

Reconciling observed patterns of temporal occurrence with cladistic hypotheses of phylogenetic relationship

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Abstract: Cladistic analyses of well-sampled groups with a complete and abundant fossil record can yield phylogenetic hypotheses that conflict with stratigraphic data, even to the extent of supporting phylogenies that appear to invert the stratigraphy. This is most probably due to the convergent evolution of similar morphologies (*i. e.* homoplasy), rather than the inadequacy of the fossil record. Several ways have been proposed to resolve this problem (stratophenetics, stratocladistics, character refinement, etc.). This paper proposes an interactive technique to construct a tree more consistent with the observed fossil record by building separate phylogenies for different stratigraphic intervals which can then be assembled into a composite phylogeny. Columbellid gastropods of the genus *Strombina* Mörch, 1852, were used to test this approach. *Strombina* originated and diversified in the Caribbean during the Miocene and Pliocene. During the Pliocene, they became nearly extinct in the Caribbean, but diversified in the eastern Pacific. Phylogenies of 42 species based only on shell morphology (49 characters, 186 states) yielded trees with high stratigraphic inconsistency and ghost lineages that require the presence of descendants 10 million years or more before the first appearance of their hypothesized ancestors. Removal of species that originated after the Pliocene resolved most of these stratigraphic inconsistencies although some ghost lineages remained. This Miocene/Pliocene tree was then used to root the trees illustrating the relationships among Pleistocene/Holocene species. This final composite tree is more consistent with the hypothesized fossil record for the group than the original tree.

Key words: phylogeny, fossil record, consistency, morphology, gastropods, *Strombina*

Most analyses of extant taxa exclude fossil data with the justification that the fossil record is too incomplete and too poorly dated to be useful (Hennig, 1966, 1981; Nelson, 1989; Patterson, 1981; Goodman, 1989). Although this is true for many taxa without durable skeletons, many marine invertebrate taxa such as mollusks, bryozoans, and corals have a rich fossil record. Moreover, fossil collections of these taxa can greatly outnumber collections of extant species. Also, the ages of many fossil collections are known within a range of 1-2 million years, and often better, which is adequate to order occurrences over the typically 20 million years of history of most genera (Cheetham, 1987; Budd, 1989; Budd *et al.*, 1994, 1996). This can depend on the density of sampling (*i. e.* number of samples and sampling interval), but even in studies of taxa with a sparse fossil record the inclusion of fossils can help discriminate morphospecies and increase the consistency of cladistic hypotheses, thus providing a more effective means of rooting trees than comparison with a living outgroup (Cheetham and Hayek, 1988; Jackson and Cheetham, 1994; Cheetham and Jackson, 1995; Marshall, 1995).

Fossils can provide reliable estimates of the order in which lineages appear in the history of life (Gardiner, 1982; Gauthier *et al.*, 1988; Norell and Novacek, 1992a, b; Novacek, 1992a; Foote, 1996), thus providing a temporal

component to calibrate phylogenetic hypotheses. However, the fossil record is often incongruent with cladistic topologies based on morphology alone. There are two sources of disagreement: (a) when the cladistic results require the presence of long ghost lineages that conflict with a rich fossil record for the time interval of interest (Cheetham and Hayek, 1988; Jackson and Cheetham, 1990, 1994; Wagner, 1995; Wagner and Erwin, 1995); or (b) when ancestor-descendant relationships are turned upside-down relative to their stratigraphic sequence (Jackson and Cheetham, 1994). This disagreement can be by as much as 5-10 million years. Such strong conflict between a good fossil record and a given cladistic hypothesis suggests that morphological convergence (*i. e.* homoplasy) could be responsible for putative relationships within the branches of the cladograms (Campbell and Barwick, 1988, 1990; Allmon, 1989; Bodenbender, 1994).

The fossil record can be employed in different ways to try to resolve this disagreement. For example, extinct taxa can be used to infer character polarity (Donoghue *et al.*, 1989; Novacek, 1992b). The fit between stratigraphic information and trees can be used to choose among most parsimonious trees based on morphological data alone (Norell, 1993; Huelsenbeck, 1994; Suter, 1994; Benton and Storrs, 1994, 1996). Stratocladistics (Fisher, 1980, 1988,

1991, 1992, 1994; Clyde, 1994; Clyde and Fisher, 1997) uses stratigraphic information to calculate the "stratigraphic parsimony debt" - a measure of the discrepancies between expected and observed order of stratigraphic occurrences. Although in this case both types of data are allowed to interact at the same level, morphological data are still assigned more weight, thus biasing the output. Common to many of these studies is the tendency to test the adequacy and completeness of the fossil data by quantifying the congruence between stratigraphic information and phylogenetic hypothesis based on morphological data (Marshall, 1990, 1994, 1997; Huelsenbeck, 1994; Benton and Hitchin, 1996; Huelsenbeck and Rannala, 1997). Several authors (Gingerich, 1979; 1994; Cheetham, 1987; Budd, 1988; Stanley *et al.*, 1988; Geary, 1990; Wei, 1994) have advocated the use of stratophenetics, a clustering technique, to reconstruct relationships using both Recent and fossil species, using overall morphologic similarity to connect populations through time. Moreover, stratophenograms give excellent results for groups with a very complete, well-preserved fossil record, like foraminiferans, cheilostome bryozoans, some gastropod groups, and small vertebrates.

