TULANE STUDIES IN GEOLOGY AND PALEONTOLOGY

Volume 27, Numbers 1-4 January 31, 1995

AN ONTOGENETIC APPROACH TO UNDERSTANDING CHANGES IN SHELL MORPHOLOGY OVER TIME: THE *STROMBUS ALATUS* COMPLEX IN THE PLIO-PLEISTOCENE OF SOUTHERN FLORIDA

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CONTENTS

I. ABSTRACT 1
II. INTRODUCTION 2
III. MATERIALS AND METHODS 2
IV. RESULTS AND DISCUSSION 9
V. CONCLUSIONS 34
VI. ACKNOWLEDGMENTS 44
VII. LOCALITY DATA 45
VIII. LITERATURE CITED 46
IX. ENDNOTES 48
X. APPENDIX: MEASUREMENT PROTOCOLS 50

I. ABSTRACT

The study seeks to focus upon the process of shell growth, as well as on the end product of that process, as a way of understanding molluscan shell morphology and how it changes over time. Techniques developed for analyzing individual ontogeny, when applied to the members of a sample, yield a multifaceted mean growth profile for that sample. The growth profiles of multiple samples of the same putative taxon are then compared to obtain a more generalized set of growth patterns for that taxon. Finally, the process is applied to the various members of a fossil lineage to provide insight into changes in the process of shell growth over time.

Presented herein are the results of a detailed ontogenetic study of Recent and fossil material from a number of biostratigraphic horizons in southern Florida involving the mesogastropod subgenus *Strombus* sensu stricto, a common component of the shallow-water marine fauna. Evidence from this study indicates that *Strombus floridanus* Mansfield, 1930, the earliest member of the subgenus in the Florida Pliocene, differs from the extant species *Strombus alatus* Gmelin, 1791, in both adult morophological characteristics and patterns of growth, and that the former represents the ancestral form of the latter. *Strombus floridanus* is restricted to the *Cancellaria* zone of the Jackson Bluff Formation in the Florida Panhandle and to the lower Pinecrest beds in southern Florida, whereas *S. alatus* makes its first appearance in the post-Bermont Pleistocene. Connecting these two taxa are a suite of fossil forms representing a single, morphologically changing lineage. Within this lineage growth patterns in the larval stage undergo a series of incremental changes in one direction during this time interval, while growth patterns in the benthic stage and adult morphological features exhibit a complex set of changes, some being incremental and others undergoing a single large-scale transformation at one point in the geologic record.

The transformation from *S. floridanus* to *S. alatus* appears to have taken place over about a one million year interval in the fossil record (from about 2.4 Ma to 1.4 Ma), and has been followed by a period of apparent morphologic stasis. Two intervening morphological forms or chronospecies can be distinguished, separable in their growth patterns and some adult morphological features from the end-point taxa and, to a lesser extent, from one another. With some reservation, *Strombus evergladesensis* Petuch, 1991, and *Strombus lindae* Petuch, 1991, have been accepted as valid names for these two forms. The former, as interpreted herein, ranges from the upper

Pinecrest to the basal Bermont, while the latter is restricted to a higher Bermont horizon. The existence of two clearly differentiable forms in different units of the Pinecrest beds, as exposed in the APAC Pit near Sarasota, supports the hypothesis of a substantial hiatus separating Units 2-4 from the underlying Units 5-10, and suggests that only the lower units are correlated with the Jackson Bluff Formation of northern Florida. The presence of *S. alatus* throughout the section exposed in the Leisey Shell Pits of southern Hillsborough County raises serious doubts about the placement of much of that section in the Bermont Formation.

II. INTRODUCTION

Of the eleven living subgenera of the mesogastropod genus *Strombus*, eight are confined to the Indo-Pacific Province, whereas three have representatives in the New World. Of those three, only members of the subgenus *Strombus* sensu stricto are restricted to the New World. There, three extant species survive. One, *Strombus gracilior* Sowerby, 1825, lives in the Pacific Panamic Province and the other two, *Strombus pugilis* Linnaeus, 1758, and *Strombus alatus* Gmelin, 1791, are found in the Atlantic Caribbean and Carolinian Provinces, respectively.

Throughout much of its range, *S. alatus* is a common component of the shallow-water molluscan assemblage, being present in quiet back bays, on intertidal sand bars, and on sandy substrates to depths of at least 35 meters along the continental margins. Local concentrations of five individuals of mixed age (adults and juveniles in excess of 30 mm) per square meter are not uncommon in intertidal habitats. The species is not present in the Bahamas, but is found 150 kilometers from the mainland in the off-shore atoll/reef areas of the Campeche Bank (Vokes and Vokes, 1983, p. 54).

Fossil members of the subgenus can be found in many Late Miocene, Pliocene and Pleistocene shallow to moderately deep-water, sub-tropical to tropical marine deposits in the New World. In the Pliocene and Pleistocene deposits of southern Florida, members of this subgenus are probably the most common medium-sized gastropods present, sometimes being found *in situ* in dense pockets or layers (Geary and Allmon, 1990).

The form studied by Geary and Allmon, from the lower units of the Pliocene Pinecrest beds (Olsson, 1964 = Fruitville Formation of Waldrop and Wilson, 1990), is generally considered to be *Strombus floridanus* Mansfield, 1930. Although the shell morphology of adult specimens of this taxon clearly differs from that of *S. alatus*, *S. floridanus* is most likely the mid-Pliocene ancestral form of the extant species. Contained in the overlying Late Pliocene and Pleistocene deposits of southern Florida belonging to the upper Pinecrest beds, the Caloosahatchee Formation (Dall, 1887), the Bermont Formation (DuBar, 1974), and the Fort Thompson/Coffee Mill Hammock Formations (Sellards, 1919),[1] is a suite of intervening forms that appears to represent a single lineage spanning some 3 to 3.5 million years.[2] The relative completeness of the fossil record in southern Florida over this period of time, together with the abundance and generally excellent state of preservation of *Strombus* specimens present in that record, make them excellent candidates for a detailed analysis of phylogenetic changes in shell morphology.

III. MATERIALS AND METHODS

Central to the study of fossil molluscan taxa is the need to be able to distinguish expressions of variation within a taxon from the character states that separate taxa. With Recent forms this can be accomplished by carrying out statistical analyses whenever a suitably large sample can be obtained from a single population. However, it is virtually impossible to determine whether fossil specimens, even when collected from the same locale, are members of a single population. Even *in situ* collections are unlikely for a number of reasons to represent a biological community (see Geary and Allmon, 1990). Nevertheless, when samples taken from biological populations of extant taxa are available for comparison, statistical analyses of carefully collected fossil material can yield useful information about probable intraspecific variation.

For work with both fossil and extant taxa, even statistical analyses can lead to misleading conclusions when care is not taken to distinguish between adult and juvenile forms. Within the family Strombidae this need not be a problem since adults can easily be differentiated from their juvenile counterparts. However, to the extent that this causes investigators to focus attention only upon those shell characteristics expressed in the adult stage, potentially valuable insights can be lost. In such instances attention tends to be focused almost exclusively on the last whorl of the teleoconch, and particularly on the form of the expanded and thickened adult lip. While vestiges of the previous whorls (12 to 14 in *Strombus* s.s.) are retained in the adult spire, it is generally only their collective impact in terms of spire shape that is noted. Yet close scrutiny reveals complex sculptural features on these earlier whorls, features that often differ from whorl to whorl. Since these features represent a partial history of the ontogeny of the individual, it would seem to be legitimate, and indeed potentially illuminating, to study their **pattern of development** over the entire protoconch and teleoconch, *i.e.*, to pay as much attention to developmental processes as to the final product. It is this ontogenetic approach to the study of molluscan shell characteristics that is at the core of the present investigation.

The analysis of gross features.

Measures. Several measurements were made of the overall shell dimensions of individual specimens. These are listed below, with the actual measuring protocols outlined in the Appendix.

Shell Length
Maximum Shell Width
Dorsal/Ventral Shell Width
Spire Height

Body Ornamentation. The presence/absence and nature of both axial and spiral sculptural elements on the body whorl of adult specimens were noted. In addition, the presence of any of three spiral sculptural elements sometimes found inside the aperture of adult specimens was noted; submarginate costae along the inside of the lip, short denticles on the anterior columella opposite the stromboid notch, and fine threads or rugosities on the parietal wall near the point of posterior lip attachment. The shape of the expanded adult lip itself was found to be of no value for differentiating taxa within this study.

Color Pattern. Elements of color pattern in Recent and, where still visible either under normal or long-wave (3660 Å) ultraviolet illumination, in fossil specimens were recorded. Of note were the presence and nature of darker axial patterns particularly on the ventral side of the body whorl in adult specimens, together with markings associated with resting varices on the spire.

Ontogenetic analysis.

The types of shell characteristics that lend themselves to an ontogenetic or developmental analysis can be placed in three categories: (1) overall whorl dimensions or shape; (2) the details of axial ornamentation; and (3) the details of spiral ornamentation. Several aspects of the spiral and axial ornamentation can be noted: (1) the onset or cessation of expression of the feature; (2) the number of elements per whorl; (3) the strength or degree of expression of the element on each whorl; and, (4) the nature of the expression of the element (*i.e.*, the overall geometry of expression) on each whorl.

Whorl Dimensions. Three linear measurements were taken for each whorl of a specimen to characterize the process of shell development. These are listed below, with the measuring protocols outlined in the Appendix.

Whorl Diameter
Whorl Height
Shoulder Height

It has been shown that the vast array of gastropod forms can be approximated in computer simulations by manipulating three variables; the shape of the curve representing the body cavity, the exponential rate of expansion in the plane of coiling, and the exponential rate of movement along the axis of coiling.[3] In these computer simulations, the rates remain constant as the "shell" grows.[4] If one were to plot the change in whorl diameter for one of these computer-generated gastropods as a function of whorl number on a semi-log graph, the result would be a straight line whose slope would represent the rate of spiral increase; for example, low for a *Turritella* and high for an *Architectonica.* Similarly, if one were to plot the change in whorl height and shoulder height for such hypothetical creatures in the same manner, the results would once again be straight lines whose slopes (the same in this case) would represent the rate of translation parallel to the axis of coiling, high for a *Turritella* and low for an *Architectonica.*

To what extent do these computer simulations reflect the ontogeny of real gastropods? By carrying out the whorl-by-whorl measurements listed above for individuals in a sample and then using them to establish mean values for the three growth characteristics, it is possible at least to determine the average behavior of a particular type of gastropod. Text-figure 1 plots the results of such an analysis for a sample of *S. alatus* for each of the three measures. Several points should be noted. First, the plots are close to, but not exactly, straight lines; in the real world, growth rates (*i.e.*, slopes) change over the course of shell development. Second, there is a similar pattern to each of these suites of changes. Third, the timing of the changes is slightly different for each of the three measures. It is the presence and nature of these rate changes that is of potential value in discriminating among different taxa. The questions central to this investigation are, do these developmental patterns differ sufficiently even among closely related forms to be of value in differentiating *Strombus* s.s. from the Florida Pliocene/Pleistocene and, if so, have they changed over time in any consistent manner?

The plots portrayed in Text-figure 1 capture aspects of the growth process but tell little about how the alterations in process give rise the characteristics observed in the finished product – the shell morphology of an adult *S. alatus.* For this purpose it is useful to create a series of curves, hereinafter referred to as **second order curves**, that portray the ways in which these individual characteristics combine with one another over the course of shell development.

Text-figure 2 portrays three such curves. The first of these (A) plots the ratio of whorl diameter to whorl height as a function of whorl number and serves to communicate about the overall shape of the spire. A horizontal plot would indicate a straight-sided spire; the lower the ratio, the smaller the spire angle. A positive slope on this graph is indicative of a concave spire aspect; the greater the slope, the greater the concavity. A negative slope indicates a convex spire aspect. In the case of *S. alatus*, there are a series of early subtle changes ranging over the protoconch and early teleoconch, followed by a transition to a moderately concave spire over most of the teleoconch.

The second curve (B) plots the ratio of whorl diameter to shoulder height and indicates whether the spire whorls appear to be sloping or tabulate; the higher the ratio the more tabulate the whorls. A plot with a positive slope would indicate a spire with an increasingly tabulate aspect and *vice versa*. In the case of *S. alatus*, the trend is towards an increasingly tabulate whorl profile, although the change is moderate and there is a distinct short-term reversal during the early teleoconch whorls and another in the later stages of teleoconch development.

The third curve (C) plots the ratio of shoulder height to whorl height as a function of whorl and indicates whether or not the spire whorls appear to be turreted in outline. A ratio of 0.5 represents a whorl in which the shoulder is situated midway between the sutures, whereas a ratio of 1.0 indicates a whorl in which the shoulder is overrun by the suture of the succeeding whorl. *Strombus alatus* yields a turreted whorl profile throughout with only a slight tendency for the suture of later teleoconch whorls to approach the shoulder of the previous whorl.

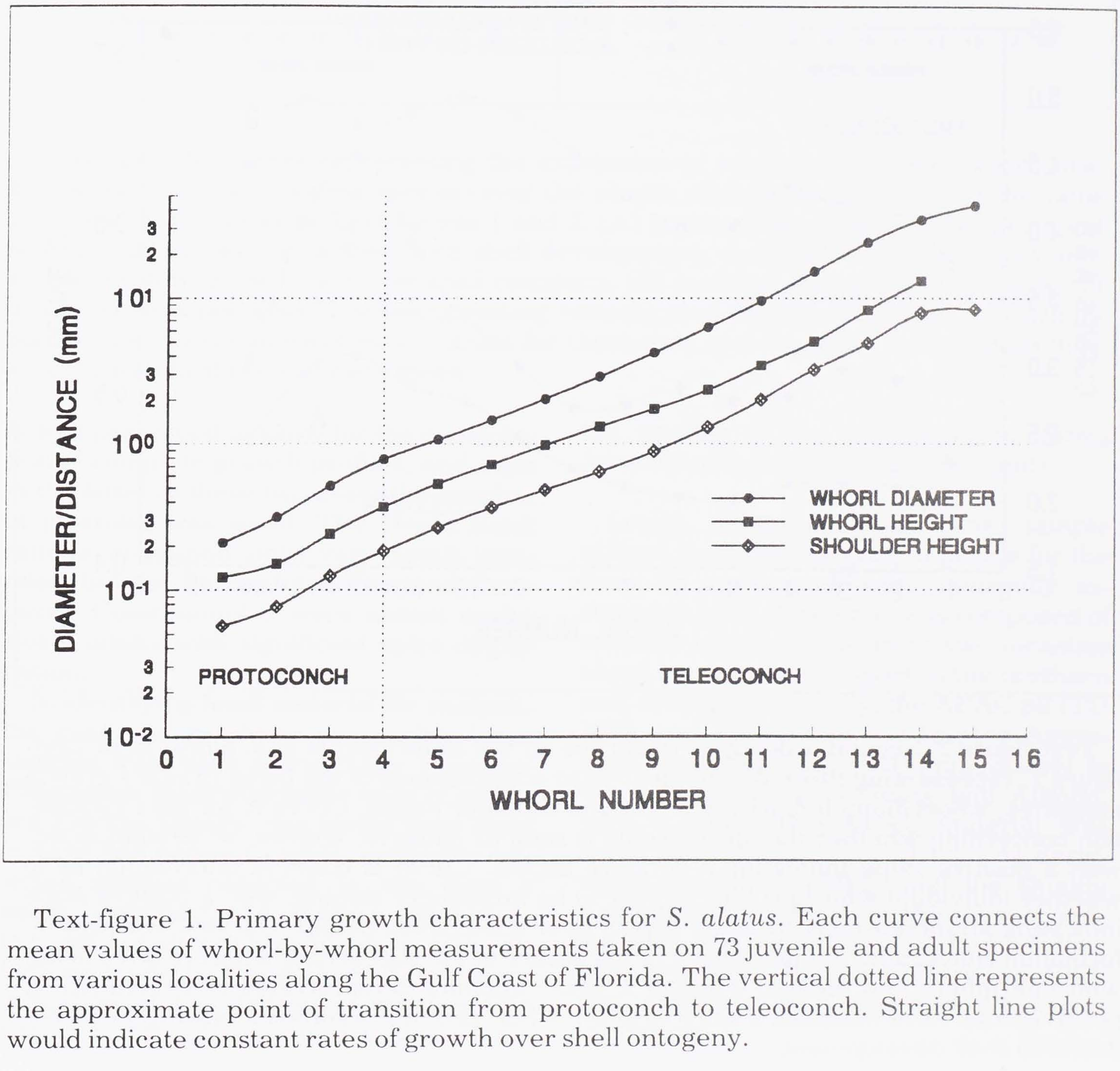
Axial Elements. The number of axial elements (ribs, knobs, or resting varices) present on each whorl was recorded and the largest element (excluding resting varices) measured. Also noted were the point at which axial sculpture was begun and the point, where applicable, at which it was terminated. The data collected from individual specimens were combined to establish a set of mean values for each sample which in turn were plotted. Text-figure 3 shows a pair of such plots for a sample of *S. alatus*, the first of which tracks the growth of axial element size as a function of whorl, and the second of which tracks the total number of axial elements present on each whorl. The second plot can be understood as portraying the relationship between the rate of growth of the axial elements themselves and the rate of growth in whorl circumference (or whorl diameter).

The curves portrayed in Text-figures 1, 2, and 3 represent a mean **growth profile** for the specimens in the sample of *S. alatus* analyzed and, to the extent that this sample can be seen as being representative of the species, as a mean growth profile for the taxon.

Spiral Elements. A number of aspects of spiral sculpture were tracked, but only the point at which spiral sculpture was initiated (or at least became visible above the attachment point of the succeeding whorl) appeared to be significant for this study. The protoconch/teleoconch boundary was defined as that point at which either axial or spiral sculpture was first noted (in those specimens sufficiently well-preserved to observe the onset of sculpture).

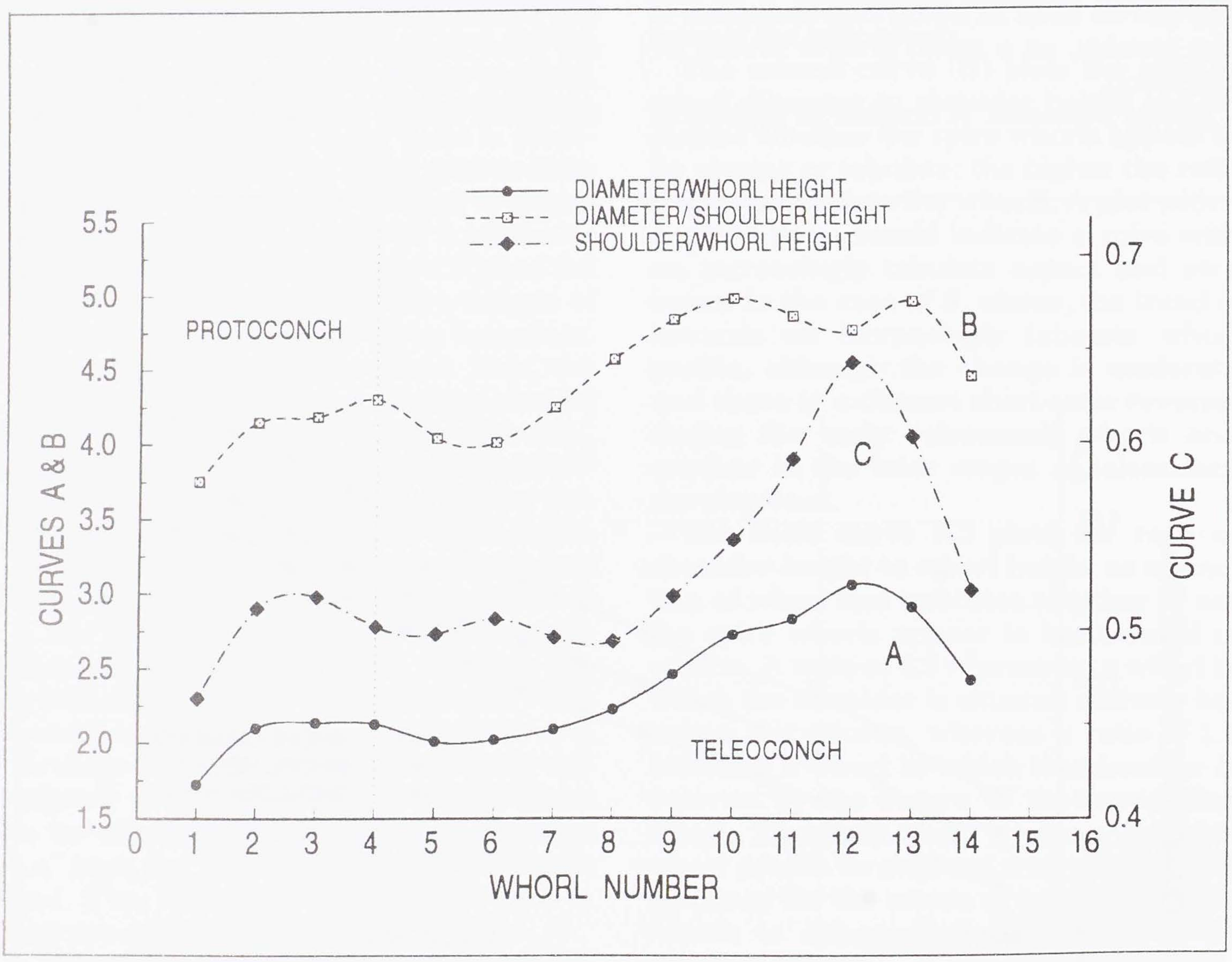
Material analyzed.

Recent *S. alatus* were obtained from five regions within the range of the species: (1) the Florida Keys; (2) southwestern Florida, from Naples to Sanibel Island; (3) St. Andrews Bay in the Panhandle of Florida; (4) Heald Bank, east southeast of Galves-

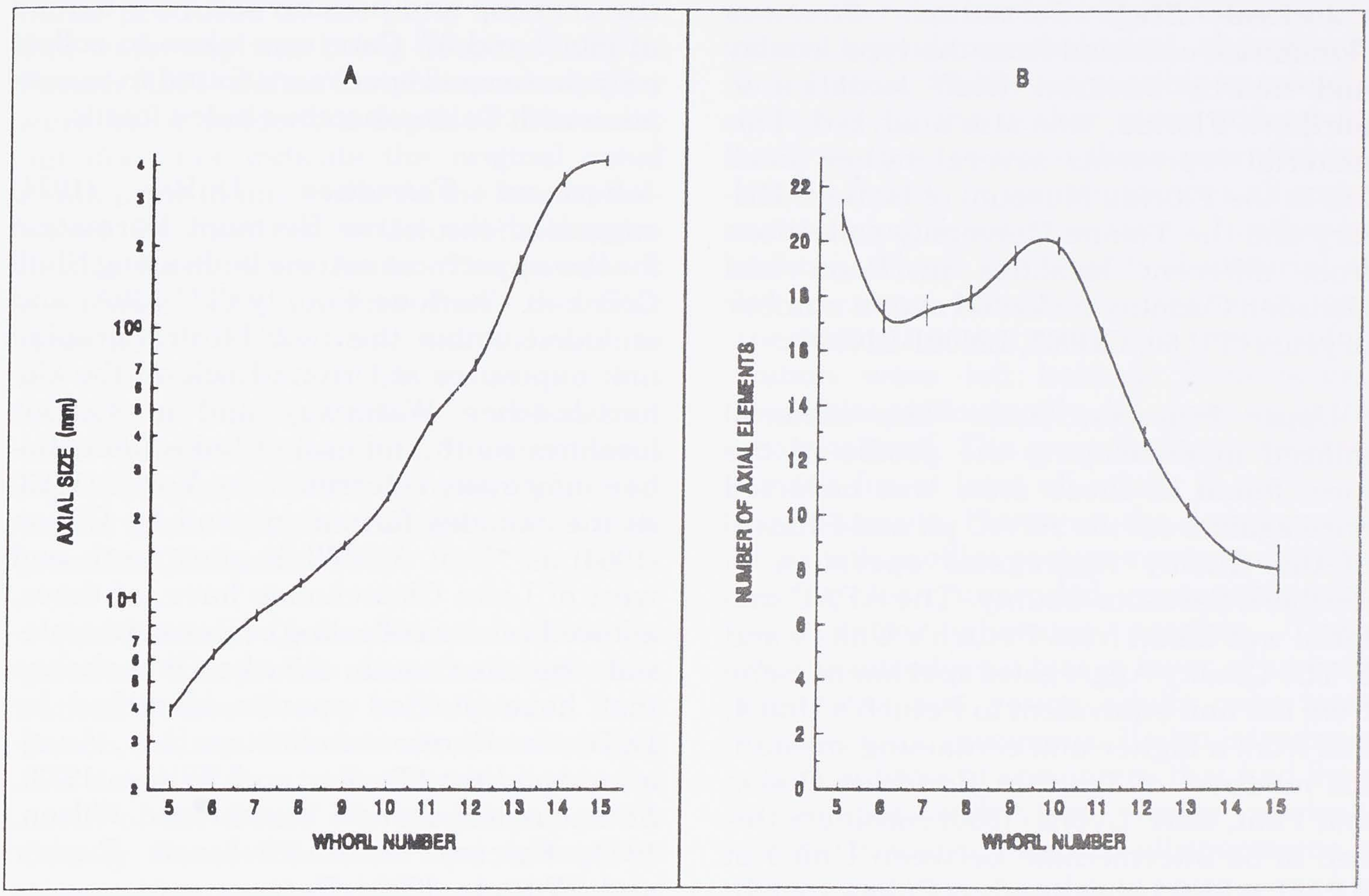


Text-figure 1. Primary growth characteristics for *S. alatus*. Each curve connects the mean values of whorl-by-whorl measurements taken on 73 juvenile and adult specimens from various localities along the Gulf Coast of Florida. The vertical dotted line represents the approximate point of transition from protoconch to teleoconch. Straight line plots would indicate constant rates of growth over shell ontogeny.

ton, Texas; and (5) the Yucatan coastline in the state of Campeche, Mexico. Only the material from St. Andrews Bay (RFG10)[5] and Heald Bank (RTG01) could be said to have come from a single biological population, each being collected from one locality at a single point in time in the 1960's. The southwestern Florida material contains a small sample (RFG01) collected at one time from the Naples area, together with a larger quantity of material (RFG02, RFG03) from Sanibel Island, designated as the type locality for *S. alatus* by Clench and Abbott (1941, p. 8), collected over the past decade. The Florida Keys material contains a number of small lots collected in different locations among the Keys and at different times (RFK01-RFK05). The material from Campeche was collected during three trips within a 21 month period from four different localities along a 135 kilometer stretch of coastline (RCM01-RCM04). The vast majority of these specimens, however, were collected near the middle of that stretch (RCM02) in January of 1993 and 1994. Only the material from southwestern Florida and the Florida Keys contained both adults and juveniles sufficient-



Text-figure 2. Second order growth curves for the same sample of *S. alatus* as in Text-figure 1, representing three distinct pair-wise combinations of the three primary growth measures; whorl diameter, whorl height and shoulder height. Curve A conveys information concerning whether the spire profile is seen as concave, convex, or straight sided, with a positive slope indicating a concave aspect. Curve B conveys information as to whether individual whorl profiles appear to be tabulate or sloping, with a positive slope indicating an increasingly tabulate aspect over shell development. Curve C conveys information concerning the placement of the suture of the succeeding whorl relative to the whorl periphery and, hence, whether a whorl appears to be turreted or embedded. A positive slope here indicates a spire wherein whorl profiles become increasingly embedded with shell development.



