Use of a Morphometric Analysis to Differentiate *Adelomelon ancilla* and *Odontocymbiola magellanica* (Caenogastropoda: Volutidae) of Southern Chile

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(Accepted May 23, 2006)

Members of the family Volutidae are large, glossy-shelled, carnivorous gastropods which inhabit seas worldwide in sandy-bottomed inter- and subtidal zones (Weaver and duPont 1970). These species have young that hatch directly from the egg case as miniature adults and disperse by crawling, which decreases the possibility of wide dispersal and may lead to narrow biogeographical ranges (Willan and Dredge 2004). Some species in this group are of commercial importance, constituting about 5% of the biomass of gastropods extracted world-wide (FAO 2002).

In Chile there are 2 volutid snails of economic value, *Adelomelon ancilla* (Lightfoot 1786) and *Odontocymbiola magellanica* (Gmelin 1791), which are the largest gastropods in the country, reaching sizes of over 20 cm (Osorio 1979). The geographic distribution of *A. ancilla* extends along the Pacific Coast from northern Chile (25°S) to the Strait of Magellan, and along the Atlantic Coast from the south of Brazil (33°S) to the Falkland Is. (52°S) (Castellanos and Landoni 1992, Osorio 2002). The distribution of *O. magellanica* extends in Chile from Chiloé I. (42°S) to the Strait of Magellan (55°S) and to Rio de la Plata (35°S) on the Atlantic Coast (Castellanos and Landoni 1992, Osorio 2002).

Although these sympatric species may be distinguished by their radular morphology, their external characteristics (used in field recognition) are so similar that they are confusedly lumped under the common name of “piquilhue” snail and registered as *A. ancilla* in the fisheries national statistics. With the aim of identifying external population characters which can facilitate discrimination between taxa, common samples of piquilhue snails were taken and separated into 330 *A. ancilla* and 54 *O. magellanica* using identification guides. The radular morphology, and shell and body characteristics of these 2 species were evaluated through traditional and landmark-based geometric morphometric methods. The results revealed that the species cannot be distinguished by meristic traits (number of whorls and columella folds), or by the thickness or weight of their shells, but they do exhibit significant differences in shell shape and body weight. *Adelomelon ancilla* has a fusiform shell shape (a small aperture and a high-spired shell) that accommodates a smaller body mass than that of *O. magellanica*, which has a globose shape (a larger aperture and a low-spired shell). The external differences found by traditional and geometric analyses are sufficient to discriminate between the 2 species, which will be useful in establishing proper fisheries statistics and adequate management strategies.


**Key words:** Geometric morphometrics, Shell shape, Allometry, Radular morphometry.

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Osorio 2002).

These species coexist in the southern zone of Chile and are exploited by local fishermen in response to a demand for these products in the international market; there are, however, no regulations governing their sustainable exploitation (Guzmán et al. 1997). This fishery has been documented since 1990 by the Servicio Nacional de Pesca (Sernapesca) as the “piquilhue” snail, associated with only the species A. ancilla. These catch reports show a historic maximum of 224 t of the piquilhue snail in the 2000 fishing season and a minimum of 3 t in 2002 (Sernapesca 2005).

The taxonomy of these 2 similar species has a history of confusion that originated with Lamarck (1811), when he proposed Voluta magellanica (A. ancilla), ignoring O. magellanica. This misunderstanding was resolved by Clench and Turner (1964), when they properly described the radulae of both species (see discussion in Weaver and duPont 1970). Although the radula provides taxonomically useful characters in many groups of gastropods (Kohn et al. 1999), recognition in the field is based on external characters. Additionally, knowledge of the intraspecific variability of most characters in gastropods is poor, thus making specific identifications based on a single character precarious, necessitating adequate sampling and evaluation of population-level characters required to identify or falsify species that are difficult to differentiate (Simison and Lindberg 1999). With this background, the aim of this study was to analyze populations of A. ancilla and O. magellanica from a fishing zone, using radular morphology, meristic traits, shell shape and weight characteristics with traditional and geometric morphometrics, in order to identify external differences which can facilitate the discrimination between species. This information should be useful as a 1st approach to conduct a proper fishing record and regulate this fishery with regards to the corresponding species involved.

