Ecology and Evolution of the Gastrochaenacea (Mollusca, Bivalvia) with Notes on the Evolution of the Endolithic Habitat

Joseph Gaylord Carter

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ECOLOGY AND EVOLUTION OF THE GASTROCHAENACEA (MOLLUSCA, BIVALVIA) WITH NOTES ON THE EVOLUTION OF THE ENDOLITHIC HABITAT

JOSEPH GAYLORD CARTER

ABSTRACT

The Gastrochaenacea are a compact group of mechanically and chemically boring bivalves that comprise a major but commonly overlooked element of tropical and subtropical endolithic faunas. As shown by their representatives in *Diploria* skeletons at Soldier Key, Florida, *Spengleria rostrata, Gastrochaena (Gastrochaena) hians* and *Gastrochaena (Rocellaria) ovata* are well suited to life in thin and rapidly eroded substrata. They have adapted to this habitat by evolving an unusual capacity for siphonal retraction and extension, a unique mechanism for directional boring, and the ability to secrete thick calcareous burrow linings and to rapidly repair damaged burrows.

The Gastrochaenacea probably evolved in the Triassic or Lower Jurassic from shallow infaunal burrowing permophorids or grammysiids through an intermediate semiendolithic nestling stage. The evolution of endolithic lithophagids (Mytilacea) and gastrochaenids may have occurred in response to an expansion in the endolithic habitat accompanying the Triassic and Jurassic proliferation of scleractinian corals. Gastrochaenids underwent a secondary adaptive radiation in the Cretaceous and Tertiary, resulting in the tube-dwelling *Kummelia* and *Eufistulana* and the "igloo"-forming *Gastrochaena (Cucurbitula)*. Tube-dwelling gastrochaenids and clavagellids represent a classic example of synchronous evolutionary convergence from ecologically and phylogenetically distinct ancestors. The Clavagellacea probably evolved from deep-burrowing representatives of the Pandoracea.

The primary nutrition of Soldier Key gastrochaenids apparently does not come from diatoms, the likely dominant representative of the phytoplankton, because diatom tests are rarely encountered in intestinal contents. Future investigations should explore the possibility that gastrochaenid nutrition comes primarily from the microbiota of resuspended sediment or from planktonic organisms lacking mineralized tests. Efficient size sorting of ingested particles correlates with ctenidial plication and smaller and more numerous major siphonal tentacles in *Spengleria rostrata*.

Spengleria should be regarded as distinct from *Gastrochaena* at the genus level because of its unique pedal musculature, completely separated siphons, plicate ctenidia, moderate anterior shell reduction, and retention of periostracal calcification in the adult stage for mechanical boring. *Gastrochaena s.s.* and *Rocellaria* differ fundamentally only in their anterior shell reduction and the presence or absence of a prominent myophoral support for the anterior pedal retractor muscle. Consequently these two taxa should be regarded as subgenerically distinct. *Cucurbitula* is regarded as subgenerically distinct from *Gastrochaena s.s.* and *Rocellaria* because of its obligatory "igloo"-forming habit, its anteriorly reflected mantle, and other characteristic shell and burrow features.

Calcification of the periostracum in *S. rostrata* is genetically distinct from calcification of the underlying shell layers. The occurrence of periostracal calcification in adults of all Recent species of *Spengleria* and in juveniles of certain fossil *Gastrochaena* and *Eufistulana* suggests that this is an ancestral feature of the superfamily.

The endolithic habitat has been colonized by the Bivalvia in three successive evolutionary phases: 1) by lithophagids and gastrochaenids [Triassic (?) and Jurassic]; 2) by pholads and hiatellids [Jurassic and Cretaceous]; and 3) by representatives of several primarily nonendolithic families at various times in the Cenozoic. The first evolutionary phase was dominated by chemical borers of largely tropical and subtropical calcium carbonate substrata, whereas the second phase consisted of mechanical borers of a variety of substrata in all major temperature realms. Pholads and hiatellids have failed to evolve an abundant and diverse endolithic fauna in tropical carbonate substrata probably because of the preoccupation of this habitat by lithophagids and gastrochaenids with competitively superior boring mechanisms.

ZUSAMMENFASSUNG

Die Gastrochaenacea sind eine geschlossene Gruppe mechanisch und chemisch bohrender Muscheln, die ein wichtiges, oft uebersehenes Element tropischer und subtropischer endolitischer Faunen darstellen. Wie uns ihre Vertreter in den *Diploria* Skeletten in Soldier Key, Florida, zeigen, sind *Spengleria rostrata, Gastrochaena (Gastrochaena) hians* und *Gastrochaena (Rocellaria) ovata* in spaerlichem und schnell ausgewaschenem Substrat gut lebensfaehig. Sie haben sich an dieses Habitat angepasst, indem sie eine ungewoehnliche Faehigkeit zur siphonalen Rueckziehung und Ausdehnung entwickelt haben, einen einmaligen Mechanismus zum direktionalen Bohren und die Faehigkeit, festen, kalkigen Roehrenbelag (burrow linings) auszusondern und beschaedigte Roehren (burrows) schnell auszubessern.

Die Gastrochaenacea entwickelten sich wahrscheinlich in der Trias oder Unteren Jura aus seicht grabenden Permophoriden oder Grammysiiden durch ein halb-endolitisches sich einnistendes Zwischenstadium. Die Entwicklung von endolitischen Lithophagiden (Mytilacea) und Gastrochaeniden kann im Zusammenhang mit einer Ausdehnung des endolitischen Habitats, das die triassische und jurassische Prolifikation von scleraktinischen (scleractinian) Korallen begleitet hat, eingetreten sein. Die Gastrochaeniden erfuhren eine zweite adaptive Ausdehnung in der Kreide- und Tertiarzeit, aus der die Roehrenbewohner *Kummelia* und *Eufistulana* und die 'igloo'-bildende *Gastrochaena (Cucurbitula)* hervorgingen. Roehrenbewohnende Gastrochaeniden und Clavagelliden stellen ein klassisches Beispiel von gleichzeitiger Konvergenz aus oekologisch und phylogenetisch verschiedenen Vorfahren dar. Die Clavagellacea entwickelten sich wahrscheinlich aus sich tief eingrabenden Vertretern der Pandoracea.

Anscheinend besteht die Hauptnahrung der Gastrochaeniden von Soldier Key nicht aus Diatomeen (Kieselalgen), dem wahrscheinlich vorherrschenden Vertreter des Phytoplanktons, denn Testa von den Diatomeen ist selten im Darmgehalt anzufinden. Kuenftige Untersuchungen sollten die Moeglichkeit erforschen, ob die Nahrung von Gastrochaeniden hauptsaechlich aus Mikrobioten suspendierter Sedimente stammt, oder aus planktonischen Organismen ohne mineralisierten Schalen. Wirksame Groessensortierung eingenommener Partikel findet man in Verbindung mit ctenidialer Faltung und kleinerer, zahlreicherer Siphonaltentakel in *Spengleria rostrata.*

Spengleria sollte als Gattung von *Gastrochaena* getrennt betrachtet werden wegen ihre einmaligen Fussmuskulatur, den vollstaendig getrennten Siphonen, den gefalteten Ctenidien, der maessigen, vorderen Schalenreduktion und dem Vorhanden-oder Nichtvorhandensein einer Erwachsenenstadium zum mechanischen Bohren. *Gastrochaena s.s.* und *Rocellaria* unterscheiden sich im wesentlichen nur in ihrer vorderen

Schalenreduktion und dem Vorhanden-oder Nichtvorhandensein einer prominenten myophoralen Stuetze feur den vorderen Fussrueckzieher. Demzufolge sollten diese zwei Taxen nur subgenerisch getrennt betrachtet werden. *Cucurbitula* ist subgenerisch getrennt zu betrachten von *Gastrochaena s.s.* und *Rocellaria* wegen ihrer obligatorischen 'igloo'-bildenden Gewonnheit, ihres vorn zurueckgebogenen Mantels und anderer charakteristischer Schalen- und Wohnorteigenschaften.

Verkalkung des Periostrakum in *S. Rostrata* ist genetisch verschieden von Verkalkung der darunterliegenden Schalenschichten. Das Eintreten von Periostrakalverkalkung in Adulten aller rezenten Arten von *Spengleria* und in Juvenilen von gewissen fossilen *Gastrochaena* und *Eufistulana* weist darauf hin, dass dies ein urspruengliches Merkmal der Ueberfamilie ist.

Das endolitische Habitat wurde von den Bivalven in drei aufeinanderfolgenden Entwicklungsphasen besiedelt: 1) Von Lithophagiden und Gastrochaeniden [Trias (?) und Jura], 2) Von Pholaden und Hiatelliden [Jura und Kreide], und 3) von Vertretern von mehreren urspruenglich nicht-endolitischen Familien zu verschiedenen Zeiten in dem Kaenozoikum. Die erste Entwicklungsphase wurde von chemisch Bohrenden in zum groessten Teil tropischen und subtropischen Kalzium-karbonatsubstrat beherrscht, waehrend die zweite Phase aus mechanisch Bohrenden in einer Mannigfaltigkeit von Substraten in allen wichtigen Temperaturbezirken bestand. Pholaden und Hiatelliden waren unfaehig, eine reiche und diverse endolitische Fauna in tropischem Karbonatsubstrat zu entwickeln, wahrscheinlich wegen der Vorbesetzung dieses Habitats von Lithophagiden und Gastrochaeniden mit konkurrenzfaehigeren Bohrmechanismus.

РЕЗЮМЕ

Gastrochaenacea представляет собой компактную группу механически сверлящих и химически протравляющих двустворок, которые включают существенный, но обычно недооцениваемый элемент тропических и субтропических фаун каменистого грунта. Как видно по их представителям, найденным в скелетах кораллов *Diploria* в Солджир Ки, Флорида, США *(Soldier Key, Florida), Spengleria rostrata, Gastrochaena (Gastrochaena) hians* и *Gastrochaena (Rocellaria) ovata* очень хорошо приспособлены к жизни в тонких и быстро размываемых субстратах. Они очень хорошо приспособились к этой среде, развив, из-за необыкновенной своей способности сифонального стягивания и удлинения, уникальный механизм для направленного сверления и способность протравливания ходов в породе и их быстрого восстановления в случае повреждения.

Gastrochaenacea вероятнее всего развилась в триасовый или ранний юрский период из живших в мелких ходах permophorids или grammysiids в промежуточный полукаменистый период гнездования. Эволюция живших в каменистом грунте lithophagids (Mytilacea) и gastrochaenids могла произойти в ответ на экспансию среды в каменистом грунте, сопутствующую триасовому и юрскому периодам пролиферации склерактинианских (scleractinian) кораллов. Gastrochaenids подверглись вторичной адаптивной радиации в меловой и третичный периоды, в результате чего образовались живущие в трубках *Kummelia* и *Eufistulana,* а также *Gastrochaena (Cucurbitula),* ходы которой напоминают по форме продольно разрезанную грушу. Живущие в трубках gastrochaenids и clavagellids представляют собой классический образец синхронной эволюционной конвергенции экологически и филогенетически различных предков. Clavagellacea вероятнее всего развились из живших в глубоких ходах представителей Pandoracea.

Диатомовые водоросли, которые, возможно, являются преобладающим элементом фитопланктона, по-видимому не являются главным источником питания для *gastrochaenids* в Солджер Ки, поскольку диатомовые раковины редко встречаются в содержимом их желудка. Дальнейшие исследования могут подтвердить вероятность того, что основным источником питания для *gastrochaenids* являются микроорганизмы *(microbiota)* осадков или планктонные организмы, не содержащие минеральных раковин. Эффективная сортировка по величине проглоченных частиц соотносится со складками жабр и с более многочисленными главными сифональными щупальцами у *Spengleria rostrata.*

Spengleria надо считать отличающимися от *Gastrochaena* на уровне рода из-за уникальной ножной мускулатуры, совершенно самостоятельных сифонов, складчатых жабр, умеренной редукции передней раковины и задерживания периостракальной кальсификации для механического сверления на взрослой стадии. *Gastrochaena s.s.* и *Rocellaria* фундаментально отличаются друг от друга на уровне подрода только характером редукции передних концов раковин и присутствием или отсутствием выпуклой мускульной *(myophoral)* подпорки для передней

отсутствием выпуклой мускульной *(myophoral)* подпорки для передней сократительной мышцы. Подрод *Cucurbitula* следует отличать от *Gastrochaena s.s.* и *Rocellaria* из-за обязательного свойства придавать ходу форму, напоминающую продольно разрезанную грушу, из-за завернутой на переднем конце мантии и из-за других характерных особенностей раковины и хода. *Gastrochaena s.s., Rocellaria* и *Cucurbitula* представляют собой 3 подрода рода *Gastrochaena.*

Кальсификация периостракума у *S. rostrata* генетически отлична от кальсификации нижних слоев раковины. Присутствие периостракальной кальсификации у взрослых организмов всех видов современных *(Recent) Spengleria* и у некоторых ископаемых *Gastrochaena* и *Eufistulana* (молодые организмы) наводит на мысль, это што является наследственной особенностью сверхсемейства.

Среда в каменистом грунте была колонизована двустворками (Bivalvia) в трех последовательных эволюционных фазах: 1) во-первых, это были lithophagids и gastrochaenids (триасовый (?) и юрский периоды); 2) во-вторых, это были pholads и hiatellids (юрский и меловой периоды); 3) и в-третьих, это были представители нескольких семейств не живших в каменистом грунте, которые заселили эту среду в различные времена кайнозойского периода. В первой эволюционной фазе преобладали химически протравливающие особи, главным образом, тропического и субтропического субстрата карбоната кальция, тогда как вторая фаза состояла из механически сверлящих особей различных субстратов всех главных температурных зон. Pholads и hiatellids не смогли развить богатую и разнообразную, жившую в камнях, фауну в тропическом карбонатном субстрате — вероятнее всего, вследствие заселения этой среды группами lithophagids и gastrochaenids со сверлильными механизмами лучшего качества.

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1. INTRODUCTION

The Gastrochaenacea are a compact group of eulamellibranch bivalves found in tropical, subtropical, and warm-temperate waters throughout the world. Like the Pholadacea, the gastrochaenids are primarily borers of hard substrata, but they are taxonomically much less diverse [Recent faunas comprise about 15 species, according to Boss (1971)] and they are restricted in their boring habit to calcium carbonate substrata. Along with the lithophagid borers, gastrochaenids form a major but commonly overlooked element of tropical endolithic bivalve faunas.

The biology of several gastrochaenid species is known from the studies by Deshayes (1846), Pelseneer (1911), Lamy (1923, 1925), Atkins (1937) Purchon (1954, 1958), Duval (1963), and Dinamani (1967). Notes on gastrochaenid ecology and biology are provided by Sluiter (1890), Kühnelt (1930, 1934), Otter (1937), Robertson (1963), Gohar and Soliman (1963c), and Soliman (1973). In spite of this abundant literature, little is known about the evolution of this group or the comparative ecology of its species, and the anatomy and ecology of the Western Atlantic gastrochaenids are largely unknown. The only recent study of evolution within the Gastrochaenacea is that by Boss (1967) on the evolution of the genus *Spengleria*.

At Soldier Key, Florida, populations of three gastrochaenids are found boring into skeletons of the coral *Diploria*. The occurrence of these closely related species in the same substrata provided a unique and rare opportunity for studying their comparative ecology under virtually identical environmental conditions. The following study of *Spengleria rostrata* (Spengler) 1793, *Gastrochaena (Gastrochaena) hians* (Gmelin) 1791, and *Gastrochaena (Rocellaria) ovata* Sowerby 1834 is based primarily on Soldier Key populations, supplemented by observations of living specimens from Discovery Bay, Jamaica, and Castle Harbor, Bermuda.

2. MATERIALS AND METHODS

At Soldier Key, Florida, skeletons of the coral *Diploria* were collected and systematically dissected to record their macroscopic epilithic and endolithic fauna. Living gastrochaenids from Discovery Bay, Jamaica, and Castle Harbor, Bermuda, were observed in running water tanks both in partially opened natural burrows and in artificial Plexiglas burrows. Specimens were examined by dissection and histological thin-section. The thin-sections were stained in haematoxylin-eosin or Alcian Blue. Shells of all three species were mounted in Epon 815 epoxy resin (Miller/Stephenson Chemical Co., Danbury, Connecticut) and sections through the shells were studied in thin-section and in acetate peels.

Internal growth band counts were taken directly on photographs of acetate peels at a magnification of slightly over 400 diameters. As relative ages are important to this study, the procedure for determining relative age will be described in detail. In order to estimate age from internal growth banding it is common practice to count light and dark band pairs in a radial section from the umbo to the shell margin (see Pannella and MacClintock, 1968, among others). Unfortunately, direct internal growth band counts cannot be made for most gastrochaenids because their outer prismatic shell layer is irregularly developed in patches, or is largely abraded, and because the crossed lamellar microstructure of their inner shell layers obscures internal growth banding. Furthermore, estimates of relative age from "annual" depositional breaks were found to be inaccurate and unreliable because these are poorly expressed on gastrochaenid shell exteriors and because interruptions in shell deposition result from nonperiodic (e.g., traumatic) as well as seasonal causes.

Although continuous, internal growth band counts were not obtainable, the total number of internal growth bands for each specimen could nevertheless be estimated by integrating empirically determined relationships between the number of comarginal ridges counted on the shell exterior and numbers of internal growth bands comprising successive comarginal ridges. Except for periostracal features, comarginal ridges comprise the major concentric ornament in most or all gastrochaenid shells (Fig. 10). A single comarginal ridge consists of numerous successively deposited internal growth bands, and it represents a major episode of shell secretion. For all three species the comarginal ridges along an umbonal-posterior radial section were counted by examination under light microscopy, and the number of internal growth bands per comarginal shell ridge was determined for a few widely spaced ridges where the outer prismatic shell layer is well enough preserved to permit continuous counts. These data, plotted in Figure 1, show that the number of internal growth bands *per comarginal ridge* increases with age. This age effect is especially pronounced in *S. rostrata.* Over the age intervals examined, the number of internal growth bands per ridge (y) is approximately a linear

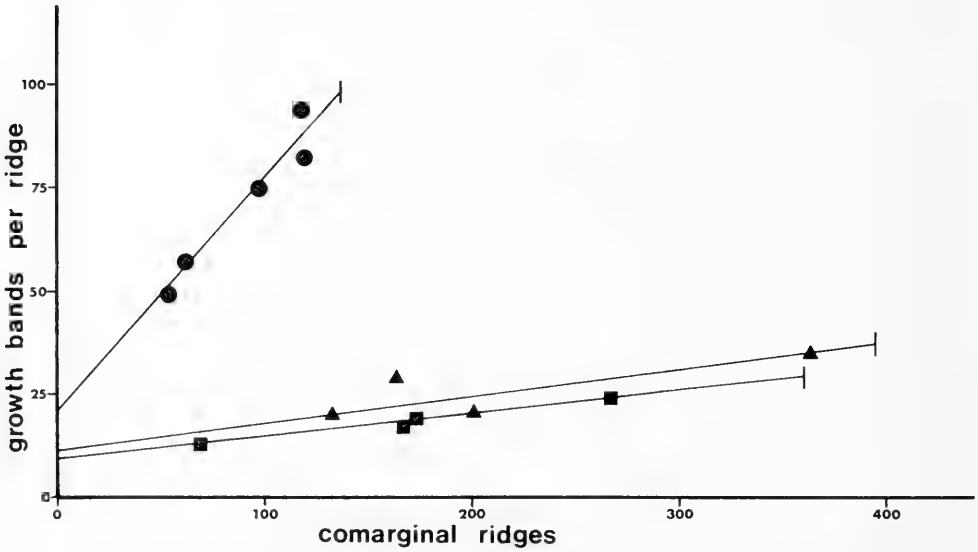


FIG. 1. Relationship between internal growth bands per comarginal shell ridge and number of comarginal shell ridges in a radial section.

Key: *Spengleria rostrata* (dots).
Gastrochaena (Rocellaria) ovata (squares).
Gastrochaena (Gastrochaena) hians (triangles).

Data are from single juvenile and single adult specimens for each species.

function of the total number of comarginal shell ridges (x). These relationships vary between the species and are described by the equations:

Spengleria rostrata:	$y = 0.56x + 21.0$
Gastrochaena (Rocellaria) ovata:	$y = 0.06x + 9.0$
Gastrochaena (Gastrochaena) hians:	$y = 0.07x + 11.0$

On the basis of these equations, the *total* number of internal growth bands along the umbonal-posterior radial section can be estimated by integrating the appropriate function over the interval (x=0) to (x=total number of comarginal ridges). For example, for individuals of the three species with 100 comarginal ridges in the radial section, the total number of internal growth bands is computed as:

Spengleria rostrata:

$$\int_0^{100} (0.56x + 21.0)dx = [0.28x^2 + 21.0x + C]_0^{100}$$
$$= 4900 \text{ internal growth bands}$$

Gastrochaena (Rocellaria) ovata:

$$\int_0^{100} (0.06x + 9.0)dx = [0.03x^2 + 9.0x + C]_0^{100}$$
$$= 1200 \text{ internal growth bands}$$

Gastrochaena (Gastrochaena) hians:

$$\int_0^{100} (0.07x + 11.0)dx = [0.035x^2 + 11.0x + C]_0^{100}$$
$$= 1450 \text{ internal growth bands}$$

Although this method of relative age determination may be less accurate than continuous internal growth band counts, it is a better indication of relative age than counts of comarginal shell ridges alone would provide. As is apparent in Figure 1, reliance upon comarginal shell ridges alone would have grossly underestimated the age of *S. rostrata* relative to the other two species. To minimize the possibility of aberrant age determinations resulting from traumatic (i.e., nonperiodic) interruptions in shell secretion, shells showing unusual interruptions in the pattern of formation of comarginal ridges (about 5 percent of the collected populations) were excluded from age-related analyses. The similarity in average internal growth band width for *S. rostrata, G. (R.) ovata* and *G. (G.) hians* (2.30, 2.47, and 2.59 μm., respectively) suggests that the time period of internal growth band formation is identical for these species. G. Pannella (personal communication) found that in the pholad *Penitella* a single pair of light and dark internal growth bands generally represents two weeks of shell deposition. As calculated using this time-conversion factor, the modes of age frequency distribution for the live gastrochaenids collected at Soldier Key (Fig. 2) are separated by an average of 1.06 years, and the age ranges of the populations are 2–5 years, 3–13 years, and 5–18 years for *S. rostrata, G. (R.) ovata* and *G. (G.) hians,* respectively.

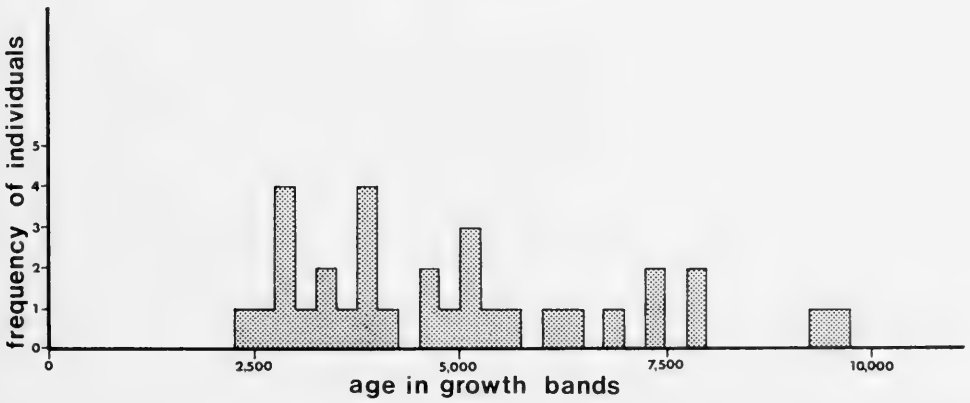


FIG. 2. Age-frequency distribution for combined populations of *Spengleria rostrata, Gastrochaena (Rocellaria) ovata* and *Gastrochaena (Gastrochaena) hians* collected during March 1970, at Soldier Key, Florida.

Apparent abrasive efficiency of the shell was computed from data of burrow length and amount of anterior shell abrasion. Burrow lengths used in these calculations exclude extensions of the burrow above the coral substratum (e.g., burrow elongations resulting from simple posterior extension of the burrow lining) and posterior burrow elongation resulting from attempted coral or sponge overgrowth of the siphons. Anterior shell abrasion was measured by comparing the number of comarginal shell ridges truncated in the shell anterior relative to the total number of comarginal ridges present in the unabraded shell posterior. The original width of abraded anterior shell ridges was estimated for each species as the average width of newly secreted and yet unabraded ridges. Apparent abrasive efficiency of the shell is expressed in micrometers of coral ab-

raded per micrometer of anterior shell abraded. The use of burrow volume abraded rather than burrow length would have been more appropriate, but the volume of shell abraded is especially difficult to estimate, and the volume of coral abraded cannot be readily calculated because gastrochaenids typically line their burrows with aragonitic laminae. However, the use of shell volume abraded rather than shell width abraded would not change the trend of the data because shells of all three species are comparable in thickness anteriorly. In *S. rostrata* the burrow is wider relative to the width and height of the valves than in the other two species. Therefore calculations of apparent abrasive efficiency based on burrow volume would only further accent the already comparatively high values plotted for this species in Figure 13.

The opening moment of the ligament was determined by orienting shells with the commissure in a horizontal position, then placing weights on the uppermost (left) valve until complete valve closure was brought about. Since the weight of a single valve is almost insignificant compared to the opening moment at closure, these opening moment values are reasonable estimates of the opening moment that would have been obtained by correcting for the weight of the upper valve. Opening moments were measured on adult specimens that had been preserved in 50 percent ethanol for approximately one week. Insofar as the ethanol solution may have altered the mechanical properties of the ligaments, these data are significant only for suggesting relative ligament strengths among the specimens at hand.

Intestinal contents from immediately anterior to the anus were spread on a glass slide in tapwater, smeared with very light pressure, and examined by normal and polarizing light microscopy. Measurements of maximum particle diameter were made directly from photomicrographs of the gut contents enlarged to a final magnification of 550 diameters.

3. DISTRIBUTION AND ECOLOGY OF THE TROPICAL WESTERN ATLANTIC GASTROCHAENIDS

The Gastrochaenidae comprise a relatively nondiverse but persistent component of endolithic faunas in corals and shells throughout the tropical and subtropical Western Atlantic. *Spengleria rostrata* (Spengler) 1793 and *Gastrochaena (G.) hians* (Gmelin) 1791, the widest ranging species, are found throughout the Caribbean and in Bermuda. *G. (G.) hians* dominates the Florida Keys gastrochaenid fauna in terms of population density, whereas *S. rostrata* is generally rare here and elsewhere in the Western Atlantic. The remaining gastrochaenids show more limited geographic distributions. *Gastrochaena (Rocellaria) ovata* Sowerby 1834 is rare to moderately common throughout the tropical Western Atlantic, but is absent from Bermuda. At Bermuda this species is apparently replaced by the similarly short-siphoned *Gastrochaena (G.) mowbrayi* Davis 1903.[1] At Castle Harbor, Bermuda, *G. (G.) mowbrayi* attains high population densities equaling or exceeding those of *G. (G.) hians.* Three other short-siphoned species are *G. (G.) stimpsonii* (Tryon 1862) from North and South Carolina and two similar species, one from the Gulf of Mexico [see "*Rocellaria hians,*" p. 218, in Andrews (1971)], and the other from Puerto Rico and the Bahamas. The following ecological notes refer to the three more common gastrochaenids of the Florida Keys, i.e., *S. rostrata, G. (G.) hians* and *G. (R.) ovata.* These notes are based primarily on populations collected near Soldier Key, Florida, where all three species are found in *Diploria* coral skeletons.

Larger *Diploria* skeletons at Soldier Key, Florida, harbor at least 19 bivalve species, eight of which are borers [*Gastrochaena (Gastrochaena) hians, G. (Rocellaria) ovata, Spengleria rostrata, Lithophaga nigra, L. antillarum, Petricola typica, P. lapicida,* and *Botula fusca*], and two of which are semiendolithic nestlers (*Arca imbricata* and *Paramya subovata*). The endolithic and epilithic bivalve assemblages show higher diversities in coral substrata largely unprotected by living coral polyps. A list of the more common Soldier Key endolithic and epilithic bivalves is presented in Appendix A (below). Larger *Diploria* skeletons commonly show dense infestation by borers on both their upper and lower surfaces. Many of these disc-shaped corals have lost their initial attachment to the hard bottom, probably

[1]Davis' plate 4, figure 21 for *G. Gastrochaena mowbrayi* Davis and his cotype for *G. mowbrayi* at the United States National Museum (USNM 109562) are different species. Davis apparently mistakenly illustrated *Spengleria rostrata* in this figure, but it is clear from his text description and from the burrows illustrated in his plate 4, figure 22, that he was referring to the species represented by his cotype. Davis' *mowbrayi* is clearly specifically distinct from *G. (R.) ovata* because of its much shorter siphons and subdued concentric ornamentation. Davis' plate 4, figure 20, described by Davis (1903, p. 128) as a juvenile *G. ovata,* is likewise a specimen of *S. rostrata.*

through disintegration by borers. Nevertheless, the concave undersurfaces of the *Diploria* skeletons provide considerable settlement area because they remain largely elevated above the sediment-water interface. The mytilacean *Lithophaga nigra,* the most abundant endolithic bivalve, bores upper and lower surfaces of *Diploria* but shows a marked preference for the center undersurfaces. Among the gastrochaenids, *Gastrochaena (G.) hians* and *Gastrochaena (Rocellaria) ovata* bore the coral margins, and *Spengleria rostrata* preferentially bores the underside of the coral margins. The synecology of bivalves inhabiting *Diploria* substrata from Soldier Key, Florida, and Castle Harbor, Bermuda, is discussed in greater detail by Carter (1976).

