

Shell variability in *Tawera gayi* (Veneridae) from southern South America: a morphometric approach based on contour analysis

SANDRA GORDILLO¹, FEDERICO MÁRQUEZ², JAVIERA CÁRDENAS³ AND MIGUEL ÁNGEL ZUBIMENDI⁴

¹Centro de Investigaciones en Ciencias de la Tierra (CICTERRA, CONICET), Córdoba, Argentina. Centro de Investigaciones Paleobiológicas, Universidad Nacional de Córdoba (CIPAL, UNC), Avenida Vélez Sársfield 299, X5000JJC Córdoba, Argentina, ²Biología y Manejo de Recursos Acuáticos (CENPAT, CONICET), Blvd Brown 2915, Puerto Madryn (U9120ACF), Chubut, Argentina, Universidad Nacional de la Patagonia San Juan Bosco, Blvd Brown 3100, Puerto Madryn (U9120ACF), Chubut, Argentina, ³Fundación Centro de Estudios del Cuaternario (CEQUA), Punta Arenas, Chile, Centro de Ciencias Ambientales EULA, Universidad de Concepción, Casilla 160-C, Barrio Universitario s/n, Concepción, Chile, ⁴Becario CONICET, Departamento de Arqueología, Museo de La Plata, FCNyM, UNLP and Universidad Nacional de la Patagonia Austral–Unidad Académica Caleta Olivia

This study analyses the significance of shell morphological variations in the venerid clam Tawera gayi, a typical element of shallow marine soft bottoms in southern South America and the most common species recovered from Late Quaternary marine deposits along the Beagle Channel, Tierra del Fuego. Fossil and modern Tawera shells from different localities around the southern tip of South America were analysed using the Elliptic Fourier Analysis (EFA) method. Taking into account the palaeontological history of this genus in the southern hemisphere, EFA was also performed on shells of Tawera congeners from South Africa (T. philomela) and New Zealand (T. spissa). The use of EFA permitted the distinction between the three Tawera species and geographical differentiation in the T. gayi groups. These morphological variations of T. gayi appear best related to ecophenotypic plasticity as a response to different environmental conditions, although the palaeobiogeographical history of Tawera in South America cannot be ruled out.

Keywords: *Tawera gayi*, Bivalvia, Magellan Region, morphometrics, shell shape

Submitted 12 November 2009; accepted 13 January 2010; first published online 2 June 2010

INTRODUCTION

Morphological variations in bivalve shells are increasingly the focus of diverse studies that bridge palaeontology and ecology. Shape in bivalves is a key morphological characteristic that reflects both phylogenetic history and life habits (Stanley, 1970; Crampton & Maxwell, 2000). Different studies (Ferson *et al.*, 1985; Innes & Bates, 1999; Palmer *et al.*, 2004; Rufino *et al.*, 2006; Krapivka *et al.*, 2007; Costa *et al.*, 2008a, b; Márquez *et al.*, 2009, among others) have proved that Elliptic Fourier Analysis (EFA) on outline bivalve shells is very useful for defining specific shape features that might distinguish species or intraspecific variations among different populations along a wide geographical range.

This study therefore uses a morphometric approach to document patterns of phenotypic change through space and time in *Tawera gayi* (Hupé in Gay, 1854) shells, and interprets these patterns in light of the concepts expressed below.

Tawera gayi is a shallow burrowing, siphonate, infaunal suspension feeder. This taxon was selected for study for different reasons, including its widespread distribution in southern

South America, its abundance and its good preservation in the fossil record.

The genus *Tawera* is a small member of the family Veneridae and it is apparently confined to the southern hemisphere. *Tawera* displays a disjointed biogeographical distribution, with occurrences in Australasia, South America, Mid-Atlantic islands and South Africa (Dell, 1964; Pether, 1993). One single species, *T. gayi*, is a typical element of shallow marine waters in southern South America, extending its range of distribution along both sides of America from 56° to about 42°–40°S. As fossils, this species was also recovered from Quaternary sediments in Argentinean Patagonia and Tierra del Fuego (Feruglio, 1950; Gordillo, 1998), and in northern Chile (Herm, 1969; Guzmán *et al.*, 2000). Along the Beagle Channel, in southern Tierra del Fuego, *T. gayi* is typically very abundant and this species completely dominates the soft benthic fossil palaeocommunities of the Holocene age.

