Phylogenetic relationships of the columbellid taxa *Cotonopsis* and *Cosmioconcha* (Neogastropoda: Buccinoidea: Columbellidae)*

Helena Fortunato

Abstract: Phylogenetic reconstructions are still lacking for many molluscan groups, making evolutionary inferences much weaker. The genera *Cotonopsis* Olsson, 1942 and *Cosmioconcha* Dali, 1913 are part of the so called Strombina group, and as such have been used as models to study patterns of speciation and extinction brought about by the rise of the Central American gateway. Earlier work, based on a few species of each genus, pointed towards a very close relationship of these genera, which prompted a complete cladistic analysis, including all species of both genera to evaluate the level of relationship. Cladistic analyses based on shell morphology support the monophyly of the group composed by *Cotonopsis + Cosmioconcha*. *Cotonopsis* as currently defined is paraphyletic and includes *Cosmioconcha*. *Cotonopsis* (Turrida) keeps its constituency and may retain its subgeneric status. *Cotonopsis* sensu stricto should be redefined to include part of *Cosmioconcha*. *Cosmioconcha* should be subdivided into two groups. One of these groups should be included in *Cotonopsis* sensu stricto. The second group should be given subgeneric status. *Cotonopsis* has a much earlier time of origination and most probably derives from *Cosmioconcha*. Obtained results give support to some of the evolutionary patterns documented earlier for the Neogene molluscan faunas of tropical America and contribute to a better understanding of the Plio-Pleistocene divergence and turnover events related to the rise of the Panamanian land bridge.

Key words: gastropods, phylogeny, columbellids, morphology

The family Columbellidae is one of the most diverse and abundant shallow-water gastropod groups. The family has undergone rapid radiation, with over 400 species having evolved since the Danian Paleocene (Keen 1971, Abbott 1974, Radwin 1977, Tracey et al. 1993). The Strombina group sensu Jung, 1989, is one of the best known columbellid taxa, as it has been used as a model system to study evolutionary trends in species composition, diversity, and ecological patterns related to the Neogene rise of the Panama land bridge (Vermeij 1978, Jackson et al. 1993, 1996, Fortunato 1998, 1999). Despite these studies, only recently have the phylogenetic relationships of these taxa been investigated (deMaintenon 1994, 1999, Fortunato and Jung 1995, Fortunato 1998). Cotonopsis Olsson, 1942, and *Cosmioconcha* (Dali, 1913) are among the genus-level taxa that belong to this group. They are abundant and include mostly recent species with a predominantly tropical American distribution.

In his latest revision, Jung (1989) included *Cotonopsis* but excluded *Cosmioconcha* from the Strombina group. Work on the anatomy as well as preliminary cladistic analyses based on a subset of taxa (Fortunato and Jung 1995) confirmed Radwin's (1977) hypothesis of a possible relationship between *Cosmioconcha* and Strombina Mörch, 1852 based on radular and shell morphology. These results pointed to a very close relationship between *Cotonopsis* and *Cosmioconcha*. The objective of this paper is to investigate the phylogenetic relationships of these genera, including all fossil and living species, based on shell morphology in order to better understand their history and evolution.

MATERIALS AND METHODS

This analysis includes all known fossil and Recent species of the genera *Cotonopsis* and *Cosmioconcha* (Table 1). *Cotonopsis* is a very young genus (Jung 1989), with the first known species dating from the early Pliocene of Ecuador. Most of the diversity within *Cotonopsis* developed during the Plio-Pleistocene turnover, around the time of formation of the Panama land barrier. *Cotonopsis* includes 18 species grouped in two subgenera. Only one species is known exclusively as a fossil. Of the 17 living species, 13 inhabit the eastern Pacific basin (Jung 1989), two were reported from the Caribbean region (Houbrick 1983, Petuch 1988, Fortunato 2002b), one was described from the west coast of Africa (Emerson 1993), and a fourth species was found in the Andaman Sea (Kosuge et al. 1998, Kronenberg and Dekker 1998, 1999).
Table 1. Taxa included in the phylogenetic analyses. Stratigraphic and geographic ranges are given only for ingroup taxa. LM, late Miocene; EP, early Pliocene; LP, late Pliocene. See Table 2 for more information on species of the genus Cosmioconcha. Extinct species indicated by an (*).