Gastrochaenids are unique among Western Atlantic endolithic bivalves because of their unusual specializations for survival in thin and rapidly eroded substrata. Their relatively long siphons effectively isolate their shells from substratum erosion, and the probing behavior of their anterior pedal organ (see below) enables them to guide their burrows away from neighboring borers and unstable coral surfaces. Gastrochaenids also show an unusual capacity for repairing even extensive damage to their burrows by forming new calcareous burrow walls. Specimens of *Spengleria rostrata* and *Gastrochaena (G.) hians* from Discovery Bay, Jamaica, were apparently able to avoid predation by forming new calcareous burrow walls after nearly half of their burrow shell chamber had been naturally broken away. Natural burrow reconstruction has been described for *Gastrochaena (Rocellaria) laevigata* from the Red Sea (Bertram 1936), and it is likely that most or all Recent representatives of the Gastrochaenacea are capable of burrow repair. Although a similar capacity for repair occurs in some more specialized species of *Lithophaga,* this does not occur in *L. antillarum* or *L. nigra.* Not surprisingly, there is a general correlation between capacity for burrow repair and the secretion of calcareous burrow linings (as opposed to paste-type detrital linings) among species of *Lithophaga.* In addition to permitting burrow repair, the ability to secrete calcareous burrow linings may be adaptive for filling in the posterior of the burrow around the siphons. Because these linings are commonly thick in gastrochaenid burrows, they probably minimize the weakening effect of the borings themselves on the coral substratum. Schroeder (1972) has discussed calcareous burrow linings in this context, i.e., in terms of reinforcing the coral substratum. This would clearly be adaptive in thinner and therefore more readily broken coral margins where the gastrochaenids preferentially settle.

In addition to their adaptations for life in rapidly eroded and broken coral margins, gastrochaenids show unique specializations for avoiding both coral overgrowth of the siphons and gastropod predation. Like *Petricola typica* but unlike the lithophagids, gastrochaenids can postpone or escape coral overgrowth by elongating their siphonal burrow toward the posterior. In *G. (G.) hians* the siphons are especially extensible and retractable, thereby enabling this species to survive extreme conditions of coral overgrowth or erosion (see Fig. 44). On the other hand *G. (G.) hians* differs from *S. rostrata* and *G. (R.) ovata* in lacking effective protection from predation by gastropods. The siphonal burrow aperture is sufficiently wide in *G. (G.) hians* to allow predation by certain naticid gastropods, judging from their characteristic borings in the posterior of some *G. (G.)*

hians shells. The small siphon diameter in *G. (R.) ovata* and the siphonal separation and projecting burrow linings ("baffles") in *S. rostrata* are apparently effective in excluding gastropod predation, at least by naticids and muricids. A similar defense against gastropod predation is not observed in the Soldier Key lithophagids. But an alternative defense may have evolved in other species of *Lithophaga* (e.g., in *L. bisulcata*) where regular posterior encrustations on the shells may constitute effective barriers to gastropod boring.

4. ANATOMY

Although the literature contains numerous references to general gastrochaenid anatomy (e.g., Tryon 1882 and Lamy 1925) and a few references to their particular organ systems (e.g., Atkins 1937, Dinamani 1967, Duval 1963) there are few detailed studies of individual species. Notable exceptions include the work by Deshayes (1846) on *Gastrochaena dubia;* Fischer (1866) on "*Fistulana*" [=*Eufistulana*] *grandis;* Pelseneer (1911) on *Gastrochaena machrochisma, G. dubia* and *Spengleria mytiloides;* and more recently Purchon (1954) on "*Rocellaria*" [=*Gastrochaena (G.)*] *cuneiformis,* and Soliman (1973) on "*Rocellaria*" [=*Spengleria*] *retzii.* The present section provides comparative anatomical data for the Western Atlantic *Spengleria rostrata, Gastrochaena (G.) hians,* and *Gastrochaena (Rocellaria) ovata.*

MANTLE. The mantle lobes of *S. rostrata, G. (R.) ovata* and *G. (G.) hians* are fused ventrally except at the pedal aperture (Fig. 3). The ventral mantle of all three species is muscular and highly contractile, but that of *S. rostrata* appears exceptionally thick and glandular. In these species the anteroventral mantle is normally expanded well beyond the shell margins, coming in contact with the adjacent anteroventral walls of the burrow shell chamber. In *G. (R.) ovata* and *G. (G.) hians* the pedal aperture is narrow, while in *S. rostrata* this is commonly greatly expanded relative to the diameter of the foot. In all three species the periostracum is initiated in a mantle groove near the periphery of the shell (Fig. 3C,D). This position of the periostracal groove requires that the mantle is fused by at most its inner and middle lobes. In *G. (R.) ovata* the periostracal groove is close to the shell margin, and the exposed ventral mantle appears otherwise smooth and featureless. In *S. rostrata* the periostracal groove is likewise situated close to the shell margin, but it is bordered by an inconspicuous mantle lobe (between the periostracal groove and the pedal aperture) that shows an apical longitudinal groove. In *G. (G.) hians* the periostracal groove lies farther from the shell margin and it is bordered, as in *S. rostrata,* by a grooved mantle lobe. In *G. (G.) hians* this mantle lobe forms a prominent projecting ridge (Fig. 3C). *G. (R.) ovata* alone shows left and right elongate white glandular areas near the periostracal groove. The position of these glands (Fig. 3G) corresponds to the zones of luminescence described for "*Rocellaria*" [=*Gastrochaena (Rocellaria)*] *grandis* by Haneda (1939), but these glands in *G. (R.) ovata* were not observed to luminesce. Similar glands were described for "*Rocellaria*" [=*Gastrochaena (Gastrochaena)*] *cuneiformis* by Purchon (1954) who presumed that they secrete mucus for binding coral debris.

In the Soldier Key gastrochaenids the lateral mantle within the mantle cavity is glandular and appears superficially irregularly folded. Deshayes (1846) and Clark (*in* Forbes and Hanley 1853, p. 135) described similar glands for *Gastrochaena dubia* and *G. modiolina,* respectively. Deshayes

noted that these glands in *G. dubia* are divided into anterior and posterior masses, and he presumed that the anterior masses secrete an acid for boring. In the Soldier Key species these glands form continuous lateral masses lining the lateral mantle within the pallial line. In *G. (R.) ovata* and *G. (G.) hians* the glands appear coarsely rugose, whereas in *S. rostrata* they are more roundly inflated.

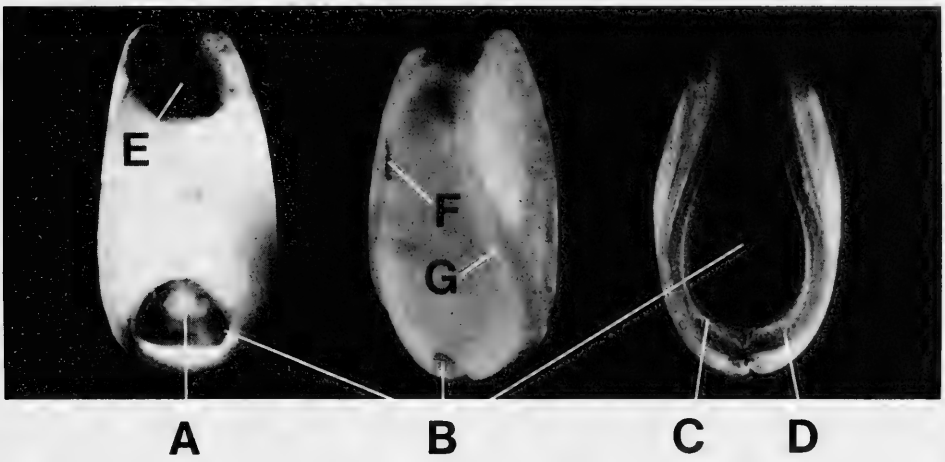


FIG. 3. Ventral views of *Spengleria rostrata* (left), *Gastrochaena (Rocellaria) ovata* (middle) and *Gastrochaena (Gastrochaena) hians* (right). The photographs of *S. rostrata* and *G. (R.) ovata* are of living specimens in artificial Plexiglas burrows; these two photographs are outlined in black to accent the outer edge of the shells. The view of *G. (G.) hians* is of a specimen preserved in alcohol; so its mantle and pedal aperture are greatly contracted. Legend:

A. Sole of the foot in *Spengleria rostrata.*
B. Expanded pedal aperture in *S. rostrata* and *G. (R.) ovata;* contracted pedal aperture in *G. (G.) hians.*
C. Grooved mantle lobe in *G. (G.) hians.*
D. Periostracum between the grooved mantle lobe and the shell margin in *G. (G.) hians.*
E. Posterior of the inhalant siphon in *S. rostrata,* fully retracted.
F. String of carmine particles visible through the semitransparent ventral mantle of *G. (R.) ovata.* The particles have been bound in mucus and are being transported to the base of the inhalant siphon for ejection.
G. Elongate white glandular area in *G. (R.) ovata.*

G. (R.) ovata, G. (G.) hians and especially *S. rostrata* possess a muscular ventral mantle, and in specimens removed from their burrows, this mantle has been observed to pump water actively through the mantle cavity and out the inhalant siphon. In the relaxed condition [see *S. rostrata* and *G. (R.) ovata* in Fig. 3] the anteroventral mantle is held agape around the base of the foot and a steady inhalant stream of water passes through this opening from the burrow into the mantle cavity. When carmine particles are introduced into this anterior inhalant stream, they are quickly bound into mucous strings and passed posteriorly along two ventrolateral mantle grooves to the base of the inhalant siphon (Fig. 3F). The mucous strings are then expelled through the inhalant siphon by contraction of the ventral mantle while the pedal aperture is closed around the stock of the

foot. Mantle contraction is immediately followed by an apparent "gulping" of water through the dilating pedal aperture as the mantle cavity expands to its normal position, to be followed by another series of contraction and "gulping." In *G. (R.) ovata* and *G. (G.) hians* this flushing cycle is repeated several times in rapid succession in the process of purging the inhalant siphon. In *S. rostrata* the mantle contractions are rarely repeated in quick succession, but the valves of this species close slightly during mantle contraction to assist the expulsion of pseudofeces.

Siphons. Unlike many Myidae, Hiatellidae and Pholadidae, gastrochaenids do not protect their long siphons with a periostracal sheath. The inhalant and exhalant siphons of *G. (R.) ovata* and *G. (G.) hians* are externally fused into a single tube over most or all of their length (Fig. 4). Similarly fused siphons have been described for *G. dubia* and *G. macrochisma* by Pelseneer (1911) and for "*Rocellaria*" [=*Gastrochaena (Rocellaria)*] *ruppelli* by Soliman (1973). In contrast, the inhalant and exhalant siphons in *S. rostrata* are completely separated. As this species matures, it spreads apart its siphons **within** the substratum through chemical erosion and accompanying deposition of aragonite. Divergence of the siphons in "*Rocellaria*" [=*Spengleria*] *retzii* has been attributed to coral overgrowth despite the observed occurrence of this species only in dead coral (Soliman 1973). All individuals of *S. rostrata* collected from Florida, Bermuda and Jamaica for the present study were found boring into coral skeletons or limestones in which living coral was not observed surrounding the inhalant and exhalant siphonal apertures. In all instances the siphons had diverged from one another within the hard substratum, forming an angle of 40 to 90 degrees. As the siphonal epithelium of *S. rostrata* erodes into the substratum on one side of the siphon, it secretes layers of prismatic aragonite to fill in the previous burrow on the opposite side. Sections through the posterior of the burrow show that siphonal boring truncates the calcium carbonate linings of the burrow shell chamber as the animal penetrates deeper into the coral.

The siphons of all three gastrochaenids are pale yellow to cream-colored externally but are brown to black internally. The extent of the internal pigmentation is proportional to the length of the siphons, being restricted to the posterior of the siphons in *G. (R.) ovata,* extending farther anteriorly in *S. rostrata,* and covering most of the interior of the siphons in *G. (G.) hians.* Some individuals of *G. (R.) ovata* are flecked with white on the interior of their siphons and on the siphon tentacles. In some *S. rostrata* and in many *G. (R.) ovata* siphonal pigmentation is lacking altogether, especially among the younger individuals.

In *S. rostrata* and *G. (R.) ovata* the posterior apertures of the inhalant and exhalant siphons are guarded by contractile annular siphonal membranes. In *G. (G.) hians* only the exhalant siphon bears an annular membrane, and this is extremely thin, transparent and very mobile (Fig. 4). The siphons of *S. rostrata* are fringed by about 250 minute tentacles arranged in four or five rows. In *G. (R.) ovata* the relatively large major siphonal tentacles are surrounded by an irregular row of minor ones, and the two annular membranes are also fringed by a delicate row of small tentacles.

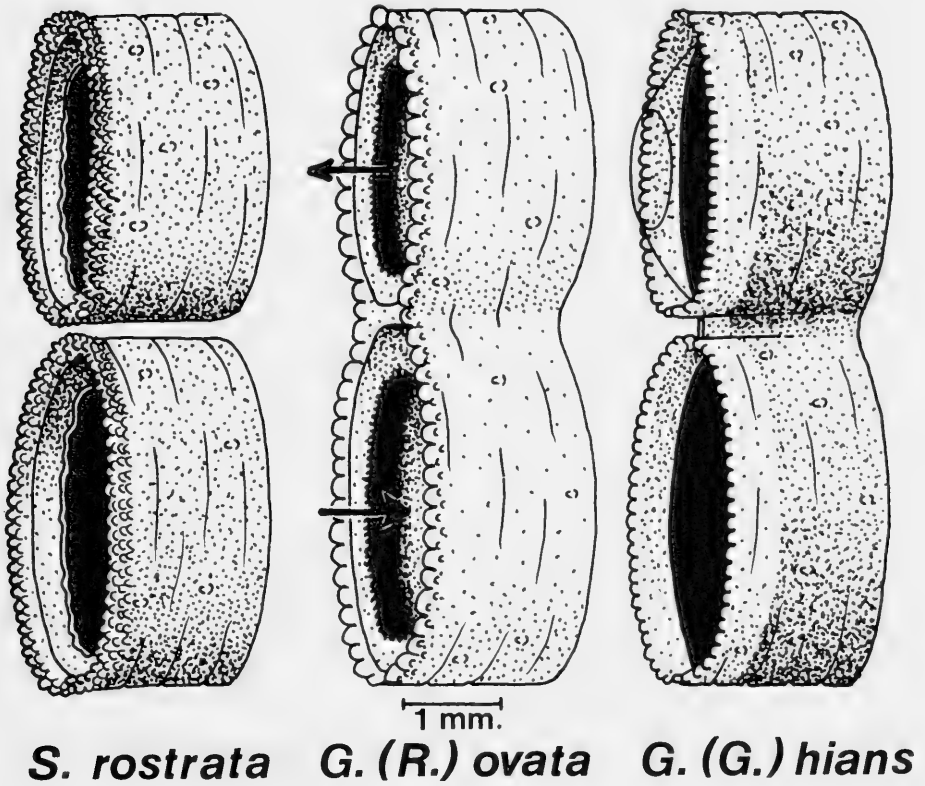


FIG. 4. Morphology of the siphon tips in *Spengleria rostrata, Gastrochaena (Rocellaria) ovata* and *Gastrochaena (Gastrochaena) hians*. The directions of the inhalant and exhalant currents are indicated by the lower and upper arrows, respectively. The siphonal tentacles are drawn as they appear in the contracted state.

The siphon tips of *G. (G.) hians* are much simpler, showing only a single row of intermediate size tentacles. As discussed below, the size and number of the major siphonal tentacles correlates with the degree of size sorting of ingested particles found in the intestines of these species. The interior of the long siphon tube of *G. (G.) hians* differs from the others in showing dorsal and ventral longitudinal grooves, expressed on the exterior of the siphons by a pair of dorsal and ventral ridges. In some specimens these features are also indicated by a pair of longitudinal grooves impressed upon the calcareous siphonal burrow lining. Similar longitudinal grooves were observed by Purchon (1954) for "*Rocellaria*" [=*Gastrochaena (G.)*] *cuneiformis*.

In *G. (R.) ovata* the inhalant and exhalant siphons are separated internally for most of their length by a horizontal pallial septum. In this species and in *S. rostrata* (where the siphons form separated tubes) the posterior of the ctenidia are free and do not extend past the posterior shell margin. In contrast, the ctenidia of *G. (G.) hians* extend far past the posterior of the shell and are attached to the pallial siphonal septum, forming a long delicate partition between the inhalant and exhalant channels (Fig. 5).

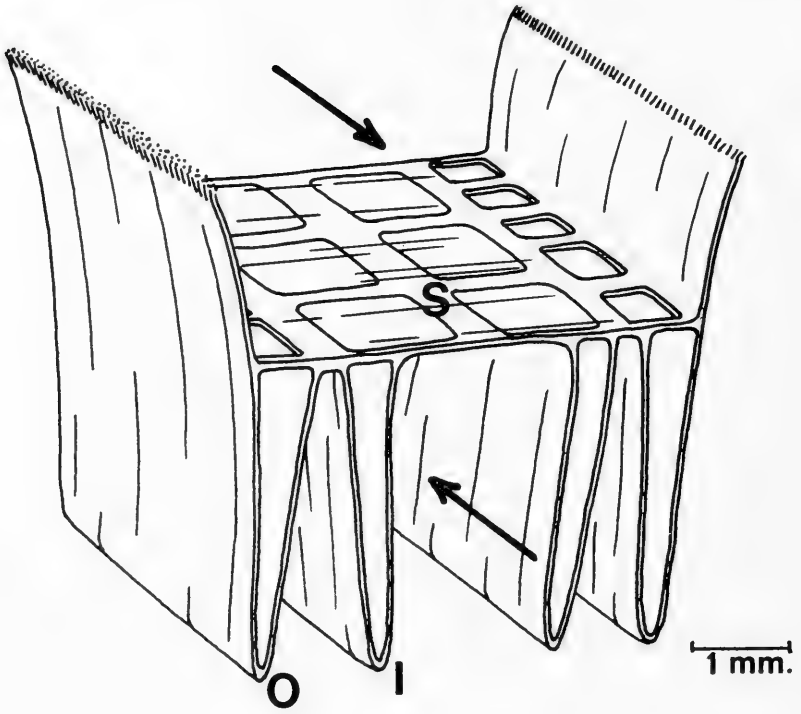


FIG. 5. Diagrammatic section through the ctenidium of *Gastrochaena (Gastrochaena) hians:* transverse section through the middle of the siphon. The directions of the inhalant and exhalant currents are indicated by the lower and upper arrows, respectively. Legend:

O. Outer demibranch.
I. Inner demibranch.
S. Ctenidial septum.

The inhalant siphon of *S. rostrata* and *G. (R.) ovata* differs from *G. (G.) hians* in having a transverse valve across its base. Similar valves have been described for *S. mytiloides* by Pelseneer (1911) and for *"Rocellaria"* [=*Gastrochaena (G.)*] *cuneiformis* by Purchon (1954). In *S. rostrata* the larger part of the valve is a crescent-shaped partition suspended ventrally from the pallial septum separating the inhalant and exhalant siphon tubes. This is accompanied by two smaller flaps projecting from ventrolateral positions on the wall of the inhalant siphon. When contracted, these valves restrict access between the inhalant siphon and the mantle cavity. The valve in *G. (R.) ovata* appears more delicate and consists of a single membranous flap suspended ventrally from the siphonal septum separating the inhalant and exhalant siphon tubes. Contraction of this process blocks only one-third of the aperture at the base of the inhalant siphon. A siphonal valve does not occur in *G. (G.) hians,* undoubtedly because its inhalant and exhalant siphons are separated anteriorly by a ctenidial rather than a pallial septum (Fig. 5). According to Haas (1935) these siphonal processes function as check-valves to arrest the flow of water through the inhalant siphon. These valves might assist purging pseudofeces, because pseudofeces collect near the base of the inhalant

siphon. Partial blocking of the inhalant siphon would increase the velocity of the purging water at this point. Siphonal valves are also known in certain Mytilacea and Mactracea (Yonge 1948, 1955).

In all three species the siphons show great sensitivity to changes in light intensity. Shadows passing over the tips of the siphons induce partial adduction of the valves and retraction of the siphons away from the burrow posterior. The siphons are remarkably contractile, and even the long siphoned *G. (G.) hians* is capable of retracting these entirely within the shell. It is noteworthy that these species can apparently fully retract their siphons only after prolonged irritation. Sudden, intense irritation of the siphons in *G. (G.) hians* causes premature adduction of the shell and damage to the siphons by being pinched between the posterior shell valves. This behavior suggests that complete siphonal retraction may require a preparatory interval during which the siphonal hemocoels are partially deflated by draining their fluid to other parts of the mantle. Unlike *S. rostrata* and *G. (R.) ovata,* complete retraction of the siphons in *G. (G.) hians* is assisted by introversion of their bases and "tucking" the siphon into the anterior mantle cavity.

Ctenidia and Labial Palps. The eulamellibranch ctenidia of *S. rostrata* are distinctly plicate and thick, while those of *G. (R.) ovata* and *G. (G.) hians* are flat and considerably more delicate. As in many bivalves, the outer demibranch shortens anteriorly relative to the inner one, and only the inner demibranch is fused to a distal oral groove. These observations corroborate Pelseneer's (1911) generalization that flat gills associate with fused siphons, whereas plicate gills associate with separated siphons in the Gastrochaenacea. Posteriorly in *S. rostrata* and *G. (R.) ovata* the outer demibranch is shorter than the inner one. In *G. (G.) hians* the outer and inner demibranchs become equal in length toward the posterior (Fig. 5). The ctenidia of *G. (G.) hians* are unique in extending far posteriorly into the siphonal tube, but the outer demibranch in *S. rostrata* is unique in forming a prominent supraaxial extension, resembling that described for *"Rocellaria"* [=*Gastrochaena (G.)*] *cuneiformis* by Purchon (1954).

In all three species the ventral tips of the anterior filaments of the inner demibranch are inserted into and fused to a distal oral groove between the elongated labial palps [ctenidium-palp association type "two" of Stasek (1963)]. The distal oral groove is especially long in *S. rostrata* and the labial palps are larger here than in the other two species.

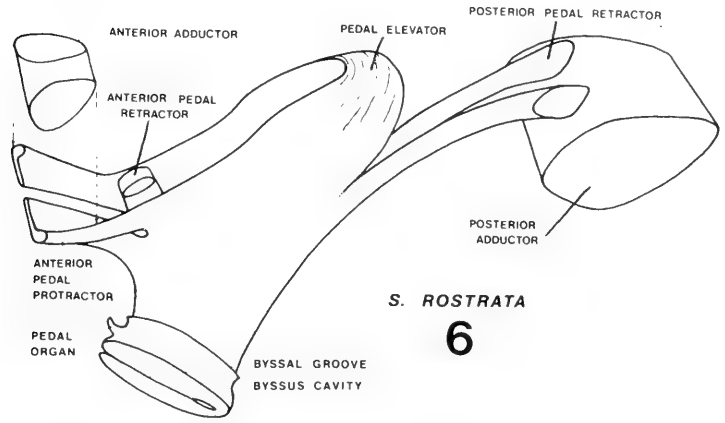
Foot. The foot of the Soldier Key gastrochaenids consists of a circular to slightly oval pedal disc with an anteriorly projecting pedal organ, a longitudinal byssal groove, and a posterior byssal gland and byssus cavity (Figs. 6–8). The anterior of the foot shows a small pedal gland located between the pedal organ and the byssal groove. These pedal apparatusses are similar to those described for *G. dubia, G. macrochisma,* and *S. mytiloides* (Pelseneer 1911), *"Rocellaria"* [=*Gastrochaena (G.)*] *cuneiformis* (Purchon 1954) and *"Rocellaria"* [=*Spengleria*] *Gastrochaena retzii* (Soliman 1973). Drawings of the foot in the tube-dwelling *"Fistulana"* [=*Eufistulana*] *grandis* do not show a well-formed pedal disc, but the presence of this in a

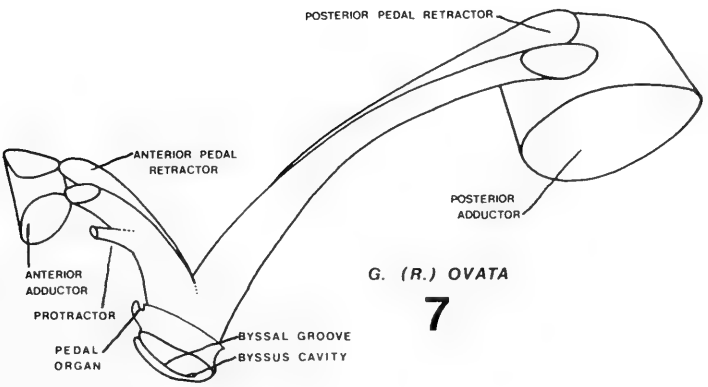
rudimentary state may be inferred from the pedal "scar" in the anterior of its tube (see plate 12, figure 3, in Fischer 1866). In *S. rostrata* the pedal disc is relatively wide, and in this species and *G. (R.) ovata* the contracted anterior pedal organ is cone-shaped (Figs. 6 and 7). Compared with *S. rostrata* the pedal discs of *G. (R.) ovata* and *G. (G.) hians* are smaller in diameter. The contracted pedal organ of *G. (G.) hians* appears relatively flattened and spatula-like (Fig. 8). *S. rostrata* is unique in that the anterior of its foot shows 5 or 6 chevron-shaped glandular corrugations immediately dorsal to the pedal organ, with the apex of each chevron pointing ventrally toward the sole of the foot.

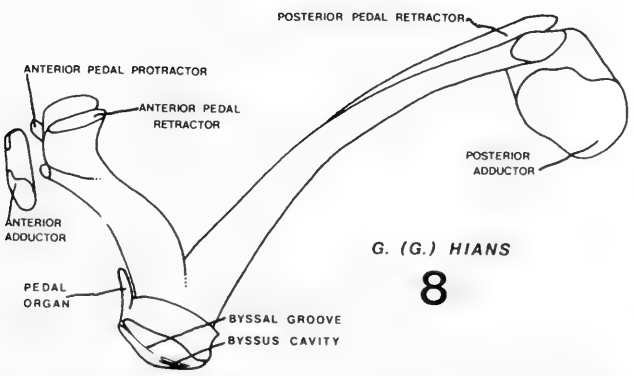
The Gastrochaenacea have been characterized as losing their juvenile byssal attachment to adhesive or suctorial attachment in the adult stage (Pelseneer 1911, Otter 1937, Soliman 1973). On the other hand, Yonge (1963) noted that the byssus gland persists in adult gastrochaenids and that byssus threads are occasionally secreted. Among the Soldier Key species the foot is byssally attached in juveniles and adults alike, although to varying degrees. In all three species the byssal attachment is minute and is hidden from view by the pedal disc. Adults of *G. (R.) ovata* are firmly byssally attached and their byssus fibers occasionally pull away pieces of the burrow wall when these animals are removed from their burrows. The byssus in *G. (G.) hians* and especially in *S. rostrata* is more delicate, and in *S. rostrata* pedal attachment is apparently supplemented by adhesion by the surface of the pedal disc. In *S. rostrata* the burrow lining may be marked by a pedal "scar" showing the outline of the pedal disc, the byssal groove, and occasionally also the site of byssal attachment. Pedal scars are less common but are occasionally observed in burrows of *G. (R.) ovata* and *G. (G.) hians*. Other Recent species of *Gastrochaena* and *Spengleria* (Gohar and Soliman 1963c, Soliman 1973), "*Fistulana*" [=*Eufistulana*] (Fischer 1866) and certain fossil species of *Gastrochaena* show pedal scars in the anterior of their burrows. These scars are potentially useful sources of information for reconstructing the pedal structure of fossil gastrochaenids.

Musculature. *S. rostrata, G. (R.) ovata* and *G. (G.) hians* are heteromyarian, with the anterior adductor muscles relatively small and attaching near the extreme anterior shell margin (Figs. 6–8 and 14–16). Reduction of the anterior adductor muscle is proportional to the degree of anterior shell reduction. Thus, the ratio of posterior to anterior adductor cross-sectional area is lowest in *S. rostrata* (averaging 5.0), slightly greater in *G. (R.) ovata* (averaging 6.7), and is greatest in the very inequilateral *G. (G.) hians* (averaging 12.1).

The pedal musculature of all three species consists of anterior and posterior pedal retractors and anterior pedal protractors. *S. rostrata* also possesses pedal elevators (Figs. 6–8). In *S. rostrata* the pedal protractors each consist of a bifurcating muscle attaching ventral and slightly lateral to the anterior adductor. In contrast, the protractors in *G. (G.) hians* consist of single muscles that attach dorsal and posterior to the anterior adductor. In *S. rostrata* the pedal retractors are diffuse and pass peripheral to the visceral mass as they attach into the food. In *G. (R.) ovata* and *G. (G.) hians* the more concentrated retractor muscles pass directly through the visceral mass and they attach more exclusively to the byssus apparatus.







FIGS. 6–8. The major pedal and shell adductor musculature in the tropical Western Atlantic gastrochaenids. The epithelium is shown intact near the base of the foot to show the position of the anterior pedal organ and the longitudinal byssal groove. The anterior adductor muscle in *Spengleria rostrata* (Fig. 6) is shown lifted out of its normal position immediately dorsal to the anterior pedal protractors (see dashes).