Shell morphology and overall appearance of *T. gayi* is very similar to *T. philomela* (Smith) from South Africa, suggesting a close relationship in the recent past. A third species *T. spissa* (Deshayes) is part of a group of ten *Tawera* species living within the Australia–New Zealand region. Based on the fossil record and available information on extant species of *Tawera*, Gordillo (2006) postulated that Cenozoic *Tawera* might first have arisen in Australia during the Early Miocene, and then expanded and radiated to New Zealand.

Corresponding author:

S. Gordillo

Email: gordillosan@yahoo.es or sgordillo@efn.uncor.edu

Later, perhaps during the Early Pleistocene, *Tawera* first crossed from Australasia to South America by means of the Antarctic Circumpolar Current, with subsequent migration to the southern African Region, and then probably coming back again to Australasia during the most extreme Pleistocene glaciations.

In this paper we attempt to answer the following questions: (1) is outline analysis (EFA) useful for discriminating between the *Tawera* species and *T. gayi* populations? (2) are morphological variations of the shell outline within populations related to a latitudinal gradient? This approach can be useful for evaluating whether *Tawera* spans the southern oceans in a series of stepwise shifts in morphology; (3) when comparing fossil and modern *Tawera* shell shapes from a single region, is it possible to recognize morphometric changes through time (temporal variations)?; and (4) is the morphometry of *Tawera* specimens collected at selected locations along the Magellan Region a potential tool for evaluating environmental changes (spatial variations)?

This preliminary approach will attempt to evaluate the potential implications of morphological variations of *Tawera* associated with different environmental conditions during the Quaternary in southern South America.

The Magellan Region

The Magellan Region is a U-shaped area starting at the southern tip of South America (55°S) and stretching northwards up to about 42°S, i.e. Península Valdés on the Atlantic seaboard and Puerto Montt on the Pacific seaboard. In the Atlantic, this region is dominated by the cool Malvinas (Falkland) Current, with mean temperatures ranging from 4° to 11°C and salinity varying from 33.8 to 34.4 psu. A second current, the Patagonian Current, affects the coastal zone northwards to 38°S, with mean temperatures between 5° and 16°C and salinity between 33 and 33.5 psu (Boltovskoy, 1979). On the Pacific seaboard, this region is dominated by sub-Antarctic water and the melting of local glaciers (Escribano *et al.*, 2003). At these latitudes, sub-Antarctic water reaches the coast and initiates the poleward Cape Horn Current, which passes around the continent through the Drake Passage, influencing both the east and west coasts of South America (Pickard, 1973). In the southernmost part of the Magellan Region, Tierra del Fuego connects the Pacific and Atlantic oceans. This area is characterized by an irregular system of islands interconnected by channels and internal seas shaped by glacial and postglacial processes during the last 800,000 years (McCulloch *et al.*, 1997). The whole area is affected by heavy continental run-off due to extreme rainfall throughout the year, making the water column strongly stratified, with salinities between 14 and 33 psu and temperatures between 4° and 11°C, from the surface to a depth of 50 m (Pinochet & Salinas, 1996). It is suggested that biotic recolonization of the Beagle Channel and the Strait of Magellan occurred quite recently, as the areas became gradually ice-free during glacial retreat after the Last Glacial Maximum (Gordillo, 1999; Gordillo *et al.*, 2005; Kilian *et al.*, 2007), i.e. the benthic communities of the southernmost tip of South America have to be considered as relatively young.

The Beagle Channel, in southern Tierra del Fuego, develops in a mainly east to west direction for about 300 km. The sea bottom is characterized by the alternation of rocky coasts and sandy littorals (Colizza, 1991). This channel is a

tectonic valley that was completely filled by ice during the last glaciation. Later, it was occupied by a glacial lake from 12,000 to 8000 years BP and then flooded by the sea, reaching a maximum sea level between 6000 and 4500 years BP.

MATERIALS AND METHODS

Tawera shells and localities

Fossil and modern specimens of *Tawera gayi* were collected at localities in Tierra del Fuego, Argentinean Patagonia and southern Chile, in order to cover a broad geographical area (Figure 1). Isolated collections from other localities in South Africa and New Zealand were also studied. Shells of *T. philomela* and *T. spissa* were provided by the South African Museum in Cape Town and the New Zealand GNS Science, respectively. In total, 133 individuals were included in the morphometric analysis. Only left valves were analysed. Details of the material studied are summarized in Table 1.

