 0.75 | 0.75 |
| 26 | 0.32 | 0.37 | 0.38 | 0.42 | 0.36 | 0.31 | 0.35 | 0.43 | 0.32 | 0.27 | 0.30 | 0.28 | 0.27 | 0.50 | 0.31 | 0.46 | 0.34 | 0.37 | 0.35 | 0.29 | 0.31 | 0.31 | 0.34 | 0.38 | 0.61 | | 0.35 | 0.42 | 0.71 | 0.70 |
| 27 | 0.29 | 0.34 | 0.38 | 0.39 | 0.31 | 0.26 | 0.31 | 0.38 | 0.29 | 0.21 | 0.26 | 0.25 | 0.24 | 0.46 | 0.27 | 0.35 | 0.24 | 0.38 | 0.25 | 0.25 | 0.33 | 0.24 | 0.22 | 0.35 | 0.59 | 0.13 | | 0.38 | 0.69 | 0.71 |
| 28 | 0.24 | 0.23 | 0.27 | 0.22 | 0.24 | 0.24 | 0.22 | 0.35 | 0.28 | 0.20 | 0.23 | 0.23 | 0.18 | 0.42 | 0.23 | 0.38 | 0.23 | 0.33 | 0.29 | 0.26 | 0.26 | 0.24 | 0.21 | 0.35 | 0.51 | 0.20 | 0.16 | | 0.62 | 0.68 |
| 29 | 0.50 | 0.50 | 0.54 | 0.41 | 0.45 | 0.50 | 0.49 | 0.47 | 0.57 | 0.69 | 0.70 | 0.67 | 0.57 | 0.61 | 0.64 | 0.61 | 0.57 | 0.72 | 0.53 | 0.73 | 0.69 | 0.68 | 0.63 | 0.87 | 0.95 | 0.79 | 0.72 | 0.55 | | 0.59 |
| 30 | 0.66 | 0.70 | 0.69 | 0.63 | 0.66 | 0.64 | 0.67 | 0.71 | 0.74 | 0.69 | 0.71 | 0.74 | 0.72 | 0.85 | 0.81 | 0.85 | 0.76 | 0.72 | 0.75 | 0.80 | 0.78 | 0.78 | 0.79 | 0.92 | 0.89 | 0.75 | 0.75 | 0.70 | 0.49 | |

Table 4: Genetic distances between the populations used in this study. The values above the diagonal are for Wright's (1978) modification of Rogers' genetic distance and those below for Nei's unbiased distance. Distances for (24) are based on the assumption that it is fixed for the most common allozyme in (20) for PK-1, PK-2, IDH-2 and AP-2. (30) is assumed to be fixed for the most common allozyme in (29) for the GOT-1, GOT-2 and PK-2 loci. These assumptions make it possible to calculate genetic distances involving these samples and all loci.

Many cladistic analyses were conducted (e.g. Figs. 5–7). Here we will describe those using allozyme presence/absence to define character states. The results using the locus as a character were similar to states determined by the most common allozyme. *B. insignis* (29) or *B. socialis* (30) was used as an outgroup for these. The HENNIG 86 algorithm most commonly used was m*; bb; (followed by xsteps w; and repeated if successive weighting were used in a given run). Broadly speaking the results were concordant with those from phenetic approaches. The Tasmanian populations and (8) form a monophyletic clade (corresponding to *B. vandiemeni*). The Pilbara Group (19–24) always forms a monophyletic assemblage. The Southern Group populations (9–11) are associated with (12) if successive weighting is applied to characters with states determined by the 0.05 presence/absence criterion (Fig. 5). This association is not maintained if successive weighting is not applied to this character state matrix (Fig. 6). The Mallee Group (14, 16, 17) always forms a monophyletic group though its position *vis-à-vis* the Southern Group is variable. Generally, the Southern Group splits at a deeper point in the cladogram than does the Mallee Group. This is the case for all most parsimonious trees when (a) the IDH-2 data for (12) are entered as unknown; (b) when (18) and (25) are omitted; and (c) character states are determined by absolute presence/absence (Fig. 7). In successive weighting of the latter analysis, however, the Mallee Group splits before the Southern Group. This is also true for successive weighting with a presence/absence criterion of 0.05 (Fig. 6). Hence it is not certain which of these two clades first split from the main *B. candida* lineage. It is notable, however, that no analysis results in a sister-grouping of the Southern Group and the Mallee Group.