MATERIALS AND METHODS

In total, 384 piquilhue snails were collected from depths of 6-12 m, at Bahía Gente Grande (53°00'S, 70°15'W) in 2001 and 2002. The snails were separated into 2 different sample groups according to external characters described in the mollusk identification guides of Castellanos and Landoni (1992) and Osorio (2002). The specimens, 330 A. ancilla and 54 O. magellanica, were measured and weighed, and their radulae were separated.

Traditional morphometrics

The number of whorls and columella folds of the shell of each specimen were counted as meristic traits, and 8 linear distances were measured: the maximum length (ML), maximum width (MW), aperture length (AL), aperture width (AW), aperture-spiral distance (ASD), spiral length (SL), siphonal notch width (NW), and shell thickness (T) (Fig. 1A). In addition, individuals were weighed, with the following measurements recorded: total wet weight (TW), shell weight (SW), body weight (BW), foot weight (FW), and gonad-digestive gland weight (GW).

Meristic traits of both species were tested under the null hypothesis that they were identical by a 2-sample permutation test using 10,000 randomizations. Shell measurements, standardized as a proportion of ML to provide more accurate relative dimensions, and individual weights of both species were compared using discriminant analysis (DA) and analysis of variance (ANOVA). Also, the relative growth of each species was estimated by the biometric relationship of the ML and linear shell distances with individual weights by fitting the data to a curve. The adjusted equation was \( Y = aX^b \), where \( b \) (slope) is the allometry coefficient, which was tested for isometric growth (with \( b = 1 \)) in the linear distance relationships, and (with \( b = 3 \)) for weight-length relationships by a t-test with a 95% confidence level (\( \alpha = 0.05 \)). The degree of association between variables was calculated by the coefficient of determination (\( r^2 \)). The species equations were compared by the F test using \( b \) and its variance as parameters. The analyses were performed using the software packages of Rundom Project 1.1 (Jadwiszczak 2003), Statistica 6.0 (StatSoft 2001), and PAST (Hammer et al. 2001).

Geometric morphometrics

A geometric morphometric analysis was performed to quantify and analyze the morphological shell shape of the species. This methodology allows generation of shape variables from a set of biologically corresponding landmarks recorded in each specimen, with the effects of any differences in translation, rotation, and scale mathematically removed (Rohlf and Slice 1990). Shape differences may be described by differences in the
coordinates of corresponding landmarks between objects. These differences may also be used as data in multivariate comparisons and in the thin-plate spline to map deformation in shape (Bookstein, 1991).

Shells of 75 specimens of *A. ancilla* and 37 specimens of *O. magellanica* were photographed using an Olympus C3030 digital camera. Only adult individuals were used so as to reduce the effects of ontogenetic allometry (Guill et al. 2003). In each image, 8 landmarks chosen for their capacity to describe the shell shape (Chiu et al. 2002) were selected using TPSDig version 1.25 (Rohlf 1998a) (Fig. 1B), including the spiral (1, 2, 3), aperture (4, 8), and shell width (5, 6, 7). For each specimen, the x and y landmark coordinates were translated to the origin, rotated, and scaled to a unit centroid by the generalized procrustes analysis (GPA). This superimposition method minimizes the squared differences between corresponding landmarks (Rohlf and Slice 1990). Once non-shape variations have been eliminated, the landmark coordinates become shape variables and may be used statistically to compare samples; graphical representations of shape may also be generated for comparison (Adams et al. 2004).

The coordinates of all aligned specimens were used in the thin-plate spline analysis (Bookstein 1991), which fits differences in the positions of landmarks in 1 organism relative to their positions in another (Rohlf and Marcus 1993, Douglas et al. 2001) by means of an interpolation function. This technique allows analysis and visualization of the direction of shape differences in both groups of snails as a set of deformation grids. Principal warps are functions of the bending energy matrix resulting from the displacement of each landmark away from the source position, thus defining a space of the possible shape deformation of the source configuration. The projection of the superimposed specimen onto the principal warps produces the partial warp scores that describe the shape change of each specimen from the source configuration, and can be used as a set of shape variables in conventional multivariate analyses (e.g., Caldecutt and Adams 1998, Rüber and Adams 2001).