Outline analysis

The shell shape variation was studied by Elliptic Fourier Analysis (EFA), which consists of decomposing a curve into a sum of harmonically related ellipses (Lestrel, 1997). For each valve, images with the inner region upward were photographed using a digital camera. The closed contours of each shell outline

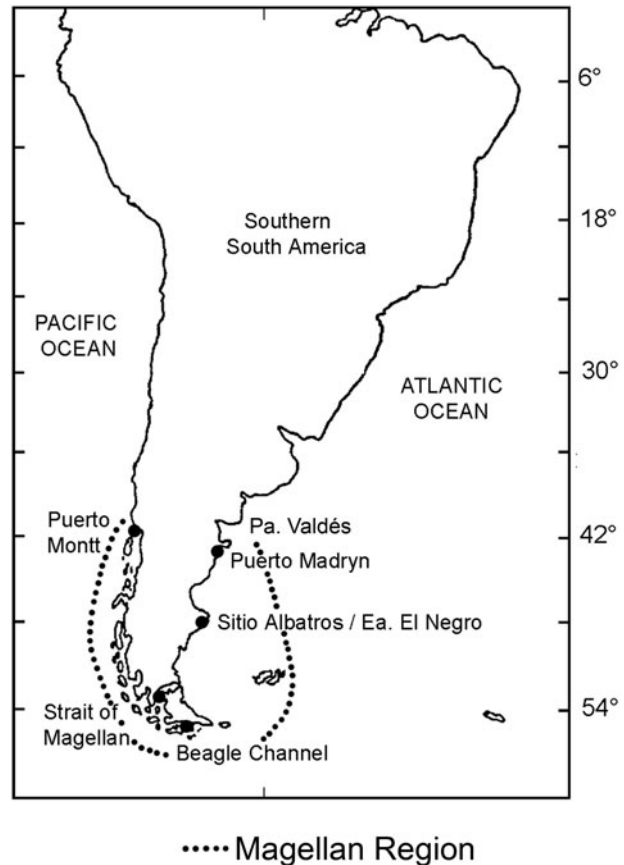


Fig. 1. Map of southern South America showing sampling sites of *Tawera gayi* shells.

Table 1. List of localities and material studied in this work.

Ref. no.	Species	Localities	Age	No. of shells	Size range (mm)
Set 10	<i>Tawera gayi</i>	Puerto Madryn, Chubut	Modern	20	19–27
Set 9	<i>Tawera gayi</i>	Puerto Madryn, Chubut	Fossil***	12	16–26
Set 8	<i>Tawera gayi</i>	Magellan Strait, Tierra del Fuego	Fossil***	7	20–32
Set 7	<i>Tawera gayi</i>	Beagle Channel, Tierra del Fuego	Fossil**	33	26–37
Set 6	<i>Tawera gayi</i>	Beagle Channel, Tierra del Fuego	Modern	19	28–35
Set 5	<i>Tawera gayi</i>	Puerto Montt, southern Chile	Modern	7	20–28
Set 4	<i>Tawera gayi</i>	Sitio Los Albatros, Sta. Cruz	Fossil*	8	23–31
Set 3	<i>Tawera gayi</i>	Ea. El Negro, Sta. Cruz	Modern	8	25–31
Set 2	<i>Tawera spissa</i>	North Island, New Zealand	Modern	11	20–34
Set 1	<i>Tawera philomela</i>	Orange Shelf, South-west Africa	Modern	8	24–44

Radiocarbon age (not corrected): ***, not dated but recent; **, 4400 years BP; *, 1400 years BP.

were obtained as chain-coded data from the digital images (Freeman, 1974). The number of harmonics (n) was calculated following Crampton (1995). The Fourier series was truncated at $n = 10$ with an average cumulative power of 99.98% of the total average power. The orientation, size and starting point of the different outlines were standardized (Kuhl & Giardina, 1982) so that three of the four elliptic Fourier coefficients describing the first harmonic ellipse were constant for all outlines. The Fourier normalized space was therefore composed of 37 morphometric variables. The software Shape v.1.3 (Iwata & Ukai, 2002) was used for all the analyses. Principal component analysis (PCA) of the variance–covariance matrix (Rohlf & Archie, 1984; Crampton, 1995) was applied to summarize shape variation based on harmonic coefficients for each shell. Differences in the coefficients between localities were tested using multivariate analysis of variance (MANOVA). The average ± 2 standard deviation (SD) shape for each group was reconstructed from the mean values of Fourier coefficients using the inverse Fourier transformations (provided by SHAPE-PrinPrint). A cluster analysis generated using an unweighted pair group method with arithmetic mean (UPMGA) was also used to show the distances (Mahalanobis) among species and localities.

RESULTS

The among-group pattern of shape similarities was displayed by means of the position of the ‘average’ shape of each group in the principal component space. Principal component axes are interpreted as shape gradients between two extreme configurations, which are visualized using the inverse elliptic Fourier transformation.

