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# Status of *Anadara trapezia* (Deshayes) (Bivalvia: Arcoida) from Oyster Harbour, Albany (Western Australia) as compared with east Australian populations

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**Abstract** – A study of allozymes of the arcoid *Anadara trapezia* was carried out to estimate the degree of divergence associated with the temporal and geographical isolation of the southwestern Australian population from the east Australian population. A survey of electrophoretic variation at 27 putative loci coding for enzymes revealed no evidence of divergence or speciation of the Western Australian population. At all surveyed loci in all sample sets, the same most common alleles were found. Questions are raised regarding the geological time of separation of those populations. Could the time span have been more recent than paleogeological records suggest or is this species made up of a set of well adapted gene complexes that have been stable for thousands of years?

## INTRODUCTION

In the marine environment, gene flow is regulated by the rate of exchange of waters between populations. In the absence of such water movement, geographic barriers to gene flow may result in genetic divergence between populations of species with pelagic larval dispersal (Burton 1986; Hedgecock 1986). The degree of divergence and speciation is related to the length of time of separation between populations. The detection of genetic differences or its lack between populations from different regions provides evidence of the isolation or continuity of those populations. Ideally a multidisciplinary approach in the delineation of a species would include data on the geographic distribution, both past and present, morphology, ecology, physiology and biochemistry, reproduction, and genetics (White 1978). However, there is a paucity of cases where all this information has been collated (see Gosling 1994).

*Anadara trapezia* (Deshayes 1839), a bivalve mollusc of the order Arcoida, is a common species found in hyposaline estuaries from Cairns, northern Queensland (Dixon 1975) to Port Philip Bay, southern Victoria (e.g., Macpherson 1966; Poore and Rainier 1974; Smith, Coleman and Watson 1975; Dixon 1975) and in southern Western Australia at Oyster Harbour near Albany (Kendrick and Wilson 1959). In South Australia, the vast areas of tidal flats and sea grass beds in Gulf St. Vincent are considered suitable habitats for *Anadara trapezia*. However, no live individual has been found in recorded history (e.g., Cotton 1957, 1961; Macpherson and Gabriel 1962; Dixon 1975), despite an attempt to reintroduce *A. trapezia* in Gulf St Vincent in 1956. The eastern and western population can be considered isolated from one another at the present time.

The Quaternary was a period of enormous change. The dramatic changes in climate were accompanied by large fluctuations in sea level, temperature and circulation. These processes resulted in the repeated production and removal of geographic barriers between the populations of temperate eastern and western Australia. Such conditions are believed to favour speciation (Heatwole 1987).

The fossil record shows that the distribution of *A. trapezia* around the Australian coast was more widespread in the past than it is today (Kendrick 1990). In Western Australia, the most northerly published fossil record is Lake McLeod at the mouth of the Lyndon River (Kendrick 1990; Kendrick *et al.* 1991). This is of particular importance as the disappearance of the species from this area provides a good indication of the drying up of rivers and change in the character of estuaries in that region (Kendrick *et al.* 1991). In South Australia during the Late Pleistocene the Glanville Formation was laid down during a period when the water in the region was much warmer than present day conditions and *A. trapezia* flourished (see Ludbrook 1984). *A. trapezia*, together with other molluscs then disappeared from South Australia. Fossils are also found in Tasmania, near Launceston (e.g., Goede *et al.* 1993) and also North Island, New Zealand (e.g., Crozier 1962; Beu and Maxwell 1990; Bryner and Grant-

Mackie 1993, Grant-Mackie and Cook 1990). *A. trapezia* apparently sporadically colonized New Zealand during the Late Pliestocene period.

The distribution of *A. trapezia* is now restricted to the eastern coast of Australia with a second, disjunct, southwestern Australian population. Questions have been raised as to whether the southwestern Australian population of *A. trapezia* has diverged during the separation time from the eastern populations. Speciation depends not only upon the spatial duration of the geographic barrier, changes in climate and related fauna and flora but also upon the characteristics of the organism itself. These include habitat selection, vagility and means of reproduction and dispersal. The phenomenon of disjunction has aroused considerable interest in studies of speciation and has been studied in great detail by classical geneticists (e.g., Mayr 1942, 1954, 1963; Huxley 1942). Even though it is generally accepted that geographic isolation favours allopatric speciation, other factors such as special ecological features are also important (e.g., Johnson and Black 1990).

The aim of the study was to determine the level of genetic divergence and hence the specific status of the geographically disjunct southwestern Australian population of *A. trapezia* relative to the east Australian populations.