Text-figure 3. Curves representing the expression of axial shell ornamentation (ribs, knobs, spines and/or resting varices) over the course of shell development for the same sample of *S. alatus* as in Text-figures 1 and 2. [A] portrays the growth of axial element size (excluding resting varices) with shell development. A straight line plot would indicate a constant growth rate over shell ontogeny. [B] portrays changes in the number of axial elements per whorl (including resting varices) over shell development. In each instance, the curves connect mean values for these data and the short vertical lines indicate the standard error of each mean.

ly well preserved to allow for the construction of complete growth profiles, and even in the latter of these two cases the number of juveniles was small. The Heald Bank sample contained only very small juveniles, but the St. Andrews Bay and Campeche Coast samples were almost exclusively adults with significant spire degradation.

In identifying fossil material for analysis, the goal was to obtain reasonably large samples from each of the major Pliocene/ Pleistocene biostratigraphic units of southern Florida. Ideally, one would have liked to have had access to large, randomly collected samples collected *in situ* from a single biostratigraphic horizon. However, this was not always possible even with collections made by the author. Below is an indication of the degree of stratigraphic precision present in samples utilized for the profiles of the morphological forms found in various biostratigraphic units.

Lower Pinecrest Beds. The sample utilized to create the growth profile for the form in southern Florida generally assumed to be *S. floridanus* was composed of material taken *in situ* from two localities about two kilometers apart in the northern part of Sarasota County, the APAC pit (TU 1000) and Phase 6 of the Quality Aggregates operation (TU 1524) immediately to the east (see map in Geary and Allmon, 1990, p. 260). The APAC material was taken from the bottom of Unit 7 as designated by Petuch (1982), and the Quality Aggregates sample from the corresponding unit (*i.e.*, just above a bed of *Vermicularia recta* Olsson and Harbison, 1953, that underlies Unit 7 over extensive areas in both pits).

Jackson Bluff Formation. *Strombus floridanus*, collected from the type locality and nearby Jackson Bluff localities in northern Florida, was also analyzed. This material represents several rather small lots in the Florida Museum of Natural History and the Tulane University collections from different localities in Leon and Gadsden Counties collected over a number of years (TU 60, GD003, LN001-LN004).

Upper Pinecrest Beds. The material utilized in developing the profile of the form found in these units was collected once again from the APAC pit and Phase 6 of the Quality Aggregates operation in northern Sarasota County. The APAC material was taken from Petuch's Units 4 and 2. The Quality Aggregates specimens came from the unit equivalent to Petuch's Unit 4, and from a higher unit containing substantial numbers of *Trochita floridana* Olsson and Petit, 1964. Lyons (1990) considers this bed to be intermediate between Unit 1 at APAC, which he contends is Caloosahatchee in age, and Unit 2, the uppermost Pinecrest unit at APAC. Although all specimens appear to have been *in situ*, the areas collected had been disturbed by the removal of overburden. This resulted at both sites in the exposure of significant lateral expanses of the rather thin Unit 4, grading upwards into Unit 2 at APAC. The *Trochita* bed was exposed as a cut beside a road running along the east wall of the Phase 6 pit at Quality Aggregates, together with a sloping surface above the road cut.

Caloosahatchee Formation. Material utilized for this profile was collected from the De Soto Shell Pits in southern De Soto County (TU 1512). Over the years several pits have been dug by the same mining company over an area of about four square kilometers. The specimens utilized in this study came from pits 2 and 3, about 16 kilometers south of Arcadia. Although the pits were pumped during extraction of the marl, *Strombus* specimens were not plentiful enough to make an *in situ* collection from a single horizon. The specimens used for this analysis were collected both from spoil and *in situ* from various horizons within the two pits. Inspection of *in situ* material did suggest that a Caloosahatchee fauna was present everywhere except at the very top and possibly the very bottom of pits 2 and 3.[6] Care was taken to collect only those spoil specimens found in association with Caloosahatchee index fossils.

Bermont Formation. DuBar (1974) suggested the name Bermont Formation for the uppermost marine beds along Shell Creek in Charlotte County (TU 539A) and included within this new biostratigraphic unit exposures at Ortona Lock on the Caloosahatchee Waterway and at various localities south and east of Lake Okeechobee informally referred to by Vokes (1963) as the "Glades formation" and by Olsson (1964) as "Unit A." While sites north and west of Lake Okeechobee have, at times, allowed *in situ* collecting of Bermont material, the sites south of Lake Okeechobee that have yielded species identified by DuBar as Bermont indicators [*i.e.*, *Anadara aequalitus* (Tucker and Wilson, 1933), *Strombus mayacensis* Tucker and Wilson, 1933, *Fasciolaria okeechobensis* Tucker and Wilson, 1932, *Fusinus watermanni* (M. Smith, 1936), *Melongena bispinosa* (Philippi, 1844), and *Vasum floridanum* McGinty, 1940] have all been worked with drag lines in an environment where the water table is essentially at the surface. Unfortunately, these drag lines have also usually brought up material of probable Caloosahatchee age, as well as younger material belonging to the Ft. Thompson or Coffee Mill Hammock Formations.

Although it was possible to obtain a small sample of *Strombus* from the type locality for study, the specimens were deemed too few and too poorly preserved to provide an adequate profile. Aside from the Leisey Shell pits in Hillsborough County (HI001, HI013-HI015), whose Bermont age placement appears to this investigator to be questionable, this was the only *in situ* Bermont material available at the time of the study. Abundant spoil-collected material from several localities south and east of Lake Okeechobee (TU 201, TU 580, TU 978) was available, though it could not be determined with certainty that the samples analyzed from any of these sites were strictly Bermont in age. Chosen for purposes of creating a Bermont profile are specimens collected about 18 kilometers south of South Bay in Palm Beach County from spoil piles along the North New River

Canal produced in the early 1980's when that waterway was being deepened (F07). Petuch (1991) claims that these excavations were being made to a depth of 15 meters, but does not indicate the original canal depth prior to this work. At the locality collected, Bermont but no Caloosahatchee indicator fossils were found. This sample is compared with another from the Star Ranch pit (TU 1536) about one kilometer to the southwest where the excavation has brought up Caloosahatchee as well as Bermont indicators, most notably *Contraconus tryoni* (Heilprin, 1886), *Echinofulgur echinatum* (Dall, 1890), and *Siphocypraea problematica* (Heilprin, 1886).

Post-Bermont Units. Material utilized to generate this profile came from two excavations in Lee County and a third in Palm Beach County. The first site is a ditch dug to a depth of four to five meters just to the north of the South Florida Mining pit on County Road 765 about five kilometers (three miles) south of the Charlotte County/ Lee County border (F15). A second lot of material, taken from a temporary excavation at the site of a new hospital between Fort Myers and Fort Myers Beach (F11), was given to the author by an amateur collector. The depth of this excavation was not recorded. The third lot comes from spoil piles associated with irrigation canal work along the south side of Florida Route 80, northeast of Belle Glade (F14). Once again the depth of the excavation is unknown. At all three sites *Strombus* specimens were the dominant faunal element and there were no indicator fossils for Bermont or older horizons. While it is clear that the material in each case came from the uppermost horizon at that locality and that that horizon was probably younger than Bermont in age, it has not been possible to assign the horizons to any specific post-Bermont unit (either the Coffee Mill Hammock Formation or the supposedly underlying Fort Thompson Formation) with certainty. For a discussion of the possible relationship between these two later Pleistocene units see Lyons (1991, p.159-161).

Experience has taught the author that specimens of fairly common species in private collections have often been kept because of their "unusual" size or appearance, thereby frustrating attempts to uncover typical morphological characteristics. Hence, whenever possible specimens collected by the author were utilized for analysis so as to avoid these potential collecting biases. In some instances all specimens encountered were taken. In other instances, where the wealth of material allowed some selectivity, fragments and specimens too worn to yield useful information were left behind. Nonetheless, some bias undoubtedly did show up in the analysis itself. The gross features were recorded for at least all adults in each collected sample. However, the development of growth profiles requires specimens possessing clean, uneroded, reasonably complete spires wherever possible. These criteria introduce a bias in favor of juvenile specimens and young adults over more mature adult specimens. It also introduces a bias in favor of specimens that had lived in comparatively low energy environments. In many instances all specimens in the lot exhibited significant spire wear but unworn body whorls, indicating that they had probably lived in a fairly high energy environment (*e.g.*, on intertidal sand bars rather than on a back bay sand/grass flat). The specimens in other lots showed overall shell wear suggesting a beach assemblage or post-depositional weathering. In those cases, the specimens retaining the most complete information were utilized in creating the growth profiles.

IV. RESULTS AND DISCUSSION

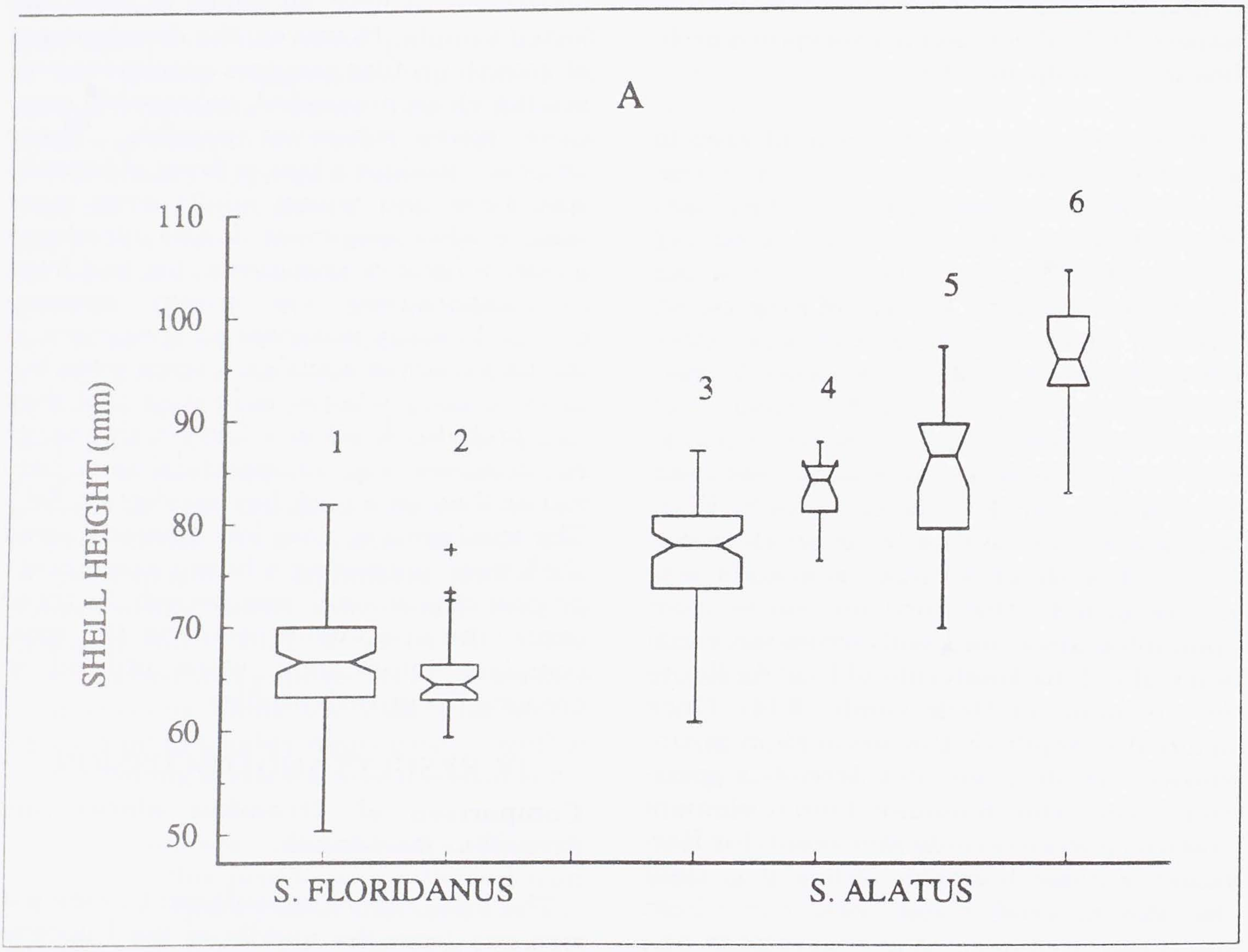
Comparison of *Strombus alatus* and *Strombus floridanus*.

The fossil record in southern Florida is a rich one from the middle of the Pliocene onward. In it, *Strombus floridanus* represents the earliest known apparent ancestral form of the Recent *Strombus alatus*. A comparison of these taxa, separated in time by some 3.0 to 3.5 million years, is a necessary first step in the analysis of morphologic change in Florida *Strombus* over time. When Mansfield described *Strombus floridanus* as a new subspecies of *Strombus pugilis* in 1930, he noted three characteristics that served to distinguish it from another assumed subspecies of *Strombus pugilis*, the Recent *Strombus pugilis alatus:*[7]

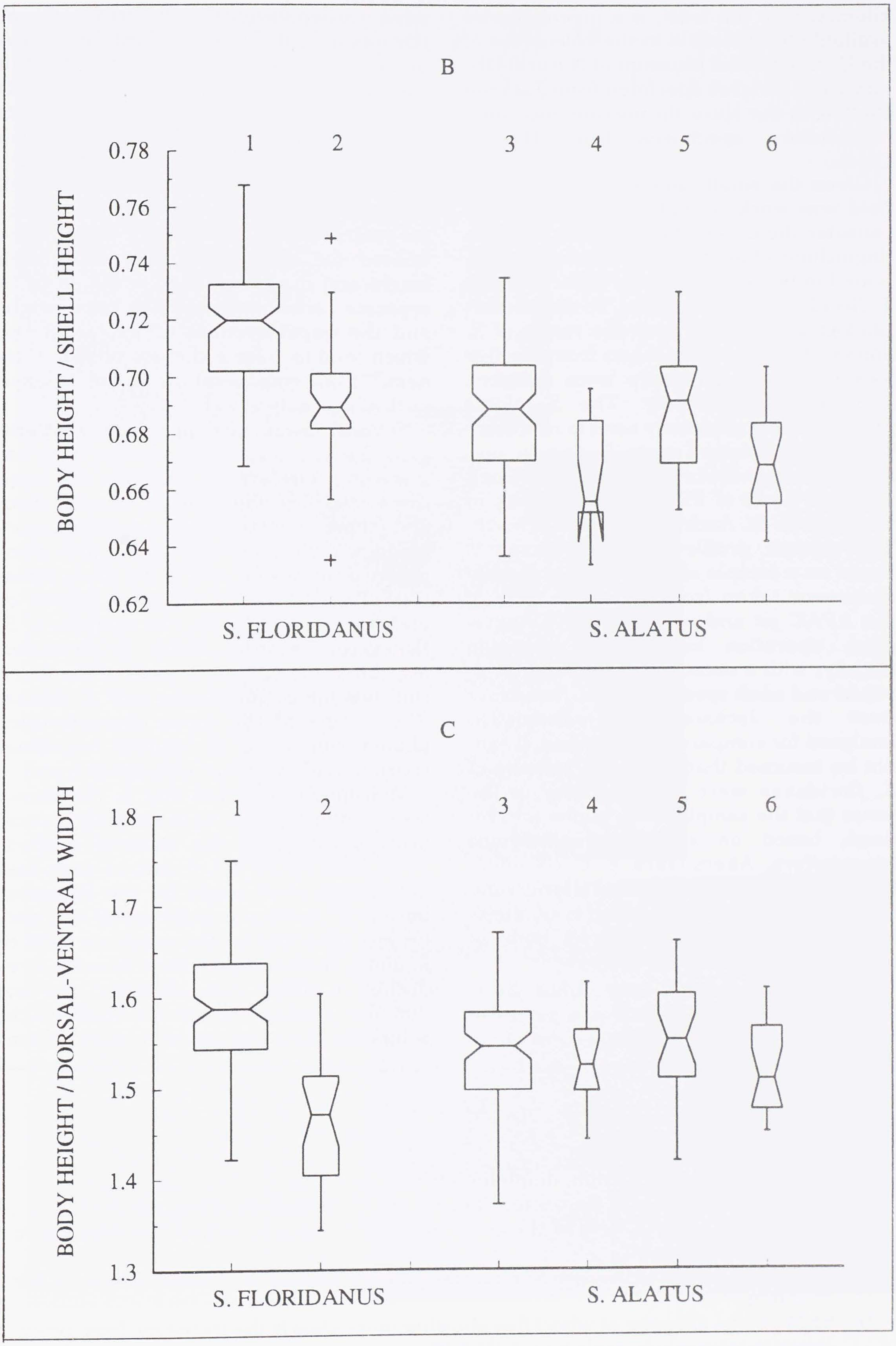
> "The new subspecies is closely related to *Strombus pugilis alatus* Gmelin but differs from the latter in having a shorter shell with a lower and less turrited [*sic*] spire, and fewer nodules or tubercles. In the new subspecies, the suture winds upon or above the spiral row of tubercles except on the earliest whorls and on the last half of the body whorl. On *S. pugilis alatus* the suture falls below the tuberculate shoulder." (Mansfield, 1930, p. 95)

In addition, he noted the presence of a distinct color pattern on the body whorl of *S. floridanus*, but did not compare this feature with the patterns found among specimens of *S. alatus*.

The material analyzed by Mansfield was from the Jackson Bluff Formation (Puri and Vernon, 1964 = the *Ecphora* and *Cancellaria* zones of the Choctawhatchee Formation of Matson and Clapp, 1909) of the Florida Panhandle. His description of *S. floridanus* was based on two specimens. The holotype, taken from Harvey Creek in Leon County, is a young, thin-lipped adult (see plate 2, figures 1a and 1b), and the paratype, from Jackson Bluff some ten



Text-figure 4. Notched box plots comparing [A] shell heights, [B] the fraction of total shell height subsumed by the body whorl, and [C] the ratio of height to dorsal-ventral width of the body whorl among samples of adult *S. floridanus* and *S. alatus*. For these, and all other box plots included in this study, the boxes inclose data for the middle 50% of the specimens in the sample, with the horizontal line indicating the median value for that sample. The width of each box is proportional to the square root of the sample size and the notches approximate the 95% confidence interval for the sample median. Vertical lines usually indicate the range of the data within the sample. However, individuals lying more than two times the height of the box beyond either end of the box are considered to be outliers, their positions being marked by a +. The sample locations and sizes are as follows: [1] lower Pinecrest beds (N = 107); [2] Jackson Bluff Formation (N = 34); [3] Campeche Coast (N = 87); [4] Florida Keys (N = 13); [5] Southwest Florida (N = 26); and [6] St. Andrews Bay (N = 19).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0.64
0.62
BODY HEIGHT / SHELL HEIGHT
S. FLORIDANUS
S. ALATUS
C
1
2
3
4
5
6
1.8
1.7
1.6
1.5
1.4
1.3
BODY HEIGHT / DORSAL-VENTRAL WIDTH
S. FLORIDANUS
S. ALATUS

kilometers to the west, is a juvenile. Also available to Mansfield in the collections of the U. S. National Museum of Natural History were an adult specimen from Jackson Bluff with the spire tip missing and some fragmentary specimens from Harvey Creek.

Given the small sample size that Mansfield was working with, it is legitimate to consider the utility of each of the four distinguishing characteristics explicitly mentioned in his description for differentiating *S. floridanus* and *S. alatus*. To assess morphological variation over the range of *S. alatus*, the specimens taken from the five localities discussed above were analyzed and plotted separately. The *S. alatus* growth profile ultimately used to represent the species is based upon 73 juvenile and adult specimens taken from localities along the west coast of Florida from Naples in the south to St. Andrews Bay in the north. The growth profile of *S. floridanus* is based on a sample of 75 juvenile and adult specimens taken from the lower units of the APAC pit and nearby Quality Aggregates operation in northern Sarasota County, with a secondary sample of 69 juvenile and adult specimens of *S. floridanus* from the Jackson Bluff Formation analyzed for comparative purposes. It cannot be assumed that these two samples of *S. floridanus* were contemporary in the sense that the samples of *S. alatus* are. Indeed, based on studies of planktonic foraminifera, Akers (1979, p. 6) considers the *Strombus*-containing *Cancellaria* zone of the Jackson Bluff Formation to be slightly younger than the Pinecrest beds of southern Florida.[8])

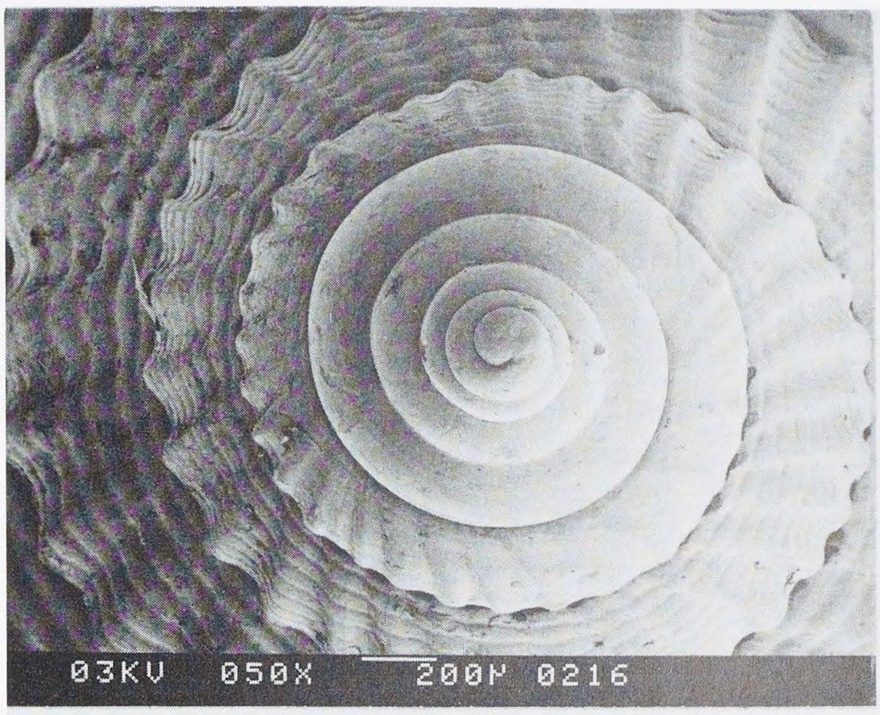
Features Associated with Adult Shell Shape. Text-figure 4 provides a series of notched box plots summarizing some of the adult morphological features of *S. floridanus* and *S. alatus* Text-figure 4-A provides a comparative picture of adult shell heights. Text-figure 4-B represents one way to compare relative spire heights among taxa, portraying the fraction of total shell height taken up by the body whorl. Text-figure 4-C compares the ratio of shell height to shell width. The height and dorsal-ventral width of the body whorl were utilized for this ratio rather than shell height and maximum shell width so as to separate variations in relative spire height and the expansiveness of the adult lip, which tend to color estimates of shell "fatness," from consideration of the relative girth of the body whorl.

Several points are apparent in these plots. First, at least for the larger samples, there is considerable variation in these three statistics within each sample. Second, there is statistically significant morphological variation among the four samples of *S. alatus* for two of the three statistics.[9] Third, there is a similar degree of variation present in the two samples of *S. floridanus*. Fourth, there is extensive overlap in the ranges of each of the three statistics for *S. floridanus* and *S. alatus*. Thus, none of the three characteristics plotted can serve to identify individual specimens of *Strombus* with either taxon.

Mansfield's assertion that *S. floridanus* is shorter than *S. alatus* is certainly true on average for all of the material studied. From Text-figure 4-A it can be seen that the median shell height for the Pinecrest form of *S. floridanus* is almost 20 millimeters less than that for the nominate form of *S. alatus* from southwestern Florida, a reduction of almost 25%. However, the fact that the median values for shell height among the four samples of *S. alatus* them-

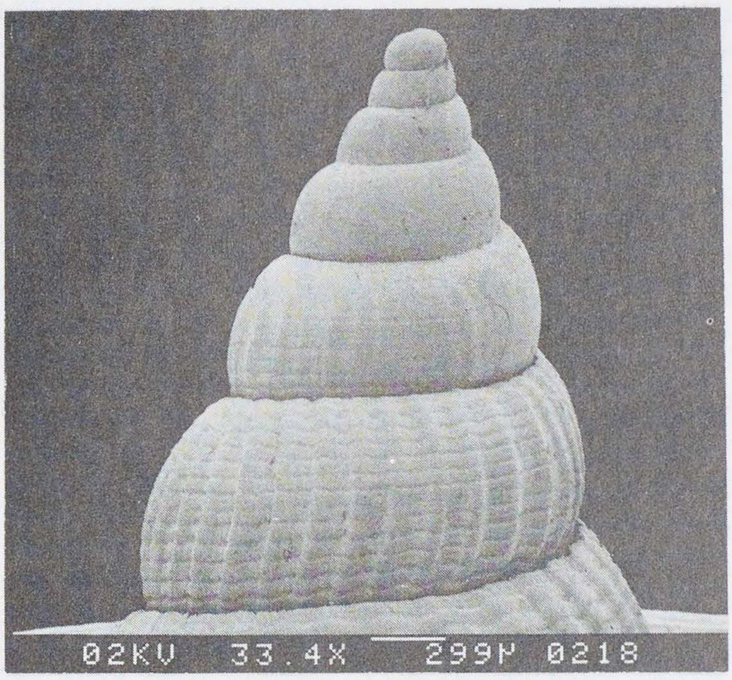
PLATE 1

Figure
1. *Strombus floridanus* Mansfield
   USNM 483764; height 12.1 mm, diameter 4.9 mm.
   Locality: Unit 7, APAC Pit, Sarasota, Florida (= TU 1000); lower Pinecrest beds.
   1a. SEM image. Apical view of the protoconch and initial whorls of the teleoconch; scale bar = .2 mm.
   1b. SEM . Side view of the protoconch and initial whorls of the teleoconch; scale bar = .3 mm.
   1c. SEM image. Closeup of whorl five showing more clearly the transition from protoconch to teleoconch; scale bar = .11 mm.