Outline analysis: interspecific variation

When *Tawera gayi* (fossil and modern) was compared with modern *T. spissa* and *T. philomela*, the MANOVA revealed significant differences in the Fourier coefficient between species (Wilks' $\lambda_{74,188} = 0.17$, $P < 0.0001$). The first three PCs (Figure 2) explicated around 87% of all the variations.

Using the extreme shapes of these figures it is possible to assign morphological meaning to the three significant PC axes. The first PC (66.2%) can be explained by the degree of roundness. Although it represents the highest variation, it does not follow any pattern which allows for the differentiation between species. However, the average shape of *T.*

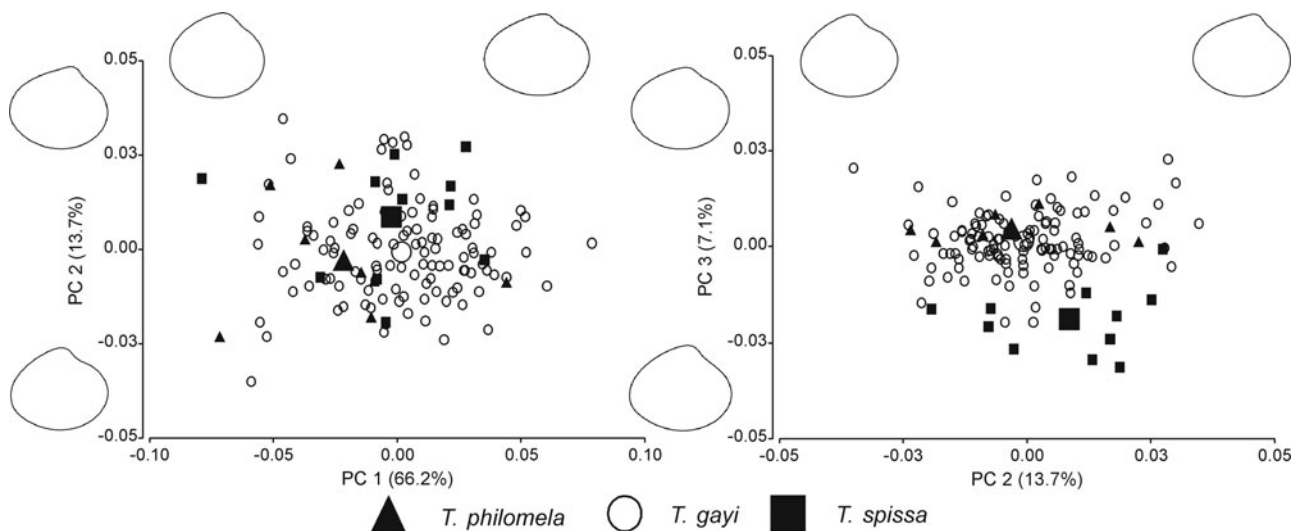


Fig. 2. Plot of principal components (PC) for *Tawera philomela* (modern), *T. gayi* (fossil and modern) and *T. spissa* (modern) based on 37 Fourier coefficients from shell outlines and the diagrams of the reconstructed extreme configurations. The largest symbols indicate the averages for each species. Left: PC 1 and PC 2; right: PC 2 and PC 3.

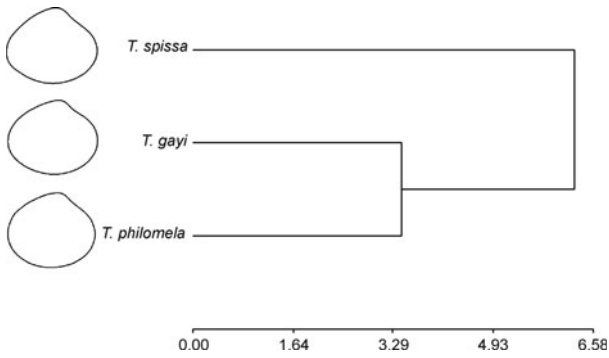


Fig. 3. UPGMA tree, obtained from the Mahalanobis distance between the averages of 37 Fourier coefficients and showing shell shape relationships among three *Tawera* species. The diagrams before the species designation refer to the mean configurations of the reconstructed shell shape.

spissa and *T. gayi* are more closely related than *T. philomela*, which is more rounded than the other two species. The second PC (13.7%) is related to the inflation of the umbo and the lunule area. *Tawera spissa* is differentiated from *T. gayi* and *T. philomela* by having lower inflation and a more prosogyrous umbo. The third PC (7.1%) represents the degree of antero-posterior elongation.