<table>
<thead>
<tr>
<th>Species</th>
<th>Status</th>
<th>Stratigraphic range</th>
<th>Geographic range</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Nassarius latostoma</strong> (Broderip &amp; Sowerby, 1829)</td>
<td>Outgroup</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Nassarius antillonum</strong> Orbigny, 1842</td>
<td>Outgroup</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Cantharius ringens</strong> (Reeve, 1846)</td>
<td>Outgroup</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Latirus concentricus</strong> (Reeve, 1847)</td>
<td>Outgroup</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) panacostaricensis</strong> (Olsson, 1942)</td>
<td>Type of species of Cotonopsis</td>
<td>LP—Recent</td>
<td>Eastern Pacific (Costa Rica—Colombia)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) edentula</strong> (Dall, 1908)</td>
<td></td>
<td>Recent</td>
<td>Eastern Pacific (G. of California—Panama)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) argentea</strong> (Houbirk, 1983)</td>
<td></td>
<td>Recent</td>
<td>Caribbean (Dominican Republic)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) crassiparva</strong> (Jung, 1989)</td>
<td></td>
<td>Recent</td>
<td>Eastern Pacific (Galapagos Is.)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) deroyae</strong> (Emerson &amp; D’Attilio, 1969)</td>
<td></td>
<td>Recent</td>
<td>Eastern Pacific (Peru)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) aff. deroyae</strong> (Emerson &amp; D’Attilio, 1969)</td>
<td></td>
<td>EP</td>
<td>Eastern Pacific (Ecuador)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) esmeraldensis</strong> (Olsson, 1964)*</td>
<td></td>
<td>Recent</td>
<td>Eastern Pacific (Mexico)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) jaliscana</strong> (Jung, 1989)</td>
<td></td>
<td>Recent</td>
<td>Eastern Pacific (Mexico—El Salvador)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) mendozaana</strong> (Shasky, 1970)</td>
<td></td>
<td>Recent</td>
<td>Eastern Pacific (Gulf of California)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) skoghundae</strong> (Jung, 1989)</td>
<td></td>
<td>Recent</td>
<td>Eastern Pacific (Mexico—Costa Rica)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) suteri</strong> (Jung, 1989)</td>
<td></td>
<td>Recent</td>
<td>Andaman Sea (Phuket Is.)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) aff. suteri</strong> (Jung, 1989)</td>
<td></td>
<td>Recent</td>
<td>Caribbean (Barbados)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) phuketensis</strong> (Kosuge, Roussy &amp; Muangman, 1998)</td>
<td></td>
<td>Recent</td>
<td>Western Africa (Senegal)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) lindae</strong> (Petuch, 1988)</td>
<td></td>
<td>Pleistocene—Recent</td>
<td>Eastern Pacific (Gulf of California—Ecuador)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Cotonopsis) monfilsii</strong> Emerson, 1993</td>
<td></td>
<td>Recent</td>
<td>Eastern Pacific (Mexico—Panama)</td>
</tr>
<tr>
<td><strong>Cotonopsis (Turrina) hirundo</strong> (Gaskoin, 1852)</td>
<td>Type species of Cosmioconcha</td>
<td>Recent</td>
<td>Eastern Pacific (El Salvador—Colombia)</td>
</tr>
<tr>
<td><strong>Cosmioconcha modesta</strong> (Powys, 1835)</td>
<td></td>
<td>Recent</td>
<td>Eastern Pacific (El Salvador—Ecuador)</td>
</tr>
<tr>
<td><strong>Cosmioconcha palmeri</strong> (Dall, 1913)</td>
<td></td>
<td>LM—Recent</td>
<td>Eastern Pacific (Gulf of California—Panama)</td>
</tr>
<tr>
<td><strong>Cosmioconcha parvula</strong> (Dall, 1913)</td>
<td></td>
<td>Recent</td>
<td>Eastern Pacific (Gulf of California—Panama)</td>
</tr>
<tr>
<td><strong>Cosmioconcha rehleri</strong> (Hertlein &amp; Strong, 1951)</td>
<td></td>
<td>Recent</td>
<td>Eastern Pacific (Mexico—Ecuador)</td>
</tr>
<tr>
<td><strong>Cosmioconcha pergracilis</strong> (Dall, 1913)</td>
<td></td>
<td>Recent</td>
<td>Eastern Pacific (Mexico)</td>
</tr>
<tr>
<td><strong>Cosmioconcha nitens</strong> (C. B. Adams, 1850)</td>
<td></td>
<td>Recent</td>
<td>Caribbean (Cuba, Puerto Rico)</td>
</tr>
<tr>
<td><strong>Cosmioconcha calligyptria</strong> (Dall &amp; Simpson, 1901)</td>
<td></td>
<td>Recent</td>
<td>Caribbean (Florida, Texas, Puerto Rico)</td>
</tr>
</tbody>
</table>
The earliest known Cosmioconcha species dates from the middle Miocene. Cosmioconcha was first described as a subgenus of Amphissa H. & A. Adams, 1853 (Dall, 1913). Radwin (1978) elevated it to generic rank. Cosmioconcha includes seven described species, two inhabiting the Caribbean Sea and five the eastern Pacific region (Table 2, Figs. 1-2). Recent patterns of diversity and abundance of this taxon indicate a radiation similar to other paciphile genera.