1a

1b



1c

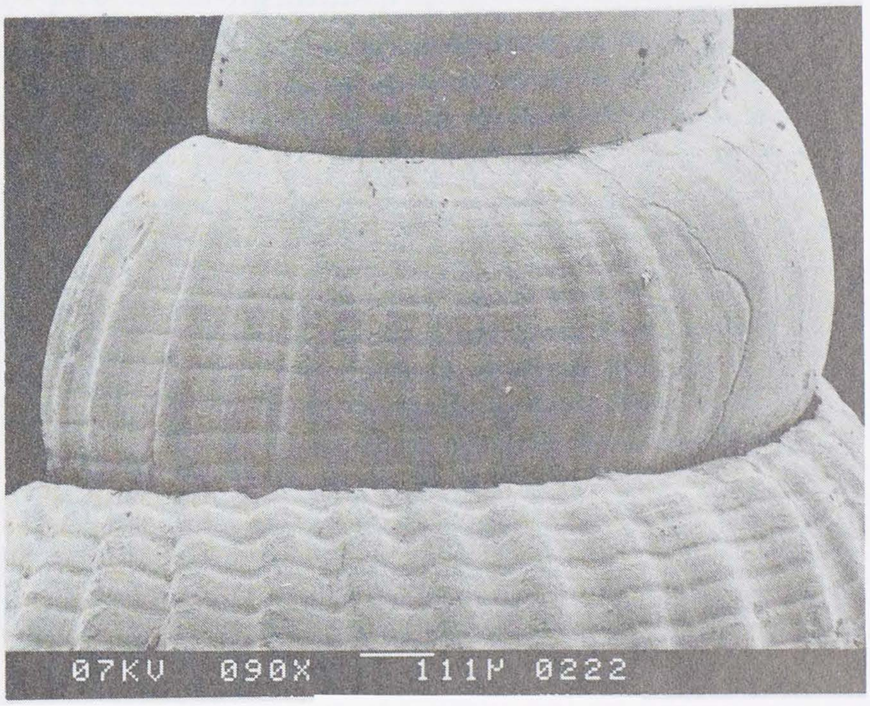


PLATE 1

selves differ by almost 20 millimeters should cause one to use extreme caution in proposing adult size as a taxonomically significant morphological characteristic among *Strombus*.

Text-figure 4-B does not substantiate the claim made by Mansfield that the Jackson Bluff form of *S. floridanus* has a proportionately shorter spire than *S. alatus*. Interestingly, the Pinecrest form of *S. floridanus*, unknown to Mansfield at the time, does have a slightly shorter (3%) spire than any known form of *S. alatus*. However, what is perceived as differences in relative spire height among *Strombus* specimens is usually rather a function of overall spire shape (*i.e.*, whether concave, convex or straight sided in aspect) and the comparative height and width dimensions of the shell. The spire of a "fat" specimen will appear to be shorter than that of a "thin" specimen of similar longitudinal dimensions because the spire angle will be greater. Also a markedly concave spire will appear to be shorter than a straight-sided or convex spire of similar longitudinal dimensions because it is inherently less substantial to the eye. It is these features that probably led Mansfield to make his claim about the relative spire heights of the two taxa. This can be seen clearly from Text-figure 4-C. The Jackson Bluff form of *S. floridanus* is markedly "fatter" than any form of *S. alatus* analyzed. The Pinecrest form of *S. floridanus*, on the other hand, is less rotund than its *S. alatus* counterparts. All of this suggests that relative spire height is a problematic and unreliable morphological characteristic for differentiating these taxa.

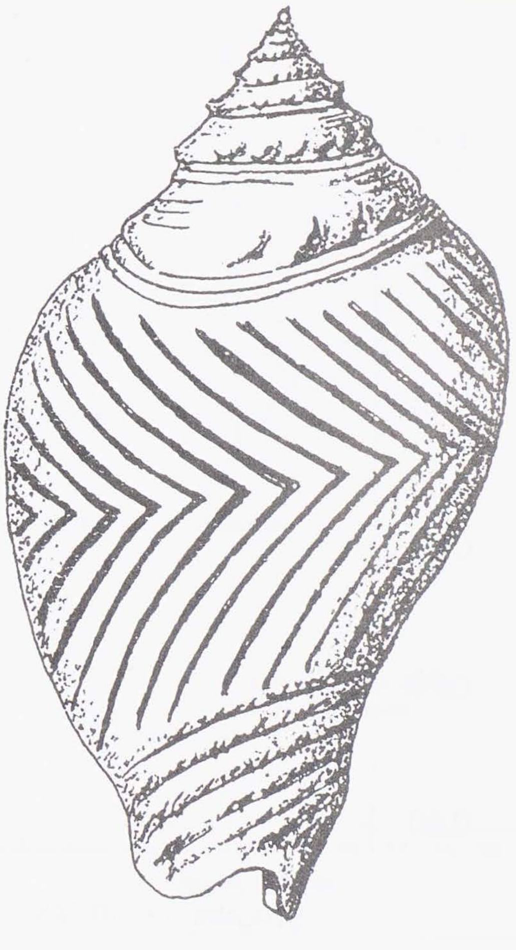
Axial and Spiral Ornamentation of Adult Specimens. Mansfield also refers to *S. floridanus* as having "fewer nodules or tubercles" than *S. alatus*. However, in the discussion of the taxon itself, it is clear that he is referring to the fact that, unlike Recent *S. alatus*, axial ornamentation in the form of shoulder knobs or blunt spines is absent from the body whorl. Indeed, of literally thousands of specimens of *S. floridanus* observed by the author, none have been found to have peripheral axial ornamentation on the body whorl.[10] As for *S. alatus*, Clench and Abbott (1941) and others have assumed that the smooth-shouldered specimen figured by Martini (1777, pl. 92, fig. 894) and utilized by Gmelin in naming the taxon represents a spineless Recent specimen from Floridian waters. If so, it is certainly an atypical specimen that was figured. Goodrich (1944) published a paper on variation within *S. alatus* based upon a sample of 1100 adult specimens collected on Sanibel Island over a period of two decades in the early twentieth century. Therein he noted that 923 specimens, or some 84% of the sample, had fully developed spinose or nodulous axial ornamentation on the body whorl. In the remaining 177 specimens, axial ornamentation was either mal-formed, reduced in extent to only a portion of the body whorl, or entirely absent from that final whorl. Unfortunately, separate statistics were not presented for these latter three categories. The author's own experience observing *S. alatus* on Sanibel Island during the past decade confirms the rarity of spineless specimens at the type locality. Also, no spineless Recent individuals have been found among several hundred *S. alatus* specimens studied from Campeche Coast of the Yucatan Peninsula. Hence, while there may be populations of *S. alatus* wherein the percentage of spineless individuals is higher, the evidence at hand suggests that this is an uncommon occurrence in the taxon.

The spiral sculpture on the body whorl, although described to some extent for the new taxon by Mansfield, was not referred to by him in differentiating that taxon from *S. alatus*. In both taxa the external spiral sculpture may be more or less strongly expressed in individual specimens and, when present, the form of the sculpture shows the same range of expression. The same can be said for the submarginate costae and columellar denticles found inside the aperture of adult specimens. It is with respect to the series of longer lirations or rugosities on the parietal wall within the aperture that *S. alatus* and *S. floridanus* differ most noticeably. Their presence is extremely rare in *S. alatus* but they appear in up to 20% of the specimens in samples of *S. floridanus*. Mansfield did not make use of this characteristic.

Adult Color Patterns. Mansfield noted on the body whorl of his adult specimens the presence of "angled colored bands" having their apices pointed backwards (*i.e.*, away from the lip) and aligned along the midpoint of the body whorl. The pattern created by these bands most often consists of a parallel series of dark chevrons one or two millimeters across and separated by slightly wider interstices (see Text-figure 5). Although nothing quite like it exists among *Strombus* sensu stricto today, this chevron pattern seems to have been a fairly common characteristic among the Caribbean *Strombus* of the Pliocene and Pleistocene. It seems to be almost ubiquitous among adult *Strombus pugiloides* Guppy, 1873, in the Bowden Formation of Jamaica. It is also common among adults of an unnamed subspecies or form of *S. pugiloides* found in the Rio Banano Formation of Costa Rica, and has been seen under UV illumination in at least one specimen of a form of *Strombus gatunensis* Toula, 1909. The persistence of color pattern in fossils appears to be strongly influenced by the conditions of preservation, making it difficult to determine how common patterning was in a taxon such as *S. floridanus*. Most Pinecrest *Strombus* specimens in collections do not show any pattern even under UV illumination. However, the author has twice come upon recently uncovered pockets of *S. floridanus* in phase 6 of the Quality Aggregates operation wherein virtually every adult specimen retained some remnant of the chevron pattern, suggesting that it was a common if not universal feature.[11]

Goodrich (1944) recorded 68 specimens from the lot of 1100 *S. alatus* analyzed as having an irregular "mottling" over nearly the entire surface of the body whorl and another 83 as exhibiting a more regular zigzag pattern (see plate 4, figure 2). While the presence of "regular" patterning in about 8% of a sample may seem to be of little diagnostic value, when compared with the other two extant species of *Strombus* sensu stricto, it is significant. Patterning has never been recorded in *S. gracilior* and has been witnessed by this investigator only once in *S. pugilis*, as a vestigial patch of pattern on the ventral shoulder of the body whorl just in front of the aperture.

In summary, normal approaches to the study of shell morphology involving adult size, shape, sculptural ornamentation, and color patterning, provide no diagnostic features that can be used unequivocally to separate *S. floridanus* from *S. alatus*. When large samples of both taxa are analyzed one is left only with tendencies, some of which yield statistically significant differences. Adult *S. alatus* tend to be larger in size, to have axial sculpture that persists onto the body whorl in the form of shoulder knobs or spines, to be less likely to exhibit parietal rugosities, and to be less likely to have distinct axial color markings on the body whorl. Other features such as relative spire height and shell "fatness" seem to provide no insight at all. Hence, although the tendencies suggest very strongly a phylogenetic relationship between the two forms, it still might not be possible to determine the identity of individual specimens based upon such information. Can an ontogenetic analysis provide additional insights into the differences between these two taxa?

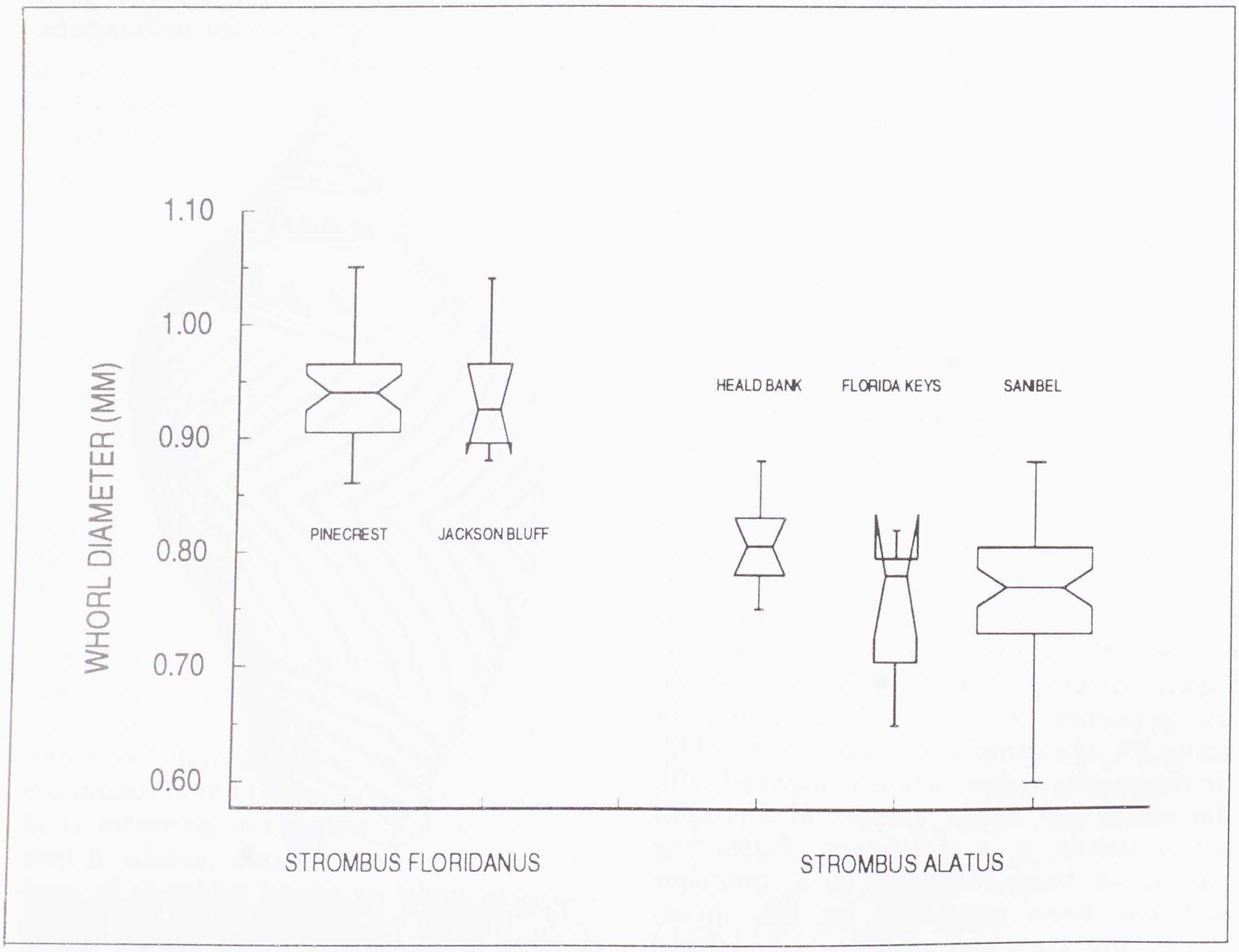


Text-figure 5. Depiction of the distinctive chevron color pattern often visible under long wave ultra-violet illumination (3660 Å). Although the specimen portrayed represents Taxon C, this pattern is reasonably common on specimens of *S. floridanus* and Taxon B as well.

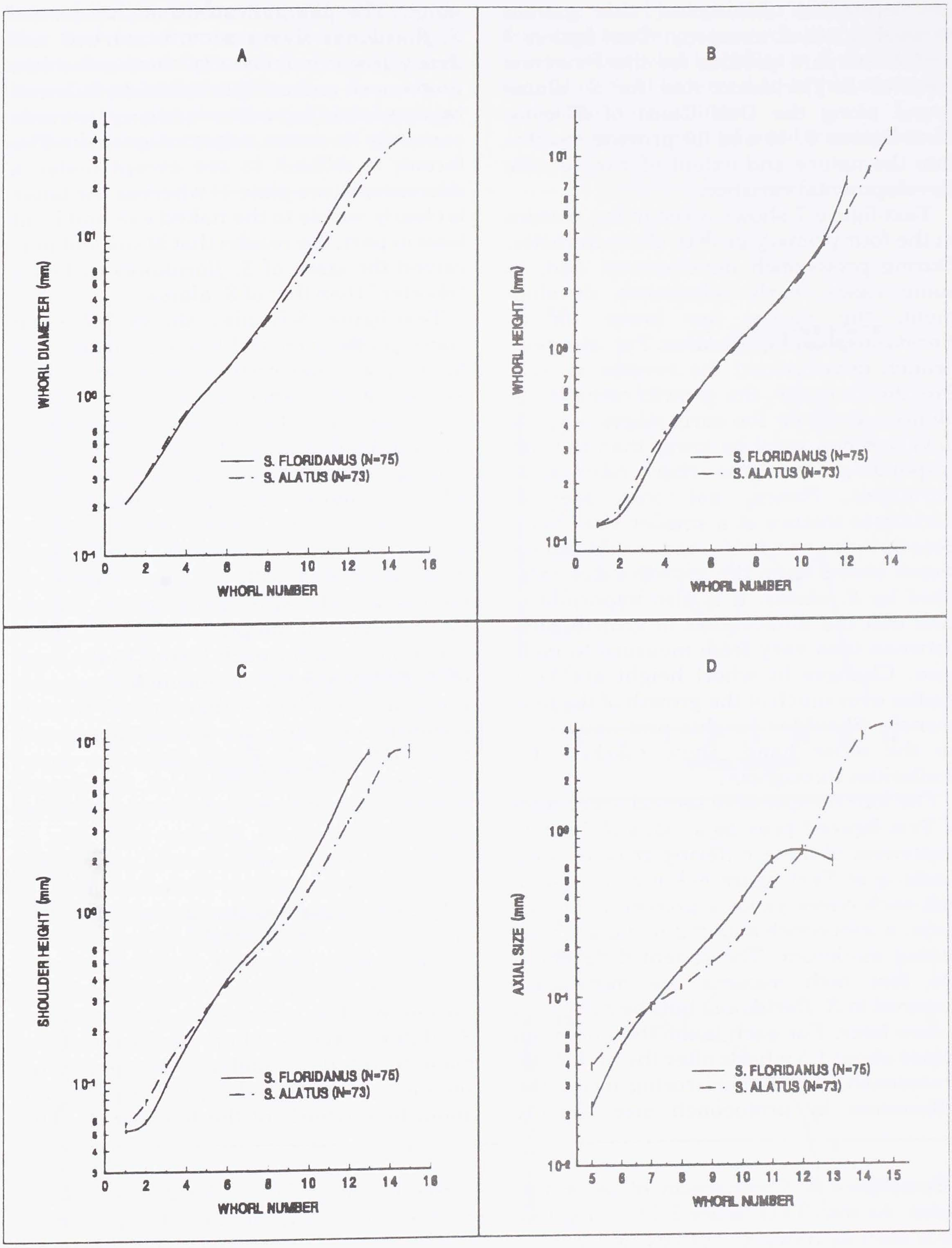
Ontogenetic Analysis. One important aspect of shell development clearly related to the ontogeny of the animal within is the transformation from protoconch to teleoconch, delineated by that point in the shell development of *Strombus* at which axial and/or spiral ornamentation is initiated. Unlike certain other gastropod families, this point of transition is not marked by an easily discernable varix. Nor is the initial ornamentation strongly expressed (see plate 1). The initial axials are usually microscopically fine and may continue that way for as much as a quarter of a whorl. Spiral sculpture tends to be most strongly expressed initially at and below the periphery of the whorl where it will be hidden by subsequent whorls.

The results of a careful microscopic analysis of well-preserved juvenile specimens are presented in Text-figure 6. While some of the sample sizes are too small to permit an assessment of intraspecific variability, it is clear that the two taxa themselves differ from one another. There is a decline in the median terminal diameter of the protoconch from 90-95 mm in *S. floridanus* to 75-80 mm in *S. alatus*, with almost no overlap in the ranges of those diameters for the two taxa. This reduction is driven primarily by a reduction in the number of whorls in the protoconch from a mean of 4.6 in the lower Pinecrest form of *S. floridanus* to 3.9 in the nominate form of *S. alatus*. However, while protoconch size does represent a good diagnostic feature for differentiating these two taxa, it tends to be a feature of limited usefulness since the early spire whorls are seldom retained in adult specimens.

Growth profiles for these two taxa (Text-figures 7 to 11) suggest a suite of other



Text-figure 6. Notched box plot comparing whorl diameters at the end of the protoconch among samples of *S. floridanus* and *S. alatus*. The sample sizes are as follows: lower Pinecrest beds (N = 36); Jackson Bluff Formation (N = 8); Heald Bank (N = 10); Florida Keys (N = 8); and Sanibel Island (N = 51).



Text-figure 7. Comparison of the primary growth characteristics for *S. floridanus* and *S. alatus*. [A] compares the growth in whorl diameter, [B] the growth in whorl height, [C] the growth in shoulder height, and [D] the growth in axial element size. The curves connect the mean values of measures made at the end of each whorl for every specimen in the sample, with the short vertical lines indicating the standard errors of those mean values.

developmental differences that persist throughout shell ontogeny. Text-figures 7 and 8 compare profiles for the Pinecrest form of *S. floridanus* and for *S. alatus* found along the Gulf Coast of Florida. Text-figures 9, 10 and 11 provide insights into the nature and extent of intraspecific developmental variation.

Text-figure 7 shows a recurring pattern in the four primary growth characteristics. During protoconch development and, in some cases, early teleoconch development, the curves are lower for *S. floridanus* than for *S. alatus*. For later teleoconch development the reverse is true. For this to occur, the growth **rates** for *S. alatus*, except for the early stages of larval development, must be lower than the corresponding (*i.e.*, same whorl) rates for *S. floridanus*. Hence, not only does *S. floridanus* mature at a smaller size, but it does so in fewer whorls than would be predicted based upon the growth rates exhibited by *S. alatus*. It is also important to note that the differentials in growth rates between taxa vary from measure to measure. Changes in whorl height are very similar over much of the growth of the teleoconch. Shoulder heights and axial size, on the other hand, show marked dissimilarities throughout.

The four comparative second order plots of Text-figure 8 provide an idea of the consequences of these differing growth rates. Looking at Text-figure 8-A it can be seen that each curve yields a protoconch maximum, a teleoconch maximum and an intervening minimum. The salient differences are that both maxima are more pronounced in *S. floridanus* but the minimum occurs later. For each taxon the minimum comes about 1.5 whorls after the end of the protoconch, the shift mirroring nicely the differences in protoconch size already noted. The plot indicates that the spire of *S. floridanus* shows a more marked tendency towards convexity during the late protoconch and early teleoconch, followed by a relatively greater tendency towards concavity in later stages of growth. The former is difficult to see except under a microscope (see plate 1) whereas the latter is clearly visible to the naked eye and is, at least in part, the reason that Mansfield perceived the spire of *S. floridanus* as being "shorter" than that of *S. alatus*.

Text-figure 8-B also shows for each curve protoconch and teleoconch maxima flanking an intermediate minimum that is located at the same points in overall development as in the previous plot, thereby suggesting that it is the decreasing and subsequent increasing growth rates in whorl diameter that give rise to this phenomenon. The maxima are in this instance curiously bimodal, particularly those associated with the development of the teleoconch. Also significant are the relative heights of the protoconch and teleoconch maxima for each taxon. In the case of *S. floridanus* the protoconch maximum is considerably higher than that for the teleoconch, providing an overall downward trend to the curve. For *S. alatus* the opposite is true. This results, for *S. floridanus*, in a spire wherein the whorls appear to be progressively more sloping and, for *S. alatus*, in a spire wherein the whorls appear to be progressively more tabulate.