A UPGMA tree based on the Fourier coefficient showed *T. philomela* and *T. gayi* more closely related than *T. spissa*, which is more elongated in an antero-posterior axis, on average (Figure 3).

When considering different localities, three major groups are formed. Argentinean localities appeared grouped into a UPGMA tree. In a second group Chile appears together with South Africa. The third one is represented only by New Zealand (Figure 4).

When modern specimens of *T. gayi* were compared with modern *T. spissa* and *T. philomela*, the same pattern was maintained. However, a lower dispersion in *T. gayi* resulted in greater differences when compared to results which included fossil specimens. The first three PCs explained around 89% of the variance. Cluster analyses show that the localities in South America, which represent *T. gayi*, define a single cluster in the tree. This group is closer to African *T. philomela* than to New Zealand *T. spissa*.

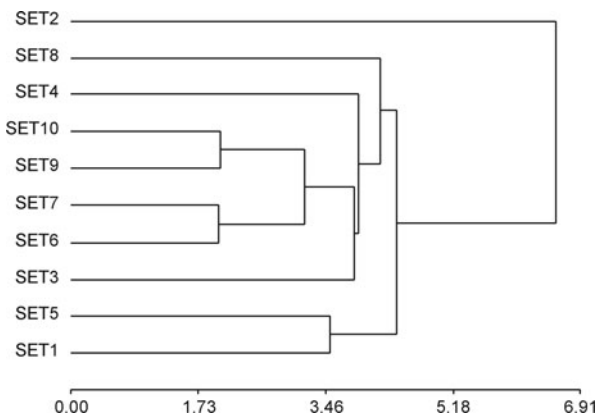


Fig. 4. UPGMA tree showing shell shape relationships among the different localities studied. See Table 1 for locality reference numbers.

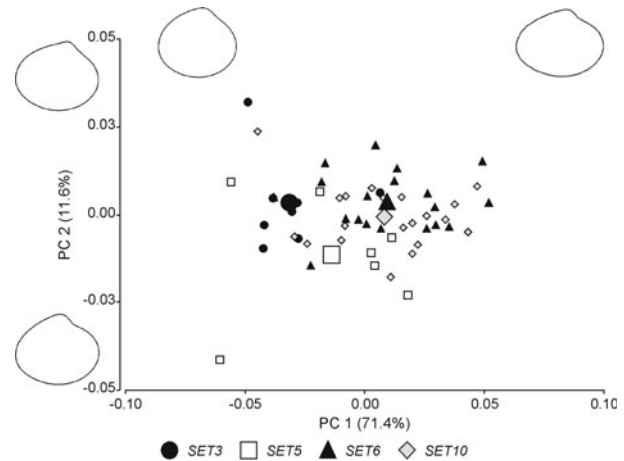


Fig. 5. Plot of principal components (PC) for modern *Tawera gayi* localities showing shell shape variation and diagrams of the reconstructed extreme configurations. The largest symbols indicate the averages for each species. Right: PC 1 and PC 2; left: PC 2 and PC 3. See Table 1 for locality reference numbers.

Outline analysis: intraspecific variation

Shell shape differences accounted for the first two PCs (explaining 83% of the variance) and are shown in Figure 5. Some overlap in shape morphospace between all four *Tawera gayi* groups (Set 3, Set 5, Set 6 and Set 10) is observed. However, PC 1 shows *T. gayi* shells from Puerto Madryn and the Beagle Channel very close to each other, since they have a similar rounded shape. The PC 2 shows that *Tawera* shells from Puerto Montt, on the Pacific, are more dorsally peaked than the other sets.

Cluster analysis (which includes all variability of the shell shape) showed *T. gayi* from Puerto Montt, on the Pacific, clearly apart from the remaining sites located on the Atlantic (Figure 6). These differences may indicate that these populations belong to different stocks.

Finally, relationships at specific times (i.e. modern shells versus fossil shells) and between particular groups (i.e. Puerto Madryn and Tierra del Fuego) were explored in more detail. When fossil and modern *Tawera* specimens from the Beagle Channel (Set 6 and Set 7) were compared, no differences were observed (Figure 7A).