G. (G.) hians differs from the other species in the attachment of its anterior pedal retractors to a pair of calcareous projections (myophores) extending laterally and posteriorly from the dorsal shell margins. In most *G. (G.) hians* the myophore consists of a simple triangular plate beneath the hinge line; but in a few individuals this plate may extend slightly above the dorsal shell margin, or it may bifurcate toward the posterior. The left myophoral plate is generally larger than the right by an average surface area ratio of 1.43/1. Distinct triangular myophores are not developed in *S. rostrata* or *G. (R.) ovata,* but in the latter species the anterior pedal retractors may attach to a pair of small, irregular knobs similar in position to the myophores of *G. (G.) hians.*

In all three species the pallial musculature consists of well-defined muscular bundles attaching to the shell in irregular patches, thereby forming a discontinuous pallial line (Figs. 14–16). In *G. (G.) hians* the posteroventral pallial muscles form a distinct accessory adductor muscle. A similar accessory adductor is not found in *S. rostrata* or in *G. (R.) ovata.*

Intestinal Contents. Fecal pellets dissected from the intestines of *S. rostrata, G. (R.) ovata* and *G. (G.) hians* are shaped in plain rods (type "four" of Arakawa 1970). Intestinal contents dissected from adult specimens collected in March of 1970 consisted of calcium carbonate debris with traces of sponge spicules, diatoms and crustacean exoskeletons. Although intestinal contents for the three species are similar in average maximum particle diameter, size sorting appears to be slightly more efficient in *S. rostrata* than in the other species (Fig. 9). This better sorting correlates with

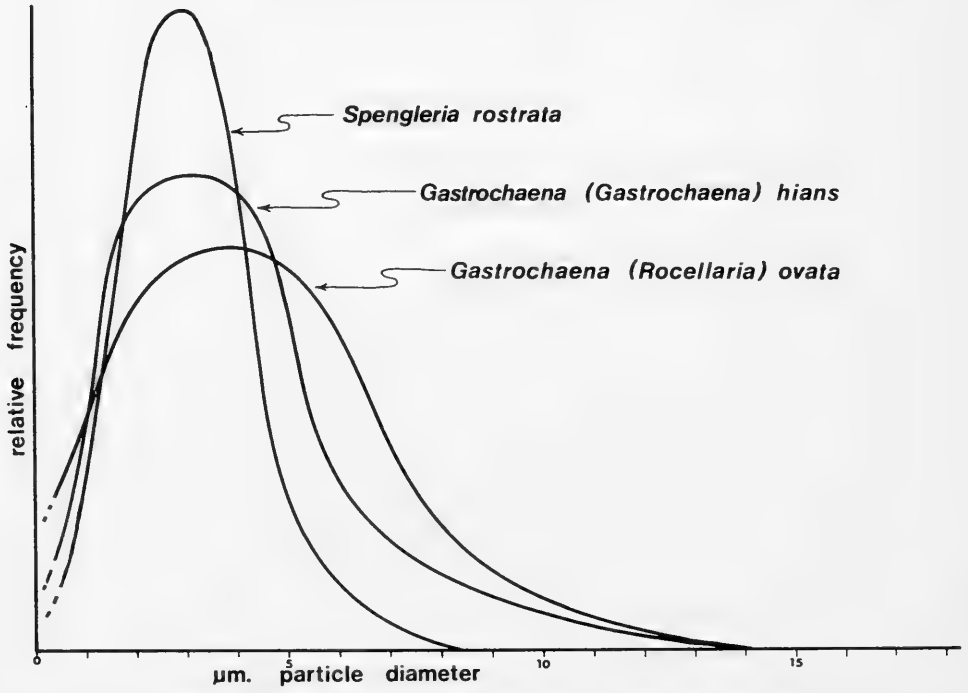


Fig. 9. Size frequency of ingested particles removed from the intestine immediately anterior to the anus. Particle size was measured as the maximum length. The curves are based on size-frequency histograms for several hundred particle measurements for three individuals of each species. See materials and methods (Chapter 2) for sampling procedure.

ctenidial plication and the presence of smaller and more numerous major siphonal tentacles in *S. rostrata* (Fig. 4). The sampled gastrochaenids were collected from near the coral margins where their siphonal openings were elevated not more than 10 centimeters from the carbonate sand substratum. Nevertheless, variation in the distance of their siphonal openings from the sand substratum may have biased the particle sorting data.

The striking aspect of the intestinal contents is the dominance of calcareous debris and the paucity of organic debris and mineralized tests of planktonic organisms. This is surprising, considering that Smith et al. (1950) determined that diatoms were the most important component of the plankton in 1945 at Soldier Key, with dinoflagellates being less abundant. The zooplankton (mostly copepods, copepod nauplii, and tintinnids) rarely dominated the plankton at this locality. In the present samples, diatoms were rarely encountered in the intestinal contents, and in each sample the number of diatoms was exceeded by the number of sponge spicule fragments. If the March 1970 plankton at Soldier Key was not very different from what it was in 1945, then the present data suggest that most of the ingested particulate matter comes from resuspended carbonate debris rather than from the plankton *per se*. Further study is needed to determine the source of primary nutrition of these bivalves, but it may likely come from the microbiota of resuspended sediment (e.g., bacteria) or from planktonic organisms lacking mineralized tests.

5. SHELLS

Unlike the common pholad borers, gastrochaenids lack conspicuous rasping "teeth" on the shell anteriors, and their delicate shells do not appear obviously adapted for deep boring into hard substrata (Fig. 10). Their shells resemble the Pholadacea only in being thin, edentulous and broadly gaping anteriorly, and they differ from most pholads in lacking a permanent posterior shell gape and modification of the shells for rocking about a vertical axis.

All three Soldier Key gastrochaenids show great variability in their proportion of shell height to length, but their shell growth is still best described as isometric (Fig. 11). As judged from shell length, the rate of growth in *S. rostrata* and *G. (G.) hians* is nearly constant over the age interval sampled, whereas shell growth rate in *G. (R.) ovata* slows markedly in older individuals (Fig. 12).

G. (R.) ovata and *G. (G.) hians* are similar in having simple comarginal shell ridges that are greatly truncated anteriorly by abrasion. Every fourth or fifth comarginal ridge protrudes farther from the surface of the shell in *G. (R). ovata,* but the shell ridges show a more uniform height in *G. (G.) hians. S. rostrata* differs from the other species in having wider, more rounded comarginal ridges. More strikingly, these ridges are covered with minute aragonitic periostracal spikes (see shell microstructure, below).

While all three gastrochaenids show considerable anteroventral abrasion of the shell, the nature of this abrasion differs between *S. rostrata* and the other species. In *S. rostrata* abrasion reduces the anterior periostracal spikes to blunt stubs at the margin of the shell while only occasionally truncating a comarginal shell ridge. On the other hand, periostracal spikes are not present in *G. (R.) ovata* and *G. (G.) hians,* so abrasion often greatly reduces the height of their comarginal shell ridges. In these two species the latest-formed ridge initially projects prominently but is quickly partially or entirely abraded. Following this abrasion, a new comarginal ridge is secreted, thereby starting a new cycle of abrasion and secretion. In all three species anterior shell abrasion is limited primarily to the surface of the latest formed comarginal ridge. Some *G. (G.) hians* and, less commonly, some *G. (R.) ovata* show evidence of additional minor abrasion on the umbones and on the lateral shell surfaces.

Anterior truncation of the comarginal shell ridges is slightest in *S. rostrata* (50 to 70 percent of the ridges truncated) undoubtedly because these are protected by the calcified periostracal spikes. Anterior truncation is much higher in the other two species, averaging 80 to 90 percent in *G. (R.) ovata* and over 90 percent in *G. (G.) hians.* The apparent abrasive efficiency of the shell (see Materials and Methods for definition) in *S. rostrata* is variable but generally much higher than in the other species, perhaps reflecting the varying importance of periostracal calcification or

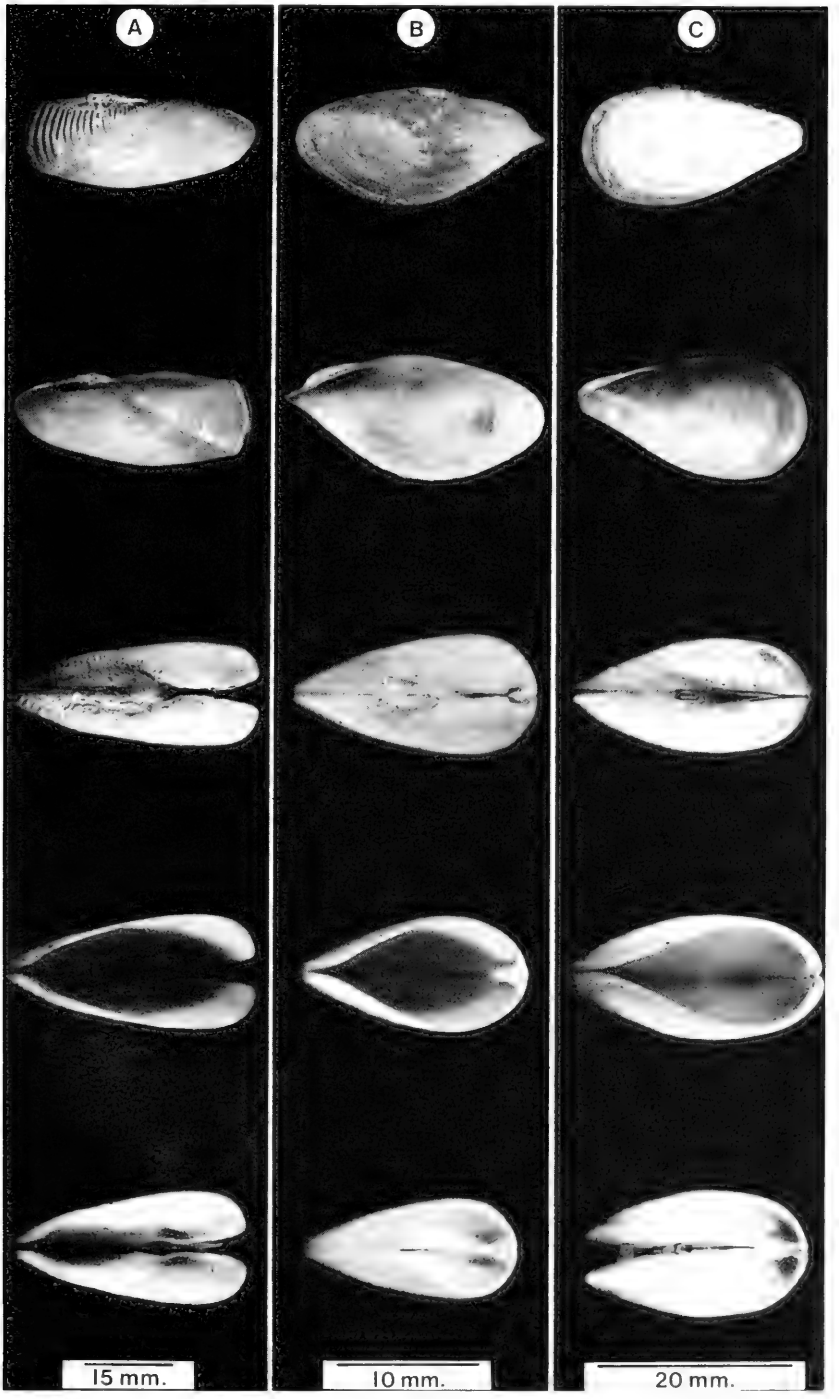


FIG. 10. *A. Spengleria rostrata* (Spengler) 1793, YPM 9480, Discovery Bay, Jamaica.
B. Gastrochaena (Rocellaria) ovata Sowerby 1834, YPM 9490, Discovery Bay, Jamaica.
C. Gastrochaena (Gastrochaena) hians (Gmelin) 1791, YPM 9483, Discovery Bay, Jamaica.
From top to bottom of figure: lateral exterior view, lateral interior view, dorsal view perpendicular to the hinge axis, ventral view perpendicular to the plane of the pedal gape, ventral view perpendicular to the hinge axis (showing hinge structure).

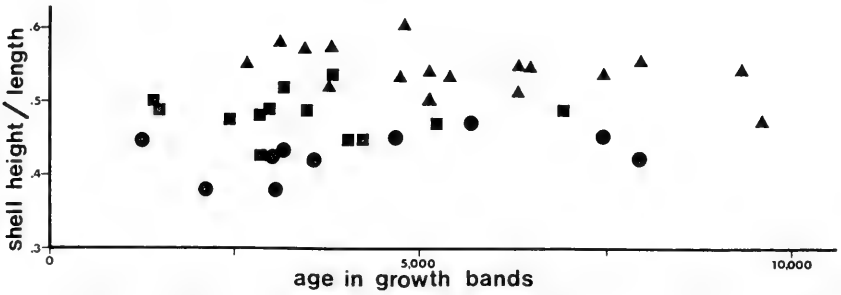


FIG. 11. Variation of shell height/length ratio with age in *Spengleria rostrata* (dots), *Gastrochaena (Rocellaria) ovata* (squares), and *Gastrochaena (Gastrochaena) hians* (triangles).

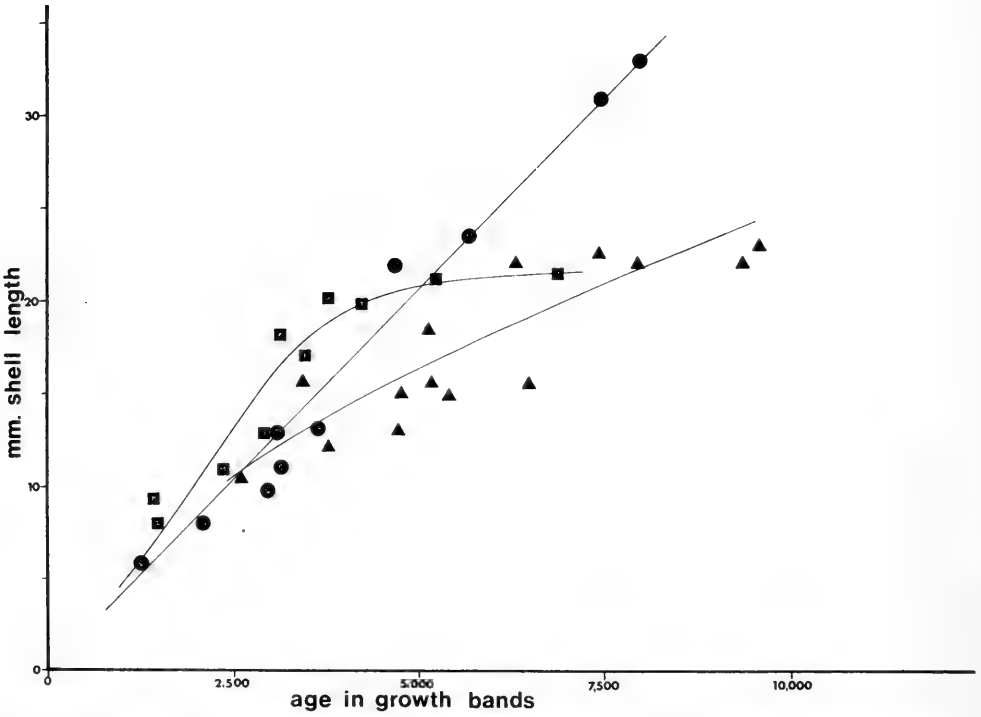


FIG. 12. Variation of shell length with age in *Spengleria rostrata* (dots), *Gastrochaena (Rocellaria) ovata* (squares) and *Gastrochaena (Gastrochaena) hians* (triangles).

chemical boring in protecting the ridges from abrasion (Fig. 13). The apparent abrasive efficiency of the shell in *G. (R.) ovata* and *G. (G.) hians* is more uniform throughout the sampled populations, and is only slightly higher in the former species. *G. (R.) ovata* may show a higher value than *G. (G.) hians* because its burrows are shallower; so its shell penetrates primarily into the outer, more friable layers of the coral skeleton.

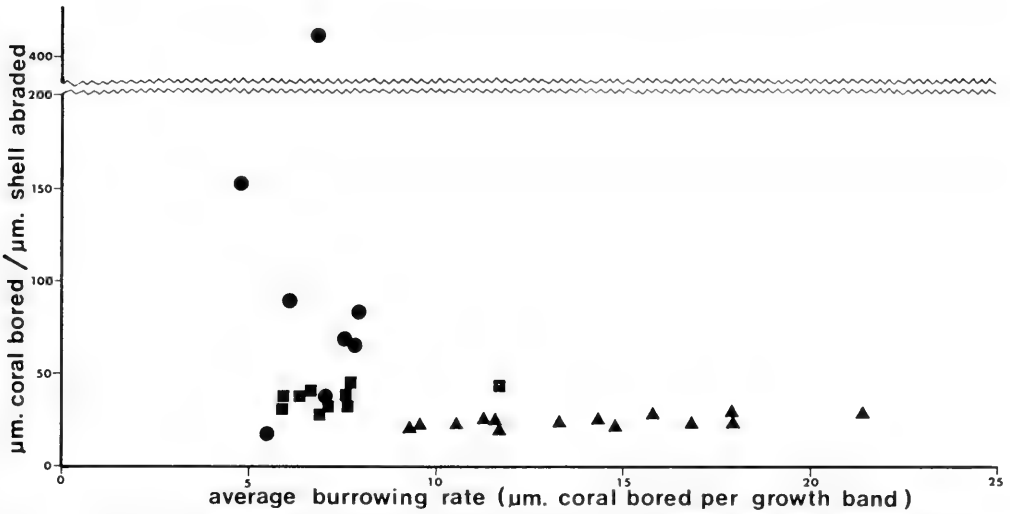
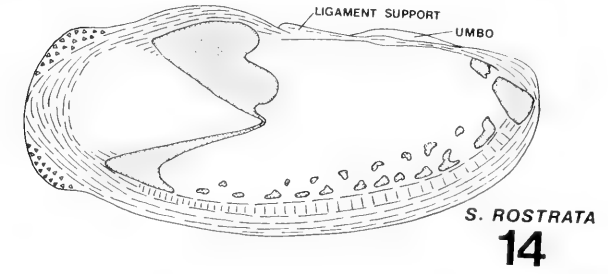


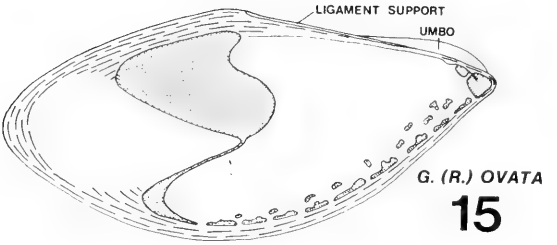
FIG. 13. Relationship between apparent abrasive efficiency (μm. coral bored/μm. shell abraded) and average burrowing rate in *Spengleria rostrata* (dots), *Gastrochaena (Rocellaria) ovata* (squares), and *Gastrochaena (Gastrochaena) hians* (triangles).

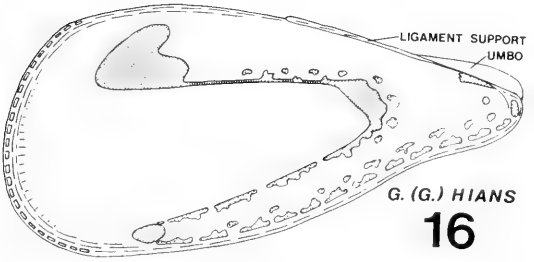
6. SHELL MICROSTRUCTURE

Shells of all three species consist primarily of periostracum, composite prismatic, crossed lamellar (CL) and fine complex crossed lamellar (fine CCL) structures (from shell exterior to shell interior), with myostracal prismatic structure occurring at sites of muscle-shell attachment (Figs. 14–16). The periostracum is generally intact only in the posterior of *S. rostrata,* where this forms regular vertical corrugations. The periostracum is commonly 15.0, 10.0 and 7.5 μm. thick in the posterior of *S. rostrata, G. (R.) ovata* and *G. (G.) hians,* respectively, and this thins anteriorly in *S. rostrata* but thickens by about 20 percent in *G. (R.) ovata* and *G. (G.) hians.* The periostracum of *S. rostrata* is studded with aragonitic spikes arranged in concentric rows in the shell posterior (Fig. 17) and in concentric to oblique rows in the shell anterior (Figs. 18, 19). Calcified spikes also occur in parts of the periostracum extending the primary ligament anteriorly and posteriorly; here the spikes are irregularly arranged and more sparse than in other parts of the shell. The aragonitic spikes are clearly entirely contained within the periostracum posteriorly (Fig. 20), but toward the shell anterior the organic component of the periostracum thins and the spikes lie closer to the surface of the shell (Fig. 21). In the midlateral and anterior parts of the shell, the bases of the spikes are partially imbedded within the underlying composite prismatic shell layer, and they are strongly abraded along the anteroventral shell margins (Figs. 18, 19). The unabraded spikes vary considerably in average dimensions, those in the shell anterior being widest, and those in the dorsal periostracum being much narrower (Fig. 22). The spikes in any given fragment of periostracum may vary considerably in width and length (Fig. 23), but average spike width and length both increase regularly with age. In the shell posterior the average spike length increases geometrically with age (Fig. 24) whereas the average spike width/length ratio increases linearly with age at the time of secretion (Fig. 25).

The secretion of individual aragonitic spikes is apparently initiated by the inner surface of the outer mantle fold near the periostracal groove, i.e., between the outer and middle mantle folds. A view of the outer surface of newly secreted periostracum between the outer and middle mantle folds (Fig. 26) shows a progressive increase in spike diameter away from the







FIGS. 14–16. Typical distributions of shell microstructure in the tropical Western Atlantic gastrochaenids. Legend:

stippling: myostracal prismatic structure.
dashes (parallel to the shell margins): branching crossed lamellar structure.
dashes (perpendicular to the shell margins): radiating crossed lamellar structure.
triangles: triangular crossed lamellar structure.
rectangles: blocky crossed lamellar structure.
white: fine complex crossed lamellar structure.

Although shown in white for the sake of simplicity, the shell exterior near the umbones may be composite prismatic, crossed lamellar, or complex crossed lamellar, depending on the depth of abrasion of the shell. The two exterior shell layers (periostracum and composite prismatic) do not appear in this view of the inner shell surface. The varieties of crossed lamellar and complex crossed lamellar structure are explained in detail by Carter (1976b).

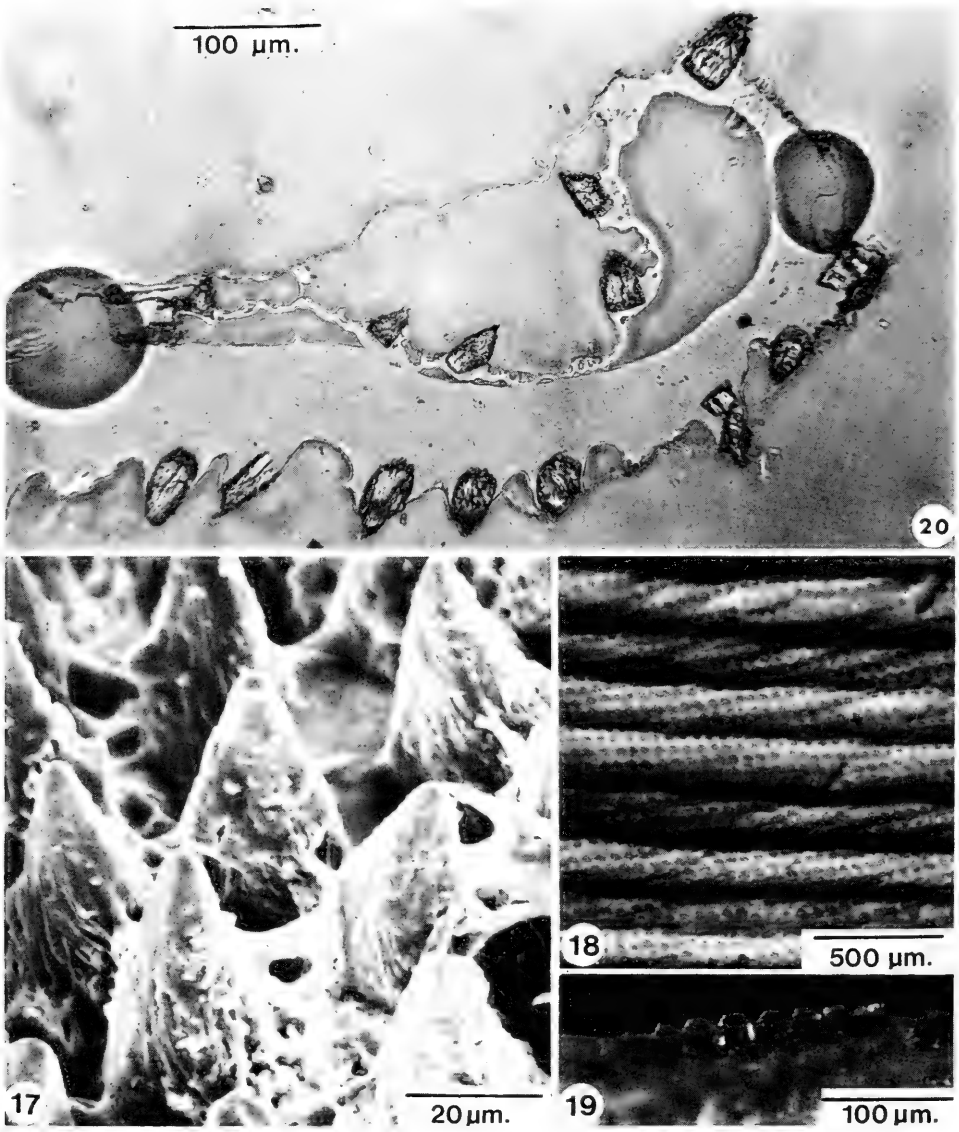


FIG. 17. Surface of the posterior periostracum in *Spengleria rostrata;* scanning electron micrograph. Rodlike structure on the right is a sponge spicule.

FIG. 18. Abraded tips of aragonitic periostracal spikes on the sides of the shell in the anterior of *Spengleria rostrata.* Note the alignment of the spikes in rows oblique to the larger comarginal shell ridges.

FIG. 19. Aragonitic periostracal spikes on the anteroventral shell margin of *Spengleria rostrata.* Note the apical abrasion.

FIG. 20. Acetate peel of a radial vertical section through the posterior periostracum of *Spengleria rostrata.* Note the thin outer layer of the organic periostracum pulled away from the tips of some of the aragonitic periostracal spikes.

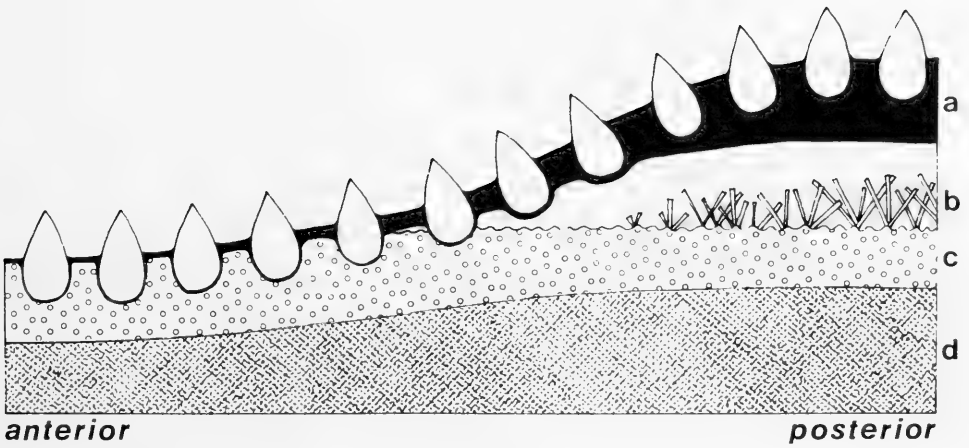


FIG. 21. Diagrammatic representation of the anterior thinning of the organic periostracum along an anterior-posterior vertical section through the shell of *Spengleria rostrata*. Note the increased imbedding of the aragonitic periostracal spikes within the composite prismatic shell layer *(c)* toward the anterior.

Legend:

a. periostracum with aragonitic spikes.
b. acicular prismatic layer.
c. composite prismatic layer.
d. crossed lamellar and fine complex crossed lamellar layer.

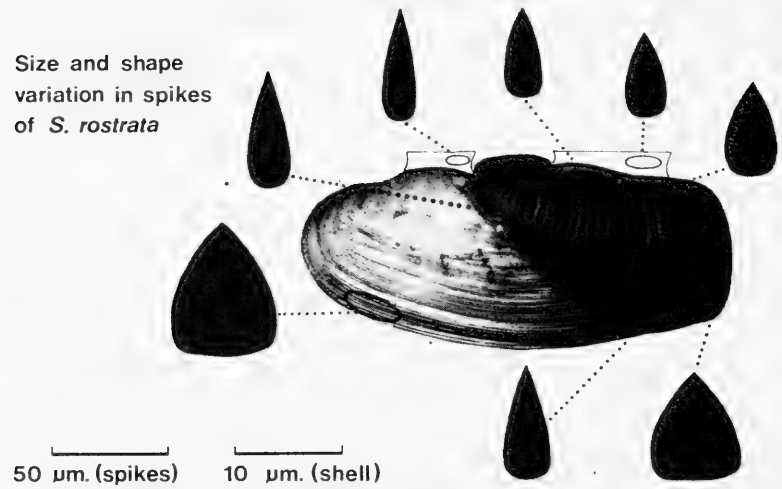


FIG. 22. Size and shape variation of periostracal spikes in *Spengleria rostrata*. The measurements indicated by the spike shapes represent averages of at least 60 measurements for each area of the periostracum circled in the diagram. Only unabraded spikes were measured.

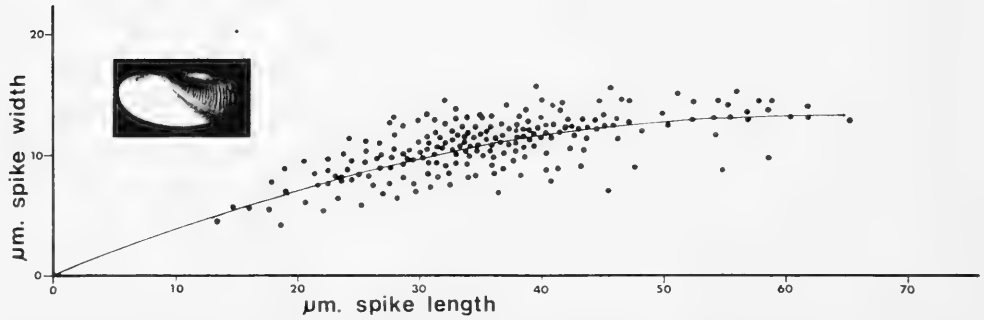


FIG. 23. Variation in aragonitic periostracal spike shape and size within a small portion of periostracum removed from the posterior of the shell in *Spengleria rostrata*. (See area circled in the accompanying photograph.)

periostracal groove and a simultaneous change in spike appearance from cloudy white to clear and refractive. The aragonitic spikes attain maximum size near the shell margin, just prior to reaching the sites of initiation of the underlying composite prisms. Individual aragonitic spikes appear crystallographically uniform under crossed-polarized light, with the crystallographic c-axis paralleling the spike length. Dissolution of isolated spikes in dilute HCl reveals an abundant water-insoluble organic matrix.