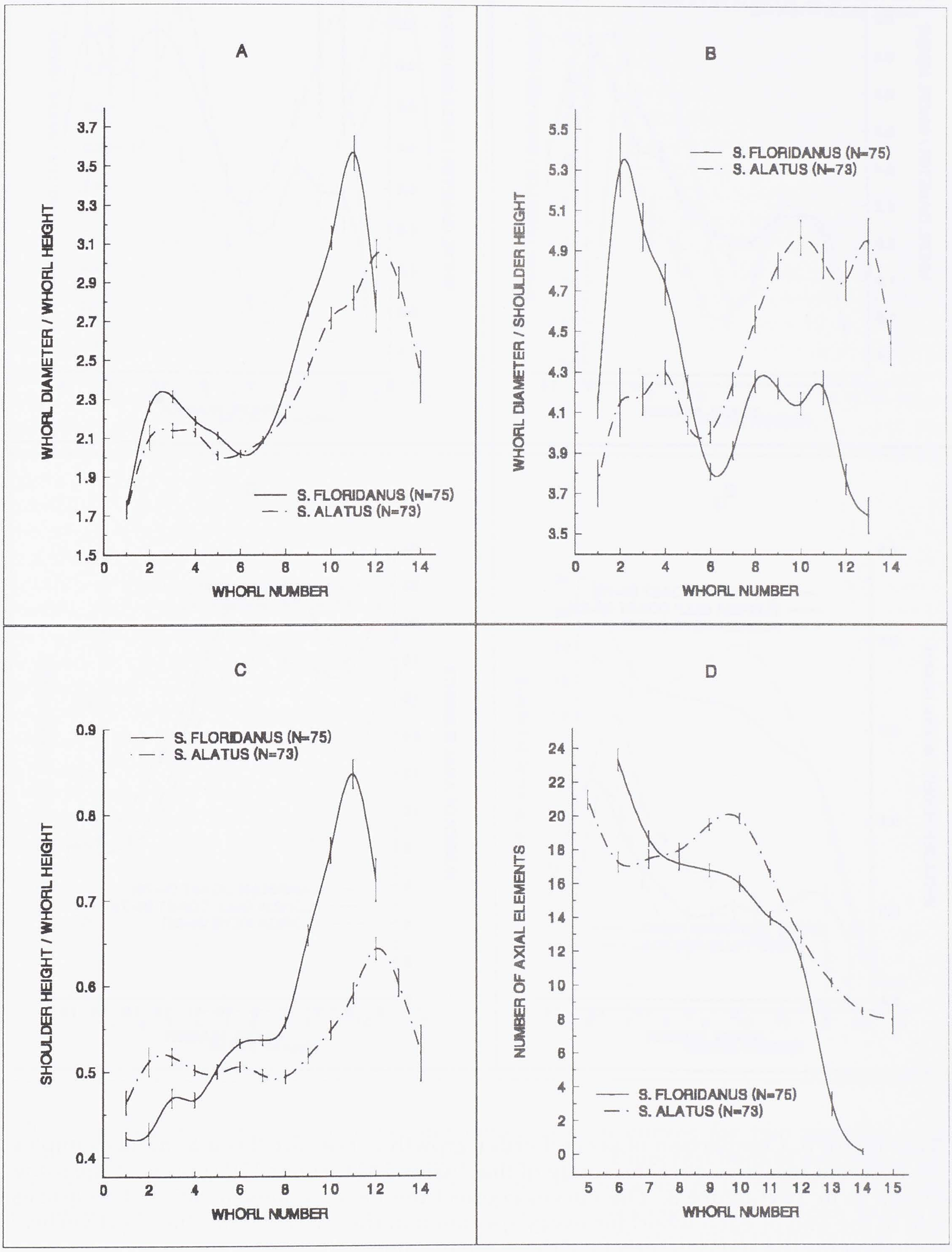
In Text-figure 8-C the important differences are in the average slope of each curve over the first eight whorls and in the extent and rapidity of the upward turn of the curves after whorl eight. The curve for *S. alatus* suggests whorl profiles that remain turreted throughout ontogeny, the situation ameliorated only slightly for about four whorls of the teleoconch. The

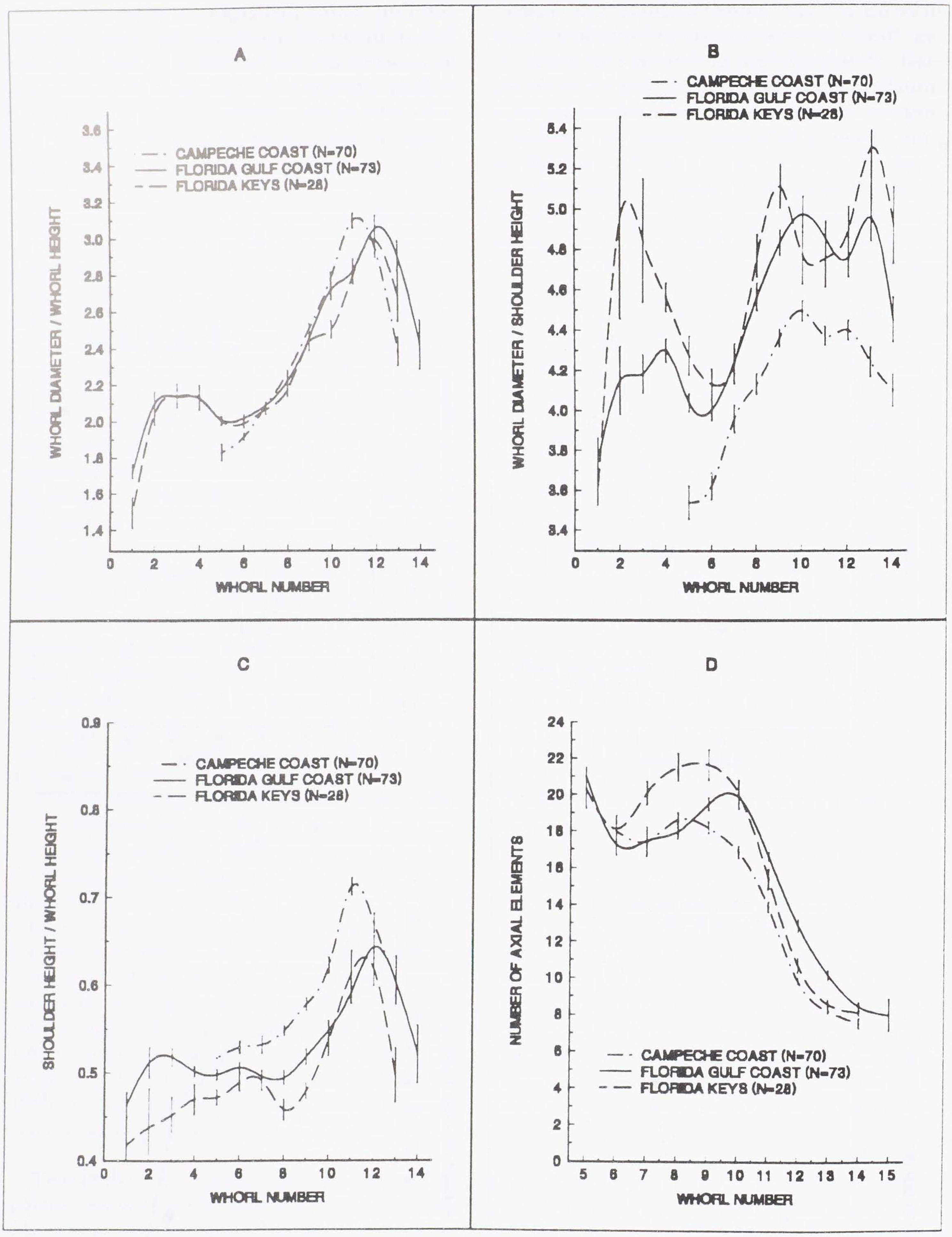
Text-figure 8. Comparison of second order growth curves for *S. floridanus* and *S. alatus*. As with Text-figure 2, [A] conveys information concerning whether the spire profile is seen as concave, convex, or straight sided, [B] conveys information as to whether individual whorl profiles appear to be tabulate or sloping, [C] conveys information concerning the placement of the suture of the succeeding whorl relative to the whorl periphery and, hence, whether a whorl appears to be turreted or embedded, and [D] portrays changes in the number of axial elements per whorl (including resting varices) over shell development. The curves connect the mean values of ratios of measures made at the end of each whorl for every specimen in the sample, with the short vertical lines indicating the standard errors of those mean values.

>

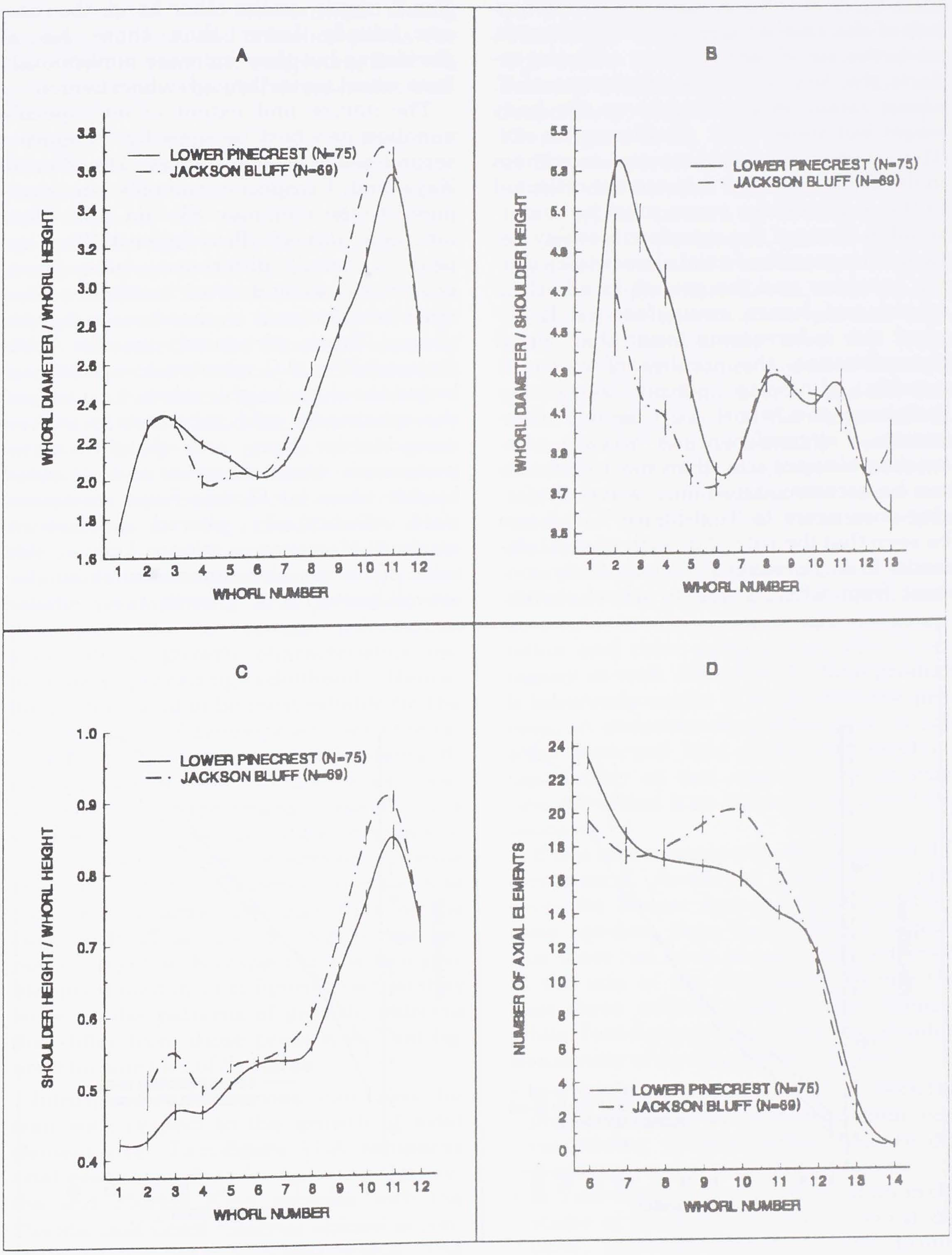
curve for *S. floridanus* suggests whorl profiles that become progressively less turreted, slowly at first and then rapidly and almost completely, culminating in a whorl wherein the peripheral axial elements are almost overrun by the suture of the succeeding whorl just prior to adulthood. It is this dual tendency towards more sloping, less turreted whorl profiles in *S. floridanus* that Mansfield referred to in his comparison of the spire outlines.

The earlier onset of axial expression in





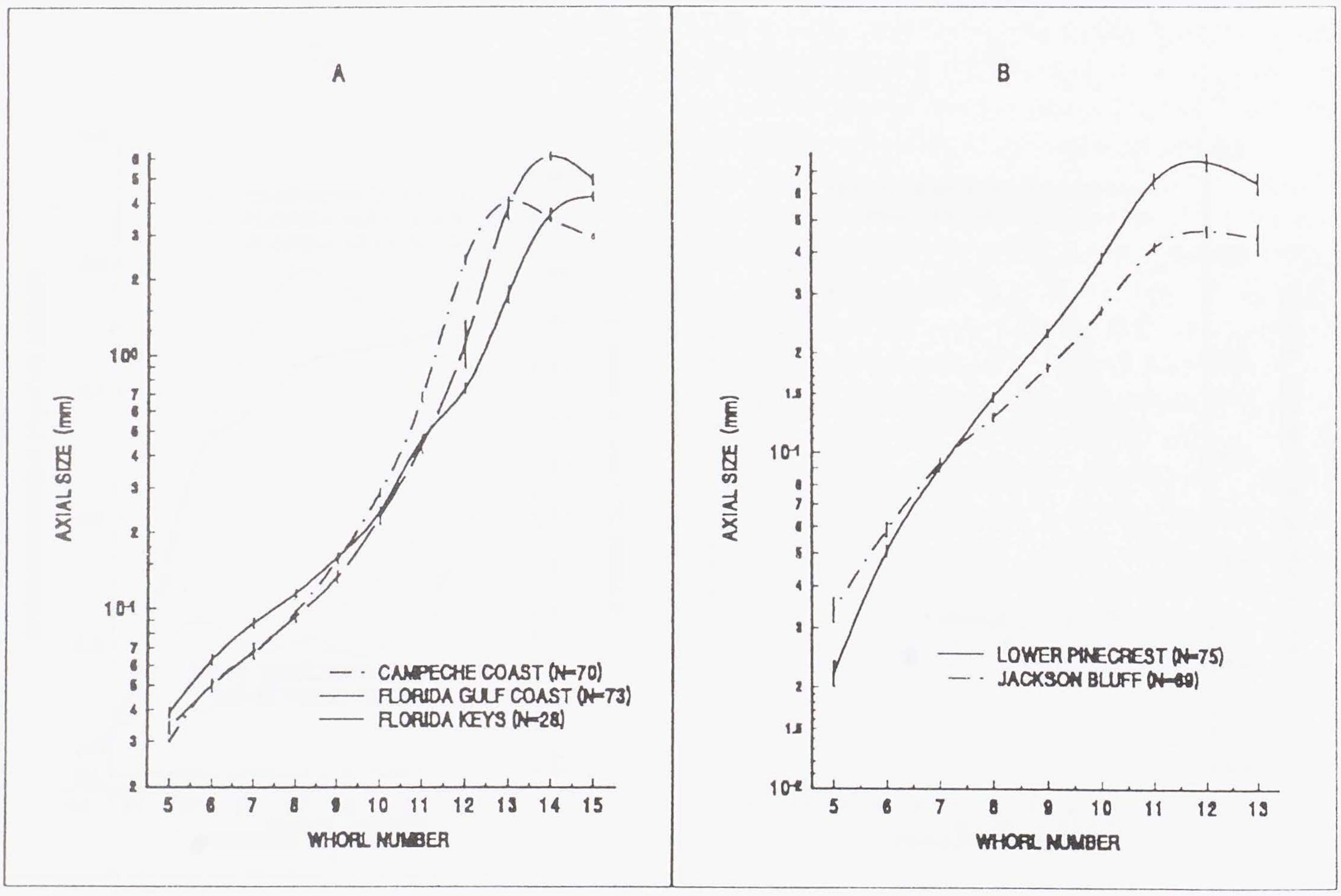
Text-figure 9. Comparison of second order growth curves for three *S. alatus* samples from different localities over the range of that taxon. [A] through [D] represent the same features as in Text-figure 8. The curves connect the mean values of ratios of measures made at the end of each whorl for every specimen in the sample, with the short vertical lines indicating the standard errors of those mean values.



Text-figure 10. Comparison of second order growth curves for two samples of *S. floridanus* from different Pliocene formations, the lower Pinecrest beds of southern Florida and the Jackson Bluff Formation of the Florida Panhandle. [A] through [D] represent the same features as in Text-figures 8 and 9. The curves connect the mean values of ratios of measures made at the end of each whorl for every specimen in the sample, with the short vertical lines indicating the standard errors of those mean values.

Text-figure 8-D for *S. alatus* is a direct result of the smaller size of the protoconch, while the significantly higher endpoint reflects the fact that most specimens of *S. alatus* retain axial elements on the body whorl but those of *S. floridanus* do not. The intervening minimum and maximum in the *S. alatus* curve that are not reflected in the *S. floridanus* curve must be understood in terms of the complex interplay between the growth of axial element size during ontogeny and the growth in whorl diameter and, hence, circumference. If element size is increasing faster than whorl circumference, the number of elements capable of being placed along the periphery of a whorl must decline. Conversely, if circumference is increasing faster than element size, then more elements can be accommodated on a whorl. Referring once again to Text-figure 7-D, it can be seen that the rate of growth of axial elements in *S. floridanus* remains fairly constant from whorl seven to whorl eleven. For *S. alatus*, on the other hand, the rates are initially lower than those for *S. floridanus* but they increase continuously from whorl seven through whorl twelve.

The nature and extent of intraspecific variation can best be seen by comparing second order growth curves. The Florida Keys and Campeche samples are compared to the nominate Florida Gulf Coast form of *S. alatus* in Text-figure 9. What appear as small differences in primary growth values and rates result in rather obvious differences in these second order curves. This is particularly true for Text-figures 9-B an 9-C wherein comparatively larger shoulder height values for Campeche specimens yield substantially shifted second order plots, and slightly altered protoconch whorl diameter and shoulder height values for Florida Keys specimens yield substantially altered protoconch maxima. However, a closer look at this suite of curves also demonstrates similar overall patterns of growth (*i.e.*, similar



Text-figure 11. Comparison of the growth in axial element size among [A] three *S. alatus* samples from different localities over the range of that taxon, and [B] two samples of *S. floridanus* from different Pliocene formations, the lower Pinecrest beds of southern Florida and the Jackson Bluff Formation of the Florida Panhandle. The curves connect the mean values of measures made at the end of each whorl for every specimen in the sample, with the short vertical lines indicating the standard errors of those mean values.

placements of and relationships among maxima, minima, and inflection points) for the different samples, suggesting that the plots may indeed be useful taxonomic indicators.

Modest differences in the values and rates for the primary growth elements in *S. floridanus* also result in clearly discernable differences in the second order growth curves (Text-figure 10). In this case, distinctly different protoconch profiles can be seen in each of the first three plots. Even though overall sample sizes may be large (75 in this case for the Pinecrest material and 69 for the Jackson Bluff material); however, individual specimens seldom if ever yield information for each and every whorl in the growth profile. Adult specimens have never been found to contain a complete, uneroded protoconch. Except for those just arriving at adulthood, it is unlikely that an adult specimen will retain any useful information concerning protoconch development. And juveniles, for their part, do not contain information about those growth characteristics immediately preceding adulthood. Hence, the profiles tend to be most reliable for the middle whorls of development, with the reliability of the protoconch profile being directly related to the number of well-preserved juvenile specimens present in the sample. In the example under discussion, the number of well-preserved juvenile specimens in the Pinecrest sample was considerably larger (39) than that for the Jackson Bluff sample (9). Again, the important point with respect to the two profiles presented in Text-figure 10 is that they show similar patterns of growth, patterns that differ from those present in Text-figure 9 for samples of *S. alatus*.

Intraspecific differences can also be seen with respect to the growth of axial element size. Text-figure 11-A compares axial growth profiles for both the Campeche and Florida Keys samples with the Florida Gulf Coast material utilized in constructing the basic *S. alatus* profile. The samples from the more southerly portions of the species' range have rather similar profiles with somewhat lower initial values than those found in the nominate form, more rapid rates of growth over whorls eight, nine and ten, and terminal "tails" suggesting that the largest axial elements on the penultimate whorl tend to be somewhat larger than those on the body whorl. The entire suite of growth rates for the Jackson Bluff sample is less than the corresponding rates for the Pinecrest sample (Text-figure 11-B). Yet, when Text-figure 11-B is compared directly with Text-figure 11-A, it can be seen that each taxon again has a typical pattern of development. In the case of *S. floridanus*, growth rates remain fairly constant from the end of whorl seven through whorl eleven, whereas, for *S. alatus*, the growth rates increase markedly and persistently over the same whorls. Taking into account all of the data plotted in Text-figures 9, 10 and 11, it is clear that samples of *S. floridanus* and *S. alatus* yield two reasonably consistent families of growth profiles, each representing, at least to some extent, the nature and extent of developmental variation within that taxon.

In summary, *S. floridanus* and *S. alatus* differ not only in adult morphological characteristics involving size, shape, ornamentation and color pattern, but also in ontogeny as well. Although the final product is inherently easier to study than the process, an understanding of the process can shed important light on the final product, particularly on that aspect of the product (the spire) that is an historical record of the process.

If one assumes not only that *S. alatus* differs from *S. floridanus* but that it represents the Recent descendent of that Pliocene species, then Text-figure 6 implies that there has been about a 15% reduction in the size of the protoconch during the past three million years in this lineage, while Text-figures 7 and 8 suggest an additional suite of developmental changes:

- in Text-figure 8-A a reduction in both the protoconch and teleoconch maxima, corresponding to spire forms that are decreasingly concave in overall aspect;
- in Text-figure 8-B a transformation in the shape of the plot from one of overall decline, corresponding to a spire profile with successively more sloping whorl shoulders, to one of overall increase, corresponding to a spire profile with successively more tabulate whorls;
- in Text-figure 8-C a flattening of the plot over the whorls of the protoconch and early teleoconch, together with a gradual

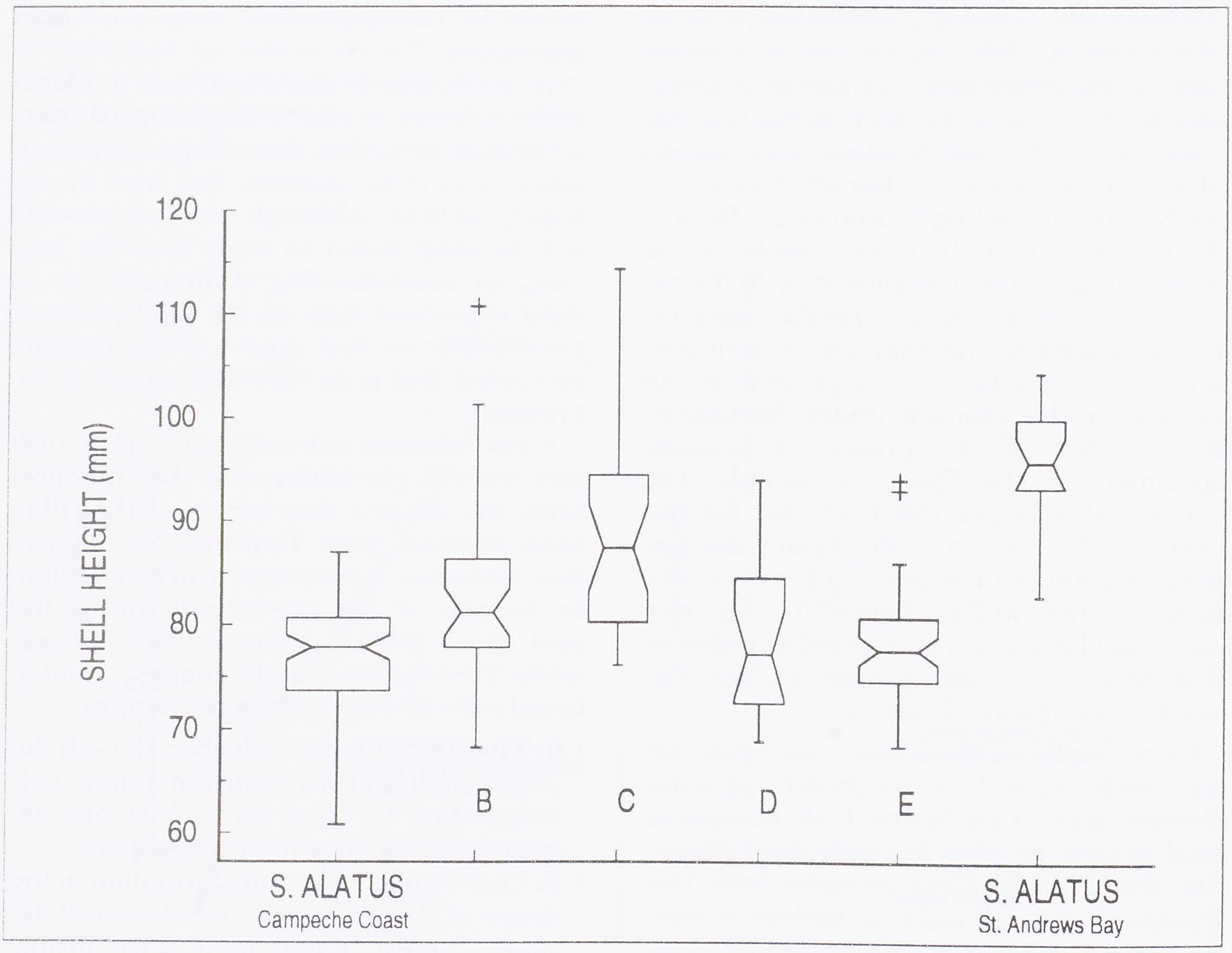
reduction of the teleoconch maximum, signifying a shift towards a more turreted spire outline;

- in Text-figure 7-D a transformation from fixed to increasing growth rates for axial ornamentation over the middle teleoconch whorls, together with an increase in the maximum value of element size.

One can postulate two hypotheses with respect to this process of morphologic change. The first assumes a series of incremental changes unfolding over all or much of the time interval. The second assumes a single shift from one morphological state to the other at some particular moment in time. This second hypothesis, in turn, offers two alternative possibilities. The first of these postulates that all of the morphological features outlined above are "coupled" and, therefore, go through the shift at the same point in time (*i.e.*, that all intervening fossil forms can be identified either with *S. floridanus* or *S. alatus*). The second postulates that some or all of the morphological features analyzed above are "decoupled" allowing the shifts in those particular features to take place at different geological times. Such decoupled changes in morphologic features would suggest that at least some of the intervening forms should be considered to be distinct chronospecies.

Analysis of Intervening Forms.