One interesting point suggested by the cladistic analysis which is not apparent in the phenetic approach is the suggestion that (18) and (25) are related more closely to each other than they are to populations which are closer geographically. These two populations appear as sister-groups in a number of cladograms (e.g. Figs. 6 and 7) including all most parsimonious trees in both unweighted

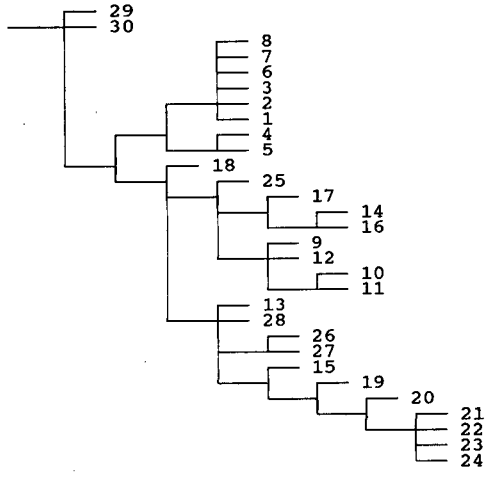


Fig. 5: Nelson consensus cladogram based on a successive weighting analysis in Hennig 86 using repetition of the m*; bb; xsteps w; sequence with character states determined by a presence criterion of 0.05. The outgroup is (29).

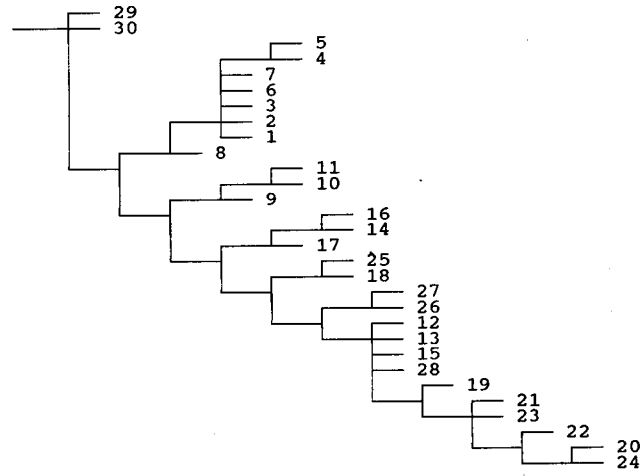


Fig. 6: Nelson consensus cladogram with character states determined by a presence criterion of 0.05. The states for the PK-1 3, PK-2 4, AP-2 2 and TPI 3 allozymes at (25) are assumed to be unknown to avoid possible homoplasy with Southern populations. The outgroup is (29).

and weighted analyses with character states determined by absolute presence/absence. Whilst inspection of the data in Table 3 does not reveal any obvious reasons why this should be so (see below), the suggestion of a close relationship between (18) and (25) is particularly interesting because these populations lie at the edges of a large gap in our collections in the central Australian region. It is tempting to speculate that the spiders in this lacuna are actually members of an arid-zone radiation (or radiations). However, exceptions to the hypothesis of the close affinity of (18) and (25) should be noted. Successive weighting with a criterion for allozymic presence of 0.05 leaves the highly autapomorphic (18) as the single member of a group in a high-level trichotomy; (25) is an outlier in one of the other two branches of the trichotomy (Fig. 5). There are no allozymes which are clearly synapomorphic for the populations. Indeed, the direct linkage between them seems to be due to their sharing the IDH-1 4 allozyme which is otherwise found in Western Australian populations only at (26) and (27). This may be independently derived in the North-West. Further, (25) is apparently semi-communal whilst (18) is solitary.

The close association of (28) with (26) and (27) which is seen in the phenetic analyses is not observed in the cladograms. The three populations do not form a monophyletic clade in any most parsimonious tree discovered during any analysis. Perhaps reflecting its geographic isolation from other samples, (28) tends to form a singleton clade at a fairly basal level. Where it does cluster with other populations, it is usually found with (15), as in all four most parsimonious trees resulting from an unweighted analysis with character states determined by absolute presence/absence. (28) is closer to (15) than to (26) or (27) but is still nearly 2,000 km distant. Further sampling might provide more structure to cladograms in the vicinity of (28). It may be commented, however, that this would probably not reveal major taxonomic sub-divisions because of the consistency with which this population is embedded, in both phenetic and cladistic approaches, within the sections of trees corresponding to *B. candida* as it is most narrowly defined.

## Discussion

The picture of the *Badumna candida* group of species which emerges from this study of its genetic structure remains that of an extremely widely-distributed continental lineage (corresponding to *B. candida*) with a number of geographically peripheral populations which are possibly genetically isolated and at least two highly distinct forms within the broad range of the main grouping. *B. vandiemeni* is a related species found in Tasmania and also in the extreme South-East of the mainland. The samples from (18) and (25) are each clearly sufficiently genetically isolated to warrant specific status. They will be formally described in another publication (Gray, in prep.).

The peripheral isolates are, firstly, a group of populations which have been referred to as the Southern Group and the Mallee Group. There is some indication of behavioural differentiation between the two groups. Mallee Group populations are commonly associated with large communal nests containing many individuals; Southern Group populations usually occur in much smaller nests. The genetic distance between these groups does not derive from an obvious contemporary geographic barrier.