Outgroup taxa were selected from Nassariidae, Buccinidae, and Fasciolariidae. Four common taxa from three bucinoidean families were selected as outgroups: Nassariidae-Nassarius luteostoma (Broderip & Sowerby, 1829) and N. antillarum d'Orbigny, 1842; Buccinidae-Cantharus ringens (Reeve, 1846); Fasciolariidae-Lattius concentricus (Reeve, 1847). These taxa were selected based on availability and not on the presumption of close phylogenetic relationship.

Forty-two qualitative characters were identified (Appendix 1). Shell sculpture is one of the most characteristic elements of this group, and provides numerous diagnostic characters. Fourteen characters code for type and sculptural details of the teleoconch and body whorl. Presence of shoulder, constriction, inflation, and angulation of the whorls, as well as presence and strength of humps were also coded. Apertural elements (thickness, denticles, apertural and columellar calledus and plicae, parietal ridge) used in traditional taxonomy of this group of gastropods are included here as well. Other characters are general shell shape, type of spire, type and depth of suture, and the relation between the total height and the height of the body whorl. All taxa were coded from direct observation.

MacClade 3.0 (Maddison and Maddison 1992) was used to create the data matrix of 25 taxa and 42 morphological characters (Appendix 2). The heuristic search in PAUP 4.0b10 (Swofford 2001) was used for the analyses, using a random addition sequence with ten replicate searches performed. All characters were unordered and weighted equally. Clade support was assessed through a bootstrap procedure (100 bootstrap replicates with 10 random addition sequences). Tree support was determined using Bremer decay analysis (Bremer 1994) in which progressively longer trees are saved and their consensus calculated in order to see how many more steps are required to collapse branches.

### Results

Cladistic analyses of the data matrix in Appendix 2 yielded six most-parsimonious trees (L=218 steps, CI=0.303, RI=0.513, and RC=0.155). Only the strict consensus tree (Fig. 3) is presented here (the 50% majority rule consensus tree shows exactly the same topology).

The ingroup is monophyletic in all trees, consisting of a single clade grouping all Cotonopsis and Cosmioconcha species. This clade is defined by fusiform shells with high spire and mostly un-sculptured earlier teleoconch whorls, body whorl mostly un-sculptured, apertures with moderately thickened outer lips, and a well developed, recurved anterior canal.

The genus Cotonopsis, as traditionally constructed, is paraphyletic and includes the polyphyletic Cosmioconcha. The subgenus Cotonopsis (Turrina) emerges as a monophyletic crown group. Cosmioconcha species are grouped in two separate clades within Cotonopsis. One clade, which contains the type species of Cosmioconcha, emerges in an unresolved trichotomy with a small clade containing the type species of Cotonopsis and a large clade that includes Cotonopsis, the remaining Cosmioconcha, and Cotonopsis (Turrina).