The shape of aragonitic periostracal spikes may be constant or quite variable within a small fragment of periostracum. Several shape variations among thousands of spikes observed are illustrated in Figure 27. The most common shape (Fig. 27, *a-i*) is a simple cone with a hexagonal cross-section. Rarely, the spikes show distinct internal growth banding (Fig. 27, *q-s*)

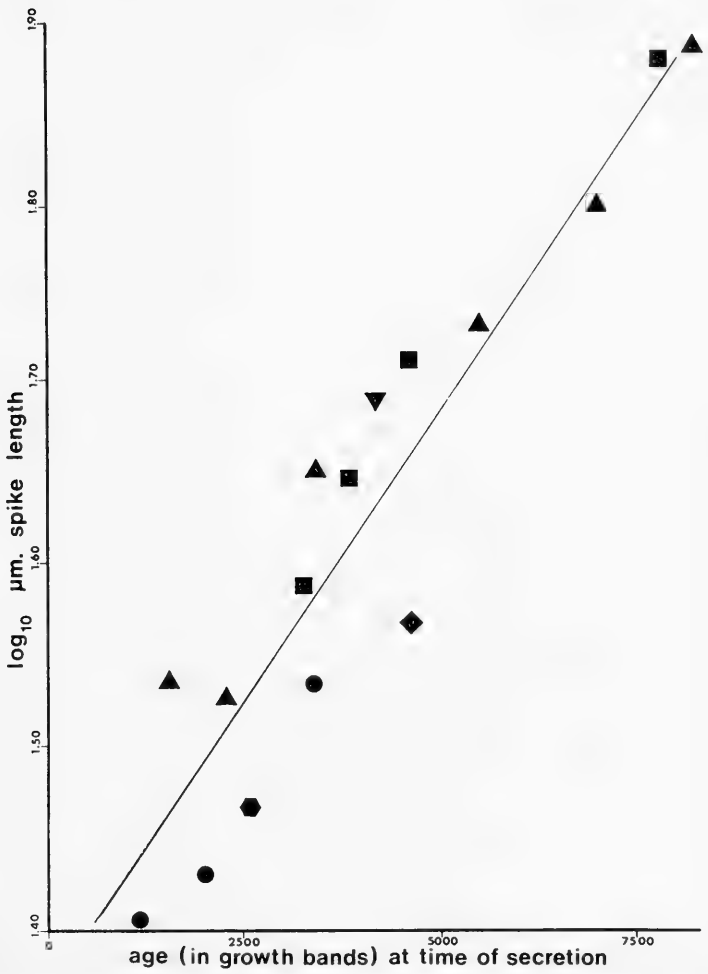


FIG. 24. Relationship between aragonitic periostracal spike length and age at time of secretion in *Spengleria rostrata*. Each data point represents an average of at least 60 length measurements for spikes isolated from within the posterior periostracum near the extreme posterior shell margin. The periostracum is sampled along a radial transect from the umbo to the posterior shell margin. Samples from the same specimen of *S. rostrata* are indicated by the same symbol (a dot, square, triangle, tilted square, upside-down triangle, or hexagon).

indicative of periodic secretion on their bases. Apparent irregularities in secretion may also result in basal (Fig. 27, *j-m, o*) or apical (*l, m*) bosses. Although the spikes are generally mutually isolated in the periostracum, they are rarely closely spaced in groups of two or three (Fig. 27, *n*) or they may appear as fused twins (*o, p*). Scanning electron microscopy of isolated spikes (Figs. 28, 29) shows an ultrastructure of elongate crystal laths usually 0.03 to 0.04 μm. thick and 0.45 to 1.06 μm. wide. Individual laths may be terminated by hexagonal crystal faces or they may show evidence of length-parallel acicular subunits about 0.03 μm. in diameter. This lathlike ultrastructure contrasts sharply with the polygonal prismatic ultrastructure of aragonitic periostracal spikes described for the pandoracean *Laternula* by Aller (1974). Spikelike periostracal calcification is rare or

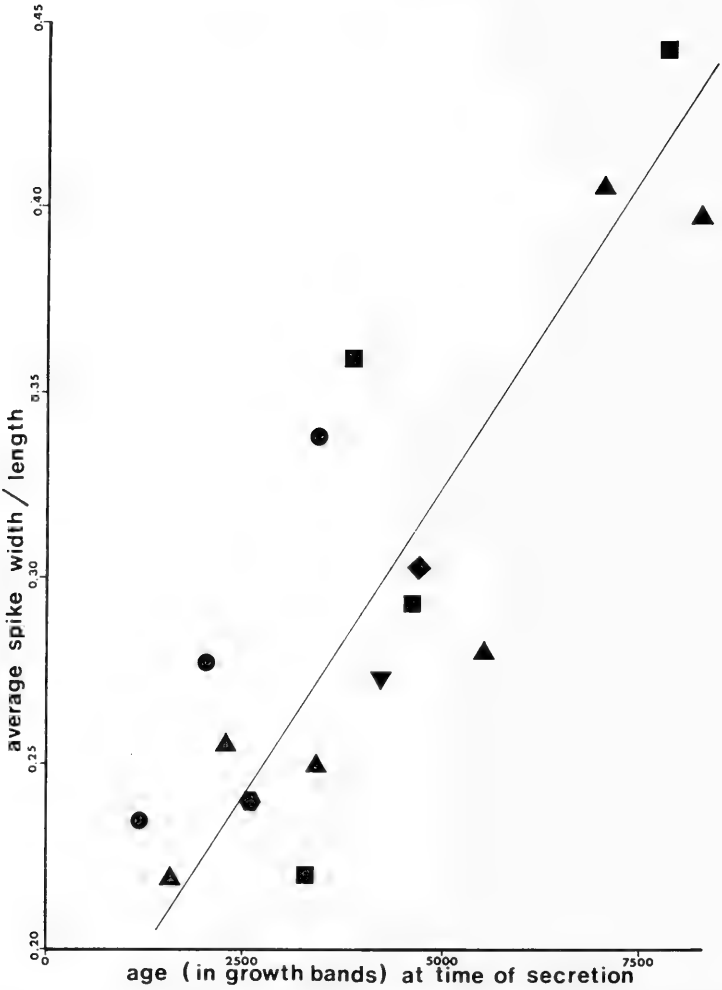


FIG. 25. Relationship between aragonitic periostracal spike width/length ratio and age at time of secretion in *Spengleria rostrata.* See explanation of Figure 24.

absent in adults of Recent representatives of *Gastrochaena.* But the presence of minute spikes on shells of the Upper Cretaceous *Gastrochaena (Rocellaria) linsleyi* (Appendix C) and *Eufistulana ripleyana* (Stephenson 1941) suggests that this is an ancestral feature of the superfamily. Aragonitic periostracal spikes have also been observed on the shell of a Pliocene *Gastrochaena (Gastrochaena)* from Florida (Fig. 30). In this fossil the spikes are restricted to the juvenile shell and were apparently not secreted by the adult. Spikelike periostracal calcification is retained in Recent gastrochaenids only in the two surviving species of *Spengleria* and perhaps in the juvenile shell of *Gastrochaena rugulosa* Sowerby (USNM 184364; Panama), *Gastrochaena denticulata* Deshayes, and certain *Gastrochaena (Rocellaria)* (Carter 1976a).

Most living bivalves lack distinct periostracal calcification of the kind present in *S. rostrata;* so this species is a striking exception to the rule. Aller (1974) described similar spike-shaped processes cemented to the shell

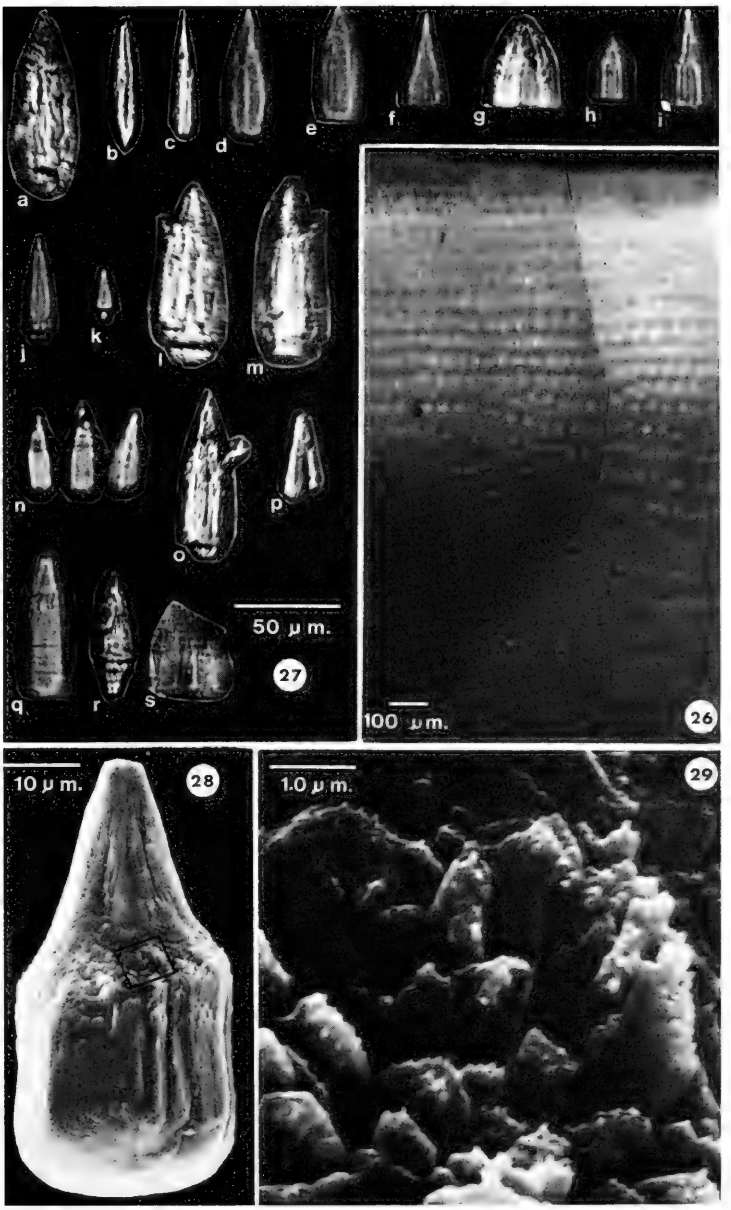


Fig. 26. Surface view of newly secreted periostracum in the posterior of *Spengleria rostrata*. The extreme posterior of the shell (out of focus) appears in the uppermost part of the photograph. The spike diameter increases from the bottom of the photograph (nearest the periostracal groove) toward the posterior shell margin.

Fig. 27. Aragonitic periostracal spikes freed from within the posterior organic periostracum of *Spengleria rostrata* by dissolution of the organic matrix in NaOCl.

Fig. 28. Aragonitic periostracal spike freed from within the posterior periostracum of *Spengleria rostrata* by dissolution in NaOCl. Scanning electron micrograph.

Fig. 29. Aragonitic periostracal spike freed from within the posterior periostracum in *Spengleria rostrata*. Higher magnification of the area circumscribed by the parallelogram in Figure 28. Scanning electron micrograph.

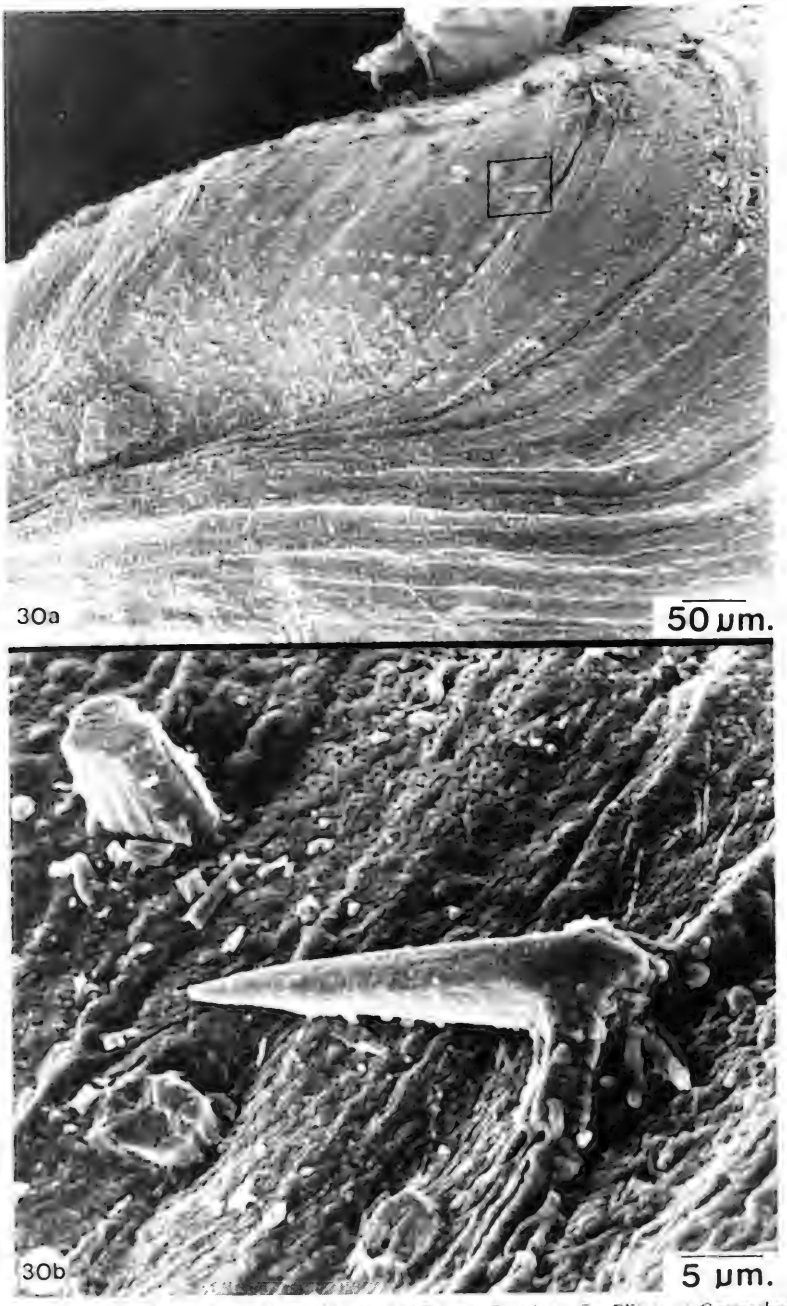


FIG. 30a,b. Aragonitic spikes on the juvenile parts of the left valve of a Pliocene *Gastrochaena (Gastrochaena)* from St. Petersburg, Florida (YPM 9597). Figure 30b is a higher magnification of the area circumscribed by the parallelogram in FIG. 30a. Note the absence of the spikes in the adult shell to the right (posterior) and bottom (ventral) in Figure 30a.

exterior in the pandoracean *Laternula*. Although these calcified spikes are probably not entirely embedded within the periostracum in the shell posterior (Aller, personal communication, states that this possibility has yet to be explored), they resemble the spikes in *S. rostrata* in three respects. 1) In *Laternula* and *S. rostrata* at least some of the spikes are cemented to or

partially embedded within the outer prismatic shell layer and they are structurally distinct from this layer. 2) The aragonitic spikes are formed in a zone of mantle epithelium (the inner surface of the outer mantle fold) peripheral to the zone of initiation of the outer prismatic layer of the shell proper. In addition, the spikes are fully formed by the time the underlying prismatic shell layer is initiated. 3) Spike formation occurs simultaneously with the secretion of organic periostracum. Since the spikes in both *Laternula* and *Spengleria* are formed simultaneously with organic periostracum by the inner surface of the outer mantle fold, they may be properly regarded as periostracal structures. The spikes are therefore *genetically* distinct from the underlying prismatic shell layer. By inference from the present data, certain granular processes on the exterior of other pandoraceans (e.g., *Thracia pubescens;* see Taylor, 1973) and the spherical granules described for a poromyacean by Runnegar (1974) (see his plate 5, fig. 8) may also be regarded as calcified periostracal structures. The wide distribution of spike- and granule-like periostracal calcification among representatives of the Mytilacea, Permophoridae, Myoida (all four superfamilies) and Anomalodesmata (all six superfamilies) suggests that these structures appeared early in the evolution of the Bivalvia. According to Carter and Aller (1975) spicule-like periostracal calcification may have constituted a primordial molluscan shell. This theory finds support in the occurrence of radial rows of minute granules cemented to the shell exterior in the Middle Cambrian monoplacophoran *Latouchella penecyrano* (fig. 10A–12 in Runnegar and Jell, 1976), an early representative of the most primitive molluscan class.

In addition to showing aragonitic periostracal spikes, *S. rostrata* is unique in having a sparsely developed aragonitic acicular prismatic layer in the shell posterior between the periostracum and the underlying composite prismatic layer (Fig. 21 and Carter, 1976a). This acicular layer, which characterizes *S. mytiloides* as well as *S. rostrata,* thins and disappears anteriorly where the periostracum comes to lie in contact with the composite prismatic shell layer (Fig. 21). The acicular prisms occur in fan-shaped aggregates that only partially fill the cavity beneath the periostracum. The orientation of individual acicular prisms appears random, but there is a tendency for prisms pointing toward the shell margin to be longer, suggesting growth in a concentration gradient. Individual acicular prisms show no evidence of an organic matrix upon dissolution, and they are morphologically identical to a common crystal form of inorganically precipitated aragonite.

The underlying composite prismatic shell layer is strongly developed in the posterior *S. rostrata* but is very weakly developed in the anterior of this species and over the entire shell of *G. (R.) ovata* and *G. (G.) hians.* The composite prismatic shell layer consists of radial first order prisms that bifurcate toward the shell margin (Figs. 31, 32). Radial, vertical sections show that these first order prisms are not strictly horizontal but rather bend toward the inner shell surface. The individual first order composite prisms consist of smaller second order prisms radiating at a high angle from a longitudinal central prism axis toward the surface of deposition.

The inner shell layers beneath the composite prismatic layer consist of crossed lamellar (CL) and fine complex crossed lamellar (fine CCL) struc-

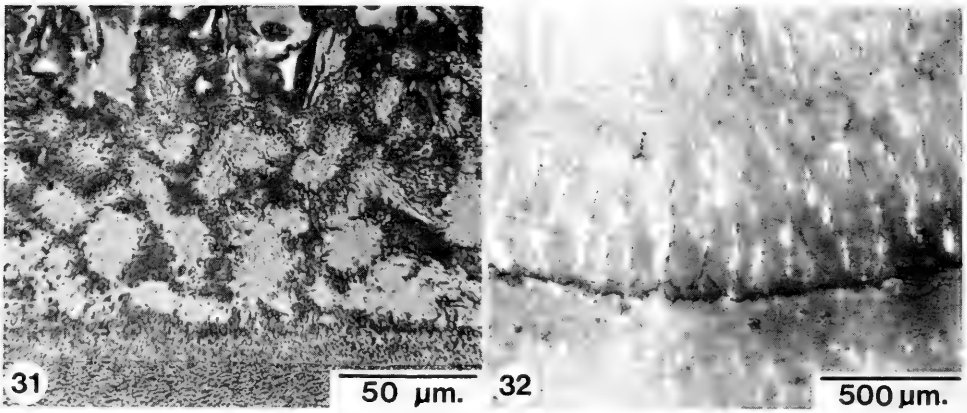


FIG. 31. Acetate peel of a vertical transverse section through the composite prismatic layer in the posterior of *Spengleria rostrata*. The shell exterior is toward the upper part of the photograph. The boundary between the porous acicular prismatic (above) and composite prismatic (middle) shell layers appears near the upper part of the photograph. The boundary between the composite prismatic and crossed lamellar shell layers appears in the lower part of the photograph.

FIG. 32. Exterior surface view of the shell posterior in *Spengleria rostrata* showing several first order composite prisms radiating from the umbo (upper part of photograph) toward the shell posterior (lower part of photograph). The periostracum and acicular prismatic shell layer have been removed to expose the composite prisms.

tures with myostracal prismatic structures developed at sites of shell-muscle attachment. As seen on inner shell surfaces, the CL structure is generally found exterior to the pallial line, while the fine CCL structure is found mostly interior to the pallial line except in the shell posterior, where it also occurs slightly exterior to the pallial line. Figures 14 to 16 show the distribution in the shell of several varieties of CL structure defined by Carter (1976b). The first order crossed lamels in *G. (R.) ovata* are mostly of the branching concentric variety (BCL), while those in *G. (G.) hians* are of the BCL variety anteriorly and of the BCL, radiating (RCL), and blocky (BlCL) varieties posteriorly. In *S. rostrata* RCL and BCL occur together in the shell anterior, while triangular (TCL) lamels flank BCL lamels in the shell posterior. The CL and CCL structures observed in the present species are uniformly present among the scores of individuals analyzed, but the distribution of each structure on the depositional surface varies with the age of the individual. Significant deviations from the distribution patterns shown in Figures 14 to 16 occur in gerontic individuals. In gerontic specimens the BCL structure may cover much of the depositional surface, even within the pallial line.

7. LIGAMENT AND DENTITION

The ligament in the Soldier Key gastrochaenids is external and inserts on ligament nymphs posterior to the umbones. The primary ligament is extended anteriorly and posteriorly only by the periostracum, which unites the valves along their entire dorsal margin. The ligament nymphs are shorter in *S. rostrata* than in *G. (G.) hians* and *G. (R.) ovata,* and in all three species the ligament and its periostracal extensions preclude pholad-like rocking of the valves about a vertical axis. The line of the ligament is oblique to the longitudinal shell axis, with the angle between the ligament and shell axis being greatest in *G. (G.) hians* and least in *S. rostrata.* Because of this high angle, *G. (G.) hians* can open its shell valves widely along the posterior margin while hardly increasing the gape between the valves anteriorly. The ligament nymph in *G. (R.) ovata* is smaller than in the other species, and this difference is expressed in the relatively small opening moment of its ligament. The ligament opening moment at shell closure for preserved specimens averages about 25 grams in adult *S. rostrata* and *G. (G.) hians* but only about 6.5 grams in *G. (R.) ovata.* At the point of maximum shell gape allowed by the width of the burrow, the ligament retains 28 to 40 percent of this opening moment, averaging about 7, 10, and 2 grams in *S. rostrata, G. (G.) hians* and *G. (R.) ovata,* respectively. These latter values represent the relative forces that would be applied to the lateral burrow walls by the shell margins during boring, assuming that no additional pressure is supplied by muscular and hydrostatic forces.

The Gastrochaenacea are commonly described as edentulous (Purchon 1954 and Olsson 1961, among others), and no species examined in this study shows a regular dentition. Rare specimens of *G. (G.) hians* from Discovery Bay, Jamaica, show a minute elongate ridge or boss in the right or left valve and a corresponding pit in the opposing valve, but this "cardinal dentition" is too irregularly developed to warrant homologies with the cardinal dentition of other bivalves. Apparently similar structures were noted for other gastrochaenids by Forbes and Hanley (1853, p. 129) and Lamy (1925). Lamy described the hinge as edentulous or showing a rudimentary cardinal tooth, forming a small callosity in older individuals.

8. BURROWS

Unlike most endolithic bivalves, gastrochaenids secrete aragonitic burrow linings that form distinctive internal burrow shapes and commonly show considerable detail in sculpture and ornamentation. Typical internal burrow shapes and burrow lining distributions are shown in Figure 33. The present observations largely confirm and extend those of Robertson (1963) for the three common Florida Keys gastrochaenids. Burrows of *S. rostrata* and *G. (R.) ovata* are less than twice as long as the shell and commonly curve gently in the dorsal direction. In contrast, burrows of *G. (G.) hians* are several times longer than the shell and may be straight or sinuously curved. All three burrows show two well-defined parts, a posterior siphonal burrow and an anterior shell chamber. Aragonitic linings in the form of an annular diaphragm or pointed "baffles" may constrict the siphonal burrow at its junction with the shell chamber. As a result, shell mobility is restricted to the shell chamber. The shell chamber is only slightly larger than the shells in every dimension, and it varies from circular to slightly elliptical in cross-section (Fig. 34). This part of the burrow is wide enough to allow rotations of the shells about an anteroposterior axis, and rotations by *S. rostrata* in partially opened burrows have been observed up to 90 degrees in either direction relative to the stationary foot. The lining of the siphonal burrow is smooth in *G. (R.) ovata,* but this

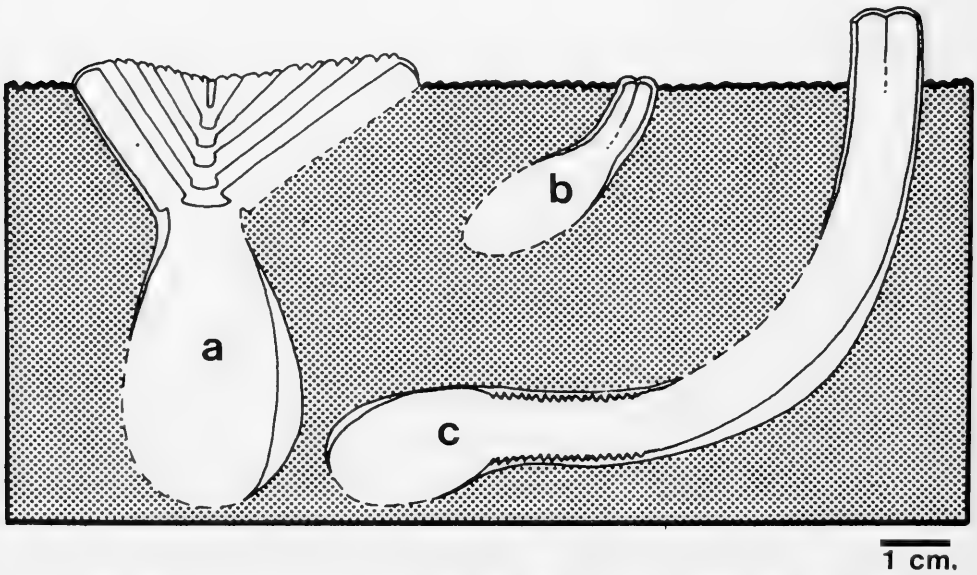


FIG. 33. Burrow cross-sections for adults of *Spengleria rostrata* (*a*), *Gastrochaena (Rocellaria) ovata* (*b*) and *Gastrochaena (Gastrochaena) hians* (*c*). The coral substratum is indicated by stipling; the aragonitic burrow linings are indicated by solid lines. The absence of a burrow lining is shown by a dashed line. The solid lines drawn between the siphon tubes of *Spengleria rostrata* suggest the configuration of accretion banding in the aragonitic deposits.

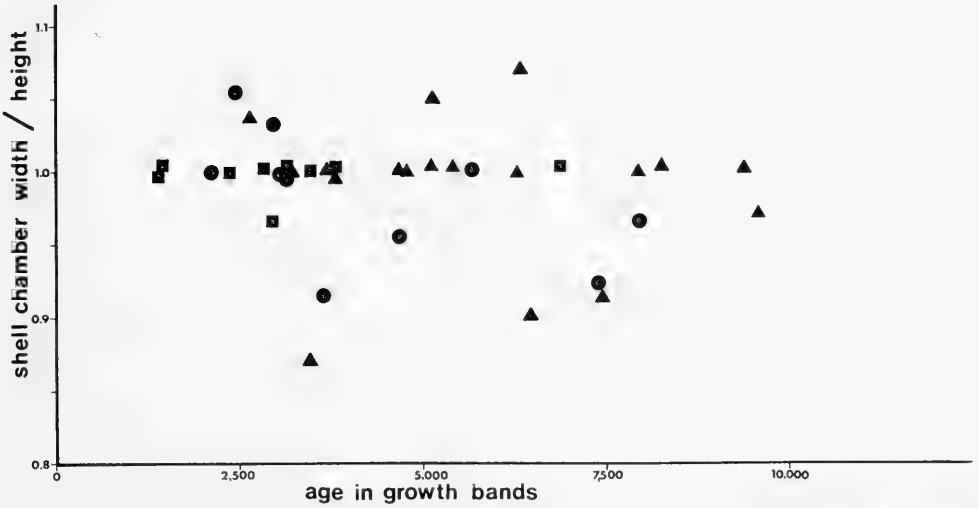


FIG. 34. Relationship between burrow shell chamber width/height ratio and age in *Spengleria rostrata* (dots), *Gastrochaena (Rocellaria) ovata* (squares) and *Gastrochaena (Gastrochaena) hians* (triangles).

may show a slight annular constriction (i.e., diaphragm) in older specimens at the base of the siphons. In contrast, the siphonal burrow in *G. (G.) hians* shows irregular concentric ridges especially near the base of the siphons (Figs. 33c, 36). In *S. rostrata* the burrow lining projects prominently in the form of two pointed baffles at the base of each siphon. These baffles appear identical to those described for another species of *Spengleria* by Soliman (1973). The siphon tube linings in *S. rostrata* also show minute knobs projecting about 0.3mm from the burrow walls, giving these linings a rough interior surface. The burrow linings in all three species show distinct accretion banding, and the linings in *S. rostrata* are commonly porous (Figs. 35, 36). The lining of the shell chamber is generally smooth, but this may appear locally rough and pitted where its prismatic microstructure is unusually coarse.

The thickness and distribution of the siphonal burrow linings depend largely upon the diameter of the siphons relative to the shell chamber and the direction of boring by the siphonal epithelium. The siphonal burrow linings increase in thickness with increasing difference in diameter between the siphons and the shell chamber. Thus, the thick-siphoned *G. (G.) hians* secretes thin siphonal burrow linings, whereas the narrower siphoned *S. rostrata* and *G. (R.) ovata* secrete thicker linings. Because the siphons in *S. rostrata* spread apart by boring into the substratum, their burrow linings are thickest between the siphons and thin or absent on the opposite (i.e., "boring") side of each siphon. The fused siphons of *G. (G.) hians* may also bore laterally into the substratum, similarly resulting in a thicker deposition of aragonite on one side (Fig. 33c). As in the siphonal burrow, the thickness and distribution of burrow linings in the shell chamber depend on the boring direction. This direction may be partly dorsal, ventral or lateral in addition to the prominent anterior direction.