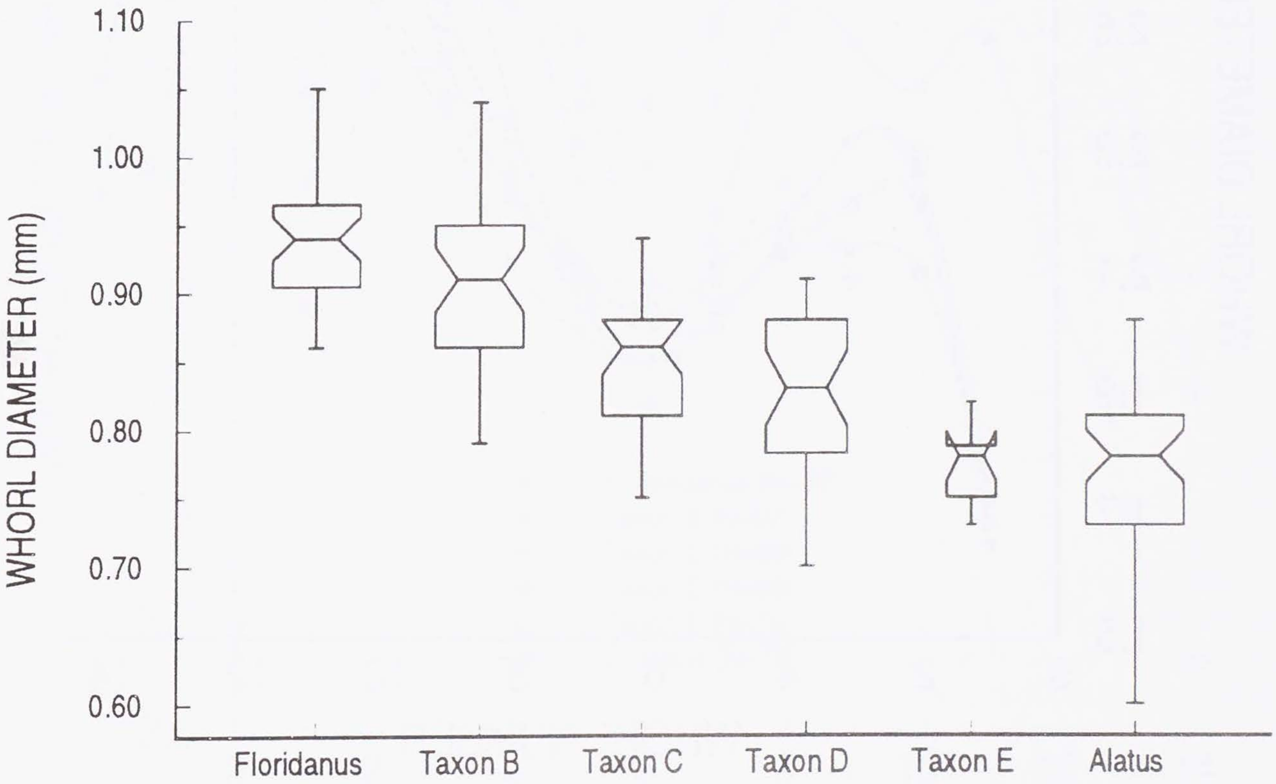
In the rich fossil record of southern Florida *S. floridanus* is present only in the lower part of the Pinecrest beds. Sub-



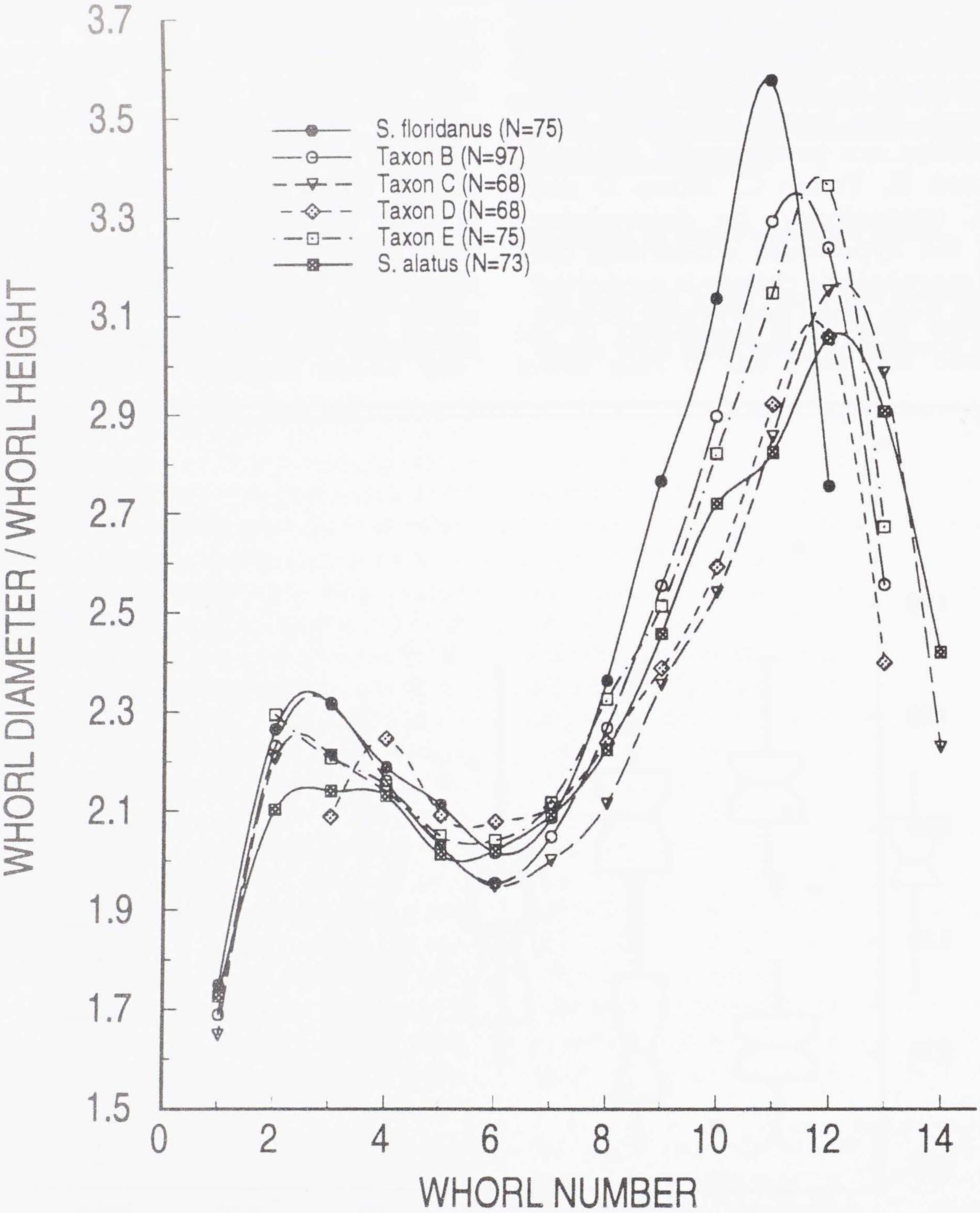
Text-figure 12. Notched box plot comparing shell heights among samples of various adult fossil *Strombus*. The fossil forms included and their sample sizes are as follows: Taxon B, upper Pinecrest beds (N = 34); Taxon C, Caloosahatchee Formation (N = 28); Taxon D, Bermont Formation (N = 20); and Taxon E, post-Bermont units (N = 50). The *S. alatus* samples with the largest (St. Andrews Bay) and smallest (Campeche Coast) median shell heights have been reintroduced from Text-figure 4-A for comparison.

sequent stratigraphic horizons contain a series of closely allied forms of *Strombus* sensu stricto that can be utilized to test the competing hypotheses set forth above. Horizons included herein for this purpose are: (1) the upper Pinecrest beds (corresponding to units 2-4 of Petuch at the APAC pit); (2) the Caloosahatchee Formation; (3) the Bermont Formation; and (4) post-Bermont units (usually referred to either the Fort Thompson or Coffee Mill Hammock Formations). The forms associated with these horizons are provisionally referred to as Taxon B, Taxon C, Taxon D and Taxon E, respectively. By determining which of the hypotheses concerning the nature of morphologic change is supported by the data from these intervening forms it should be possible to determine how many of these forms deserve to be considered as distinct taxa.

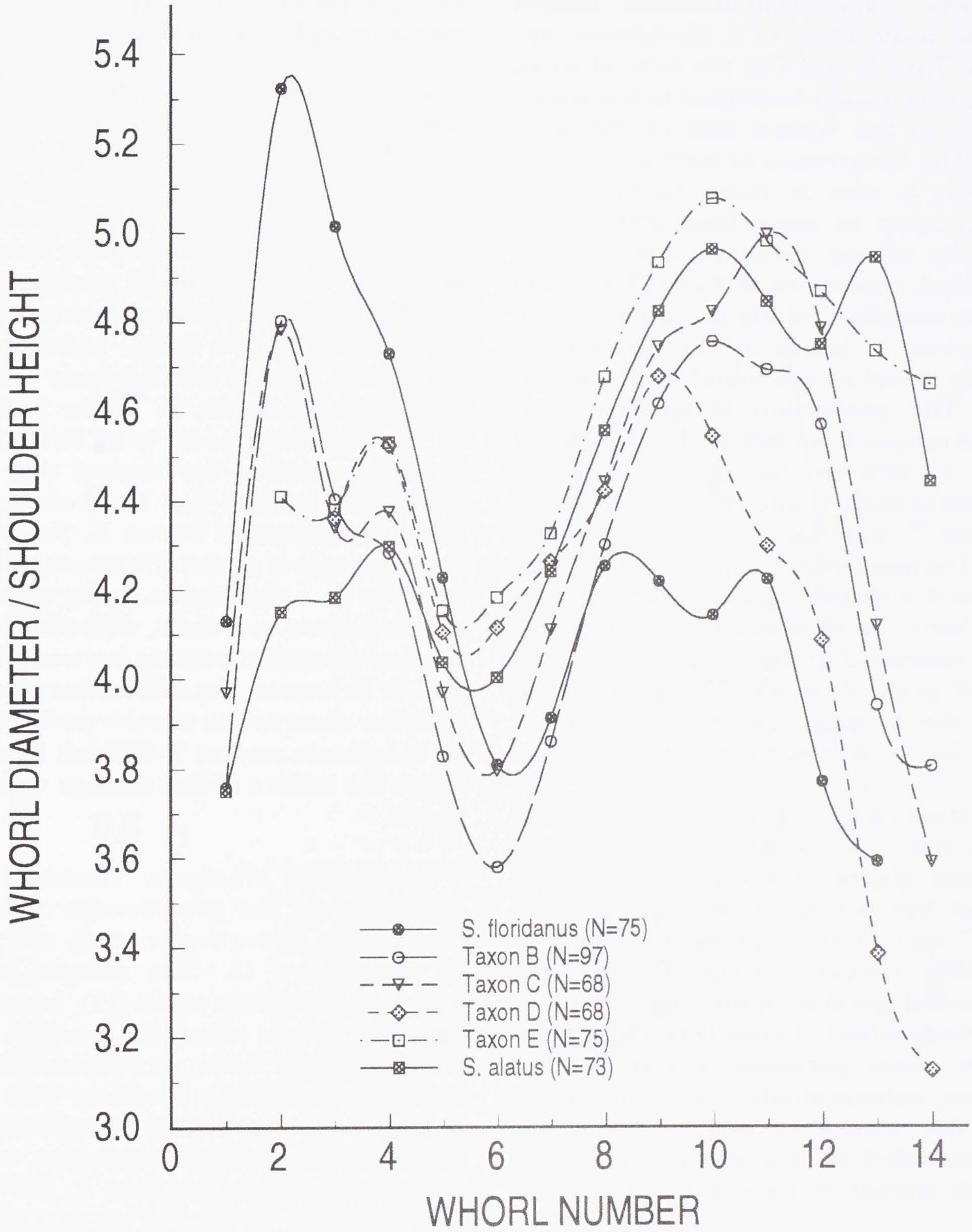
Features Associated with Adult Shell Shape. Text-figure 12 provides a notched box plot comparing the shell heights of the four intervening forms. The shell heights of the *S. alatus* samples having the largest and smallest median values in Text-figure 4-A are included for purposes of comparison. The median values of all of the intermediate forms analyzed fall within the range of variation for that statistic for *S. alatus*. When sufficiently large collections of adult specimens are utilized, none of these forms exhibit the characteristics of *S. floridanus*, suggesting that adult size is a useful characteristic for distinguishing *S. floridanus* from all subsequent fossil and



Text-figure 13. Notched box plot comparing whorl diameters at the end of the protoconch among samples of Florida fossil and Recent *Strombus* forms. The forms included and their sample sizes are as follows: *S. floridanus*, lower Pinecrest beds (N = 36); Taxon B, upper Pinecrest beds (N = 35); Taxon C, Caloosahatchee Formation (N = 29); Taxon D, Bermont Formation (N = 28); Taxon E, post-Bermont units (N = 11); and *S. alatus*, Sanibel Island (N = 51).



Text-figure 14. Comparison of the second order growth curve tracking the mean ratio of whorl diameter to whorl height for samples of Florida fossil and Recent *Strombus* forms. As in Text-figures 2, 8, 9 and 10, the plot conveys information concerning whether the spire profile is seen as concave, convex, or straight sided, with a positive slope indicating a concave aspect. In this and the next three Text-figures, the end-point taxa, *S. floridanus* and *S. alatus*, are represented by solid lines.



Text-figure 15. Comparison of the second order growth curve tracking the mean ratio of whorl diameter to shoulder height for samples of Florida fossil and Recent *Strombus* forms. As in Text-figures 2, 8, 9 and 10, the plot conveys information as to whether individual whorl profiles appear to be tabulate or sloping, with a positive slope indicating an increasingly tabulate aspect over shell development.

recent forms. The data contained in Text-figure 12 seem to support the hypothesis of a single shift in morphological states, with adult sizes going from "*floridanus*-like" to "*alatus*-like" between the lower Pinecrest and upper Pinecrest beds.

Axial and Spiral Ornamentation of Adult Specimens. Axial ornamentation, absent from the body whorl of *S. floridanus*, appears in Taxa B and C in the form of weak curving ribs usually restricted to the shoulder area of the ventral side of the body whorl. The occurrence of such axial ornamentation is rare in these forms, never being present in more than 25% of the specimens of any given sample. On the other hand, specimens of Taxon E from all localities sampled exhibit the same type of blunt spines or knobs on the shoulder of the body whorl as are found on Recent *S. alatus*. The proportion of specimens so adorned ranges from 50% in the Bass Road sample to 96% in the sample collected northeast of Belle Glade. With one possible exception,[12] material from localities containing Bermont material tends to be transitional in this respect. Axial ornamentation on the body whorl is still rare and almost always restricted to the ventral side of the whorl if present at all. However, while weak, the ornamentation is knob-like rather than the curving riblets of earlier forms.

The lirations or rugosities found on the parietal wall of up to 20% of *S. floridanus* specimens are present on almost 50% of the adult Taxon B specimens analyzed. In Taxa C and D their presence drops to about 10%. However, while Taxon C exhibits muted spiral sculpture in all respects on the body whorl, Taxon D tends to have stronger, more persistent external spiral sculpture, submarginate costae, and columellar denticles than any of the other forms included in this study. This vigor does not appear to have extended to the parietal lirations. In post-Bermont Taxon E spiral sculpture is again muted and parietal lirations have yet to be observed.

Hence, with respect to shell sculpture, there appear to be a series of small changes in either the form of the sculpture, the frequency of expression, or both within the four intervening forms of *Strombus* providing support for the hypothesis of incremental morphological change over time.

Adult Color Patterns. The chevron pattern commonly encountered in specimens of *S. floridanus* continues to be observed in a significant fraction of the adult specimens of both Taxa B and C. However, in spite of states of preservation that allow one to see other remnants of color such as the darkening of the leading edges of resting varices on the spire, patterning has been seen on only 2% the body whorls of specimens of Taxon D. When present at all, the pattern appears to be limited to the shoulder area on the ventral side of the whorl. No pattern has been observed in adult specimens of Taxon E. As with the development of parietal lirations, there appears to be a diminution in the expression of this feature over time, with the most significant alteration coming between Taxa C and D. However, the difficulties associated with the observation of color pattern in fossil specimens makes it difficult to characterize the nature of this change with confidence.

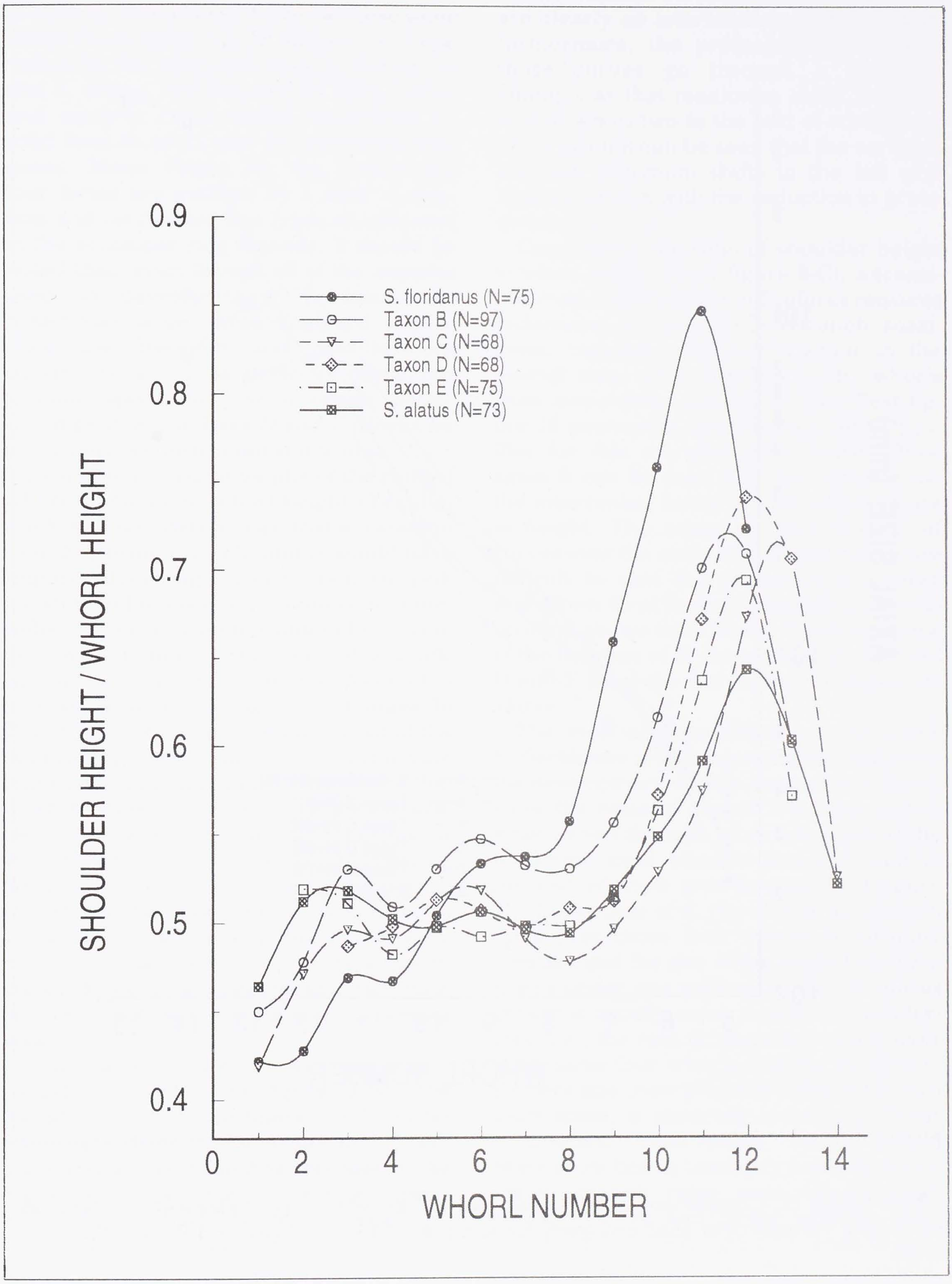
Ontogenetic Analysis. Terminal whorl diameters for the protoconchs of the four intervening forms under study are plotted in Text-figure 13. The sample size for Taxon E was fairly small (11), but there is little doubt but what the median protoconch for the form represented by this sample is essentially identical with that of *S. alatus*. The remaining three forms, all of which have, on average, smaller terminal protoconch diameters than *S. floridanus*,

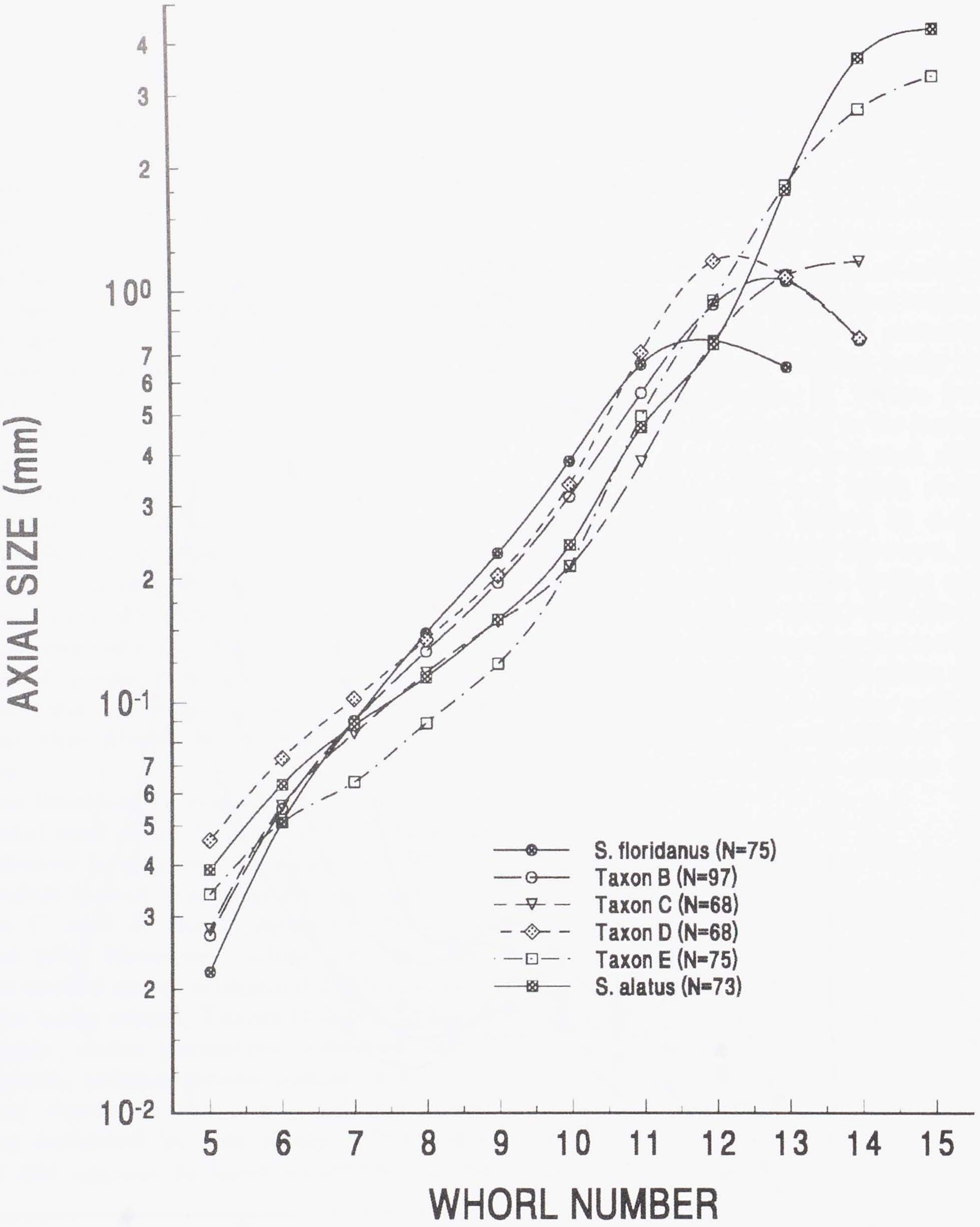
Text-figure 16. Comparison of the second order growth curve tracking the mean ratio of shoulder height to whorl height for samples of Florida fossil and Recent *Strombus* forms. As in Text-figures 2, 8, 9 and 10, the plot conveys information concerning the placement of the suture of the succeeding whorl relative to the whorl periphery and, hence, whether a whorl appears to be turreted or embedded. A positive slope here indicates a spire wherein whorl profiles become increasingly embedded with shell development.

>

appear to exhibit a series of incremental reductions in that statistic over geologic time.[13] This offers strong support for the hypothesis of incremental morphologic change over time rather than for a single quantum shift at one point in the time continuum.

To assess other changes in developmental patterns over time, three of the four second order plots that were utilized to





Text-figure 17. Comparison of the mean rates of growth in axial element size (excluding resting varices) over shell ontogeny for samples of Florida fossil and Recent *Strombus* forms.

provide comparative growth profiles of *S. floridanus* and *S. alatus* have been redrawn and expanded in Text-figures 14-16 to include the profiles for the intervening forms. To these three, one of the primary plots has been added portraying the growth in axial element size for these same forms (Text-figure 17). In all plots the mean values for the end-point taxa, *S. floridanus* and *S. alatus*, are denoted by filled circles and squares respectively, connected by solid lines in each case for reference purposes. Mean values for the intervening four forms are marked by a suite of symbols and connecting line types as indicated in the accompanying legends. It should be noted that, even though all of the samples used to develop these profiles were reasonably large, those analyzed to produce the Bermont and post-Bermont curves contained no perfectly preserved juvenile specimens. As a result, protoconch profiles for Taxa D and E cannot be accurately reconstructed at this time.

