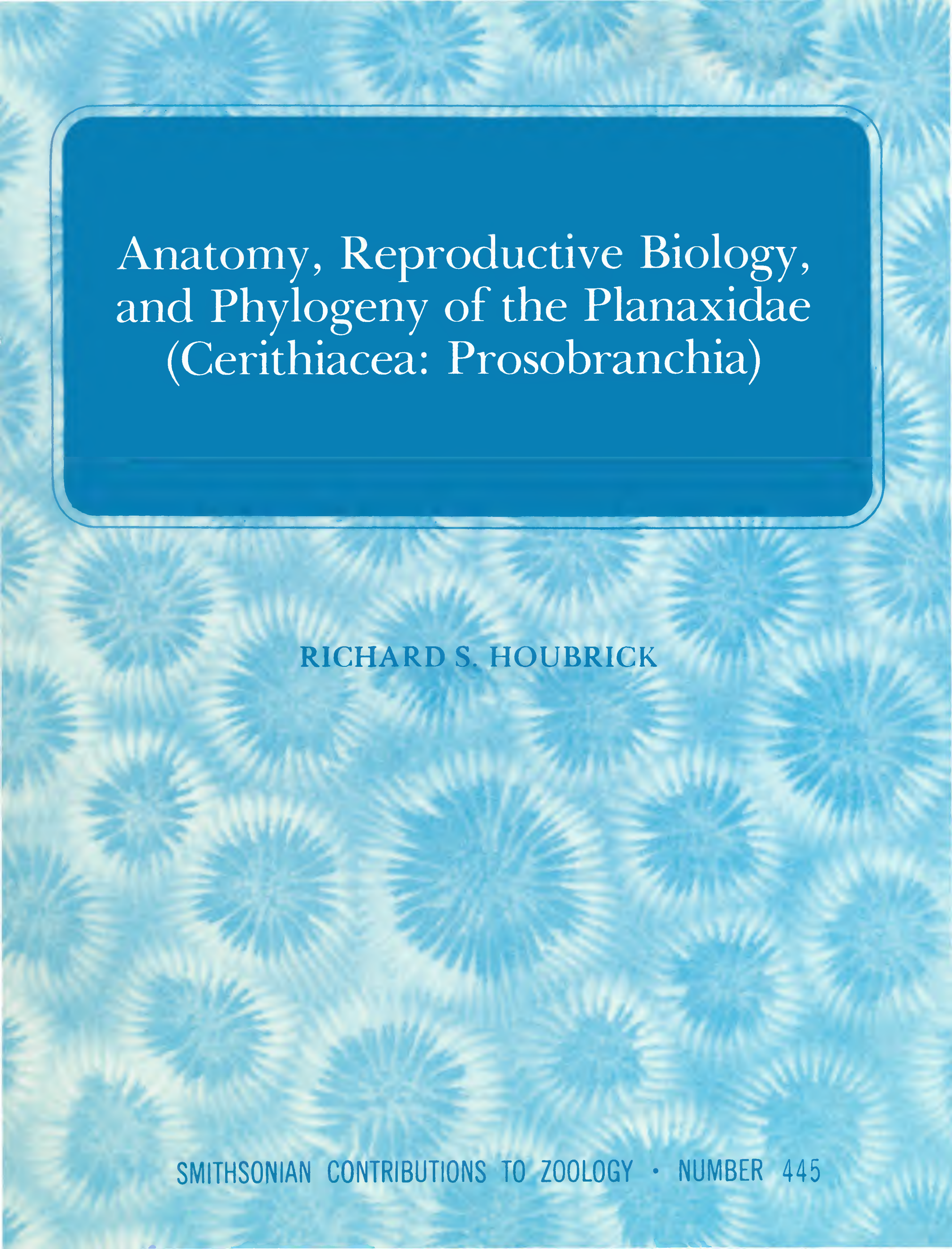

Anatomy, Reproductive Biology, and Phylogeny of the Planaxidae (Cerithiacea: Prosobranchia)

RICHARD S. HOUBRICK

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 445

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SMITHSONIAN INSTITUTION PRESS
Washington, D.C.
1987

ABSTRACT

Houbrick, Richard S. Anatomy, Reproductive Biology, and Phylogeny of the Planaxidae (Cerithiacea: Prosobranchia). *Smithsonian Contributions to Zoology,* number 445, 57 pages, 27 figures, 6 tables, 1987.—The family Planaxidae Gray comprises a small, monophyletic, mainly pantropical marine group of six extant genera in the superfamily Cerithiacea Fleming that are adapted to an intertidal environment. They are microphagous herbivores and usually occur in large populations on hard substrates. Planaxids are gonochoristic and have open pallial gonoducts, aphallic males, produce spermatophores, and brood their young in specialized cephalic brood pouches of ectodermal origin. Embryos of most species are released at the veliger stage and undergo a planktotrophic phase before settlement, but some species undergo a direct, lecithotrophic development. Species in the genus *Angiola* are unique among prosobranchs in having a bioluminescent mantle organ.

On the basis of morphological homology, ontogeny, and advocacy, *Batillaria* (of the subfamily Batillariinae, family Potamididae) and *Melanoides* (of the freshwater family Thiaridae) were chosen as outgroups for phylogenetic analysis of all genera except *Holcostoma.* The polarities of characters were established by outgroup comparison, and transformation series of multi-state characters were ordered by structural complexity and by reciprocal illumination. Two equally parsimonious cladograms were produced that arrange the taxa in essentially similar sequence. *Planaxis* and *Fissilabia* share many apomorphies as do *Angiola* and *Hinea.* Six Recent genera are recognized as comprising the Planaxidae: *Planaxis* Lamarck, 1822; *Fissilabia* Macgillivray, 1836; *Supplanaxis* Thiele, 1929; *Hinea* Gray, 1847; *Angiola* Dall, 1926; *Holcostoma* H. and A. Adams, 1853. Synonymies, conchological, radular and anatomical descriptions, and the ecology and life histories of each genus are presented.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year.* SERIES COVER DESIGN: The coral *Monastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data
Houbrick, Richard S.
Anatomy, reproductive biology, and phylogeny of the Planaxidae (Cerithiacea: Prosobranchia).
(Smithsonian contributions to zoology ; no. 445)
Bibliography: p.
Includes index.
Supt. of Docs. no.: SI 1.27:445
1. Planaxide. I. Title. II. Series.
QL1.S54 no. 445 591 s 86-600266 [QL430.5.P46] [594'.32]

Contents

Anatomy, Reproductive Biology, and Phylogeny of the Planaxidae (Cerithiacea: Prosobranchia)

Richard S. Houbrick

Introduction

The Planaxidae is a family of tropical or subtropical, largely marine, amphibious prosobranchs that is adapted to an intertidal, rocky environment. Known by the vernacular name of "clusterwinks," the Planaxidae includes six higher Recent taxa comprising about 20 species throughout the world, most of which occur in large populations in intertidal habitats. Most species are common and as Sowerby (1877) remarked: "Few genera so restricted in numbers are so widely spread in their habitats." Nearly all species in the family have relatively small- to medium-sized shells, which look somewhat like those of *Littorina* except for the presence of a wide, shallow siphonal canal. Planaxid snails are microphagous herbivores. They have open pallial gonoducts, aphallate males, and are allocated to the superfamily Cerithiacea Fleming, 1822. They are generally placed with the Modulidae, between the freshwater families Thiaridae and Pleuroceridae and the marine Cerithiidae and Potamididae (Thiele, 1929; Wenz, 1940; Taylor and Sohl, 1962:10).

Despite their abundance and accessibility in the intertidal zone, the biology of *Planaxis* species is not well known. Some species are unique among prosobranchs in possessing a luminescent mantle organ, and all planaxids are unusual in that the females have cephalic brood pouches of ectodermal origin in which the young are brooded, usually up to the veliger stage. Several, short, anecdotal citations about brood pouches and enclosed larvae of *Planaxis* exist (Bandel, 1976:258; Ponder, 1980; Boss, 1982:992), but most observations have centered on the larvae rather than on the brood pouch itself. Risbec (1935:392–393) and Thorson (1940:162–169) described the brood pouch embryos of *Planaxis sulcatus* (Born) in some detail, and Thorson (1940) presented a brief account of the brood pouch of *Supplanaxis nucleus*. No other species have been examined nor has any modern descriptive account of the comparative functional anatomy of these structures or of the brooded larvae been published. Besides Thorson's (1940) paper on *Planaxis sulcatus*, there are no substantial accounts of the embryology or life histories of any planaxid species. Likewise, the functional anatomy of the pallial gonoducts has never been elucidated. Indeed, the anatomy of other systems is virtually unknown and nothing has been published about the animals of other planaxid genera.

The only recent paper on the ecology of planaxids is that of Rohde (1981), who discussed the population dynamics of *Planaxis sulcatus* and its trematode parasites.

The genus *Planaxis* Lamarck, 1822, sensu lato, has been divided into eight higher taxa by Thiele (1929), five genus group taxa by Cossmann (1889:196), nine genus group taxa (including one extinct genus) by Wenz (1940), and nine genera and subgenera by Taylor and Sohl (1962:10). These classifications were based on shell characters and a few radular differences, and are here critically evaluated. It is the aim of this paper to describe and analyze characters derived from the shell, radula, anatomy, reproductive biology, and ecology of select members of various planaxid groups. These data, interpreted by cladistic analysis, will test and establish the biological validity of the proposed genera and subgenera. Clarification of generic relationships within the family will develop a synthetic picture of the Planaxidae and their systematic relationships with other cerithiacean families.

MATERIALS AND METHODS

This study examines the comparative anatomy and reproductive biology of five species representing the five major genera of planaxids: *Planaxis sulcatus* (Born, 1780), *Fissilabia decollata* (Quoy and Gaimard, 1833), *Hinea brasiliana* (Lamarck, 1822), *Angiola lineata* (da Costa, 1778), and *Supplanaxis nucleus* (Bruguière, 1789).

With the exception of *Angiola lineata*, each of these

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species is the type-species of the genus group it represents. The first three taxa represent Indo-Pacific species; *Planaxis sulcatus* with a wide Indo-Pacific distribution, *Fissilabia decollata* with a more limited range in the western Pacific, and *Hinea brasiliana* with a peculiar South Pacific distribution (see Rehder, 1980:49, fig. 7). *Angiola lineata* and *Supplanaxis nucleus* occur throughout the Caribbean. Additional species were also studied: *Planaxis planicostatus* Sowerby, 1825, type-species of *Proplanaxis* from the tropical eastern Pacific; *Hinea akuana* Rehder, 1980, from Easter Island; *Angiola fasciata* Pease, 1868 (= *A. lineolata* Gould, 1851), from Guam. While field and anatomical studies of all type-species were made, only the shell, protoconch, radula, and superficial morphological observations of *Planaxis planicostatus* were available for comparison.

The two Caribbean species of *Planaxis* were collected in the vicinity of Miami, Florida, and examined alive at the Smithsonian Marine Station, Link Port, Florida. They were kept in bowls of seawater that were changed daily. Anatomical and embryological studies were made on these specimens. A population of *Supplanaxis nucleus* was studied on a regular basis and collections were periodically made over a three-year period, from 1982 to 1984. Periodic samples of a nearby population of *Planaxis lineatus* were taken at the same time as those of *Planaxis nucleus*. These two species were also examined at Carrie Bow Cay, Belize, in April 1985. In the Southwest Pacific, a population of *Hinea brasiliana* was observed at Sydney, New South Wales, Australia, during March and June 1984 and examined alive at the Australian Museum. *Fissilabia decollata* and *Planaxis sulcatus* were studied at Lizard Island, North Queensland, Australia, in April 1979 and at South Mission Beach, North Queensland, Australia, in June 1984. Living animals were maintained in aquaria and dissected at the Lizard Island Marine Laboratory and at the James Cook University of North Queensland, Townsville, Queensland. These two species and *Angiola lineolata* were also studied at Pago Bay, Guam, in August 1985 and dissections carried out at the University of Guam Marine Laboratory.

For comparative anatomical studies only ripe, adult snails were used. Snails were relaxed in a 7.5% $MgCl^2$ solution isotonic with sea water, and were dissected under a Wild M-8 dissecting microscope. Tissues for sectioning were fixed in Bouin's solution or in buffered 10% formalin sea water, embedded in paraffin, sectioned at 8–10 μm, and stained with Harris' hematoxylin and eosin for histological study. Photomicrographs of sections were made with a Zeiss Photomicroscope III. Some tissues and structures were fixed in 10% formalin, brought through a percentage series of ethanol to 100%, and transferred to amyl acetate prior to critical point drying. Larvae and embryos were relaxed in 10% ethanol or 0.5% chlorotone prior to fixation in Carnoy's solution. Spermatozoa concentrated in sea water were pipetted onto a coverslip, which was placed in a large petri dish to which 25% gluteraldehyde droplets were added. The dish was covered and the sperm fixed in the gluteraldehyde vapor. The preparation was then passed through an ethanol series ending in acetone after which it was critical point dried and coated. Terminology used about sperm types is that proposed by Healy (1983:57–59). Scanning electron micrographs (SEM) were taken of gametes, larvae, tissues, radulae and protoconchs using a Zeiss Novascan-30 instrument.

Two cladistic analyses were made with either *Batillaria* or *Melanoides* as the outgroup, using the Wagner-78 algorithm (Farris, 1970; Wiley, 1981:178–192). The characters were derived from analysis of the shell, radula, soft anatomy, and larvae of species representing five genera: *Planaxis, Fissilabia, Angiola, Hinea,* and *Supplanaxis*. The genus *Holcostoma,* known only from its shell and radula, was excluded from the analysis. Characters and scoring of character states are presented in Tables 5 and 6. Although two-state characters are common, many are multi-state characters and were not easily polarized or ordered. Thus, for series of branching character states, both higher numbers and negative numbers were used in the coding. More details about the characters and their selection is presented in the Phylogeny section of this paper.

ACKNOWLEDGMENTS

Much of this work was done from 1983 to 1985 at the Smithsonian Marine Station, Link Port, Florida. I am grateful for the support funds and thank Dr. Mary Rice, Scientist-in-Charge, for her assistance during this project. My thanks to Woody Lee, Julie Piraino, and Hugh Reichardt for their help with sectioning, scanning electron microscopy and photography, respectively, and for general laboratory assistance. I also thank June Jones, Administrative Officer, for typing some of the initial drafts of the manuscript. This is Smithsonian Marine Station Contribution, Number 154.

Some research was also done at the Smithsonian's Carrie Bow Cay laboratory in Belize. I gratefully acknowledge the support of the Smithsonian Caribbean Coral Reef Ecosystems Program in this project. This is contribution number 173, Reef and Mangrove Study, Belize, partly supported by the Exxon Corporation.

Field studies in Guam were conducted at the University of Guam Marine Laboratory. I am indebted to the laboratory staff for assistance in the field, lab space, equipment, and supplies.

I thank the following curators and institutions for access to material and collections in their charge: Dr. Philippe Bouchet, Museum National d'Historie Naturelle, Paris; Mr. Ian Loch, Collection Manager, The Australian Museum, Sydney; Dr. James McLean, Los Angeles County Museum of Natural History.

I am especially indebted to Dr. Winston Ponder, Australian Museum, Sydney, for his helpful discussions about cerithiacean and planaxid anatomy and for sharing with me his drawings, photos, and histological sections of Australian planaxid taxa. He assisted me in the field and helped me obtain live-collected material of some of the species in this paper. I gratefully acknowledge the use of all this material in this publication. I also wish to thank Dr. David Reid, formerly of James Cook University, Queensland, Australia, for logistic support and assistance during field work in Queensland.

Field work in Australia was made possible by an Australian Museum Fellowship and by the Smithsonian Institution Secretary's Fluid Research Funds. Field work in Guam was supported by the Smithsonian Research Opportunities Fund.

Within the National Museum of Natural History, technical assistance was kindly provided by Miss Diane Bohmhauer and help with the manuscript by Miss Juel Rembert, Department of Invertebrate Zoology. Photography was done by Mr. Victor Krantz, Smithsonian Photographic Services. Scanning electron micrographs were taken by Miss Heidi Wolf and supplied by the Smithsonian Scanning Electron Microscope Laboratory. I thank Dr. Stephen Cairns, Department of Invertebrate Zoology, for advice in the preparation of the Wagner-78 algorithm. Statistical packages and the Wagner-78 Program were provided by the Science Applications Division of the Smithsonian's Office of Information Resources Management.

The original draft of the manuscript was critically reviewed by Dr. Winston F. Ponder, The Australian Museum, Sydney; Dr. M.G. Harasewych, Associate Curator of Mollusks, Department of Invertebrate Zoology, Smithsonian Institution; Dr. Rudiger Bieler, Postdoctoral Fellow, Department of Invertebrate Zoology (Mollusks), Smithsonian Institution; Dr. David Reid, Postdoctoral Fellow, Department of Invertebrate Zoology (Mollusks), Smithsonian Institution and British Museum (Natural History). I thank Dr. Stephen Cairns, Associate Curator, Department of Invertebrate Zoology, Smithsonian Institution, and Mr. Silvard P. Kool, Department of Zoology, George Washington University, for critically reviewing the section of the manuscript on phylogeny and cladistic analysis. Their comments, corrections, and advice have substantially improved this paper.

Family PLANAXIDAE Gray, 1850

In this section, the family and each genus are diagnosed and the type-species of each higher taxon is described, with the exception of *Angiola*, for which *Angiola lineata* (da Costa) is used.

DIAGNOSIS.—Shells of medium size, thick, conic-ovate, often covered with heavy periostracum. Sculpture and pigment, if present, spirally arranged. Aperture ovate, internally lirate and with denticles on inner edge of rounded outer lip. Slight notch in anterior end of aperture due to truncated columella. Moderate columellar shelf and short, wide anterior canal. Operculum horny, ovate, paucispiral with subterminal nucleus. Radula taenioglossate (2+1+1+1+2). Rachidian tooth narrow with long lateral extensions, large central cusp and pair of basal cusps. Laterals with strong, large main cusp and long, lateral extensions. Marginals elongate with spatulate tips having saw-like denticles and large outer flange. Snout pointed downward, lips flared and expanded at tip into a crescent. Eyes, on outer peduncular bases of cephalic tentacles, directed downward. Foot short, with well-defined anterior pedal mucus gland. Mantle edge smooth or weakly scalloped. Osphradium a simple long ridge, slightly shorter than ctenidium. Ctenidium monopectinate, long, usually narrow and composed of elongate filaments. Hypobranchial gland well developed and produces copious amounts of mucus. Pallial gonoducts open, males aphallate with small prostate gland at proximal end of pallial gonoduct. Female pallial oviduct with long sperm groove, spermatophore bursa, and single seminal receptacle in medial lamina. Ciliated groove leaves distal end of pallial oviduct and runs down right side of foot to birth pore in neck beneath right cephalic tentacle. Brood pouch present in head-foot, separate from cephalic hemocoel, ciliated internally, subdivided, and of ectodermal origin. Brooded larvae may be planktotrophic, lecithotrophic, or ovoviviparous. Sperm dimorphic. Euspermatozoa have conical acrosomal cone invaginated in the basal half. Sperm nucleus laterally compressed and posteriorly invaginated. Midpiece composed of two large and two small elements. Pair of salivary glands pass through nerve ring. Midesophagus enlarged to form large esophageal gland divided by strong dorsal ridge. Complex, thin-walled stomach has large bilobed typhlosole, cuticular gastric shield, one opening to digestive gland, short style sac, and short protostyle. Style sac and intestinal opening only partially separated by typhlosole. Kidney with a single lobe that overlaps proximal part of pallial gonoduct and pericardium. Large kidney opening to mantle cavity. Ganglia of nerve ring large, well defined. Cerebral commissure short, pleural ganglia closely juxtaposed to cerebral ganglia, long connectives to pedal ganglia and long supraesophageal connective present. Subesophageal ganglion close to left pleural ganglion. Visceral ganglion at right of esophagus at proximal end of mantle cavity with secondary ganglionic mass crossing over esophagus. Pedal ganglia, each have a pair of long extensions with accessory nodes. Statocysts each with single statolith. Distribution worldwide tropical to subtropical, intertidal, amphibious, microphagous herbivores, usually on hard substrate. There are 6 Recent genera comprising about 20 species.

REMARKS.—The Planaxidae is a small group of marine taxa usually placed in the superfamily Cerithiacea near the freshwater families Thiaridae and Pleuroceridae and the marine families Potamididae and Cerithiidae (Thiele, 1929;

Wenz, 1940; Taylor and Sohl, 1962:10).

Golikov and Starabogatov (1975:212–213) allocated the Planaxidae to a new superorder, Cerithiimorpha, assigning it superfamilial rank. Within their proposed superfamily Planaxoidea they included the families Thiaridae, Planaxidae, and with a query, the fossil group Brachytremidae Wenz, 1940. Planaxoidea was listed close to the superfamilies Cerithioidea Ferussac [sic], 1819, and Melanopsoidea H. and A. Adams, 1854. Their reasons for this assignment were the lack of a true pallial gonoduct (an erroneous statement, as there is a complex open pallial gonoduct present) and the presence of a brood pouch in the planaxids (Golikov and Starabogatov, 1975:220). While I agree with them as to possible affinities between the Thiaridae and the Planaxidae, the anatomical differences of these two groups are not sufficiently great to justify creation of a separate superfamily.

The Planaxidae is not species-rich as are the related families Cerithiidae, Thiaridae, and Potamididae. The phylogenetic placement, composition, and ranking of taxa within the family has had an unstable history. Tryon (1882:246–247) recognized three genera: *Planaxis,* under which he included the subgenera *Hinea, Fissilabia,* and *Holcostoma,* and the genera *Litiopa* Rang, 1829, and *Alaba* H. and A. Adams, 1862. Under *Alaba,* Tryon included the subgenera *Diala* A. Adams, 1862, and *Styliferina* A. Adams, 1860. *Litiopa* and *Alaba* are small snails with distinctive shell morphologies, that have epipodial tentacles and occupy very different niches from the intertidal rocky habitat of planaxids. They should be excluded from the Planaxidae. *Styliferina* is a parasitic group with epipodial tentacles and differs greatly in external anatomy from planaxids (Kosuge, 1964:34). It should be allocated to the Litiopidae. Fischer (1887:686–687) recognized only two genera in the family: *Planaxis* including section *Hinea,* subgenera *Fissilabia* (cited as *Quoyia*) and *Holcostoma,* and genus *Plesiotrochus* Fischer, 1878, which he listed with a query. The latter group does not have the shell morphology, radula, or habitat of planaxids and should be excluded from them. Cossmann (1906:195–200) presented the most thorough analysis of the Planaxidae including living and fossil groups. He erroneously attributed the Planaxidae to Sowerby and followed Fischer's (1887) classification, putting the Planaxidae in the Cerithiacea between the Trichotropidae and Modulidae rather than in the vicinity of the Littorinidae, as did Tryon (1882). Cossmann (1906:196) pointed out that the aperture is not holostomous but has a short canal. He suggested that for a paleontologist the most essential familial shell character is the notch formed by the truncated columella and that the placement of the lip is a good subgeneric criterion. Spiral sculpture distinguishes the sections in his classification. Cossmann (1906) divided the family into two subfamilies: Planaxinae Tryon, 1887, and Litiopinae Tryon, 1887. I pointed out above that the Litiopinae should be excluded from the Planaxidae. Within the Planaxinae, Cossmann (1906) gave generic status to *Planaxis,* and the two fossil groups, *Orthochilus* Cossmann, 1889, and *Dalliella* Cossmann, 1895. He considered *Planaxis* to comprise three subgenera, *Hinea, Quadrasia,* and *Fissilabia* and regarded *Holcostoma* as a section of *Planaxis.* Under the subgenus *Dalliella* he included the fossil section *Sirius* Hedley, 1900, but this taxon should be assigned to the Trichotropidae (Ponder, in litt.). Cossmann (1906) considered the Planaxidae to have been extant since the Tertiary but expressed puzzlement about their origins since they seem to have no close morphological relatives among the Metacerithinae.

The monotypic genus *Quadrasia* Crosse, 1886, was assigned to the Planaxidae with a query by Thiele (1929:204). Only two samples of *Quadrasia hidalgoi* Crosse, 1886, were available for examination. This species was described from Balabac, Philippine Islands, from a freshwater habitat. The holotype and one specimen preserved in alcohol from the Paris Museum and a single shell in the National Museum of Natural History, Smithsonian Institution, were the only material I could find. The animal has a long inhalant siphon, closed pallial gonoducts, a pleurembolic proboscis, and a radula typical of the Buccinidae. Thus, *Quadrasia hidalgoi* Crosse, 1886, should be considered a Philippine representative of the buccinid genus *Clea* H. and A. Adams, 1855. It closely resembles the type-species, *Clea nigricans* A. Adams, 1855, from the rivers of Sarawak, Borneo.

RECOGNIZED GENERA OF PLANAXIDAE.—*Planaxis* Lamarck, 1822; *Fissilabia* Macgillivray, 1836; *Hinea* Gray, 1847; *Angiola* Dall, 1926; *Supplanaxis* Thiele, 1929; and *Holcostoma* H. and A. Adams, 1853.

Genus *Planaxis* Lamarck, 1822

Planaxis Lamarck, 1822:50 [not *Planaxis* Risso, 1826].
Proplanaxis Thiele, 1929:203.—Wenz, 1940:721. [Type-species: *Planaxis planicostatus* Sowerby, 1825, by original designation.]

TYPE-SPECIES.—*Buccinum sulcatum* Born, 1780, by subsequent designation (Gray, 1847:138).

DIAGNOSIS.—Shell conical, solid, obese, dark brownish black with white spiral spots. Whorls inflated, sculptured with spiral grooves. Body whorl large, inflated with ovate purple aperture, a little less than one-half the shell length. Outer lip thick, scalloped at edge and deeply grooved within. Columella white, concave, with large parietal tooth at anal canal. Rachidian tooth with single broad, blunt cusp, a pair of tiny, midlateral basal cusps and two moderately elongate lateral extensions on long basal plate. Seminal receptacle distal, situated below spermatophore bursa. Large brood pouch divided into many lamellar chambers on both sides of head-foot and extending up on right side over buccal mass and midesophagus. Pair of large coiled salivary glands and wide esophageal gland. Stomach with large bilobed, raised pad and two anterior typhlosoles. Habitat mid-intertidal rocky substrate. Development lecithotrophic in brood pouch until veliger stage; then planktonic.

Development may also be ovoviviparous.

REMARKS.—The type-species of the genus, *Planaxis sulcatus,* is a widespread Indo-West Pacific species that also occurs throughout the Indian Ocean, the Red Sea, and the Persian Gulf. Although this species broods its embryos, there appears to be a geographic difference in developmental strategies, in regard to the extent of brooding prior to expulsion from the brood pouch. Populations from the Persian Gulf and Pakistan have been cited to have a viviparous type of development (Thorson, 1940; Barkati and Ahmed, 1982), which differs from the planktotrophic development observed in populations from the western Pacific (Risbec, 1935; this study). As the shells and radulae from these widely separated populations are morphologically identical, it is assumed that they are conspecific. The possibility remains, however, that the Indian Ocean populations may constitute a separate, sibling species; therefore, this phenomenon needs to be studied in detail.