An unusual feature of many gastrochaenid burrows is the presence of minute tubules penetrating the burrow lining around the area of pedal

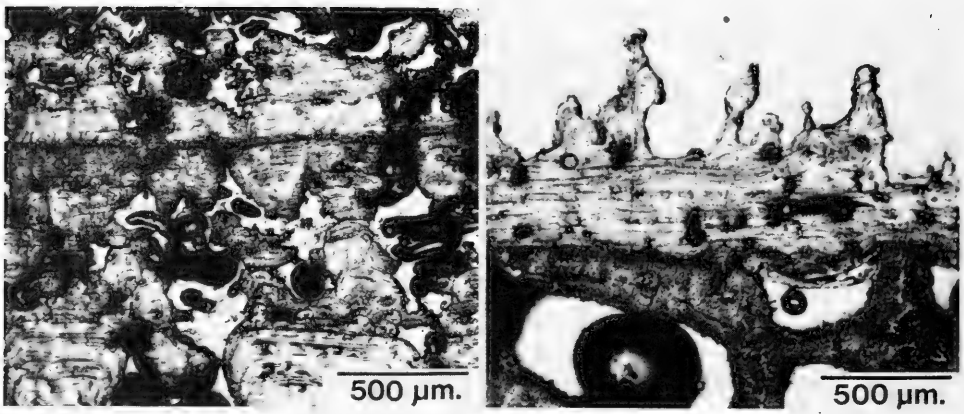


FIG. 35. Acetate peel of a transverse section through the burrow shell chamber lining of *Spengleria rostrata.* Note the lines of accretion paralleling the surface of deposition (horizontal in this photograph).

FIG. 36. Acetate peel of a vertical section through the siphonal burrow lining of *Gastrochaena (Gastrochaena) hians.* The coral substratum appears in the lower one-third of the photograph. The section is taken from near the base of the inhalant siphon, and is aligned parallel to the siphon length.

attachment (Fig. 37). These are common features in burrows of G. *(G.) hians,* and are especially numerous in burrows approaching other borers or opposite surfaces of the substratum. For example, anterior burrow tubules were abundant in the two specimens boring near the coral margin in Figure 44. These tubules probably serve a probing function for guiding the boring direction (see below).

All three gastrochaenids are capable of extending their siphonal burrow above the substratum, but this habit is typical only in *G. (G.) hians.* In this species the burrow lining invariably projects one to two centimeters above the substratum. When coral overgrowth threatens *G. (G.) hians,* it may further extend its siphons several centimeters beyond their normal length (Figs. 38, 44). These siphonal burrow extensions differ from those described by Otter (1937) for *G. (G.) cuneiformis* in showing only a partial calcareous partition between the inhalant and exhalant siphonal apertures. For *S. rostrata,* overgrowth by encrusting sponges is more of a problem than coral overgrowth because this species commonly settles the underside of coral margins. Because encrusting sponges seldom reach a considerable thickness (i.e., rarely over two or three centimeters), they induce only a slight lengthening of the siphonal burrow in *S. rostrata* (Fig. 40).

The Soldier Key gastrochaenids show an amazing capacity for repairing even severe damage to their burrows. Burrow repair was observed for a Bermuda specimen of *G. (G.) hians* in a running water tank. On three successive days the mantle secreted aragonitic laminae along the anterior margins of a break in its burrow shell chamber (Fig. 41a,b). As shown in Figure 41b, these laminae overlap so that subsequent sheets reinforce and extend the previous ones. The formation of each lamina was accompanied by inflation of the anteroventral mantle and was initiated by the secretion of a mucous sheet. Initially supported by the mantle, the mucous sheet

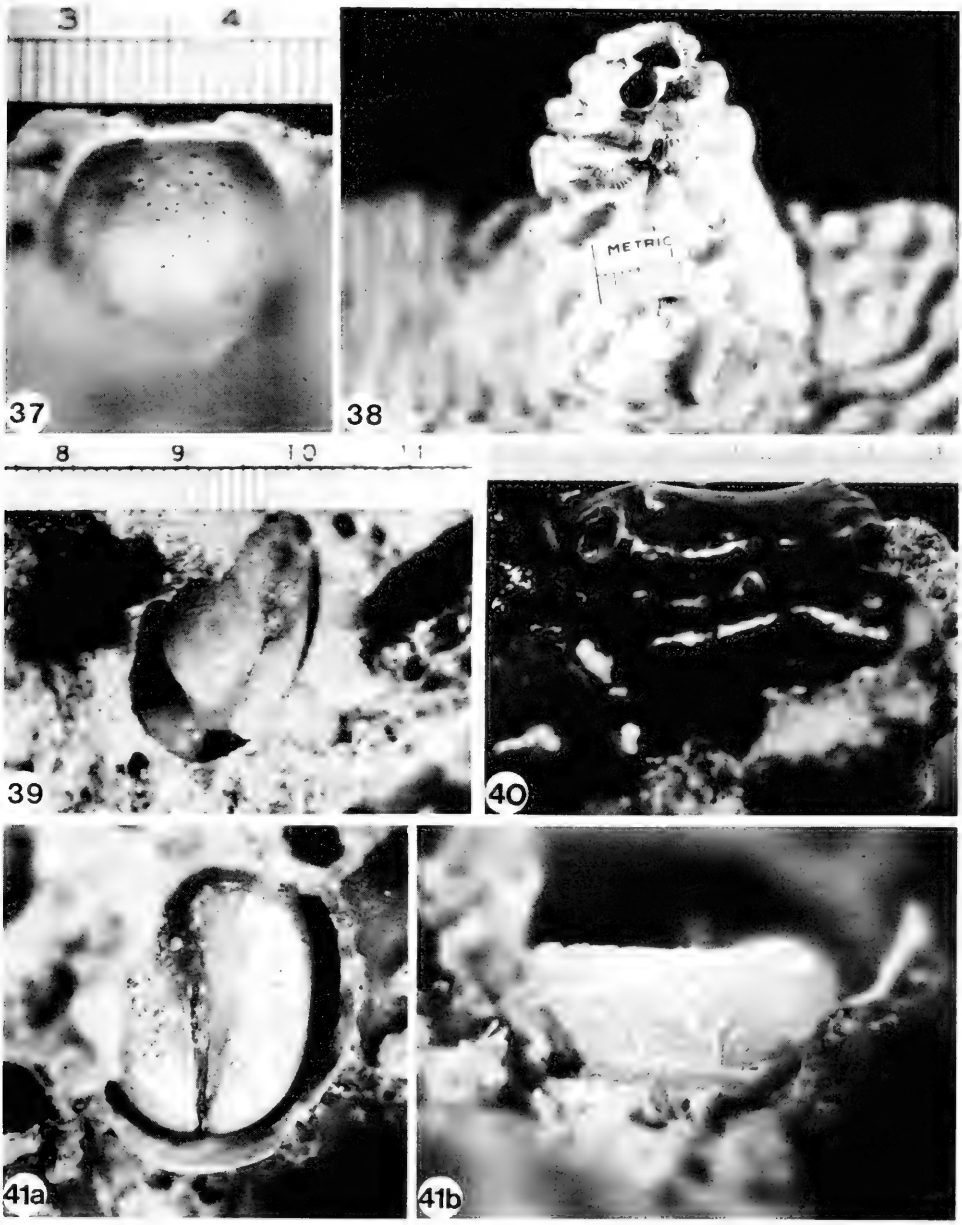


FIG. 37. Probing tubules distributed over the anteroventral wall of the shell chamber of *Gastrochaena (Gastrochaena) truncata,* YPM 9281, from Pearl Islands, Panama. This view is from the burrow posterior. The tubules penetrate the calcareous burrow lining and the coral substratum.

FIG. 38. The siphonal burrow aperture of *Gastrochaena (Gastrochaena) hians* extended posteriorly apparently to avoid overgrowth by the coral *Diploria clivosa.*

FIG. 39. Broken burrow shell chamber of *Spengleria rostrata,* showing the attached pedal apparatus and the contracted anteroventral mantle.

FIG. 40. The siphonal burrow apertures of the *Spengleria rostrata* shown in Figure 39. An encrusting sponge surrounds the exhalant (left) and inhalant (right) apertures.

FIG. 41a,b. Broken anterior shell chamber of *Gastrochaena (Gastrochaena) hians* showing the partially exposed shells and a newly secreted aragonitic burrow wall. *a,* dorsal view. *b,* anterior view.

became wrinkled when semirigid, and then hardened as the crystallization of aragonite was completed.

As might be expected from their differing burrow lengths (see Figs. 33 and 42) the three gastrochaenids differ considerably in their life averaged rates of boring (Fig. 43). *G. (G.) hians* is the most rapid borer, and its boring rate decreases considerably with age. Although much slower borers, *S. rostrata* and *G. (R.) ovata* show only a slight increase or decrease in boring rate with age, respectively. As illustrated by the latex burrow casts for *G. (G.) hians* in Figure 44, burrow lengths can also be greatly affected by erosional truncation (most common near the coral margins) or siphon elongation induced by threatened coral overgrowth.

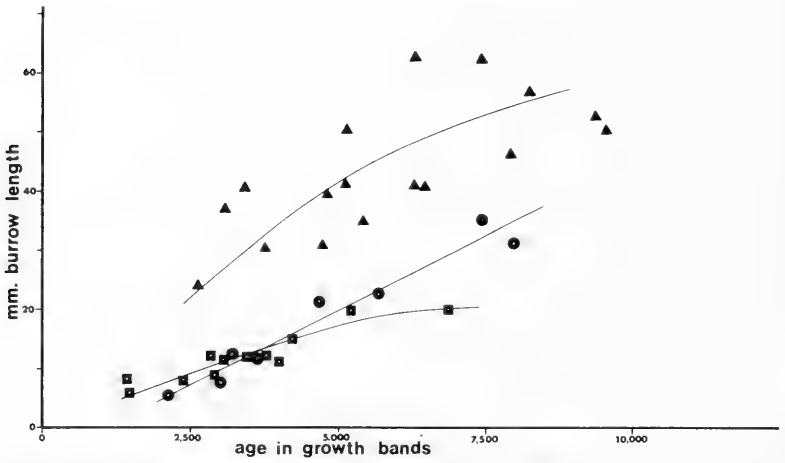


FIG. 42. Relationship between burrow length and age for *Spengleria rostrata* (dots), *Gastrochaena (Rocellaria) ovata* (squares), and *Gastrochaena (Gastrochaena) hians* (triangles).

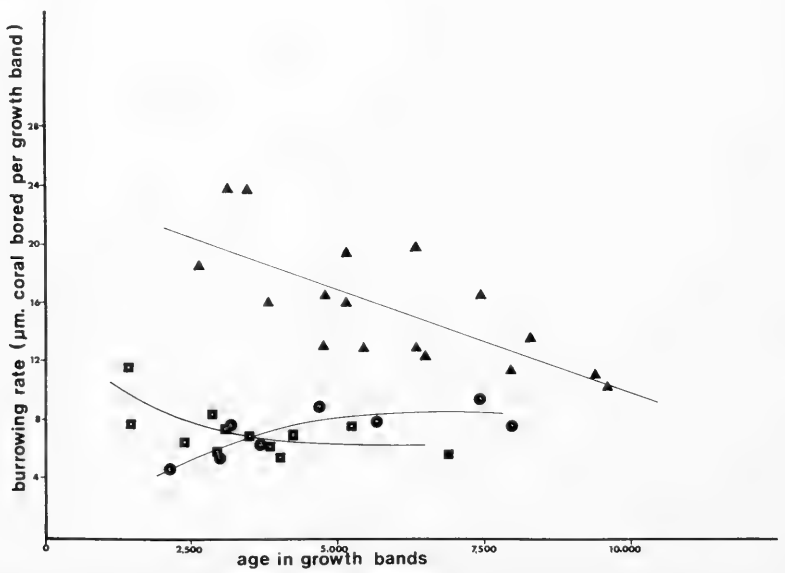


FIG. 43. Relationship between life-averaged burrowing rate and age at time of collection for *Spengleria rostrata* (dots), *Gastrochaena (Rocellaria) ovata* (squares), and *Gastrochaena (Gastrochaena) hians* (triangles).

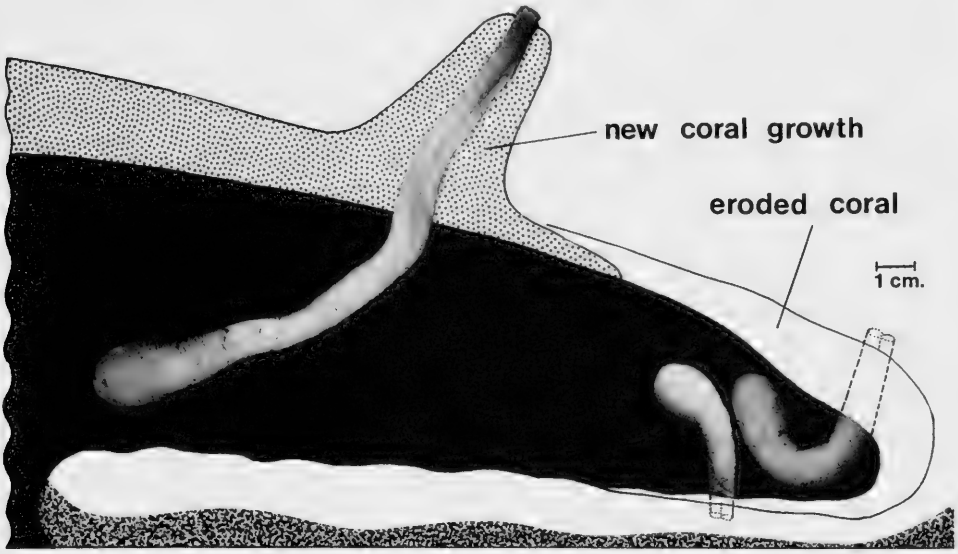


FIG. 44. Latex casts of three adult specimens of *Gastrochaena (Gastrochaena) hians* in a diagrammatic representation of their actual positions in a *Diploria* substratum. Only one-half of the *Diploria* substratum is shown in this figure. Note the attachment of the *Diploria* skeleton to the substratum on the far left.

9. MANNER OF BORING

The role of mechanical abrasion in gastrochaenid boring is apparent from the strong anteroventral abrasion of their shells, but the precise manner of mechanical boring has never been observed. Gastrochaenid anatomy and shell morphology suggest that the anteroventral shell margins are abraded against the substratum by contraction of the pedal retractor muscles about the byssally or suctorially attached foot. Purchon (1954) and Yonge (1963) presumed that abrasion by the shell then occurs by closing or opening the valves, but Gohar and Soliman (1963c) suggested that abrasion is caused by anteroposterior shell movements with some rotation. Otter (1937) inferred from the oval burrow cross-sections in *Gastrochaena (Gastrochaena) cuneiformis* that this species bores by means of a rocking movement comparable to that observed in *Pholas*. Pholads typically rock their shells about a vertical axis (Nair and Ansell, 1968), but a comparable boring mechanism cannot occur in gastrochaenids because of their relatively straight, long hinges and prominent ligaments. Gohar and Soliman noted that abrasion by the shell margins is supplemented by dorsal and lateral shell abrasion, and they added that gastrochaenid burrow circularity requires rotation of the shells about an anteroposterior axis. The observed rotation of *S. rostrata* in its burrow (see above) suggests that this may be a significant aspect of the boring mechanism. Hancock (1848) suggested that gastrochaenids and other endolithic bivalves abrade substrata by means of siliceous particles imbedded in their pedal and mantle epithelium. Subsequent authors (e.g., Jeffreys 1865) were unable to substantiate Hancock's theory, and siliceous particles were not found in the mantle of the Florida Keys gastrochaenids. One specimen of *G. (G.) hians* from Discovery Bay, Jamaica, showed crystals of aragonite superficially impressed in its siphonal and anterior mantle epithelium (Fig. 45) but these structures are atypical and may have been formed only in response to irritation of the epithelium by crab commensals found within its mantle cavity. It is likely that the "siliceous" particles described by Hancock were in fact sand grains adhering to the epithelium or refractive lipid globules within the epithelium.

The distribution of shell abrasion in *G. (G.) hians* and *G. (R.) ovata* suggest that their mechanical boring is accomplished primarily by the latest-formed, projecting, comarginal shell ridge. In *S. rostrata* abrasion also occurs on the lateral valve surfaces, but here the aragonitic periostracal spikes rather than the underlying ridges are the primary agents of abrasion.

Abraded coral debris probably enters the anterior mantle cavity through the dilated pedal gape, where it is bound into mucous strings and passed posteriorly to the base of the inhalant siphon. The same mantle pumping activity that serves to expel these and other pseudofeces (see above) will also cause a strong water current to pass between the animal

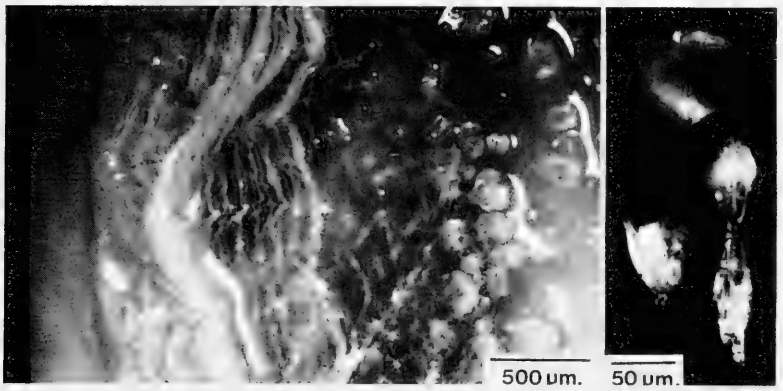


FIG. 45. Left: Ventral exterior view of *Gastrochaena (Gastrochaena) hians* showing the shell margin (far left), the folded periostracum (most of the middle portion of the photograph) and bundles of aragonite crystals on the exposed anterior mantle (far right). Right: three bundles of aragonite crystals removed from the anterior mantle by lightly scraping its surface.

and the burrow wall, thereby sweeping abraded coral debris toward the pedal aperture and into the mantle cavity.

Because of their restriction to calcareous substrata and the apparent ability of their delicate siphons to enlarge the posterior of the burrow, gastrochaenids have been considered to bore partially by chemical means (Otter 1937, Yonge 1963, Gohar and Soliman 1963c). The divergence of the siphons of *Spengleria* within the substratum (Fig. 33a) clearly requires a chemical boring mechanism, since the siphonal epithelium is relatively thin and is not protected by a periostracal sheath. Chemical boring is also required for the formation of the minute tubules that penetrate the anterior burrow linings in *G. (G.) hians*. The diameter of these tubules and their location near the pedal apparatus suggest that they are produced by the anterior pedal organ. Probing by this pedal organ would clearly be adaptive for directing burrowing, since gastrochaenids commonly bore relatively thin shells and unstable coral margins. This function is compatible with the commonness of probes in *G. (G.) hians* burrows nearing outer surfaces of the substratum or approaching burrows of neighboring borers. As shown by vertical sections through the anterior of the burrow, these probing tubules commonly follow a sinuous course, penetrating several millimeters of the coral substratum in addition to the calcareous burrow lining (Fig. 46). An unusual example of pedal probing is provided by a Pliocene *Gastrochaena (Gastrochaena)* sp. from North Carolina. The specimen whose burrow is shown in Figure 47 initially bored into a pectinid shell, but formed its own aragonitic tube when it outgrew this substratum. A latex cast of the interior of this tube (Fig. 47, right) shows numerous anterior tubules that penetrate both the secreted tube walls and shell debris incorporated into the surface of the tube. Some of these tubules branch distally, suggesting multiple probings from the same penetration through the aragonitic tube.

Additional evidence for chemical boring comes from certain Indo-Pacific species of *Gastrochaena (Cucurbitula)* boring into *Spondylus* shells. *Gastrochaena (Cucurbitula)* commonly penetrates the outer calcitic shell

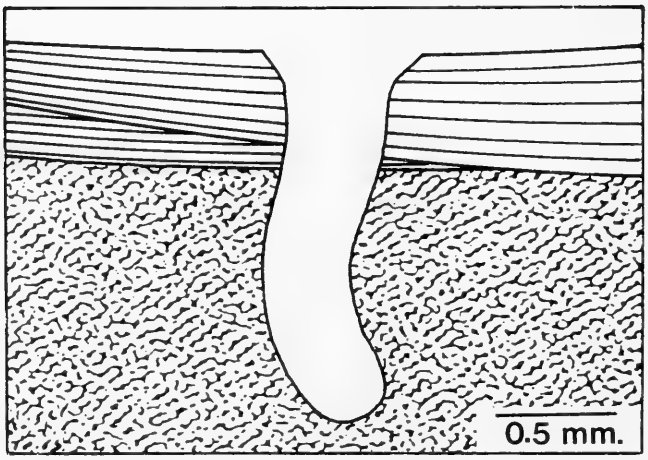


FIG. 46. Penetration of the burrow lining and part of the coral substratum by a probing tubule of *Gastrochaena (Gastrochaena) truncata*, YPM 9281, from Pearl Islands, Panama. Note the truncation of accretion lines within the general burrow lining, indicative of a previous cycle of resorption and resecretion. The diagram is based on an acetate peel of a vertical section through the burrow anterior.

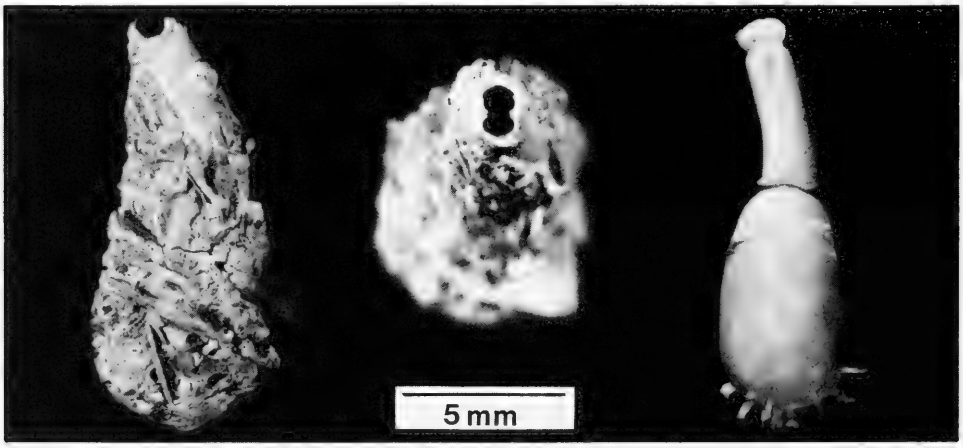


FIG. 47. Lateral (left) and posterior siphonal (middle) view of the calcareous laminated and agglutinated tube of a Pliocene *Gastrochaena (Gastrochaena)* sp. from Duplin County, North Carolina (USNM 2279).

layer of *Spondylus* and partly enters the underlying aragonitic layer. Chemical boring by *Gastrochaena (Cucurbitula)* is indicated by a distinct indentation in its burrow wall that follows the contact between the calcitic and aragonitic layers of the host shell. This indentation is too sharply defined to result from differences in the mechanical abradability of the *Spondylus* shell layers, but it may result from more rapid chemical erosion of the aragonitic layer. This would be compatible with the higher thermodynamic instability of aragonite.

Although chemical boring by the pedal, siphonal and anterior mantle epithelium in gastrochaenids seems certain, the nature of the boring agent is presently unknown. Deshayes (1846) proposed that the anterior half of

the interior pallial glands in *Gastrochaena dubia* produce acid for chemical boring, and similar suggestions were offered by Cailliaud (1856) and Carazzi (1903). Extensive lateral pallial glands are found in the tropical Western Atlantic species and in other gastrochaenids (see above and Pelseneer 1911), but the position of these glands *within* the mantle cavity suggests that they are not directly involved in chemical boring. These glands probably function like the similar glands in the burrowing and boring Hiatellacea, i.e., to secrete mucus for binding pseudofeces within the mantle cavity (see Hunter 1949 and Yonge 1971). According to Jaccarini et al. (1968) *Lithophaga lithophaga* bores chemically by means of calcium-complexing secretions emanating from two dorsal pallial glands. Distinctive glands in a similar position have not been observed in the Soldier Key gastrochaenids. However, future investigations might explore the possibility that the chevron-shaped glands located immediately dorsal to the anterior pedal organ in *S. rostrata,* or other pedal glands, may secrete a chemical boring agent. Another possibility, suggested by Kühnelt (1934), is that the glands participating in chemical boring are not concentrated, but rather occur throughout the entire exposed mantle epithelium. Such a mechanism is plausible, considering that the mantle epithelium in many bivalves is capable of bringing about general decalcification of the inner shell surface (Dugal 1939, Crenshaw and Neff 1969) or eroding tubules through previously deposited shell layers (Oberling 1964, Taylor et al. 1969).

10. GASTROCHAENID ORIGINS

Numerous fossils with probable gastrochaenid affinities are described in the literature of European Jurassic bivalve faunas, e.g., *"Gastrochaena" infraliasina* Terquem 1855 and several species of *"Gastrochaena"* described by Phillips (1829), Eudes-Deslongchamps (1838), Buvignier (1852), de Loriol and Bourgeat (1888), de Loriol (1891), and Arkell (1929–1937). Many of these Jurassic forms have not been critically re-examined since their original description in the nineteenth century, and the mytilid versus gastrochaenid affinities of the more elongate of these species have yet to be satisfactorily demonstrated. But some of these fossils, like the Jurassic *Gastrochaena moreana* Buvignier 1852 (Figs. 54–56) and *"Gastrochaena"* [=*Spengleria*] *recondita* (Phillips 1829) show unmistakable gastrochaenid affinities in terms of their flasklike burrow, *Rocellaria*-like or *Spengleria*-like shell outline, and well developed siphons (judging from the shape of the siphonal burrow). These Jurassic forms generally differ from the modern species of *Gastrochaena* and *Spengleria* in their more restricted pedal gape and greater lateral compression in the shell anterior.

Most current hypotheses regarding the origins of the Gastrochaenacea are based on comparisons of anatomy and life habits between Recent representatives of the Gastrochaenacea and Pholadacea. Purchon (1954) considered the Pholadacea as possible gastrochaenid relatives on the basis of their 1) common representation by borers with calcareous burrow linings, 2) presumed homologies between the pholad apophysis and gastrochaenid myophore, and 3) possible similarities in siphon structure. But Purchon noted that differences in manner of boring, stomach structure, and visceral ganglia do not support the view that gastrochaenids are an early offshoot from a pholadacean stock. Purchon (1954) concluded that "there is insufficient evidence to justify any view as to relationship between the Gastrochaenidae and the Adesmacea [Pholadacea]." Purchon's negative conclusion is supported by the fact that the pholad apophysis and gastrochaenid myophore are not homologous, because they attach to different pedal muscles, i.e., to the anterior and posterior pedal retractors in *Gastrochaena* and *Zirfaea* respectively (see above and Nair and Ansell 1968). In addition, possible pholadomyoid ancestors of the Pholadacea (e.g., *Myopholas* and *Girardotia;* see Morris in Taylor et al. 1973, p. 291, and Runnegar 1974) are probably too specialized for a deep burrowing life habit to have given rise to the Jurassic gastrochaenids.

Although the pholads are unlikely gastrochaenid ancestors, several other taxa remain as possible ancestors on the basis of their anatomical similarities (e.g., the Hiatellacea) or because of their representation by fossil forms morphologically similar to the early gastrochaenids [e.g., the Isofilibranchia (Modiomorphacea and Mytilacea), Permophoridae and Grammysiidae]. Certain representatives of these taxa resemble gas-

trochaenids in their general shell form, reduced dentition or edentulous hinge, external opisthodetic ligament inserting on a ligamental nymph, and reduced anterior adductor muscle scars. In addition, certain living or fossil representatives of all these taxa show evidence of gastrochaenid-like periostracal calcification (Carter 1976a). Data of shell features and known or inferred anatomy and ecology for all these taxa are compiled in Figure 48. Features of soft anatomy for the extinct Modiomorphacea (Isofilibranchia), Grammysiidae, and Permophoridae are inferred from their closest living relatives, i.e., the Mytilacea (Isofilibranchia), Pholadomyidae or Pandoracea, and Carditidae, respectively. Data of labial palp and stomach structure were not available for the recent Pholadomyidae; so these are inferred from the Pandoracea, a later evolving pholadomyoid superfamily. Excluded from this tabulation are features (enumerated

	shell microstructure[7]	deep pallial sinus[8]	discrete pallial scars[8]	extensive pallial glands	ligament fusion layer	represented by borers[8]	ventral mantle fusion	"fourth" mantle aperture	elongate siphons	ctenidium grade[9]	labial palp grade[10]	stomach grade[11]
ISOFILIBRANCHIA	N	A	A	A?	A[5]	P	A	A	A	F	1	3
PERMOPHORIDAE[1]	CL[4]	A	A	P	A	A	A	A	A	E	2	4
HIATELLIDAE[2]	CL	P	P_A	P_A	A	P	P	A	P_A	E	3	4
GRAMMYSIIDAE[3]	N?	A	P_A	P?	P?	A	P	P?	A	E	2_3[6]	4[6]
GASTROCHAENIDAE	CL	P	P	P	A	P	P	A	P	E	2	4

FIG. 48. Summary of characters varying among the Gastrochaenidae, Isofilibranchia (Mytilacea and Modiomorphacea), Permophoridae, Hiatellidae and Grammysiidae. Excluded here are characters found in all five groups (e.g., aragonitic periostracal spikes and anterior shell reduction) and specialized features found only in the Gastrochaenacea (e.g., the pedal probing organ). Symbols: present (*P*), absent (*A*), nacreous shell structure (*N*), crossed lamellar shell structure (*CL*), filibranch ctenidia (*F*) and eulamellibranch ctenidia (*E*).

