

New insights in the phylogenetic relations within the Orthalicoidea (Gastropoda, Stylommatophora) based on 28S sequence data

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New phylogenetic data are presented on the land snail superfamily Orthalicoidea, using sequences of 22 taxa. In general, the results corroborate the findings of previous authors, but provide a better resolution for several groups within this superfamily. Most basal in the phylogeny are Orthalicidae s.str. and Amphibulimidae. The Placostylidae sensu Bouchet et al. (2005) and the African genus *Prestonella*, the Australian *Bothriembryon* and the South American *Plectostylus* form one clade, classified with the Placostylidae. Odontostomidae and Bulimulidae are the remaining well-supported clades.

Keywords: Gastropoda, Stylommatophora, Orthalicoidea, molecular phylogenetics.

INTRODUCTION

The land snail superfamily Orthalicoidea is a large taxon, distributed on most of the southern continents. At present it comprises five families with approximately 1,500 species, represented in Melanesia, New Zealand, Australia, Africa, South America, the West Indies and Central America up to

the southern United States. The group is predominantly present in the Neotropics. Its current taxonomic status is under dispute. Zilch (1960) included in his Bulimulacea [= Orthalicoidea] six families, of which the combined Cerionidae and Urocoptidae have recently been separated as a distinct superfamily (Uit de Weerd, 2008). Breure (1979), restricting himself to the Bulimulidae, Odontostomidae, Amphibulimidae and Orthalicidae sensu Zilch, considered these groups subfamilies of the Bulimulidae. Schileyko (1999) made a distinction between Bulimulidae (with subfamilies Bulimulinae, Placostylinae and Peltellinae [= Amphibuliminae]) and Orthalicidae. He also included the Brazilian Megaspiridae in the superfamily. Bouchet et al. (2005), following Neubert & Janssen (2004), gave family rank to the Placostylidae, degrading the Orthalicinae to a subfamily while bringing the nomenclature up to date following the priority rules. Moreover, Uit de Weerd (2008) suggested a close relationship of the Coelociontidae to this group. Finally, Herbert & Mitchell (2009) have shown that the South African genus *Prestonella* belongs to the orthalicsids. Table 1 summarizes the classification of the superfamily through time. It is not hard to endorse the view held by Herbert & Mitchell (2009), who refer to “the nomenclatural uncertainties that bedevil this group”.

ZILCH, 1960	BREURE, 1979	SCHILEYKO, 1999	BOUCHET ET AL., 2005	This study
Bulimulacea		Bulimuloidea	Orthalicoidea	Orthalicoidea
Bulimulidae	Bulimulidae	Bulimulidae	Orthalicoidea	
	<i>Bulimulinae</i>	<i>Bulimulinae</i>	<i>Bulimulinae</i>	Bulimulidae
	<i>Placostylinae</i>	<i>Placostylinae</i>	Placostylidae	Placostylidae
Odontostomidae	<i>Odontostominae</i>	<i>Bulimulinae</i>	<i>Bulimulinae</i>	Odontostomidae
Amphibulimidae	<i>Amphibuliminae</i>	<i>Peltellinae</i>	<i>Amphibuliminae</i>	Amphibulimidae
Orthalicoidea	<i>Orthalicinae</i>	Orthalicoidea	<i>Orthalicinae</i>	Orthalicoidea
		Megaspiridae	Megaspiridae	?Megaspiridae
			Coelociontidae	
Cerionidae		Cerionidae	Cerionidae	
Urocoptidae		Urocoptidae	Urocoptidae	

Table 1. Classification of the (sub)families within the superfamily Orthalicoidea, according to different authors.

The phylogenetic relationships within the Orthalicoidea are not well understood, because molecular studies in which species of this group are treated are scant, and usually include only a few representatives (Wade et al., 2001, 2006; Ponder et al., 2003; Parent & Crespi, 2006; Herbert & Mitchell, 2009; Ramirez et al., 2009; Trewick et al., 2009). At present, data for genes sufficiently conserved to resolve deep-level phylogeny (ITS2/28S) are available in GenBank for only eight species.