Another way of using the fossil record is to construct separate analyses of subsets of a clade between major pulses of evolution (Budd and Coates, 1992). The justification for this method is the assumption that convergent taxa tend to originate during such pulses or turnovers. These separate analyses can then be used to assemble a composite tree across the pulse by building on the tree for the previous interval, such that later taxa cannot totally change hypothesized relationships among much older taxa. This method assumes that observed stratigraphic ranges correspond closely to "true" stratigraphic ranges and that members of different but contemporary clades had approximately the same probabilities of preservation and recovery. Consequently, it considers the possibility that the phylogenetic hypothesis could be incorrect, rather than blaming the fossil record for its deficiency. The aim of this paper is to present a case study where this methodology was used to choose among competing hypotheses of relationships. The final accepted tree is one that better reconciles observed and expected patterns of temporal occurrences for the group in question. This methodology applies only to species-level analyses, differing in this from stratocladistics, which can be used in cases of uncertain specific affinities and also with supraspecific taxa.

MATERIALS AND METHODS

TAXA AND CHARACTERS

The Isthmus of Panama provides a well-document-

ed example of a turnover event that occurred approximately 3-2 Ma (Allmon *et al.*, 1993, 1996; Jackson *et al.*, 1993, 1996; Budd *et al.*, 1996; Cheetham and Jackson, 1996; Fortunato and Jackson, 1996). The large molluscan fossil collections now available for the Neogene to Recent of tropical America, with greatly improved geochronological data (Coates *et al.*, 1992; Collins and Coates, 1993; Coates and Obando, 1996; A. G. Coates, unpub.) and from tens to hundreds of localities, contain thousands of specimens belonging to several highly diverse clades (J. B. C. Jackson *et al.*, unpub.). They permit a look at evolution at the species level and test the hypothesis that homoplasy arises during mass extinction/origination events.

The taxon used in this study is a group of small buccinoidean gastropods, mostly 1-5 cm long, the so-called *Strombina*-group (Jung, 1986, 1989). This group comprises approximately 110 species ranging from the early Miocene (about 20 Ma) through the Holocene, with an excellent fossil record and several thousand specimens collected. Their alpha taxonomy has been revised recently (Jung, 1989), and is assumed to be correct (or correctable with little effort) for this study. The wide distribution of the group, both in space and time, is an important aspect for the technique used here. Species diversity slowly increased over time, mainly in the Caribbean. In the eastern Pacific there were always many fewer species until approximately 1.8 Ma, at the Plio-Pleistocene boundary, when there was a sudden geographic shift in diversity from the Caribbean to the eastern Pacific (Jackson *et al.*, 1993). The fact that there are fewer collections (and specimens) from the eastern Pacific than from the Caribbean sea could affect the observed diversity pattern through time. Nevertheless, in spite of being very abundant, most taxa of the *Strombina*-group occur only in one region and only during one time interval, which, given the extensive records overall, cannot be merely a sampling artifact.

Of the five genera that comprise the *Strombina*-group, only the genus *Strombina* Mörch, 1852, was used for this study. This is the most abundant and diverse genus in the group, with 42 species, of which 20 originated during the last three million years. Previous results based in both shell morphology and anatomy strongly support the monophyly of this genus (Fortunato and Jung, 1995).

The material analyzed here (Table 1) consisted of all available fossil and Holocene collections from more than 20 institutions and private collections used by Jung (1989) for his taxonomic revision of the genus *Strombina*. These collections were supplemented by the fossil collections from the Panama Paleontological Project (PPP), maintained in the Naturhistorisches Museum, Basel, Switzerland.

The characters used in this study were selected from a larger suite of characters, including both measurements

Table 1. Number of lots and specimens used in this study.

| Subgenus | Lots | Specimens |
|----------------------|------|-----------|
| <i>Strombina</i> | 362 | 7085 |
| <i>Spiralta</i> | 459 | 2646 |
| <i>Lirastrombina</i> | 291 | 1363 |
| <i>Arayina</i> | 11 | 117 |
| <i>Recurvina</i> | 310 | 2969 |
| <i>Costangula</i> | 98 | 603 |

(continuous) and qualitative (discrete) characters of shell morphology and anatomy, as defined in a previous work to test the monophyly of the *Strombina*-group (Fortunato and Jung, 1995). Only shell morphology was considered here to allow equal evaluation of both extant and fossil species. Of these 49 characters, six are measurements of overall shell and aperture dimensions; 38 are qualitative (discrete) characters related to various aspects of shell ornamentation and armor, as well as aperture armor; and five are composite characters referring to overall shell size, shape, and spire, as well as apertural size and shape. All characters were unordered and equally weighted. Unknown states were coded as missing. Continuous characters were coded using the Duncan's procedure for multiple-comparison tests of species means (Winer, 1971). Detailed descriptions of these characters, as well as coding procedures and the data matrix, will be published elsewhere.

ANALYTIC PROCEDURES

Species-level cladistic phylogenies for 42 *Strombina* species were generated using Hennig86 version 1.5 (Farris, 1988). Trees were rooted on the three oldest

species of the genus *Sincola* Olsson & Harbison, 1953, which is the second oldest genus of the *Strombina*-group. Both *Sincola* and *Strombina* first occur in the proto-Caribbean region approximately 18 million years ago. Heuristic searches were performed using the "mhennig" followed by "bb" options to generate trees. Exhaustive searches were impossible to carry out because of the excessive amounts of time required. No consensus trees were requested; all most-parsimonious trees obtained in each analysis were evaluated and only the trees that were congruent with the time of origination and extinction hypothesized for the group in question were retained. The single tree that was most consistent with the observed fossil record was then used for the reconstructions.