No substantial characters justify recognition of the taxon *Proplanaxis,* proposed by Thiele (1929:203) as a subgenus of *Planaxis* on the basis of radular differences. Examination of the radula with SEM revealed no significant differences. The name *Proplanaxis* was cited by Wenz (1940:721) but has been largely ignored by subsequent workers. The type-species of *Proplanaxis, Planaxis planicostatus* Sowerby (Figure 1I), is common throughout the tropical eastern Pacific and appears to live in the same kind of habitat as does *P. sulcatus.* The shell of *Planaxis planicostatus* (Figure 1I) is only slightly more elongate than that of *P. sulcatus,* which it closely resembles. The radula and most anatomical features are likewise virtually identical to those of *P. sulcatus.* The two small denticles flanking the central cusp of the rachidian as depicted by Thiele (1929:203, fig. 196) were not seen in SEM studies of specimens from Panama. Instead, they show a radula with a rachidian tooth virtually identical to that of *P. sulcatus.* The brood pouch of *P. planicostatus* fills the center of the propodium reaching both sides, extending dorsally backwards beneath the midesophagus. (The brood pouches I examined were not fully developed and no pregnant specimens were seen.) Internally, the brood pouch is lined with many folds of epithelium, suggesting potential formation of the thin partitions and chambers found in *P. sulcatus* and *Fissilabia decollata.* The mantle edge of *P. planicostatus* is fringed with large, broad, darkly pigmented scallops and a deep indentation at the inhalant siphon where it becomes thick and appears to be innervated by a large ganglion. The organs of the mantle cavity are very similar to those seen in other planaxids. The ctenidium is comprised of long triangular filaments that are less wide and three times as long as those of *P. sulcatus.*

Planaxis sulcatus (Born, 1780)

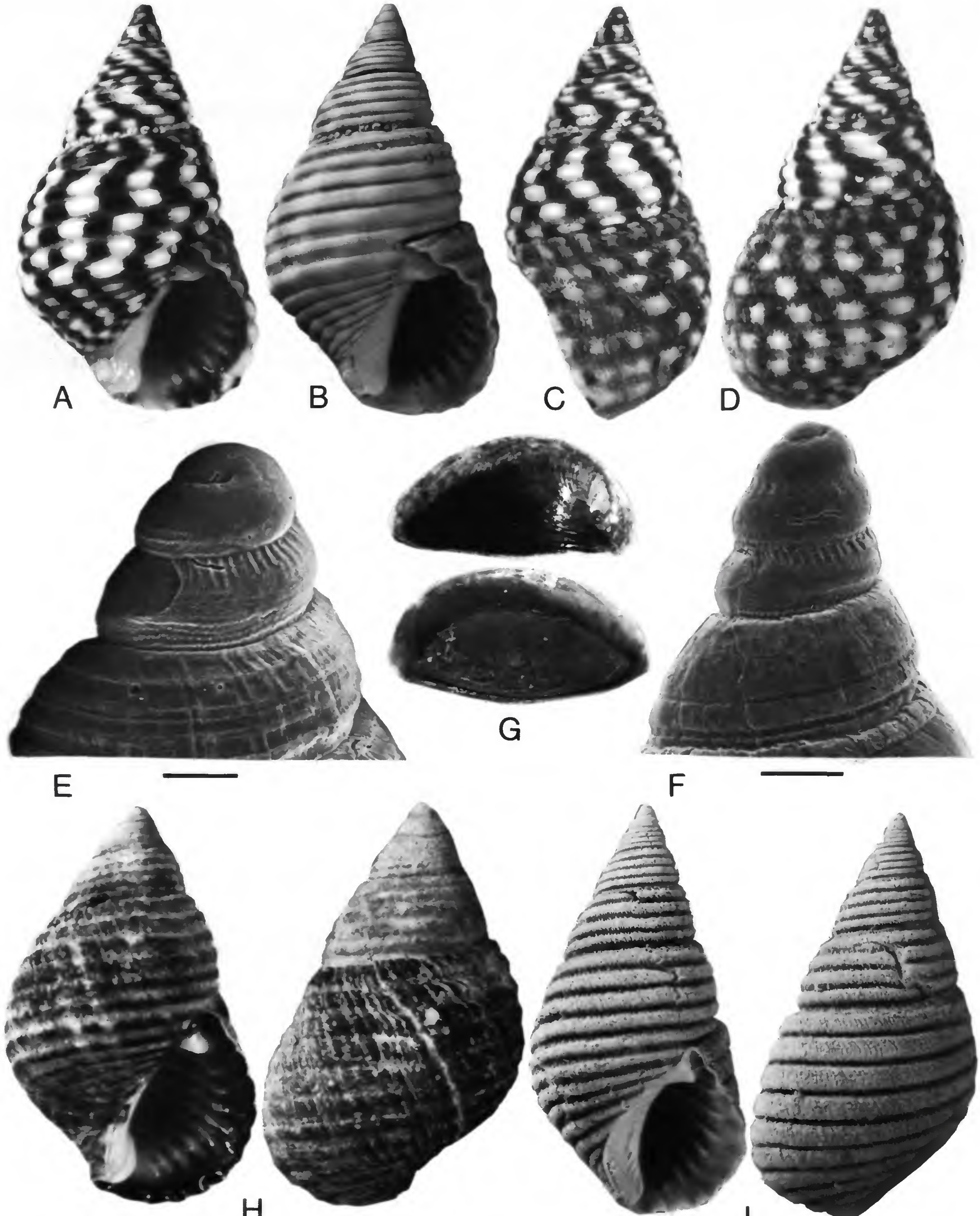
Buccinum sulcatum Born, 1780:258, pl. 10: figs. 3, 6.
Buccinum pyramidale Gmelin, 1791:3488.
Planaxis sulcata Lamarck, 1822:51.—Quoy and Gaimard, 1833:486, pl. 33: figs. 25–39.
Planaxis undulata Lamarck, 1822:51.
Planaxis sulcatus Lamarck.—Sowerby, 1822(12), pl. 1: fig. 1.
Planaxis buccinoides Deshayes, 1828:13.
Planaxis sulcatus (Born).—Sowerby, 1877, pl. 1: fig. 4.—Morlet, 1889:144.— Fischer, 1891:164.—Dautzenberg and Fischer, 1905:139–140.

This ubiquitous snail occurs in large populations throughout the Indo-Pacific among intertidal, rocky environments where it is frequently found on large rocks, stones, and beachrock in the low to midtidal zones. It grazes on microalgae covering rocky substrates in moderate to low energy habitats. When exposed to air during low tides, groups of snails frequently cluster together in crevices and depressions and are highly visible.

SHELL MORPHOLOGY (Figure 1).—Shell solid, wide, moderately elongate, reaching 35 mm in length, and comprising about 7 inflated whorls. Whorls are sculptured with incised spiral lines and grooves, the penultimate whorl having 6 grooves. Body whorl very large, wide, with an ovate aperture a little less than one-half the shell length. Outer lip smooth, slightly scalloped and denticulate within. Interior of aperture sculptured with deep grooves paralleling outer spiral grooves. Columella concave with slight callus and prominent parietal tooth at edge of anal canal. Base of body whorl moderately constricted with short, wide, anterior canal. Suture deeply incised. Larval shell has 3.5 whorls. Protoconch I with 1.5 smooth whorls. Protoconch II sculptured with fine subsutural axial plaits and two primary spiral cords, and a secondary presutural spiral of minute pustules (Figure 1E, F). Well-developed sinusigeral notch present in planktotrophic forms. Shell has white background color but usually of an overall brown-black aspect due to many spiral dark brown to black blotches. Interior of aperture purple, columella white. Periostracum thin, brown. Operculum large, lenticular, paucispiral with subterminal nucleus (Figure 1G).

EXTERNAL ANATOMY (Figure 2A).—The head-foot is black although the bases of the cephalic tentacles may be dusky white and the metapodium a yellowish dirty white. The sole of the foot is white. In females, there is a ciliated groove on the right side of the foot beginning at the distal end of the oviduct and ending in a swollen birth pore on the neck beneath the right cephalic tentacle (Figure 2A, bp). The mantle edge is slightly scalloped (Figure 2A, me).

MANTLE CAVITY ORGANS.—The osphradium is in the form of a very thin ridge flanked on each side by a thin, densely ciliated strip. The ctenidium is broad and composed of shallow, triangular filaments. There is a raised ridge at the basal side of the ctenidium adjacent to the osphradium. The hypobranchial gland is wide, thick, whitish in color, and divided into raised transverse ridges. A raised glandular pad of the hypobranchial gland lies adjacent to the distal end of the osphradium where it curves into the inhalant siphon. The intestine is wide and filled with many trans-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versely stacked fecal pellets. The distal end of the pallial oviduct opens anterior to the rectum.

ALIMENTARY TRACT.—The buccal mass is very large, filling the snout (Figure 3D, bm). A small pair of chitinous jaws is situated at the edge of the inner lips. A long, robust radula curves under the buccal mass and dorsally around the nerve ring, terminating in the radular sac, which lies to the right of the nerve ring (Figure 3F). Buccal muscles are well developed.

Radula (Figure 3A, B). The radular ribbon is long, a little over one-half the shell length and has about 5 rows of teeth per millimeter. The rachidian tooth (Figure 3A) is squarish in shape, with a pentagonal basal plate on which there are a pair of basal lateral cusps, a rounded basal margin and a long thin lateral extension on each side. The cutting edge is convex and has a single broad spoon-like cusp. The rachidian formula is $\frac{1}{1-1}$. The lateral tooth (Figure 3B) is rhomboidal and has a cutting edge with a broad, straight-edged central cusp flanked on each side by two small outer and inner denticles. There is a long lateral extension that extends downward and twists where it anchors the tooth to the basal membrane. The marginal teeth (Figure 3B) are long, narrow and expanded at the tips. The tip of the inner marginal tooth has five wide denticles while the tip of the outer marginal tooth has nine digitate denticles. Wide flange on outer margin of marginal tooth.

The paired salivary glands (Figure 3F, sg) are minute, coiled tubes with separate origins that begin behind the nerve ring but join into a single mass that is spread over the anterior dorsal surface of the esophageal gland. The salivary glands pass through the nerve ring as two uncoiled simple tubes, coiling again and uniting anterior to the nerve ring as a large mass that lies on the posterior dorsal surface of the buccal mass. The two anterior salivary ducts lie close together, but separate before emptying into the dorsolateral sides of the buccal mass.

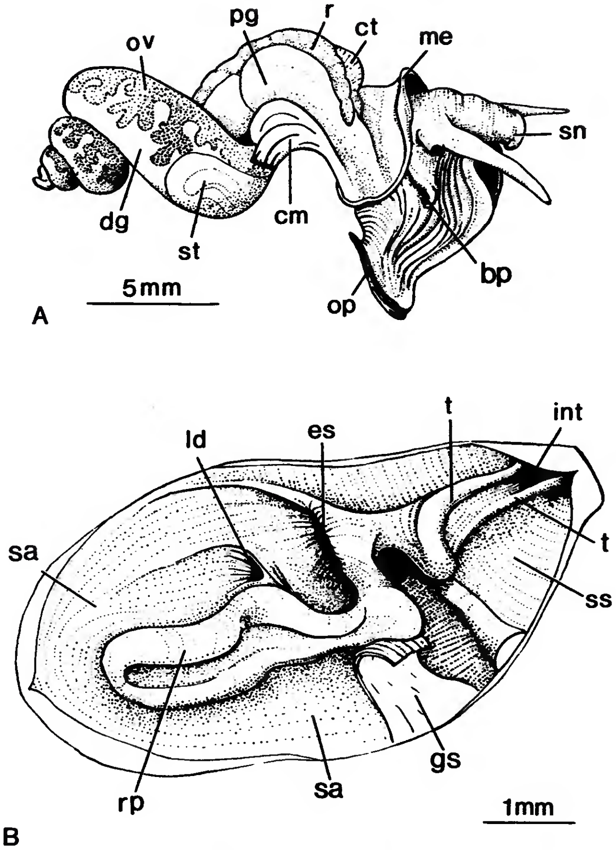
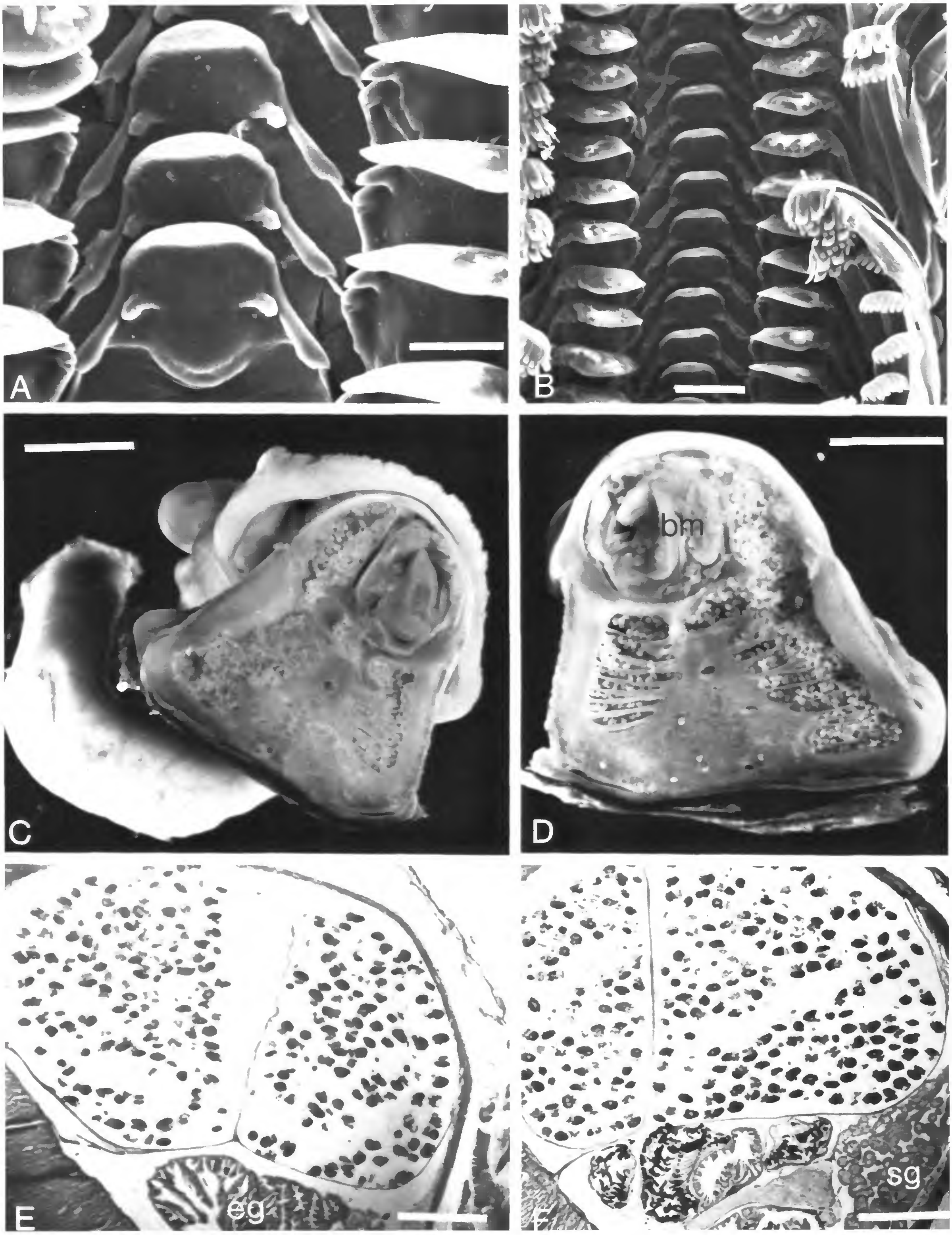


FIGURE 2.—*Planaxis sulcatus:* A, female; B, stomach. (Abbreviations: bp = brood pore; cm = columellar muscle; ct = ctenidium; dg = digestive gland; es = esophageal opening; gs = gastric shield; int = intestinal opening; ld = digestive gland opening; me = mantle edge; op = operculum; ov = ovary; pg = pallial oviduct; r = rectum; rp = raised muscular pad; sa = sorting area; sn = snout; ss = style sac; st = stomach; t = typlosole.)

The midesophagus widens immediately behind the nerve ring expanding laterally and thickening to form a wide esophageal gland. In section, the inner wall of the esophageal gland is folded into many deep longitudinal lamellae. The epithelial cells lining the esophageal gland stain deep purple with hemotoxylin (Figure 3E, eg). The esophageal gland extends posteriorly nearly the length of the mantle cavity before constricting to form the posterior esophagus.

The large stomach (Figure 2B) has a wide, posteriorly bilobed, raised pad that is T-shaped in profile and is highly muscular and mobile, particularly in its dorsal lips (Figure 2B, rp). This pad serves to separate the particulate matter entering the stomach from the esophagus on the right from the sorted particles being transported on the left toward the anterior typlosoles. The two typhlosoles (Figure 2B, t), located in the anterior portion of the stomach, most of the sorting area of the stomach (Figure 2B, sa), and the style sac (Figure 2B, ss) are weakly ciliated. The cuticularized gastric shield (Figure 2B, gs) is large. A short protostyle is present in freshly collected specimens. The single opening to the digestive gland (Figure 2B, ld) is close to the esophageal opening (Figure 2B, es) and lies adjacent to the left base of the bilobed pad.

FIGURE 1.—Shell morphology. A–D, Highly colored *Planaxis sulcatus* from Port Hedland, Queensland, Australia (length: 22.4 mm, USNM 835608): A, B, apertural views (B whitened with ammonium chloride to enhance sculptural details); C, D, side and dorsal views; E, SEM micrograph of protoconch of *P. sulcatus* from Mission Beach, Queensland, Australia (bar: 100 µm, USNM 836627); F, SEM micrograph of protoconch of *P. planicostatus* from Naos Id, Panama (bar: 100 µm, USNM 742818); G, free and attached sides of operculum of *P. sulcatus* from Mission Beach, Queensland, Australia (length 7 mm, USNM 836627); H, melanistic specimen of *P. sulcatus* from Mission Beach, Queensland, Australia (length 23.3 mm, USNM 836627); I, *P. planicostatus* from Naos Id, Panama (length: 18.8 mm, USNM 742818, specimen whitened with ammonium chloride to enhance periostracum and sculptural details).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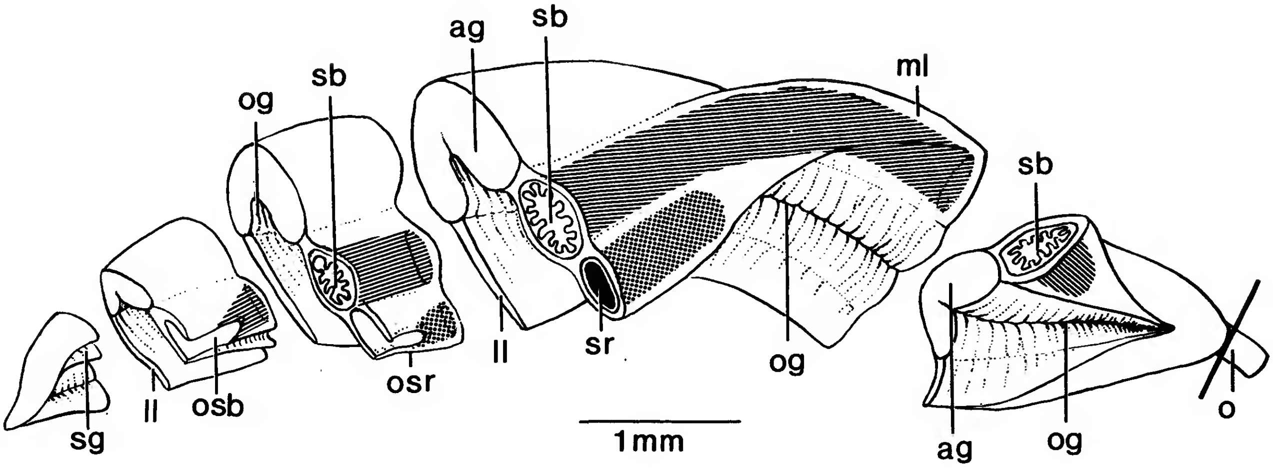


FIGURE 4.—Schematic of pallial oviduct of *Planaxis sulcatus* with distal portion of open duct folded back to expose oviducal groove. (Abbreviations: ag = albumen gland; ll = lateral lamina; o = coelomic oviduct; og = oviducal groove; ml = medial lamina; osb = opening to spermatophore bursa; osr = opening to seminal receptacle; sb = spermatophore bursa; sg = sperm gutter; sr = seminal receptacle.)

REPRODUCTIVE SYSTEM.—The pallial gonoducts are tubular extensions of the coelomic gonoducts and developed from tissues of the floor and right wall of the mantle cavity. In all cerithiaceans, the pallial gonoduct is an open, slit tube comprising two laminae joined dorsally to each other: a lateral lamina attached to the mantle wall and a medial, free lamina. These laminae consist of loosely organized connective tissue covered by epithelium and contain the reproductive structures that are formed as sacular invaginations of the epithelium. The basal attachment of the pallial gonoduct, where the two laminae are connected, is highly glandular and thickened, forming the albumen gland. The channel at the base of the two laminae is the oviducal groove and is the part of the pallial oviduct in which eggs are fertilized, surrounded by albumen, and encapsulated while moving through the duct by ciliary transport. The distal end of the pallial gonoduct lies a few millimeters behind the mantle edge.

In *Planaxis sulcatus,* the male pallial gonoduct is a simple open tube with a proximal glandular prostate. The pallial oviduct, which is shown diagramatically in Figure 4, has a proximal albumen gland (Figure 4, ag) and a median capsule gland. The oviducal groove (Figure 4, og) is moderately glandular along its length. A long sperm gutter (Figure 4, sg) begins at the distal end of the medial lamina (Figure 4, ml) and extends to the median edge where it enters the lamina as a duct (Figure 4, osb) that branches into a large proximal spermatophore bursa (Figure 4, sb) and a smaller, median seminal receptacle (Figure 4, sr), lying beneath the spermatophore bursa. A highly ciliated groove emerges from the distal pallial oviduct and runs down the right side of the foot into the birth pore (Figure 2A, bp) of the brood pouch. The brood pore is a slit in the center of an elevated, lightly pigmented portion of the neck, beneath the peduncle of the right cephalic tentacle. The brood pouch (Figure 3C–F) in pregnant snails is a very large, complex structure partially divided into left and right chambers located in the head-foot (Figure 3C, D). It becomes extended and swollen when filled with embryos and is separated from the cephalic cavity and midesophagus by only a thin membrane (Figure 3E). In the anterior part of the foot both right and left chambers are subdivided into a series of many narrow, longitudinal chambers separated by thin partitions (Figure 3D). These small chambers on both sides of the foot unite posteriorly to form a single large chamber that extends dorsally to the base of the buccal cavity and posteriorly over the right side of the buccal mass and esophagus just below the dorsal body wall. The dorsal portion of the chamber is further subdivided by a few thin membranous partitions and is separated from the buccal cavity and esophagus by a thin membrane. Embryos are found throughout the entire

FIGURE 3.—*Planaxis sulcatus.* A–D, Specimen from Mission Beach, Queensland, Australia: A, detail of rachidian tooth (bar: 50 μm); B, half row of radula (bar: 100 μm) illustrating relationship of marginal teeth to central and lateral teeth (USNM 836627); C, D, female of *P. sulcatus* divided by transverse cut (C, posterior and D, anterior of snail) showing relationship of brood pouch to buccal mass (bm) and lamellar aspect of brood chambers (note extension of brood pouch over dorsal right side of buccal mass; bars: 1 mm). E–F, Specimen from Lizard Id., Queensland, Australia: histological sections through neck showing brood pouch and embryos extending over esophageal gland and salivary gland (note thin dividing partition in brood pouch and thin wall separating radula, salivary gland (sg), and esophageal gland (eg) from brood pouch) (bar: 0.5 mm).

brood pouch and may comprise several cohorts of different growth stages. The more advanced embryos appear to be in the dorsal portion of the chamber. Each embryo is contained in a thin egg capsule from which it breaks out prior to expulsion from the brood pore in the right side of the neck. The stage at which embryos hatch from the brood pore and the kind of development that follows appears to vary between populations in the Indian and Pacific Oceans. Indirect evidence derived from field observation and the study of larval shells indicate that the population from South Mission Beach, North Queensland, Australia, has a moderate lecithotrophic type of development and a short planktonic phase. Larval shells from this population have a sinusigeral notch and protoconch sculpture indicative of a free swimming larval stage. My observations agree with those of Risbec (1935) who noted a similar type of development from a New Caledonian population. He found that cleavage started in the pallial oviduct and that the embryos reached the brood pouch at the morula stage. Risbec (1935:387–388) stated that well-developed larvae, ready to hatch, as well as early embryos, fresh from the oviduct, were present in the brood pouch. In the New Caledonian population, larvae left the brood pouch and became pelagic when each larval shell reached 0.1 mm across and the velum was well developed. Risbec (1935:387–388) noted emerging larvae had not developed eyes. Other types of development have been attributed to populations of *P. sulcatus* in the northwestern Indian Ocean. Thorson (1940) recorded that larvae of a population from the Persian Gulf developed into small snails and fed on nurse eggs within the brood pouch prior to hatching. In some cases, a few embryos reached the free crawling stage and attained considerable size (3.25 mm) within the brood pouch. Barkati and Ahmed (1982) recorded direct development in a population from Buliji, near Karachi, Pakistan. In this population crawling snails hatched out at a length of 0.38 mm. Other populations from the northwestern Indian Ocean need to be studied to determine if direct development is the usual mode in that region. There may be two cryptic species involved: an Indian Ocean species with ovoviviparous development, and an Indo-Pacific species with indirect development, including partial brooding followed by a planktonic phase.

NERVOUS SYSTEM.—The nervous system of *P. sulcatus* has been described in detail by Risbec (1935:391) and my observations are in agreement with his. The subesophageal ganglion is attached to the left pleural ganglion and the visceral ganglion lies at the posterior end of the mantle cavity, forming a ganglionic mass to the right of the esophagus, with a secondary mass crossing over the esophagus. The cerebral-pleural connectives are very long. The large pedal ganglia each have two swollen extensions or strands, the external one being more developed than the internal one. These appear to innervate the brood pouch. The RPG ratio (Davis et al., 1976:263) is 0.57 (n = 5), indicating a tight central nervous system.

Genus *Fissilabia* Macgillivray, 1836

Fissilabia Macgillivray, 1836:42 [type-species: *Fissilabia fasciata* Macgillivray, 1836 (= *Planaxis decollata* Quoy and Gaimard, 1833), by monotypy].

Quoyia Gray, 1839:125.—Cossmann, 1906:197.—Thiele, 1929:203.—Wenz, 1940:721. [Type-species: *Planaxis decollata* Quoy and Gaimard, 1833, by monotypy].

Leucostoma Swainson, 1840:172, 336 [not *Leucostoma* Meigen, 1803].

Quoya.—Deshayes, 1843:236 [misspelling].

Fissilabria Brown [sic].—Gray, 1847:138 [wrong author and misspelling].—Oostingh, 1925:43.

Fissilabra Brown [sic].—Paetel, 1875:81 [wrong author and misspelling].

TYPE-SPECIES.—*Planaxis decollata* Quoy and Gaimard, 1833, by monotypy.

DIAGNOSIS.—Shell tall, thick, light tan to brown, decollate and sculptured with many spiral grooves. Aperture narrow, ovate with slight columellar callus and columellar plait below parietal area. Outer lip smooth, internally grooved. Periostracum yellowish brown. Radula long, comprising about 800 rows of teeth. Cutting edge of rachidian tooth with single, large, wide, blunt cusp; basal plate with two medium-sized cusps and two lateral extensions slightly bifurcated at their tips. Seminal receptacle in median portion of pallial oviduct. Larger portion of partitioned brood pouch in right side of head-foot. Embryos lecithotrophic. Salivary glands coiled, esophageal gland wide. High rocky supratidal habitat.

REMARKS.—This genus is usually called *Quoyia* Gray, 1839, and has sometimes been used as a subgenus of *Planaxis*. An earlier name, *Fissilabia* Macgillivray, 1836, has not been used in the past 50 years and, under the old International Code rules, would have been considered a nomen oblitum. It does, however, have priority and since *Quoyia* is an obscure genus, not frequently cited in the literature, it will not upset taxonomic stability or cause confusion to strictly apply the principle of priority and accept *Fissilabia* as the valid name. There are several misspellings of this name in the literature, and these have been noted in the above synonymy. Gray (1847:138) in error cited Brown as the author of *Fissilabia*. *Fissilabia fasciata*, cited by Macgillivray (1836), is conspecific with *Planaxis decollata* Quoy and Gaimard, 1833, which is the type-species.

Fissilabia is a monotypic genus and was accorded sectional status under *Planaxis* by Wenz (1938:721, cited as *Quoyia*), but shell, radular, and anatomical characters as well as ecology differ substantially from other planaxid taxa. *Fissilabia* is here regarded as a genus. The decollate spire and the columellar plait below the parietal thickening are apomorphic shell characters. The brood pouch of *Fissilabia* is very similar to that of *Planaxis*, but the protoconch of the former is larger and smooth. *Fissilabia* is limited in geographic distribution to the Indo-West Pacific.