Breure (1979) investigated the relationships of the Orthalicoidea s.str., using morphological data of shells and anatomy. Based on cladistic treatment of 14 characters, he found evidence for the monophyly of the Orthalicinae, Odontostominae, Amphibuliminae and Placostylinae (sensu Breure, 1979). Neither the monophyly of the Bulimulinae, nor Bulimulinae + Odontostominae could be corroborated with the data at hand.

The aim of the present paper is to obtain a better understanding about the relationships within the Orthalicoidea (sensu Bouchet et al., 2005), taking into account the results of Uit de Weerd (2008) who removed the Urocoptidae and Cerionidae and placed them into a distinct superfamily. However, due to lack of suitable material, the Megaspiridae are excluded from the present analysis. This paper will deal only

with the higher-level relationships and their nomenclatural consequences at (sub)family rank. More detailed studies on the phylogenetic relationships within the superfamily, using more genetic markers, as well as details on the phylogeny of some selected genera, will be given in forthcoming papers.

MATERIAL AND METHODS

In total, 22 taxa were sampled (Table 2), spanning all groups within the Orthalicoidea. Genomic DNA was extracted using a DNeasy Tissue Kit (Qiagen). Primers (LSU 1-3 and LSU 2-4), reaction conditions and cycling parameters were obtained from Wade & Morgan (2000). PCR-products were sequenced in both directions on an ABI3730 capillary sequencer by MacroGen Europe. Forward and reverse sequences were assembled with Sequencher v.4.2 (Gene Codes corp.). All sequences were deposited in GenBank under accession numbers HM027490-HM027510. From GenBank, 11 additional taxa (including outgroup taxa) were added to the analysis. Contig-sequences were aligned using CLUSTALW and ambiguously aligned regions were excluded, using MacClade 4.0.8, resulting in 969 bp for ITS2/28S. The most appropriate model of sequence evolution was selected using jModeltest 0.1.1 (Posada, 2008).

Species	Country	Locality data	Genbank accession
Bostryx bilineatus (Sowerby, 1833)	Ecuador	Isla de Puna	HM027501
Bostryx strobili (Parodiz, 1956)	Argentina	Sierra de Maza	HM027498
Bothriembryon dux (Pfeiffer, 1861)	Australia	Mt Caitlin ca. 3km N of Ravensthorpe	HM027490
<i>Bothriembryon indutus</i> (Menke, 1843)	Australia	Walyunga National Park	EU6220231
<i>Bulimulus guadulupensis</i> (Bruguière, 1789)	Puerto Rico	San Juan Viejo	AY841298.1
Bulimulus tenuissimus (Férussac, 1832)	Brazil	ES, Vitoria	HM027507
<i>Cerion incanum</i> (Binney, 1851)	USA	Florida Keys	AY014060
Clessinia pagoda Hylton Scott, 1967	Argentina	Quilpo	HM027497
<i>Coelocion australis</i> (Forbes, 1851)	Australia	Queensland	EU409896
Corona pfeifferi (Hidalgo, 1869)	Peru	rio Curany	HM027495
<i>Drymaeus discrepans</i> (Sowerby, 1833)	Guatemala		AY841300.1
Drymaeus inusitatus (Fulton, 1900)	Costa Rica	S of Liverpool	HM027503
Drymaeus laticinctus (Guppy, 1868)	Dominica	Carnholm	HM027492
Drymaeus serratus (Pfeiffer, 1855)	Peru	Tingo Maria, Cueva de la Pavas	HM027499
Eumecostylus uliginosus (Kobelt, 1891)	Solomon Islands	hill near Rokera	HM027505
Gaeotis nigrolineata Shuttleworth, 1854	Puerto Rico	Sierra de Luquillo, El Yunque	HM027509
<i>Leucotaenius proctori</i> (Sowerby, 1894)	Madagascar	Beheloa	AY014085.1
<i>Megalobulimus oblongus</i> (Müller, 1774)	Antigua		AY014078.1
Naesiotus quitensis (Pfeiffer, 1848)	Ecuador	Cayambe	HM027510
Naesiotus stenogyroides (Guppy, 1868)	Dominica	path to Lake Boeri	HM027494
Orthalicus ponderosus Strebel & Pfeffer, 1882	Mexico	Punta Perula area	HM027506
Placocharis strangei (Pfeiffer, 1855)	Solomon Islands	Munda	HM027504
<i>Placostylus ambagiosus</i> Suter, 1906	New Zealand	Manaaki Whenua	AY014059.1
<i>Placostylus eddystonensis</i> (Pfeiffer, 1855)	New Caledonia	Mont Koghis	AY841297.1
Plagiodontes multiplicatus Döring, 1874	Argentina	Sierra de Cuniputo	HM027496
Plectostylus peruvianus (Bruguière, 1789)	Chile	Pichilemu	HM027493
Plekocheilus vlceki Breure & Schlögl, 2010	Venezuela	Churi-tepui	HM027491
Porphyrobaphe iostoma (Sowerby, 1824)	Ecuador	c. 4km Puerto Lopez to Machalilla	HM027500
<i>Prestonella bowkeri</i> (Sowerby, 1890)	South Africa	Glen Avon	EU622021
<i>Prestonella nuptialis</i> (Melvill & Ponsonby, 1894)	South Africa	Cradock area	EU622022
Spixia popana Döring, 1876	Argentina	Dean Funes-Inti Huasi	HM027502
Thaumastus thompsonii (Pfeiffer, 1845)	Ecuador	Gualaceo-Macas, San Francisco	HM027508