All species assigned to Cotonopsis sensu stricto emerge as a grade that also includes a small clade of three species of Cosmioconcha, including its type species. These species have mostly stout shells with axially sculptured late spire whorls and well defined cords at the base of the body whorl. They have broad apertures with denticles and thin outer lip edges.

This grade (all Cotonopsis sensu stricto + three Cosmioconcha taxa) has several smaller groupings. Its base is weakly resolved with several Cotonopsis species branching succes-

### Table 2. Synopsis of species belonging to the genus Cosmioconcha Dall, 1913. *, type species.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>Author &amp; Year</th>
<th>Synonyms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cosmioconcha</td>
<td>modesta*</td>
<td>Powys, 1835</td>
<td>Buccinum modestum Powys, 1835; Strombina lacriviata Li, 1930</td>
</tr>
<tr>
<td></td>
<td>palmeri</td>
<td>Dall, 1913</td>
<td></td>
</tr>
<tr>
<td></td>
<td>parvula</td>
<td>Dall, 1913</td>
<td></td>
</tr>
<tr>
<td></td>
<td>rehderi</td>
<td>Hertlein &amp; Strong, 1951</td>
<td></td>
</tr>
<tr>
<td></td>
<td>pergranilis</td>
<td>Dall, 1913</td>
<td></td>
</tr>
<tr>
<td></td>
<td>nitens</td>
<td>C. B. Adams, 1850</td>
<td>Fusus nitens C. B. Adams, 1850; Columbella (Asystis) perpicta Dall &amp; Simpson, 1901; Mitrella perpicta (Dall &amp; Simpson) Woodring, 1928 Anachis calliglypta Dall &amp; Simpson, 1901</td>
</tr>
<tr>
<td></td>
<td>calliglypta</td>
<td>Dall &amp; Simpson, 1901</td>
<td></td>
</tr>
</tbody>
</table>
Figure 1. Species of Cosmoconcha Dall, 1913. A-C Cosmoconcha modesta (NMB 17442). D-F Cosmoconcha palmeri (NMB 17793). G-I Cosmoconcha parrula (NMB H18181). J-L Cosmoconcha rhideri (NMB H18182). M-O Cosmoconcha nitens (NMB 18567). Views are front, rear, and from right side. All specimens belong to the Gibson-Smith Recent collection housed at the Naturhistorisches Museum Basel, Switzerland.
Phylogeny of Cotonopsis and Cosmioconcha

Among these are C. monfils and C. lindae, an African and a Caribbean species respectively. The next branch has two small subclades, one with three Cosmioconcha and a second one joining two Cotonopsis taxa. Next to diverge is the Cotonopsis living in the Andaman Sea, followed by another small group formed by two eastern Pacific Cotonopsis. The last grouping of this grade joins a Caribbean and two eastern Pacific Cotonopsis taxa.

The two other groups are sister clades and are located as crown groups. One of these clades groups, but does not resolve, the three Cotonopsis (Turrina) taxa. The second group is composed by four Cosmioconcha species, among which appear the two Caribbean species. Species of the crown clades have slender shells, almost no axial ornamentation on the spire whorls, and narrower apertures with a thicker edge. The species of Cosmioconcha have more convex spires, numerous denticles on the aperture, and a collar-like band below the spire suture. Cotonopsis (Turrina) taxa are characterized by taller, straight-sided shells and a well-developed thickening behind the outer lip. Results of the Bremer decay analysis are plotted onto the strict consensus tree (Fig. 3).

The first round resulted in 284 trees with 219 steps or less. These trees support the monophyly of the entire ingroup as well as the monophyly of both crown clades, i.e. Cotonopsis (Turrina) and the four Cosmioconcha species. Two small groups that appear among the basal branches (one joining three eastern Pacific Cosmioconcha, and another with two Cotonopsis sensu stricto taxa) are equally supported here. The second round of the decay yielded 6,278 trees, 220
steps or less. The ingroup is still monophyletic but only the group with the two Caribbean Cosmioconcha species is supported. The third round yielded 117,655 trees, 221 steps or less. It supports the monophyly of the ingroup but there is no resolution. The fourth round of decay analyses overflowed the memory with over 500,000 trees. The monophyly of the ingroup is still supported here. The bootstrap support for some of the clades is plotted in the strict consensus tree (Fig. 3).