## MATERIALS AND METHODS

Seven individuals of *Anadara trapezia* were obtained from Oyster Harbour, near Albany, Western Australia. To examine the degree of genetic divergence in this population, the sample set from Oyster Harbour (35°30'S, 118°E) was compared with two sample sets, each of seven specimens, one from Corinella, Western Port Bay Victoria (38°22'S and 145°34'E), and the other from Fingal Bay, Tweed Heads estuary, northern New South Wales (28°16'S and 153°35'E). These two samples were taken as representatives of the southern and northern sections of the east coast population respectively.

As discussed in Richardson *et al.* (1986), the sample size needed for the electrophoretic detection of a suspected cryptic species is a minimum of five individuals. Since the detection of cryptic species relies heavily upon finding fixed differences, the method depends upon the number

**Table 1** Electrophoretic conditions and staining methods. * Indicates polymorphic locus. Locus was considered polymorphic if more than one allele was detected.

| Enzyme | Abbreviation | E.C. Number | Buffer system | Number of loci |
|---|---|---|---|---|
| Alanopine dehydrogenase | ALPD* | 1.5.1.17 | A | 1 |
| Enolase | ENOL | 4.2.1.11 | B | 1 |
| Glutamate dehydrogenase | GDH | 1.4.1.3 | A | 1 |
| Isocitrate dehydrogenase | IDH* | 1.1.1.42 | B | 1 |
| Glucose-6-phosphate dehydrogenase | G6PD | 1.1.1.49 | A | 1 |
| Sorbitol dehydrogenase | SORDH | 1.1.1.14 | A | 1 |
| Glucose dehydrogenase | GLDH | 1.1.1.118 | A | 1 |
| 6-phospho gluconate dehydrogenase | 6-PGD | 1.1.1.44 | A | 1 |
| Malic enzyme | ME* | 1.1.1.40 | A | 1 |
| Fumarate hydratase | FUM | 4.2.1.2 | A | 1 |
| Strombine dehydrogenase | STR | 1.5.1.X | A | 1 |
| Aconitate hydratase | ACON | 4.2.1.3 | A | 1 |
| Esterase methylumbelliferyl butyrate | EST | 3.1.1.1 | B | 1 |
| Alanine amino transferase | GPT 1<br>GPT 2 | 2.6.1.2 | B | 2 |
| Malate dehydrogenase | MDH 1*<br>MDH 2* | 1.1.1.37 | A | 2 |
| Octopine dehydrogenase | ODH* | 1.5.1.11 | A | 1 |
| Cytosol amino peptidase/leucine amino peptidase | CAP*<br>Formerly LAP* | 3.4.11.1 | A | 1 |
| Mannose phosphate isomerase | MPI* | 5.3.1.8 | C | 1 |
| Phosphoglucomutase | PGM* | 2.7.5.1 | A | 1 |
| Glucose phosphate isomerase | GPI* | 5.3.1.9 | A | 1 |
| Arginine kinase | AK | 2.7.3.3 | A | 1 |
| Aspartate amino transferase | GOT 1<br>GOT 2 | 2.6.1.1 | A | 2 |
| Pyruvate kinase | PYR | 2.7.1.40 | B | 1 |
| Guanine deaminase | GDA* | 3.5.4.3 | D | 1 |

**Table 2** Allelic profile of 21 individuals at 27 electrophoretic putative enzyme loci.
Key: 1 indicates presence, 0 indicates absence of allele. Alleles named alphabetically and putative enzyme loci numbered in order of increasing anodal mobility.

| | | Individuals | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Western Australia | | | | | | | Victoria | | | | | | | Northern New South Wales | | | | | | |
| Loci | Alleles | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| ALPD | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| | B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| ENOL | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| GDH | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| IDH | A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | B | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| G6PD | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| SORDH | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| GLDH | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 6PGD | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| ME | A | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | B | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| FUM | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| STRDH | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| ACON | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| EST | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| GPT1 | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| GPT2 | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| MDH1 | A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| | B | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| | C | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| MDH2 | A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| | B | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| | C | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| ODH | A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| | B | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| | C | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| CAP | A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | B | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| | C | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| | D | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| MPI | A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | B | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| | C | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| | D | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | F | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PGM | A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| | B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| | C | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| | D | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| | E | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 |
| | F | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GPI | A | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| | B | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |
| | C | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ARK | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| GOT1 | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| GOT2 | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| PYR | A | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| GDA | A | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |

of loci screened rather than on the number of individuals surveyed. Seven animals from each locality were used as this was the maximum number that could be run on a single gel, which is necessary if mobilities are to be compared.

Twenty seven putative enzyme loci including 11 polymorphic enzymes were surveyed using cellulose acetate electrophoresis (Cellogel, Chemtron, Italy). The enzymes studied are detailed in Table 1.