Table 2 summarizes the sequence of procedures and results for all four sets of cladistic analyses. All assumptions were the same for the four sets of analyses, only the species included varied. For Analysis 1, all 42 species rooted on three *Sincola* species were used regardless of stratigraphic level. Evaluation of the most parsimonious trees yielded by this analysis (the "Total" tree; Fig. 1) showed that taxa from different stratigraphic levels were evenly scattered across the trees, indicating extremely high stratigraphic inconsistency. The taxa were therefore subdivided into two groups, pre- and post-turnover, depending on their time of origination. Analysis 2 was run using only the 22 species that originated before the turnover event that took place in tropical America ("pre-turnover" species; origination times older than three million years). The trees yielded by this analysis (the "Mio-Pliocene" tree; Fig. 2) were evaluated and taken as a fixed point for further work. Analysis 3 was subdivided into two phases, each consisting of a

Table 2. Sequence of procedures used in each analysis and the results obtained.

| | Analysis 1 | Analysis 2 | Analysis 3A | Analysis 3B | Analysis 4 |
|-------------|---|--|--|--|--|
| Input: | 42 ingroup taxa 3 outgroup taxa 49 characters | 22 ingroup taxa older than 3 Ma 3 outgroup taxa 49 characters | 11 Mio-Pliocene ingroup taxa (left clade) 3 outgroup taxa 49 characters | 9 Mio-Pliocene group taxa (right clade) 3 outgroup taxa 49 characters | All trees |
| Procedures: | Morphologic parsimony | Morphologic parsimony Removal of taxa younger than 3 Ma | Morphologic parsimony Break between taxa 28/27 Include oldest <i>Strombina</i> (taxon 4) Add younger taxa to each lineage | Morphologic parsimony Break between taxa 28/27 Include oldest <i>Strombina</i> (taxon 4) Add younger taxa to each lineage | Connect each tree sequentially following stratigraphic order Retain main clades delineated in Analysis 1 |
| Result: | "Total tree" 2 main clades Stratigraphic inconsistency | "Mio-Pliocene tree" 2 main clades Stratigraphic consistency | Final tree for <i>Strombina</i> / <i>Recurvina</i> clade | Final tree for <i>Lirastrombina</i> / <i>Spiralta</i> / <i>Costangula</i> clade | Composite tree Stratigraphic consistency |

series of separate cladistic analyses including the younger species which originated after the turnover event (the "post-turnover" species; origination times younger than three million years). In each of these phases, the extant species were added to each subclade as defined by the "Mio-Pliocene" tree and supported by the "Total" tree. The results of the third set of analyses were then used to build a composite tree (Analysis 4) based on the "Mio-Pliocene" tree and with all of the extant species added. Ancestor-descendant relationships were interpreted for each of these subclades based on the results of Analyses 2 and 3. The taxon of the same subgenus which lay at the tip of the "Mio-Pliocene" tree was considered to be the ancestor of the subsequent Holocene species. The trees yielded by Analysis 3 were attached to these ancestor taxa.

In another words, all analyses were performed as though a systematist decided to test for homoplasy three million years ago, before the major turnover event took place in Central America. One of the assumptions is that the relationships that existed then could not be changed by any subsequent events. The removal of younger species from the "Mio-Pliocene" tree minimized most of the possible effects of the subsequent radiation during this period which could obscure older relationships.

RESULTS AND DISCUSSION

Analysis 1 ("Total" tree). Four equally most parsimonious trees, with length 703, CI = 0.21, and RI = 0.52, were obtained. The main differences in tree topology were related to the relative positions of taxa 17 and 18. In one case taxon 17 was hypothesized to be sister of the group formed by taxa 10 and 18, whereas in the other case taxon 18 was hypothesized to be sister of the group formed by taxa 10 and 17. The former tree was accepted because it was more consistent with the observed fossil record of the group. Fig. 1 shows a reconstruction of the accepted tree plotted against the stratigraphic column (the "Total" tree).

Fig. 1 shows striking stratigraphic inconsistency. One-third of the branches are ghost lineages that extend for more than ten million years without a single fossil occurrence or with fossils that appear several million years after their origination times as hypothesized by the cladogram (*i. e.* taxa 9, 12, 40/41). The tree also hypothesizes that several extant species are ancestors of species that became extinct 10-15 Ma. This is the case for taxon 12, a living species reported from a region that yielded many other fossil species, but of which there are no fossil occurrences. According to the relationships postulated in Fig. 1, this