Bass Strait does not presently constitute the boundary of the distribution of *B. vandiemeni*. Clearly the speciation event leading to this taxon has not been due to the most recent inundation of the strait which occurred about 10,000 years ago (Frakes, 1987). It is, however, likely that the presence of *B. vandiemeni* on both the mainland and Tasmania is due to a range extension during a period when low sea levels permitted land passage between the two areas. *B. vandiemeni* may have become genetically distinct during one of the earlier inundations of Bass Strait. The lack of heterozygotes for 6-PGDH in Tasmania suggests the presence of cryptic species. It is interesting in this context to note that 6-PGDH heterozygotes are found in population (8). This suggests that the split within *B. vandiemeni* may be comparatively recent. Otherwise there could well have been backflow of allozymes from the Victorian populations of *B. vandiemeni*, re-establishing the 6-PGDH polymorphism in the Tasmanian taxa. Of course, it is also possible that no such backflow could occur because the Victorian *B. vandiemeni* are a species distinct from both Tasmanian forms. There is no genetic evidence to support this contention.

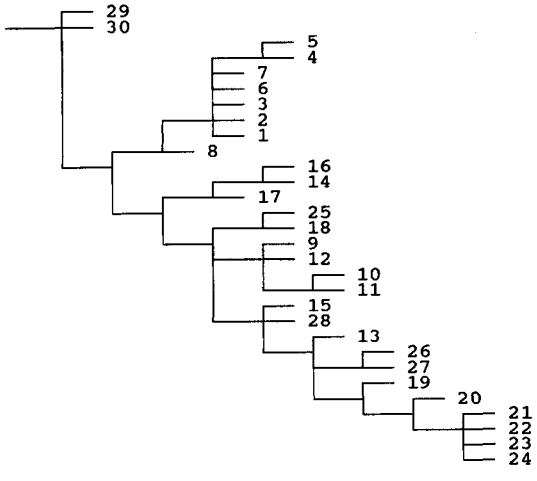


Fig. 7: Nelson consensus cladogram based on a successive weighting analysis as in Fig. 5 with character states determined by absolute presence/absence. The outgroup is (29).

Another possibility is that the solitary *B. vandiemeni* may be related to other solitary populations from the South-West of Western Australia. The present distribution of these animals may be relictual. Unfortunately, specimens of the Western Australian solitary populations have not yet become available for electrophoresis to test this possibility.

There is apparently a barrier to gene flow between the Pilbara Group populations (19–24) and those in the Kimberley region (26) and (27) in Western Australia. This is seen in all analyses in the separation of populations (26) and (27) from the remainder of the Western Australian populations. Such a barrier in *B. candida* may be considered somewhat anomalous in view of the relative proximity of the two regions, the dispersibility of *B. candida* and the apparent connection between the regions through populations (22 and 23) along the Canning Stock Route. It is possible that the Great Sandy Desert has been a barrier in the past and that there has been a recent range expansion (following European settlement) from the South along the Canning Stock Route.

There are no apparent contemporary geographic barriers to gene flow between the Southern Group, Mallee Group and other *B. candida* populations. Southern Group samples, for instance, have been taken North and South of the Murray River and on both sides of the Great Dividing Range. Suitable habitat is widespread in this part of the continent. The phenetic and cladistic analyses of the relationships between the three groups are also ambiguous. At this stage, and particularly in view of the variability in the affiliation of (12), it may be advisable to regard the genetic distances between populations in the groups as reflecting geographic distance. This is supported by the variation, which has been revealed by more extensive sampling, in morphological characters that had previously been used to discriminate between *B. candida* and *B. gausapata* (Gray, in prep.). Notwithstanding this caveat, however, most phenetic and virtually all cladistic analyses suggest that the Southern and Mallee Groups have experienced significant isolation from other *B. candida* populations during their evolutionary history. Clusters which join at Nei and Rogers distances of about 0.30, as these three do, must be regarded as sufficiently genetically distinct to warrant taxonomic recognition, at least at the level of sub-species. In other spider groups this level of distinctiveness is at least sometimes characteristic of species-level differentiation (Terranova & Roach, 1987). In the funnel web spiders (Atracinae), morphospecies were discriminated electrophoretically at Nei distances ranging from 0.10 to 0.48 (Gray, 1986, 1988).

Whether or not the Southern and Mallee Groups are accorded separate specific status from *B. candida*, the distribution of the latter is remarkably widespread. There is little doubt that populations from as far afield as northern Western Australia, North Queensland and most of New South Wales belong to a single species. There is some question as to the degree of penetration of this species into the most central areas of the continent. As, however,

samples of this species have been taken from very arid localities, such a penetration may be expected. The pattern of intermediate-scale distribution that can be envisaged depends on the mode of dispersal of these spiders. If, for example, gossamer ballooning occurs and suitable habitat is patchy in the arid zone then it would be expected that the continued influx of *B. candida* migrants would be at a low level. Patches of habitat could remain free of such immigrants for sufficient periods to develop genetic isolation. But it would not be anticipated that the biogeographic patterns of this type of speciation would conform with any phylogenetic pattern owing to the vagaries of successful dispersal by this method.

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