[1]Soft anatomy data inferred from the Recent *Cardita* (Carditidae; see Yonge 1969).
[2]Soft anatomy data from Yonge (1971) unless otherwise noted.
[3]Soft anatomy data inferred from Recent *Pholadomya candida* (Pholadomyidae; see Runnegar 1972) unless otherwise noted.
[4]Data from Nakazawa and Newell (1968).
[5]Data from Yonge (1948).
[6]Data inferred from the Recent Pandoracea (see Stasek 1963 and Purchon 1958).
[7]Data from Taylor et al. (1969, 1973) unless otherwise noted.
[8]Data from various authors in the *Treatise on Invertebrate Paleontology* (R. C. Moore, ed.) *Part N, Mollusca 6,* (1969).
[9]Data from Pelseneer (1911) unless otherwise noted.
[10]Data from Stasek (1963).
[11]Data from Purchon (1958).

above) found in all the compared taxa and specialized features unique to the Gastrochaenacea. The data of Figure 48 are abstracted diagrammatically in Figure 49 to show relative unweighted similarities with the Gastrochaenacea.

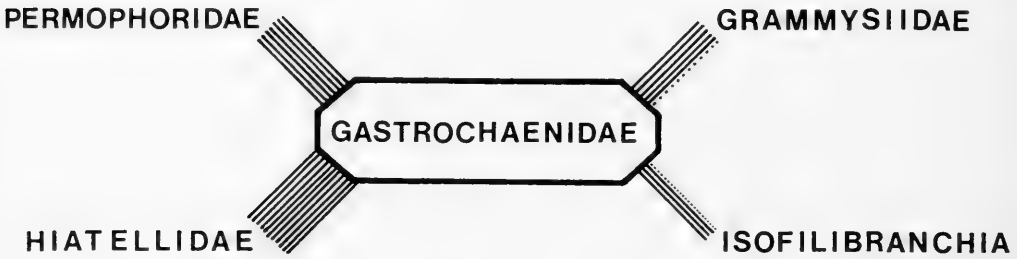


FIG. 49. Abstract of the data compiled in Figure 48, showing unweighted similarities between the Gastrochaenidae and four possible ancestors. Each line connecting the Gastrochaenidae and another taxon represents one similarity from Figure 48. The two dotted lines represent possible but unverified similarities.

Although the Hiatellacea and the Isofilibranchia resemble the gastrochaenids in their representation by rock borers, these borers appear too early or too late in the fossil record or are too dissimilar in shell form to be likely gastrochaenid ancestors. The semiendolithic nestling Ordovician modiomorphid *Corallidomus* (Whitfield 1893) appears much too early to have given rise to the gastrochaenids. The Mytilacea are represented by Carboniferous through Permian forms morphologically similar to *Lithophaga,* but an endolithic habit has yet to be demonstrated for any Upper Paleozoic lithophagid (see Pojeta and Palmer 1976). Among other early lithophagids, the Permian *Lithodomina* is too specialized in terms of its internal ligament, and the Jurassic *Inoperna* is too dissimilar in its large size and shell form to be likely gastrochaenid ancestors (see generic diagnoses in Soot-Ryen 1969 and Pojeta and Palmer 1976). Furthermore, data of soft anatomy and shell mineralogy suggest that the Isofilibranchia are the least likely gastrochaenid ancestors among the possibilities considered in Figure 49. Many Mytilacea have an outer calcitic prismatic shell layer that differs mineralogically and microstructurally from the aragonitic outer prismatic layer observed in gastrochaenids (Oberling 1964 and Taylor et al. 1973).

The Hiatellacea show greater anatomical similarity to the Gastrochaenacea than any other taxon represented in Figure 49, but they are doubtful direct gastrochaenid ancestors for a variety of reasons. Prior to the Jurassic, the hiatellids may be represented only by a Triassic *Panopea.* Keen (1969b) considered the Permian *Roxoa* to be a hiatellid, but Runnegar and Newell (1971) subsequently allied this genus with the Pholadomyidae. *Panopea* and *Roxoa* are unlikely gastrochaenid ancestors because of their permanent posterior siphonal gape, a feature unknown in any fossil or Recent gastrochaenid. *Hiatella,* the only hard substrate borer in the Hiatellacea, does not appear until the Upper Jurassic (Keen 1969b), too late to have given rise to the Gastrochaenacea. In addition, the present data of functional morphology support Purchon's (1954) suggestion that the endolithic habit evolved independently in *Hiatella* and the Gas-

trochaenacea. Unlike *Gastrochaena, Hiatella* moves its shell freely in its burrow, apparently using its siphons as a fulcrum for abrasion, and rocking its valves about a dorsoventral axis (Hunter 1949). Some anatomical similarities are also expressed differently in *Hiatella* and the Gastrochaenacea. Whereas accessory ventral adductors in *Hiatella* form a muscular floor to the mantle cavity (Hunter 1949), the ventral adductor in *Gastrochaena (G.) hians* is a single, relatively small muscle near the base of the siphons. Extensive pallial glands are found in *Hiatella* along either side of the midventral region of the mantle cavity (Pelseneer 1911), whereas analogous pallial glands in *Gastrochaena* do not occur in a midventral position. In addition, the Hiatellacea differ microstructurally from the gastrochaenids. Whereas gastrochaenids show reclined composite prisms in their outer shell layer, hiatellids show irregular prisms with no distinct substructure (in *Hiatella* and *Cyrtodaria*) or a unique vertical composite prismatic structure (in *Panopea*). The first order lamellae of the crossed lamellar layer are relatively large and sharply defined in gastrochaenids, but these are smaller and poorly defined in hiatellids (Carter 1976b). Finally, and perhaps most significantly, the Hiatellacea had just evolved and were not diverse at the generic level when the earliest gastrochaenids appeared in the Triassic or Jurassic (Fig. 50).

On the other hand, certain Permian permophorids resembled the modern *Gastrochaena (G.) hians* (Fig. 10c) in their mytiliform lateral profile, and may have also been similar in their adaptations for adult byssal attachment. The Permian permophorid *Myoconcha* sp. of Winters (1963) shows an anteroventral byssal sinus and anterior umbones reminiscent of modern gastrochaenids (Fig. 51). But these similarities are probably convergent, because many Middle and Upper Jurassic *Gastrochaena* and *Spengleria* had not yet evolved a comparable degree of anterior reduction and lateral shell inflation. Other Permian forms, including some "*Permophorous*" (Permophoridae) and certain forms questionably allied with the Grammysiidae were morphologically similar to the Jurassic through Recent species of *Spengleria. Sanguinolites*? sp. of Chronic (1952) (Grammysiidae?) resembles *Spengleria* in its rounded anterior margins, flattened posterior triangular area set off by radial ridges, concentric ornament, moderately anterior and low umbones, and possibly in its edentulous hinge (see Chronic 1952 and the present Figs. 52 and 53). Forms like *Sanguinolites*? might be considered unlikely gastrochaenid ancestors because their shell shape is suggestive of a shallow burrowing rather than an epibyssate life habit. But curiously, *Spengleria* has retained many shell and anatomical features commonly associated with shallow burrowing in the modern Bivalvia. Separated siphons have apparently characterized *Spengleria* since its earliest (Jurassic) appearance in the fossil record (see below), and this feature is clearly more characteristic of modern shallow burrowers than hard substrate borers. Completely separated siphons occur in many shallow burrowing Tellinacea, but in no other endolithic bivalve besides *Spengleria.* This genus also resembles modern shallow burrowers in its diffuse pedal retractor musculature (see Yonge's 1969 discussion of evolutionary trends in pedal musculature in the Carditacea).

Considering the shell and anatomical similarities between *Spengleria*

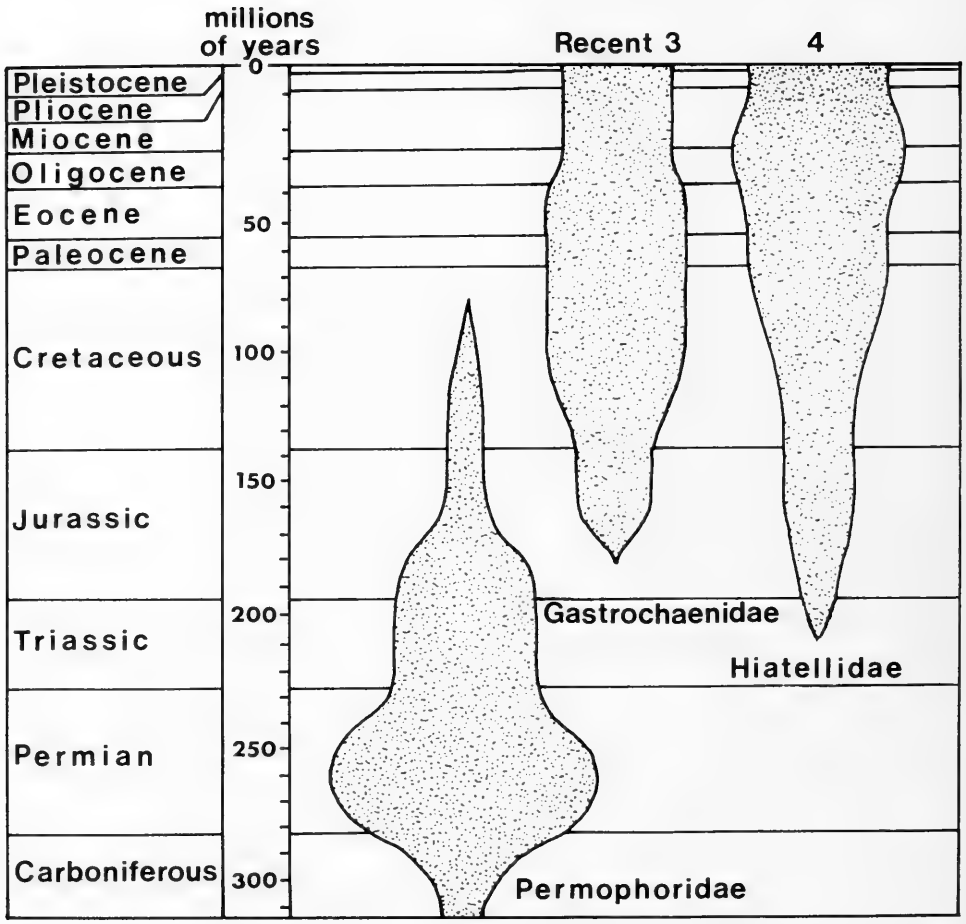
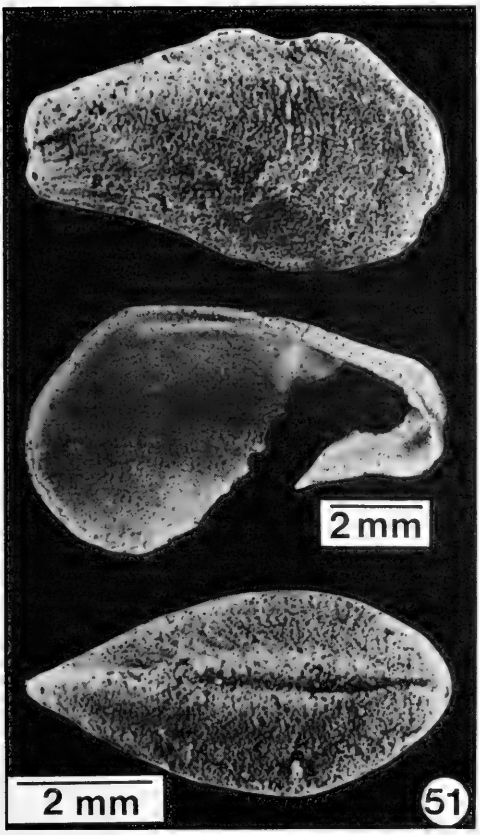


FIG. 50. Generic diversity through time for the Gastrochaenidae, Permophoridae and Hiatellidae. The Gastrochaenidae are regarded as comprising three extant genera *(Spengleria, Gastrochaena,* and *Eufistulana)* and one extinct genus *(Kummelia).* The genus *Gastrochaena* includes the subgenera *Gastrochaena* s.s., *Rocellaria* and *Cucurbitula.* Following Runnegar and Newell (1971) the "hiatellid" *Roxoa,* a possible ancestor of the Hiatellidae, is classified with the Pholadomyidae. The data are otherwise abstracted from Keen (1969a, 1969b) and Chavan (1969).

and many modern shallow-burrowing bivalves, it is not unreasonable to assume that this genus evolved more or less directly from shallow-burrowing ancestors, i.e., from Permian or Triassic forms morphologically similar to *Sanguinolites*? sp. of Chronic (1952). By this hypothesis, the immediate gastrochaenid ancestors had not become morphologically specialized for epibyssate nestling prior to their assumption of the endolithic habit. Instead, forms like *Sanguinolites*? sp. may have evolved through a semiendolithic nestling stage in protected microhabitats. This would bring their mantle epithelium in contact with coral or shell substrates, thereby permitting evolution of chemical boring. Unlike mechanical boring, chemical boring would require little change in the ancestral shell and anatomical features except for elaboration of glandular tissues involved in the process of calcium carbonate erosion. Gastrochaenids retaining a primarily chemical boring mechanism (e.g., *Spengleria*) would keep the lateral shell profile, separated siphons, and diffuse pedal musculature of



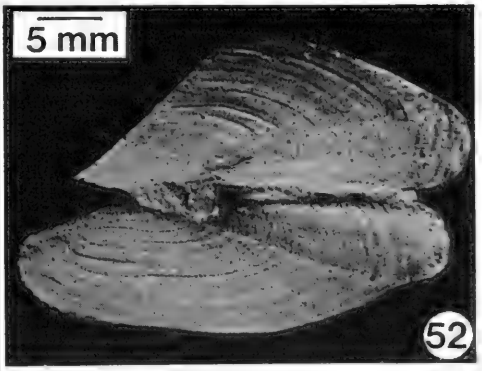


FIG. 51. *Myoconcha* sp. (Myoconchinae, Permophoridae) Permian Supai Formation, Arizona. Photographic reproduction of plate 8, figure 15 (middle; valve interior; AMNH 28035:1), figure 16a (above; valve exterior; AMNH 28035/1:1) and figure 16b (below; dorsal view of both valves; AMNH 28035/1:1) from Winters (1963). The lower scale bar refers to the upper and lower figures; the upper scale bar refers only to the middle figure.

FIG. 52, *Sanguinolites*? sp., Permian Kaibab Formation, Arizona, rubber squeeze from an external mold. Photographic reproduction of plate 10, figure 16 from Chronic (1952).

their shallow burrowing ancestors. They would become morphologically specialized for boring primarily in their anteroventral pedal gape. This permits permanent pedal attachment and the application of a wide area of mantle epithelium to the burrow walls for chemical boring. A corollary of this hypothesis is that *Spengleria* represents a primitive stock from which the more mechanically boring gastrochaenids evolved. Natural selection for efficient mechanical boring would result in the anterior reduction, streamlined lateral profile, united siphons, and concentrated pedal musculature characteristic of modern *Gastrochaena*.

Unfortunately, the taxonomic affinities of *Sanguinolites*? sp. and similar Upper Paleozoic forms possibly ancestral to *Spengleria* have not been satisfactorily determined. It is therefore uncertain whether the Gastrochaenacea can be regarded as likely derivatives of the Permophoridae (subclass Heteroconchia) or the Grammysiidae (subclass Anomalodesmata). Chronic (1952) indicated that his *Sanguinolites* may be related to

FIG. 53. *Spengleria spengleri* (Deshayes) 1857, Eocene, France. Photographic reproduction of plate XVII, figure 1 (middle; valve interior), figure 2 (below; ventral view of both valves) and figure 3 (above; valve exterior) from Deshayes (1860).

Permophorous, and Elias (1957) subsequently erected *Eopleuorphorous* to include *Sanguinolites tricostatus* (Portlock) and similar edentulous Permo-Carboniferous forms resembling *Permophorous* in general shell outline, subdued anterior umbones, anterior myophoric buttress, and a shell ornament of minute papillae, concentric ridges, and posterior radial keellike ridges. Newell and La Rocque (1969) considered *Eopleurophorous* a possible synonym of *Sanguinolites,* presumably largely on the basis of its edentulous hinge. But this criterion may not be definitive, because the hinge dentition is also subdued in certain forms presently classified with the Permophoridae. Also, some taxa possibly related to the Grammysiidae show heterodont-like differentiated cardinal and lateral teeth (e.g., *Alula squamulifera;* see Fig. 27 *in* Runnegar and Newell 1971). Therefore, if the Gastrochaenacea evolved from shallow infaunal permophorids or grammysiids similar to *Sanguinolites?* sp., the subclass affinities of these ancestors cannot presently be resolved.

11. EVOLUTION AND ADAPTIVE RADIATION WITHIN THE GASTROCHAENACEA

General Evolutionary Trends. As presently hypothesized, *Spengleria* evolved as a chemical borer from shallow infaunal burrowing ancestors through an intermediate semiendolithic nestling stage. Except for its stocky foot and anteroventral pedal gape, *Spengleria* retained the major shell and anatomical features of shallow burrowers like the Permian *Sanguinolites*? sp. of Chronic (1952). The Jurassic gastrochaenid faunas of Europe are presently well enough known to compare the early representatives of *Spengleria* and *Gastrochaena* with their modern counterparts. These earlier gastrochaenids were generally characterized by narrower and shorter pedal gapes than the modern species (compare Figs. 10 and 54). Within *Spengleria,* the Jurassic through Eocene species were also more laterally compressed than the modern *Spengleria rostrata* (compare Figs. 10A and 53). In addition, certain Jurassic *Gastrochaena* show burrow casts with slight separation of the posterior siphon tubes (Fig. 56), perhaps representing an early transition from the fully separated condition in *Spengleria* to the fused siphons characteristic of modern *Gastrochaena.*

By Miocene time, and probably much earlier, *Spengleria* and *Gastrochaena* had expanded their pedal gapes laterally and lengthwise, and *Spengleria* had also laterally inflated its shell anterior (e.g., see *Spengleria emilyana* from the Miocene of Florida; Vokes 1976). This parallel evolutionary expansion of the pedal gape in *Spengleria* and *Gastrochaena* permitted application of the anteroventral mantle and shell margins over a wider area of the anterior burrow chamber, thereby facilitating both chemical and mechanical boring. A wider pedal gape allows for boring in the entire burrow anterior with minimal rotation of the valves about the stationary foot.

Inasmuch as some permophorids and grammysiids secreted calcified periostracal spikes (Carter 1976a), *Spengleria* probably inherited these structures from its burrowing ancestors. Among modern gastrochaenids, *Spengleria* is unique in its retention of prominent periostracal spikes over the exterior of its adult shell. The modern *Gastrochaena* seldom, if ever, secretes aragonitic spikes in its adult stage, but these are secreted by juveniles in a few modern species (Carter 1976a). Periostracal spikes are more common in fossil representatives of *Gastrochaena,* and these cover the entire shell in the Cretaceous *Gastrochaena (Rocellaria) linsleyi* (see below). It is likely that calcified periostracal spikes initially functioned to increase friction between the shells and the substratum in shallow burrowing and semiendolithic nestling ancestors of the gastrochaenids. Aragonitic spikes may likewise have assisted chemical boring by scraping debris from the burrow walls in forms like *Spengleria* and, presumably, in early representatives of *Gastrochaena.* But the spikes became less important as *Gastrochaena* became increasingly specialized for mechanical boring, because they were

FIGS. 54–56. *Gastrochaena moreana* Buvignier 1852, YPM 10002, Jurassic (Malm), Stramberg, Czechoslovakia.

FIG. 54. Shell valves. Upper left: lateral exterior view of right valve. Irregularity on the posterior of the shell is sediment filling the burrow. Center left: dorsal view of right valve and internal cast of left valve. Lower left: ventral view perpendicular to the plane of the pedal gape. The shell interior is partially filled with crystals of calcite.

FIG. 55. Natural internal limestone casts of three burrows. The burrow on the right shows the internal cast of the left valve visible in Figure 54 (left, center). The substratum is a scleractinian coral.

FIG. 56. Diagrammatic reconstruction of the center burrow in Figure 55, drawn after removal of the surrounding coral substratum. The figure represents an internal cast of the burrow. The burrow was lined only near the extreme posterior of the siphonal portion (i.e., toward the upper right, near the burrow aperture).

The three scale bars are graduated in millimeters.

functionally replaced by stronger comarginal shell ridges. By Pliocene time, calcified spikes were restricted to the juvenile shell (Fig. 30) or entirely lost in most species of *Gastrochaena.* Calcified periostracal spikes have likewise been secondarily reduced during the course of evolution of *Eufistulana.* Stephenson (1941) described minute spikes covering parts of the Cretaceous *Eufistulana ripleyana,* but these are limited to the juvenile shell or are entirely lost in the Recent *Eufistulana* (see below).

Whereas *Spengleria* and *Gastrochaena* specialized for chemical and combined chemical and mechanical boring, respectively, certain other gastrochaenids partially or entirely abandoned the endolithic habitat for a

tube-dwelling existence. The fossil *Kummelia* retained a shell similar to *Gastrochaena* (Fig. 61), but evolved a combined tube-dwelling and free-burrowing existence. The modern *Eufistulana* is more strictly a permanent tube dweller, and its shell has evolved a graceful sculpture unique in this superfamily (Figs. 62, 63). Evolutionary transitions leading from *Spengleria* or *Gastrochaena* to *Kummelia* and *Eufistulana* are presently unknown. But the modern semiendolithic *Gastrochaena (Cucurbitula)* may provide some indication of what the transitional life habit may have been like. *G (Cucurbitula)* has evolved an obligatory "igloo"-forming habit in which the shell chamber is partially enclosed by the substratum and partially contained by calcareous laminae (Figs. 58–60). In some species of *G. (Cucurbitula),* the calcareous "igloo" comprises the largest portion of the burrow, so the animal is almost entirely a tube-dweller.

As a final note, the available fossil data are sufficient to indicate that shell rotation was incorporated into the mechanism of boring early in the evolutionary history of *Spengleria* and *Gastrochaena.* With the exception of the Upper Cretaceous *Gastrochaena (Rocellaria) linsleyi* (Fig. 57) and the modern *Gastrochaena (Cucurbitula)* (Fig. 59), post-Jurassic gastrochaenid burrows typically show rounded anterior cross-sections. Nonrotation of the shell in the modern *Gastrochaena (Cucurbitula)* is clearly a secondary specialization made possible by its strongly reflected mantle (see below).

Evolution of *Spengleria. Spengleria* is particularly interesting because it has retained many of the shell and anatomical features of its presumed permophorid or grammysiid ancestors, *Spenglerea* is represented in the Middle Jurassic by "*Gastrochaena*" sp. (Palmer 1974) and in the Upper Jurassic by *S. recondita* (Phillips) 1829 and *S. corallensis* (Buvignier) 1843. The latter two species resemble the Recent *Spengleria rostrata* in their lateral profile, moderately anterior umbones, posterior triangular area, posterior truncation, and winglike projection of the posterodorsal shell margins. Undoubted fossil *Spengleria* are also known from the Paleocene *(S. cumitariopsis,* Georgia, Harris 1896), Eocene *(S. spengleri,* France, Deshayes 1857), Miocene *(S. emilyana,* Florida, Vokes 1976; see also Cossmann and Peyrot 1909 and Boss 1967), and Pleistocene *(S. rostrata,* Key Largo Limestone, Florida; Carter, personal observation). The two Recent species of *Spengleria* [*S. rostrata* (Spengler) 1793 and *S. mytiloides* (Lamarck) 1818] occur in the tropical and subtropical Western Atlantic and Indo-Pacific regions, respectively.

As noted previously, the Jurassic through Eocene *Spengleria* differs from the modern *S. rostrata* in its more restricted pedal gape and more pronounced anterior lateral compression (see Arkell 1929–1937, his pl. 43, figs. 1–4; and Buvignier 1852, his pl. VI, figs. 1–6). Judging from the burrow casts illustrated by Buvignier (1852), the Jurassic *Spengleria* possessed completely separated siphons, but the siphon bases were not constricted by baffles projecting from the burrow wall, as in the modern *Spengleria* (see Buvignier 1852, his pl. VI, figs. 19–20). Except for these minor differences in shell and burrow form, the Jurassic and modern *Spengleria* are surprisingly similar, and this genus has been evolutionarily conservative.

Evolution of *Gastrochaena (Rocellaria)* and *Gastrochaena (Gastrochaena).* If *Spengleria* is in fact a primitive genus morphologically similar to the

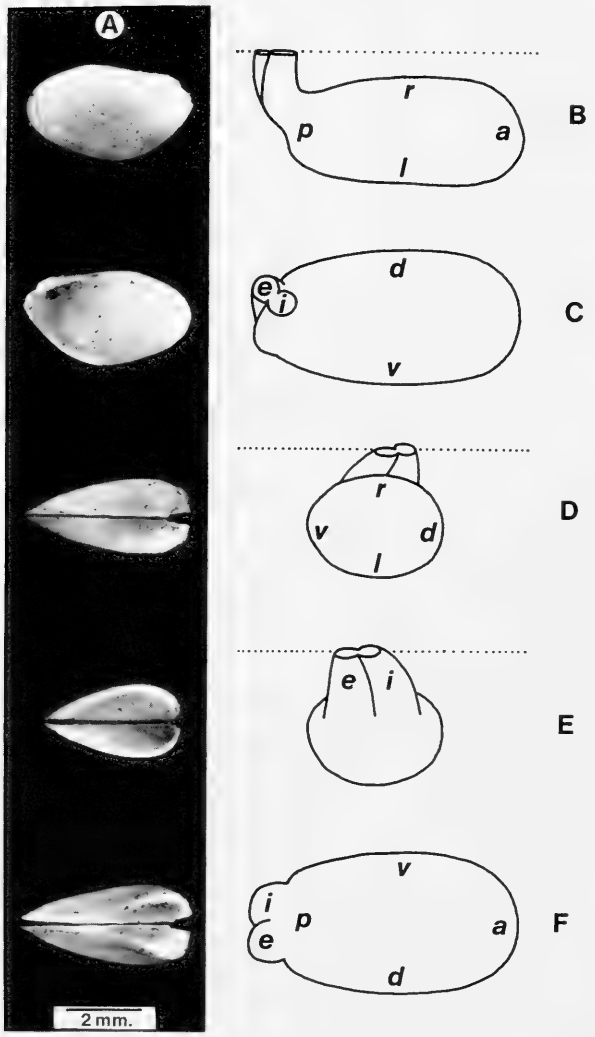


FIG. 57. Shell and burrow of *Gastrochaena (Rocellaria) linsleyi* n. sp., holotype, YPM 10216a, Upper Cretaceous Ripley Formation, Coon Creek, Tennessee. Specimen removed from a shell of *Cucullaea vulgaris* Morton.

A. From top to bottom of figure: lateral exterior view, lateral interior view, dorsal view perpendicular to the hinge axis, ventral view perpendicular to the plane of the pedal gape, ventral view perpendicular to the hinge axis (showing hinge structure).

B–F. Diagram of a latex cast of the burrow interior of the holotype, same magnification as *A*. The dotted lines in *B, D,* and *E* indicate the outer (exterior) surface of the *Cucullaea vulgaris* substratum. Legend:

B View from the ventral shell margins
C View from the outer (exterior) surface of the *Cucullaea* substratum
D View from the anterior shell margins
E View from the posterior shell margins
F View from the inner (interior) surface of the *Cucullaea* substratum
a Anterior of burrow shell chamber
d Dorsal aspect of burrow shell chamber
e Exhalant siphon
i Inhalant siphon
l Position of left shell valve
p Posterior of burrow shell chamber
r Position of right shell valve
v Ventral aspect of burrow shell chamber

shallow burrowing gastrochaenid ancestors, then *Gastrochaena* probably evolved from *Spengleria* or from *Spengleria's* immediate ancestors through specialization for efficiency in mechanical boring. Increased reliance upon mechanical boring required streamlining of the shell and siphons into a cylindrical tube, reduction of the shell anterior, and eventually replacement of calcified periostracal spikes with stronger comarginal shell ridges. Anterior shell reduction in *Gastrochaena* s.s. and *Rocellaria* increased the mechanical leverage of the anterior pedal retractor muscles by bringing their attachment sites closer to the rasping shell margins. *Gastrochaena* s.s. is more specialized for mechanical boring than *Rocellaria* in terms of its generally stronger anterior reduction and more prominent myophores.

Gastrochaena has been reported from the Triassic and Lower Jurassic (e.g., *G. infraliasina* Terquem 1855; see also references to Triassic species compiled by Diener, 1923). But the oldest presently confirmed member of this genus is *G. moreana* Buvignier 1852 from the European Middle and Upper Jurassic (Figs. 54–56). *G. moreana* and the Upper Cretaceous *G. (Rocellaria) linsleyi* (Fig. 57) differ from most post-Mesozoic *Gastrochaena* in their smaller pedal gapes. Like *Spengleria,* the genus *Gastrochaena* shows a general evolutionary increase in the width and length of its pedal gape, and the introduction of siphonal baffles in certain later Cenozoic species. The subgenera *Gastrochaena* s.s. *Rocellaria* are difficult to distinguish in the older fossil record because their hinge structures are often not preserved, and also because transitional forms were more common than at present. But the subgenus *Gastrochaena* s.s. was well differentiated at least by Oligocene or Miocene time, when it was represented by the Western Atlantic *G. (G.) ligula* Lea 1846, *G. (G.) rotunda* Dall 1898, and numerous other species. *Gastrochaena* s.s. comprises the majority of gastrochaenid species in modern endolithic faunas.