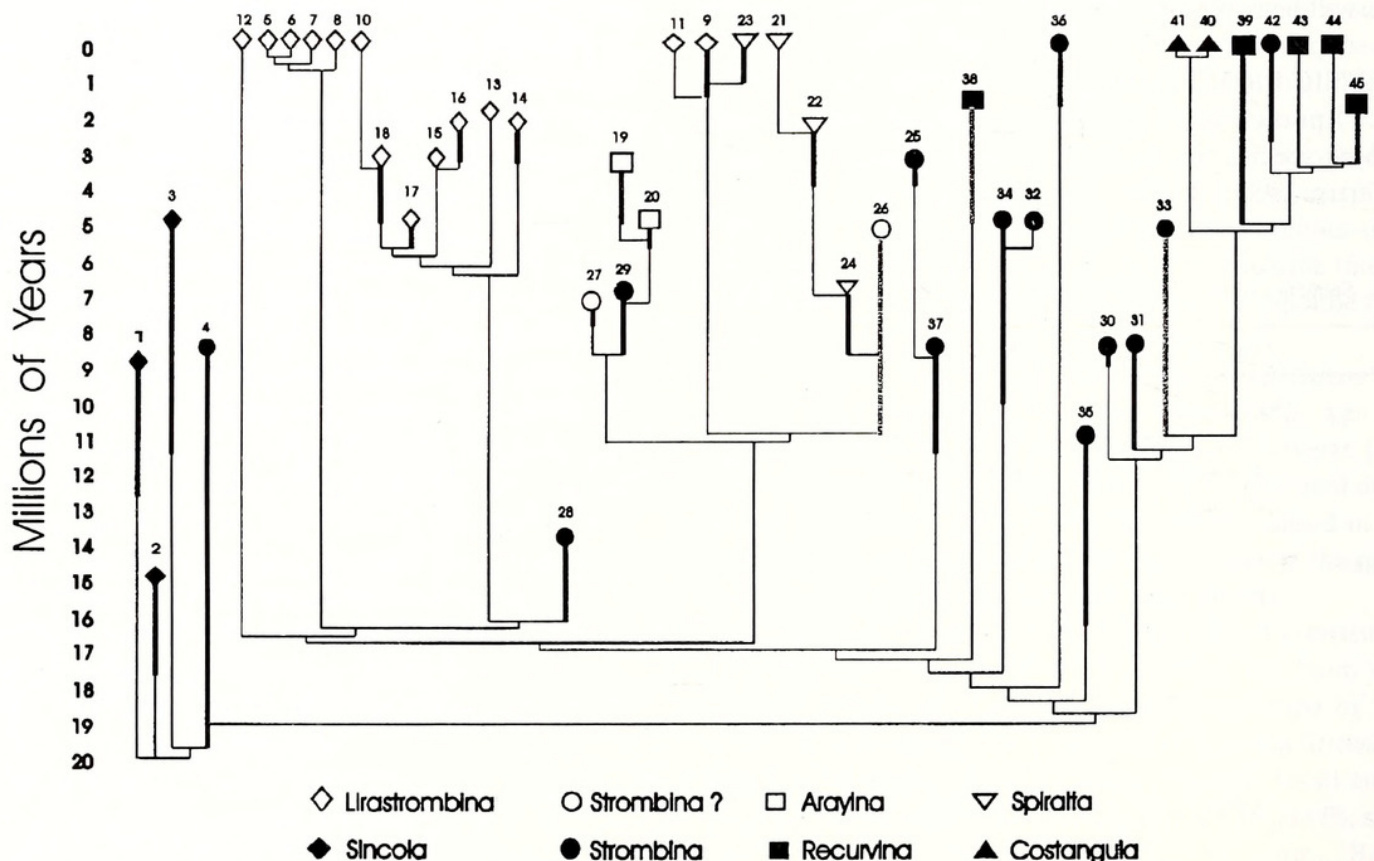


Fig. 1. Reconstructed 42-species cladogram ("Total" tree) showing the geologic time scale for calibration. Numbers on terminal branches represent species; symbols on terminal branches represent subgenera; thick black lines are real fossil data through time; gray lines represent ranges with uncertain age assignment; thin vertical lines represent ghost lineages hypothesized by the cladogram.

taxon is the ancestor of clades 13/18 and 5/8, as well as of taxon 28; however, most of these hypothesized descendent species became extinct several million years before taxon 12 originated. The same situation occurs with several other taxa (*i. e.* taxa 36, 38, etc.). These long ghost lineages also push back the radiation of the whole group to a time, approximately 15 Ma, when, although there is an excellent fossil record for many other molluscan groups in the same region, there is no sign of such a radiation in the *Strombina*-group.

Despite these stratigraphic inconsistencies, the subgeneric assignments of the species are mostly conserved, and several major clades are delineated, thus the problem is mainly one of stratigraphic inconsistency between clades and subclades. Such stratigraphic inconsistency is probably due to an extensive morphologic convergence caused by the evolution of similar forms during the turnover as existed in the earlier history of the group. Similar problems of homoplasy are common among corals, bryozoans, etc. (Budd and Coates, 1992; Jackson and Cheetham, 1994; Cheetham and Jackson, 1995, 1996).

Analysis 2 ("Mio-Pliocene" tree). This analysis yielded eight most-parsimonious trees, of 419 steps, CI = 0.31, and RI = 0.48. The major differences among these trees were in the basal taxa. In several trees the node that joined taxa 30 and 31 was basal to the rest of the tree,

whereas in other trees the node joining taxa 28 and 35 was basal. The tree in which taxa 28 and 35 were basal was accepted because these taxa have older origination times.

The "Mio-Pliocene" accepted tree is plotted stratigraphically in Fig. 2. Most of the long ghost lineages have disappeared. None of the younger species included in the analysis are hypothesized to be ancestors of much older taxa. Once again, the subgeneric taxonomic assignments hold together and two major clades are clearly defined.

Analysis 3A (18 species, "*Strombina/Recurvina*" clade). The right subclade of the "Mio-Pliocene" tree (Fig. 2) comprised all species of the subgenus *Recurvina* Jung, 1989 (closed squares), and nearly all species of *Strombina s. s.* (closed circles). Three *Strombina s. s.* species (taxa 25, 26, 27) grouped with the left clade. This result supports the initial questionable subgeneric assignments of taxa 26 and 27 (Jung, 1989) and suggests that taxon 25 could also belong to another subgenus. The analysis of the 11 Mio-Pliocene species of these subgenera, plus the oldest *Strombina s. s.* (taxon 4) (which consistently appeared in a basal position in all previous analyses) rooted on *Sincola*, yielded only one tree with exactly the same topology, thus confirming the stability of this clade.