The matrix of the partial warp scores with the

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**Fig. 1.** Diagram of a volutid snail shell. (A) Measurements used in the traditional morphometric analysis: maximum length (ML), maximum width (MW), aperture length (AL), aperture width (AW), aperture-spiral distance (ASD), spiral length (SL), siphonal notch width (NW), and shell thickness (T); (B) 8 landmarks used in the geometric analysis.
uniform components was used to examine morphometric differences between the 2 species by DA. In addition, a multivariate analysis of covariance (MANCOVA) was performed using the centroid size as the covariate. The centroid size for each specimen was calculated as the square root of the sum of the squared distances from each landmark to the specimen’s centroid (Bookstein 1989). Centroid size exhibits all of the desirable properties of a size variable, in particular that of being uncorrelated with shape under the null hypothesis of no allometry (Mosimann 1970, Bookstein 1991). Deformation grids using thin-plate splines were used to graphically portray the patterns of shape variations among the landmarks (Cavalcanti et al. 1999).

The partial warp scores and centroid size were computed using the TPSRelw program vers. 1.21 (Rohlf 1998b) and TPSRegr vers. 1.22 (Rohlf 2000), respectively. DA and MANCOVA were performed with Statistica 6.0.

Radular morphology

A head portion containing the radular ribbon was dissected and preserved in 90% ethanol from specimens of the 2 species. Later, entire radulae were isolated, placed in 5% sodium hypochlorite for ≤ 10 min, and rinsed in distilled water. The radulae were observed under a Leitz DMRBE microscope, and digital images were taken using a Nikon Coolpix 5000 digital camera.

RESULTS

Adelomelon ancilla and O. magellanica have spiral shells reaching over 21 cm in maximum length. The shells are smooth, and a light yellow to orange color; some have thin reddish ochre zigzag bands. The color of the foot edge is reddish brown in O. magellanica and pinkish brown in A. ancilla.

Traditional morphometrics

Because the number of whorls and columella folds did not differ between species, the null hypotheses could not be rejected ($p = 0.45$ and $p = 1.0$, respectively). The number of whorls for both species varied between 3 and 6, with the greatest proportion having 5 whorls (65.7% in A. ancilla and 76.4% in O. magellanica). Similarly, the number of columella folds was between 2 and 5, with the largest proportion having 3 folds (47.9% in A. ancilla and 44.4% in O. magellanica).

The DA showed significant differences between the linear measurements of the shells of the 2 species (Wilks $\Lambda = 0.399$, $F_{[7,376]} = 80.97$, $p < 0.00001$), correctly classifying 97.1% of specimens into the corresponding groups. Figure 2A

![Fig. 2. Histograms of Adelomelon ancilla and Odontocymbiola magellanica along the discriminant axis. (A) Shell linear distances; and (B) weight measurements.](image)

![Fig. 3. Average values and standard errors obtained from the linear measurements of Adelomelon ancilla and Odontocymbiola magellanica shells. *** $p < 0.001$.](image)
shows a histogram of the species along the discriminant axis, where it is possible to distinguish 2 groups. The differences according to the DA-standardized coefficients were principally due to the variables ASD and MW (Table 1). ANOVA showed significant differences in all variables except NW ($F_{[1,382]} = 0.697, p = 0.404$) and T ($F_{[1,382]} = 1.655, p = 0.199$) (Fig. 3). In comparing the average values of the variables for both groups, A. ancilla shells were narrower (< MW), with a smaller aperture (< AL and AW), a greater aperture-spiral distance (> ASD), and a higher spire (> SL), while O. magellanica shells were wider, with a larger aperture, and a lower spire.

With regard to weights, the DA showed significant differences between species (Wilks $\Lambda = 0.8377$, $F_{[5,346]} = 13.44, p < 0.00001$), correctly classifying 87.8% of the specimens into the corresponding groups. When the discriminant axis was plotted, the 2 groups were not completely separated (Fig. 2B). The differences according to the DA-standardized coefficients were principally due to body weight (Table 1). Similarly, ANOVA showed significant differences in all variables except for shell weight ($F_{[1,350]} = 0.013, p = 0.9705$). The average weights of the soft parts were all greater in O. magellanica than in A. ancilla (Fig. 4).