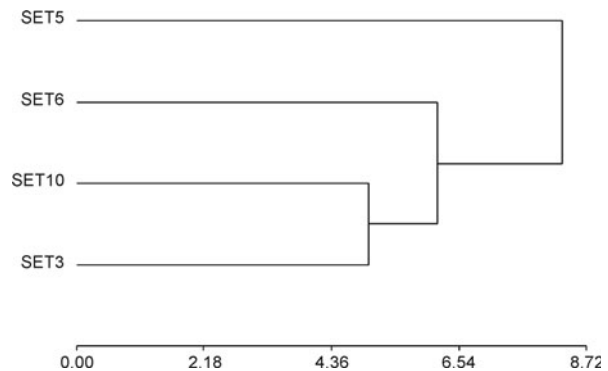


Fig. 6. UPGMA tree showing shell shape relationships between different modern *Tawera gayi* localities. See Table 1 for locality reference numbers.

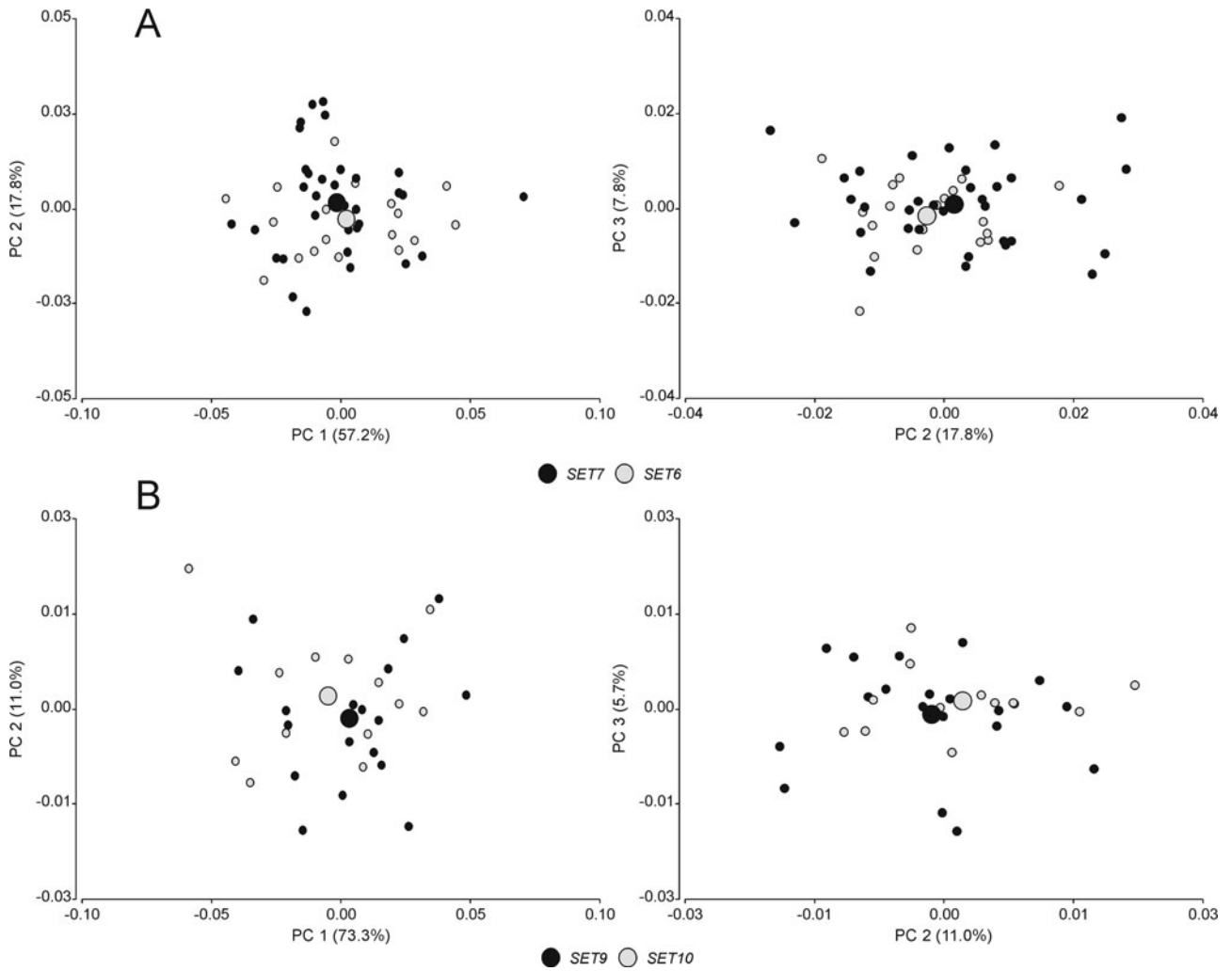


Fig. 7. Plot of principal components (PC) for *Tawera gayi* (fossil and modern) from (A) Puerto Madryn and (B) Beagle Channel localities showing shell shape variation. The largest symbols indicate the average for each species. See Table 1 for locality reference numbers.