Table 2. Species used in the DNA-analysis for this study.

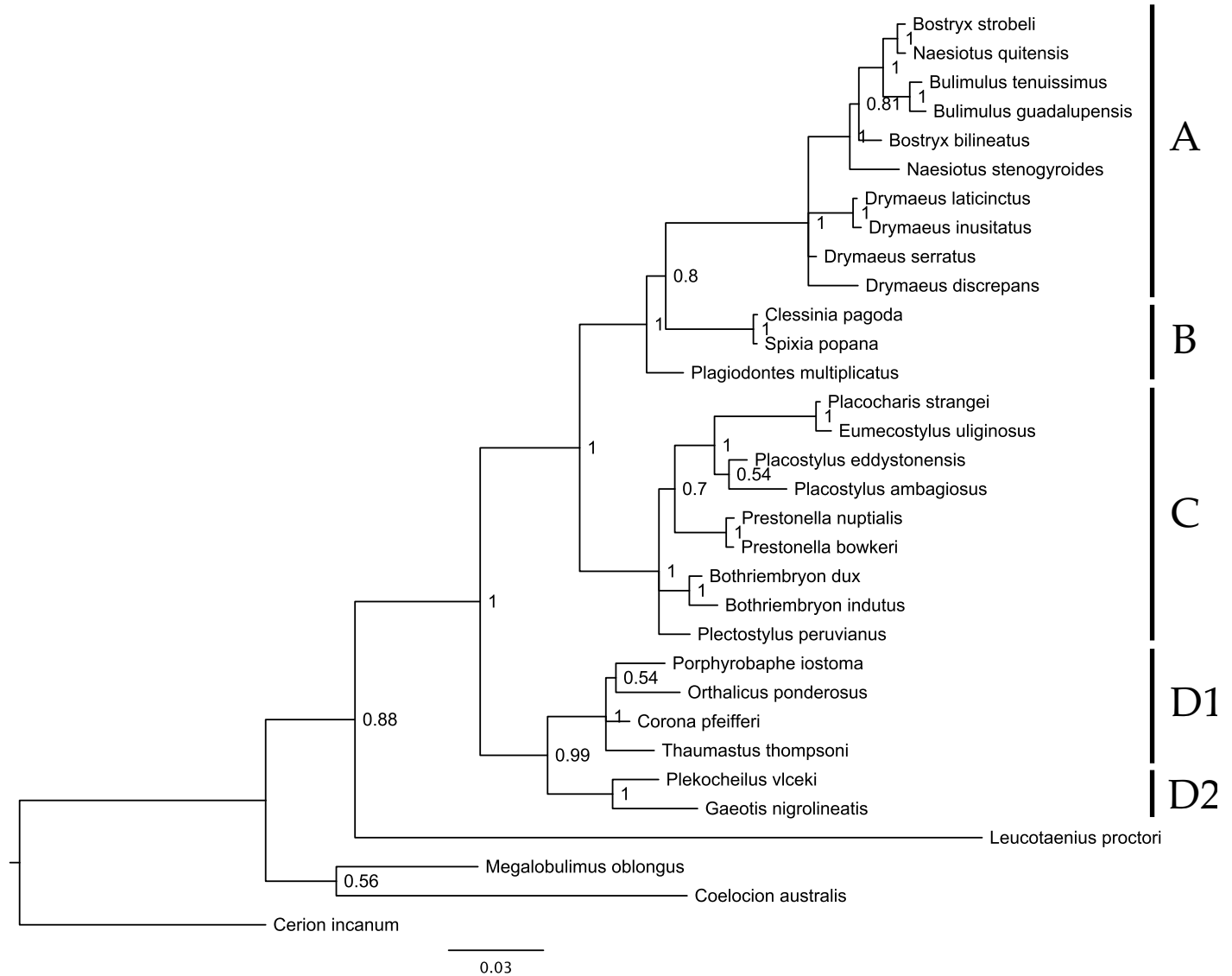


Fig. 1, Bayesian tree for the Orthalicoidea, based on 969 unambiguously aligned nucleotide sites of nuclear DNA. Posterior probabilities (PP) shown to the right of the nodes (polytomies = PP < 0.50). Note the position of *Coelocion*.

Neighbour-joining analysis (NJ) was performed in Geneious 4.3.8 (Drummond et al., 2009), using 100 bootstrap replicates and a majority-rule consensus tree was constructed. Maximum likelihood (ML) analyses were executed using PhyML in Geneious 4.3.8 (Drummond et al., 2009; Guindon & Gascuel, 2003), using 250 bootstrap replicates. Bayesian inference (BI) was done using MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001), using four MCMC runs, each with 1,100,000 chains (three with increasing temperature from 0.1-0.4, one cold), a subsampling frequency of 200 and discarding 100,000 as burn-in. All analyses were done with the model selected (GTR+Gamma+Inv) by jModeltest and an outgroup consisting of *Megalobulimus*, *Leucotaenius* and *Cerion*, rooted on the latter.

RESULTS

NJ, ML and BI analyses all indicated a grouping into four main clades (Fig. 1; NJ and BI trees not shown). Clade A is strongly supported (100/100/1 for bootstrap support [BS] and posterior probabilities [PP] in the three methods applied) and encompasses the genera *Bulimulus*, *Naesiotus*, *Bostryx* and *Drymaeus*. Their posterior probabilities within this clade are generally high, with the exception of one group within *Drymaeus*. The clade corresponds to part of the Bulimulinae sensu Breure, 1979. The well-supported clade B (95/97/1) is formed by *Plagiodontes*, *Spixia* and *Clessinia*; this group is paraphyletic. These