**DISCUSSION**

The main objective of this work was to re-evaluate all species that have traditionally been assigned to the genera Cotonopsis and Cosmioconcha, in order to assess their relationships and the true constituency of these genera. Earlier analyses based on a selected subset of species from each of these genera (Fortunato and Jung 1995) suggested a close relationship of these taxa, confirming Radwin's (1977) hypothesis of a relationship between Cosmioconcha and the Strombina group of which Cotonopsis is part (Jung 1989). Our objective was to test this relationship, including in the analysis all known species currently included in both genera.

The results of this study indicate that Cotonopsis + Cosmioconcha form a monophyletic group. Cotonopsis as it was initially defined by Jung (1989) is paraphyletic and contains Cosmioconcha. Of the two subgenera of Cotonopsis, only Cotonopsis (Turrina) is monophyletic and retains its entire constituency. Cotonopsis sensu stricto, as currently constructed, is paraphyletic. Its status as a monophyletic taxon could be restored only by synonymizing both Cosmioconcha and Turrina. Alternatively, inclusion of more closely related outgroups might alter the rooting of the tree. Rooting at Position A (Fig. 3) would be required to retain monophyletic Cotonopsis and Cosmioconcha as sister taxa although the majority of species currently assigned to Cosmioconcha would still emerge Cotonopsis.

Species assigned to Cosmioconcha are divided into two groups. The first group is composed of three eastern Pacific
species, and is located near the base of the tree, among *Cotonopsis* sensu stricto taxa. This group includes the type species, *Cosmioconcha modesta*. The second group is one of the crown subclades and unites two Caribbean and two eastern Pacific species. This group is sister of *Cotonopsis* (*Turrina*).

Within the grade *Cotonopsis* sensu stricto, *C. monfilisi*, a deep water species from West Africa, and *C. linnae*, a shallow water species from Barbados, form adjacent branches but are flanked by eastern Pacific species from California, Mexico, and Peru that have no known fossil record. It is tempting to speculate about the possible existence of geminate pairs [i.e., closely related taxa separated by a barrier (Jordan 1908)] among the extinct fossil ancestors of these taxa. These relationships also suggest an earlier radiation of American species, probably from the eastern Pacific towards the Atlantic before the closure of the Panamanian Strait. Unfortunately, none of these species have a known fossil record which could help calibrate the time of such radiation. However, both the geographic distribution of these species, and the fact that several of the following taxa (within the context of this tree topology) have fossils dating back to the middle Miocene (i.e., *Cosmioconcha palmeri* (Dall, 1913)) suggest that such a radiation may have taken place during the middle Miocene. It is also reasonable to assume the possible existence of fossil lineages yet to be found. Molecular studies could provide an alternative tool to elucidate these relationships.

Three eastern Pacific species of *Cosmioconcha*, including the type species, emerge as a clade. The stem species, *C. palmeri*, has the oldest fossil record of all the species in this study, being known from the middle Miocene deposits of Darien [Radwin, 1977; Panama Paleontological Project (PPP) data]. Based on these results, it is reasonable to assume that *Cotonopsis* sensu stricto is much older than postulated by Jung (1989) in his revision of the *Strombina* group. Jung indicated an early Pliocene age for *Cotonopsis*, based on the occurrence of *Cotonopsis esmeraldensis* (Olsson, 1964) in the early Pliocene of Ecuador. Results of the present analysis indicate that *Cosmioconcha* is part of *Cotonopsis* sensu stricto, thus moving the time of origin of this genus most probably to middle Miocene.

Another closely related small clade unites the Recent *Cotonopsis* (*Cotonopsis*) crassiparva and a late Pleistocene *Cotonopsis* (*Cotonopsis*) panacostaricensis (Olsson, 1942), the type species of *Cotonopsis*.