Fissilabia decollata (Quoy and Gaimard, 1833)

Planaxis decollata Quoy and Gaimard, 1833:489–491, pl. 33: figs. 33–37.
Fissilabia fasciata Macgillivray, 1836:42.
Quoyia decollata (Quoy and Gaimard).—Chenu, 1859:304, fig. 2147.
Quoyia michaui Crosse and Fischer, 1863:375, pl. 13: fig. 6.
Planaxis (Quoyia) decollata (Quoy and Gaimard).—Sowerby, 1877, pl. 5: fig. 37.—Cernohorsky, 1972:59–60, pl. 12: fig. 21.
Fissilabria decollata (Quoy and Gaimard).—Oostingh, 1925:43 [misspelling].

This large, brown, decollate species lives in the high intertidal zone of upper littoral rocky habitats, where it is found at the bases and interstices of large boulders and rocks; it also occurs under rubble and debris in the high intertidal of protected shorelines. Snails tend to cluster in moist areas away from bright light during low tides and may be abundant in some places. *Fissilabia* grazes on the microalgae covering rocky substrates.

SHELL MORPHOLOGY (Figure 5).—The strong shell is tall, narrow and decollate in adults, reaching 30 mm in length. It comprises about four weakly inflated whorls, each sculptured with 8 or 9 spiral grooves. The large body whorl is moderately inflated and angulate at its periphery and is sculptured with spiral grooves. The base of the body is moderately concave and constricted toward the siphon. The aperture is ovate, one-third the shell length (nondecollate), and has a smooth outer lip that is spirally grooved within. The siphonal canal is short, the columella concave with a slight callus. A prominent columellar parietal plait, near the parietal thickening, extends into the aperture and throughout the shell, as seen in cross-section. Suture distinctly impressed. Larval shell (Figures 5D, 8), comprising about 2.5 whorls, sculptured with fine, pustulate, spiral striae, protoconch 1 (Figures 5D,F; 8) smooth, bulbous. There are faint subsutural axial plaits on the second protoconch whorl and a slight sinus at the aperture. Entire adult shell covered with thick, tan periostracum. Shell color tan to dark brownish gray. Aperture purple-brown and columella whitish. Operculum paucispiral with subterminal nucleus (Figure 5E). The opercular notch, depicted by Quoy and Gaimard (1833, pl. 33: fig. 37) and said to conform to the columellar plait, was not seen.

EXTERNAL ANATOMY.—The head is black except for a white- tipped snout and whitish cephalic tentacles. The surface of the foot is pinkish gray and the sole white. Females have a ciliated groove on the right side of the foot and the brood pouch opening is raised and lightly pigmented. The dorsal surface and edge of the mantle are pinkish white except for the inner part of the mantle edge, which is lined with black. The mantle edge is smooth. The kidney is dark reddish brown.

MANTLE CAVITY ORGANS.—The ctenidium is narrow, well developed, and comprised of long triangular leaflets. The wide, thick hypobranchial gland secretes copious amounts of mucus. The distal end of the female pallial oviduct opens in front of the rectum.

ALIMENTARY TRACT.—The buccal mass is large, massive, and much like that of *Planaxis sulcatus*.

Radula (Figure 6A–D). The radula is long and robust, about one-half the shell length, and has about 10 rows of teeth per millimeter. The rachidian tooth (Figure 6D) has a large wide blunt central cusp and a basal plate with two blunt cusps and a long median basal projection. The lateral extensions of the basal plate have slightly bifurcate tips. The dental formula for the rachidian tooth is $\frac{1}{1-1}$. The rhomboidal lateral tooth has a cutting edge with a wide, blunt central tooth, two sharp inner denticles, and 2 or 3 outer denticles (Figure 6B). The base is short, having a central supporting column and a very long, tapering lateral extension. The marginal teeth are long, narrow, and spatulate at their tips (Figure 6A,C). There are 6 or 7 digitate denticles on the tip of the inner marginal tooth and 8 or 9 digitate denticles on the outer marginal tooth. A long, broad outer flange extends outwardly from the tip of the outer marginal tooth and tapers along its length to the tooth base.

Each of the paired salivary glands consists of a minute tube that begins in a coiled mass dorsal and to the left of the midesophagus. The salivary glands pass through the nerve ring as single tubes, but become large coiled flattened masses anterior to it. The dorsal fold of the anterior esophagus is wide and thin-walled. Sections of the midesophagus show that it is comprised of numerous thick, deep, longitudinal folds in the walls of the esophagus (Figure 6F). The midesophagus is long, with a deep dorsal food groove (Figure 6F, dfg), but narrows abruptly towards the posterior end of the mantle cavity, where it becomes the posterior esophagus. The posterior esophagus is an oval-shaped tube, which in section is seen to have lateral and dorsal longitudinal folds, and a large ventral fold protruding from the thin floor into the lumen.

The stomach is very large, about 1.5 whorls in length and distinguished by a long, massive, bilobed pad in its posterior end.

REPRODUCTIVE SYSTEM.—The pallial oviduct is shown diagramatically in Figure 7. It has a highly glandular proximal albumen gland (Figures 7, ag; 9C,F, ag) and the oviducal groove is glandular throughout its length (Figures 7, og; 9A, og). A long sperm gutter (Figure 7, sg) lies along the edge of the anterior-median portion of the medial lamina (Figure 7, ml). This gutter leads into a duct that widens posteriorly to become a spacious spermatophore bursa (Figures 7, sb; 9B,C, sb), which is internally lined with longitudinally folded, highly ciliated epithelium. Sections

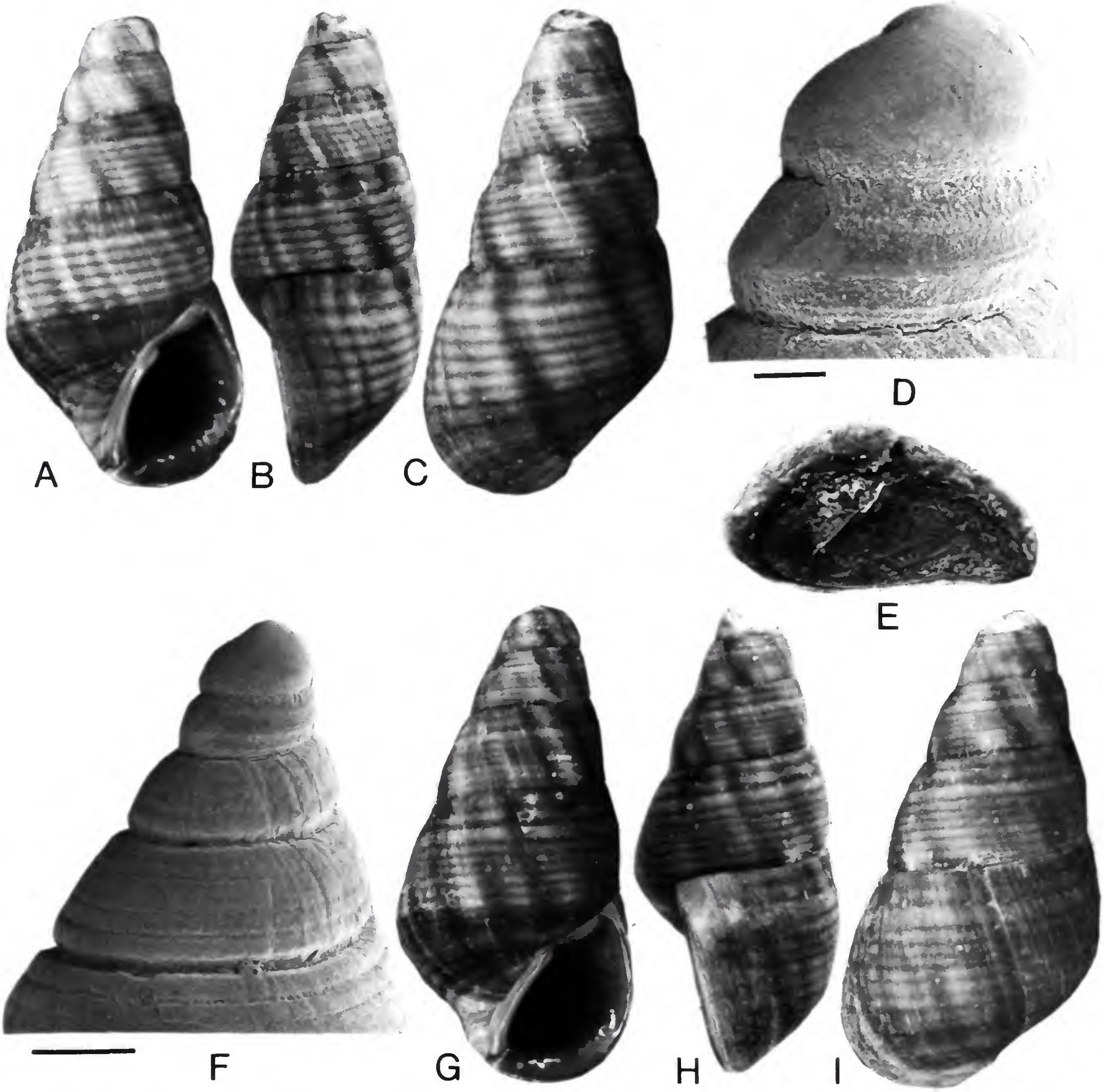


FIGURE 5.—*Fissilabia decollata*. A–F, Specimen from SW corner of Lizard Id, Queensland, Australia, USNM 795161: A–C, apertural, side, and dorsal views (length: 23.2 mm); D, SEM micrograph of protoconch showing short sinusigeral notch (bar: 50 μm); E, attachment side of operculum (length: 6.4 mm); F, SEM micrograph of early whorls showing sculpture of upper whorls (bar: 100 μm). G–I, Specimen from Mission Beach, Queensland, Australia, USNM 836888 (length: 23.2 mm).

show long columnar epithelial cells with dark staining nuclei and long cilia that overlie dense connective tissue (Figure 9D, sb). The duct leading into the spermatophore bursa (Figure 7, sb) also opens into a smaller seminal receptacle (Figures 7, sr; 9F, sr) located in the midproximal portion of the medial lamina (Figure 7, ml), adjacent to and beneath the spermatophore bursa. The seminal receptacle, densely packed with oriented sperm (Figure 9D, sr), is connected to the spermatophore bursa by a narrow channel (Figure 9G, con) and opens into the oviducal groove through a small

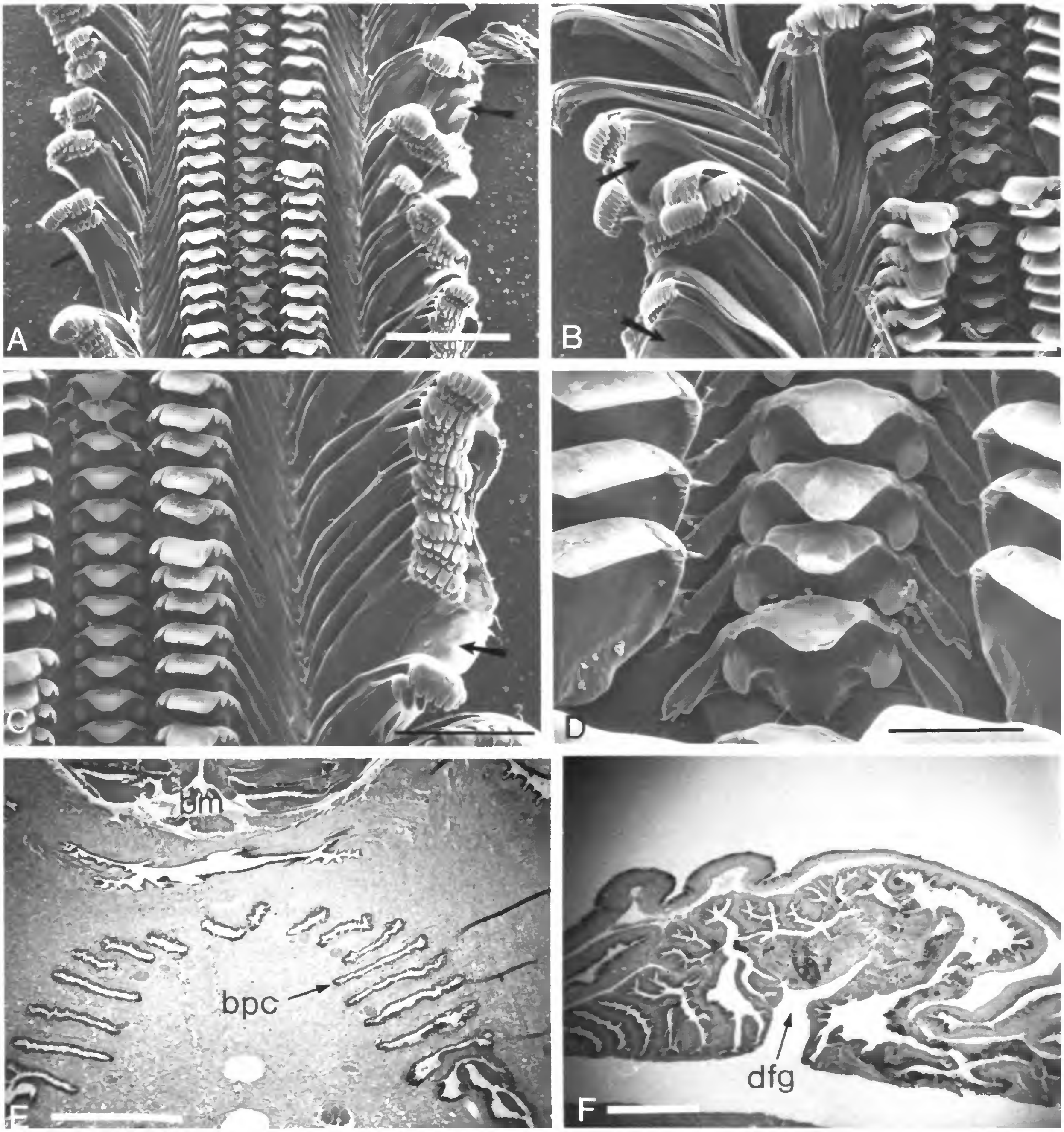


FIGURE 6.—*Fissilabia decollata* from Mission Beach, Queensland, Australia, USNM 836888: A, general view of radular ribbon with marginal teeth spread open (arrows indicate flanges on outer side of marginal teeth) (bar: 200 μm); B, half row of radula showing complete aspect of lateral teeth and flanges (arrows) on outer side of outer marginal tooth (bar: 100 μm); C, half row showing articulation between bases of marginal and lateral teeth (arrow indicates flange on outer side of marginal tooth) (bar: 100 μm); D, detail of rachidian tooth (bar: 50 μm); E, histological transverse section through anterior of head-foot viewed anteriorly, showing anterior compartments of brood pouch (bm = buccal mass; bpc = brood pouch compartments) (bar: 1 mm); F, transverse section through esophageal gland showing dorsal food groove (dfg) (bar: 1 mm).

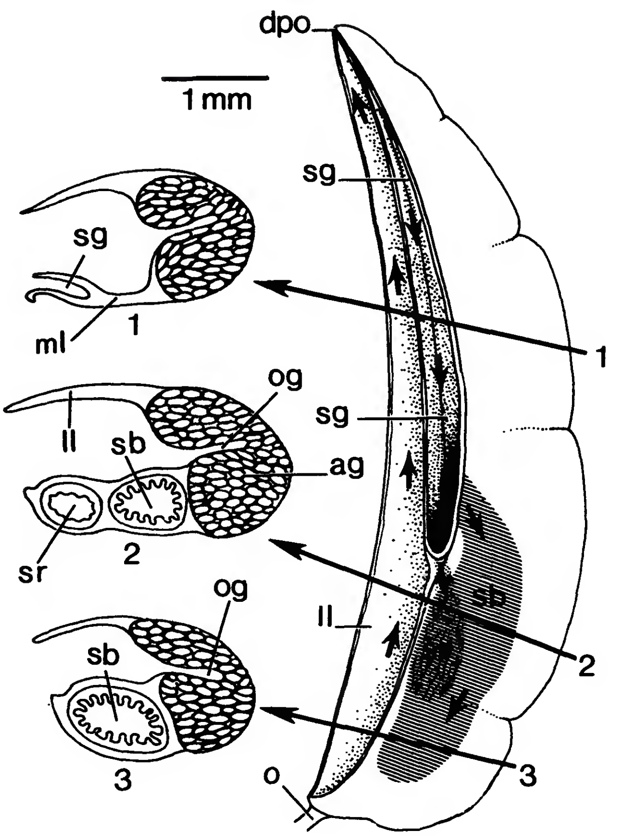


FIGURE 7.—Schematic of pallial oviduct of *Fissilabia decollata* (Abbreviations: ag = albumen gland; dpo = distal pallial oviduct; ll = lateral lamina; o = coelomic oviduct; og = oviducal groove; ml = medial lamina; sb = spermatophore bursa; sg = sperm gutter; sr = seminal receptacle; numbers adjacent to large arrows correspond to numbered cross-sections on right; short arrows indicate direction of ciliary currents).

aperture (Figure 9F, osr). The birth pore leads into a large brood pouch similar to that of *Planaxis*, but more confined to the anterior and right side of the head-foot (Figure 9H). This is a large kidney-shaped chamber divided anteriorly by thin lamellae into numerous, stacked, narrow chambers (Figure 9I). The chambers are blind in the anterior foot (Figure 6E, bpc) but are not completely separated from one another, interconnecting posteriorly where lamellae are lacking. There, a large chamber is formed that extends along the right side of the buccal mass. Variable numbers of embryos are found throughout the brood pouch (Table 3) including the narrow stacked chambers and in females pregnant with advanced embryos, the head-foot may become quite swollen and thin walled so that embryos may be seen through the epithelium of the anterior and sides of the foot. In the specimens examined, all phases of development were observed, including the veliger stage. Late veligers have small eye spots and embryos well past the veliger stage and ready to hatch have shells of 2.5–3 whorls (Figure 8). Several hundred embryos were found in each pregnant female examined. Although the exact time of release from the brood pouch was not observed, the large size of the embryos (0.23 mm) and the well-developed appearance of their shells, along with the smooth sculptured protoconch seen in shells of immature snails (Figure 8), indicate long brooding followed either by a brief lecithotrophic larval stage (Jablonski and Lutz, 1980:330–331) or by direct development.

NERVOUS SYSTEM.—The ganglia comprising the nerve ring are all large. Although the cerebral, pleural, and subesophageal ganglia are close together, the connectives to the pedal ganglia and the supraesophageal connective are very long. The RPG ratio is 0.67 (n = 5), indicating a relatively loose organization. The pedal ganglia have long anterior extensions with minor swellings that lie adjacent to the brood pouch (Figure 9I, exp).

Genus *Hinea* Gray, 1847

Hinea Gray, 1847:138.—H. and A. Adams, 1854(1):323.—Cossmann, 1906:197.—Thiele, 1929:204.—Wenz, 1940:722.—Rehder, 1980:49–50.

TYPE-SPECIES.—*Planaxis mollis* Sowerby, 1823 (= *Buccinum brasilianum* Lamarck, 1822), by original designation.

DIAGNOSIS.—Shell smooth, high spired, covered with brownish yellow periostracum. Whorls flattened, outer lip grooved internally, and thickened where it extends high onto previous whorl. Parietal area of columella thickened where it meets outer lip edge. Labial lip folded over anal canal. Rachidian tooth long, having large, single, serrated central cusp and basal plate with narrow lateral extensions and two tiny basal cusps. Pallial oviduct with proximal seminal receptacle. Brood pouch small, limited to right side of foot. Larvae lecithotrophic, demersal. Salivary glands uncoiled simple tubes. Mid-intertidal rocky habitat.

REMARKS.—The taxonomic history and status of the name *Hinea* Gray, 1847 has been thoroughly discussed by Rehder (1980:50) who, following H. and A. Adams (1854(1):323), regarded it as a subgenus of *Planaxis*. Hedley (1918:51), McMichael (1960:66), and Powell (1979:130), accorded it full generic status, and the results of this study support their view. *Hinea* is represented by two living species that have a peculiar South Pacific distribution in the "Easter-Kermadec Province" of Rehder (1980:51).

Hinea brasiliana (Lamarck, 1822)

Buccinum brasilianum Lamarck, 1822:272.

Planaxis mollis Sowerby, 1823:209, pl. 209: fig. 2.—Tryon, 1887:279, pl. 52: figs. 34, 35.

Planaxis brasilianus (Lamarck).—Sowerby, 1877, pl. 5: fig. 35.

Hinea brasiliana (Lamarck).—Hedley, 1904:186; 1918:51.—McMichael, 1960:66, fig. 128.

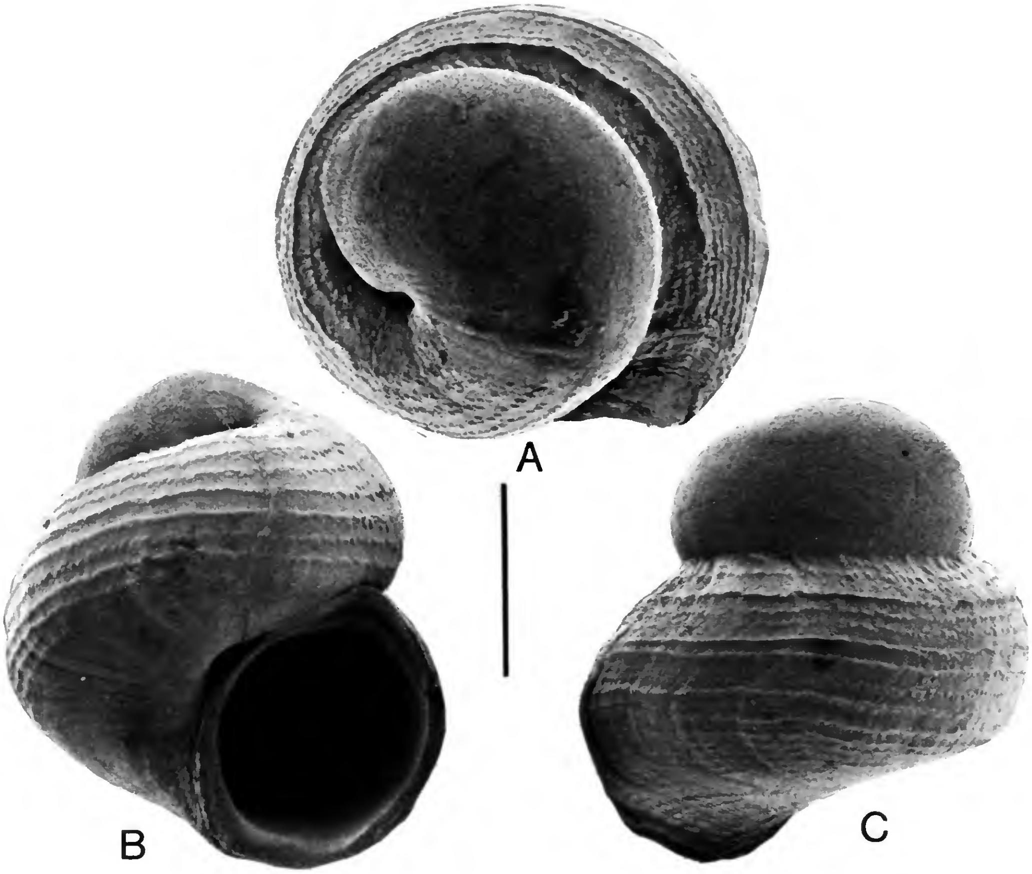


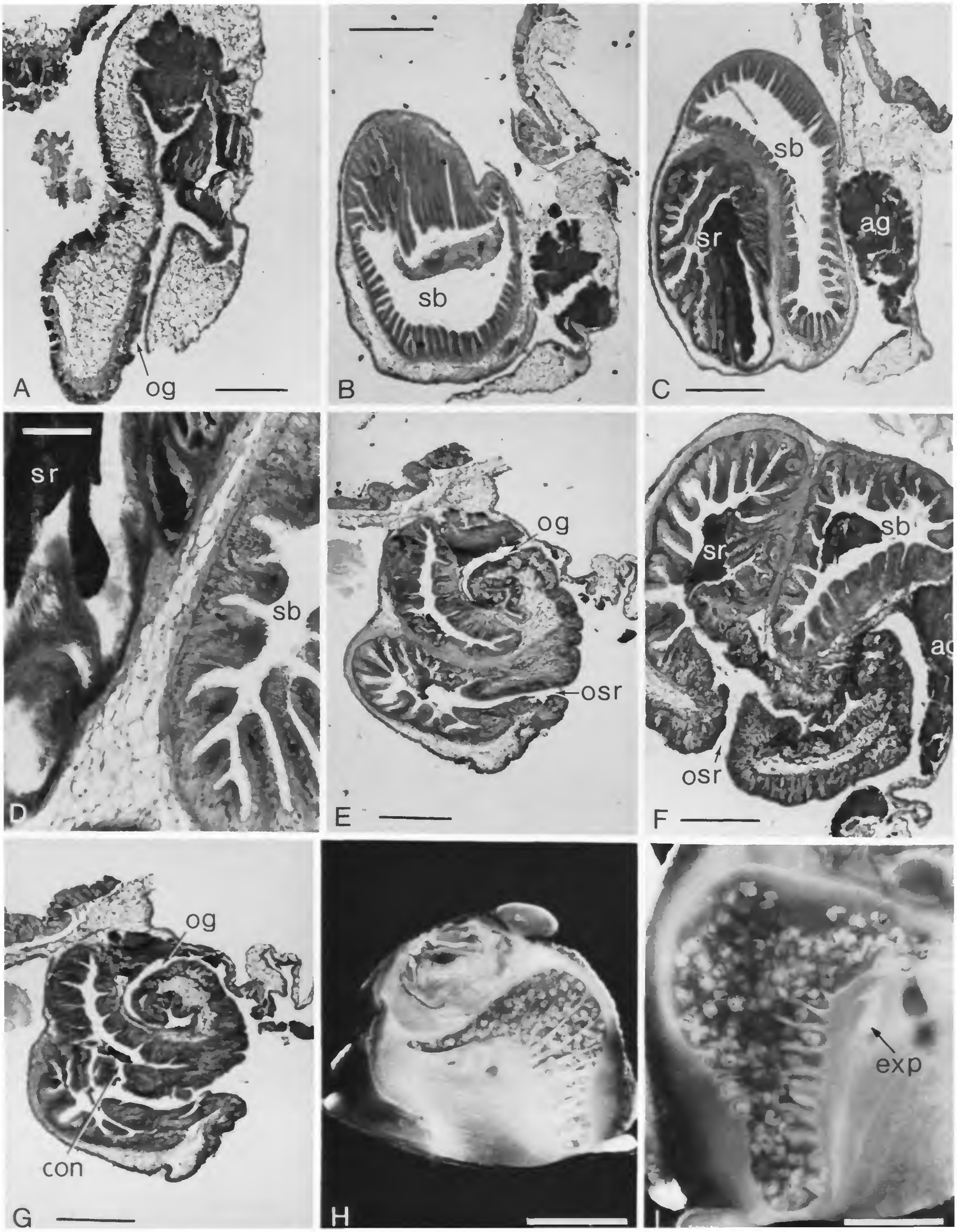
FIGURE 8.—Late embryonic shell of *Fissilabia decollata* removed from brood pouch prior to hatching (bar: 100 μm): A, apical, B, apertural, and C, dorsal views.

Planaxis (*Hinea*) *mollis* (Sowerby).—Thiele, 1929:204.—Wenz, 1940:722.
Planaxis (*Hinea*) *brasilianus* (Lamarck).—Cernohorsky, 1972:59, pl. 12: fig. 20.

Hinea brasiliana has a geographic distribution from South Australia to southern Queensland and also occurs at Lord Howe Island, Norfolk Island, the Kermadecs, and northern New Zealand. The species is gregarious and occurs in discrete populations among rocks and rubble in the midlittoral zone along exposed, rocky, high-energy coastlines. Populations usually live in somewhat protected areas not in direct contact with large waves. Individuals are found in clusters under rocks, in moist, dark places during low tide, but become very active and rapidly disperse when submerged by incoming tides. *Hinea brasiliana* lives well under laboratory conditions and needs little care. Coleman (1975:8) kept specimens alive for a year in a jar of unchanged seawater to which no food was added.