Similarly, *Tawera* specimens from Puerto Madryn (Set 9 and Set 10) display no differences between modern and fossil shells (Figure 7B).

Cluster analysis showed two major groups separating Chubut from Tierra del Fuego, with fossil and modern *Tawera* from each region more closely related (Figure 8).

DISCUSSION

In this study we considered both modern and fossil *Tawera gayi* shells in order to improve the use of this species in palaeo-environmental reconstructions. Morphological changes through space and time were analysed.

Changes through space

Detection of morphometric differences between *Tawera* sets indicates that different environments are reflected in the shell morphology. Thus *T. gayi* is able to live in different shallow environments, from intertidal to depths of more than 100 m, and within different kinds of substrates. Each set must represent a distinct subgroup belonging to a different local community. For example, for the Atlantic, at Golfo Nuevo, Chubut (42°47'S 64°53'W), *T. gayi* is the third member in order of abundance of a shallow soft infaunal community dominated by venerids (*Venus antiqua*, *Retrotapes exalbidus* and *T. gayi*) and mainly preyed upon by volutids (*Odontocymbiola*) (Schuldt, 1975; Verdinelli & Schuldt, 1976). In Tierra del Fuego, *T. gayi* was sampled at Laredo Bay, Strait of Magellan (5–10 m depth; 52°58'S 70°47'W) (Urban & Tesch, 1996). In contrast, in the same region, *T.*

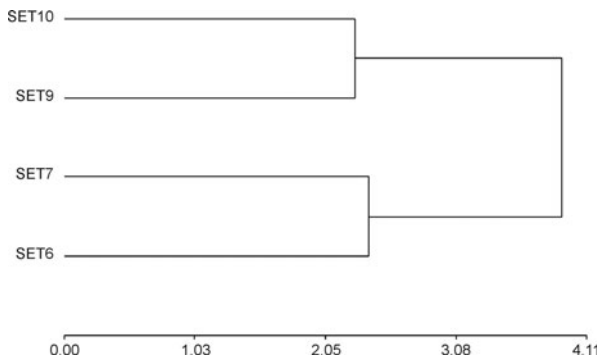


Fig. 8. UPGMA tree showing shell shape relationships among *Tawera gayi* (fossil and modern) from Puerto Madryn and Beagle Channel localities. See Table 1 for locality reference numbers.

gayi appears as a secondary member in a typically hard-bottom community of boulder–cobble intertidal fields resting on a sandy-sediment matrix, dominated by mytilids (*Mytilus chilensis* and *Perumytilus purpuratus*) (Ríos & Mutschke, 1999). From a structural point of view this type of physical habitat can be considered as an intermediate situation between soft substrate (e.g. sandy beaches) and typical hard-bottom substrate (i.e. rocky shores). In Tierra del Fuego, *T. gayi* also inhabits shallow coarse sandy substrates along the Beagle Channel (Gordillo, 1994; Lomovasky *et al.*, 2003), and was also collected at Isla Navarino from grey mud (6–10 m depth; 54°55'S 67°37'W), together with other shelled molluscs such as *Xymenopsis*, *Yoldia* and *Plaxiphora* (Dell, 1971). This species was also found in this channel within holdfasts of *Macrocystis pyrifera* (Adami & Gordillo, 1999). As fossils, in the same region, *T. gayi* was recovered from Holocene mollusc assemblages along the Beagle Channel, as the dominant species, and together with other bivalves (e.g. *Retrotapes exalbidus*, *Venus antiqua* and *Hiatella solida*) and predator gastropods such as muricids (*Trophon geversianus*). On the Pacific, in Chile (43°28'S–45°55'S), *T. gayi* was found at different depths (i.e. 10–15, 70, 130 and 160 m), at the bottom of cobbles, gravel and coarse sands, sometimes with *Venus antiqua* (Reid & Osorio, 2000; Osorio *et al.*, 2006; Cárdenas *et al.*, 2008), and as dominant taxa at 16–20 m, within medium to coarse sands together with echinoids (*Loxechinus albus*), asteroids (*Stichaster striatus*), nematodes, amphipods and other molluscs (i.e. *Mulinia edulis*, *Tindaria striata*, *Tagelus dombeii* and *Nassarius* species).

This ability to adapt to different environments, including varied substrate and predators, is probably the main reason for morphological variability between *Tawera* populations.

Our preliminary analysis of *Tawera* suggested that several factors must be considered in order to decipher the ecological significance of its morphological variations.