*Cotonopsis* (*Cotonopsis*) phuketensis (Kosuge et al., 1998), a shallow water species from the Andaman Sea, is the second species in this genus with a distribution outside of tropical America. There are infrequent reports of planktotrophic larvae crossing the central Pacific barrier (Scheltema, 1978). Most *Cotonopsis* have planktotrophic larvae (exceptions are *C. jaliscana*, *C. esmeraldensis*, and *C. argentea*; authorities in Table 1) able to spend a considerable amount of time in the plankton (Fortunato 2002a). Again, the lack of fossil data precludes the dating of this dispersal event. Nevertheless, the presence of an early Pliocene species within a sister clade indicates that it may date back to the early Pliocene, at the very least. Here again, molecular data would be useful to help resolve these events.

The next clade comprises *Cotonopsis esmeraldensis* (early Pliocene of Ecuador) and a recent eastern Pacific species, *C. aff. sutera*. This is probably a case of speciation with a switch in developmental mode, as *C. esmeraldensis* is a non-planktotroph whereas its sister species has planktonic larvae. *Cotonopsis esmeraldensis* is the only extinct taxon in the analyzed data set. The basal species of this clade, *C. pukhetensis*, is also a planktotroph. A trans-isthmian event in the history of the group is documented in the next branch of this phylogenetic tree. *Cotonopsis argentea*, a non planktotroph taxon found in deep water of the Dominican Republic coast is the sister taxon of two eastern Pacific species (*C. mendozana* and *C. skoglundiae*).

The crown of the tree is composed by two subclades with a relatively strong Bremer and bootstrap support. The stem taxon is *Cotonopsis deroeye*. One of the groups includes the three *Cotonopsis* (*Turrina*) species, confirming the composition and monophyly of this subgenus. The second group, composed by four *Cosmioconcha* species, documents another trans-isthmian event: *C. nitens* and *C. calliglypta* are shallow water taxa inhabiting the Caribbean Sea that diverged from an eastern Pacific taxon.

Based on the obtained results and the phylogenetic reconstruction presented here, *Cotonopsis* sensu stricto, as presently understood, represents a grade that includes several *Cosmioconcha* taxa (i.e., *C. palmeri*, *C. modesta*, and *C. rehderi*), among them the type species of *Cosmioconcha*. All have stout shells with high spires, axially sculptured early teleoconch whorls, body whorls with strong cords on the base, and wide apertures.

The four “*Cosmioconcha*” species that constitute one of the crown groups of the tree are not closely related to the type species of *Cosmioconcha*. These species are characterized by smaller fusiform shells, absence of sculpture on the early teleoconch, absent or weak cords on the body whorl, and narrow apertures. The character “presence of a collar-like band below the suture”, traditionally used to unify *Cosmioconcha* taxa is not reliable and should not be given more value than any other morphological character.

*Cotonopsis* is a taxon that reflects the pulse of origination that occurred in the eastern Pacific at the Pleio-Pliocene boundary. Most of the recognized taxa originated during the last two million years, probably along the shallow waters of the eastern Pacific coast. Unfortunately, the stratigraphic record of the eastern Pacific region is not very well preserved (Coates et al., 1992, Jackson et al., 1993, 1996) and there is no fossil record for most of the known species. *Cosmioconcha* also originated in this region and has a fossil record that
dates back to the middle Miocene. Based on the phylogenetic reconstruction presented here it is reasonable to assume that *Cotonopsis* derives from a *Cosmiococcha*-like ancestor. The group then radiates and speciates with the documented increase in species diversity towards the recent, a pattern well documented for the entire Strombina group (Jung 1989, Jackson et al. 1993, 1996).

The *Strombina* group has been used as a model system to document patterns of diversification during the Neogene rise of the Panamanian isthmus. Phylogenetic inferences have started to give historical support to earlier studies. The taxa studied here are part of this group and the results confirm the validity of the evolutionary patterns documented earlier (Jackson et al. 1993, 1996, Fortunato and Jung 1995, Fortunato 1998, 1999). It is also reasonable to assume the existence of fossil lineages and even Recent taxa yet to be found that could contribute to a better understanding of the natural history of the molluscan fauna of the region and its relationships.