SHELL MORPHOLOGY (Figure 10).—The adult shell (Figure 10A–D,F) is thick, smooth, and turreted, reaching 20 mm in length, and is covered with a thick, brownish yellow periostracum. The whorls are slightly inflated and the suture adpressed. The protoconch comprises 3 whorls, each sculptured with a suprasutural spiral cord and subsutural axial plaits (Figure 10E). A distinct sinusigeral notch is present. The aperture is ovate, white inside, and has a short anterior canal. The outer lip is thick, smooth, and denticulate within. The thick upper edge of the outer lip extends onto the middle of the penultimate whorl folding over the anal canal. Operculum thin, having attachment scar a little less than half the operculum length.

EXTERNAL ANATOMY.—Animal is cream colored with a yellowish head. The head, snout, tentacles, and propodium are covered with a network of fine black lines. A large red buccal mass is seen through the snout. The eyes, located at the bases of the tentacle peduncular stalks, are black and smaller than in other planaxid taxa. The sole of the foot is white and has a propodial mucus gland that extends halfway around the foot. Although no sign of a ciliated groove for egg transport was found, a small brood pouch on the right side of the head-foot is highlighted by a raised, white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pigmented area. The mantle edge is smooth. Gonads are orange in females and brown in males.

MANTLE CAVITY ORGANS.—Within the mantle cavity, the osphradium (Figure 13C, os) separates from the ctenidium distally and runs into the inhalant siphon. In contrast to *Planaxis sulcatus*, the ctenidium is comprised of narrow, tall filaments. The hypobranchial gland, although wide and covering the mantle roof, is very thin and underdeveloped in comparison to other planaxid taxa and in section is seen to comprise numerous, granular, secretory, elongate cells (Figure 13B, hg).

ALIMENTARY TRACT (Figure 12A).—The body wall of the snout is thin and the buccal mass (Figure 12A, bm) of moderate size.

Radula (Figure 11). The radula is small, about one-sixth the shell length and has about 16 rows of teeth per mm. The semilunar rachidian tooth (Figure 11B) has long lateral extensions and is much wider than tall. It has a concave top with a single triangular cusp that is serrated along its cutting edge by 3–5 minute denticles. The basal plate of the rachidian has a shallow central extension and a pair of sharp cusps along its base. The dental formula of the rachidian tooth is $\frac{n-1-n}{1-1}$. The rhomboidal lateral tooth (Figure 11D) has a long lateral extension and a concave cutting edge with a large central pointed cusp, flanked by 2 or 3 proximal (inner) denticles and 3 or 4 distal (outer) denticles. The marginals (Figure 11C) are elongate with curved spatulate tips. The inner marginals have about 10 sharp denticles, while in the more spatulate outer marginals the denticles are not as clearly separated and the distal portion is smoother. The tips of the outer and inner marginals appear to be fused to each other.

The paired salivary glands (Figure 12A, sg) are long thin tubes having a proximal origin on the left side of the esophagus, far behind the nerve ring. The glands pass through the nerve ring and empty into the mid-dorsolateral part of the buccal mass. Unlike those of other planaxids, they are uncoiled.

The esophagus is wide, with a distinct dorsal food groove. The esophageal gland (Figure 12A, eg) arises as a series of lateral longitudinal folds in the sides of the esophagus.

The stomach has a small, bilobed posterior pad, but in other respects it is similar to that of *Planaxis sulcatus*.

REPRODUCTIVE SYSTEM.—The male pallial gonoduct is a simple open duct lined with transverse thin glandular folds at its basal attachment. The free portions of the medial lamina are composed of thick, white, glandular tissue proximally and medially, but become thin distally. These thickened portions of the gonoduct appear to delineate the prostate-spermatophore gland. In the female pallial oviduct, the lateral lamina (Figure 12B, ll) is closely fused to the mantle wall, while the medial lamina (Figure 12B, ml) has a long, thin-walled, highly ciliated, sperm gutter (Figure 12B, sg) along its distal edge, which runs into a moderate sized median-proximal spermatophore bursa (Figure 12B, sb). The seminal receptacle (Figure 12B, sr) is proximal to the spermatophore bursa and connected to it by a tiny opening. A ciliated tract leading from the oviduct to the brood pouch is present, but no groove is present as in *Planaxis*, *Supplanaxis*, and *Fissilabia* species. The brood pouch is lined with ciliated epithelium and arises as an invagination of the outer epithelium of the head-foot. It is located in the lower right portion of the head-foot. It is not large, about 1.5 mm in length (one-third the foot width), and lies only in the right side of the head-foot, adjacent to the extensions of the right pedal ganglion (Figure 13A, bp, exp). Thin, convoluted, heavily ciliated lamellae of connective tissue that stain darkly in section arise from the inner walls of the chamber (Figure 13D, E). These lamellae occur throughout the lumen, separate the larvae, and may provide some kind of fluid medium in the brood pouch. In section, the interior surface of the brood pouch consists of tall columnar epithelial cells bearing long cilia (Figure 13D). The latter cells are not present in the part of the brood pouch closest to the birth pore. A thick branch of the right pedal ganglion appears to innervate the brood pouch. Advanced embryos and newly hatched larvae range in size from 0.2–0.3 mm and are intermediate in size between typical planktotrophic larvae and lecithotrophic larvae. Moreover, the protoconch does not have a deep sinusigeral notch, suggesting that development is lecithotrophic, perhaps with a brief demersal stage.

NERVOUS SYSTEM (Figure 12A).—The subesophageal ganglion (Figure 12A, ueg) is joined to the left pleural ganglion (Figure 12A, lpg). The pedal ganglia have elongate extensions (Figure 12A, pg) with a series of smaller ganglia

FIGURE 9.—*Fissilabia decollata* from Mission Beach, Queensland, Australia, USNM 836888 (all sections looking toward anterior of pallial oviduct; bars (except D): 0.25 mm). A–G, Distal to proximal transverse sections of pallial oviduct: A, section through distal end of oviduct showing oviducal groove (og) (note dark glandular portion of bottom of groove); B, midsection through spermatophore bursa (sb) in medial lamina; C, section through more proximal part of oviduct where spermatophore bursa (sb) and seminal receptacle (sr) lie adjacent to each other—note albumen gland (ag) at base of oviducal groove; D, detail of oriented sperm in seminal receptacle (sr) and ciliated epithelium of longitudinally folded inner wall of spermatophore bursa (sb) (bar: 0.12 mm); E, section through proximal pallial oviduct showing opening of seminal receptacle (osr) to pallial cavity near opening to oviducal groove (og); F, detail of opening of seminal receptacle (sr) to pallial cavity adjacent to oviducal groove (ag = albumen gland; sb = spermatophore bursa); G, connection (con) between spermatophore bursa and seminal receptacle (og = oviducal groove); H, I, transverse cut through head-foot: H, viewed anteriorly, showing disposition of brood pouch and embryos to buccal mass (bar: 4 mm, note partitions subdividing brood pouch into thin lamellar compartments); I, viewed posteriorly and enlarged to show pedal nerve extensions (exp) adjacent to brood pouch (bar: 0.5 mm).

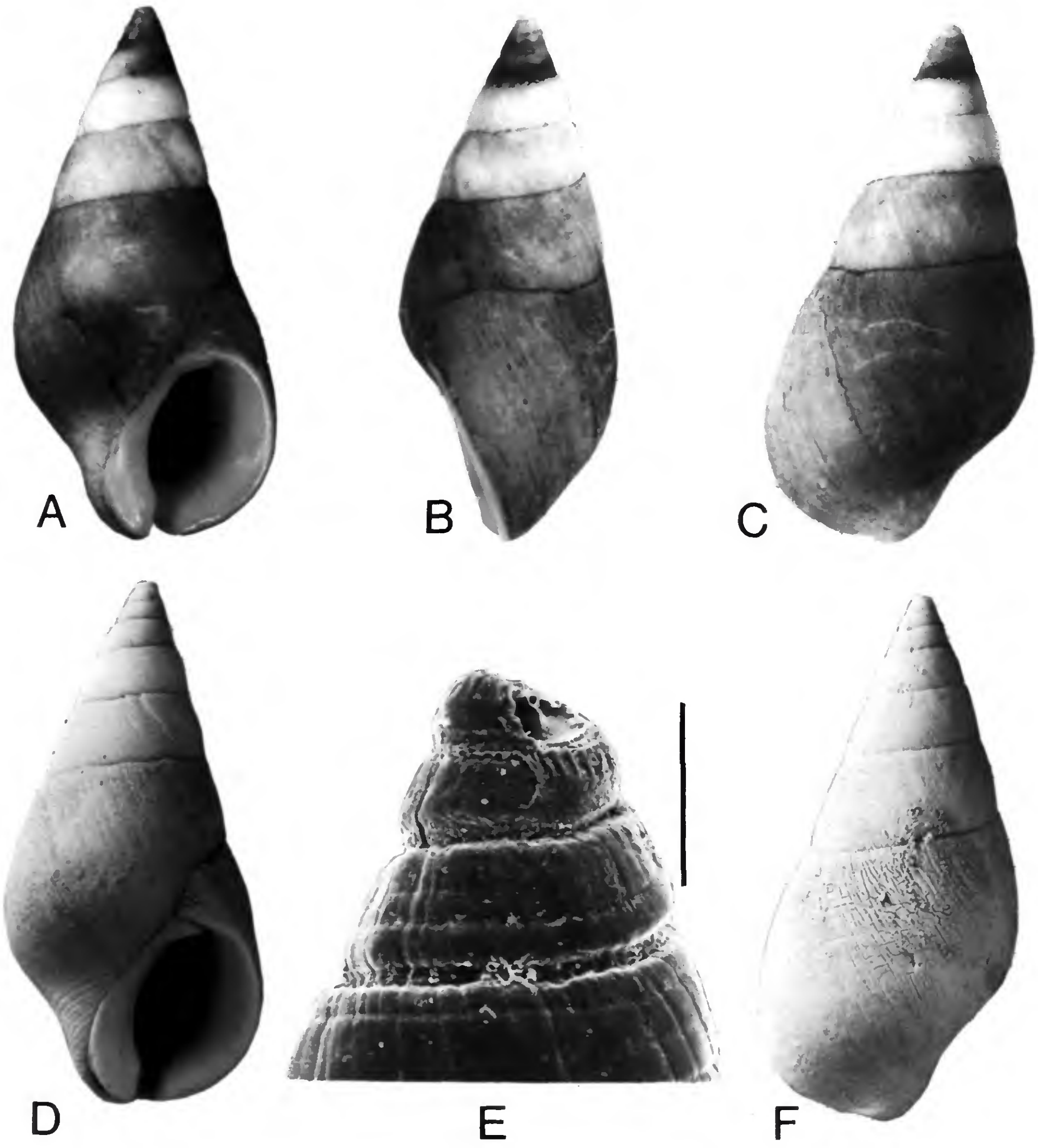

FIGURE 10.—*Hinea brasiliana*. A–D, F, Specimen from Shark Point, Colvelly, Sydney, NSW, Australia, USNM 836893 (length: 8.6 mm): A–C, apertural, side, and dorsal views showing shell morphology; D, F, shells whitened with ammonium chloride to show periostracum and sculptural details; E, SEM micrograph of specimen from Shell Harbor, NSW, Australia (AMS) showing details of early whorl sculpture (bar: 200 μm).

extending anteriorly and innervating the brood pouch (Figure 13A, exp). The RPG ratio is 0.65 (n = 4), indicating a looser concentration of ganglia than in other planaxid taxa.

Genus *Angiola* Dall, 1926

Angiola Dall, 1926:63.—Thiele, 1929:204.— Wenz, 1940:722.—Rehder, 1980:48.

TYPE-SPECIES.—*Planaxis periscelida* Dall, 1926, by original designation.

DIAGNOSIS.—Shell small, thick, mostly smooth, glossy, and colored white, with numerous spiral bands of brown, tan and black. Periostracum thin, hispid. Rachidian tooth wider than tall, with single serrated triangular cusp and basal plate with two cusps. Luminous organ near edge of middorsal mantle. Seminal receptacle in proximal part of

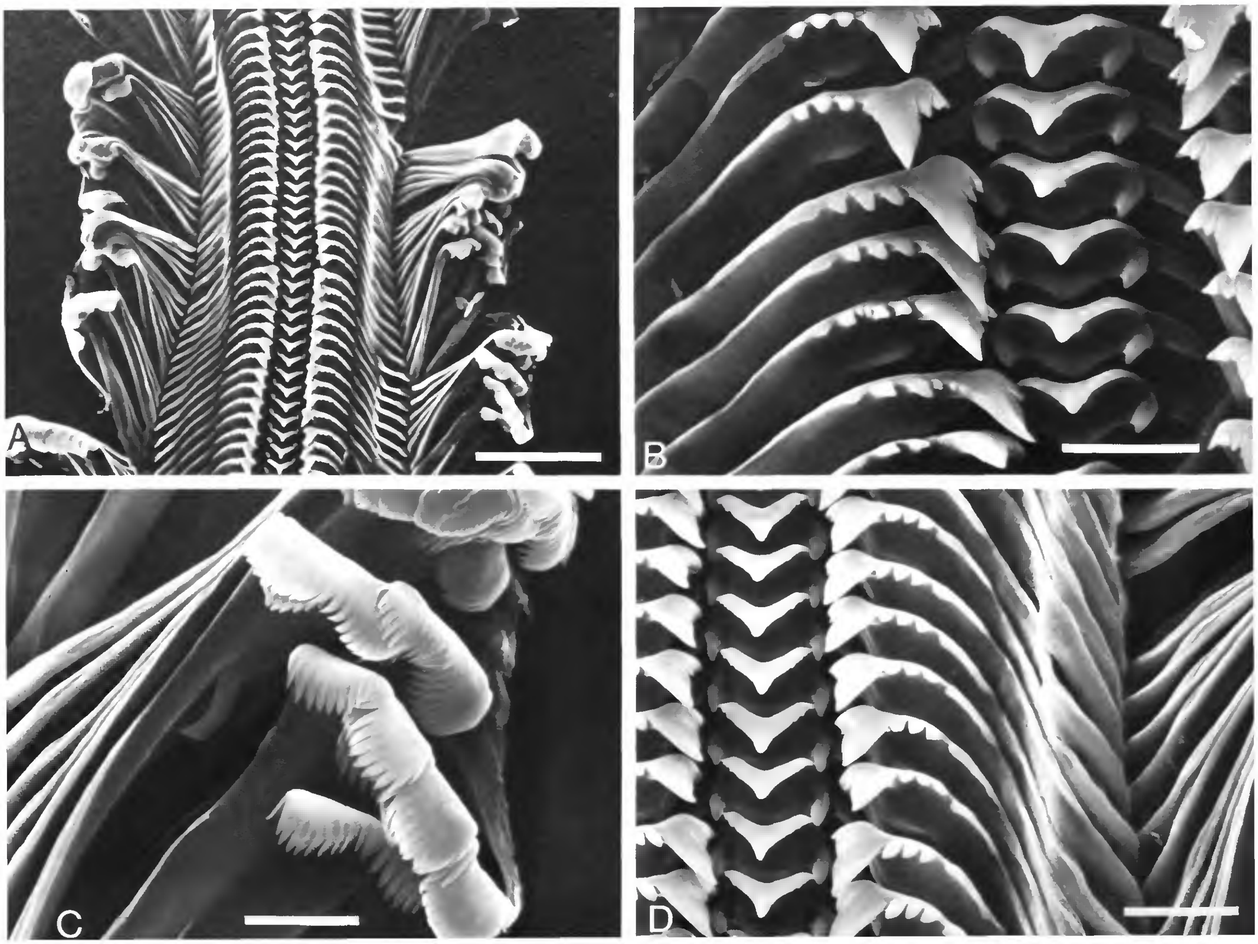

FIGURE 11.—Radula of *Hinea brasiliana* from Shark Point, Clovelly, Sydney, NSW, Australia, USNM 836893: A, general view of radular ribbon with marginal teeth folded back (bar: 100 μm); B, detail of rachidian and lateral teeth (bar: 20 μm); C, detail of marginal teeth showing cusp denticles (bar: 20 μm); D, lateral teeth showing lateral extensions and articulation with marginal teeth (bar: 20 μm).

outer lamina. Brood pouch small, in right side of head-foot. Larvae brooded to veliger stage, released, and undergo planktotrophic phase. Paired salivary glands coiled posterior to nerve ring. Esophageal gland moderately developed. Low intertidal rubble habitat.

REMARKS.—This genus contains small species with glossy shells and spiral color patterns, which occur throughout the Indo-Pacific and Caribbean provinces, usually under rocks at the low tide mark. The taxonomy of these small species is confusing and in need of revision. The common Indo-Pacific species *A. fasciata* (Pease, 1868) is frequently called *Planaxis lineolatus* Gould, 1851 (not *Planaxis lineolatus* Risso, 1826), and this is, in turn confused with the Caribbean species *A. lineata* (da Costa, 1778). Rehder (1980:48) has discussed the nomenclatural history of *Angiola* and referred to Thiele's (1929:204) and Wenz's (1940:722) uncertainty as to the placement of this taxon, to which they gave sectional and subgeneric rank, respectively, near *Supplanaxis*. *Supplanaxis*, however, is clearly unlike *Angiola* in anatomy and radula and, as Rehder (1980:48) noted, the shell of *Angiola* species bears little resemblance to that of *Supplanaxis nucleus* (Lamarck), the type-species of *Supplanaxis*. The type-species of *Angiola*, *A. periscelida* Dall, 1926 is, as Rehder (1980:48) suggested, probably synonymous with *A. zonata* (A. Adams, 1851) and *A. inepta* (Gould, 1861).

Angiola species are easily distinguished by their small size (reaching 12 mm in length) and spiral color patterns. The radula is very similar to those of *Holcostoma* and *Hinea* with the exception of the rachidian tooth, which is markedly concave in *Angiola* (Figure 25D-F). The small brood pouch occurs only on the right side of the head-foot and the

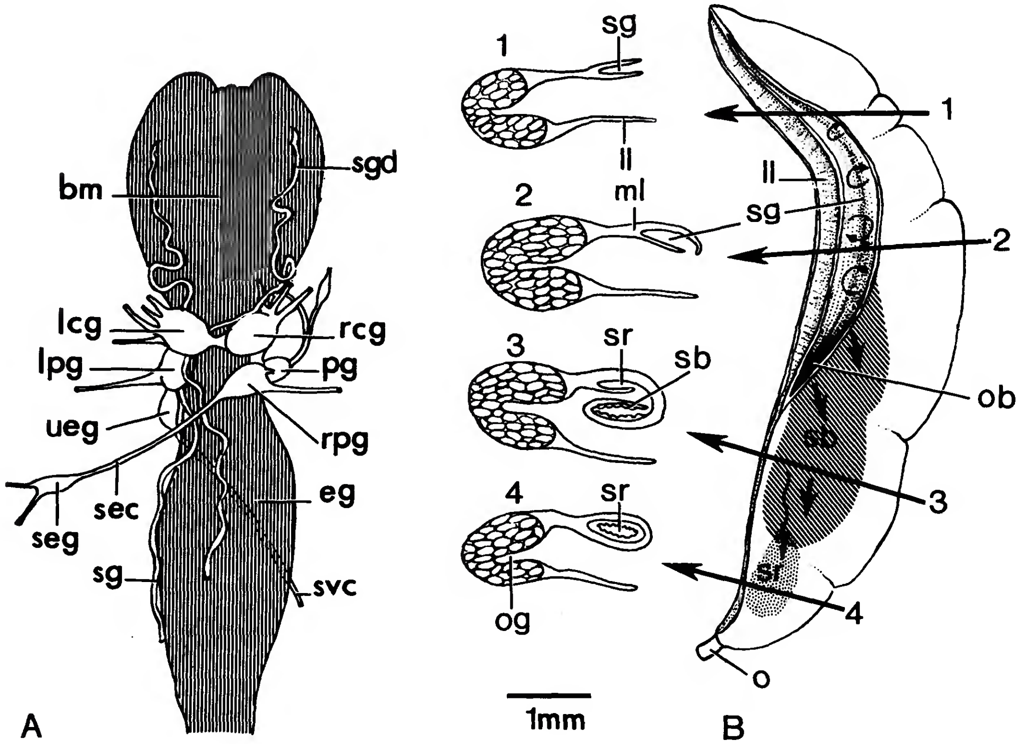

FIGURE 12.—*Hinea brasiliana:* A, schematic of anterior alimentary tract (bm = buccal mass; eg = esophageal gland; lcg = left cerebral ganglion; lpg = left pleural ganglion; pg = pedal ganglion; rcg = right cerebral ganglion; rpg = right pleural ganglion; sec = supraesophageal connective; seg = supraesophageal ganglion; sg = salivary gland; sgd = salivary gland duct; svc = subvisceral connective; ueg = subesophageal ganglion). B, schematic of pallial oviduct (numbers by arrows correspond to numbered cross-sections; ll = lateral lamina; o = coelomic oviduct; ob = opening to spermatophore bursa; og = oviducal groove; ml = medial lamina; sb = spermatophore bursa; sg = sperm gutter; sr = seminal receptacle).

presence of a luminous mantle organ is a unique distinguishing character. With the exceptions of the above characters, *Angiola* differs little from *Hinea* and is probably closely related to it. It could be regarded as a subgenus of *Hinea,* but the subtropical-temperate habitat of *Hinea* and the allopatry of the two taxon prompt me to give *Angiola* generic rank.

Angiola lineata (da Costa, 1778), new combination

Buccinum lineatum da Costa, 1778:130.
Planaxis lineatus (da Costa).—Abbott, 1974:102: fig. 974.

This small, colorful, gregarious species is common throughout the Caribbean and southeastern Florida. Large discrete populations live in the rubble of sheltered littoral habitats such as bays, lagoons, and other low energy environments. *Angiola lineata* is an active crawler while submerged, but when exposed by falling tides, it gathers into large aggregations under stones and in the interstices of gravel, where it can remain moist until the next high tide. In the laboratory, it is strongly photonegative and lives well in petri dishes with daily changes of water for as long as three months.

SHELL MORPHOLOGY (Figure 14).—The small, thick shell is up to 10 mm in length and comprises 8 or 9 moderately inflated whorls. It is glossy and smooth, with a creamy white base color broken by numerous brown to black spiral bands (Figure 14A,C,D). The shell matrix is more dense than that of *S. nucleus* and does not fracture into fine lamellae when broken. The tan protoconch (Figure 14F,H) comprises protoconch I (sensu Robertson, 1974:227) of 1.5 smooth whorls, and protoconch II of 2 whorls. It is sculptured with two strong median spiral cords, with prominent axial plications above and below the spiral elements. There is a strong sinusigeral notch. The early whorls have strong spiral cords that gradually become broader on succeeding whorls and begin to merge (Figure 14F). The last two whorls are smooth except for the shell base which has spiral incised lines (Figure 14B). The suture is deeply impressed and there is a

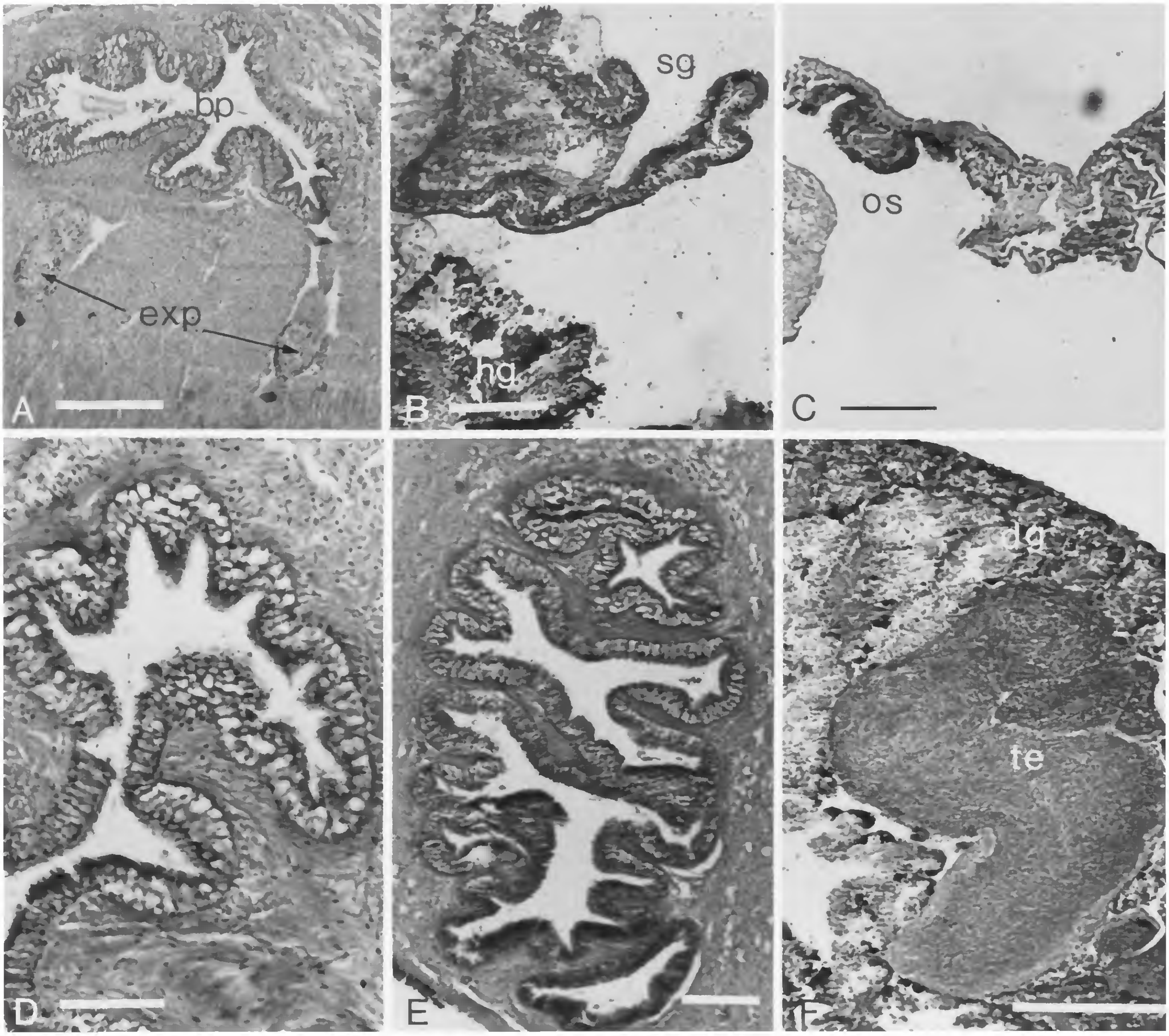

FIGURE 13.—Histological sections of *Hinea brasiliana* from Shark Point, Clovelly, Sydney, NSW, Australia, USNM 836893: A, section through brood pouch (bp) showing extensions of pedal ganglia (exp) ennervating brood pouch (bar: 0.5 mm); B, section through distal pallial oviduct showing sperm groove (sg) on outer lamina and hypobranchial gland (hg)(bar: 0.13 mm); C, section through pallial cavity showing osphradium (os) adjacent to ctenidium (bar: 0.13 mm); D, detail of ciliated epithelial lining of brood pouch (bar: 0.13 mm); E, brood pouch showing internal partitions (bar: 0.13 mm); F, section through upper coils of male showing digestive gland (dg) and testis filled with sperm (te)(bar: 0.5 mm).

narrow abapical ramp. The aperture is large, spanning a little less than one-half the shell length. The outer lip is thick, beveled on the inside and denticulate within. Shells of females are significantly larger than those of males ($T = 2.19$; $p = 0.02$, $n = 20$). A very thin hispid periostracum is sometimes seen in specimens from protected areas but is abraided from the shell in most cases. The thin, tan operculum is lenticular with a subterminal nucleus (Figure 14E).

EXTERNAL ANATOMY.—The animal has an overall light tan color. The dark brown head-foot is overlain by a network of iridescent blue with the large red buccal mass showing through the snout. The sole of the foot is white.