genera are placed in the Odontostominae (sensu Breure, 1979). The relation between the sister-groups *Plagiodontes* and *Spixia/Clessinia* is not strongly supported (100/63/0.8). Clade C consists of African-Australasian members, comprising the genera *Bothriembryon*, *Prestonella*, *Placostylus* and other genera; also the South American genus *Plectostylus* groups within this moderately supported (85/89/1) clade. The support values are relatively low for the grouping of *Plectostylus* (51/34/1). Also, the grouping of *Prestonella* and *Placostylus* s.l. with *Bothriembryon* is not well resolved; in the NJ analysis *Prestonella* clusters with *Bothriembryon* and *Plectostylus* (BS: 63), in ML and BI analyses this genus groups with *Placostylus* s.l. (BS: 62, PP: 0.7). Finally, the strongly supported clade D (100/95/0.99) consists of two sister-groups. One, comprising genera re-

garded as Orthalicinae (sensu Breure, 1979): *Orthalicus*, *Corona* and *Porphyrobafe*, supplemented by one genus hitherto classified within the Bulimulinae: *Thaumastus*. Support values are, however, partially low and tree topologies vary in the three analyses. The other, strongly supported group consists of *Plekocheilus* and *Gaeotis*; these genera are hitherto classified within the Bulimulinae and Amphibuliminae respectively.

The outgroup, including *Coelocion*, shows partially different tree topologies in the three, unconstrained analyses. In NJ, the clade composed of *Coelocion* and *Leucotaenius* is well supported (BS: 93); in both ML and BI, *Leucotaenius* appears as sister-group to the Orthalicoidea, albeit with low support values (BS: 38, PP: 0.88). In all analyses, *Leucotaenius* showed a topology that suggests long-branch attraction.