**ACKNOWLEDGMENTS**

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**LITERATURE CITED**


Appendix 1. Character and character state list.

1- Shell shape: (0) fusiform (elongate, spire high); (1) strombiform, spire low; (2) buccinoid (stout, spire tapered); (3) columbelloid (stout, spire high)

2- Shape of spire whorls: (0) straight sided; (1) straight going to convex; (2) straight going to concave

3- Depth of suture: (0) shallow; (1) impressed; (2) incised

4- Shoulder on spire whorls: (0) absent; (1) present, inconspicuous; (2) present, strong

5- Number of whorls in protoconch: (0) < 2; (1) 2-3; (2) > 3

6- Axial sculpture on early teleoconch whorls: (0) absent; (1) present, inconspicuous and subordinate; (2) present, well developed

7- Spiral sculpture on early teleoconch whorls: (0) absent; (1) present, inconspicuous and subordinate; (2) present, well developed

8- Axial sculpture on late spire whorls: (0) absent; (1) present, inconspicuous and subordinate; (2) present, well developed

9- Spiral sculpture on late spire whorls: (0) absent; (1) present, inconspicuous and subordinate; (2) present, well developed

10- Spiral sculpture on body whorl: (0) absent; (1) present, inconspicuous and subordinate; (2) present, well developed

11- Axial sculpture on body whorl: (0) absent; (1) present, inconspicuous and subordinate; (2) present, well developed

12- Shoulder on body whorl: (0) absent; (1) present

13- Cords on base of body whorl: (0) absent; (1) present, weak; (2) present, well developed

14- Concavity on central part of body whorl: (0) absent; (1) present

15- Constriction on lower part of body whorl: (0) inconspicuously constricted; (1) strongly constricted

16- Inflation of body whorl: (0) not inflated; (1) inflated

17- Type of sculpture on early vs. late spire whorls: (0) same; (1) different

18- Shape of aperture: (0) broad; (1) narrow; (2) slit-like

19- Thickness of outer lip: (0) not thickened; (1) slightly thickened; (2) conspicuous thickness

20- Teeth on inner surface of outer lip: (0) absent; (1) present, small and inconspicuous; (2) present, strongly developed

21- Number of teeth on inner surface of outer lip: (0) none; (1) few (1-5); (2) numerous (>5)

22- Posterior canal: (0) absent; (1) present, inconspicuous; (2) present, well developed

23- Apertural callus: (0) absent; (1) present, as a slight thickness; (2) present, continuous, well developed

24- Columellar denticles: (0) absent; (1) present

25- Parietal callus: (0) absent; (1) present, slightly thickened; (2) present, well developed

26- Parietal denticles: (0) absent; (1) present

27- Parietal ridge: (0) absent; (1) present, small and inconspicuous; (2) present, well developed

28- Sinus on outer lip: (0) absent; (1) present

29- Flaring of outer lip: (0) absent; (1) present

30- Length of anterior canal: (0) short; (1) intermediate; (2) long

31- Width of anterior canal: (0) wide; (1) narrow

32- Extension of adapical part of outer lip (aperture edge at suture): (0) outer lip not extended; (1) outer lip somewhat extended after suture

33- Shape of anterior canal: (0) slightly curved; (1) strongly curved; (2) straight

34- Notch of anterior canal (at the end): (0) shallow; (1) deep depression

35- Thickening behind outer lip: (0) absent; (1) present, slight thickness; (2) present, well developed

36- Dorsal hump: (0) absent; (1) present, slight thickness; (2) present, well developed

37- Edge of outer lip: (0) sharp; (1) rounded

38- Hump on left side of outer lip: (0) absent; (1) present, slight thickness; (2) present, well developed

39- Repeated thickenings behind outer lip: (0) absent; (1) present

40- Plicae on columella: (0) absent; (1) present

41- Relation aperture height/total height: (0) aperture < 1/2 total shell height; (1) aperture much smaller than 1/2 total shell height; (2) aperture bigger than 1/2 but smaller than 3/4 total shell height

42- Collar-like band below spire suture: (0) absent; (1) present

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