The allometric relationships between the ML and linear distances for the shells of both species were significant ($p < 0.001$), except for the ML/NW relationship in O. magellanica, where only 3% of the total variation in the NW could be explained by this linear relationship ($r^2 = 0.03, p = 0.157$). Table 2 shows the allometric equations for the shell linear distances of both species. Adelomelon ancilla exhibited negative allometric growth ($b < 1$) in MW,

![Fig. 4. Average values and standard errors obtained from weights of Adelomelon ancilla and Odontocymbiola magellanica. Total wet weight (TW), shell weight (SW), body weight (BW), foot weight (FW) and gonads-digestive gland weight (GW). ** $p < 0.01$; *** $p < 0.001$.](image)

![Fig. 5. Histogram of the shell shape between Adelomelon ancilla and Odontocymbiola magellanica along the discriminant axis.](image)

| Table 1. Discriminant analysis (DA)-standardized coefficients of the length and weight variables |
|-------------------------------------------------|------|-----------------|------|-----------------|
| Length variable | DA coefficient | Weight variable | DA coefficient |
| MW | 0.527 | TW | 2.422 |
| AL | -0.045 | SW | -0.276 |
| AW | 0.340 | BW | -3.793 |
| NW | -0.290 | FW | 0.921 |
| ASD | -0.599 | GW | 0.169 |
| SL | 0.144 | | |
| T | 0.100 | | |

MW, maximum width; AL, aperture length; AW, aperture width; NW, siphonal notch width; ASD, aperture-spiral distance; SL, spiral length; T, shell thickness; TW, total wet weight; SW, shell weight; BW, body weight; FW, foot weight; GW, gonads-digestive gland weight.
On the other hand, *O. magellanica* showed negative allometry in MW, NW, and ASD and isometric growth in AL, AW, and SL. Coefficients of all allometric equations differed between species.

Table 3 shows the length-weight relationship equations, which were all significantly related (*p* < 0.001). *Adelomelon ancilla* had a negative allometric pattern (*b* < 3) for all weight measures, while *O. magellanica* had negative allometry for total wet weight and shell weight, and isometric growth in the body, foot, and gonads-digestive gland weights. Coefficients from all allometric equations differed between species except for shell weight.

### Geometric morphometrics

The DA showed significant differences between the shell shape of *A. ancilla* and *O. magellanica* (*Wilks Λ = 0.3565, *F*$_{[12,99]}$ = 14.89, *p* < 0.0001). The model correctly classified 92.9% of the specimens into the corresponding groups, which are depicted as a histogram along the discriminant axis in figure 5. Likewise, applying MANCOVA using the centroid size as a covariate indicated significant differences in shape for the 2 species (*Wilks Λ = 0.3588, *F*$_{[12,98]}$ = 14.60, *p* < 0.0001). The multivariate test of parallelism showed that the centroid size and shape trajectories were not parallel for the species (*Wilks Λ = 0.8068, *F*$_{[12,97]}$ = 1.94, *p* = 0.039).

Differences between *A. ancilla* with respect to *O. magellanica* as depicted by the thin plate spline deformation grids are related to spiral lengthening, last-whorl shortening, a centric starting point, and size constriction in the aperture, which describe an extended fusiform shape in *A. ancilla* shells and a globose shape in *O. magellanica* shells (Fig. 6).

### Radular morphology

Radulae of the 2 species are uniserial with tri-

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### Table 2. Allometric equations for shells of *Adelomelon ancilla* and *Odontocymbiola magellanica*. Allometric (A) and isometric (I) growth patterns were evaluated by *t*-test. Differences between species were determined by *F* tests