When the two younger species of *Strombina*, three of *Recurvina*, and two of *Costangula* Jung, 1989 (which had consistently grouped with the other two subgenera in

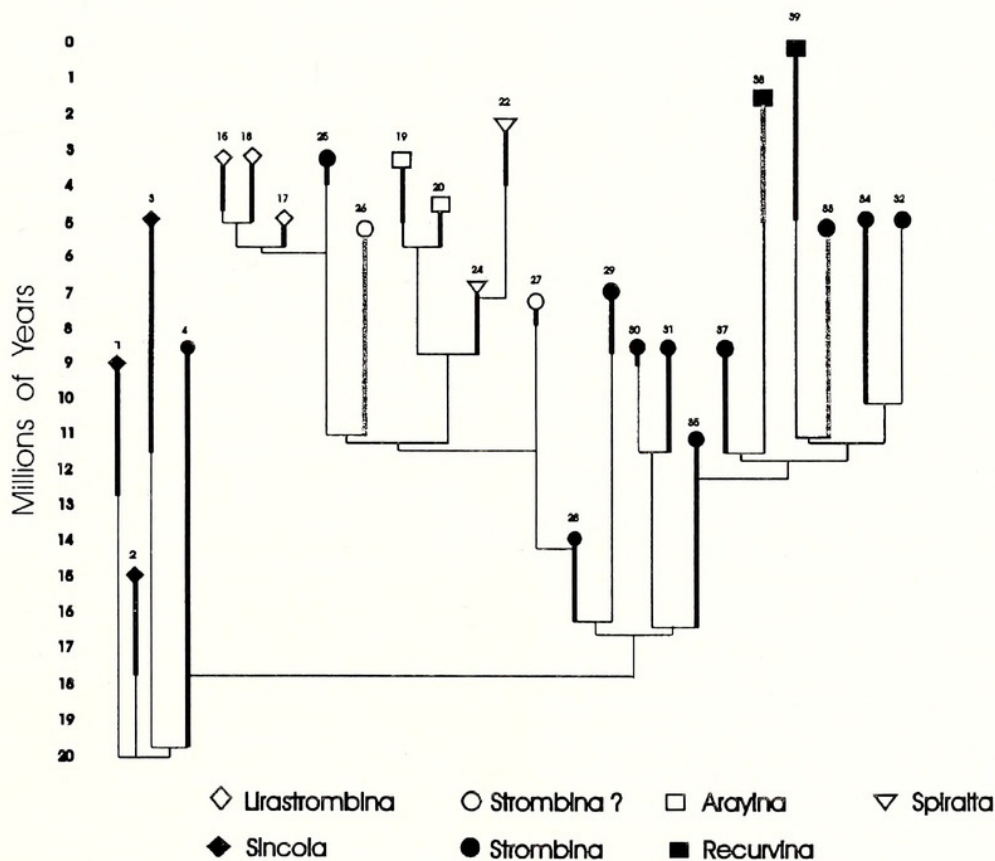


Fig. 2. Reconstructed 22-species cladogram ("Mio-Pliocene" tree) with geologic time scale for calibration. All symbols as in Fig. 1. This tree was the fixed point for Analyses 3A and 3B.

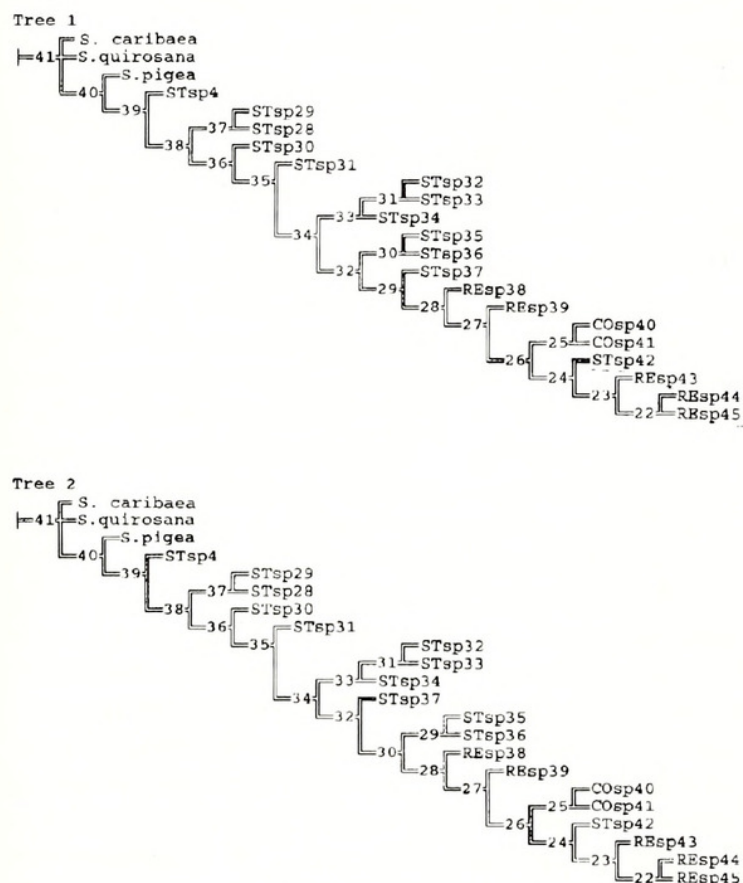


Fig. 3. Two most parsimonious trees yielded by Analysis 3A, including 19 species: 11 Mio-Pliocene species of the subgenera *Strombina* (ST) and *Recurvina* (RE) (= right clade of the "Mio-Pliocene" tree) plus seven extant species: two *Strombina s. s.*, three *Recurvina*, and two *Costangula* (CO) rooted on three species of *Sincola* (*S. caribaea* Gabb, 1873; *S. quirosana* H. K. Hodson, 1931; *S. pigea* Olsson, 1964). The oldest *Strombina s. s.* in the analysis (taxon 4) was also used here.

the "Total tree" analysis), were added to the analysis and rooted on *Sincola*, the resulting two most-parsimonious trees (Fig. 3) differed only in the relative position of taxon 37 versus 35 and 36. The tree in which taxon 35, the oldest, branched first (Fig. 3, Tree 1) was accepted. Fig. 4 shows the reconstructed "Mio-Pliocene" tree (Fig. 2) with the "*Strombina/Recurvina*" clade (Fig. 3) added to the right side.