Recipes for staining these enzymes can be found in Richardson *et al.* (1986) and Manchenko (1994). Four buffer systems were used (A) 0.05 M Tris-Maleate-EDTA-MgCl2 pH 7.8, (B) 0.01 M Citrate-phosphate pH 6.4, (C) 0.025 M Tris-glycine-MgCl2 pH 8.5, (D) 0.05 M Tris-maleate pH 7.8 (see Richardson *et al.* 1986 for details).

All 21 specimens were run on a single gel and mobilities compared. At each locus, putative alleles were labelled alphabetically in order of increasing electrophoretic mobility of their corresponding electromorphs. Allelic differentiation was quantified using pair-wise comparison within sample sets and among sample sets by the sum of similarities (0, different mobility, 1 same mobility). As the data is approximately normally distributed, the mean and standard error of all observations within and among regions were calculated to evaluate the level of divergence and, hence, species status. This simple statistic was used as the presence of null alleles at many loci (Yardin unpublished) made any more complex analyses invalid.

## RESULTS

The allelic profile of each individual is summarised in Table 2. Pair-wise comparisons at all loci were calculated and the results are tabulated in matrix form (Table 3). The means and standard deviation of similarities within and between localities are shown in Table 4. Because the values are not independent, simple parametric tests of similarity cannot be used.

It is clear that the same suite of allelomorphs occur in all three population sets (Table 2) and that there is no greater differentiation between individuals from the same population than there is between individuals from different populations. Western Australian individuals shared 24.81 alleles on average while the average number of alleles they shared with Victoria and northern New South Wales were 24.69 and 25.41 respectively. There is no evidence of any divergence between the populations and therefore no evidence of speciation.

## DISCUSSION

The electrophoretic comparisons within and among the three populations of *A. trapezia* did not provide any evidence of genetic divergence in this

**Table 3** Pair-wise comparison of individuals showing commonality of alleles within and among populations.

| | | Western Australia | | | | | | | Victoria | | | | | | | Northern New South Wales | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| WA | 1 | – | | | | | | | | | | | | | | | | | | | | |
| | 2 | 26 | – | | | | | | | | | | | | | | | | | | | |
| | 3 | 28 | 26 | – | | | | | | | | | | | | | | | | | | |
| | 4 | 24 | 23 | 24 | – | | | | | | | | | | | | | | | | | |
| | 5 | 24 | 23 | 23 | 23 | – | | | | | | | | | | | | | | | | |
| | 6 | 23 | 23 | 23 | 23 | 28 | – | | | | | | | | | | | | | | | |
| | 7 | 26 | 26 | 27 | 26 | 26 | 26 | – | | | | | | | | | | | | | | |
| VIC | 1 | 25 | 25 | 25 | 25 | 25 | 25 | 28 | – | | | | | | | | | | | | | |
| | 2 | 25 | 25 | 24 | 24 | 23 | 23 | 26 | 26 | – | | | | | | | | | | | | |
| | 3 | 24 | 25 | 23 | 23 | 25 | 25 | 26 | 27 | 25 | – | | | | | | | | | | | |
| | 4 | 27 | 25 | 26 | 23 | 24 | 22 | 25 | 25 | 26 | 24 | – | | | | | | | | | | |
| | 5 | 27 | 26 | 27 | 24 | 24 | 24 | 27 | 28 | 26 | 26 | 28 | – | | | | | | | | | |
| | 6 | 24 | 24 | 24 | 25 | 23 | 23 | 26 | 27 | 25 | 24 | 24 | 26 | – | | | | | | | | |
| | 7 | 24 | 24 | 24 | 24 | 24 | 24 | 27 | 26 | 24 | 24 | 25 | 27 | 28 | – | | | | | | | |
| Northern | 1 | 25 | 23 | 24 | 25 | 22 | 22 | 25 | 24 | 24 | 23 | 24 | 24 | 23 | 23 | – | | | | | | |
| NSW | 2 | 27 | 25 | 26 | 25 | 22 | 22 | 25 | 24 | 24 | 24 | 27 | 27 | 24 | 25 | 27 | – | | | | | |
| | 3 | 26 | 26 | 28 | 26 | 25 | 25 | 29 | 27 | 26 | 25 | 26 | 28 | 25 | 26 | 26 | 26 | – | | | | |
| | 4 | 27 | 26 | 27 | 26 | 25 | 25 | 28 | 27 | 27 | 25 | 26 | 28 | 27 | 26 | 27 | 27 | 28 | – | | | |
| | 5 | 27 | 27 | 27 | 25 | 25 | 25 | 28 | 28 | 26 | 25 | 26 | 28 | 27 | 26 | 24 | 26 | 27 | 28 | – | | |
| | 6 | 26 | 25 | 26 | 27 | 24 | 24 | 26 | 27 | 25 | 24 | 25 | 26 | 27 | 25 | 25 | 26 | 26 | 28 | 28 | – | |
| | 7 | 26 | 26 | 27 | 24 | 23 | 23 | 27 | 25 | 25 | 24 | 26 | 26 | 24 | 24 | 25 | 26 | 28 | 27 | 26 | 26 | – |