<table>
<thead>
<tr>
<th></th>
<th><em>A. ancilla</em></th>
<th></th>
<th><em>O. magellanica</em></th>
<th></th>
<th><em>F</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>MW</strong></td>
<td>0.614ML$^{0.823}$</td>
<td>0.81***</td>
<td>-A</td>
<td>0.559ML$^{0.915}$</td>
<td>0.87***</td>
</tr>
<tr>
<td><strong>AL</strong></td>
<td>0.786ML$^{0.922}$</td>
<td>0.9***</td>
<td>-A</td>
<td>0.818ML$^{0.944}$</td>
<td>0.88***</td>
</tr>
<tr>
<td><strong>AW</strong></td>
<td>0.196ML$^{0.993}$</td>
<td>0.76***</td>
<td>I</td>
<td>0.227ML$^{1.011}$</td>
<td>0.75***</td>
</tr>
<tr>
<td><strong>NW</strong></td>
<td>0.190ML$^{0.824}$</td>
<td>0.46***</td>
<td>-A</td>
<td>0.929ML$^{0.23}$</td>
<td>0.03</td>
</tr>
<tr>
<td><strong>ASD</strong></td>
<td>0.169ML$^{1.029}$</td>
<td>0.79***</td>
<td>I</td>
<td>0.334ML$^{0.622}$</td>
<td>0.41***</td>
</tr>
<tr>
<td><strong>SL</strong></td>
<td>0.170ML$^{1.071}$</td>
<td>0.66***</td>
<td>I</td>
<td>0.260ML$^{0.867}$</td>
<td>0.72***</td>
</tr>
</tbody>
</table>

$r^2$, coefficient of determination. *** *p* < 0.001. Parameters are defined in the footnotes to table 1.

### Table 3. Length-weight equations for *Adelomelon ancilla* and *Odontocymbiola magellanica*. Allometric (A) and isometric (I) growth patterns were evaluated by *t*-test. Differences between species were determined by *F* tests

<table>
<thead>
<tr>
<th></th>
<th><em>A. ancilla</em></th>
<th></th>
<th><em>O. magellanica</em></th>
<th></th>
<th><em>F</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>TW</strong></td>
<td>0.447 ML$^{2.258}$</td>
<td>0.81***</td>
<td>-A</td>
<td>0.281 ML$^{2.528}$</td>
<td>0.94***</td>
</tr>
<tr>
<td><strong>SW</strong></td>
<td>0.263 ML$^{2.091}$</td>
<td>0.58***</td>
<td>-A</td>
<td>0.577 ML$^{1.858}$</td>
<td>0.74***</td>
</tr>
<tr>
<td><strong>BW</strong></td>
<td>0.317 ML$^{2.191}$</td>
<td>0.77***</td>
<td>-A</td>
<td>0.073 ML$^{2.671}$</td>
<td>0.94***</td>
</tr>
<tr>
<td><strong>FW</strong></td>
<td>0.309 ML$^{2.148}$</td>
<td>0.76***</td>
<td>-A</td>
<td>0.051 ML$^{2.941}$</td>
<td>0.94***</td>
</tr>
<tr>
<td><strong>GW</strong></td>
<td>0.029ML$^{2.305}$</td>
<td>0.50***</td>
<td>-A</td>
<td>0.011ML$^{2.802}$</td>
<td>0.81***</td>
</tr>
</tbody>
</table>

$r^2$, coefficient of determination. ** *p* < 0.01; *** *p* < 0.001. Parameters are defined in the footnotes to table 1.
cuspid teeth, where the central cusp is the longest (Fig. 7A, B). The teeth differ in morphology and size between species. *Adelomelon ancilla*’s teeth are flat and straight with triangular cusps; the central cusp is slightly longer than the other two. The tooth width is approximately 9 µm in adult snails (Fig. 7C). In *O. magellanica*’s teeth, the 2 lateral cusps are conical, small, and curved in the center, while the central cusp is much flatter, larger, and straighter, with 2 invaginations like half-empty cones projected from the base up to its midsection. The tooth width is approximately 1.2 µm (Fig. 7D).

**DISCUSSION**

In this study, differences in shell morphometry and body weight were found between *A. ancilla* and *O. magellanica*. Furthermore, the radular morphologies observed in these snails agreed with the schemes proposed by Weaver and duPont (1970), which allowed us to corroborate their

![Fig. 6. Deformation grids illustrating shape variations depicted by the thin-plate spline. (A) Corresponding to the *Adelomelon ancilla* phenotype; and (B) corresponding to the *Odontocymbiola magellanica* phenotype.](image)

![Fig. 7. Frontal view of the radular teeth. (A) The full width of the radula of *Adelomelon ancilla*; (B) the full width of the radula of *Odontocymbiola magellanica*; (C) a single tooth of *A. ancilla*; (D) a single tooth of *O. magellanica*. Scale bar, 2 µm.](image)
species determination. The use of all the available external characters in these volutid snails was consistent in distinguishing between the 2 taxa.