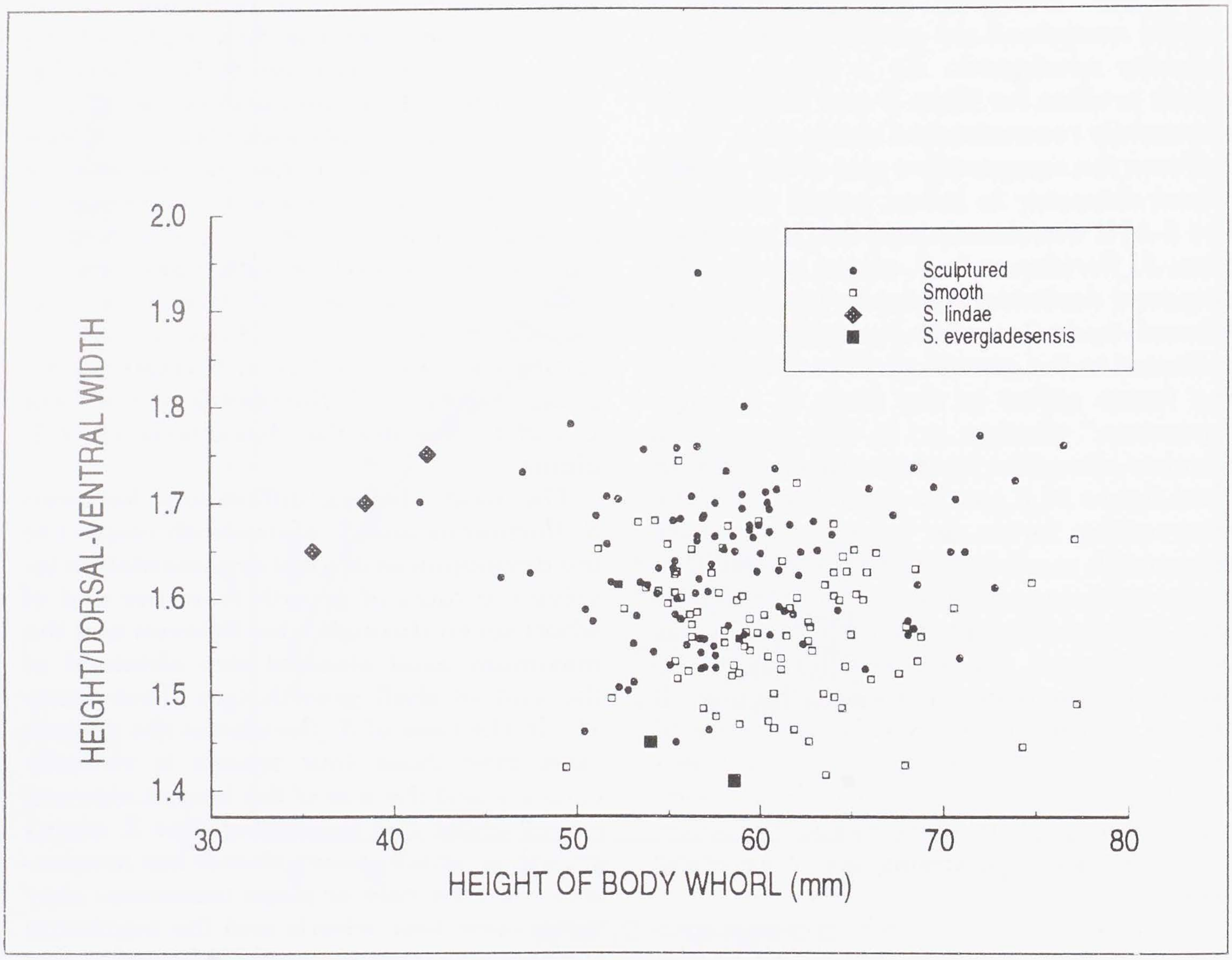
From the comparative plot of the ratio of whorl diameter to whorl height (Text-figure 8-A) it was determined that a transition from *S. floridanus* to *S. alatus* would have required declining values for both the protoconch and teleoconch maxima over time, reflected in the growth profiles of intervening forms either in the form of a single "quantum" change or in the form of a number of smaller incremental changes. In Text-figure 14 it can be seen that all of the intervening forms do have intermediate teleoconch maxima and, to the extent that it can be determined from the data available, intermediate protoconch maxima as well. However, the teleoconch maxima do not all decline from one form to the next. It should also be noted that the sequence of shifts to the left among the early teleoconch minima over time provide supporting evidence of an incremental reduction in protoconch size among the intervening taxa.

In terms of the plot of whorl diameter to shoulder height (Text-figure 8-B), the transition from *S. floridanus* to *S. alatus* requires a drop in the protoconch maximum and a corresponding increase in the teleoconch maximum, yielding spires whose later whorls become increasingly more tabulate over geologic time. Text-figure 15 presents a comparative set of profiles for this morphologic feature. Although the individual curves themselves are all rather complex, it can be seen that the teleoconch maxima rise quickly to values in the neighborhood of *S. alatus*. The protoconch maxima for the intervening forms are clearly all intermediate in height and, furthermore, the protoconch portions of those curves go through a series of changes as that maximum shifts from the end of whorl two to the end of whorl four. Once again it can be seen that the early teleoconch minimum shifts to the left over time in concert with the reduction in protoconch size.

Considering the ratio of shoulder height to whorl height (Text-figure 8-C), a transition from *S. floridanus* to *S. alatus* requires reductions in the late teleoconch maximum, together with a reduction in the overall slope over the first eight whorls from moderately positive to flat. Text-figure 16 presents a comparative set of profiles for this morphologic feature. Once again it can be seen that the maxima for the intervening forms are all intermediate in height. The complex intermingling of curves over the early whorls makes it more difficult to spot the reduction in overall slope from form to form. However, careful scrutiny shows that Taxon B retains some of the features of *S. floridanus*, while Taxa D and E have the flat characteristics of *S. alatus*.

The most obvious differences between *S. floridanus* and *S. alatus* with respect to the development of axial ornamentation involve the rates of growth from the end of whorl seven through whorl eleven and the maximum axial element size obtained at the end of shell growth (see Text-figure 11). In the case of *S. floridanus* the growth rates over those four whorls is virtually constant and the size of the largest element is well under one millimeter. For *S. alatus* growth is initially much slower but accelerates (*i.e.*, the rate or slope increases) over those same four whorls and the maximum element size (now properly referred to as a blunt spine) is generally in excess of four millimeters. Intervening forms would likely show both a tendency towards accelerated growth rates over whorls eight through eleven and larger ultimate axial element sizes. Text-figure 17 tends to support both of these theses. Not surprisingly, Taxon E and *S. alatus*, both of which retain axial sculpture on the body whorl, have the largest axial elements. However, all of the other intervening forms have maximum axial sizes that exceed those of *S. floridanus*. Once again, the close proximity of the growth curves makes reading the intermediate growth rates rather difficult. However, if studied carefully it can be seen that the growth rates for Taxon B increase only slightly from the end of whorl seven through the end of whorl twelve. For the other intervening taxa there is a considerable increase in rates over the same set of whorls.

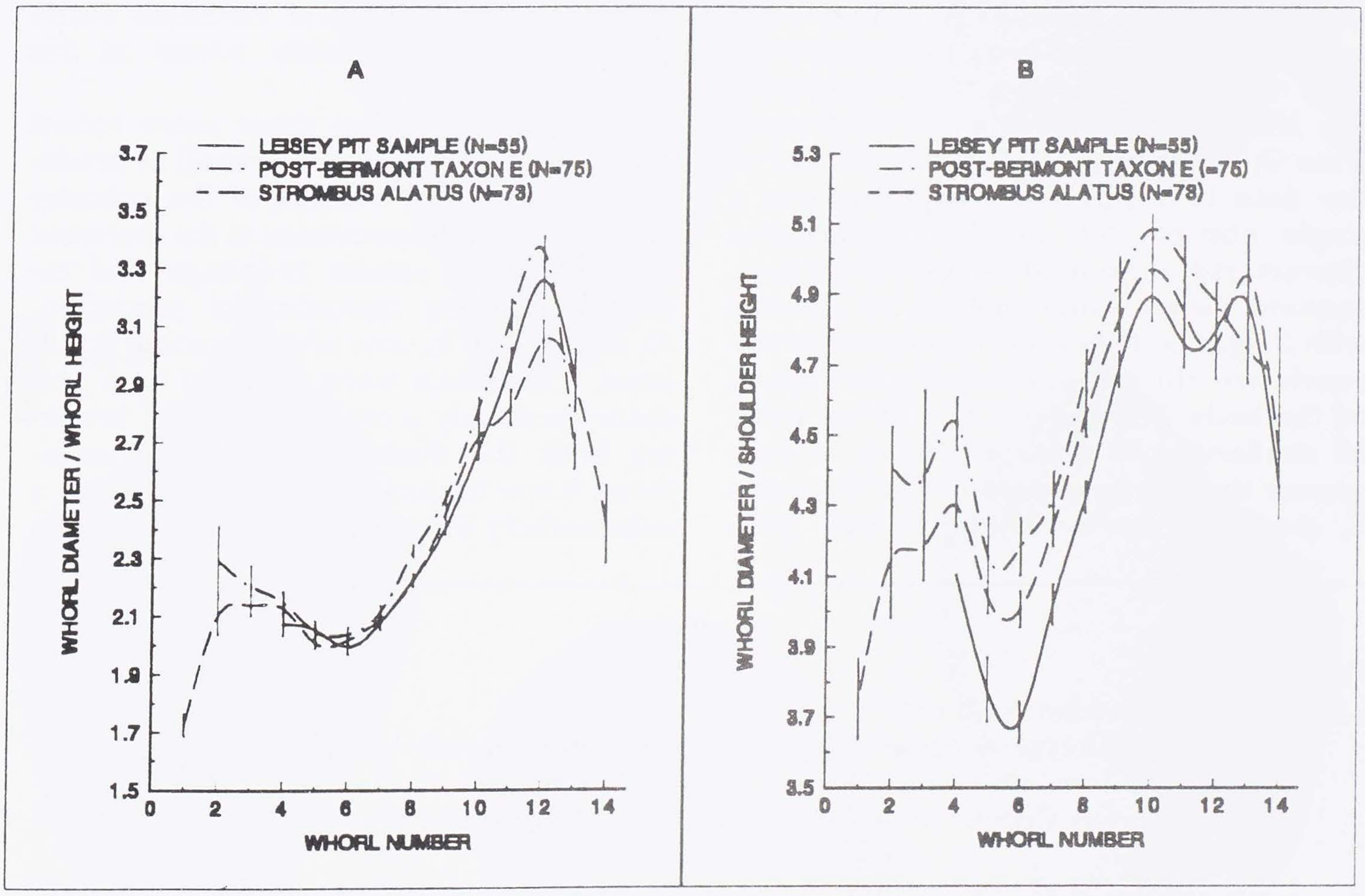
When the four plots making up Text-figures 14 through 17 are analyzed in their entirety, there is little doubt that the intervening forms found in the upper Pinecrest beds, the Caloosahatchee Formation, the Bermont Formation, and the post-Bermont Pleistocene represent a single morphologically changing lineage linking the Pliocene *S. floridanus* with the Recent *S. alatus*. What is more difficult to determine with precision is the exact nature of that change. The data gathered concerning adult size suggests a single shift in that morphological feature between the lower and upper Pinecrest beds. However, the suite of growth profiles does not support the conclusion that other features of ontogeny were coupled to adult size. Of the features present in those growth profiles, only the placement of the teleoconch maxima in Text-figures 14, 16 and 17 appear to



Text-figure 18. Scatter plot showing the relationship among shell size, relative fatness, and the vigor of spiral sculptural expression on the body whorl of 205 adult *Strombus* collected at the Star Ranch borrow pit in Palm Beach County. The height of the body whorl was used as a measure of shell size, while the ratio of body whorl height to dorsal ventral width was used as a measure of relative fatness. For comparative purposes, the type specimens of *S. lindae* Petuch (shaded diamonds) and *S. evergladesensis* Petuch (shaded boxes) are included.

be influenced in part by adult size. The high terminal values of some of the curves in Text-figures 15 and 17 appear to be tied to the extension of spinose axial sculpture to the body whorl of adults, which first becomes prevalent in the post-Bermont form (Taxon E). The analysis of protoconch sizes (Text-figure 13) suggests an incremental reduction in that feature over time. This is supported by, and apparently coupled to, the placement of the early teleoconch minima in Text-figures 14 and 15. Although the data are incomplete, it also appears that there has been a parallel series of incremental changes in larval shell shape over time, as seen particularly in Text-figure 15. Changes in later teleoconch characteristics, as expressed in terms of the heights of teleoconch maxima in Text-figures 14, 15 and 16, are more enigmatic. A chronologically consistent suite of changes in those heights would imply incremental change similar to that which appears to be operating in the larval stage over time, whereas one or more tight clusters could be interpreted as evidence of larger-scale shifts in character states. The curves do not support the former and support for the latter is ambiguous at best. However, the earlier analysis of intraspecific variation among samples of *S. alatus* pointed to the fact that it is the patterns of growth, not specific numerical values, that reoccur from sample to sample. Hence, it would be dangerous to read too much into the numerical values of specific maxima or minima for the samples selected to represent the four intervening fossil forms in this analysis.

In summary, morphologic change in the *S. floridanus*/*S. alatus* lineage over the past 3.0 to 3.5 million years has been complex. The data clearly do not support the hypothesis of a single change of all morphological characteristics at one point in the geologic record, but they do offer varying degrees of support for the remaining two hypotheses of "decoupled" abrupt



Text-figure 19. Comparison of Leisey Shell pits *Strombus* with the post-Bermont Taxon E and Recent *S. alatus*. [A] portrays changes in the mean value of the ratio of whorl diameter to whorl height over shell ontogeny, while [B] tracks changes in the mean value of the ratio of whorl diameter to shoulder height. The vertical lines indicate the standard errors of those mean values.

changes and incremental change. Changes in larval growth patterns appear to be incremental, while certain features of adult morphology seem to have undergone large-scale changes at different times in the past.

V. CONCLUSIONS

The taxonomic status of analyzed forms.

The most conservative hypothesis based upon the evidence at hand is that the various forms of southern Florida fossil *Strombus* sensu stricto analyzed herein form a single morphologically changing lineage. There is neither morphologic evidence for any branching speciation event among these forms during the past 3.0 to 3.5 million years, nor any evidence from *in situ* collections that the forms coexist in the same biostratigraphic units.[14] The growth profiles, together with the data accumulated concerning adult sizes, demonstrate that *S. floridanus*, as found in the *Cancellaria* zone of the Jackson Bluff Formation and lower Pinecrest beds, is morphologically distinct from all later forms, supporting Mansfield's separation of that taxon from the Recent *S. alatus*. The failure of the data to support the hypothesis of a single abrupt shift in all morphological characteristics studied suggests that subsequent forms should not all be equated with *S. alatus*. However, in terms of protoconch size, the presence of shoulder spines on the body whorl of adults, and the overall similarities in growth profiles, it does appear that the post-Bermont form, Taxon E, can be grouped within *S. alatus*. Taxa B, C, and D then would appear to represent one or more morphologically distinct chronospecies ranging from the upper Pinecrest beds through the Bermont Formation.

Are there any characteristics that would allow workers in the field to separate Taxa B, C, and D on the basis of cursory visual inspection? For the Bermont Taxon D two features can be noted: (1) the nature and strength of the spiral sculptural elements on the body whorl of adult specimens; and (2) the presence of pronounced resting varices on the last three teleoconch whorls of adults. Specimens of Taxa B and C tend to have much less pronounced resting varices on the later whorls and very muted spiral sculpture on the body whorl both externally and within the aperture of adult specimens. Conversely, many Bermont specimens exhibit exterior spiral sculpture that is both persistent and complex over much of the dorsal surface of the body whorl and is particularly strong on the expanded adult lip. With the exception of the parietal rugosities, the sculptural elements inside the aperture are equally robust in this form.

It may well be that these more robust sculptural features are the result of predation; a significant fraction of the robustly sculptured adult specimens at the Bermont sites surveyed exhibit breakage and repair, suggesting unsuccessful predation. At some point in time after reaching adulthood, individuals were attacked by a predator (probably a crab) capable of breaking back the thickened adult lip (sometimes 4 mm in thickness), often as far as a substantially thickened resting varix some

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PLATE 2

Figures

1-2. *Strombus floridanus* Mansfield
  1. (X 1.2) Holotype – *Strombus pugilis floridanus* Mansfield, 1930. USNM 370260; height 62 mm, diameter 36 mm (young adult specimen). Locality: USGS station 3422, Harvey Creek, Leon County, Florida; *Cancellaria* zone of the Jackson Bluff Formation.
  2. (X 1) USNM 483765; height 61.1 mm, diameter 33.0 mm. Locality: Unit 7, APAC Pit, Sarasota, Florida (= TU 1000); lower Pinecrest beds.

3. *Strombus* sp. aff. *S. evergladesensis* Petuch (X 0.8)
USNM 483766; height 85.1 mm, diameter 49.7 mm.
Locality: Unit 4, APAC Pit, Sarasota, Florida (= TU 1000); upper Pinecrest beds.

(Diameter of all specimens includes the expanded adult lip)

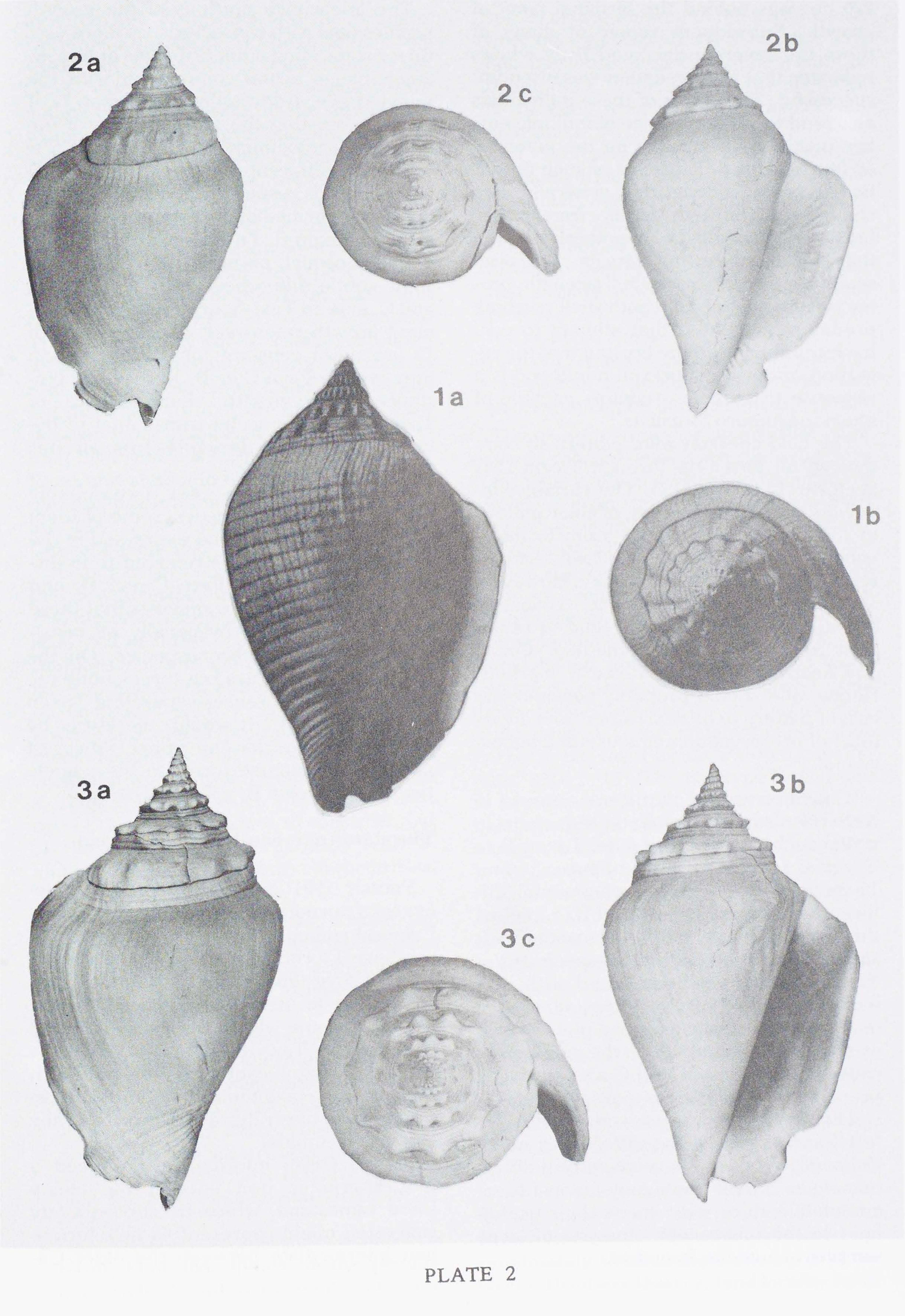

PLATE 2

220 degrees behind the terminal point of growth. Subsequent repair of many of these the severely damaged body whorls indicates that this predation was often unsuccessful. The spires of these individuals also tend to yield evidence of multiple earlier unsuccessful attacks on the juveniles as they matured. Evidence of such predation is rare among the generally less robustly sculptured forms from other biozones. It might be hypothesized then that thickened resting varices and spiral sculpture provide extra shell strength, protecting the animal from both shell crushing predators and those that attempt to peel back the shell from the lip, and that the retention of these features in adulthood is a response to specific predators capable of attacking mature *Strombus*.[15]

The bold chevron color pattern so common in all forms up through Taxon C is seen rarely in Taxon D. The variables involved in the preservation of color pattern in fossil specimens would seem to make conclusions based upon the absence of pattern in certain fossil forms risky. However, specimens from the same collecting localities of other taxa that tend to retain their color patterns over time (*e.g.*, *Conus* and *Scaphella*) are often clearly marked. Hence, one should probably consider the lack of pattern to be real rather than an artifact of preservation and a useful diagnostic tool.

It has been noted that there appears to have been small incremental reductions in protoconch size in going from Taxon B to Taxon C to Taxon D. Text-figures 14 and 15 indicate additional developmental differences between Taxa C and D that affect the overall shape of the protoconch. It should be pointed out that no specimens of Taxon D have yet been found with perfectly preserved protoconchs, making it impossible to construct a complete profile of that form. In addition, the number of specimens of Taxa B and C with perfectly preserved protoconchs analyzed was small; 4 in the former case and 10 in the latter. Finally, even if the differences noted are accepted as expressions of real differences in larval ontogeny over time, cumulative spire wear limits their usefulness to the microscopic analysis of large samples of juvenile *Strombus*.

The teleoconch portions of the growth profiles deal with characteristics more useful for separating adult *Strombus* and more amenable to visual comparison with the unaided eye. Addressing first Taxon D, it can be seen that the general form of the teleoconch maximum in Text-figure 15 is somewhat different than those for Taxa B and C. In this respect Taxon D is morphologically intermediate between *S. floridanus* and Taxon B. The late protoconch and early teleoconch portions of Text-figure 16 show subtle differences between Taxa B and C, and, in Text-figure 17, the axial element growth rates over whorls 8 through 12 are more constant for Taxon B than they are for Taxa C or D. In these two instances, the growth characteristics of Taxon B appear to be transitional in nature, separating *S. floridanus* from all later forms.

In summary, there exist a reasonably large suit of characteristics, some of them developmental and some expressed in the adult state, that can be referred to in distinguishing between Taxa C and D, and the weight of evidence suggests that these two forms should provisionally be considered as distinct chronospecies. On the other hand, there are but three subtle developmental differences separating Taxon B from Taxon C. It would, therefore, be prudent to consider the upper Pinecrest and Caloosahatchee forms to be a single taxon (*i.e.*, Taxon B = Taxon C).

The status of recently proposed taxa.

Petuch (1991) has described two *Strombus* taxa purporting to come from the post-Caloosahatchee, lower Pleistocene of southern Florida, *Strombus evergladesensis* and *Strombus lindae*.[16] Although it is reasonable to assume that these taxa are related in some way to the forms referred to herein as Taxa B, C and D, Petuch's work poses significant problems, both with respect to the taxa themselves and with respect to the biostratigraphic horizons they supposedly inhabit.

Petuch (1990) informally introduced a biostratigraphic unit entitled the Holey Land Limestone, which he subsequently suggested might represent "a new formation intermediate between the older Caloosahatchee Formation and the younger Bermont Formation" (Petuch, 1991, p. 6). Under the discussion of these units in the latter work he lists *S. evergladesensis* among the index fossils for the supposedly younger Bermont Formation and *S. lindae* as an index fossil for the underlying Holey Land unit, implying that the two taxa did not coexist in geologic time and that *S. evergladesensis* is the younger taxon. Seven pages later, however, he contradicts himself, placing the type locality of *S. evergladesensis* in the Holey Land unit rather than in the Bermont Formation. The type locality for *S. lindae*, although different from that of *S. evergladesensis*, is also placed in the Holey Land Unit, implying that the two taxa are sympatric. In a popular work published a year later (Petuch, 1992) there is no mention of the Holey Land unit at all and the two *Strombus* taxa under consideration are portrayed as sharing the same habitat in the Bermont Okeechobean Sea.

In spite of the fact that Petuch places the two new *Strombus* taxa in the same stratigraphic unit (albeit a different one) on at least two of three occasions, he does not compare one with the other while describing and discussing either species. Instead, he compares each with a form or subspecies of *S. alatus* (probably the post-Bermont Taxon E) that he seems to think coexisted with both *S. evergladesensis* and *S. lindae*. Using Petuch's language (1991, pp. 14, 15), I have sought to construct, out of these pair-wise comparisons with *S. alatus*, a set of diagnostic characteristics for the two taxa:

Adult Size – *Strombus lindae* is small (all specimens referred to by Petuch being under 70 mm), whereas *S. evergladesensis* is typical of the subgenus (*i.e.*, around 80 mm).

Outline – *Strombus lindae* is elongated, slender with high, elevated, protracted spire, whereas *S. evergladesensis* is very bulbous, inflated or globose, but having a spire with the early whorls elevated, protracted and scalariform. (This would seem to suggest a more concave spire aspect for *S. evergladesensis* than for *S. lindae*.)

Axial Elements – *Strombus lindae* has blunt, knob-like spines on the penultimate whorl and occasionally obsolete spines on the dorsum of the body whorl. In *S. evergladesensis* the axial sculpture becomes obsolete and disappears on the penultimate whorl so that the shoulder of the body whorl is without axial ornamentation.

Spiral Sculpture on the Body Whorl – *Strombus lindae* is said to be heavily ornamented with large, evenly spaced spiral cords, although the mid-dorsum is acknowledged to have a smooth spot. *Strombus evergladesensis*, by contrast, has a body whorl that is smooth and polished with spiral sculpture limited to the siphonal canal.

Stromboid Notch – Deep and well-developed in *S. lindae*, but shallow and poorly developed in *S. evergladesensis*.

The present study has shown that adult size and relative fatness are characteristics of dubious value in separating the forms of *Strombus* sensu stricto present in southern Florida, especially when statistical analyses of large samples are not carried out. Petuch's descriptions appear to be based upon very small data sets, in spite of the abundance of *Strombus* at almost all collecting localities. The description of *S. lindae* is based upon four specimens while that of *S. evergladesensis* is based upon three. It is claimed in the discussion of *S. lindae* that it is the smallest conch shell known from the Florida Pleistocene (Petuch, 1991, p. 15). The holotype is recorded as 54 mm (which it is). However, when the holotype is figured once again in his 1992 work, it is said to be 42 mm (Petuch, 1992, p. 42, figure 21, nos. 2, 6). On the next page in that work it is claimed that an unnamed Bermont *Strombus* reaches adulthood at 25 mm.[17] The holotype of *S. evergladesensis* was reported by Petuch in 1991 to be 72 mm (it is, but about 5 mm of the anterior end is missing). Yet in 1992 this same specimen is listed as being 68 mm (Petuch, 1992, p. 42, figure 21, no. 3). These discrepancies throw doubt on taxa supposedly differentiated primarily by adult size.