**Table 4** Statistical description of pair-wise comparisons of allelic similarities within and between populations

| | WA/ WA | VIC/ VIC | NSW/ NSW | WA/ VIC | WA/ NSW | VIC/ NSW |
|---|---|---|---|---|---|---|
| Mean | 24.81 | 25.76 | 26.52 | 24.69 | 25.41 | 25.47 |
| Standard error | 0.39 | 0.30 | 0.24 | 0.19 | 0.24 | 0.20 |

species. Moreover, populations that have been isolated for considerable time usually show some degree of divergence, at least in allozymes (Richardson *et al.* 1986) and the lack of any evidence of divergence for populations that have presumably been separated for at least 10,000 years is very surprising.

The results obtained give rise to several hypotheses. It is possible that (1) the population in Albany has been recently introduced rather than the remains of a relict of the Western Australian population seen in the fossil record. Cotton (1957,1961) reported an unsuccessful attempt to reintroduce *A. trapezia* to St Vincents' Gulf in South Australia. While no evidence is known for such an attempt in Western Australia, the limited distribution of the species does leave such a possibility open. Alternatively, a set of well adapted gene complexes exists in the species resulting in very slow rates of evolution.

(2) If the observed allozyme variation is adaptive, rather than selectively neutral (Kimura and Ohta 1973) then, as long as the environment at Oyster Harbour is similar to those of *A. trapezia* habitats in eastern Australia, then there is no ground for expecting changes in the genotypes.

(3) The evolutionary literature is full of discussion of issues related to the rate of evolution. Is it gradual (e.g., Wright 1931; Ayala *et al.* 1975; Provine 1986; Wake, Yanev and Freelow 1989) or is it punctuated (Eldredge and Gould 1972; Stanley 1975). It has been much debated that most well-established species evolve at a very slow rate (e.g., Mayr 1982; Grant 1963; Barton and Charlesworth 1984). Mayr (1982) relates this to what he termed "the unity of the genotype" i.e., individuals within a species carry within their genetic make-up a well-integrated set of adapted genes (Dobzhansky 1951). Restructuring of the genotype is less likely to happen in large populations as gene flow will tend to counteract the effect of mutations in a stable environment. Isolated and small populations are thus most vulnerable to adaptive and selective changes. However most isolated populations either reestablish contact with the parent population or become extinct. Mayr (1982), while acknowledging that evolutionary events such as speciation are usually linked with swift dramatic changes in environmental conditions, i.e., changes in the adaptive landscape, identified two different aspects of allopatric speciation. Firstly, widely discontinuous portions of a species often fail to diverge, and secondly, highly isolated populations are sometimes very drastically different from the parent population. Thus, it appears that every founder population does not speciate. Moreover, homeostatic mechanisms prevent well established species from undergoing rapid evolutionary change. As Carson (1975) pointed out, "the loosening up of the cohesion of the genotype is an important and perhaps the decisive component in much of speciation".

(4). Alternatively, Eldredge and Gould (1972) and Gould and Eldredge (1977) proposed the concept of punctuated equilibrium. This concept postulates that evolution does not happen gradually but rather, it appears that large wide-ranging species remain static for a very long time and new forms arise in peripheral small isolated populations at a very rapid rate. However the influences of founder events on the magnitude and pattern of speciation are in theory directly related to the size and duration of such events and also on the resulting rate of population recovery (Nei, Maruyama and Chakraborty 1975). In addition, as discussed by Avise (1994), the survival of particular lineages following a bottleneck may be a purely stochastic event.

In the eastern regions of Australia *A. trapezia* has survived for a relatively long time in most estuaries even though it may have undergone drastic population crashes in various places in periods due to catastrophes such as major floods. Recolonisations have been observed in some places on the east coast due to the ability of the organism to disperse by pelagic larvae and also the presence of ocean currents that enable connectedness among geographically separated populations. The population in Oyster Harbour, near Albany, however requires special management strategies as there are no adjacent populations to replenish the genetic pool in the event of a major catastrophe. Indiscriminate exploitation by commercial fishers may also result in the extinction of this species from the southwestern region of Australia.

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