Traditional morphometrics show that differences in shell shape are principally due to the aperture-spiral distance, which is longer in *A. ancilla* than in *O. magellanica*. Considering the species weights, the main differentiation is due to body weight, which is significantly greater in *O. magellanica* than in *A. ancilla*. Nevertheless, these 2 characters exhibit differential growth in these species. *Adelomelon ancilla* shows isometric growth in the aperture-spiral distance and allometric growth in body weight. On the contrary, *O. magellanica* shows allometric and isometric growth in those same characters, making differentiation of small-sized individuals more complex than large ones using these characters. Additionally, in the geometric analysis, the shape-size relationships were not parallel between species, as they showed different allometric trajectories. This kind of ontogenetic effect of allometric growth has been documented in several groups of mollusks and it is often a cause of confusion in species delineation (Chiu et al. 2002).

Considering the traditional and geometric morphometric analyses of shell shape, these species may be distinguished by means of the spiral length and aperture dimension and position. *Adelomelon ancilla* has a higher-spired shell and smaller aperture (a fusiform shape), whereas *O. magellanica* has a low-spired shell and an expanded aperture, the starting point of which is close to the suture of the last whorl (a globose shape). The size of the aperture is visibly related to the foot weight, which is significantly larger in *O. magellanica*; this probably makes this species more suitable to catch. Although Osorio (2002) characterized *A. ancilla* and *O. magellanica* shells as having differences in thickness and in the range of number of whorls and columella folds, we did not find differences in these characters between species, which display high intraspecific variations. For this reason we do not consider them useful for discriminating between these 2 species.

Characters which support differences in several other species of gastropods have been shown to present morphological variability among populations of the same species, due to environmental influences acting on the phenotypic expression of the genotype (e.g., Kemp and Bertness 1984, Janson 1987, Palmer 1990, Boulding and Hay 1993, Trussell 2000, Trussell and Smith 2000, Trussell and Nicklin 2002, Dalziel and Boulding 2005). Experiments with *Littorina littorea* showed that fast growth develops thin-shelled, globose morphs with low-spired shells, rapidly expanding apertures, and large body masses, in comparison to more slowly growing snails (Kemp and Bertness 1984). In addition, it has been found that species within the genus *Littorina*, which are direct developers like the Volutidae, show strong phenotypic variations among populations inhabiting different types of habitats. Ecotypes of different species found in the same habitat exhibit very similar shell sizes and shapes, indicating that selection pressures may be strong enough to cause species of different phylogenetic backgrounds to converge toward a common design (Johannesson 2003). Considering this information and the results obtained in this study, although it is possible to differentiate these 2 species, an overlapping area was found as depicted in the discriminant plots. We suggest that such similarities may be attributable to convergent processes due to the species living in the same habitat, having similar conditions of food availability, and being subjected to similar predation pressures and environmental conditions for shell construction. However, there are no ecological studies of these species that can help us reach a conclusion on this matter. This hypothesis may be contrasted through shape analyses of populations living in the same and different habitats and their variations at the molecular genetic level.

In summary, shell morphometry and body weight are variables that can be used to discriminate between *A. ancilla* and *O. magellanica* in field surveys. This information should be taken into consideration for differentiating the species involved in the “piquilhue” snail fishery in southern Chile, because there is no recent or historical information on the proportion of these species in the catches or whether there is differential fishing pressures being exerted on them. In addition, it is very important to determine the latitudinal and bathymetrical distributions of these populations, their food habits, reproductive strategies, and fishing parameters in order to contribute to sustainable harvesting strategies.

**Acknowledgments:** We thank Dr. Leonardo Guzmán (IFOP) for providing information about the species and for survey coordination; Donald Brown for support in data collection, radula preparation, and photographs; Katherinne Valderrama, René Durán, and Rodolfo Fariola for help with data collection; David Kemp, Bill Maslach, and Tray Biasiolli for contributing suggestions that greatly...
improved the manuscript; Paul Kemp and Cecilia Osorio for providing important bibliographic documents; and David Kaisel and Lafayette Eaton for the final English revision. Finally, we also thank Lobo Orensanz for introducing us to the Volutidae problems in South America. This work was supported by a grant from Dipuv 39/2000, University of Valparaiso.

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