Evolution of *Gastrochaena (Cucurbitula), Kummelia,* and *Eufistulana.* The subgenus *Cucurbitula* and the genera *Kummelia* and *Eufistulana* are characterized by their replacement of the ancestral endolithic habit with an obligatory "igloo" or tube-dwelling habit. It is not uncommon for *Gastrochaena* s.s. and *Rocellaria* to construct nearly complete calcareous tubes after boring through substrata too thin to contain their shells (Fig. 47). Even *Spengleria* occasionally secretes a partial calcareous tube in repairing severe damage to its burrow. But tube formation is clearly facultative in these three latter taxa, and does not characterize individuals inhabiting adequate shell and coral substrata. In contrast, "igloo" and tube dwelling are the preferred life habits among representatives of *Cucurbitula, Kummelia* and *Eufistulana.*

Cucurbitula typically bores shallowly into the exterior of other shells and then completes the dorsal half of its burrow by secreting a calcareous "igloo" (Figs. 58–60). Superficial "igloo" formation is obligatory in *Cucurbitula,* because this habit characterizes individuals boring even thicker substrata. The Indo-Pacific *Gastrochaena (Cucurbitula) cymbium* precedes "igloo" formation by boring shallowly into a shell substratum, and then emerges on the bored surface to secrete the calcareous "igloo" walls. Thus, *G. (C.) cymbium* is fully endolithic as a juvenile, and its "igloo" is constructed only as the later juvenile and adult burrow increases in size (Fig. 58). The "igloo"-forming stage is assumed after a more abbreviated juvenile en-

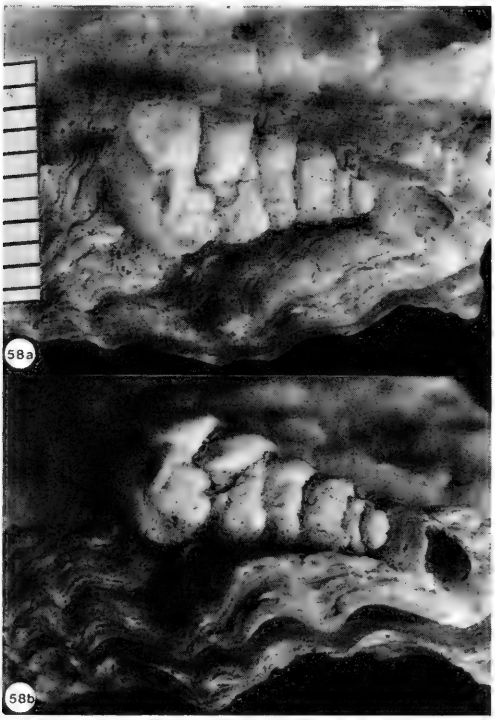


FIG. 58. Dorsal *(a)* and lateral *(b)* views of the calcareous "igloo" secreted by *Gastrochaena (Cucurbitula) cymbium* Spengler 1783, YPM 10218a, Calapan, Mindoro, Philippines, boring into *Plicatula muricata* Sowerby. Same specimen as in Figures 59 and 60. The cupules comprising the "igloo" represent successive stages of anterior burrow enlargement. The scale bar represents 10 millimeters.

FIG. 59. Latex cast of the burrow interior of *Gastrochaena (Cucurbitula) cymbium* Spengler 1783, YPM 10218a, Calapan, Mindoro, Philippines.

From top to bottom of figure: lateral, ventral, and dorsal views. The lateral view is slightly oblique to show the impressions of the umbones in the burrow shell chamber. The ventral view shows the impression of the pedal attachment scar in the middle of the burrow shell chamber. Photographs prepared by William Pirowski, 1974, at Colgate University (Hamilton, N.Y.).

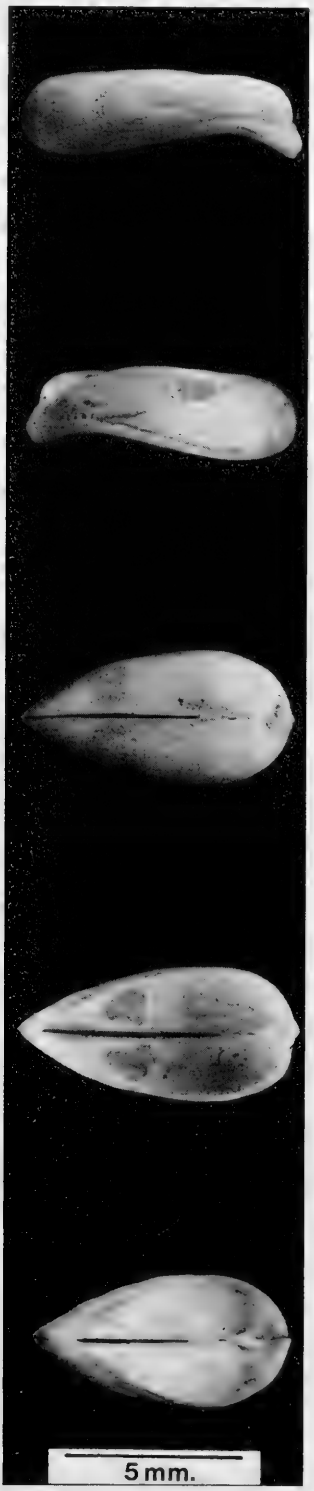


FIG. 60. *Gastrochaena (Cucurbitula) cymbium* Spengler 1783, YPM 10218a, Calapan, Mindoro, Philippines.

dolithic stage in certain other representatives of this subgenus [e.g., in *G. (C.) tasmanica;* see Laseron and Laseron 1952.]

The flattened shape of the shell chamber in *Cucurbitula* requires that its shell does not rotate during the process of boring and "igloo" formation (Fig. 59). Boring and "igloo" formation are both accomplished by the ventral mantle, which is strongly reflected over the anterior of the shell valves (Gould 1861). *Cucurbitula* "igloos" are typically constructed of cup-shaped calcareous walls, with the size of the cups increasing toward the anterior of the burrow (Fig. 58). Burrow enlargement in *Cucurbitula* is apparently accomplished by periodic resorption of the burrow anterior, followed by the secretion of new anterior calcareous cups.

In addition to its obligatory semiendolithic habit, *Cucurbitula* is readily distinguished by its unusually long and wide pedal gape and dorsoventral compression of the shells and burrow (Fig. 60). *Cucurbitula* resembles certain *Gastrochaena* s.s. in its possession of pointed baffles projecting from the burrow lining at the base of the siphons. Tryon (1862) indicated that *Cucurbitula* is widely distributed in the fossil record. But Tryon possibly included under this name many facultative tube-dwelling representatives of *Gastrochaena* s.s. and *Rocellaria.* Fossil *Cucurbitula* as originally defined by Gould (1861) and as described here is presently known only from a single Tertiary species from Italy (see Brocchi 1814, his pl. XI, fig. 14a,b). The Recent species of *Cucurbitula* are restricted to the Indo-Pacific region and Australasia (Sturany 1899, Lynge 1909, Lamy 1923, Laseron and Laseron 1952). Although apparently closely related to the other subgenera in *Gastrochaena,* the phylogenetic origins and time of appearance of *Cucurbitula* are presently unknown. Among the Mesozoic *Gastrochaena,* the Upper Cretaceous *G. (R.) linsleyi* resembles modern *Cucurbitula* in its flattened burrow shell chamber and shallow burrowing habit (Fig. 57). However, the shells of *Cucurbitula* and *G. (R.) linsleyi* are strikingly different, and there are presently no known morphological intermediates.

Unlike *Cucurbitula,* both *Kummelia* and *Eufistulana* have entirely abandoned the endolithic habit for a specialized free-burrowing, tube-dwelling existence. Both taxa appeared in the fossil record during Cretaceous time, but only *Eufistulana* is represented in Upper Cenozoic and Recent faunas. *Kummelia* is known only from the Cretaceous through Eocene *Kummelia americana* (Gabb) 1860 from Europe and eastern North America (Holzapfel 1889, Wade 1926, Stephenson 1937, Richards et al. 1958, Palmer and Brann 1965–1966). Shells of *Kummelia* are similar to modern *Gastrochaena* except for their greater elongation (Fig. 61, middle and right). Natural internal casts of *K. americana* tubes show widely spaced annular constrictions (Fig. 61, left). Stephenson (1937) interpreted these to represent successive anterior tube walls partially removed during the process of periodic anterior tube resorption and secretion. Unlike many gastrochaenids (including *Eufistulana*), *Kummelia* probably lacked a single, major constriction of the burrow lining at the junction of its siphonal and shell chambers. Complete *Kummelia* tubes are presently unknown, but partially dissolved tubes from the Paleocene of Maryland (Fig. 61, middle and right) indicate that the animal secreted an exteriorly smooth, conical tube at least in the burrow posterior. In a few *Kummelia* the shells are preserved some distance from the end of an irregularly shaped tube

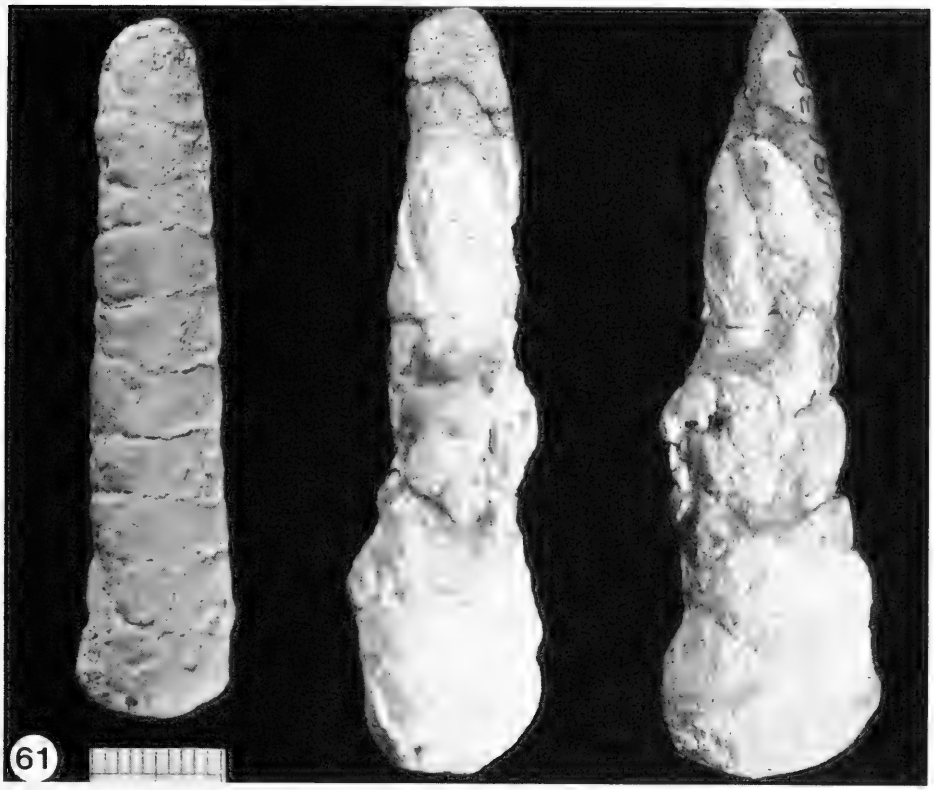


FIG. 61. Natural internal casts of tubes of *Kummelia americana* (Gabb) 1860. Left: regularly shaped tube showing several widely spaced annular constrictions of the tube lining. Each constriction may represent a previous position of the anterior tube wall. Successive anterior tube walls were probably resorbed as the siphons increased in length. USNM 496382, Vincentown Formation, Lower Eocene, New Jersey. Middle and right: two views of an irregularly shaped tube showing the right shell valve. The straight edge on the upper right portion of the right figure probably represents the impression of a posterior tube wall. USNM 496381, Aquia Formation, Paleocene, Maryland. The scale on the left represents 10 millimeters.

anterior. This suggests that *Kummelia* employed considerable anterior-posterior shell movement to accomplish its periodic burrow expansion. This also reinforces the inference that *Kummelia* tubes did not show distinctly separated siphonal and shell chambers.

The shells of *Eufistulana* differ from *Kummelia* and all other gastrochaenids in their extreme elongation, sharply truncated anterior, and unusually long and wide pedal gape. The Indo-Pacific *Eufistulana mumia* (Spengler) 1783 is strongly compressed dorsoventrally, and it lacks projecting myophores (Fig. 63). The elongate, conical tube of *Eufistulana* shows well-defined siphonal and shell chambers separated by a double-walled, elliptical diaphragm (Fig. 62). This partition greatly restricts shell movement in the anterior-posterior direction, but does not interfere with rotational activity within the shell chamber.

Burrow elongation in *Eufistulana* is apparently accomplished by episodic resorption and resecretion of the medial diaphragm and the anterior tube wall. Kühnelt (1934) suggested that *Eufistulana* increases its

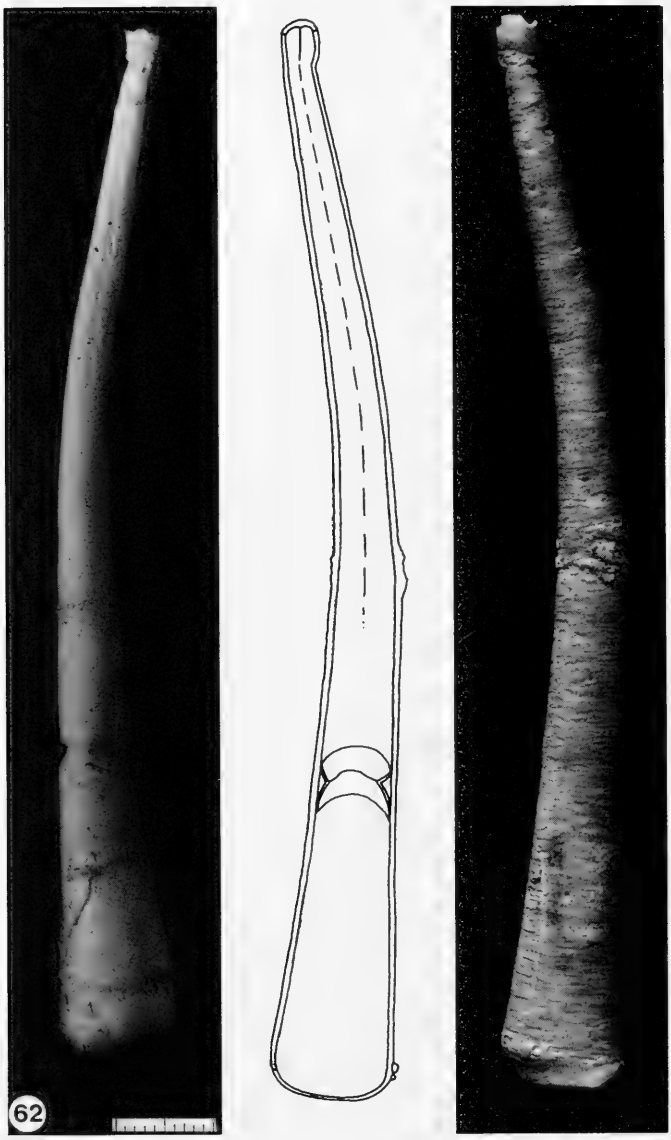


FIG. 62. Right: lateral view of calcareous tube of *Eufistulana mumia* (Spengler), 1783, YPM 9589, Singapore. Left: lateral view of latex cast of tube interior. Middle: diagrammatic longitudinal cross-section through tube, showing the elliptical diaphragm between the posterior siphonal burrow and the anterior shell chamber. Scale represents 10 millimeters.

burrow length in increments comparable to the shell length. By this hypothesis, the medial diaphragm represents the position of the previous anterior tube wall, and an entirely new shell chamber is formed during each phase of burrow elongation. Alternatively, *Eufistulana* may increase its tube length in smaller increments, i.e., by more frequent resorption and resecretion of its diaphragm and burrow anterior. This latter hypothesis seems likely, because the shell and shell chamber are nearly the same length in all representatives of *Eufistulana* examined by the author. In addition, *Eufistulana*'s tube shows numerous closely spaced concentric

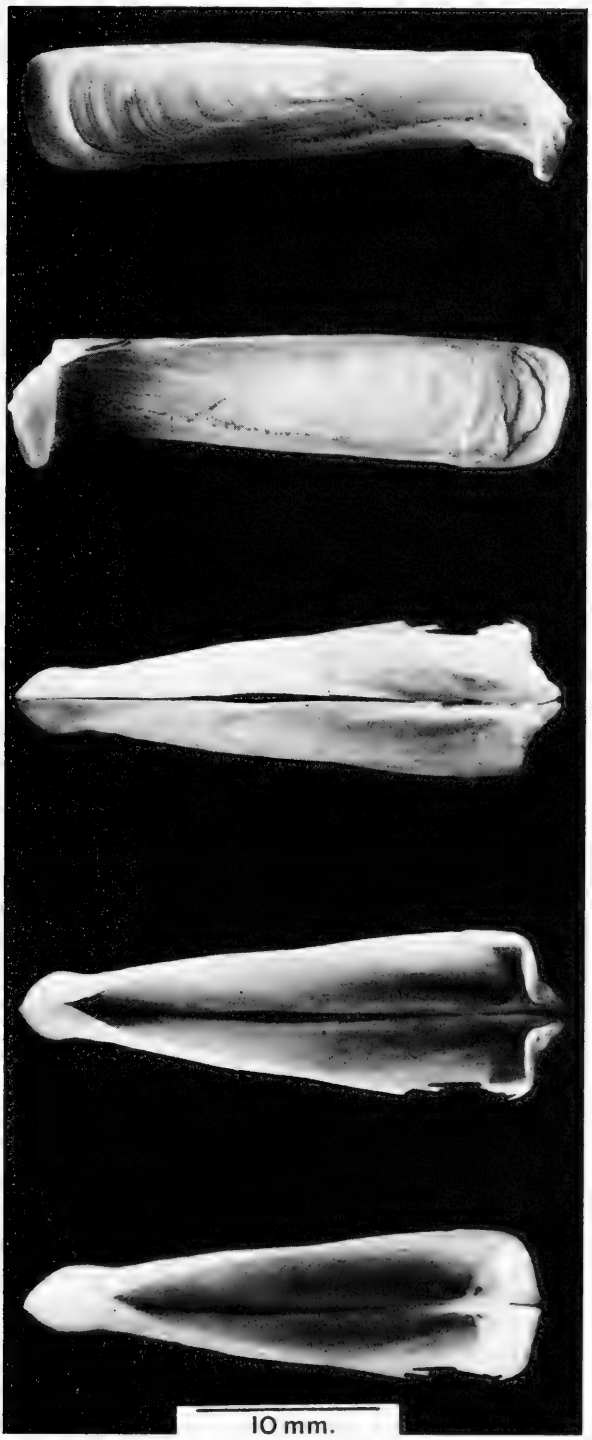


FIG. 63. *Eufistulana mumia* (Spengler 1783), YPM 9589, Singapore. From top to bottom of figure: lateral exterior view, lateral interior view, dorsal view perpendicular to the hinge axis, ventral view perpendicular to the plane of the pedal gape, ventral view perpendicular to the hinge axis (showing hinge structure).

accretion bands on its anterior, and its medial diaphragm occasionally shows evidence of closely spaced successive diaphragm positions.

Eufistulana is represented in the Upper Cretaceous by *E. linguiformis* (Weller) 1907 and *E. whitfieldi* (Weller) 1907 (both from New Jersey) and by *E. ripleyana* (Stephenson) 1941 from Mississippi and Texas. Of these three species, at least *E. ripleyana* retained calcified periostracal spikes in radiating and irregular rows. Among Recent species of this genus, spikelike calcified periostracal structures are generally absent or are restricted to the posterior of the juvenile shell (e.g., in an Australian *Eufistulana clava;* USNM 714790). Definite fossil *Eufistulana* are also known from the Eocene of Europe, northern and eastern Africa, and Pakistan (Glibert 1936, Eames 1951) and from the Oligocene of Germany (Koenen 1894). Like *Cucurbitula,* the modern species of *Eufistulana* are probably restricted to the Indo-Pacific region and Australasia.

There can be little doubt that *Eufistulana* evolved from endolithic or semiendolithic ancestors. Even the modern *Eufistulana* is capable of penetrating calcium carbonate substrata that interfere with its burrowing direction (see Sowerby and Fulton 1903 and Smith 1907). In these instances, *Eufistulana*'s boring mechanism is almost certainly chemical, because its shells are delicate and show little evidence of mechanical abrasion on their margins. Possibly *Eufistulana* evolved from *Kummelia* or from a less specialized representative of *Gastrochaena* retaining the ancestral chemical boring mechanism and adult periostracal calcification.

12. CONVERGENCES BETWEEN THE CLAVAGELLACEA AND GASTROCHAENACEA

Some representatives of the Clavagellacea are so strikingly similar to the Gastrochaenacea that they deserve special consideration. Like *Eufistulana,* most Clavagellacea construct flasklike calcareous tubes that surround the soft tissues, and which may be perforated anteriorly (compare Figs. 47 and 64). Like the Gastrochaenacea, some Clavagellacea pump water through their pedal aperture, and in both the Clavagellacea (Purchon 1960) and some tube-dwelling gastrochaenids this habit may serve as an accessory burrowing mechanism. Additionally, both superfamilies contain primarily tropical, long-siphoned, eulamellibranch bivalves that are represented by mechanical and chemical borers (Soliman 1971). Some clavagellids resemble gastrochaenids in their periostracal calcification (Carter 1976a) and some even resemble *Gastrochaena (Gastrochaena)* in having a myophore-like structure projecting from beneath the hinge (Fig. 65). Based on an analysis of their Recent and fossil shells and anatomical data, further similarities between these superfamilies can be summarized as follows:

1. Anterior umbones (see Deshayes 1857).
2. Mostly well-developed pallial sinus (see Deshayes 1857).
3. Extension of the ctenidia past the posterior shell margin (Purchon 1956b).
4. Annular siphonal membranes (Purchon 1956b).
5. Stomach construction, grade "four" (Purchon 1958).
6. Accessory ventral adductor muscles (Soliman 1971).

But the Clavagellacea and Gastrochaenacea also show certain dissimilarities suggesting that they are not closly related. For example, the free shell valves of many Cretaceous and early Tertiary Clavagellacea (i.e., the valves not fused to the calcareous tube; see Deshayes 1857) closely resemble *Mya* and *Panopea.* This shell form indicates that the immediate ancestors of the clavagellids were probably specialized for deep rather than shallow burrowing. Like *Panopea* (Hiatellacea), the early Clavagellacea commonly show a permanent posterior siphonal gape and subequal adductor muscle attachment scars, and they lack gastrochaenid-like concentric ornamentation. Although the Gastrochaenacea have evolved tube-dwelling species, their shell valves are never incorporated into the tube. Partial or complete fusion of one or both shell valves to the tube occurs in most Clavagellacea except certain early forms (e.g., *Clavagella cornigera* Schafheutl, see annotation, p. 170, *in* Smith 1962). Also unlike *Gastrochaena* and *Spengleria,* endolithic clavagellids abrade only the free shell valve and perhaps also the periostracum-covered mantle against the substratum, using the attached valve to provide leverage (Soliman 1971). Even among endolithic clavagellids, the foot is totally unlike that in the Gastrochaenacea. The clavagellid foot lacks both a circular pedal disc and an anterior pedal probing organ (Soliman 1971). The Clavagellacea re-

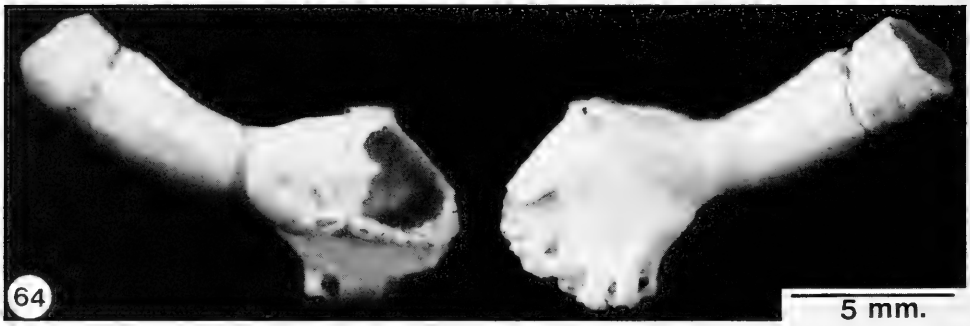


FIG. 64. Calcareous tube constructed by *Clavagella multangularis* Tate (USNM 159380). Note the fusion of the left valve to the aragonitic tube.

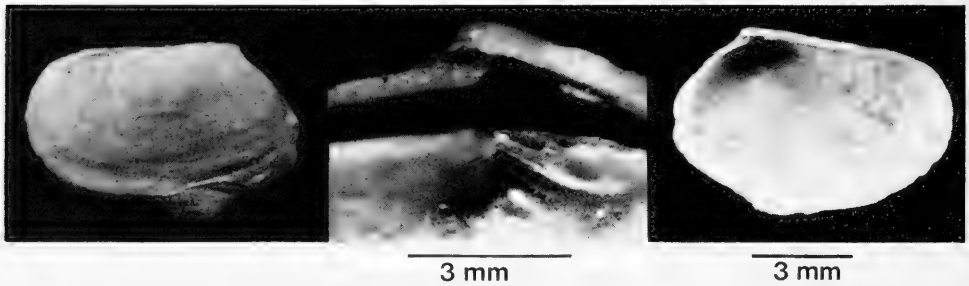


FIG. 65. The free valve of *Clavagella mutangularis* Tate removed from the aragonitic tube in Figure 64. Note the radiating lines of aragonitic periostracal spikes on the valve exterior (left) and the deep pallial sinus (right). The center photographs show the hinge from lateral (upper) and ventral (lower) views.

semble some Pholadomyidae or Pandoracea more than the Gastrochaenacea in their type "E" ctenidial structure (Atkins 1937), "fourth" mantle aperture (Allen 1958, Lacaze-Duthiers 1883), nacreous shell microstructure (Taylor et al. 1973) and periostracum-covered siphons (Purchon 1956b; Runnegar 1972). If, as is apparent from a description of a young *Humphreyia* by Smith (1911), some clavagellids also have a lithodesma, then this superfamily probably evolved from the Pandoracea. The tube-dwelling Clavagellacea and Gastrochaenacea, both of which appeared in the Upper Cretaceous, would then have descended from ecologically and phylogenetically dissimilar ancestors. Whereas the Gastrochaenacea evolved from shallow-burrowing permophorids or grammysiids, the Clavagellacea evolved from deep-burrowing pandoraceans.

13. DISCUSSION

Diversification within the Endolithic Habitat. The endolithic habit is one of the most specialized and, appropriately, one of the last major life styles to evolve in the Bivalvia. Facultative epifaunal and boring bivalves have been described from the Ordovician (e.g., *Corallidomus scobina;* see Pojeta and Palmer 1976) but these are not truly endolithic. By the present definition, endolithic bivalves both excavate and are largely enveloped by their hard substratum. The Ordovician *Corallidomus* merely abraded hard substrata with its ventral shell margins, i.e., much like the modern epilithic *Arca imbricata* Bruguière. The Carboniferous and Permian fossil record shows several species morphologically similar to the modern chemical borer *Lithophage* (see Merla 1931, Frebold 1933, and Wanner 1940 for the Permian forms). But according to Pojeta and Palmer (1976), the presumed endolithic habits of these Paleozoic *Lithophaga* are yet unverified. The Pholadacea are questionably represented by a Carboniferous *Martesia* (Turner 1969), but it is possible that this superfamily evolved only during the Mesozoic, i.e., from pholadomyoids similar to *Myopholas* and *Girardotia.* The latter two genera show striking similarities in shell form to certain modern pholads like *Pholas latissima* Sowerby (YPM 9590, Philippines). In any event, the fossil record of abundant and diverse endolithic bivalves clearly does not appear until the Triassic or Jurassic. Middle and Upper Jurassic tropical corals and hardgrounds are commonly infested by truly endolithic species of *Gastrochaena, Spengleria,* and *Lithophaga* (Arkell 1929–1937, Palmer 1974, Palmer and Fürsich 1974, Fürsich and Palmer 1975). Aside from the Mytilacea and Gastrochaenacea, only two other bivalve superfamilies are presently known to have evolved endolithic species during the Mesozoic. These are the Hiatellacea, represented by the Jurassic through Recent *Hiatella* (Keen 1969b; Hunter 1949; Yonge 1971) and numerous Jurassic and Cretaceous Pholadacea (Turner 1969). Endolithic bivalves evolved from various other primarily epifaunal or infaunal bivalve stocks during the Cenozoic. These include the mytilid subfamilies Modiolinae and Crenellinae [including *Botula, Gregariella, Fungiacava,* and certain *Modiolus* (see Otter 1937, Yonge 1955, Gohar and Soliman 1963a, Keen 1971, and Goreau et al. 1972], certain Arcidae (Frizzell 1946, Olsson 1961), Tridacnidae (Purchon 1955b), Petricolidae (Otter 1937, Yonge 1958, Narchi 1975), Myidae (Yonge 1951), and Clavagellacea (Soliman 1971). In summary, the fossil record indicates that bivalves have invaded the endolithic habitat in a succession of adaptive radiations, i.e., in the Triassic (?) or Jurassic (by lithophagids and gastrochaenids), in the Jurassic and Cretaceous (by the pholads and *Hiatella),* and in the Cenozoic (by representatives of several primarily nonendolithic stock groups).

Insofar as chemical boring is generally considered more "specialized" than mechanical boring among modern bivalves, it is surprising that the

earliest adaptive radiation into the truly endolithic habitat apparently consisted of chemical borers. The modern Gastrochaenacea comprise chemically and combined chemically and mechanically boring forms, but their early representatives were probably largely chemical borers (see above). Based on their shell form, verified endolithic lithophagids have probably always been largely chemical borers. But the early evolution of chemical borers might be expected because chemical boring requires less specialization of shell form than mechanical boring. Except for their chemical boring apparatus and pedal structure, the early endolithic *Spengleria* and *Lithophaga* may have retained much the same anatomy and shell form as their presumed shallow burrowing or epilithic nestling ancestors. As suggested above, *Spengleria* may well have evolved its endolithic habit without greatly modifying its ancestral lateral profile, siphon structure, and pedal musculature.