In order to test the correlations among the individual characteristics cited by Petuch, a sample consisting of 205 adult *Strombus* was analyzed from a single collecting locality for this study. The Star Ranch borrow pit (TU 1536) is located approximately 18 kilometers due north of the Griffin Brothers Quarry, type locality for *S.*

evergladesensis, and approximately four kilometers northwest of the type locality for *S. lindae*. The excavation at that site has penetrated the sandy facies of the Bermont, the Holey Land Limestone, and into the underlying Caloosahatchee Formation. Since the pit itself is flooded, all collecting at that site is restricted to spoil piles that contain a mixture of Bermont and Caloosahatchee index fossils. Specimens assignable to each of Petuch's taxa were present in numbers.

Text-figure 18 shows the results of this analysis, plotting a measure of relative "fatness" (the ratio of the height of the body whorl to the dorsal-ventral width of that whorl, the same ratio that is plotted in Text-figure 4-C), against a measure of shell height, in this case the height of the body whorl. Those specimens exhibiting strong internal and external spiral sculpture are differentiated from those specimens having a smooth body whorl with weak or absent internal spiral elements, the former being marked by small solid circles, the latter by small open boxes. According to the criteria set forth above for differentiating Petuch's two Bermont taxa, one would expect a cluster of specimens in the top left hand portion of the plot marked by solid circles representing *S. lindae* (*i.e.*, small, slender, heavily sculptured specimens), and another cluster in the bottom right hand portion of the plot marked by open boxes representing *S. evergladesensis* (*i.e.*, large, bulbous, smooth-surfaced specimens). Data for the holotype and two deposited paratypes of *S. lindae* (solid diamonds), together with the holotype and one deposited paratype of *S. evergladesensis* (large solid boxes), are included on the scatter plot for reference. Several points are immediately apparent. First, the specimens do not sort themselves into two morphologically distinct populations. Second, there is no discernable correlation between adult shell size and fatness or between shell size and the strength of expression of spiral sculpture. There is only the weakest of correlations between shell shape (*i.e.*, fatness) and the expression of spiral sculpture. Third, Petuch appears to have chosen the most extreme forms available to him to describe his two taxa. From the evidence contained in this plot one cannot rule out the possibility that *S. lindae* and *S. evergladesensis* simply represent two extreme forms of the same morphologically variable Bermont taxon. If this is the case, then *S. evergladesensis* would have priority. And, since it has been demonstrated herein that the Bermont Taxon D is a distinct chronospecies, *S. evergladesensis* would be equated with that form.

Other interpretations, however, are also possible. Given the fact that both Bermont and Caloosahatchee index fossils are pre-

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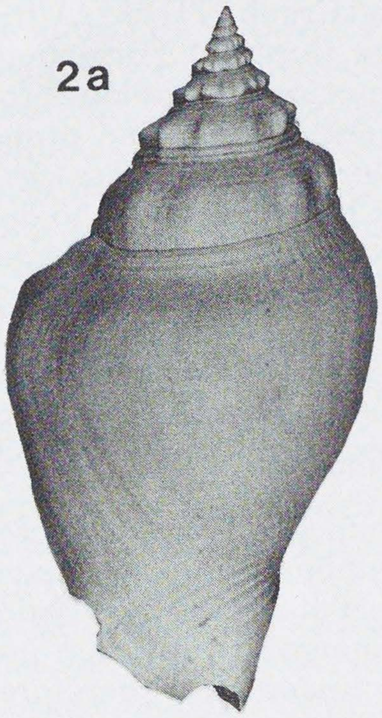
PLATE 3

Figures

1. *Strombus evergladesensis* Petuch (X 1.2)
   CM 35698 (holotype); height 72.8 mm (anterior tip missing), diameter 46.6 mm.
   Locality: Griffin Brothers Quarry, Broward-Palm Beach County line, Florida; Holey Land Unit (= Bermont Formation?).
2. *Strombus* sp. aff. *S. evergladesensis* Petuch (X 0.8)
   USNM 483767; height 77.5 mm, diameter 43.8 mm.
   Locality: DeSoto Shell Pit # 3, DeSoto County, Florida; Caloosahatchee Formation.

3-4. *Strombus lindae* Petuch
   3. (X 1) Holotype – *Strombus lindae* Petuch, 1991.
      CM 35700; height 53.4 mm, diameter 28.1 mm.
      Locality: North New River Canal, Palm Beach County, Florida; Holey Land Unit (= Bermont Formation?).
   4. (X 0.8) USNM 483768; height 75.6 mm, diameter 42.9 mm.
      Locality: North New River Canal (about 4 km nw of the type locality), Palm Beach County, Florida; Bermont Formation.

(Diameter of all specimens includes the expanded adult lip)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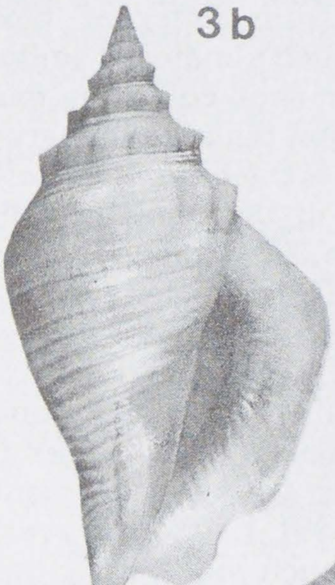
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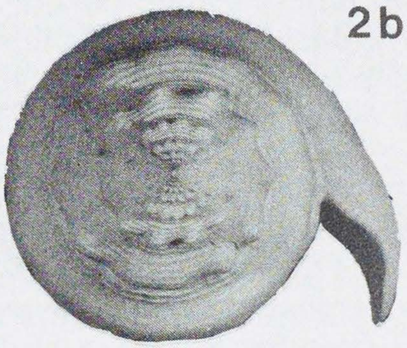
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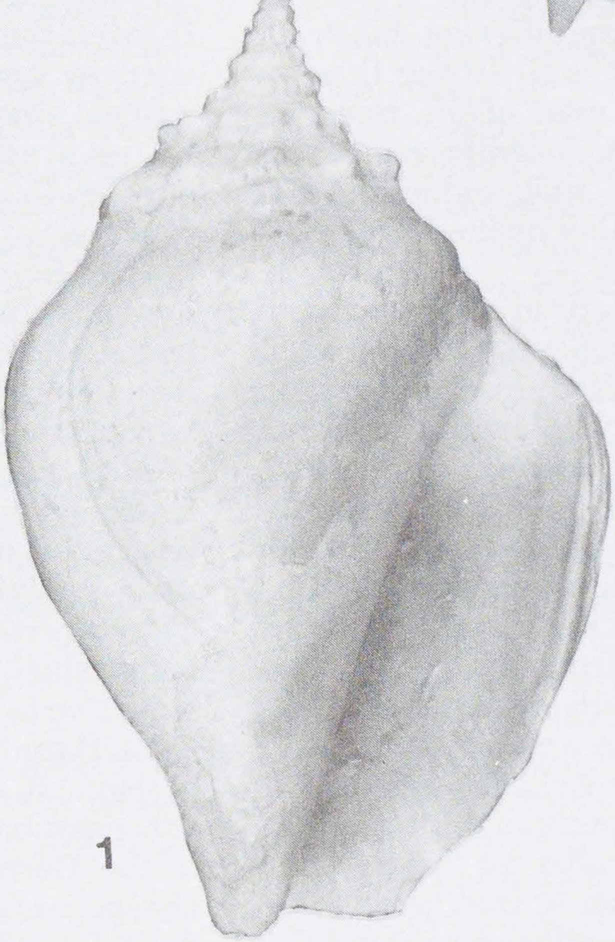
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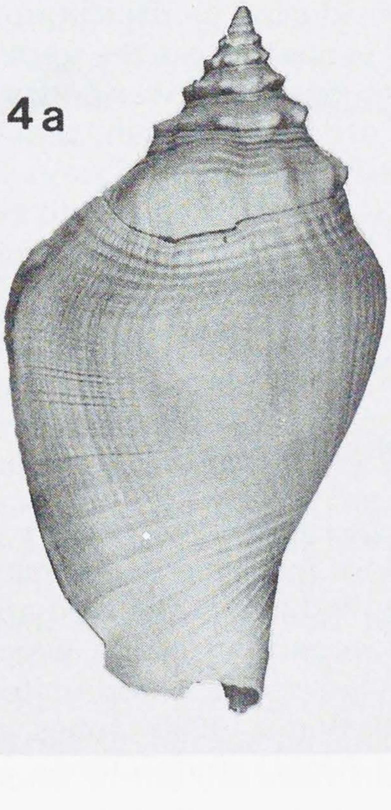
3a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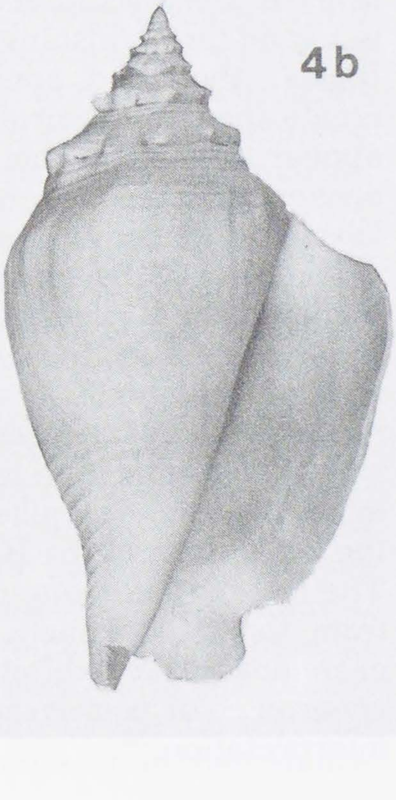
4b


4c

PLATE 3

sent at the site, the Star Ranch sample utilized above almost certainly contains material from different biostratigraphic units. Petuch's material undoubtedly also came from spoil collecting making it quite possible that his two taxa are not sympatric. If this is the case, then several hypotheses open up involving the Caloosahatchee Formation, the Holey Land unit, and the sandy shell marl facies of the Bermont Formation. Petuch himself offered one possibility when he included *S. lindae* as an index fossil for the Holey Land unit and *S. evergladesensis* as an index fossil for the supposedly younger Bermont Formation (Petuch, 1991, p. 7). However, this author thinks it much more likely that, if the two forms do come from different biostratigraphic units, that it is *S. lindae* that resides in sandy shell marl of the Bermont Formation, while *S. evergladesensis* is found in some lower unit, either the Caloosahatchee Formation or the lower Bermont Holey Land unit.

The sample utilized in this study to create the growth profile for the Bermont Taxon D was collected from a location (F07) along the North New River Canal about one kilometer northeast of the Star Ranch pit and roughly four kilometers upstream from the type locality for *S. lindae*. Like the material taken from the *S. lindae* type locality, this sample was collected from spoil dredged from the North New River Canal in the early 1980's. If the presence of spiral sculpture on the body whorl is a valid distinguishing characteristic of *S. lindae*, then the specimens utilized to create the growth profile for Taxon D all appear to be referable to that taxon. The absence of both *S. evergladesensis* and Caloosahatchee index fossils at this locality, would seem to be significant. In all probability the canal dredging did not reach the same depths as the borrow pit nearby. Hence, Petuch's *S. evergladesensis* might represent very fat specimens of the underlying Caloosahatchee form (Taxon C) or it might represent an allied form confined to the basal units of the Bermont Formation. The fact that only one of the 93 specimens from the Star Ranch pit referred to *S. evergladesensis* exhibited even a hint of chevron color pattern supports the second interpretation.[18]

Further support for this interpretation comes from material taken from the upper shell bed along Shell Creek (TU 539A), the type locality for the Bermont Formation. Although the 17 specimens available for study yield no information on the protoconch whorls, in terms of the gross shell characteristics that have been used to distinguish *S. evergladesensis* from *S. lindae*, all of the Shell Creek specimens more closely resemble the former. The distinctive chevron color pattern often present in upper Pinecrest and Caloosahatchee specimens was not observed in this Shell Creek sample.

It is clear that Petuch's *S. lindae* represents the form identified herein as Taxon D, even though most of the characteristics used by him to distinguish the taxon are suspect. *Strombus lindae* can, therefore, be seen as a valid taxon. Whether one equates *S. evergladesensis* with the upper Pinecrest and Caloosahatchee form (Taxon B = Taxon C) at this point in time depends upon the importance one places in the apparent rarity of color patterns in this taxon. In other respects the taxon would seem to capture the salient features of the older Caloosahatchee and upper Pinecrest forms. The situation could be clarified if it were possible to create complete growth profiles for *S. lindae* and *S. evergladesensis*. Until this can be accomplished the most conservative position would be to equate *S. evergladesensis* with Taxa B and C, considering its distribution in the fossil record to range from the upper Pinecrest beds to at least the lower portion of the Bermont Formation. Again, if the characteristics used to separate Taxon D from Taxa B and C are not deemed to be sufficient for that purpose, then all three forms should be equated with *S. evergladesensis*, with *S. lindae* being considered a form of that taxon.

Chronostratigraphy.

The APAC Pit. In the past few years a team of investigators from the University of Florida have applied a multi-faceted approach to the Pliocene/Pleistocene geochronology of selected south Florida sites (Webb *et al.*, 1989; Jones, 1990; Jones *et al.*, 1991). For the APAC study (Jones *et* *al.*, 1991), paleomagnetic assessments were undertaken and strontium isotope ratios measured for all of the eleven units identified by Petuch (1982), and ostracode samples were collected for all but the lowest unit. The critical unit, however, was Petuch's "black layer" (Unit 4), an organically-rich marine deposit containing abundant vertebrate remains. The mammalian remains present in that unit, their concurrent range elsewhere in the country, and the reversed magnetic polarity associated with all units, suggested an age for Unit 4 ranging from 2.5 Ma to 2.1 Ma (Jones *et al.*, 1991, p. 642). Of the units above the black layer, only Unit 1 appeared to be of appreciably different age. Based upon strontium isotopic ratios, a rather broad age range of 2.0 Ma to 1.0 Ma was proposed for that unit (Jones *et al.*, 1991, p. 644). The ostracode fauna present in the units below Unit 4 occur elsewhere in coastal plain deposits dated between 3.5 Ma and about 2.8 Ma. Based upon this and the paleomagnetic evidence, the authors came up with three possibilities for what has been referred to herein as the lower Pinecrest beds at APAC:

> "(1) if the faunas are 2.5 Ma or younger, these units could be placed in the lower Matuyama Chron, along with Units 4 and above; (2) if the faunal age is truly around 3 Ma, a correlation with the Kaena or Mammoth Subchrons within the Gauss Chron is possible; or (3) if the faunal age is closer to 3.5 Ma, these units might belong in the upper portion of the Gilbert Chron." (Jones *et al.*, 1991, p. 645).

In the present study of *Strombus* sensu stricto, samples were collected for study from Units 2, 4, 6 and 7 at APAC and the equivalent units at the nearby Quality Aggregates operation. Analysis of that material demonstrated clearly that, at least in the case of *Strombus*, the fauna of the lower units is not the same as that of Unit 4 and above. *Strombus floridanus*, described from the *Cancellaria* zone of the Jackson Bluff Formation, was present in Units 6 and 7, but not in the upper units. From Unit 4 upward it is replaced by a form referred to herein as Taxon B that is not found in the Jackson Bluff Formation. In terms of shell morphology Taxon B is more closely related to the Caloosahatchee form (Taxon C) and even to the Bermont form (Taxon D) than it is to the underlying *S. floridanus*. This suggests a hiatus between Unit 4 and the units below, lending support to either the second or the third of the hypotheses above, or to some combination of the two.

Lyons (1990, 1991) has demonstrated that Unit 1 at APAC contains a Caloosahatchee-age molluscan fauna. Although *Strombus* specimens have not been collected from that unit for study, one would not expect them to be of use in clarifying the relationship between this unit and underlying units, given the morphological similarity between the Caloosahatchee Taxon C from other localities and the upper Pinecrest Taxon B from APAC. Helium-uranium dates by Bender (1973) in the range of 1.9 Ma to 1.7 Ma for corals taken from another Caloosahatchee site, together with the evidence presented by the University of Florida team concerning the age of the Leisey Pit strata to be discussed below, support an age for Unit 1 towards the older end of the 2.0 Ma to 1.0 Ma range presented by Jones *et al.*, probably before the onset of the Olduvai Subchron at 1.88 Ma.

The Leisey Shell Pits. Extensive vertebrate bone beds separating massive marine shell beds were uncovered during the 1980's in two of three adjacent borrow pits excavated near Little Cockroach Bay in southern most Hillsborough County (Webb *et al.*, 1989). The accumulated weight of evidence would seem to restrict a substantial portion of the Leisey section, including the bone beds and the underlying marine deposits, to an age range of 1.66 Ma to 1.4 Ma (Webb *et al.*, 1989, p. 109). Based upon the presence of small numbers of three fossil species thought to be index fossils for the Bermont, the authors tentatively referred all of the marine sections below the bone beds, as well as some above the bone beds, to the Bermont Formation. However, they admitted that most of the taxa identified with more southerly Bermont sites are absent from the Leisey fauna, suggesting that this might be due either to temperature differences or to age differences, with the strata at the Leisey Pits being somewhat younger than their southern counterparts.

Specimens of *Strombus* sensu stricto are among the most common gastropods present in the Leisey fauna, although juveniles with well-preserved protoconchs are rare. A total of 115 specimens were studied for this paper, 100 adults and 15 juveniles. Of the 115 specimens, 39 were borrowed from the collections of the Florida Museum of Natural History and 29 of those were collected *in situ* during the field work carried out in conjunction with the Webb *et al.* study. The remaining 86 specimens were collected from spoil. Only one of the 100 adult specimens could be referred to the Bermont form described by Petuch as *S. lindae*. It was collected from spoil in Pit #03. Of the remaining 99 adults, 73 have shoulder spines on the body whorl and appear to be identical to the form identified herein as Taxon E (= *S. alatus*) present in the post-Bermont deposits of southern Florida. Among the specimens collected *in situ* from different horizons within the Leisey pits, spined specimens were found above, below, and in the bone beds. While the remaining 26 adults that do not have shoulder spines on the body whorl could represent Petuch's supposed Bermont *S. evergladesensis*, it is much more likely that they are simply smooth shouldered specimens of *S. alatus*. Recall that the fraction of spined adults among sampled populations of Taxon E ranges from 50% to 96%.

To seek further clarification concerning the identity of the Leisey form of *Strombus*, 55 specimens, including all of those borrowed from the Florida Museum, were analyzed to obtain a growth profile. These were then compared with the profiles developed for Taxon E and for Recent *S. alatus*. Two of these comparative second order plots are presented in Text-figure 19 to show the similarities among the three forms. There would seem to be little doubt that all three profiles belong to the same species, *S. alatus*.

One is forced to conclude that a large majority of the *Strombus* at the Leisey Shell Pits, both above and below the bone beds, represent *S. alatus* and not either of the forms assigned by Petuch to the Bermont Formation, *S. lindae* or *S. evergladesensis*. *Strombus lindae*, the one taxon unquestionably identified with the Bermont Formation at more southerly locations, is present in the Leisey pits, but appears to be very rare. As pointed out above, although some of the specimens lacking shoulder spines on the body whorl might represent *S. evergladesensis*, the form found in the upper shell beds at Shell Creek, their presence with *S. alatus* suggests that they are simply spineless specimens of that taxon.

Given that Taxon E (*S. alatus*) is present even in the lower shell beds, it is unlikely that much of the Leisey section is referable to the Bermont biozone, as it is defined either at the type locality or at sites south of Lake Okeechobee. Whether one wants to consider the fauna present as "younger" Bermont or post-Bermont is of little real significance here. The important point is that the University of Florida studies would seem to compress a number of biozones representing a significant amount of evolutionary activity and/or geographic replacement into a rather short time interval. Units 4 through 2 at APAC are regarded by most investigators to be part of a biostratigraphic unit known as the Pinecrest beds (albeit the upper Pinecrest beds

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PLATE 4

Figures

1-3. *Strombus alatus* Gmelin (X 0.8)

1. Hargreave Collection; height 89.9 mm, diameter 50.5 mm.
   Locality: Sanibel Island, Florida; Recent.
2. Hargreave Collection; height 78.6 mm, diameter 45.5 mm.
   Locality: Sanibel Island, Florida; Recent.
3. USNM 483769; height 71.6 mm, diameter 44.3 mm.
   Locality: Temporary excavation, Bass Road, Lee County, Florida; Ft. Thompson Formation?

(Diameter of all specimens includes the expanded adult lip but not shoulder spines)

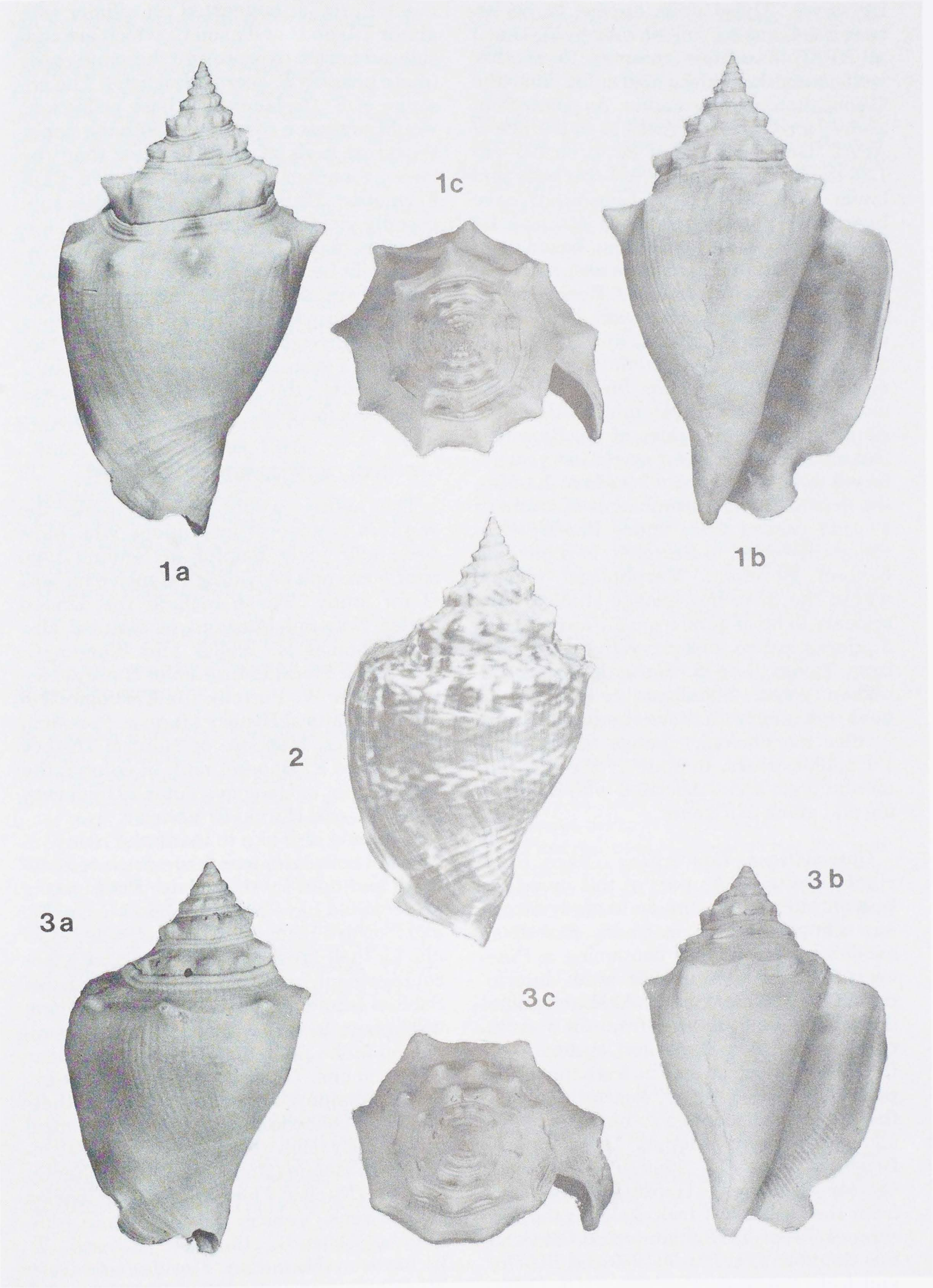

PLATE 4

by some). These units appear to be between 2.4 and 2.1 million years old. Unit 1 at APAC has been referred to another well-established biostratigraphic unit, the Caloosahatchee Formation. As pointed out above, a reasonable guess as to the age of APAC Unit 1 would be between 2.0 and 1.88 million years old. The bone beds and lower shell beds at the Leisey pits have been dated at between 1.66 Ma and 1.4 Ma, and it is suggested herein, based upon the *Strombus* fauna, that this represents a post-Bermont (or younger Bermont) assemblage. If this is the case, then somewhere in between 1.88 Ma and 1.66 Ma the "real" Bermont biozone must be accommodated, not to mention the Holey Land unit if it proves to be something other than simply a limestone facies of the Bermont. Put another way, in a one million year interval or less (*i.e.*, from 2.4 Ma to 1.4 Ma), the marine faunal assemblages of southern Florida passed from upper Pinecrest, to Caloosahatchee, to Bermont, to something beyond Bermont. Morphologic change within the *Strombus* lineage studied here appears to have gone from *S. floridanus* to *S. alatus* in two million years or less, and from Taxon B to *S. alatus* in about one million years. Significantly, the lineage does not seem to have undergone any further morphologic change for the past 1.4 million years, in spite of the environmental pressures associated with the coming and going of ice ages.