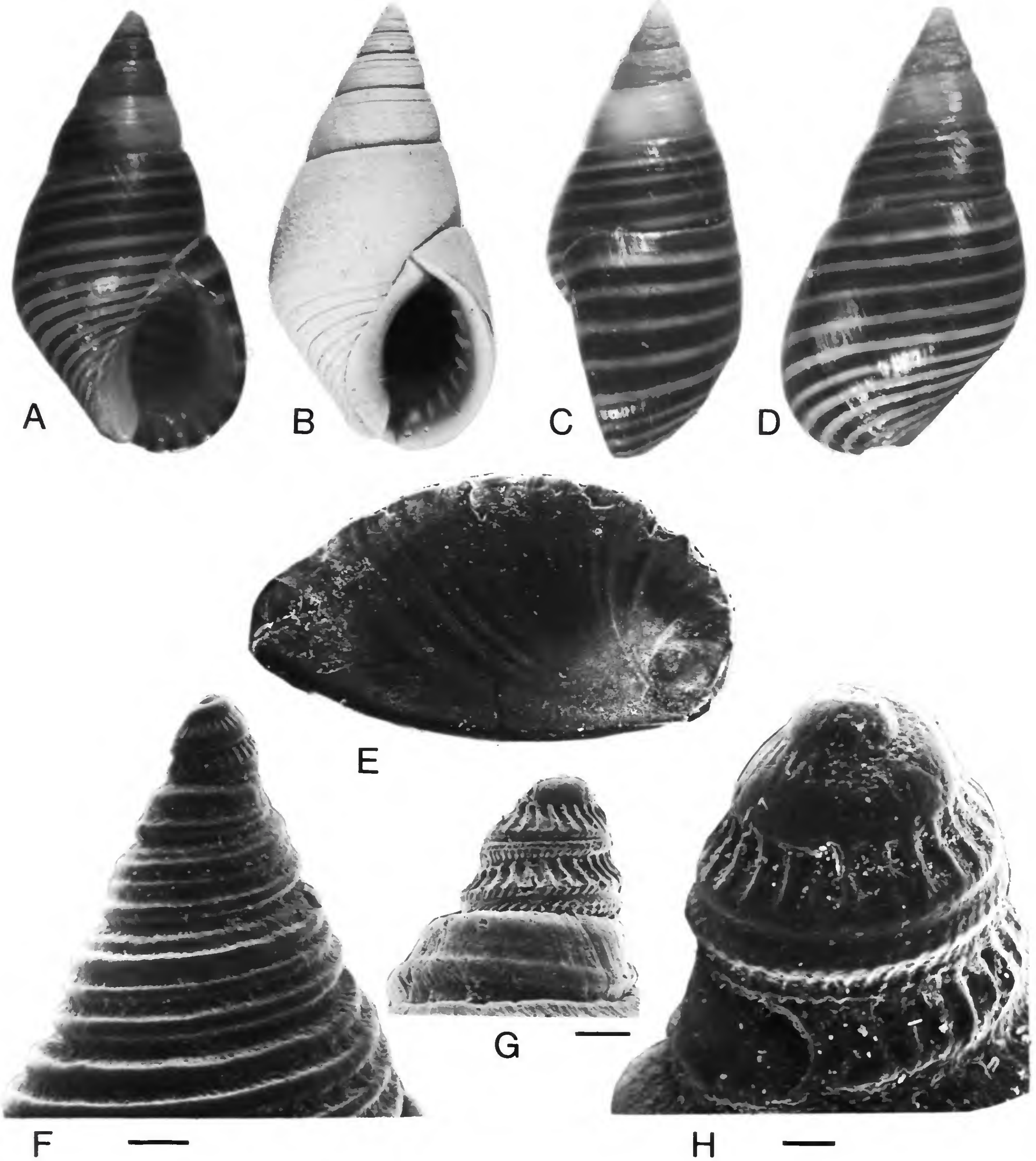

FIGURE 14.—Shell Morphology. A–D, *Angiola lineata* from inlet into Biscayne Bay at Baker's Haulover Beach, Florida, USNM 828838: A, B, apertural views (B whitened with ammonium chloride to show sculptural details), C, D, side and dorsal views; E, free side of operculum (length: 3.1 mm); F, SEM micrograph of upper whorls showing early sculpture and protoconch (bar: 100 μm); G, SEM micrograph of protoconch of *A. lineolata* from Funafuti, Ellice Islands (bar: 67 μm; AMS); H, SEM micrograph of protoconch of *A. lineata* from Baker's Haulover Beach, showing sculpture and deep sinusigeral notch (bar: 20 μm, USNM 828838).

The tentacles are tapering and very long in relation to the animal, spanning about one-third the shell length.

The mantle is large, covering much of the head-foot, thin, somewhat transparent, and its edge is smooth. The middorsal surface of the mantle edge contains a luminous organ, comprised of tissue located just below the epithelium, that emits blue-green light when stimulated. Haneda (1958:154–155) stated that the luminous organ is localized in a limited area of the mantle, is comprised of many folds of tissue that run parallel to each other, and that this structure is identical in all five species examined. The luminescence is intracellular. Histological sections showed that it is confined to small, closely packed cells beneath the thin epithelium (Haneda, 1958:155–156). The area of the mantle which Haneda's (1958, fig. 3) illustration indicates as containing the luminescent cells appears to be the hypobranchial gland. His figure of the longitudinal section through the mantle containing this luminescent organ (Haneda, 1958, fig. 5) also looks like typical hypobranchial gland tissue. The cells he identified as being bioluminescent appear to lie between the outer mantle epithelium and the hypobranchial gland. Although I observed bioluminescence in these snails, I was unable to detect any specific area of the mantle that could be considered the light organ. My histological studies of *Angiola lineata* do not show any specific tissue that I can identify as distinctive tissue supporting bioluminescent cells. Emission of the blue-green light is caused by strong stimulation, such as shaking or mechanical irritation of the body, which I observed in *Angiola fasciata* in Guam and *A. lineata* in Florida. The natural function of the bioluminescence was not ascertained, but it may serve as a recognition mechanism or have an antipredation function.

There is no ciliated groove leading to the brood pore, which is a simple raised area on the right side of the neck, conspicuous because of the unpigmented epithelium that surrounds it. A tiny central hole enters the brood pouch (Figure 16G,H, bp). In ripe snails, female gonads occupy about 3 coils and male gonads about 2.5 coils.

MANTLE CAVITY ORGANS.—The osphradium is typically planaxoid with a raised broad band of cilia on each side (Figure 16F, os). The distal osphradium deviates from the ctenidium and becomes narrow as it curves into the inhalant siphon. The long, narrow ctenidium is whitish in color, somewhat transparent, and comprised of about 30 long triangular filaments. The hypobranchial gland begins about 7 mm from the mantle edge and consists of thick, transverse ridges of papillate, glandular tissue that partially covers the rectum.

ALIMENTARY TRACT.—The mouth is a small slit at the edge of the flattened, ovoid snout tip. There is a moderately sized buccal mass (Figure 16H, bm).

Radula (Figure 16A–E). The radula is short, about one-fourth the shell length, and has about 14 rows of teeth. The rachidian tooth (Figure 16B,D) is wider than tall, having a basal plate with tapering lateral extensions that curve downward on each side. There is a central, triangular basal extension. The tip of the rachidian is concave and has a cutting edge with a wide, central, triangular cusp flanked by 3 or 4 tiny serrations on each side. The rachidian formula is $\frac{n-1-n}{1-1}$. The lateral tooth (Figure 16C) is subtriangular and has a long distal lateral extension and a cutting edge of one large, pointed cusp with two inner denticles and two outer denticles. The marginal teeth (Figure 16C,E) are long and tapering with curved, wide tips and have cutting edges of numerous fine, nearly fused, denticles. A description of the radula of *A. lineata* from Santa Marta, Colombia, was given by Bandel (1984:35–36, fig. 57).

The paired salivary glands originate behind the nerve ring and lie closely adpressed to it as coiled tubes. They pass through the nerve ring as single thin tubes and run over the dorsal surface of the central buccal mass where they enter the buccal cavity.

The esophagus widens immediately behind the nerve ring to form the esophageal gland, which is similar to that described in *Planaxis sulcatus*. In section, the epithelium of these folds stains deeply with hematoxylin (Figure 16F, eg).

The stomach has a moderately sized, narrow, bilobed pad that becomes single lobed as it approaches the short style sac.

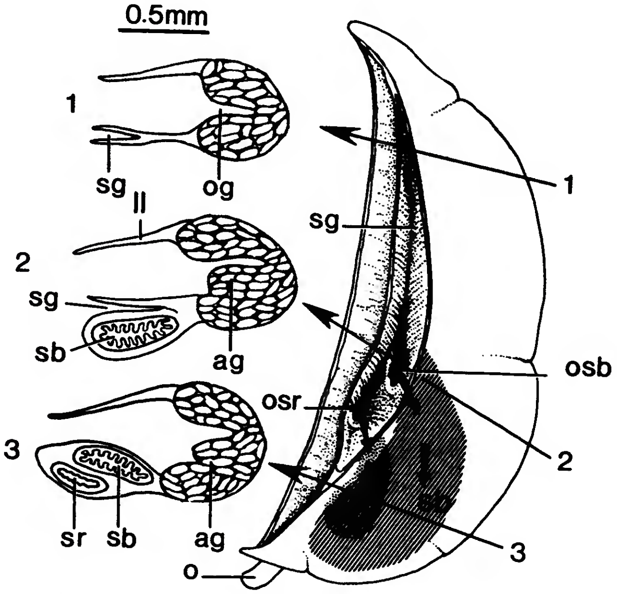

FIGURE 15.—Schematic of pallial oviduct of *Angiola lineata*. (Abbreviations: ag = albumen gland; ll = lateral lamina; o = coelomic oviduct; og = oviducal groove; osb = opening to spermatophore bursa; osr = opening to seminal receptacle; sb = spermatophore bursa; sg = sperm gutter; sr = seminal receptacle; numbers adjacent to large arrows correspond to numbered cross-sections on right; short arrows indicate direction of ciliary currents.)

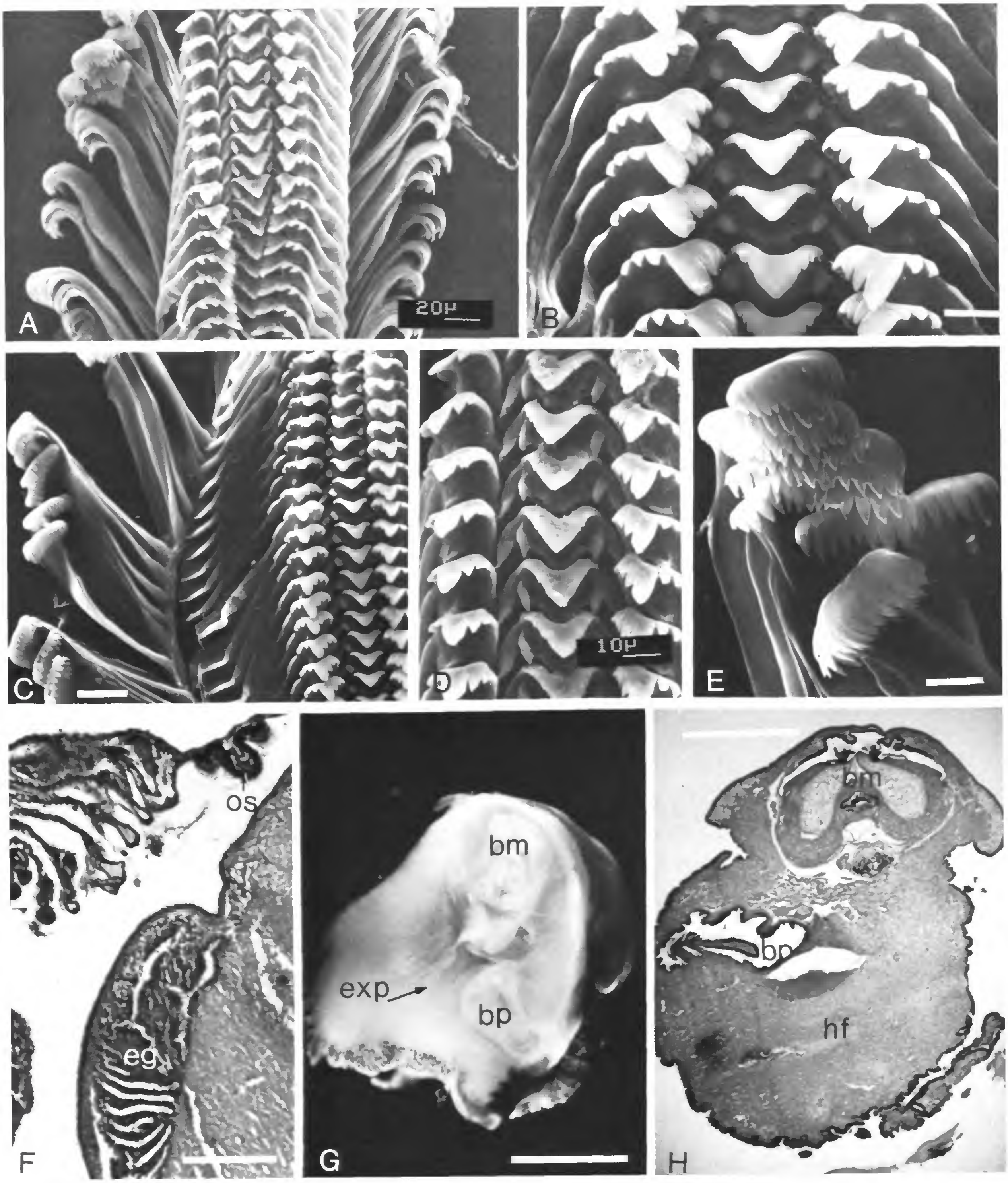

FIGURE 16.—A, C–E, Radula of *Angiola lineata* from Bakers Haulover Beach, Biscayne Bay, Florida, with marginal teeth folded back, USNM 828838: A, general view (bar: 20 μm); C, half row of radula (bar: 5 μm); D, detail of rachidian tooth (bar: 10 μm); E, detail of tips of marginal teeth showing cusp denticles (bar: 10 μm). B, Detail of rachidian and lateral teeth of *Angiola periselida* from Japan (bar: 14 μm; USNM). F–H, Transverse sections of *Angiola lineata:* F, through anterior mantle cavity showing esophageal gland (eg), and osphradium (os) adjacent to ctenidium (bar: 0.04 mm); G, transverse cut, anterior view, showing brood pouch (bp) on right side, extension of the left pedal ganglion (exp) and buccal mass (bm) (bar: 4 mm); H, histological transverse section through head-foot (hf), anterior view, showing buccal mass (bm) and brood pouch (bp)(bar: 4 mm).

REPRODUCTIVE SYSTEM.—The male pallial gonoduct is folded transversely interiorly and divided by a transverse internal ridge into a proximal and distal portion. The proximal portion is a whitish, glandular area that stains dark purple with methylene blue and probably serves as the prostate-spermatophore gland; the distal portion is less glandular and stains light blue. Euspermatozoa and paraspermatozoa are present in about equal numbers in the vas deferens. Euspermatozoa are about 12 µm long and have a short, well-defined acrosome and a relatively long midpiece. Paraspermatozoa are a little larger and have a broad triangular head and five flagellae.

The female pallial oviduct (Figure 15) is conspicuously swollen in ripe females. The oviducal groove (Figure 15, og) lies at the base of the two lamina that comprise the open duct and is demarcated by a transversely folded, thickened glandular area along its length. The proximal end of the pallial oviduct comprises the albumin gland (Figure 15, ag) and, in section, appears as a dark staining bulge along the base of the lateral lamina (Figure 15, ll). The median part of the pallial oviduct is much thicker and glandular, and is probably the capsule gland. The wall of the lateral lamina is thin and highly ciliated. The medial lamina has a short, wide, sperm collecting gutter (Figure 15, sg) along its distal edge that becomes a duct (Figure 15, osb) leading into a large median spermatophore bursa (Figure 15, sb). Adjacent to this duct is another highly ciliated opening (Figure 15, osr) in the outer median part of the medial lamina that leads into a median distal seminal receptacle (Figure 15, sr) located in the inner wall of the medial lamina, adjacent to the spermatophore bursa.

The small dumbbell-shaped brood pouch is located in the right side of the head-foot (Figure 16G, bp) and is lined with ciliated tissue. It is small in comparison to those of *Planaxis, Fissilabia,* and *Supplanaxis* species. Histological sections through the chamber show a deeply stained ciliated epithelium throughout. The brood pouch is subdivided into interconnected locula or chambers by thin invaginations of the internal wall (Figure 16H, bp), which greatly increase its surface area. Larvae were rarely observed in the brood pouch, but the few examined contained about 30 larvae that are brooded until the veliger stage. The brood pouch is adjacent to and innervated by large, swollen extensions of the pedal ganglia (Figure 16G, exp). This species was examined at various times throughout the year and no trace of a brood pouch on the left side of the foot was seen. It thus seems certain that it is limited to the right side.

NERVOUS SYSTEM.—*Angiola* species have a typical planaxoid nervous system and an RPG ratio of 0.50 (n = 5).

Genus *Supplanaxis* Thiele, 1929, new status

Subgenus *Supplanaxis* Thiele, 1929:203–204.—Wenz, 1940:721.—Abbott, 1974:102.

TYPE-SPECIES.—*Planaxis sulcatus* (Bruguière, 1789), by original designation.

DIAGNOSIS.—Shell conical, obese, black and smooth except for early whorls, part of body whorl and area beneath suture, where there are incised spiral grooves. Aperture wide with thick outer lip, grooved within, and thick columella with broad siphonal notch. Rachidian tooth broad, wider than long, with pair of small basal cusps close to outer edges. Cutting edge with large, rounded, central denticle flanked by smaller denticles. Seminal receptacle in proximal oviduct. Large dumbbell-shaped brood pouch in both sides of head-foot beneath buccal cavity and esophagus. Many small embryos incubated to veliger stage in brood pouch, followed by planktotrophic development. Large pair of coiled salivary glands pass through nerve ring. Midesophagus forms wide esophageal gland. Habitat low rocky, high energy, intertidal zone.

REMARKS.—This taxon was previously given subgeneric rank by Thiele (1929:204), Wenz (1940:721), and Abbott (1974:102). It is here accorded full generic status on the basis of the many significant morphological differences in shell, radula, soft anatomy, and embryonic development, which are described in more detail below. *Supplanaxis* species occur in the Caribbean, eastern Pacific, and Indo-Pacific biogeographic provinces.

Supplanaxis nucleus (Bruguière, 1789), new combination

Buccinum nucleus Bruguière, 1789:254–255.
Planaxis nucleus (Bruguière).—Deshayes, 1828:13.
Planaxis (Supplanaxis) nucleus (Lamarck) [sic].—Thiele, 1929:204.—Wenz, 1940:721.—Abbott, 1974:102.

This conspicuous black snail lives in high-energy, well-oxygenated, intertidal environments. Throughout the Caribbean, it is found among large boulders and rocks at the low to midtide marks, where it is an active crawler, moving rapidly over rocky surfaces during incoming tides. Its large, powerful foot tenaciously grips the substrate preventing dislodgement by waves. Exposed to air for several hours during low tides, it finds refuge in the interstices and crevices among the rocks, remaining inactive until the next incoming tide. Although it occurs in populations of moderate size, it is not a particularly gregarious animal. *Supplanaxis nucleus* has been kept alive in petri dishes with daily changes of water for as long as three months.

SHELL MORPHOLOGY (Figure 17).—The black adult shell (Figure 17G,I) of *Supplanaxis nucleus* reaches 20 mm in length, is moderately elongate with a wide body whorl, and has a general littorinid shape except for the shallow anterior canal. Although the shell is relatively smooth, it is sculptured with numerous wide, spiral furrows or grooves, particularly on the latter portion of the body whorl (Figure 17B,C). The shell is thick and strong, but not very dense; it fractures

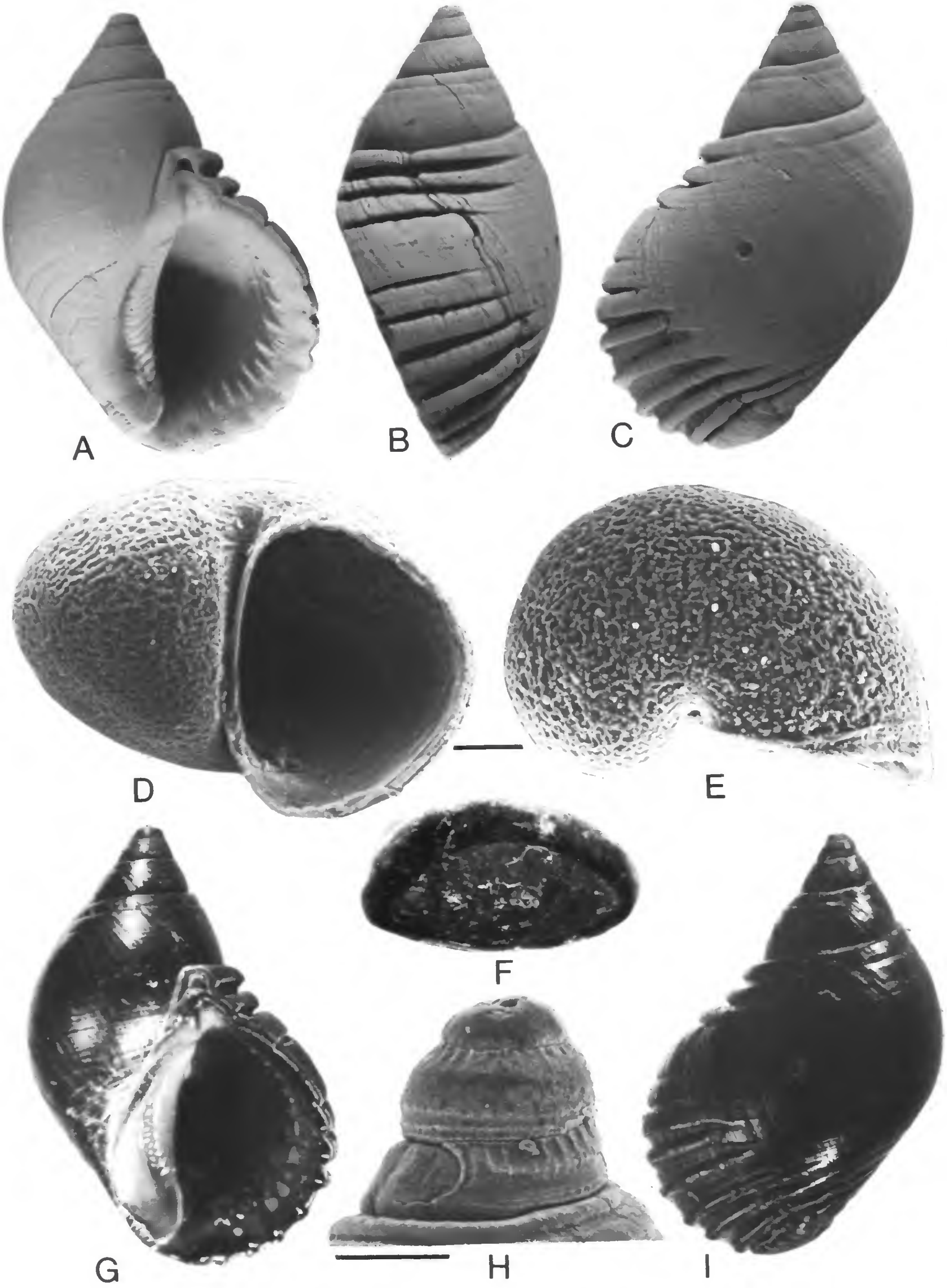

FIGURE 17.—***Supplanaxis nucleus:*** A–C, G, I, from S. Miami Beach, Florida, USNM 809780: A–C, apertural, side, and dorsal views of specimen whitened with ammonium chloride to enhance sculptural details (length: 16.4 mm); G, I, apertural and dorsal views of same specimen as in A–C, but in natural state to show color. D, E, embryonic shells (protoconch I) of newly hatched larva (bar: 10 μm); F, attached side of operculum (length: 6.7 mm); H, SEM micrograph of protoconch of specimen from Redonda, British West Indies, USNM 714035 (bar: 100 μm).

easily into many fine lamellae when placed under pressure. In cross-section, a broken piece of shell is composed of three orthogonal layers of cross lamellar aragonite and has a thin, black periostracum (Figure 18F). The protoconch (Figure 17H) comprises a little over 2.5 whorls. Protoconch I is unsculptured, but under SEM is seen to be covered with minute pustules (Figure 17D,E). Protoconch II is sculptured with two major spiral cords and a wide subsutural band of axial plications (Figure 17H). Small axial plications may also be present in a narrow presutural band. There is a deep sinusigeral notch. The operculum is relatively large, about three-fifths the animal's length, lenticular with a subterminal nucleus, and completely closes the aperture when the snail is retracted (Figure 17F).

EXTERNAL ANATOMY.—Removed from the shell, the animal has a large, wide head-foot and a small visceral mass of about 2.5 coils. The black head-foot (Figure 21B) is overlain by a microscopic, lattice-like network of iridescent blue, and the sole of the foot is white. The sole is thin at its edges and folded into numerous fine grooves. Its surface, as seen under SEM, is heavily ciliated. At the leading edge of the propodium there is a crescent-shaped anterior pedal gland that extends along both sides of the sole for well over half the sole length (Figure 21C, apg). The edge of the metapodium is scalloped where the large operculum is attached (Figure 21A). The thin mantle wall is thickened and somewhat scalloped along its black edge.

The large head has a moderately extensible snout with an expanded tip. The lips are flared and widespread forming an oral crescent. Deep grooves on the undersurface of the lips lead into the mouth, which is a longitudinal slit (Figure 21C, m). The cephalic tentacles are thick but long, each with a large black eye on a partially detached lobe of its latero-ventrally swollen base (Figure 21C, t, e).

Females have a deep, ciliated groove (Figure 21B) on the right side of the foot that emerges from the genital aperture and leads into a glandular, semicircular flap located on the neck of the head-foot (Figure 21B, bpo). Under the flap is a pit that leads into a large, subcephalic brood pouch (Figure 21D, bp), which is a very large, semicircular, central chamber connected to two smaller side chambers. When the brood pouch is filled with embryos, the sides of the foot become swollen (Figure 21B) and thin walled, and the brood pouch may be seen through the sole of the foot.

MANTLE CAVITY ORGANS.—The mantle cavity is wide but shallow. The distal osphradium separates from the ctenidium about 4 mm from the mantle edge and runs into the incurrent siphon. The hypobranchial gland, formed of tall glandular, granulated cells (Figure 22A, D, F, hg) tapers at both ends. The proximal end is thin and less glandular, while the distal end separates from the ctenidium and lies closer to the rectum, where it is highly glandular. The ctenidium is formed of long, narrow, triangular filaments and has a thick ridge at its base adjacent to the osphradium.

ALIMENTARY TRACT.—The robust buccal mass (Figure 19B, b) is attached with numerous thin muscle strands to the walls of a large, spaceous buccal cavity. A pair of large, strap-shaped buccal retractor muscles (Figure 19B, br) attaches to the posterior dorsal surface of the buccal mass, each muscle extending posteriorly to insert into the body wall behind the nerve ring. A smaller pair of lateral retractor muscles extends from the buccal cavity walls, adjacent to the nerve ring, and attaches to the back of the buccal mass and the anterior esophagus.

Radula (Figure 18A–E). The radula is long, about one-half the shell length, and has about 9 rows of teeth per millimeter. The pentagonal rachidian tooth (Figure 18D,E) has a broad basal plate with long basolateral extensions and a short median basal projection. There is a basal denticle on each side of the upper lateral part of the basal plate. The cutting edge of the rachidian is concave with a large squarish median cusp that extends nearly 90 degrees out from the tooth base, flanked on each side by three, sometimes four, smaller sharp denticles. The dental formula of the rachidian is $\frac{3\text{-}1\text{-}3}{1-1}$. The lateral tooth (Figure 18D) has a broad, high basal plate with a central supporting ridge, rounded margins, and a long lateral basal extension. The cutting edge is broad with a large, squarish, central cusp flanked by three inner sharp denticles and two sharp outer denticles. The elongate marginal teeth (Figure 18B,C) are narrowest at their bases, have curved paw-like tips that appear to be fused to each other at their broad median surfaces. The inner marginal tooth has a rake-like tip comprising about nine rounded denticles. The outer marginal is broader, concave at its tip, and has a cutting edge of numerous (about 30) small denticles. Another description of the radula of *S. nucleus* from Santa Marta, Colombia, has been given by Bandel (1984:34–35, fig. 59).