Analysis 3B (23 species, "*Lirastrombina/Spiralta/Arayina*" clade). The left clade of the "Mio-Pliocene" tree comprised all species of three subgenera: *Lirastrombina* Jung, 1989 (open diamonds), *Spiralta* Jung, 1989 (open inverted triangles), and *Arayina* Jung, 1989 (open squares), as well as the three *Strombina s. s.* (taxa 25/27) mentioned above. Analysis of the ten Mio-Pliocene species of these subgenera plus the oldest *Strombina* species (which had been basal in all prior analyses), rooted on *Sincola*, yielded five trees. The major differences among these trees were in the relative positions of taxa 25 and 26. The tree in which the node that joined taxa 25 and 26 was basal was accepted based on the older origination times of taxon 26. This

topology also retained taxa 26 and 27 close together. In spite of these changes, all topologies maintained all species belonging to the left clade in the same relative positions they had in the "Mio-Pliocene" tree, thus confirming the stability of this clade.

The "*Lirastrombina/Arayina/Spiralta*" clade involved three different and large subgenera, and it was analyzed in two separated phases. In phase 1, when the ten extant species of *Lirastrombina* were added to the three Mio-Pliocene species plus the *Strombina s. s.* (taxon 4) and rooted on *Sincola*, the resulting two most-parsimonious trees (Fig. 5) differed only in the relative positions of taxa 13 and 14. In one of these trees, taxon 14 was hypothesized as a sister taxon of taxon 13, whereas in the second tree, taxon 13 was hypothesized as branching earlier. Because taxon 14 has an earlier origination time than taxon 13, the tree in which it is hypothesized to arise at least at the same time (as a sister taxon of 13 and not later) was accepted (Fig. 5, Tree 1). Due to extreme homoplasy, the extant taxon 10 always nested very deep within the *Lirastrombina* tree, resulting in a decrease of overall stratigraphic consistency. This problem was solved by the elimination of this species from this phase of the analysis; this species was later added to the "Total tree" based on its position in the first analysis (see Fig. 1).

In phase 2, when the two extant species of *Spiralta* were added to the Mio-Pliocene species of *Spiralta* and *Arayina* plus taxon 4 and rooted on *Sincola*, the result was a single tree (Fig. 6).

Analysis 4 (composite tree). The trees resulting from Analyses 2 and 3 were then added to the left side of the "Mio-Pliocene" tree. Fig. 7 shows the final reconstructed tree. This tree has a high stratigraphic consistency even though ages were not used directly as characters. It has two major clades: one composed of members of the *Strombina*, *Recurvina*, and *Costangula* subgenera; the other is composed mainly of members of the *Lirastrombina*, *Arayina*, and *Spiralta* subgenera. These same major clades were delineated in the original 42-species tree (Fig. 1), but some of their relationships were originally obscured by morphologic convergence which then confused the stratigraphic relationships. A few ghost lineages, presumably due to missing fossil data, still remain.

CONCLUSIONS

The observed stratigraphic order of species occurrences (first and last appearances) should be used as one more source of data in phylogenetic inferences. The technique proposed here is a simple and independent way of assessing rival phylogenetic hypotheses obtained through parsimony methods. The final tree is more consistent with