Observations Concerning Other Pinecrest Localities. As part of this investigation an attempt was made to study *Strombus* samples taken in years past from localities identified as containing a Pinecrest fauna by Olsson (1964) in his description of the Pinecrest beds. Although potentially important material from the type locality in western Dade and eastern most Collier Counties, as well as from the Acline pits in Charlotte County, was not available, the author did manage to obtain material for study from Slough Ditch in the Brighton area of southern Highlands County (localities TU 520 and TU 752), from the vicinity of lock 65-D on the Kissimmee River in Highlands and Okeechobee Counties (TU 728, TU 769 and TU 770), and from the Mule Pen Quarry in Collier County (TU 1177). In all instances developmental profiles suggested an affinity with either Taxon B or Taxon C, which are considered herein to represent the same entity (quite possibly *S. evergladesensis)*. The absence of *S. floridanus* in these collections would suggest a correlation with the upper Pinecrest beds at APAC rather than the lower Pinecrest beds and Jackson Bluff Formation. Since all of these localities supposedly yielded a mixed Pinecrest/Caloosahatchee fauna, an alternative interpretation might be that all of the *Strombus* taken came from the Caloosahatchee components of those faunas. Given the ubiquitous nature of *Strombus* sensu stricto in the Pliocene and Pleistocene fossil record of southern Florida, this alternative seems less likely than the first.

VI. ACKNOWLEDGMENTS

The author would like to thank the workers at several institutions who have been extremely helpful in lending type specimens and providing extensive material for study. These include the United States National Museum of Natural History (Thomas R. Waller and Warren C. Blow), the Florida Museum of Natural History (Roger W. Portell), the Carnegie Museum of Natural History (Juan J. Parodiz), the Houston Museum of Natural History (Constance E. Boone), and, of course, the Department of Geology, Tulane University (Emily H. and Harold E. Vokes).

He would also like to thank the many individual collectors who have provided material and data for this study. First among these would have to be the late Miriam W. and Howard Schriner Jr. of La Belle, Florida, for their great generosity and early encouragement, and Susan B. Stephens of Sanibel Island, Florida, for her unflagging willingness to be an advance scout, companion in the field, and generous provider of specimens. Others who have been extremely helpful and generous with their personal collections are, in alphabetical order, Billy Bell (Naples, Florida), Constance E. Boone (Houston, Texas), Wendy Conway (Naples, Florida), the late Charles J. Hertweck (Venice, Florida), Anne Joffe (Sanibel Island), the late Cheryl T. Richardson (Marathon, Florida), and Gary W. Schmelz (Naples, Florida). If anyone has been omitted, it has been due to the

author's lack of organization not appreciation.

Finally, the author would like to thank Dana H. Geary (University of Wisconsin) and Warren D. Allmon (Paleontological Research Institution) for their careful reading of and valuable comments concerning the original manuscript. Any remaining factual or grammatical errors, faulty interpretations, or obscure and convoluted passages are strictly the fault of the author.

Abbreviations for institutions holding type material, figured specimens, and lots utilized in this study are:

CMNH - Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA
HMNS - Houston Museum of Natural Science, Houston, Texas, USA
TU - Tulane University, New Orleans, Louisiana, USA
UF - Museum of Natural History, University of Florida, Gainesville, Florida, USA
USNM - U. S. National Museum of Natural History, Washington, DC, USA

VII. LOCALITY DATA

The following are Tulane University fossil locality numbers:

60. Jackson Bluff Fm., borrow pits at Jackson Bluff, Ochlockonee River (NW1/4 Sec. 21, T1S, R4W), Leon Co., Florida.
201. Bermont Fm., spoil banks at pit just south of Belle Glade (at Belle Glade Camp), Palm Beach Co., Florida.
520. Pinecrest beds, spoil banks, canal 0.9 mile east of Brighton on Florida Highway 70 (Sec. 25, T37S, R32E), Highlands Co., Florida.
539A. Bermont Fm., Shell Creek (upper beds), about 8 miles east of Cleveland (Sec. 30, T40S, R25E), Charlotte Co., Florida. (Designated as type locality of the Bermont Formation by DuBar, 1974, p. 221.)
580. Bermont Fm., North New River Canal spoil banks, 1 mile south of South Bay, Palm Beach Co., Florida.
728. Pinecrest beds, spoil banks on west side of Kissimmee Canal and east side of Kissimmee River, just across from U.S. Corps of Engineers Structure 65-D (Sec. 33, T36S, R33E), Okeechobee Co., Florida.
752. Pinecrest beds, spoil banks on south side of canal 41-C ("Slough Ditch") at crossing of county road, 4.3 miles east of Brighton and 1.4 miles south of Florida Highway 70 (SE1/4 Sec. 33, T37S, R33E), Highlands Co., Florida.
769. Pinecrest beds, spoil banks east side of Kissimmee River, 1 1/2 to 2 miles south of U.S. Corps of Engineers Structure 65-D (NE 1/4 Sec. 35, T36S, R33E), Okeechobee Co., Florida.
770. Pinecrest beds and Caloosahatchee Fm. mixed, spoil banks west side of Kissimmee River, 1 1/2 to 3 1/2 miles north of Florida Highway 70 (Secs. 10, 14, 15, and 28, T37S, R33E), Highlands Co., Florida.
797. Pinecrest beds, material exposed during construction of "Alligator Alley," 13.3 miles east of Florida Highway 29 (T49S, R32E), Collier Co., Florida.
978. Bermont Fm., spoil banks at pit on south side of waterworks, about 1 1/2 miles northeast of South Bay, Palm Beach Co., Florida.
991. Caloosahatchee Fm., Cochran rock pit, 2 1/2 miles west of La Belle, on north side of Florida Highway 80, Hendry Co., Florida.
1000. Pinecrest beds, APAC pits at east end of 17th street (T36S, R19E), about 8 miles east of U.S. Highway 301 at Sarasota (now northwest corner of Fruitville Road exit I-75), Sarasota Co., Florida.
1177. Pinecrest beds and Caloosahatchee Fm. mixed, Mule Pen Quarry, north side of Florida Highway 846, 9.1 miles east of U.S. 41 at Naples Park (SE1/4 Sec. 24, T48S, R26E), Collier Co., Florida.
1512. Caloosahatchee Fm. and Bermont Fm. mixed, De Soto Shell Company, pits 2 miles east of Florida Highway 31, about 12 miles south of Arcadia (T39S, R25E), De Soto Co., Florida.
1524. Pinecrest beds, Quality Aggregates Pit, off Richardson Road, north side of Fruitville Road and east of highway I-75, east of Sarasota, Sarasota Co., Florida.
1536. Pinecrest beds, Caloosahatchee Fm. and Bermont Fm. mixed, Star Ranch, Bergeron Rock Co. pit, 11.4 miles south of South Bay, and 0.8 mile west of U.S. Highway 27, Palm Beach Co., Florida.

The following are fossil collecting localities of the Invertebrate Paleontology Division, Florida Museum of Natural History, University of Florida:

GD003 Jackson Bluff Fm., Lake Talquin, Gadsden Co., Florida.
HI001 Bermont Fm., Leisey Shell Pit 01, bone bed, lower shell bed, and upper shell bed, Hillsborough Co., Florida (SE1/4, SW1/4 Sec. 15, T32S, R18E; Ruskin Quadrangle, USGS 7.5 minute series).
HI013 Bermont Fm., Leisey Shell Pit 03, bone bed, Hillsborough Co., Florida (N1/2 Sec. 15, T32S, R18E; Ruskin Quadrangle, USGS 7.5 minute series).

HI014 Ft. Thompson Fm., Leisey Shell Pit 03, upper shell bed, Hillsborough Co., Florida (N1/2 Sec. 15, T32S, R18E; Ruskin Quadrangle, USGS 7.5 minute series).

HI015 Bermont and Ft. Thompson Fms. mixed, Leisey Shell Pit 03, spoil, Hillsborough Co., Florida (N1/2 Sec. 15, T32S, R18E; Ruskin Quadrangle, USGS 7.5 minute series).

LN001 Jackson Bluff Fm., Jackson Bluff 01, material taken from borrow pit at power plant, Leon Co., Florida (NW1/4 Sec. 21, T1S, R4W; Bloxham Quadrangle, USGS 7.5 minute series).

LN002 Jackson Bluff Fm., Jackson Bluff 02, Leon Co., Florida (SW1/4 Sec. 16, T1S, R4W; Bloxham Quadrangle, USGS 7.5 minute series).

LN003 Jackson Bluff Fm., *Cancellaria* zone, Harvey Creek, Lake Talquin, Leon Co., Florida (SW1/4 Sec. 9, T1S, R3W; Bloxham Quadrangle, USGS 7.5 minute series).

LN004 Jackson Bluff Fm., Jackson Bluff, general, Leon Co., Florida (Sec. 16, 20, and 21, T1S, R4W; Bloxham Quadrangle, USGS 7.5 minute series).

The following are fossil localities collected by the author:

F01 Caloosahatchee Fm., Hendrickson Quarry, about .5 mile east of CR 768, just north of airport, Punta Gorda, Charlotte Co., Florida.

F07 Bermont Fm., spoil banks along the east sideof the North New River Canal, about 11 miles south of South Bay and just east of U.S. 27, Palm Beach Co., Florida.

F11 Ft. Thompson Fm., spoil from temporary excavation for new hospital, Bass Road near the intersection of SR 869, southwest of Ft. Myers, Lee Co., Florida.

F14 Ft. Thompson Fm., spoil piles along canal paralleling south side of new SR 80, 2.5 miles east of intersection with U.S. 441, northeast of Belle Glade, Palm Beach Co., Florida.

F15 Ft. Thompson Fm., spoil banks from ditch dug to depth of 4 to 5 meters, about 1/2 mile west of Burnt Store Road (CR 765) and 3 miles south of Charlotte County line, Lee Co., Florida. This locality is just to the north of FMNH site LE010, Burnt Store Road Pit 01A, (N1/2 Sec. 30, T43S, R23E; Matlacha Quadrangle, USGS 7.5 minute series).

The following are Recent collecting localities:

RFK01 Directly south of Key West, Florida; taken from stomachs of bat fish feeding among eel grass in 35-40 feet of water.

RFK02 Big Pine Key, Florida; Coupon Bight, off marker 3, Sheriff's Island, on sand in 3-6 feet of water.

RFK03 Hawk Channel, 3-4 miles south of Bahia Honda Key, Florida; 40 feet on soft mud bottom.

RFK04 East of Coffin's Patch, Marathon, Vaca Key, Florida; 32 feet on sand.

RFK05 Hawk Channel, off Duck Key, Marathon, Florida; 35 feet on sand.

RFG01 Off Beach Club Hotel, Naples, Florida; 8-10 feet on sand.

RFG02 San Carlos Bay, just west of Punta Ybel, Sanibel Island, Florida; 4-6 feet on sand.

RFG03 Gulf side, SanibelIsland, Florida; on intertidal sand bars 1 mile west of Punta Ybel.

RFG10 St. Andrews Bay at St. Andrews Recreation Area, Panama City, Florida; on grassy sand flats in 4-6 feet of water.

RTG01 Heald Bank, 31 miles ESE of Galveston, Texas; by divers in 12 fms. at Pleistocene rock outcrop, 2 miles south of #1 buoy. A lot of small juveniles from the Houston Museum of Natural Science (lot #15,249).

RCM01 Isla del Carmen, Campeche, Mexico; beach about 3 km west of Paso Real. (Close to Tulane locality R-52.)

RCM02 Sabancuy, Campeche, Mexico; beach at restaurant just south of where the road to Sabancuy meets Route 180.

RCM03 Punta Chanchec, 56 km NE of Isla Aguada, Campeche, Mexico. (= Tulane locality R-49.)

RCM04 Beach just south of Punta Sihoplaya, Campeche, Mexico.

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IX. ENDNOTES

[1] As Lyons (1991, p. 136) points out, the *North American Code of Stratigraphic Nomenclature* requires that lithostratigraphic units such as formations be differentiated in terms of lithologic characteristics. However, there are few lithologic criteria that can be used to separate the major biostratigraphic units in southern Florida that have been described over the years as formations. The author has decided to continue to utilize these long-standing formational names in this article because of their widespread use in the geological and paleontological literature and because of their potential for distinguishing chronologically distinct faunal units.

[2] These intermediate forms have generally all been equated with *S. pugilis* or *S. alatus* in broad-scale faunal studies (Heilprin, 1886, p. 83; Dall, 1890, p. 177; Olsson and Harbison, 1953, p. 273; DuBar, 1958, p. 214; and Hoerle, 1970, p. 63). Recently, however, Petuch has described two morphological variations purportedly found in the Bermont Formation as *Strombus evergladesensis* (1991, p. 14, pl. 1, figs. 11 and 12) and *Strombus lindae* (1991, p. 14, pl. 1, figs. 13 and 14). Therein and elsewhere (1992, p. 44) Petuch suggests that these two forms, together with *S. alatus*, represented three sympatric species, only one of which survived subsequent extinction events. This scenario of phyletic divergence and subsequent extinction used to explain morphological variation among early Pleistocene *Strombus* sensu stricto found in southern Florida excavations will be dealt with later in this paper.

[3] Some interesting examples of such computer-generated shell-forms can be seen in the introduction to the popular coffee-table shell book by M. G. Harasewych (1989, p. 17).

[4] The term "rate" as used here does not signify a measure of change **per unit of time,** but rather a measure of the change in a given measurement **per whorl.** It is in this sense that the term will be used throughout this study.

[5] For detailed locality data see Section VII.

[6] The presence of occasional specimens of *Vasum floridanum* McGinty, 1940, indicates the presence of Bermont material at the sites. On the other hand, the existence at the Florida Museum of Natural History of a single specimen of *Strombus hertweckorum* Petuch, 1991, from pit 1 suggests that an underlying Pinecrest fauna was uncovered on at least one occasion.

[7] When describing *S. alatus* in 1791, Gmelin referred to a figured specimen without shoulder spines on the body whorl (Martini, 1777, pl. 91, fig. 894). No type locality was given by him. This led to ongoing confusion regarding the identity of the taxon. Dall (1890) assumed that Gmelin's taxon was simply a spineless form of *S. pugilis*,

more prevalent in both the Recent and fossil record of Florida, but present throughout that species' range. Clench and Abbott (1941) maintained that the figured specimen referred to by Gmelin was the Florida form of *S. pugilis* (with or without spines on the body whorl) and, based on a number of distinguishing features, assigned a subspecific rank to it. Sanibel Island was designated as the type locality. Olsson and Harbison (1953), while retaining the subspecific rank in their work, suggested the re-elevation of *S. alatus* to full specific rank based upon the constant agreement of the Caloosahatchee form, referred to herein as Taxon C, with Gmelin's type figure. However, Morris (1951) had already taken this step based entirely upon the distinctions noted by Abbott and Clench, and Abbott himself soon followed suit (1954), thus presenting *S. alatus* as a distinct species in two of the most popular and authoritative American shell guides available in the early 1950's.

[8] As will be demonstrated later in this paper, it is only the lower portion of the Pinecrest beds (Units 5-10 at APAC) that correlate with the Jackson Bluff Formation. Whether these units are older than the *Cancellaria* zone of the Jackson Bluff Formation is also open to debate based upon the *Strombus* fauna. Although further study is required on this point when better-preserved material becomes available, the *S. floridanus* collected just below the lower *Vermicularia* bed (Unit 8) at APAC seem to show a greater affinity to the Jackson Bluff form of that taxon in some respects than to the form found in Units 6 and 7 at APAC.

[9] The horizontal line of a notched box plot indicates the median value for a sample and the notches approximate the 95% confidence interval for the sample median. McGill *et al.* (1978) have demonstrated that, in general, the difference in median values of two samples can be considered statistically significant if the notches do not overlap. However, they note that little confidence should be placed in "folded boxes" wherein the notch extends beyond the quartile box.

[10] It is possible to find *Strombus* specimens in spoil at the Quality Aggregates site that do have axial ribs or even weak shoulder knobs extending onto the body whorl. While some of the specimens are small enough to be confused with *S. floridanus* from the lower units of the pit, this form comes from the *Trochita* bed at the top of the section.

[11] Typically, once these specimens dry out the pattern is no longer visible to the naked eye.

[12] In a sample recently collected from spoil piles at the Florida Rock Quarry in western Dade County, made up at least in part of specimens which can be equated with the form identified by Petuch (1991) as *Strombus lindae*, 20% of the 42 adults exhibit axial sculpture on the body whorl. In at least two cases the sculpture consists of knobs indistinguishable in size and shape from those found on the body whorl of Recent *S. alatus.* The age of this material, however, has not been clearly established.

[13] The overlapping notches for the samples of *S. floridanus* and Taxon B, on the one hand, and for the samples of Taxon C and Taxon D, on the other, forces one to question the statistical significance of those pairs of sample medians. However, even if one were to equate the protoconch sizes of *S. floridanus* with Taxon B and Taxon C with Taxon D, there would remain a two-step incremental reduction over time. Larger data sets would be desirable to help resolve the nature of this change.

[14] It is often possible to collect more than one form from the same locality. However, this mixed material seems to be derived from spoil pile sampling. For the younger (*i.e.*, Bermont and post-Bermont) deposits found in the Everglades south of Lake Okeechobee this is the only strategy possible as the water table is at the surface and even borrow pits are flooded, being worked with drag lines. For the generally older deposits outside the Everglades northwest of Lake Okeechobee, where the water table is lower allowing borrow pits to be kept dry by pumping while being worked, *in situ* sampling does not yield a mixture of forms.

[15] The author has in his possession Recent *S. alatus* that have identical morphological characteristics, strong spiral sculpture on the body whorl combined with pronounced resting varices, and the same signs of predation. However, the collecting data are insufficient to allow conclusions to be drawn concerning the environmental conditions that might give rise to such morphological expressions.

[16] In an as-yet unpublished work Petuch will describe four more *Strombus* sensu stricto taxa from the Pliocene/Pleistocene of southern Florida. Although the type specimens have been studied, the author will await publication of the descriptions of the taxa and locality data before commenting.

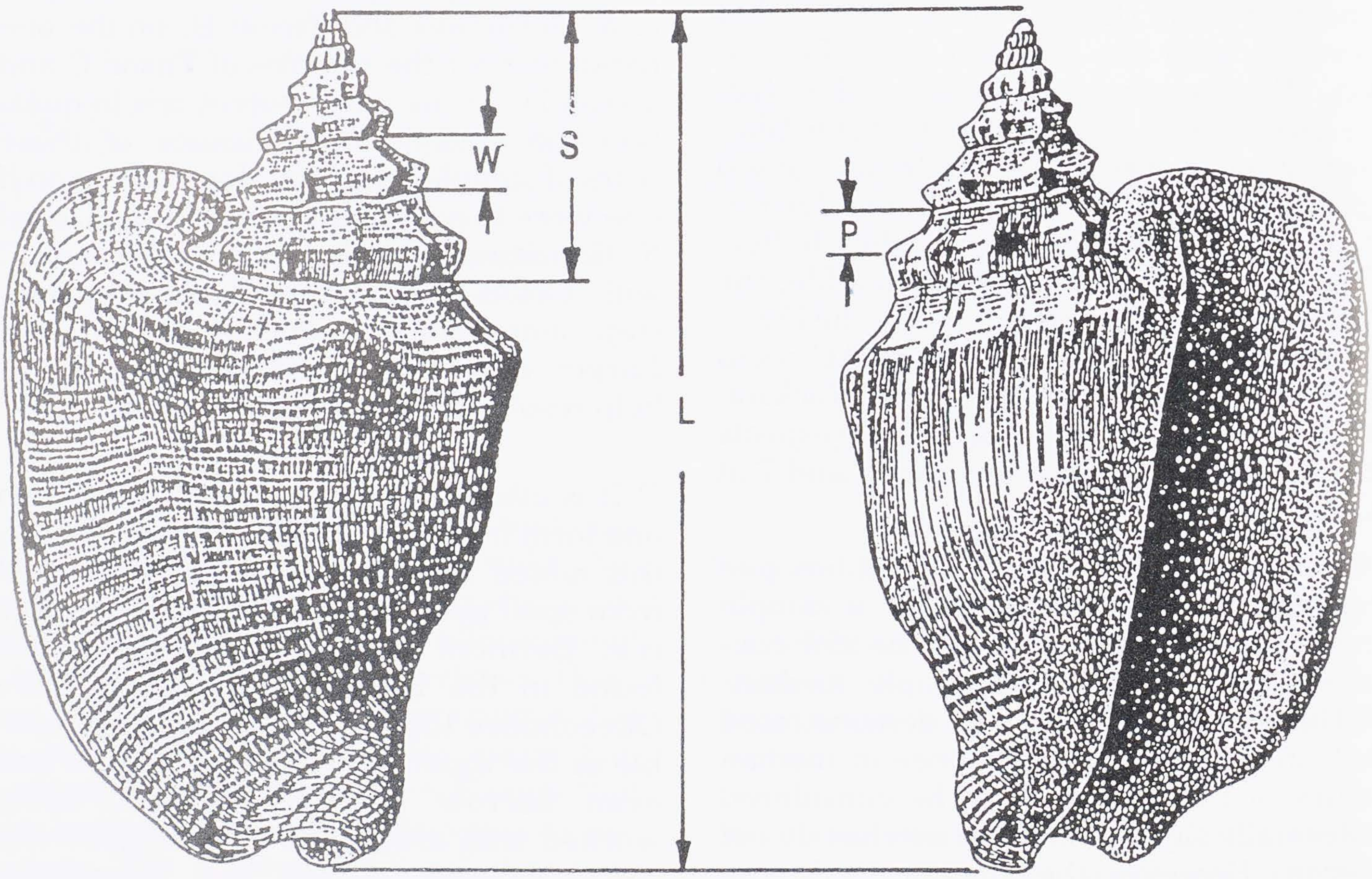
[17] Having studied thousands of specimens from the Miocene, Pliocene, Pleistocene, and Recent, this author finds it highly unlikely that any *Strombus* s.s. taxon yields adults smaller than about 45 mm.

[18] Interestingly, Petuch, in his popular work (1992, p. 43), includes a drawing of a "herd" of *S. evergladesensis* grazing on algal films in the Okeechobean Sea. All six of the specimens in the scene sport chevron patterns on the body whorl. Whether this represents artistic license on his part, based upon his having seen the pattern in older forms, or is an accurate reflection of the material collected from the type locality, is hard to say.

X. APPENDIX: MEASUREMENT PROTOCOLS

The following linear measures were made for all specimens analyzed. All measurements were carried out with vernier calipers, except as noted. For incomplete specimens, estimates were made of the amount of shell missing whenever possible. The letters in square brackets [ ] refer to Text-figure 20.

Shell length [L]. The distance from the apical tip to the anterior end of the siphonal



Text-figure 20. The linear measures carried out on those juvenile and adult *Strombus* analyzed in detail in this study. All measurements were made parallel to the axis of coiling using either vernier calipers, dividers and a millimeter scale, or a reticle mounted in the eyepiece of a binocular microscope.

canal, measured parallel to the axis of coiling.

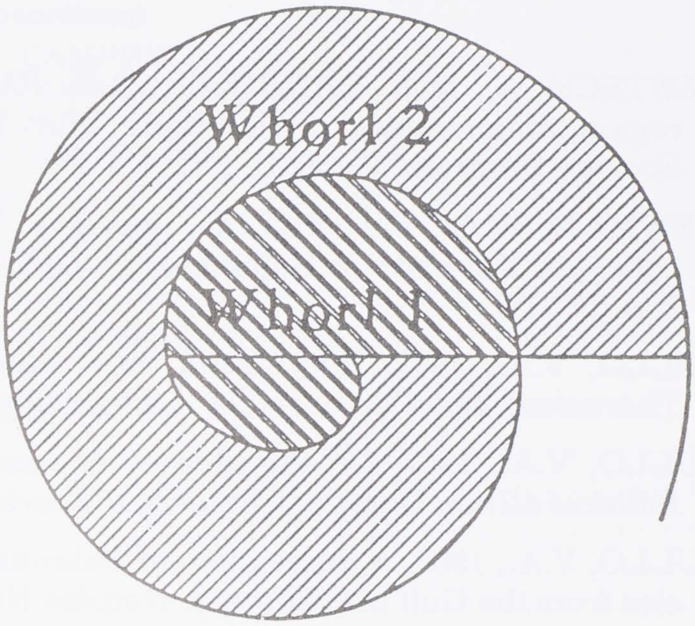
Maximum shell width. Measured perpendicular to the axis of coiling across the widest point of the shell (including the expanded lip in adults).

Dorsal/ventral body width. Measured in a direction that is both perpendicular to the axis of coiling and at right angles to the measurement of maximum shell width.

Spire height [S]. Measured parallel to the axis of coiling from the spire tip to the suture of the body whorl at the dorsal midline of adults (*i.e.*, roughly one quarter whorl before cessation of shell development in the expanded adult lip). For juvenile specimens, the distance measured was from the spire tip to the suture terminus. For very small specimens the measurement itself was performed under a binocular microscope fitted with a linear reticle scale. For larger specimens a divider and millimeter scale were used.

The following linear measurements were carried out for each spire whorl present. All measurements were made using a linear reticle scale mounted in the eye piece of an Olympus 7 to 40 power binocular microscope:

Whorl diameter. Specimens mounted so that the spire could be viewed from directly above. Those with intact protoconchs were oriented so that the initial whorls corresponded to Text-figure 21. With the whorls so defined, the diameter of each whorl present, defined as the distance from the mid-point to the end of the whorl, was measured. Incomplete specimens were oriented for analysis by setting the diameter of the smallest measurable whorl present equal to the mean value for that whorl as determined from measurements of perfect or more complete specimens in the sample. Once a specimen was oriented and the whorls thereby defined, the other two measurements and counts could be undertaken.



Text-figure 21. Shell orientation for the analysis of whorls (after Fisher *et al.*, 1964). Whorl diameter was measured from the mid-point to the end-point of a whorl at right angles to the axis of shell coiling.

Whorl height [W]. Specimens mounted so that the axis of coiling was oriented horizontally and the end points of the whorls facing upwards. Whorl height was determined by measuring the distance at the end of the whorl from the suture representing the point of attachment of that whorl (*i.e.*, the posterior suture) to the suture representing the point of attachment of the succeeding whorl (*i.e.*, the anterior suture).

Shoulder height [P]. Specimens mounted so that the axis of coiling was oriented horizontally and the end points of the whorls facing upwards. Shoulder height was defined as the distance measured at the end of the whorl from the posterior suture to the whorl periphery (for rounded whorls) or shoulder (for angled whorls).

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