Long thread-like tubes of the paired salivary glands (Figure 19B, sg) are tightly coiled masses behind the nerve ring but pass through it as single thin tubes. Distally, these become tightly coiled again on each side of the buccal mass before emptying into it middorsally. They are closely associated with the transverse muscles immediately behind the nerve ring (Figure 19B, nr).

The midesophagus is thin walled and expands laterally, immediately posterior to the nerve ring. Cross-sections of the midesophagus show a well-defined dorsal food groove, located ventrally that becomes progressively wider and then narrows posteriorly. As in other planaxids, the inner walls of the midesophagus are longitudinally folded, forming a large esophageal gland (Figure 19B, eg) whose folds and glandular surface diminish toward the posterior esophagus (Figure 19B, pe).

The stomach has a long bilobed pad at its posterior end. The wide rectum is folded latitudinally.

EXCRETORY SYSTEM.—The kidney is tan and about 5

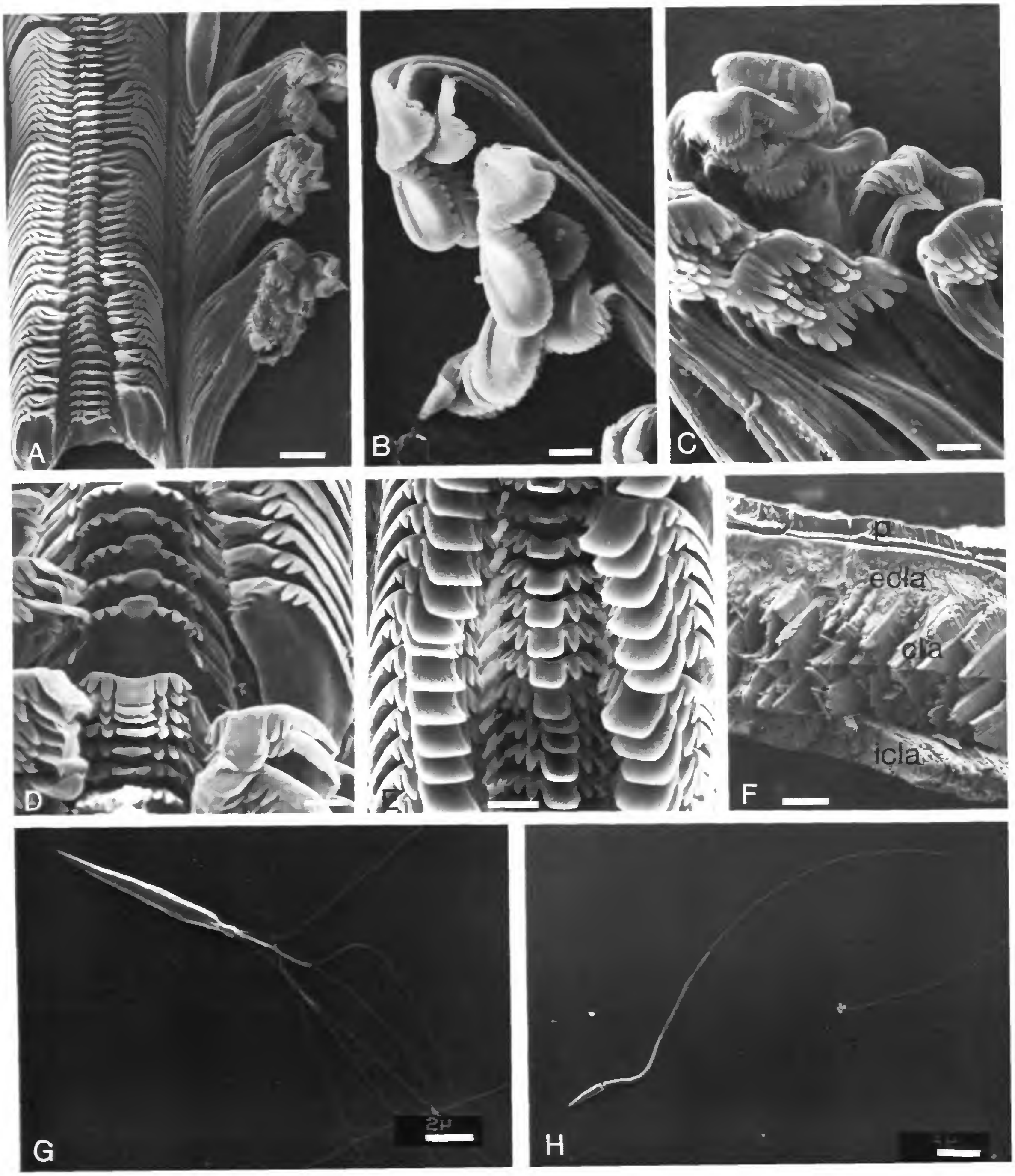

FIGURE 18.—SEM micrographs of *Supplanaxis nucleus* from S. Miami Beach, Florida, USNM 809780: A, general aspect of radular ribbon, marginal teeth spread back (bar: 20 μm); B, detail of tips of marginal teeth (bar: 14 μm); C, detail of tips of marginal teeth showing differences of denticles between inner and outer marginals (bar: 20 μm); D, rachidian and lateral teeth (bar: 20 μm); E, dentition of rachidian and lateral teeth (bar: 25 μm); F, fractured shell whorl showing crystalline ultrastructure of three orthogonal layers (p = periostracum, ecla = early cross lamellar aragonite, cla = cross lamellar aragonite, icla = inner cross lamellar aragonite) (bar: 100 μm); G, paraspermatozoan; H, euspermatozoan.

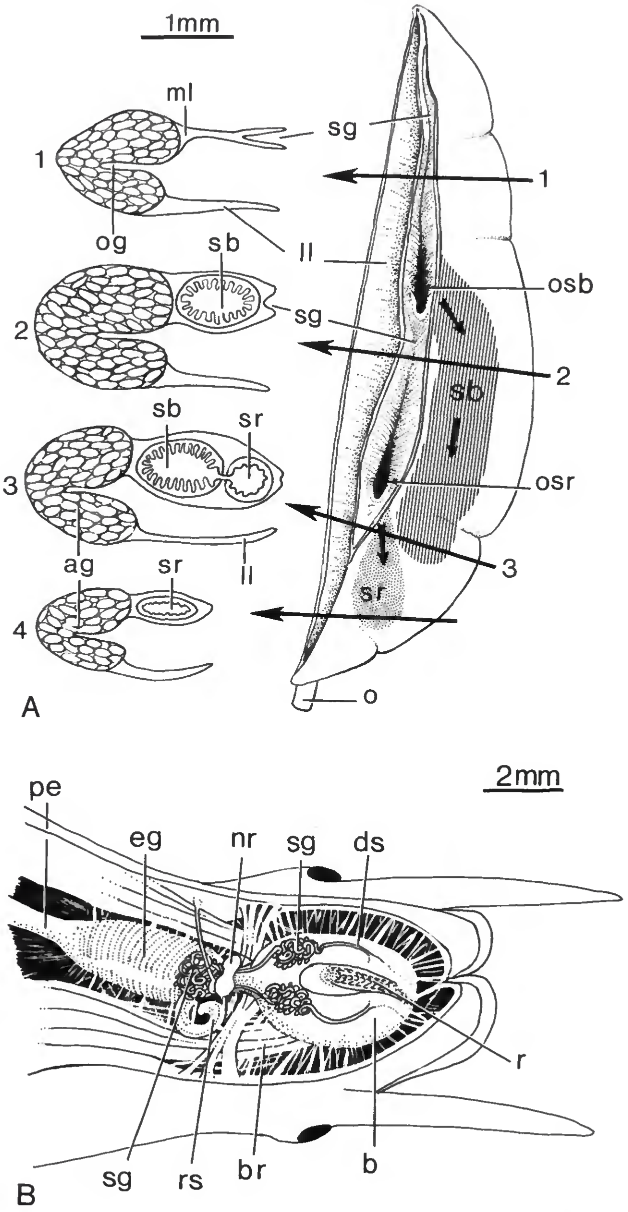

FIGURE 19.—*Supplanaxis nucleus:* A, schematic of pallial oviduct (ag = albumin gland; ll = lateral lamina; o = coelomic oviduct; og = oviducal groove; ml = medial lamina; osb = opening to spermatophore bursa; osr = opening to seminal receptacle; sb = spermatophore bursa; sg = sperm gutter; sr = seminal receptacle; numbered large arrows indicate cuts through oviduct corresponding to numbered cross-sections; small arrows indicate direction of ciliary currents; B, schematic of anterior alimentary tract (b = buccal mass; br = buccal retractor muscles; ds = duct of salivary gland; eg = esophageal gland; nr = nerve ring; pe = posterior esophagus; r = radula; rs = radula sac; sg = salivary gland).

mm long. It overlays the proximal portion of the pallial gonoduct and is adjacent to the pericardium, which slightly overlays the osphradium and ctenidium. There is a large kidney opening to the mantle cavity.

REPRODUCTIVE SYSTEM.—The medial lamina of the male pallial gonoduct is slightly folded and glandular at its proximal end. This is probably the prostate gland. The distal end of the gonoduct becomes deeper, slightly thicker, and glandular and curves to the left beyond the anus. This may be the site of spermatophore formation.

The pallial oviduct (Figure 19A) is a swollen tubular structure that tapers and curves to the left at its distal end, where the genital pore discharges into a ciliated groove leading into the brood pouch on the right side of the foot. The wall of the lateral lamina (Figure 19A, ll) is thin and attached to the mantle along its entire length. At the proximal end it thickens at its base to form the albumen gland (Figure 19E, ag), identified by a mass of transversely folded tissue. The distal end of the medial lamina has a relatively short, wide, heavily ciliated sperm gutter at its edge that runs via a distal opening (Figures 19A, osb; 22A, sg) into a deep spermatophore bursa located in the central portion of the swollen lamina (Figures 19A, sb; 22C,D, sb). The spermatophore bursa is large and lined with ciliated epithelium thrown into deep transverse folds (Figure 22D, sb) and contains the spermatophore, sperm mass, and the remains of other disintegrating spermatophores. The bursa is connected by a small passage to the seminal receptacle (Figures 19A, sr; 22F, con) that lies partly adjacent to it at the proximal end of the medial lamina. In critical point dried SEM sections, the seminal receptacle is seen to contain densely packed euspermatozoa oriented with their heads attached to the epithelial lining. Eggs from the oviduct enter the mantle cavity at its proximal end where they are fertilized by sperm from the seminal receptacle and then covered with albumen from the albumen gland (Figure 19A, ag). They move down the oviducal groove by ciliary action and encapsulation presumably is affected by the capsule gland, which is comprised of the thick, glandular, central base of the medial lamina. Egg capsules are then moved by cilia down the right side of the foot and into the brood pouch.

The brood pouch is a large, ciliated chamber located inside the central anterior part of the foot and neck region adjacent to the head (Figure 21D, bp). It is not an outgrowth of the cephalic hemocoel, but is formed by an ectodermal invagination of the brood pore in the neck of the snail, and is innervated by a pair of ganglia arising from extensions of the pedal ganglia. In brooding snails, it swells to great size and may be seen through the sole of the foot. In this state, the sides of the foot become swollen, distended, and very thin (Figure 21B), and the dumbbell-shaped chamber may occupy more than one-half the interior of the foot (Figure 20A–D). After the expulsion of larvae, the brood pouch

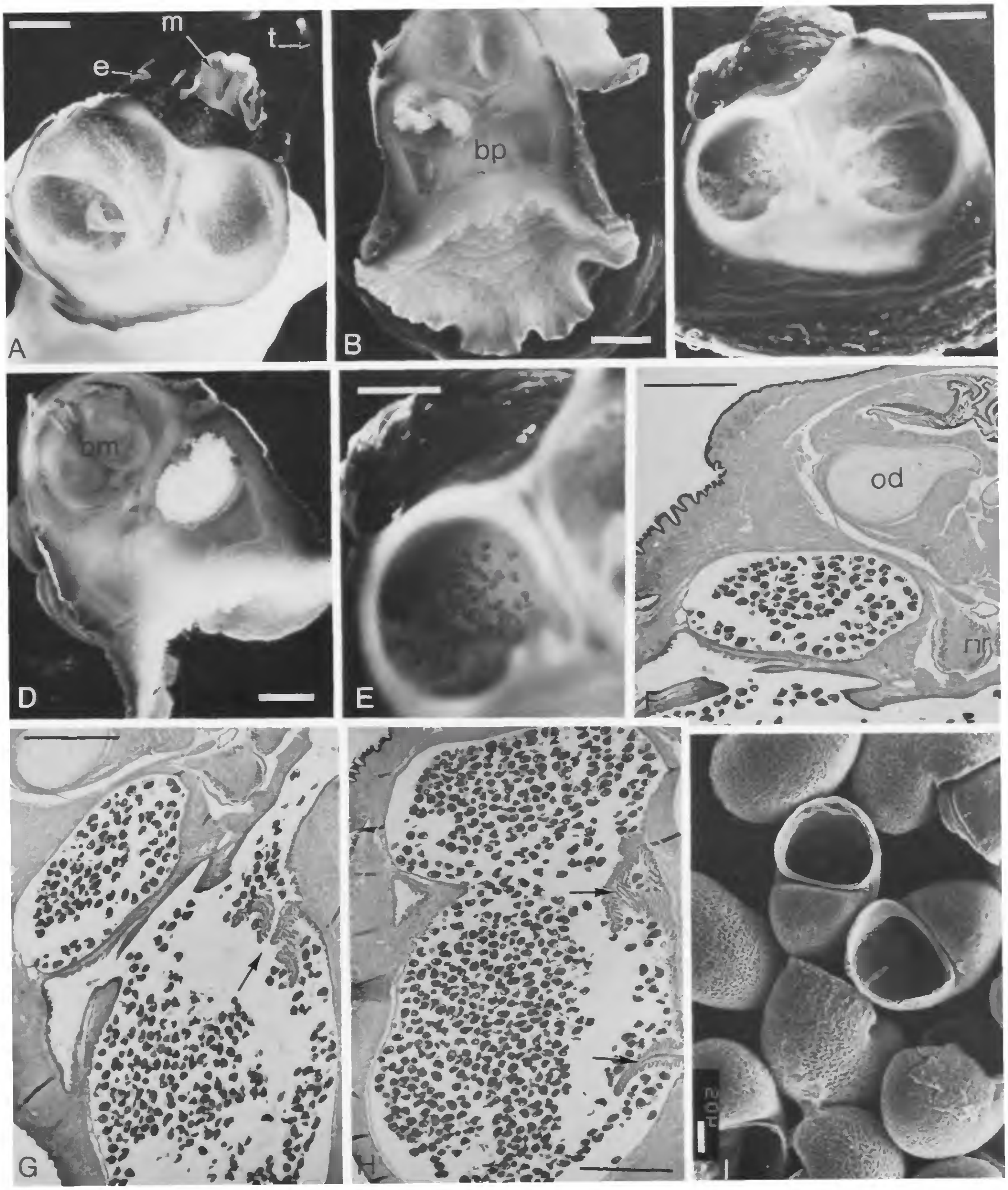

FIGURE 20.—Aspects of brood pouch of *Supplanaxis nucleus* from S. Miami Beach, Florida, USNM 809780: A, frontal section through foot just beneath head showing eye (e) and mouth (m) and revealing large dumbbell-shaped brood pouch containing embryos (t = tentacle) (bar: 1.5 mm); B, transverse section through head-foot, posterior view, showing brood pouch (bp) beneath buccal mass (bar: 2 mm); C, frontal section through foot (bar: 1.5 mm); D, transverse section through head-foot, anterior view, showing buccal mass (bm) and newly brooded larvae in one of brood pouch chambers (bar: 2 mm); E, detail of advanced embryos in brood pouch (bar: 1.1 mm); F, section through head-foot showing relationship of brood pouch to nerve ring (nr) and odontophore (od) of buccal mass (bar: 0.5 mm); G–H, sections through brood pouch showing large and small chambers filled with embryos and illustrating dark-staining membranous structures (arrows) of presumed secretory function (bars: 0.5 mm); I, larval shells removed from brood pouch (bar: 20 µm).

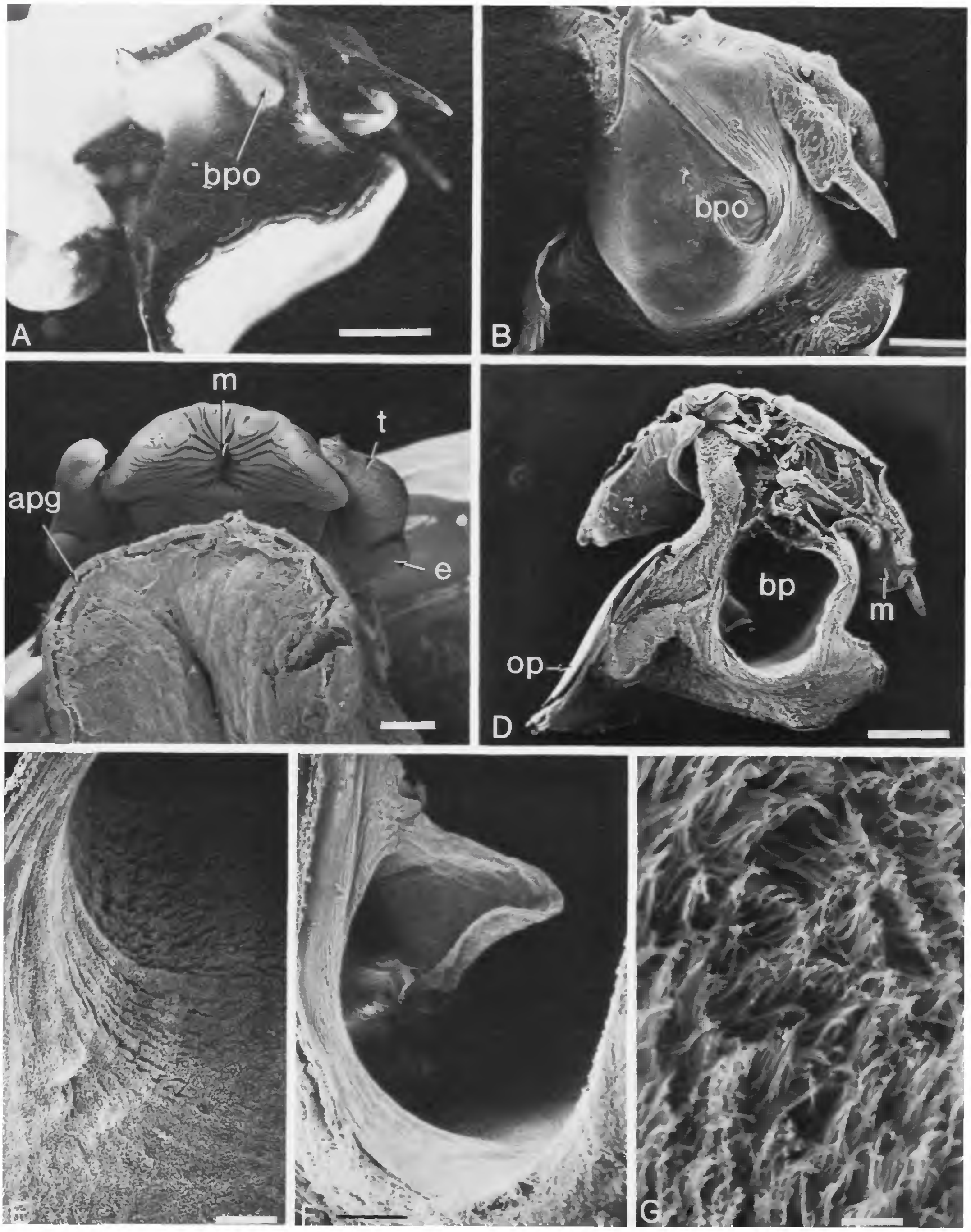

FIGURE 21.—SEM micrographs of brood pouch in critical point dried specimens of *Supplanaxis nucleus* from S. Miami Beach, Florida, USNM 809780: A, living, relaxed snail viewed from right showing location of brood pouch opening (bpo) or birth pore (bar: 1 mm); B, right view of critical point dried pregnant snail showing swollen condition of head-foot and brood pouch opening (bpo) (bar: 1 mm); C, snout, tentacles (t), eyes (e), and foot of critical point dried snail showing mouth (m) and anterior pedal gland (apg) (bar: 400 μm); D, midsaggital section through critical point dried snail showing head, mouth (m), operculum (op), and location of brood pouch (bp) (bar: 1 mm); E, enlargement of inner surface of brood pouch (bar: 100 μm); F, detail of membranous structure (bar: 250 μm); G, magnification of inner wall of brood pouch showing cilia (bar: 3 μm).

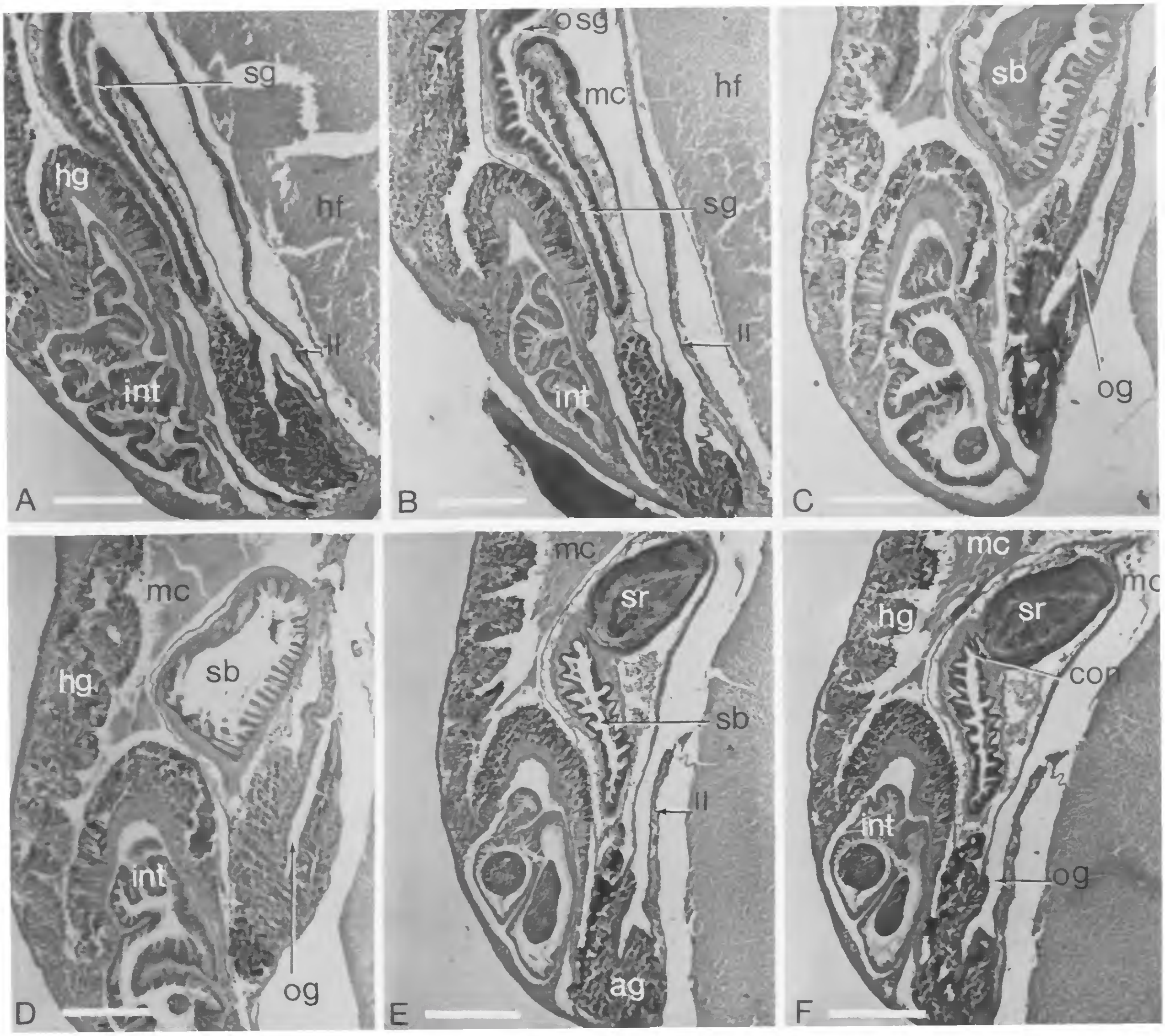

FIGURE 22.—Transverse histological sections through pallial oviduct of *Supplanaxis nucleus*, distal to proximal views: A, B, distal pallial oviduct showing sperm groove (sg) in medial lamina and its opening (osg) to pallial cavity (mc), close connection of lateral lamina (ll) to head-foot (hf), and relation of gonoduct to other pallial organs such as hypobranchial gland (hg) and intestine (int) (bars: 1 mm); C, D, midsections showing relationship of oviduct to mantle cavity (mc), hypobranchial gland (hg), and intestine int), oviducal groove (og) and spermatophore bursa (sb) containing disintegrating spermatophore in medial lamina, (bars: 1 mm and 0.5 mm); E, F, proximal section through pallial oviduct showing albumen gland (ag), spermatophore bursa (sb), seminal receptacle filled with sperm (sr), and the connection between them (con) (bars: 1 mm) (hg = hypobranchial gland; int = intestine; ll = lateral lamina; mc = mantle cavity; ag = albumin gland; sr = seminal receptacle).

contracts and becomes smaller. When filled, it comprises two large pockets (Figure 20C) on the left and right of the foot, joined centrally by a wide passage. Dorsal and posterior (proximal) to each of these pockets is a pair of smaller chambers (Figure 20F,G) connected to each other by a narrow passage. In the right passage there is an opening to the outside neck, the so called birth pore (Figure 21A,B, bpo). On each side of the wide passage joining the two major pouches is a thin T-shaped membrane which is highly convoluted (Figures 20G,H [arrow]; 21D, F). In section, the membrane stains darkly at its edges and is highly villous with a large surface area. These membranes may be secretory and provide the fluid medium in which the embryos are maintained and nourished. Under high magnification the entire inner surface of the brood pouch is seen to be roughly textured due to dense cilia (Figure 21E,G).

The brood pouch may contain great numbers of embryos, each enclosed in an individual capsule, 0.1 mm in diameter. Snails with filled brood pouches were opened at various stages. While still in early cleavage stages, embryos appear white (Figure 20B,D). There are no nurse eggs but several growth stages may be present. In the larger of the brood pouch compartments I have seen advanced embryos, ready to hatch (Figure 20C,E,G,H), while a white mass of newly deposited embryos was in another chamber adjacent to the birth pore; however, in most of the females I dissected, all embryos were of the same growth stage. Development continues within the egg capsules until the veliger stage is reached, at which point the embryos are expelled from the brood pouch through the birth pore in a milky, particulate exudate. In the lab, expelled embryos tend to stick together and pile up at the foot of the snail, but gradually dissociate as the egg capsule walls break down. Veligers emerge from their individual capsules in about 5 minutes and begin swimming vigorously in the water. In the lab, veligers were maintained alive in vessels of sea water for three days and attained 0.13 mm size before dying. Veligers have light tan shells with reddish brown apertures. Larval shells have about one whorl and are coarsely textured (Figure 20I). The number of larvae expelled by a female was determined by suspending the larvae in a known amount of seawater, taking an aliquot, and counting the larvae. A single large female snail was estimated to contain 12,886 embryos in its brood pouch. The number of larvae varies with the state of fecundity and size of the snail. It was not ascertained if all embryos are expelled in one birth event, although this appeared to be the case in laboratory snails. It would be difficult to witness a birth event in the field due to the high energy habitat. In the natural habitat, embryos are probably expelled during high tide and dispersed by wave and current action. The great numbers of veligers, small size, sparse yolk, and long velar cilia suggest a long planktonic life, but the amount of time spent in the plankton before settlement is unknown.