DISCUSSION

Morphological data

In his study of the systematic relationships within the Orthalicoidea, Breure (1979) used a series of morphological (shell and anatomical) characters to establish a cladistic phylogeny of the five subfamilies. In the resulting hypothesis, the Placostylinae were sister-group to the four other subfamilies, based on five, anatomical autapomorphies. The monophyly of Orthalicinae was corroborated by three anatomical autapomorphies, the monophyly of Amphibuliminae by two and the monophyly of these subfamilies combined by an additional two. Although Breure found two character states that he considered apomorphic in the Odontostominae, neither this subfamily nor the Bulimulinae were supported by autapomorphies.

Herbert & Mitchell (2009), when discussing the taxonomy of the African *Prestonella*, focused on the distal genital tract and found six characters to be supportive of their hypothesis of orthalicoid affinities. They also noted the sigmoid pulmonary cavity of *Prestonella*, which corresponds with that structure in several orthalicid taxa, plus similarities in protoconch sculpture, radula structure and jaw morphology. These morphological characters were compared to *Bothriembryon* and South American orthalicids. Furthermore, they hypothesized a pre-Gondwanan stock to

explain the joint origin of *Prestonella*, *Bothriembryon*, *Placostylus* and the South American taxa.

Neubert et al. (2009) have made thorough studies on the anatomy of Placostylidae, especially those of New Caledonia. They conclude that three of the five characters used by Breure (1979) should not be used to establish the relationships between this group and the other orthalicids. By carefully reassessing anatomical characters, they conclude that the group is typified by three autapomorphies. Due to the fact that the reproductive tract morphology of the Pacific orthalicids is quite distinct from that of the other orthalicids, they regard this group as sufficiently distinct to justify the family status of Placostylidae. Furthermore, they reject the close affinity between *Placostylus* and the other orthalicids as proposed by Herbert & Mitchell (2009).

Molecular data

When Wade et al. (2001) published their "most comprehensive molecular analysis of land snail phylogeny", the only orthalicoid representative *Placostylus ambagiosus* grouped with *Leucotaenius* and the Elasmognatha (Succineidae, Athoracophoridae). Later on Wade et al (2006) added five more orthalicoid species, corroborating this grouping. In this extended analysis, *Gaeotis* appeared as sister-group to *Bulimulus* and *Drymaeus*. Recently, Herbert & Mitchell (2009) showed that the African genus *Prestonella* grouped within the Orthalicoidea; they found a strongly supported (BS: 100; PP: 1) sister-group relationship between *Prestonella* and an Australasian clade comprising *Bothriembryon* and *Placostylus*. This relationship between the three genera was refuted by Neubert et al. (2009) on morphological grounds. The results published by Ponder et al. (2003) and Ramírez et al. (2009) are generally consistent with the results in this paper, but cannot be directly compared as these authors used different genetic markers.

The Orthalicoidea sensu Bouchet et al. (2005) are not monophyletic. Our analysis shows that the Coelociontidae are less closely related than suggested by Uit de Weerd (2008). The grouping of *Leucotaenius* as a sister-group in two of the three analyses, suggests a close relationship to the Acavidae. However, since no phylogenetic data for Neotropical Acavidae are known, future research should corroborate this assumption.