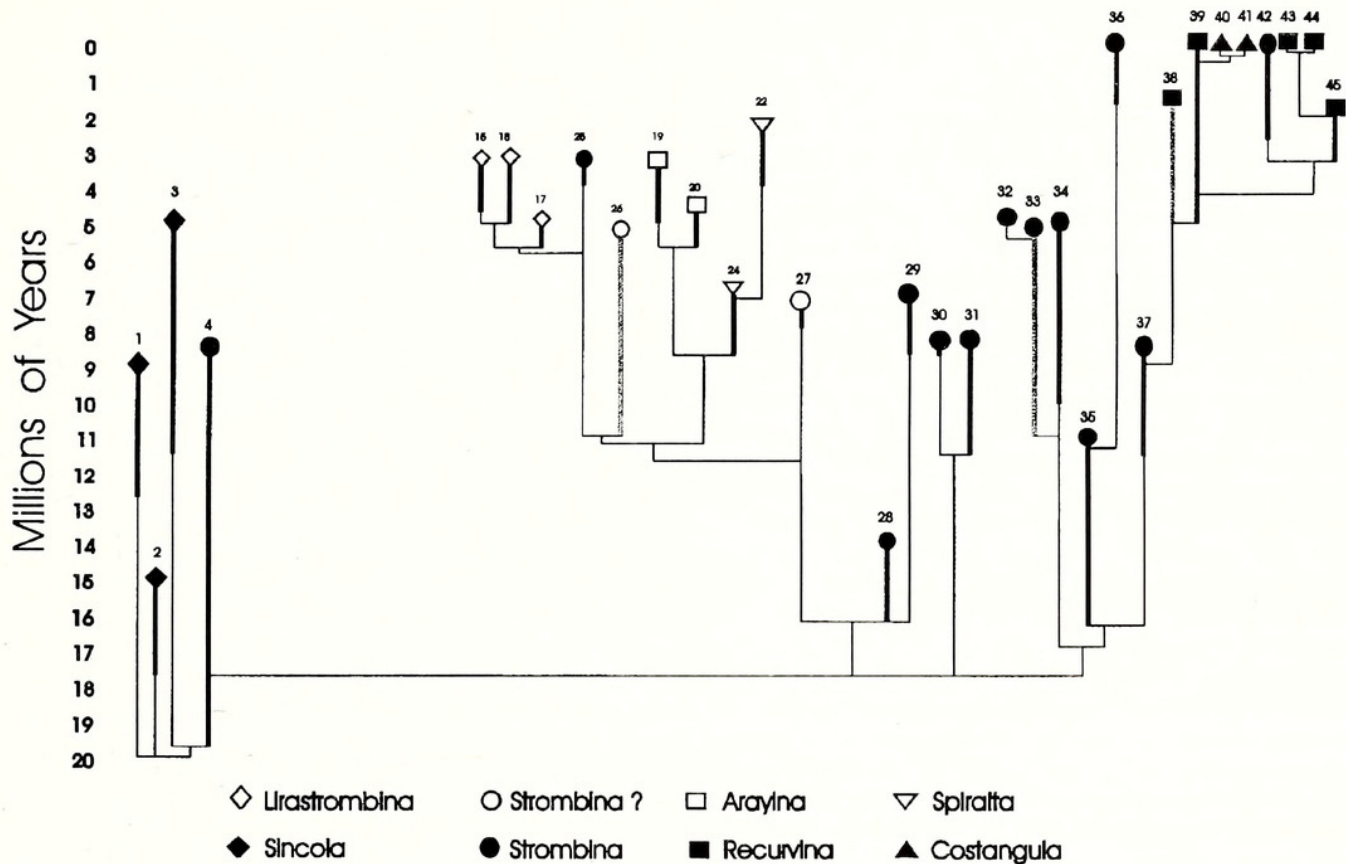


Fig. 4. Reconstructed cladogram of the 22 Mio-Pliocene species plus the seven extant species of the right clade ("Strombina/Recurvina" clade), with geologic time scale for calibration. All symbols as in Fig. 1.

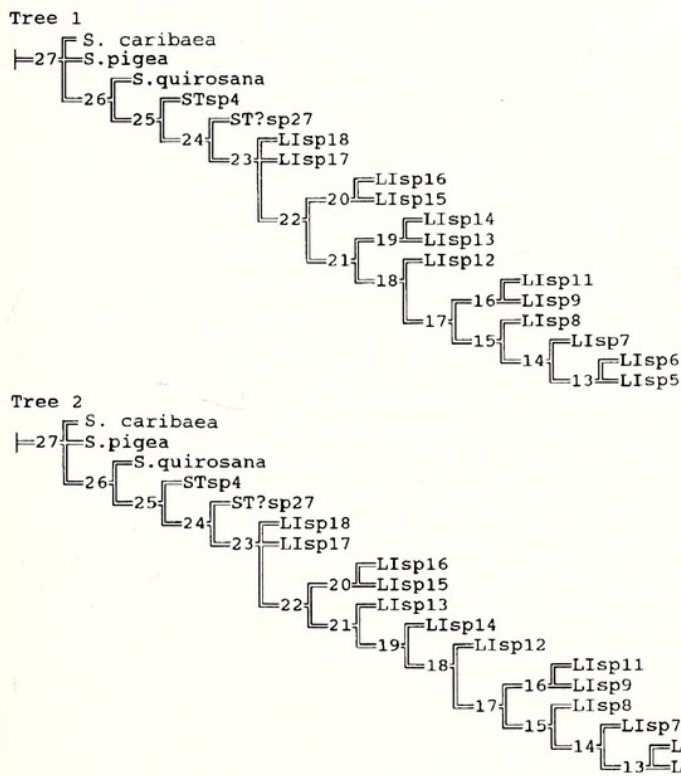


Fig. 5. Two most-parsimonious trees yielded by the analysis of 13 species (Mio-Pliocene plus extant) of the subgenus *Lirastrombina* (LI) rooted on *Sincola*. This was the first phase of Analysis 3B. Other taxon labels as in Fig. 3.

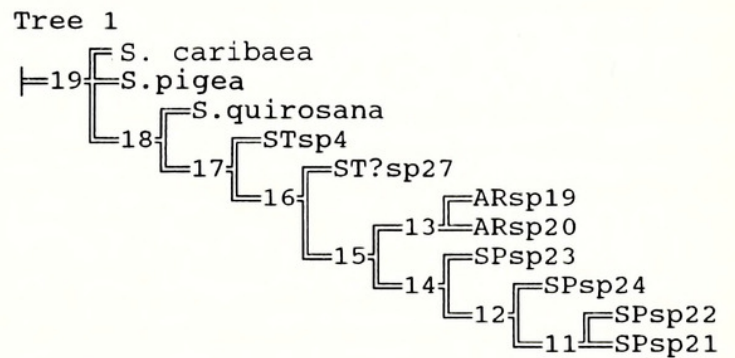


Fig. 6. Single most-parsimonious tree yielded by the analysis of eight species (Mio-Pliocene plus extant) of the subgenera *Spiralta* (SP) and *Arayina* (AR) rooted on *Sincola*. This was the second phase Analysis 3B. Other taxon labels as in Fig. 3.

the fossil data and uses fewer statements about relative probabilities of preservation, thus conforming to the principle of parsimony.