Two other studies on *Supplanaxis* have been made: brooding in *Supplanaxis nucleus* has been discussed by Thorson (1940:168) and Bandel (1976:258). To confirm his suggestion that the normal mode of reproduction in *Planaxis* species is brooding followed by a pelagic larval stage, Thorson (1940) examined some dried specimens of *S. nucleus* from St. Croix and found their brooding pouches densely packed with tiny shells of dried embryos ranging from 0.1–0.15 mm in diameter. Bandel (1976) cited a population of *Supplanaxis nucleus* from Santa Marta, Colombia, in which some females shed veligers at all seasons of the year. The veligers had a small, soft shell with one whorl.

NERVOUS SYSTEM.—The RPG ratio is 0.58 (n = 5), indicating a tightly concentrated system. As in other planaxids, the pedal ganglia give rise to long extensions that innervate the brood pouch.

Genus *Holcostoma* H. and A. Adams, 1853

Holcostoma H. and A. Adams, 1853(1):174.—Tryon, 1882:246.—Fischer, 1887:687.—Cossmann, 1906:196–197.—Thiele, 1929:204.—Wenz, 1940:722, fig. 2089.

TYPE-SPECIES.—*Planaxis piliger* Philippi, 1848, by monotypy.

DIAGNOSIS.—Shell thin, short, ovate, spire spirally channeled. Outer lip expanded, aperture ovate about three-fourths the shell length. Outer lip free at posterior end and drawn out onto the body whorl as a narrow, extended channel. Shell color light brown, with broad purple bands. Periostracum light brown-yellow, hispid, thin. Radula very small, rachidian tooth crescent-shaped with single large serrated cusp and two small denticles on basal plate.

REMARKS.—This monotypic genus is little known and appears to be endemic to Mauritius, Reunion, and adjacent Indian Ocean Islands. The radula resembles that of *Angiola* but does not have the concavity on the top of the rachidian as does that taxon (Figure 25D,E). The radula is also similar to those of *Hinea* species from which it differs in having a wider basal plate (Figure 25E,F).

Holcostoma piliger (Philippi, 1848), new combination

Planaxis piliger Philippi, 1848:164.—Cossmann, 1906:196.
Planaxis (Holcostoma) piliger (Philippi).—Sowerby, 1877, pl. 5: fig. 38.—Thiele, 1929:204.—Wenz, 1940:722.

SHELL MORPHOLOGY (Figure 23).—Shell small, thin, ovoid with low spire, protruding nipple-like from an extremely large body whorl. Shell sculptured with deep spiral grooves on early whorls, weak, spiral grooves on penultimate and body whorls, with grooves becoming deeply channeled at siphonal constriction. Suture deeply impressed. Aperture large, about three-fourths of the shell length. Pseudoumbilicus present in mature specimens. Columella concave, broad at anterior siphon, with deep narrow anal canal. Outer lip smooth, expanded, slightly denticulate within and sinuous at upper end, when seen in side view. Anterior siphonal canal short, broad, distinct, with slight siphonal fasciole. Periostracum thin, brownish, markedly hispid, with individual hairs in regularly spaced spiral pattern. Shell color brownish with lighter yellow-white broad spiral bands, especially on body whorl. The lenticular oper-

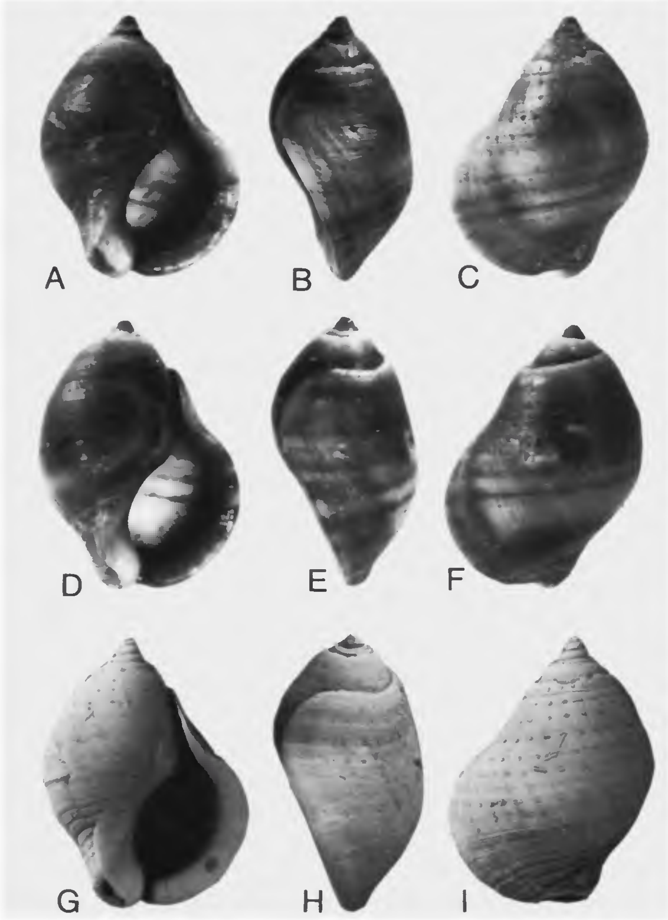

FIGURE 23.—Apertural, side, and dorsal views of shells of *Holcostoma piliger* (Philippi, 1848), all from Reunion, USNM 130064: A–C, 7.5 mm length; D–F, 8.6 mm length; G–I, shells whitened with ammonium chloride to show periostracum and sculptural details, 7.5 mm length.

culum (Figure 24D) has a subterminal nucleus, is multispiral and nearly transparent.

ANATOMY.—Based on head-foot of one dried specimen reconstituted with trisodium-phosphate. The head has a narrow snout and small buccal mass. The long cephalic tentacles are tapered, each bearing a small black eye at the outer base. The edge of the mantle is slightly fringed but nearly smooth. The ctenidium is black and comprised of long triangular filaments.

Radula (Figure 24A–C). The radula is very small, about one-fifth the shell length. Rachidian tooth (Figure 24B) crescent-shaped, longer than wide, with a concave cutting edge comprising a single large serrated cusp. Rachidian formula $\frac{n-1-n}{1-1}$. Basal plate with short central basal projection, long, narrow, lateral projections and two lateral basal denticles. Lateral tooth (Figure 24A,B) rectangular with a long narrow lateral projection that is attached to the basal membrane. Cutting edge with long, central cusp flanked on each side with 2 or 3 smaller denticles. Outer side of tooth with slight flange. Basal plate with central supporting column that extends slightly at the base. Marginal teeth (Figure 24C) with long basal shafts, curved and wider at tips and with many fine serrations. Shafts of marginals appear to be fused midway beneath the curled tips.

REMARKS.—Only a few specimens of this species have been examined, several of which had dried animals from which radulae were extracted and the incomplete anatomical features listed above derived. The tiny radula indicates a grazing habitat on soft material.

Discussion

FUNCTIONAL ANATOMY

The Planaxidae is a relatively small but distinct family in the Cerithiacea Fleming, 1822, having the generalized anatomical groundplan of that superfamily. A number of erroneous statements about planaxid anatomy have persisted in the literature. The Planaxidae was compared with and incorrectly considered close to the Littorinidae by H. and A. Adams (1854(1, 11):321). They noted that planaxids were distinct from littorinids only by the presence of a siphonal canal and anterior columellar notch and erroneously stated that the foot was "furnished with tentacular filaments." The Planaxidae differs from the Littorinidae by having open pallial gonoducts, aphallate males, and cephalic incubatory pouches. In regard to H. and A. Adams' (1854(1, 11):321) remark about pedal tentacles, none of the taxa I dissected had pedal tentacular filaments, although there is a metapodial scalloped edge adjacent to the operculum. Risbec (1935:387) also referred *Planaxis* to the Littorinidae. Aside from pointing out that the long extensions of the pedal ganglia were also found in littorinids, Risbec offered no supporting evidence for this claim.

Kay (1979:112), following the misleading opinion of Morrison (1954:358), stated that reproduction in planaxids is parthenogenetic (no males). Boss (1982:992) repeated the error and added that *Planaxis* lacks a true pallial gonoduct, which is certainly not the case, as all planaxid species examined have equal sex ratios and well-defined pallial gonoducts.

EXTERNAL ANATOMY

When crawling, the long cephalic tentacles of all examined planaxid snails wave back and forth, frequently touching the substrate. The ventral-lateral position of the eyes on the tentacle bases enables the snails to see the substrate at all times while the large, extended mouth at the snout tip is in constant touch with the substrate and is moved left

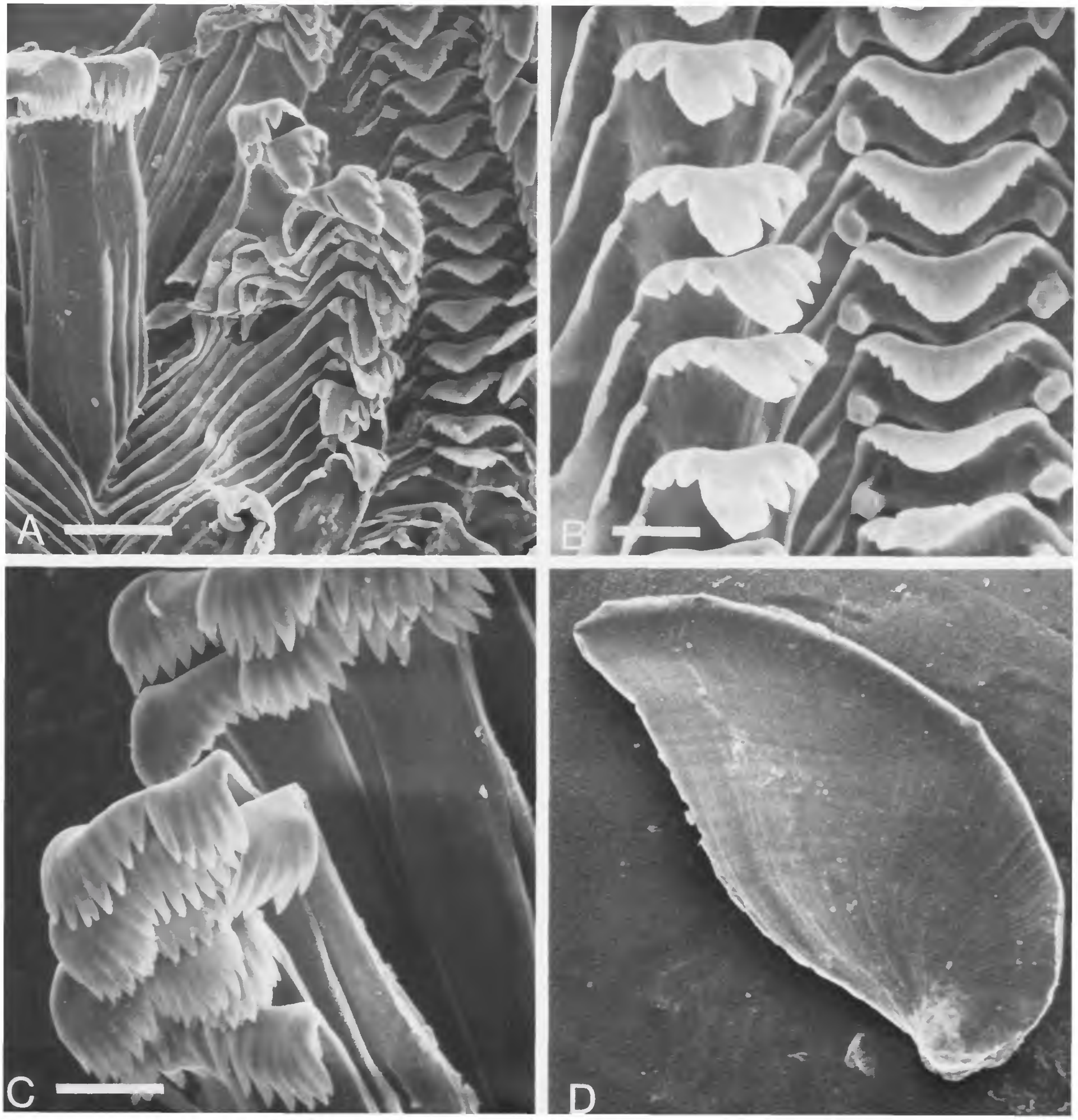

FIGURE 24.—A–C, Radula of *Holcostoma piliger* from Reunion, NMHNP: A, general view of half of radular ribbon (bar: 25 μm); B, detail of rachidian and lateral teeth (bar: 12 μm); C, detail of tips of marginal teeth (bar: 15 μm); D, operculum of *Holocostoma piliger* from Reunion, NMHNP (3 mm length).

and right in vacuum cleaner fashion, allowing constant grazing on microalgae such as diatoms.

An unusual character found in some Planaxidae is the presence of a luminous organ situated on the middorsal part of the mantle, not far from the mantle edge. Bioluminescence in marine snails is a rare phenomenon (Harvey, 1952) and limited to a few taxa. Its presence in the planaxids has not been well known despite the interesting paper by Haneda (1958) who documented this phenomenon in five species. I can find no further references to bioluminescence in the Planaxidae aside from the recent remark by Kilburn and Rippey (1982:53), who stated that the dorsal surface of the planaxid mantle bears a luminous organ of unknown function. Their remark was based on Haneda's (1958) paper. The two luminescent species examined by me and the five listed by Haneda (1958:154) are all members of the genus *Angiola*. All are from the Indo-Pacific except for *Angiola lineata*, which is from the Caribbean. During my field studies, I observed luminescence in *Angiola fasciata* from Pago Bay, Guam, and also observed the same phenomenon in *Angiola lineata* from Miami, Florida. I did not observe bioluminescence in species of the genera *Planaxis, Fissilabia*, and *Supplanaxis*. Ponder (in litt.) has examined *Hinea*, as this genus shares so many other characters with *Angiola*, but has not observed bioluminescence. Haneda (1958:154) also noted the absence of luminescence in *Planaxis sulcatus*. It would thus appear that this character is restricted to *Angiola* species and perhaps to *Hinea*.

MANTLE CAVITY ORGANS

The osphradium in planaxid species is a simple ridge flanked by a pair of ciliated lateral strips, and is similar to the osphradia of members of the Potamididae, Thiaridae (Houbrick, 1984:5; Haszprunar, 1985:477), Littorinidae, and Rissoidae (Johansson, 1956:150). Haszprunar (1985:489) classified these kinds of osphradia as the Si1–Si2–Si3–type, indicative of his suborder Neotaenioglossa. The planaxid osphradium is less complex than the bipectinate osphradia of members of the Cerithiidae (Houbrick, 1974:43, 1978:6, 1985:27).

The planaxid ctenidium is typically cerithiacean, extending the full length of the mantle cavity, and comprising long triangular filaments in most species. An exception is *Planaxis sulcatus*, in which the filaments are broad and shallow.

The hypobranchial gland is well developed in all planaxid taxa examined and produces copious amounts of mucus in all taxa except *Hinea*, where the gland is thin and not as active in producing mucus.

ALIMENTARY TRACT

Planaxid species have a distinctive snout that is flared into an oral hood at its tip. The head and snout are remarkably similar in all planaxid taxa. The mouth is a longitudinal slit in the concave ventral portion of the oral hood. The whole structure functions in vacuum cleaner fashion. The mouth is clearly illustrated in a critical point dried specimen in Figure 21C. There are a pair of tiny jaws made of scale-like pieces on the dorsal inner side of the lips.

TABLE 1.—Rachidian cusp formulae among Planaxid genera (n = numerous serrations).

Genus	Rachidian formula
Planaxis	$\frac{1}{1\text{-}1}$
Fissilabia	$\frac{1}{1\text{-}1}$
Angiola	$\frac{n\text{-}1\text{-}n}{1\text{-}1}$
Hinea	$\frac{n\text{-}1\text{-}n}{1\text{-}1}$
Holcostoma	$\frac{n\text{-}1\text{-}n}{1\text{-}1}$
Supplanaxis	$\frac{3\text{-}1\text{-}3}{1\text{-}1}$

Among the six planaxid genera, *Holcostoma, Hinea*, and *Angiola* species have relatively small radular ribbons that are equal to or less than one-fourth the shell length. There are about 15 rows of teeth per millimeter. In contrast, *Planaxis, Fissilabia*, and *Supplanaxis* species have long radular ribbons equal to about half the shell length and with an average of 8 rows of teeth per millimeter. In all planaxids, the outer and inner marginal teeth of the taenioglossate radula extend well beyond the other teeth as the radula passes over the bending plane. The long mid-shaft areas of the marginals are fused together into groups of 3 or 4 teeth, forming claw-like bunches at their apices, with many small denticles at their tips. These appear to function in a brush-like fashion and are the working part of the radula. When the radula is withdrawn into the mouth, the long marginal teeth interlock and fold up like a zipper. Although the marginal and lateral teeth are somewhat similar among all species, there are major differences in the rachidian teeth among some genera. These differences are illustrated in Figure 25 and the rachidian cusp formula for each planaxid

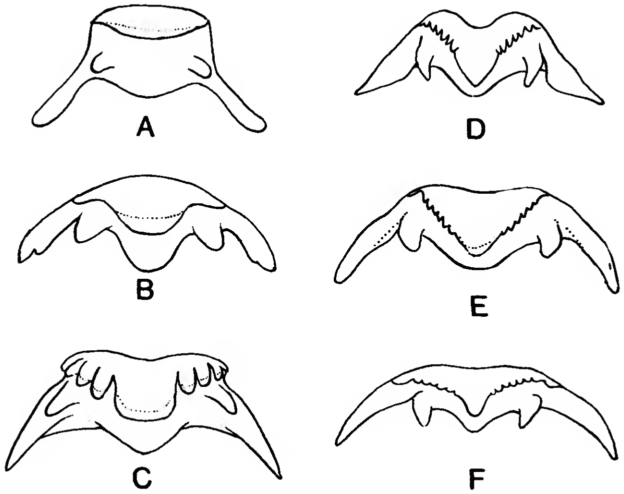

FIGURE 25.—Rachidian teeth of six planaxid genera (not to scale): A, *Planaxis*; B, *Fissilabia*; C, *Supplanaxis*; D, *Angiola*; E, *Holcostoma*; F, *Hinea*.

genus is presented in Table 1. The rachidian of *Planaxis* species (Figure 25A) has a dental formula of $\frac{1}{1-1}$ and is a squarish plate with a spoon-like, shallow single cusp. The basal plate has a pair of basolateral club-like extensions. The rachidian of *Fissilabia* species (Figure 25B) somewhat resembles that of *Planaxis* in having a single cusp, but the cusp is chisel-shaped and the entire rachidian is more compressed into a crescent shape. The basal plate has a triangular base and a pair of flaring lateral extensions. The dental formula is $\frac{1}{1-1}$. In *Supplanaxis* species (Figure 25C), the rachidian is squarish, has a rounded central major cusp flanked by three smaller but well-defined denticles on each side. The basolateral extensions of the basal plate are very long and there is a tiny denticle on each side of the basal plate. The dental formula is $\frac{3-1-3}{1-1}$. The rachidian teeth of *Angiola, Hinea,* and *Holcostoma* are very similar. In *Angiola* species (Figure 25D), the rachidian has a concave top and a single, large, triangular-shaped cusp with fine serrations. The basal plate has short lateral extensions and a large pair of basal denticles. The dental formula is $\frac{n-1-n}{1-1}$. *Hinea* (Figure 25F) and *Holcostoma* (Figure 25E) species have rachidia compressed into elongate crescents. The basal plate is narrow and has a pair of large cusps and a cutting edge of a single large serrated pointed cusp. The dental formula is $\frac{n-1-n}{1-1}$.

These generic differences were not recognized by Bandel (1984:48) who, in a comparison of the radulae of some Planaxidae, considered all species to belong to *Planaxis*. Bandel's descriptions are accurate, but I do not agree with him that the rachidian tooth of *Planaxis sulcatus* is intermediate in form between those of the two Caribbean genera. I find the rachidian of the former to be quite dissimilar from those of other genera in having a wide, blunt single cusp and a square basal plate.

One of the pecularities of planaxid radulae is the lamellae-like flange on the outer margin of the outer marginal tooth (Figure 6A–C, arrows). This is a difficult structure to see clearly, even on SEM micrographs, and is frequently lost during preparation of the radular ribbon. As Bandel (1984:48) pointed out, Troschel (1856–1863:151) did not mention this structure, but it has been alluded to by Thiele (1929:202–203) as characteristic of the Planaxidae. Risbec (1935, figs. 14, 15 on p. 389) depicted a very wide flange on the outer marginal tooth of *Planaxis sulcatus* from New Caledonia. This structure was not figured by Bandel (1984:48) for any of the species he described; moreover, his drawing of *Planaxis sulcatus* from the Red Sea (Bandel, 1984, fig. 58) shows an accessory plate that I have not seen in my specimens. This may be further evidence that the populations cited as *P. sulcatus* from the northeastern Indian Ocean are in reality another species. I have noted this lamella-like flange on the outer margin of the outer marginal tooth on SEM micrographs of various planaxid species, including *P. sulcatus* from Queensland, Australia. A similar structure appears on the outer marginal teeth of many potamidids such as *Cerithidea* species (Houbrick, 1984:15, fig. 3h). Bandel (1984:50) thought that the radulae of some thiarids, such as *Amphimelania,* resembled that of *Supplanaxis nucleus,* and thought that the close morphological agreement of the radulae of the three planaxid species he described and that of *Amphimelania* suggested a relationship between these two families. Although I agree that there appears to be a close relationship between the Thiaridae and the Planaxidae, I do not find an obvious similarity between the the radulae of these two groups and disagree with Bandel on this point.

REPRODUCTIVE SYSTEM

Misconceptions concerning the reproductive biology and the placement and derivation of the brood pouch in planaxids are common in the literature. The erroneous idea that planaxids are parthenogenetic can be traced to the comments of Thorson (1940:169) who had noted a lack of males in the Persian Gulf and commented on the low number of males observed by Risbec (1935:392–393) in New Caledonia. This may have been due to a sampling problem, because gonadal sections (Figure 13F, te) clearly show that males exist in all taxa of the Planaxidae. This does not mean that some remote populations, such as those observed by Thorson in the Persian Gulf, may not be parthenogenetic. Morrison (1954:358), probably relying on Thorson's (1940) suggestion, wrongly assumed that all members of the Planaxidae were parthenogenetic, with no males present, and his error was repeated by Kay (1979:112) and Boss (1982:992), as mentioned previously.

Some planaxids, such as *Angiola lineata* and *Hinea brasiliana,* exhibit sexual dimorphism in shell size, females being larger than males. In *Supplanaxis nucleus,* no significant differences between sexes were found. No statistical tests were run on the shell measurements of other taxa.

Although the layout of the female pallial oviduct is basically the same among all planaxid taxa, there are some differences that are outstanding: (1) All planaxid taxa have long sperm gutters leading to the opening of the spermatophore bursa except for *Supplanaxis,* where the opening to the bursa is more distal and well separated from the opening to the seminal receptacle. (2) In *Planaxis* and *Fissilabia,* the seminal receptacle is adjacent and medial to the spermatophore bursa. In *Angiola* and *Hinea,* it is adjacent and lateral to the bursa. In *Supplanaxis,* the seminal receptacle is proximal to the spermatophore bursa. (3) *Planaxis, Fissilabia,* and *Hinea* have the openings to the seminal receptacle and spermatophore bursa close together or in common, whereas the openings are well separated in *Angiola* and *Supplanaxis.*

Barkati and Ahmed (1982:355) stated in error that embryos of *Planaxis sulcatus* are brooded in the pallial oviduct and Bandel (1976:258) wrongly reported that females of *Supplanaxis nucleus* brood their young in a special pouch within the mantle cavity. Morrison (1954:358) correctly pointed out that the brood pouch in planaxids is not uterine in origin, but adventitious (subhemocoelic) in the neck region. He also noted the same kind of brood pouch in members of the Thiaridae, which he proposed were freshwater relatives of the Planaxidae. Boss (1982:992) also noted that the brood pouch is not of mantle origin and that it is located in the neck region and opens on the right side. Ponder (1980:257–258) correctly surmised that the brood pouch is formed by an epithelial invagination. These opinions are supported by my own investigations that show the interior of the brood pouch to be ciliated (Figure 21G), attesting to its ectodermal origin.

There are three different kinds of brood pouches found in the Planaxidae. The simplest kind is small, with few interior membranous folds, and located only in the right side of the head-foot. This kind occurs in *Hinea* and *Angiola* species and contains comparatively few, partially brooded embryos that hatch as longterm planktotrophic larvae. The second, more complex kind of brood pouch occurs in *Supplanaxis* species. It is a large dumbbell-shaped chamber located on both sides of the head-foot, and holds large numbers of embryos that are expelled at the veliger stage to become planktotrophic larvae. The third and most complex kind of brood pouch occurs in *Fissilabia* and *Planaxis* species and consists of a large, primary chamber subdivided into many secondary, lamellar chambers that fill both sides of the head-foot (extending over the right side of the esophagus in *Planaxis*). This kind of chamber holds many embryos that may hatch at the veliger stage to become planktotrophic larvae, at a late veliger state as lecithotrophic larvae, or may be brooded through all embryonic stages to hatch as juvenile snails. In comparing brood pouch morphology between taxa it is important to examine snails at approximately the same stage of pregnancy, because the brood pouch changes shape and size according to its stage of development and level of utilization.

The presence of an incubatory chamber or cephalic brood pouch in *Planaxis* females has been noted by several authors (Risbec, 1935:392–393; Thorson, 1940:162; Ponder, 1980:257; Boss, 1982:992). Similar brood pouches have been cited in the Fossaridae (Ponder, 1980:257), Thiaridae (Morrison, 1954:357; D.S. Brown, 1980; Starmühlner, 1969:218, 239; 1974:158) and the presence of this structure has been suggested in the Diastomatidae (Houbrick, 1981b:609). Several workers (Ponder, 1980:258; Morrison, 1954:358) have indicated that cephalic brood pouches may be homologous between some families and have inferred close relationship on this basis. For example, Morrison (1954:358) stated that the freshwater Thiaridae was "obviously" a relative of the Planaxidae because they had similar brood pouches. However, the homology between these similar brood pouches needs careful investigation because not much attention has been given to the anatomical structure and histology of these organs. Berry and Kadri (1972:373) recorded that the irregular compartments of the brood pouch of the thiarid, *Melanoides tuberculata,* are lined by unciliated epithelium. This is in marked contrast to the heavily ciliated brood pouch walls seen in the Planaxidae.

Brooding in specialized incubatory chambers of ectodermal origin is not uncommon among many groups in the superfamily Cerithiacea Fleming, 1822. This phenomenon is summarized in Table 2. Much of the information upon which this table is based is scattered throughout the literature. Some is clearly anecdotal and in need of further confirmation. In many taxa, the exact nature and disposition of the brood pouches are unclear. There are probably other cerithiacean taxa that have similar brood pouches that have not been recorded. Are these brood pouches, found in so many widely distributed groups among the Cerithiacea, homologous and of phylogenetic significance? This is a difficult question to answer and some caveats are apparent. All incubatory structures are secondary sexual characters of ectodermal origin and are thus subject to independent evolutionary modification and loss. Despite this, I believe that certain trends in brood pouch evolution may be discerned among taxa of cerithiacean lineage. In most marine members of the family Cerithiidae Fleming, 1822, a ciliated furrow emerges from the distal pallial oviduct and runs down the right side of the metapodium. This layout is common in *Cerithium* Bruguière, 1789 (Marcus and Marcus, 1964:504), *Bittium* Gray, 1847 (Marcus and Marcus, 1963:507), *Rhinoclavis* Swainson, 1840 (Houbrick, 1978:8), and *Clypeomorus* Jousseaume, 1888 (Houbrick, 1985:27). Members of the freshwater family Pleuroceridae Fischer, 1885, also have this anatomical feature (Morrison, 1954:358). A similar ciliated groove on the right side of the metapodium occurs in other cerithiacean families, and may be elaborated at its distal end to form a bulbous, glandular ovipositor. Intermediate states of the ciliated groove and ovipositor occur among several taxa. For example, ovipositors occur in species of *Cerithidea* Swainson, 1840, family Potamididae H. and A. Adams, 1854 (Houbrick, 1984:3), on some *Cerithium* species, family Cerithiidae Fleming, 1822 (Marcus and Marcus, 1964), and on species of *Modulus* Gray, 1842, family Modulidae Fischer, 1884 (Houbrick, 1980:121). Ovipositors also occur among freshwater cerithiaceans in pleurocerid and thiarid species. In the family Thiaridae Troschel, 1857, an ovipositor similar to that of *Modulus* was described by Belgin (1973:390, fig. 7) for

TABLE 2.—Distribution of brooding and reproductive strategies among the Cerithiacea.