Considering that lithophagids may have evolved their endolithic habit at least as early as the gastrochaenids, it is puzzling that they never evolved deep-burrowing, long-siphoned forms with comparable directional mobility. In comparison with gastrochaenids, the Lithophaginae have remained unspecialized in terms of their simple grades of mantle fusion and siphon formation and their pedal structure (Yonge 1955; 1963). One may only speculate that the ancestors of the endolithic lithophagids differed from early gastrochaenids in possessing filibranch rather than eulamellibranch gills. According to Stanley's (1968) hypothesis, only the more efficient (i.e., eulamellibranch) gills would have been preadaptive for the evolution of long siphons, and hence deep burrowing. Gill pumping efficiency may have also permitted gastrochaenids, but not lithophagids, to evolve narrow constrictions (i.e., baffles) in their burrow linings at the base of their siphons. Many early gastrochaenid burrows resemble fossil and Recent lithophagid burrows in their lack of siphonal baffles. But by Upper Cretaceous or early Tertiary time, siphonal baffles and medial diaphragms became common among representatives of both *Eufistulana* and *Gastrochaena*. This evolutionary innovation apparently occurred during or immediately following the Upper Cretaceous radiation of naticid and muricid gastropods (see Sohl 1969). It is therefore interesting to speculate that siphonal baffles were adaptive for excluding the probosci of these increasingly important predators. Faced with this same increase in predation pressure, certain lithophagids may have evolved an alternative "baffle" against predatory gastropods in the form of thick posterior encrustations, as in the modern *Lithophaga plumula* (see Turner and Boss 1962, Soot-Ryen 1969).

Unlike the lithophagid-gastrochaenid phase in the evolution of the endolithic habitat, the following Jurassic-Cretaceous phase saw the appearance of primarily mechanical rather than chemical or chemical-mechanical borers. The Mesozoic pholads became highly specialized for mechanical boring through their evolution of prominent rasping spines and a unique mechanism for rocking the valves about a dorsoventral axis (Purchon 1955a, 1956a; Evans 1968a,b; Ansell and Nair 1969). *Hiatella* (superfamily Hiatellacea) is a facultative borer-nestler found generally in temperate and colder waters (Hunter 1949; Keen 1969b). Insofar as the

Triassic (?) and Jurassic lithophagids and gastrochaenids were limited to carbonate substrata, they were largely restricted to warmer (i.e., carbonate rich) marine environments. In contrast, the mechanical boring mechanism of the pholads and *Hiatella* permitted their successful colonization of a wider variety of substrata in cool and warm water marine environments.

Interestingly, despite the Cretaceous and Cenozoic proliferation of pholads, the lithophagids and gastrochaenids maintained their dominance in terms of species-level diversity and population density in tropical marine carbonate substrata. Conversely, despite the great ecologic and taxonomic diversity of modern pholads, they have evolved relatively few species in tropical corals and shells. Among modern pholads, the Western Atlantic *Diplothyra smithii* Tryon and the Eastern Pacific *Penitella conradi* Valenciennes are endolithic in calcium carbonate substrata, and the latter has apparently evolved a combined chemical-mechanical boring mechanism (Smith 1968). But both taxa are more common in subtropical and cooler marine than in tropical marine environments (Turner 1954, 1955; Andrews 1971; Abbott 1974). Certain other modern pholads are occasionally found in tropical marine corals and shells (see Olsson 1961 and Abbott 1974), but these species seldom occur in densities comparable to gastrochaenids and lithophagids. This preliminary analysis suggests that the modern marine endolithic habitat is ecologically and taxonomically partitioned largely between the lithophagids and gastrochaenids (ancestrally chemical borers; now inhabiting largely tropical marine coral and shell substrata) and the pholads and hiatellids (ancestrally mechanical borers; now inhabiting a number of substrata in a variety of marine temperature realms, but not as successful as gastrochaenids and lithophagids in tropical marine carbonates). One may only surmise that lithophagids and gastrochaenids maintained their dominance in tropical corals and shells because of their prior occupation of this habitat, and because of their competitive chemical or combined chemical and mechanical boring mechanisms.

Erosional Instability and Tropical Endolithic Communities. The same advantage of mantle fusion and siphon formation that enabled many Mesozoic bivalves to successfully inhabit unstable soft sediments (see Stanley 1968, 1972) probably contributed to the success of gastrochaenids in colonizing erosionally unstable hard substrata. The Jurassic *Spengleria* and *Gastrochaena* were undoubtedly limited in their directional mobility within the substratum. This is suggested by their generally straight or only slightly curving burrows, and by their generally short siphons. The siphons in some Jurassic *Spengleria* were relatively long, but their complete separation precluded abrupt departures from the initial boring direction. In many later *Gastrochaena* the siphons became much longer in relation to burrow length, and the inhalant and exhalant channels became fused into a single, narrow tube. In conjunction with this siphon streamlining, siphonal elongation permitted deeper burrowing and increased directional mobility. Increased siphon length also permitted freedom of burrow shortening in the case of erosional truncation, or burrow elongation in the case of threatened siphon overgrowth.

Studies of modern Western Atlantic tropical endolithic communities suggest that the evolution of directional mobility and siphonal elongation provided gastrochaenids with an ecological advantage over lithophagids for life in erosionally unstable substrata (Carter 1976). Certain other gastrochaenid features have likewise contributed to their success in thin and rapidly eroded coral and shell substrata. Probing of the hard substratum by the pedal probing organ enables gastrochaenids to guide their burrows away from other borers and opposite coral or shell surfaces. Pedal probing holes are presently known in fossil gastrochaenids only in the Upper Cenozoic [e.g., in the *Gastrochaena (Gastrochaena)* tube in Fig. 47]. But this adaptation may have evolved earlier in this superfamily, judging from the occurrence of pedal probing organs in both the modern *Spengleria* and *Gastrochaena*. Gastrochaenids also show an exceptional capacity for burrow repair and for anterior and posterior extension of their burrows in thin or overgrown substrata. Certain lithophagids are capable of repairing their broken burrows, and some even extend their siphonal burrow above the substratum by secreting calcareous laminae (e.g., *Diplothyra smithii* Tryon 1862, North Carolina). But most lithophagids do not extend their siphonal burrows far beyond the substratum, and none show a capacity for posterior burrow extension comparable to *Gastrochaena*.

The successful adaptation of gastrochaenids to erosionally unstable substrata is reflected in their spatial zonation in *Diploria* skeletons from Florida, Jamaica, and Bermuda. As described by Carter (1976) gastrochaenids generally settle later in the cycle of coral disintegration when these substrata are more rapidly eroded. Gastrochaenids generally reach their highest population densities near the thinner, exposed coral margins. In contrast, lithophagids commonly enter early in the cycle of coral disintegration when the upper coral surfaces are still protected by a complete cover of living polyps. In addition, many lithophagids reach their maximum population densities near the protected centers of the coral undersurfaces. As in soft sediment environments, erosional instability therefore appears to be an important factor influencing the spatial distribution of bivalves in tropical endolithic communities.

As a final note, it is interesting to speculate that the adaptive radiation of the Triassic or Jurassic lithophagids and gastrochaenids may have been stimulated by the contemporaneous major expansion in tropical marine carbonate substrates. The Triassic and Jurassic periods saw the appearance and diversification of reef-building scleractinian corals. This evolutionary radiation culminated in the development of extensive hermatypic reefs in the Middle and Upper Jurassic (Wells 1969a,b). According to Jackson et al. (1971) the cryptic habitats created by Jurassic reefs presented vast new areas comparatively free from competition with many common epifaunal taxa. These cryptic habitats and the coral substrata may have set the stage for the initial major radiation by the Bivalvia into the endolithic habitat.

Taxonomic Distinction of *Spengleria, Cucurbitula, Gastrochaena,* and *Rocellaria*. There is disagreement in the literature concerning the sub-

generic (Tryon 1862, Dall 1898, Lamy 1925, Prashad 1932, Keen 1969a) versus generic (Pelseneer 1911, Olsson 1961, Boss 1967, Abbott 1974) taxonomic distinction accorded *Spengleria* Tryon 1862. Tryon (1862) proposed *Spengleria* as a new subgenus "to separate from *Rocellaria* s.s. those species which are elongate-cuneiform, truncated at the posterior end of the shell, and having a triangular space, radiating from the beaks posteriorly to the margin, elevated slightly above the general surface of the shell, and ornamented with transverse lamellae" (1862, p. 472). But Tryon's diagnosis was not sufficient to exclude *Gastrochaena truncata* Sowerby 1834, which has a truncated posterior and a triangular area of elevated periostracum. This species is properly regarded as *Gastrochaena (Gastrochaena)* because of its strong anterior reduction and prominent myophoral plates. Examination of *G. (G.) truncata* from *Spondylus* shells collected near the species type locality (the Bay of Panama) shows that its posterior raised triangular area consists of rugulose periostracum. Furthermore, the siphons of *G. (G.) truncata* are fused for most of their length, as in the Western Atlantic *G. (G.) hians.* The other three species included by Tryon (1862) in *Spengleria* (i.e., *G. mytiloides* Lamarck 1818, *G. plicatilis* Deshayes 1855, and *G. rostrata* Spengler 1793) are properly regarded as representatives of *Spengleria* as presently emended.

After thoroughly studying *Spengleria mytiloides, Gastrochaena dubia,* and *G. macrochisma,* Pelseneer (1911) suggested that the following characters of *Spengleria* warrant its generic distinction from *Gastrochaena:*

1. Less anterior umbones.
2. Anterior adductor muscle more equal in size to the posterior adductor than in *Gastrochaena.*
3. Completely separated siphons.
4. Plicated ctenidia.
5. Anterior point of the foot (the anterior pedal organ) reduced or absent in *Spengleria.*
6. Pedal protractor muscle present in *Spengleria.*

The present study shows that the fifth and sixth characters are not unique to *Spengleria.* The anterior pedal organ is likewise small in *Gastrochaena (Rocellaria) ovata,* and both *G. (R.) ovata* and *G. (G.) hians* possess pedal protractor muscles.

In order to better resolve the taxonomic distinction of *Spengleria,* data of shell morphology, anatomy and ecology for *Spengleria rostrata, Gastrochaena (G.) hians,* and *G. (Rocellaria) ovata* are tabulated in Figure 66 and summarized in Figure 67. Excluding the features in common among all three species, *S. rostrata* resembles *G. (G.) hians* only in its ligament, whereas *S. rostrata* and *G. (R.) ovata* are alike only in their common lack of certain specializations for mechanical boring unique to *G. (G.) hians.*

Comparing *Spengleria* with the genus *Gastrochaena* (including *Gastrochaena* s.s. and *Rocellaria*), it is apparent that many of their anatomical differences are directly or indirectly related to specializations in the latter for mechanical boring. *Gastrochaena* is more specialized for mechanical boring in terms of its increased anterior shell reduction, centralized pedal musculature, laterally expanded pedal gape, and (in most Recent species)

SHELL & LIGAMENT	periostracal spikes	truncated posterior	posterior sulcus	myophore	anterior reduction	ligamental nymph	ligament strength
S.	P	P	P	A	W	S	S
R.	A	A	A	A	M	W	W
G.	A	A	A	P	S	S	S

FOOT & MUSCULATURE	pedal retractors	pedal elevators	adductor inequality	pedal protractors	ventral adductor	pallial sinus	pedal disc (width)
S.	1	P	M	3	A	M	S
R.	2	A	S	4	A	M	W
G.	2	A	S	4	P	S	M

SIPHONS & CTENIDIA	coarse tentacles	separated siphons	annular membrane (inhalant)	velar flap	siphon length	ctenidial plication	ctenidia length
S.	A	P	P	P	M	P	Sh
R.	P	A	P	P	Sh	A	Sh
G.	P	A	A	A	L	A	L

ECOLOGIC CHARACTERS	zonation on *Diploria*	capacity for direction change	burrow length	burrowing rate	size sorting in hindgut	average population age	apparent abrasive efficiency
S.	5	W	M	W	S	M	S
R.	6	W	Sh	W	W	W	M
G.	6	S	L	S	M	S	W

FIG. 66. Summary of characters varying among *Spengleria rostrata, Gastrochaena (Rocellaria) ovata* and *G. (Gastrochaena) hians* (indicated on the left by *S., R.* and *G.*, respectively). Symbols: present (P), absent (A), strong or great (S), moderate or intermediate (M), weak or less (W), long (L) and short (sh).

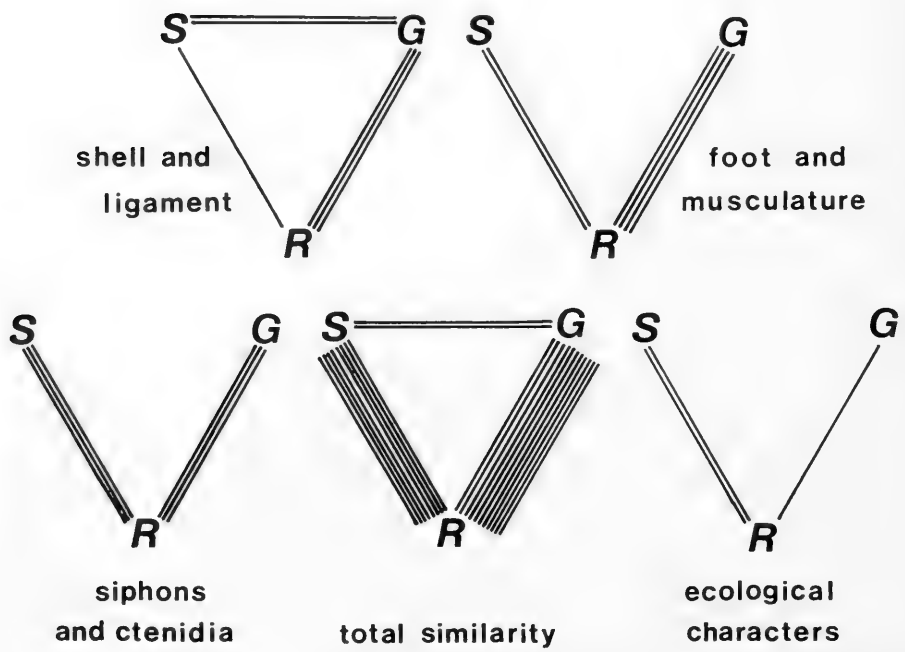


FIG. 67. An abstract of data compiled in Figure 66, showing the unweighted similarities between species pairs of *Spengleria rostrata (S.), Gastrochaena (Rocellaria) ovata (R)* and *Gastrochaena (Gastrochaena) hians (G.)*. Each line connecting the species indicates a similarity.

functional replacement of calcified periostracal spikes with comarginal shell ridges. To accommodate anterior shell reduction, *Gastrochaena* has decreased the width of its anterior adductor muscle, and has shifted dorsoposteriorly the attachment site of its anterior pedal protractor muscles. *Gastrochaena* also differs from *Spengleria* in its fused siphons, flat ctenidia, and less numerous major siphonal tentacles. Considering also the distinct fossil record of *Spengleria,* these anatomical differences also certainly warrant the generic level distinction of *Spengleria* from *Gastrochaena.*

There is also disagreement in the literature concerning the taxonomic distinction accorded *Cucurbitula* Gould 1861. Gould (1861, p. 22) originally based this taxon on a complex of distinctive characters, including:

1. A mantle that entirely envelopes the anterior shell valves.
2. The exterior ornament and curved, elongate shape of the shells.
3. The "artichoke-like" or bulbous structure of the "igloo," which is made up of successive calcareous cups.

Among subsequent authors, only Tryon (1862) and Kuroda et al. (1971) have followed Gould in recognizing the type species of *Cucurbitula* [*Fistulana lagenula* Lamarck] and similar forms as generically distinct from *Gastrochaena.* Fischer (1866) maintained that *Cucurbitula* should not be separate genus because its identity depends largely upon its "igloo"-forming habit. According to Fischer this habit occurs in many other gastrochaenids. Fischer's (1866) recommendation was apparently followed by numerous subsequent workers, including Lynge (1909), Lamy (1922, 1923, 1925), Olsson (1961), and Keen (1969a).

Not all *Cucurbitula* secrete a capsule with an "artichoke-like" exterior, but capsule formation does appear to be obligatory here. Unlike *Gastrochaena* s.s. and *Rocellaria, Cucurbitula* invariably secretes a calcareous capsule regardless of the substratum thickness. *Cucurbitula* can penetrate entirely through thinner substrata to construct a capsule on the surface opposite that initially settled. But even when settling thicker substrata, *Cucurbitula* nevertheless forms a capsule by changing its burrowing direction and exiting on the surface initially penetrated. Because of its reflected mantle, curved, elongate shell, and this obligatory capsule formation, *Cucurbitula* can properly be regarded as subgenerically distinct from *Gastrochaena* s.s. and *Rocellaria.*

Considering *Gastrochaena* s.s. and *Rocellaria,* the available data show their representatives to be similar in their ctenidia and siphons but different in their degree of specialization for mechanical boring. Both taxa have undergone evolutionary specialization for mechanical boring, i.e., by evolving anterior reduction, lateral and posterior expansion of the pedal gape, a centralized pedal musculature, and replacement of periostracal calcification with comarginal shell ridges. But *Gastrochaena* is further specialized for mechanical boring in terms of its greater anterior reduction and prominent myophores. Because these taxa differ only in this degree of specialization and because their species are morphologically quite similar in the earlier fossil record, they should be regarded as only subgenerically distinct. Inasmuch as *Gastrochaena* s.s. represents a grade of specialization for mechanical boring, further study of the fossil record may show this taxon to be polyphyletic.

APPENDIX A
LIST OF SOLDIER KEY BIVALVIA ASSOCIATED WITH *DIPLORIA* SKELETONS, WITH REFERENCES TO THEIR ILLUSTRATIONS IN OTHER WORKS.

Endolithic species:

Botula fusca Gmelin. Warmke and Abbott (1961) pl. 31, fig. d.

Gastrochaena (Gastrochaena) hians (Gmelin). Morris (1973), pl. 32, fig. 1, listed as *Rocellaria hians.*

Gastrochaena (Rocellaria) ovata (Sowerby). Warmke and Abbott (1961), pl. 44, fig. k, listed as *Gastrochaena hians.*

Lithophaga antillarum Orbigny. Morris (1973), pl. 13, fig. 16.

Lithophaga nigra Orbigny. Warmke and Abbott (1961), pl. 31, fig. m.

Petricola lapicida Gmelin. Warmke and Abbott (1961), pl. 44, fig. e.

Petricola typica (Jonas). Warmke and Abbott (1961), pl. 44, fig. b, listed as *Rupellaria typica.*

Spengleria rostrata (Spengler). Warmke and Abbott (1961), pl. 44, fig. g.

Semiendolithic species:

Arca imbricata Bruguière. Warmke and Abbott (1961), pl. 30, fig. e.

Paramya subovata Conrad. Morris (1973), pl. 30, fig. 11.

Epilithic species:

Arca zebra (Swainson). Warmke and Abbott (1961), pl. 30, fig. l.

Barbatia cancellaria Lamarck. Warmke and Abbott (1961), pl. 30, fig. j.

Barbatia candida Helbling. Warmke and Abbott (1961), pl. 30, fig. i.

Barbatia domingensis (Lamarck). Warmke and Abbott (1961), pl. 30, fig. d.

Chama macerophylla Gmelin. Warmke and Abbott (1961), pl. 4, fig. c; pl. 37, fig. b.

Cumingia antillarum Orbigny. Warmke and Abbott (1961), text-fig. 31, fig. c, d.

Isognomon radiatus (Anton). Warmke and Abbott (1961), pl. 32, fig. a.

Lima lima (Linnaeus). Warmke and Abbott (1961), pl. 34, fig. f.

Plicatula gibbosa Lamarck. Warmke and Abbott (1961), pl. 34, fig. g.

APPENDIX B
TAXONOMIC OUTLINE

The following taxonomic outline summarizes the generic versus subgeneric rank presently suggested for the gastrochaenid taxa discussed in this paper. Designations of genotypes are taken directly from the taxonomic review of this superfamily by Keen (1969a). This summary is not intended to represent a taxonomic revision of this superfamily, nor is this a particular endorsement of the genotypes outlined by Keen (1969a). In some instances, the genera and subgenera are accompanied by references to the more important taxonomic literature.

I. Genus *Gastrochaena* Spengler 1783.
Type species: *Gastrochaena cuneiformis* Spengler 1783 by subsequent designation, Children 1822. See Kennard, Salisbury and Woodward (1931) for discussion of Children's type designations, and see Keen (1969a).
   A. Subgenus *Gastrochaena* s.s. Spengler, 1783 (as presently restricted).
   Type species: *Gastrochaena cuneiformis* Spengler 1783.
   B. Subgenus *Rocellaria* de Blainville 1828 (issued in 1829).
   Type species: *Gastrochaena modiolina* Lamarck, 1818, by monotypy.
   C. Subgenus *Cucurbitula* Gould 1861.
   Type species: *Fistulana lagenula* Lamarck, 1801, by monotypy. See Olsson (1961) and Keen (1969a).

II. Genus *Spengleria* Tryon 1862 (as presently restricted).
Type Species: *Gastrochaena mytiloides* Lamarck, 1818, by subsequent designation, Stoliczka (1871; see his "Synoptical list" of "type-species").

III. Genus *Eufistulana* Eames 1951 [new name for *Fistulana* Bruguière 1789 (1792)].
Type species: *Gastrochaena mumia* Spengler, 1783, by original designation, Eames, 1951.

IV. Genus *Kummelia* Stephenson, 1937.
Type species: *Gastrochaena americana* Gabb, 1860, by original designation.
Discussion: The names *Kummelia* and *Polorthus* are presently a source of taxonomic confusion. Turner (1966; 1969, p. N741) indicated that *Gastrochaena americana* Gabb 1860 is the genotype of *Polorthus* Gabb 1861 by Gabb's original designation. Earlier, however, Whitfield (1885, p. 203) expressed the opinion that Gabb (1861) founded the genus *Polorthus* on *Teredo tibialis* Morton. *Teredo tibialis* forms clusters of tubes, and on this basis is probably not at all closely related to *Gastrochaena americana,* i.e., to *Kummelia* as dis-

cussed in the present paper. Although Turner (1969) erred in indicating that Gabb (1861) designated *G. americana* as the type of Polorthus, her type designation must stand unless Whitfield's (1885) discussion can be constructed as a previous type designation. Clearly, if *G. americana* is the type of *Polorthus,* then this species is unavailable as the type of *Kummelia.*

APPENDIX C
DESCRIPTION OF NEW SPECIES

Family Gastrochaenidae Gray, 1840

Shell fairly small, thin, more or less elongate, equivalve, inequilateral, prosogyrous, and widely gaping anteroventrally or along the entire ventral margin. Hinge edentulous or nearly so; ligament external and opisthodetic and inserting on ligamental nymphs. Anterior adductor scars reduced relative to posterior ones. Siphons well developed; siphon formation reflected in Recent and fossil representatives by a deep pallial sinus and an elongated posterior siphonal burrow. The siphonal and shell chambers of the burrow are generally clearly differentiable in casts of the burrow interiors. In many gastrochaenids these two chambers are separated by pointed "baffles" or by an annular constriction (diaphragm) produced by the calcareous burrow lining. Chemical and mechanical borers in calcium carbonate substrata, facultative tube-dwellers, and obligatory tube-dwellers in tropical, subtropical and less commonly warm temperate waters.

Genus *Gastrochaena* Spengler, 1783

Endolithic boring, facultative tube-dwelling, and obligatory "igloo" forming gastrochaenids with low to moderate elongation of the shells and anterior or nearly anterior umbones. Spikelike calcification of the periostracum, moderate lateral inflation of the shell anterior, a restricted anteroventral pedal gape, and a flaring posterior siphonal burrow are primitive features, most of which are modified by Cenozoic time. Most Cenozoic species show restriction of periostracal calcification to the juvenile shell or a complete loss of this feature, greater lateral inflation of the shell anterior, and posterior and lateral expansion of the pedal gape.

Subgenus *Rocellaria* de Blainville, 1828 (1829)

Endolithic and facultative tube-dwelling gastrochaenids with relatively short siphons and umbones lying near but not at the anterior shell margin. The hinge line is straighter and somewhat thicker than in the other subgenera of *Gastrochaena* (i.e., *Gastrochaena* s.s. and *Cucurbitula*), and is

commonly horizontally flattened toward the anterior shell margin. The hinge line forms a sharp angle with the anteroventral shell margin (as viewed from the side), except in specimens showing extreme abrasion on this part of the shell. The exterior ornament commonly consists of distinct and rather regular comarginal ridges, and the posterior periostracum is generally thin and inconspicuous. The burrow generally takes the form of a simple flask-shaped tube without a prominent diaphragm or "baffles" at the base of the siphons. Some species show an elongated, horizontally flattened area on the anterior of the hinge extending in an anterior-posterior direction, and this may be developed posteriorly into a small, triangular myophore. Other species show more irregular thickenings at the attachment sites of the anterior pedal retractor muscles. But most species lack distinct, spatulate myophores projecting prominently into the umbonal cavity.

Gastrochaena (Rocellaria) linsleyi, n. sp.
Fig. 57, A–F

Description. Shell small (mean length of 4 specimens 4.9 mm, ranging from 4.3 to 6.1 mm), elliptical posteriorly and widely gaping anteroventrally (Fig. 57A). Umbones prosogyrous and lying near but not at the anterior shell margin. Shell valves ornamented with concentric ridges except on the prodissoconchs, which appear as distinct, smooth, shiny caps on the umbones. Anteriorly and laterally the concentric ridges are studded with numerous conical spikes aligned in concentric to slightly oblique rows and imbedded within or cemented to the shell exterior. These spikes (presumably periostracal in origin) are absent from the shell posterior, but may originally have been present in the organic periostracum in this part of the shell. The external opisthodetic ligament inserts on two well-developed ligament nymphs that extend nearly 1/4 the shell length from the umbo toward the shell posterior. These nymphs and the anterior edentulous hinge form an angle of about 16 degrees with the anteroposterior shell axis. The shell anterior is only slightly laterally inflated, and the anteroventral pedal gape is restricted to the shell anterior, extending less than one-half the shell length toward the posterior. The juvenile valves show a broad, radial furrow in the midlateral position extending ventrally from the edge of the prodissoconch. This furrow does not persist into the adult growth stage and is consequently visible in larger shells only near the umbones (Fig. 57A). The shell structure is branching crossed lamellar near the shell margins and irregularly crossed lamellar toward the shell interior (see Carter 1976b for definitions). An outer prismatic shell layer may be present, but this has not yet been confirmed by sectioning. The shell interior appears glossy white and shows no pedal, adductor or pallial muscle attachment scars.

The burrow of *G. (R.) linsleyi* shows distinct siphonal and shell chambers, but these are not separated by a calcareous annular ring or by pointed baffles projecting from the burrow lining (Fig. 57B–F). Latex casts of the

burrow interior indicate short, presumably fused inhalant and exhalant siphon tubes. The orientations of the siphons indicate that the shell commissure plane was essentially parallel to the exterior surface of the *Cucullaea* substratum. The burrow shell chamber is elliptical and relatively spacious in comparison with the shell dimensions, so it would have permitted both rotational and slight anterior-posterior shell movement.

Types. Holotype: YPM 10216a. Type locality: Coon Creek, 250 yards east of Dave Weeks' house, 3½ miles south of Enville, Tennessee. This is the "Dave Weeks place" locality described by Wade (1926, p. 9). Stratigraphic position: Upper Cretaceous. Additional specimens: YPM 10216b–d.

Material. The species is based on four specimens, one of which (the holotype, Fig. 57A) is nearly perfect and is accompanied by a latex cast of the burrow interior. All four specimens are permanently deposited in the Yale Peabody Museum. *G. (R.) linsleyi* and several associated endolithic species (*Lithophaga conchafondentis* Gardner, *Martesia procurva* Wade, an endolithic sponge, and possibly *Lithophaga ripleyana* Gabb) were found boring into the ventrolateral exterior surfaces of an articulated shell of *Cucullaea vulgaris* Morton.

Occurrence. Shells of this species are presently known only from the type locality. The distinctive burrows of *G. (R.) linsleyi* observed in the upper valves of *Exogyra costata* Say from the Prairie Bluff Chalk, 2.8 miles south of the intersection of Highways 21 and 263, northwest of Greenville, Alabama.

Comparisons. The burrow of *G. (R.) linsleyi* resembles the Cretaceous *G. dilatata* Leymerie 1842 in its short siphonal burrow and more or less horizontal orientation of the burrow shell chamber relative to the surface of the substratum. But judging from Reuss' (1845–1846) drawing of *G. dilatata* (see "*Fistulana dilatata* d'Orbigny," Reuss's plate 37, fig. 9) its siphonal burrow differs from *G. (R.) linsleyi* in showing no evidence of distinct inhalant and exhalant tubes. The Upper Cretaceous *Gastrochaena ostreae* (Geinitz) shows distinct inhalant and exhalant tubes in the siphonal burrow (see plate I, figs. 1 and 3 in Zazvorka 1943) but its siphons are separated at their base by a short extension of the posterior burrow shell chamber. In addition, Zazvorka's (1943) description of *G. ostreae* indicates that this species is considerably larger than *G. (R.) linsleyi*. *G. ostreae* and *G. (R.) linsleyi* similarly show a radial furrow in the shell valves, but this is more pronounced in the former and persists into the adult stage. *G. (R.) linsleyi* differs from most Cenozoic gastrochaenids in its relatively restricted anteroventral pedal gape and relatively subdued lateral inflation in the shell anterior.

Discussion. The lateral compression, restricted pedal gape, and calcified periostracal spikes in *G. (R.) linsleyi* are primitive features that strengthen the hypothesis of evolution of *Gastrochaena (Rocellaria)* from *Spengleria*. *G. (R.) linsleyi* represents an early stage in the evolution of *Gastrochaena* in which calcified periostracal spikes were functional for mechanical boring throughout life. Most Cenozoic *Gastrochaena* utilize projecting comarginal

ridges on the valve margins to abrade the substratum often without the aid of projecting periostracal spikes.

It is interesting that *G. (R.) linsleyi* shows an ontogenetic loss of the radial furrow in the shell, since a similar furrow is found in adults of the Upper Cretaceous *G. ostreae* (Geinitz).

G. (R.) linsleyi is assigned to the subgenus *Rocellaria* on the basis of its simple hinge line, nearly anterior but not terminal umbones, relatively short siphons, and simple burrow lining at the base of the siphons. It may be noted, however, that the delicate hinge and relatively subdued concentric ornament of *G. (R.) linsleyi* are more typical of the modern species of *Gastrochaena* s.s. than *Rocellaria*.

The naming of this species is dedicated to Robert M. Linsley of Colgate University.

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