From the analyses presented herein, it may be inferred that the Orthalicoidea sensu stricto (= Orthalicidae + Placostylidae sensu Bouchet et al., 2005) are monophyletic. The four taxa recognized above (A-D) are sufficiently well-supported to consider them monophyletic. Clade A, containing the type genus, should be classified as Bulimulidae. Clade B should be called Odontostomidae, at present comprising two sister-groups; further study should resolve the relationships when more genera are added to the analysis. Clade C aggregates genera of different origin. At present most enigmatic is the position in this group of the Chilean *Plectostylus*. However, as Breure (1979) already pointed out, morphological characteristics suggest a close relationship between *Plectostylus* and *Bothriembryon*. It is expected that also *Discoleus*, occurring in Argentina, belongs to this group. A cladistic analysis using morphological characters corroborates the affinities between these genera and *Prestonella* (Cuezzo, pers. comm.). Also included in this group are the Placostylidae (sensu Bouchet et al., 2005), with representatives from various localities within their distributional range. The weak support between the Melanesian and the other members of this clade, prohibits a nomenclatural conclusion. It is here treated as Placostylidae sensu lato, but further research should clarify this issue. The first cluster of clade D, corresponding to the Orthalicinae sensu Bouchet et al. (2005), comprise the genera traditionally referred to this group (*Orthalicus*, *Corona*, *Porphyrobaphe*) and a genus (*Thaumastus*) hitherto classified within the Bulimulinae. It may be noted however, that the latter (*Thaumastus*) is represented by only a single species in the analysis. Further studies should clarify in which clade the subgenera of *Thaumastus* belong. Clade D2 relates to species of *Plekocheilus* and *Gaeotis*. Since this group appears to be monophyletic, and because also species of *Amphibulima* may be attributed to this group (unpublished data; Breure, forthcoming), this clade may be classified as Amphibulimidae.

Following the argument for family status of the Placostylidae by Neubert et al. (2009) and given the phylogenetic results presented herein, the clades distinguished here should either also be given family rank or all should be treated as subfamilies within the Orthalicidae (sensu lato). We tentatively follow the first option, awaiting forthcoming morphological, phylogenetic and phylogeographical studies.

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BOOK REVIEW

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ESPINOSA, JOSÉ & JESÚS ORTEA, 2009. *Moluscos terrestres de Cuba*: 191 pp., 363 figs. Published by the authors, with support of Spartacus Foundation and Sociedad Cubana de Zoología. Photographs by Julio Larrimendi. In Spanish. ISBN 978-952-92-5427-9. Price: approx. € 70.

This is the second book within a short time about the Cuban terrestrial malacofauna. Like the book of González (2008), this is a publication that gives an introduction to the land snail diversity on this island, rather than a systematic treatment, although there is a species list at the end.

The book is entirely in Spanish, which will limit the readership. This may be counterbalanced by the many beautiful photographs of Julio Larrimendi, making this book attractive to view. The book has a large format (24.5 × 29.5 cm) and hard covers.

After the introduction and a brief chapter on diversity and endemism, the book has ten chapters on different land snail families. For each family, the diversity is described and illustrated with pictures of mostly living animals. Some families, like the Orthalicidae and Xanthonychidae, are centered around one genus (*Liguus* and *Polymita* respectively). Finally there is a chapter on the relation between man and snails, describing examples from gastronomy, medicine, architecture, art, religion, and coin and stamp collecting. A synopsis on taxonomy (listing 33 families and 1393 species) and a glossary complete this book.

A comparison with the book of González is inevitable. There are both positive and negative remarks to be made. For a taxonomist, the more or less systematic arrangement is a positive, but the treatment is very incomplete and very

much focused on visual attractive species; González has a more ecological orientation in his book. The list of species at the end of the book is just an enumeration of names. A previous version of this list was published in 1999 by both authors in an obscure Cuban journal. The current publication makes the list more accessible, but references to the original publication, the type locality and depository (if known) are still missing; for a taxonomist this is indispensable information in such a list. Subspecific taxa are not mentioned at all and an index to taxa is omitted. Compared to the book of González, the list provides a sort of introduction to a taxonomic treatment. However, the plates of shells showing the diversity in major families in González' book are probably more informative for a general public than an incomplete list of taxon names.

The photographs are very well done. Many have been made in the field and most of them show the colours of the animal well, which may be a help for their identification. Julio Larrimendi, who also has contributed to the book of González, has taken the liberty to use part of the pictures again. This adds to the overlap between the two books.

Espinosa and Ortea, who are both marine biologists, consider terrestrial molluscs "one of the better studied zoological groups and well-known in Cuba" (p. 15). Cuba has indeed a long-standing tradition in malacology, but has suffered from a decline during the last decades. This book is another window on the enormous biodiversity of this island, which deserves far more attention from taxonomists, ecologists and conservationists than it currently receives. For those who have already González' book or who prefer to have an English text, this book has limited added value. Others, who master Spanish, will see this as a welcome addition to their library.

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