Several main aspects of the methodology used and its implications for the study of phylogenetic relationships should be noted here. Others will be considered in a later work dealing mainly with further refinement of this technique, as well as with its comparison with similar methods. The quality of geochronological data used is very important for the correct interpretation of the results obtained with

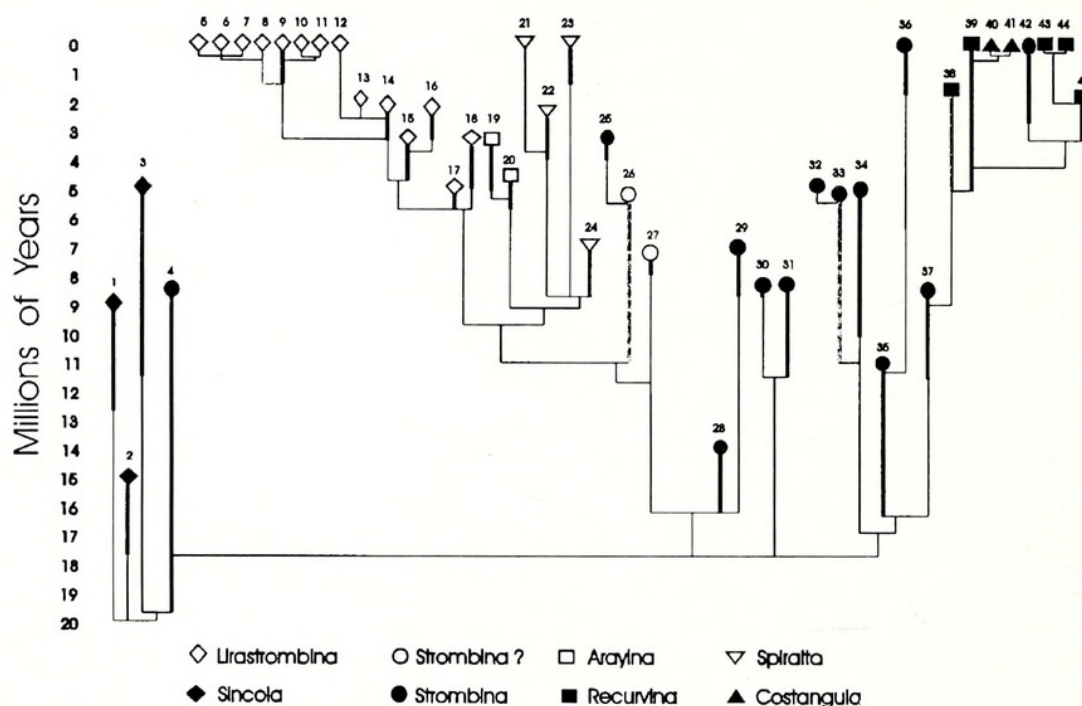


Fig. 7. Reconstructed cladogram including the 42 initial species. This is the final composite tree based on the "Mio-Pliocene" tree plus the trees yielded by Analyses 3A and 3B. All symbols as in Fig. 1.

this methodology. Uncertain age assignments and low stratigraphic resolution will make difficult the decision about time intervals into which to divide the analyses, thus increasing the uncertainty in recovering the true history of the clades under study. Sampling can also be a problem: uneven geographic and stratigraphic sampling will give an incomplete picture of the true abundance and diversity of the groups studied, and its effects can be confounded with homoplasy. Another important point is the question of how well the species-level taxonomy is employed. The "Total tree" preserved most of the subgeneric units (with only a few exceptions, some of which were already doubtful). This result matches earlier work (Fortunato and Jung, 1995) using both shell morphology and anatomy, thus adding confidence to the methodology employed to recover the true history of the clade. In spite of this agreement with the structural component of the analysis, the temporal aspect was violated both by the extremely long-lasting ghost lineages and by the hypothesized order of originations of several ancestor-descendant pairs. The removal of all taxa that originated during the last three million years resolved many of these incongruences with the known order of fossil occurrences. Most of the hypothesized cladistic relationships (*i. e.* ancestor-descendant pairs and sister taxa) among the Mio-Pliocene taxa have a high level of agreement with their origination time as shown by the fossil record. This also helped to resolve most of the long-lasting ghost lineages. These results all agree with the assumption that most of the stratigraphic inconsistencies present in the first tree (Fig. 1) were due to high levels of

homoplasy after and before the turnover event rather than to the incompleteness of the fossil record, incorrect taxonomic assignments, or sampling bias.

It is important to notice that the evolutionary patterns hypothesized by the trees obtained before and after the removal of the young species are very different. These evolutionary scenarios and its implications for the history of the group will be analyzed elsewhere. It is enough to mention here that whereas the tree represented in Fig. 1 implies an extensive radiation of the whole group approximately 15 Ma, that represented in Fig. 6 suggests that there were two radiations (or three), one approximately 10 Ma, and the second probably just before the final closure of the isthmus of Panama, and extending for some time thereafter in the eastern Pacific. This scenario of several possible radiations agrees with the fossil record.

The technique outlined in this paper is still in its preliminary stage. As such it suffers from several biases which are currently being resolved. One of these is the lack of stratigraphic confidence intervals for the samples. The approach used here assumes that the sampling bias is not large enough to significantly override the effects of homoplasy. As part of the development of this technique, stratigraphic intervals will be calculated following Wagner's (1995) methodology. This will separate the effects of homoplasy from those of inadequate sampling, thus testing the consistency of the method. Also as part of the work in progress, the same data set will be employed using Fisher's methodology (Fisher, 1992; Clyde and Fisher, 1997) and the resulting trees compared with the composite tree

obtained through the technique presented here. This will provide a test of the power of both methodologies and evaluate their capability of recovering the true history of this group.

Regardless of the need for further development of this technique, it is clear that conventional parsimony analyses are only the first step towards recovering the true history of a clade. Cladistic hypotheses should be tested against the stratigraphic data if at all possible. Failure to do this can distort the evolutionary histories and falsify our predictions about evolutionary patterns.

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