Changes through time

In this study, we compared *Tawera* shells from different regions within a short scale of hundreds to thousands of years. *Tawera* specimens from the Beagle Channel displayed little morphological variability during the last 4500 years, indicating environmental stability in this region. Similarly, fossil and modern *Tawera* specimens from Puerto Madryn display no significant difference between the recent past and the present.

Fossil and modern *Tawera* specimens from each region are more similar than modern specimens from different regions. It must be thought of as temporal stability and spatial variability of the *Tawera* shell shape.

As *Tawera* was apparently able to achieve a circumpolar distribution during the Cenozoic, this dispersal ability via planktonic larvae can be correlated with phenotypic and physiological plasticity of this group. Crampton & Gale (2005) pointed out that the presence of planktonic larval development in a marine mollusc may favour the evolution of phenotypic plasticity as a way of maximizing phenotypic adaptability while minimizing physiological costs to the individual. In other words, this relationship may result because high levels of gene flow in readily dispersed species will promote genetic homogenization, but, at the same time,

wide dispersal exposes the organism to a broad spectrum of environmental stresses.

There was no evidence of a latitudinal trend or a gradient of shape change from north to south in either ocean, although the observed difference between the Pacific and Atlantic sites turned out to be significant in relation to the arrival of *Tawera* in South America, probably first into the Pacific, and then expanding along both oceans. Differences between *Tawera* subgroups would therefore be the result of both the dispersal route in South America and local environmental conditions. However, data on fossil *Tawera* from the Pacific as well as from the Atlantic oceans would be required to reinforce this interpretation.

Thus it could be argued that the broad distribution of *T. gayi* in the Magellan Region with spatial phenotypic variations between *Tawera* subgroups is an evolutionary morphological change that was not associated with speciation.

CONCLUSION

Shell shape variations of *Tawera* species can be quantified by the Fourier coefficient obtained from 2-D digital images. Elliptic Fourier Analysis thus seems to be a powerful method for detecting intra- and interspecific differences between *Tawera* populations (or subgroups). Furthermore, another important advantage of EFA is that one can visualize the results of different statistical multivariate analyses reconstructed graphically from the series with high precision.

Looking back at the questions presented in the Introduction we conclude that outline analysis is useful for differentiating the three *Tawera* species and for separating intraspecific groupings, indicating that considerable phenotypic plasticity exists among the populations of *T. gayi*. The morphological variations of *T. gayi* appear to be related to ecophenotypic plasticity as a response to different environmental conditions.

Over the short geological period that represents the interval of the last 4500 years, the shell shape of *T. gayi* from the Beagle Channel exhibits stasis, suggesting stable environmental conditions at the southern tip of South America.

As morphological variation of *Tawera* shells is the product of both heredity and environment, morphological change need not be interpreted solely as a species-level phenomenon, but can and should be considered in a community or palaeocommunity context, in which phenotypic variation between localities may represent a source of ecological information suitable for the evaluation of environmental changes.

Future research

In the future, stronger methodology for this investigation could be obtained by incorporating information from different disciplines, including ecology, genetics and geochemistry.

Some basic documentation is also still needed in several areas. For example, a genetic analysis of *Tawera* would help to determine if there is an association between genetic and morphological variations of shells, possibly linked to environmental parameters.

Another gap is the poor knowledge of shallow soft benthic communities, including community structure, diversity, density and biotic relationships. The lack of this kind of basic information makes it difficult to compare *Tawera* communities, to identify the different factors associated with

morphological variations of *Tawera* and to discover which of them are more sensitive to ecological changes over short time intervals.

There is great potential in the application of morphometry to palaeo-environmental studies. Future studies should also include stable oxygen and carbon isotopic composition of *Tawera* shells, in order to evaluate morphological changes associated with environmental conditions such as temperature and hydrologic changes.

Finally, more work on the *Tawera* group is needed to evaluate morphological changes associated with environmental conditions and those which represent evolutionary innovations.

ACKNOWLEDGEMENTS

We sincerely thank James S. Crampton (GNS Science, New Zealand) who helped us with criticism during the writing of a previous version. We also thank two anonymous referees for their valuable comments. This work was supported by the National Research Council, CONICET (S.G., grant no. PIP 05-6323); and the National Agency for the Promotion of Science and Technology (grant no. PICT 06-00468).

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Correspondence should be addressed to:

S. Gordillo
 Centro de Investigaciones en Ciencias de la Tierra
 (CICTERRA, CONICET)
 Córdoba, Argentina
 email: gordillosan@yahoo.es or sgordillo@efn.uncor.edu