Taxon	Location of brood pouch	Type of brooding	Type of development	Sexes	Source
PLEUROCERIDAE					
Semisulcospira	pallial oviduct	complete	ovoviviparous	gonochoristic	Morrison 1954
THIARIDAE					
THIARINAE					
Aylacostoma	head-foot	complete	ovoviviparous	parthenogenetic	Morrison 1954
Brotia	head-foot	complete	ovoviviparous	gonochoristic	Morrison 1954
Cubaedomus	head-foot	complete	ovoviviparous	parthenogenetic	Morrison 1954
Melanoides	head-foot	complete	ovoviviparous	parthenogenetic (males rare)	Morrison 1954, this study
Pachymelania	head-foot	complete	ovoviviparous	gonochoristic	Binder 1959
Sermyla	head-foot	complete	ovoviviparous	parthenogenetic	Morrison 1954
Stenomelania	mantle	partial	planktotrophic	gonochoristic	Starmühlner 1976
Sulcospira	head-foot	complete	ovoviviparous	parthenogenetic	Morrison 1954
Tarebia	head-foot	complete	ovoviviparous	parthenogenetic	Morrison 1954
Thiara	head-foot	complete	ovoviviparous	parthenogenetic	Morrison 1954
MELANOPSINAE					
Faunus	head-foot	partial	planktotrophic	gonochoristic	this study
PALUDOMINAE					
Lavigera	oviduct	complete	ovoviviparous	gonochoristic	Moore 1899
Potadomoides	oviduct	complete	ovoviviparous	gonochoristic	Leloup 1953
PARAMELANIINAE					
Bathanalia	mantle cavity	complete	ovoviviparous	parthenogenetic	Moore 1898
Tanganyicia	head-foot	complete	ovoviviparous	parthenogenetic	Moore 1898
Tiphobia	oviduct	complete	ovoviviparous	gonochoristic (penis in males)	Moore 1898
DIASTOMATIDAE					
Diastoma	head-foot	complete?	lecithotrophic	gonochoristic	this study
FOSSARIDAE					
Fossarus	head-foot	partial?	lecithotrophic	gonochoristic	Ponder 1980
PLANAXIDAE					
Angiola	head-foot	partial	planktotrophic	gonochoristic	this study
Fissilabia	head-foot	partial	lecithotrophic	gonochoristic	this study
Hinea	head-foot	partial	planktotrophic	gonochoristic	this study
Planaxis	head-foot	partial	planktotrophic	gonochoristic	Risbec 1935, this study
Planaxis	head-foot	complete	ovoviviparous	parthenogenetic?	Thorson 1940, Barkati and Ahmed 1982
Supplanaxis	head-foot	partial	planktotrophic	gonochoristic	this study
SILIQUARIIDAE					
Pyxipoma	head-foot	complete	ovoviviparous	gonochoristic	Morton 1951

Zemelanopsis, and Binder (1959:753) cited a similar ovipositor in *Melanopsis*. In all cases, the ovipositor is a raised glandular area on the right side of the metapodium and in some taxa (*Diastoma, Modulus, Cerithidea*) there is a pit bordered by a muscular lobe associated with the ovipositor. In *Diastoma* this pit leads into a large pedal brood pouch, which I had initially interpreted as a glandular, jelly-secreting part of the ovipositor, as I found no larvae in it (Houbrick, 1981b:609, fig. 2). I now consider that this structure is probably a brood pouch, very similar to those found in some planaxid species.

Considering the array of brood pouch morphologies, it is not difficult to envisage the following transformation series in their evolution: nearly all cerithiacean snails have open pallial oviducts and many taxa in diverse families have a ciliated groove that emerges from the distal pallial oviduct on the right side of the metapodium. This groove functions to remove feces and debris from the pallial cavity, but is also used to move egg strings from the oviduct for deposition onto the substrate. Frequently, the groove terminates in a bulbous, glandular flap of tissue that functions as an ovipositor. In some taxa, the ovipositor has become modified by ectodermal invagination into a pit (birth pore) that leads into a ciliated incubatory chamber. There thus appear to be three stages in the development of a brood pouch: (1) some cerithiaceans have developed parts of the open pallial oviduct itself into a brood pouch (*Tiphobia, Lavigera, Potadomoides*); (2) in others, the formation of a moderately sized, simple, internal brood pouch in the subcephalic hemocoel has arisen by modification of the pedal ovipositor due to

TABLE 3.—Variations of development within the Planaxidae (+ = presence; – = no information)

Species	Type of development			Nurse eggs	Embryo diameter (mm)	Number of embryos per brood pouch	Locality	Source
	complete ovovivi-parity	lecitho-trophy	plankto-trophy					
Planaxis sulcatus	–	–	–	+	0.38	328	Karachi, Pakistan	Barkati and Ahmed 1982:357
	–		+	–	0.10	–	New Caledonia	Risbec 1935:393
	+	+	–	+	0.10–0.75	11–580	Persian Gulf	Thorson 1940:164–165
	–	–	+	–	0.15 (n=5)	2000	Queensland, Australia	this study
Planaxis planicostatus	–	–	+	–	–	–	Panama	this study
Fissilabia decollata	–	+	–	–	0.23 (n=6)	436	Queensland, Australia	this study
	–	+	–	–	0.40 (n=10)	326	Guam	this study
Angiola lineata	–	–	+	–	0.10 (n=5)	30	Miami, FL	this study
Angiola lineolata	–	–	+	–	–	30	Miami, FL	this study
Hinea brasiliana	–	+	–	–	0.25 (n=3)	–	Sydney, Australia	this study
Supplanaxis nucleus	–	–	+	–	*0.10 (n=6)*	*12000*	*Miami, FL*	*this study*
	–	–	+	–	0.10–0.15	1000	St. Croix, Virgin Id	Thorson 1940:168
	–	–	+	–	–	–	Santa Marta, Colombia	Bandel 1976:258

invagination of the glandular pit (*Stephopoma, Angiola, Hinea*); (3) in some taxa, further modification of the brood pouch has culminated in the development of a complex, subdivided chamber that fills the entire head-foot and surrounding tissues of the cephalic hemocoel (*Planaxis, Fissilabia, Supplanaxis, Melanoides, Thiara*).

Planaxis sulcatus has been cited in the literature (Robertson, 1974:227) as an example of a prosobranch species that has the ability to utilize several reproductive modes in response to environmental or geographic differences. This is based on observations of *Planaxis sulcatus* in the Persian Gulf (Thorson, 1940) and needs to be reconfirmed by careful observation. Intraspecific variation in larval types or poecilogony is an uncommon phenomenon and it is not certain that this occurs in *P. sulcatus*. I previously discussed the data relevant to this claim under the section on *P. sulcatus* and suggested that there may be two cryptic taxa involved. It is significant that all studies of the developmental biology of *P. sulcatus* in the western Pacific show a pattern of partial brooding followed by a planktotrophic stage. The two papers citing viviparity in this species (Thorson, 1940; Barkati and Ahmed, 1982) were based on studies of populations from the Persian Gulf and the Pakistan coast. This suggests that these populations may represent a distinct, undescribed northwestern Indian Ocean *Planaxis* taxon.

The presence of ovoviviparity and brooding in the Planaxidae and among other cerithiacean taxa raises several interesting evolutionary questions as both phenomena are usually associated with K-selection and iteroparity. In the case of cerithiaceans, the evolution of ovoviviparity and brooding seems clearly to be associated with the radiation into fresh water by the families Thiaridae and Pleuroceridae (Table 2). Planktotrophy is a distinct disadvantage in many freshwater environments where free swimming veligers would be carried away by currents. Interesting exceptions to absence of planktotrophy in the Thiaridae are seen in *Stenomelania* (Starmühlner, 1976:576; 1979:254) and *Faunus* species (personal observation), which have veliger larvae but live near river mouths or in brackish water environments. It is assumed that freshwater cerithiaceans evolved from marine ancestors; consequently, ovoviviparity and brooding in marine groups are not as easy to explain. Was the evolution of ovoviviparity and brooding in the Cerithiacea first associated with the evolution of K-strategy in marine groups such as the Planaxidae and Diastomatidae, and this "preadaptation" capitalized upon with subsequent adaptive radiation of the superfamily into freshwater habitats? What advantage to planaxids is there in partial brooding followed by a planktotrophic stage? There is an obvious reduction in larval mortality, which results even from partial brooding, but the adaptive value to variation in the size and number of larvae (Table 3) and the length of brooding among the Planaxidae are difficult to explain.

Although several broods or cohorts of embryos may be found in a single brood pouch, each brood seems to hatch separately. My observations of *Supplanaxis*, *Fissilabia*, and *Planaxis* species indicate that brooding is synchronous rather than sequential, but I was unable to determine the pattern in *Hinea* and *Angiola* species.

An hypothesis proposed by Strathmann and Strathmann (1982:92) associating small adult size with brooding is that as adult size increases, the capacity to produce young becomes proportionately greater than the capacity to brood them. This does not seem to follow in the planaxids, for the genera with the larger sized species, *Planaxis*, *Fissilabia*, and *Supplanaxis*, brood and release large numbers of embryos in large, complex brood pouches, whereas the genera comprising smaller shelled species, *Hinea* and *Angiola*, have fewer eggs and smaller, simpler brood pouches.

The morphology of male gametes provides significant, conservative characters for comparison with other higher taxa. The sperm of Planaxidae species are typically cerithiacean in morphology and consist of two basic types, euspermatozoa ("typical"), which fertilize eggs, and paraspermatozoa ("atypical"), of unknown function. In using the above terms, I follow the terminology proposed by Healy and Jamieson (1981:101). Among the Planaxidae, the sperm of three species are known: *Supplanaxis nucleus*, *Angiola lineata*, and *Planaxis sulcatus*. I have examined the sperm of *Supplanaxis nucleus* and *Angiola lineata* at the scanning electron microscope (SEM) level. Micrographs show that euspermatozoa each have a pointed acrosome, a short cylindrical nucleus separated by a narrow neck from a very long midpiece, and a long flagellum. The midpiece appears to be subdivided into several sections (Figure 18H). The paraspermatozoan has a pointed acrosome, a long lance-like nucleus with a short, narrow mitochondrial base and 5 (6?) very long flagellae (Figure 18G). At the SEM level, no differences between the two taxa were seen. Healy (1983), using transmission electron microscopy (TEM), studied the ultrastructure of *Planaxis sulcatus* sperm. His pictures and drawings agree with what I have been able to discern in the other species at the SEM level. Healy (1983:59–60) showed that planaxid sperm share all the features of other cerithiacean euspermatozoa he examined; i.e., a well-defined acrosome, a short, very electron-dense nucleus, an elongate midpiece, and an elongate glycogen piece. Healy stated that true cerithiaceans are distinguished from other mesogastropods on the basis of euspermatozoan midpiece structure. Based on ultrastructural differences, he split the cerithiaceans into two groups and placed the Planaxidae into what he called "Group 1," which comprises the Turritellidae, Cerithiidae, Potamididae (subfamily Batillariinae), and Planaxidae. He further subdivided Group 1 into two subgroups: Group 1(i), Turritellidae and Cerithiidae, and Group 1(ii), Planaxidae and Potamididae (Batillariinae) (Healy, 1983:63–65). Group 1(ii) is distinguished by euspermatozoa in which the acrosomes are conical, the midpieces shorter, and the crystal plates of all four midpiece elements are comprised of two large and two small elements. In addition, the smaller elements are larger than those of subgroup I(i) (Healy, 1983:63). Thus, ultrastructural morphology of *Planaxis* euspermatozoa is closest to those of members of the Batillariinae, subfamily of the Potamididae. On the basis of these ultrastructural differences, Healy (1983:73) suggested that there may be a close systematic relationship between the Batillariinae, which he thinks should be elevated to familial rank, and the Planaxidae. I support this hypothesis.

NERVOUS SYSTEM

Planaxis species have an epiathroid nervous system. Distinguishing features are the large major ganglia (especially in *Angiola lineata*), the closeness of the subesophageal and left pleural ganglia to each other, the long pedal-pleural connectives, and the series of smaller, lobe-like ganglia, and nerves emerging from the anterior of each pedal ganglion and extending down and forward to the brood pouch. This is similar to the situation in *Littorina* as described by Fretter and Graham (1962:42). Binder (1959:753) also called attention to this similarity and suggested that the Planaxidae were closer to the Littorinidae than to the Thiaridae (cited as Melaniidae) in this respect. However, in *Littorina*, the subesophageal ganglion, in contrast to planaxids, is far away from the left pleural ganglion (Risbec, 1935:392). In planaxids, conspicuous statocysts are present on the posterior portions of the pedal ganglia. The right pleuro-supraesophageal connective is moderately long. The RPG ratio as defined by Davis et al. (1976:263) constitutes the length of the pleuro-supraesophageal connective divided by the sums of the lengths of the supraesophageal ganglion, pleuro-supraesophageal connective, and right pleural ganglion. Accordingly, the RPG ratio is 0.67 ($n = 4$) in *Fissilabia decollata*, 0.65 ($n = 6$) in *Hinea brasiliana*, 0.58 ($n = 10$) in *Supplanaxis nucleus*, 0.57 ($n = 2$) in *Planaxis sulcatus*, and 0.50 ($n = 10$) in *Angiola lineata*. While the RPG values of *Fissilabia* and *Hinea* are higher, the average value in the Planaxidae is comparable to that of the Cerithiidae (0.59). This indicates a tighter concentration of the nervous system than seen in members of the Potamididae, which have an average RPG value of 0.78 (Houbrick, 1984:7).

ECOLOGY AND BEHAVIOR

Very little has been written about the ecology of planaxid snails. The only paper with which I am familiar is Rohde's (1981) on *Planaxis sulcatus*. All planaxid species appear to be common in the rubble and rocks of the intertidal zone, where they occur in large populations. Both adult and young snails occur together. They are active crawlers, emerging from crevices or beneath large rocks and rubble at the incoming tide when they begin to graze on microalgae covering the substrate. Movement is by retrograde, ditaxic waves. When crawling, planaxid snails touch the substrate with their long tapering cephalic tentacles, one at a time, in a rhythmic manner. Among cerithiaceans, this kind of behavior appears to be unique to members of the Planaxidae. The ventral lateral position of the eyes places them close to the substrate while the large extended oral hood, in constant touch with the substrate, is moved left and right. All species appear to be photonegative and are probably more active at night and on cloudy days. The function of the luminous organ on the mantle edge in members of the genus *Angiola* is unknown, but undoubtedly plays some role in their behavior during the night.

The tropical intertidal environment is harsh due to great fluctuations in temperature, salinity, turbidity, and exposure. The hardiness of these snails is attested to by the ease with which they may be maintained in the laboratory in containers of seawater with little or no attention. *Supplanaxis nucleus* and *Angiola lineata* lived in petri dishes without food and only occasional changes of water for as long as three months. Coleman (1975:8) kept *Hinea brasiliana*, a more temperate species from southeastern Australia and New Zealand, alive in 100 ml of seawater in a jar stoppered with a loosely fitting lid and with no artificial aeration for 6 years and one month. Remarkably, no food or additional water were added and it is thought that the animals lived on algal film and their own feces, which had become modified by bacterial action back to consumable food.

Laboratory maintained specimens of *Hinea brasiliana* from a Sydney, Australia, population collectively crawled in a counterclock-wise direction in their containers several times a day. This behavior was correlated with daily tide changes, the snails becoming active and crawling during the high tide periods. These movements paralleled the local tide changes over several weeks indicating that some kind of internal biological clock is at work. This kind of behavior was not observed in the Florida species kept under laboratory conditions. Perhaps the magnitude of tidal changes in New South Wales, Australia, compared with the relatively slight changes in Florida account for these differences.

Throughout the world, two size classes of planaxid taxa coexist: small *Angiola* species (up to 10 mm) and the other larger genera such as *Planaxis*, *Fissilabia*, *Hinea*, and *Supplanaxis* (up to 30 mm). They are usually found to be geographically (but not ecologically) sympatric. Of the two Caribbean species, *Supplanaxis nucleus* is the larger (14–17 mm in length), and lives in a high-energy, mid-intertidal habitat, among boulders and large rocks. Its large foot and smooth, slippery shell make it difficult to dislodge from the substrate. It is not found in large clusters as are most planaxids. This species is highly fecund, producing very large numbers of small embryos that are incubated in a large brood pouch. In contrast, *Angiola lineata* is small (7–9 mm), extremely gregarious, and lives in colonies under rubble and small stones in more sheltered, low intertidal habitats. It produces fewer eggs and larvae and has a comparatively small brood pouch. In the tropical Indo-Pacific, the most common large planaxid species is *Planaxis sulcatus*, sympatric with the equally large *Fissilabia decollata* and with other small *Angiola* species. Indo-Pacific *Angiola* species live in different microhabitats than the other, larger genera. When found with *Fissilabia decollata* in the same habitat, *Planaxis sulcatus* always occurs lower in vertical distribution along the shore. *Planaxis sulcatus*, a large snail, is less cryptic than other planaxid species. It is frequently seen exposed on rocks during low tides and does not appear to be as photonegative as other species. Rohde (1981) studied the population dynamics of this species, which is extremely abundant in large populations at Heron Island, Queensland, Australia. Over a two-year period he found that populations of *P. sulcatus* remained remarkably stable, indicating equilibrium conditions and saturation of habitats. Rohde (1981:347) showed that there was little mixing of snails over short distances and that populations in different parts of the habitat remained well separated. After a one-year period, about 80% of the snails had not migrated more than 4 m from their original site.

During the course of this study, predation was never observed in the field. No chipped or drilled shells were found, but it is very likely that predation by crabs occurs as they are common in the rocky intertidal habitat. The bioluminescence observed in *Angiola* species may have a startling effect on predators as it occurs only when the snails are disturbed. Rohde (1981:348) showed that *Planaxis sulcatus* in Queensland, Australia, is heavily infected by trematode parasites, but found that these infections did not significantly affect the snails and that population size and biomass remained constant.

FOSSIL HISTORY

In contrast to the abundance of fossil cerithiids, the sparse amount of fossil planaxids does not allow much to be said of the history of this group. The Planaxidae was thought to be as old as the Eocene by Cossmann (1906:198), but a Cretaceous species attributed to *Planaxis*, *P. simplex* Mahmoud, 1956, has been described from the Moghara Massif of Egypt (Mahmoud, 1956:148, pl. 16: figs. 23–25). The shell illustrated by Cossmann (1906, pl. 12: figs. 53–54) as the "geno-plesiotype" of the genus *Planaxis*, *P. aulacophorus* Cossmann, looks somewhat like Recent *Planaxis* species. As it is impossible to ascertain if this species is ancestral to living ones, I prefer to refer it and other similar Eocene species to *Planaxis*, sensu lato. Along with *Planaxis*, under which he included *Hinea*, *Fissilabia* (cited as *Quoyia*), and *Quadrasia* as subgenera, Cossmann (1906:196) recognized two other Eocene genera: *Orthochilus* Cossmann, 1889 and *Dalliella* Cossmann, 1895. *Orthochilus*, as exemplified by *O.*

TABLE 4.—Fossil records of Cenozoic planaxid taxa (* still extant).

Taxon	Epoch	Locality	Source
Planaxis aulacophorus Cossman, 1889	Eocene	Paris basin	Cossmann 1889:10–11, pl. 1: fig. 3; 1906:198, pl. 12, figs. 53–54
Planaxis littorinoides Cossmann [?]	Eocene	Lower Loire	Cossmann 1906:198
Planaxis fischeri de Raincourt, 1870	Eocene	Paris basin	Cossmann 1889:10–11, pl. 1: figs. 1–2; 1906:198
Planaxis rosthorni Cossman, 1906	Eocene	Hungary	Cossmann 1906:198
Planaxis blackenhorni Cuvillier, 1933	Eocene	Egypt	Cuvillier 1933:42, pl. 4.
Orthochilus denudatus Cossmann, 1889	Eocene	Paris basin	Cossmann 1889:12, pl. 2: fig. 13
Orthochilus bezanconi (de Raincourt, 1870)	Eocene	Paris basin	Cossmann 1889:11–12, pl. 1: fig. 22; 1906:199, pl. 12: figs. 55–56
Orthochilus breviculus Cossman 1907	Eocene	Paris basin	Cossmann 1907:60–61
Dalliella brusinai Cossmann, 1895	Eocene-Miocene	Paris basin	Cossmann 1906:199–200, pl. 13: figs. 12–13
Dalliella turriculata Cossmann, 1896	Eocene	Paris basin	Cossmann 1906:200
Dalliella insolita (Deshayes, 1864)	Eocene	Paris basin	Cossmann 1906:200
* *Supplanaxis nucleus* (Bruguière, 1789)	Late Miocene[1]	Cabo, Blanco, Venezuela	Weisbord 1962: 168–169, pl. 14: figs. 17–18
Supplanaxis ame (Woodring, 1928)	Miocene[1]	Bowden, Jamaica	Woodring 1928:342, pl. 25: fig. 16
* *Planaxis sulcatus* (Born, 1780)	Pliocene	Sonde (Madioen), Java	K. Martin 1905:222, pl. 40: fig. 660
Planaxis sondeianus K. Martin, 1905	Pliocene	Sonde (Madioen), Java	K. Martin 1905:222, pl. 40: fig. 661; Altena Regreten 1941:5–6, figs. 1a,b
Planaxis bantamensis Oostingh, 1933	Pliocene	Tjimantjeuri (Bantam), Java	Oostingh, 1933; Altena Regreten 1941:6
* *Fissilabia decollata* (Quoy and Gaimard, 1833)	Pliocene	Sonde (Madioen), Java	K. Martin 1905: 222–223, pl. 40: fig. 662

[1] No longer considered Miocene; probably Pliocene.

bezanconi (Cossmann, 1889), looks very much like *Hinea* and *Angiola* species and may be in the same lineage with them. Wenz (1938:722) also included *Orthochilus* in the Planaxidae. *Dalliella,* which Cossmann (1906:199–200, pl. 13: figs. 12, 13) illustrated, does not appear to closely resemble any living planaxid taxon. Its sculpture of many spiral grooves probably influenced Cossmann to place it near *Planaxis*.

Table 4 presents a summary of Cenozoic planaxid fossils known to me. It would appear that the earliest representatives of the Planaxidae are the Eocene genera *Planaxis,* sensu lato, *Orthochilus,* and *Dalliella. Supplanaxis* may be traced back to the Pliocene (cited as Miocene in the literature) while *Planaxis,* sensu stricto, and *Fissilabia* are recorded from the Pliocene. Three of the fossils, *Planaxis sulcatus, Fissilabia decollata,* and *Supplanaxis nucleus,* represent species still extant.

Phylogeny

RELATIONSHIPS WITH OTHER CERITHIACEAN FAMILIES

As has been shown, uncertainty as to the exact placement of the family Planaxidae within the superfamily Cerithiacea is reflected in the literature. The subdivision of the family into genera has likewise differed among authors (see p. 4 for details), largely due to the lack of anatomical knowledge about planaxid groups and other cerithiacean families. This has led to a somewhat superficial classification based mostly on shell and a few radular characters. A number of cerithiacean families, such as the Vermetidae, Dialidae, and Turritellidae, remain poorly defined or anatomically unknown; others such as the freshwater Thiaridae and the Pleuroceridae, are slightly better known, but the available data on these two families remains unfocused and needs synthesis.

My papers on the Modulidae (Houbrick, 1980), Cerithiidae (Houbrick, 1974, 1978, 1985), Potamididae (Houbrick, 1984), Diastomatidae (Houbrick, 1981b), and Campanilidae (Houbrick, 1981a) have clarified the status of these groups; thus, some meaningful comparisons between these families and the Planaxidae may now be made.

Within the Cerithiacea, similar pallial gonoducts, ciliated furrows, and glandular ovipositors on the right side of the foot of females occur in the Cerithiidae, Potamididae, Pleuroceridae, and Modulidae, but members of these families do not brood their young. However, members of the families Thiaridae, Diastomatidae, and Fossaridae all share similar brood pouch morphology and placement.

As seen earlier, Healy's (1983) studies of the ultrastructure of euspermatozoa and paraspermatozoa of *Planaxis* indicate close morphological similarity and a possible close systematic relationship between planaxids and members of the Batillariinae, family Potamididae.

The operculum, ctenidium, short style sac and cuticular stomach of planaxids are like those seen in the Cerithiidae, but the smooth mantle edge and simple ridge-like osphradium are features shared with the Potamididae and Thiaridae.

The lateral flanges on the marginal teeth and the denticles on the basal plate of the rachidian tooth of many planaxids are similar to those found in some members of the Potamididae (Houbrick, 1984). The cusp structure of the marginal teeth is somewhat similar to that observed in the Modulidae (Houbrick, 1980) and in some thiarids such as *Amphimelania* (Bandel, 1984:50, fig. 62).

OUTGROUP SELECTION

In a phylogenetic analysis of the five genera of the Planaxidae several cerithiacean taxa are possible candidates for outgroup comparison. The choice of an ideal sister group of the planaxids is complicated by inadequate anatomical knowledge about some nonplanaxid taxa and difficulties with resolving morphological homology and ontogeny. Anatomical data exist for only a few species of most genera in other families, and frequently conchological and radular characters are the only information available for some outgroups. Conchological and radular data, used without anatomical and ontogenetic characters, result in unsatisfactory trees because of frequent evolutionary convergence of the shell and radula; e.g., shells of planaxid taxa look very much like those of some littorinids. Indeed, Davis (1979:35) suggested that, among the Hydrobiidae, shell convergence may be one of the most underestimated phenomena in evolution.

Despite the above caveats, close relationships among the Planaxidae, Diastomatidae, Fossaridae, Potamididae, Cerithiidae, and the freshwater Thiaridae are suggested by the anatomical, radular, and shell characters available; thus, an appropriate outgroup for phylogenetic analysis was sought within these families.

The Fossaridae were rejected as an outgroup because of the absence of sufficient characters. There is a brief, but intriguing paper by Ponder (1980) in which a close relationship between the Fossaridae and Planaxidae is suggested on the basis of homologous brood pouches, but he does not discuss other aspects of fossarid anatomy. Their anatomy and biology are basically unknown, and detailed anatomical work on fossarid species is necessary before any meaningful comparison may be made.

The Cerithiidae, among the better known of cerithiacean families, could certainly be used as an appropriate outgroup. But in comparison to the potamidids, thiarids, and *Diastoma*, which share more anatomical traits with the planaxids, the cerithiids are a less desirable outgroup.

The anatomy of *Diastoma*, family Diastomatidae, is well known (Houbrick, 1981b). There are many similarities with planaxid anatomical characters, including a putative homologous brood pouch. *Diastoma melanioides*, although a marine species, is a relict species, monotypic for the whole family. *Diastoma* is morphologically close in shell, radula, and soft anatomy to members of the freshwater family Thiaridae, which appears to have close systematic relationships with the Planaxidae. For these reasons, it was one of the species initially considered for outgroup comparison, but was later rejected because of its unique position as a relict, monotypic taxon.

The two families judged most appropriate for outgroup comparison are the Thiaridae and the Potamididae.

The Thiaridae share many characters with planaxids and appear to be closely related to them but, because of their freshwater habitat, their ecology, and larval development, are very different from the marine Planaxidae. The anatomy of the pallial oviduct of some thiarids is highly modified and differs considerably from the more generalized pallial oviducts of planaxids. Moreover, many species of Thiaridae are parthenogenetic. The inner wall of the brood pouch of *Melanoides tuberculata* is unciliated according to Berry and Kadri (1972:373), suggesting a similar condition in other thiarids and casting suspicion on the homology of these organs with those of the Planaxidae. With the exception of *Melanoides tuberculata* and *Tarebia granifera*, I am not familiar with thiarid anatomy on a first-hand basis, but numerous anatomical papers on various thiarid species have supplied the characters necessary for comparative analysis. My own dissections of *Melanoides* have enhanced the information available for an adequate comparison among taxa. Table 6 presents the character distributions used in the analysis.

The family Potamididae, largely a brackish water group, is difficult to compare to the Planaxidae because it is a large, diverse group comprising many higher taxa of numerous species, some well known and others unstudied. Moreover, the family is divided into two very different subfamilies, the Potamidinae and the Bartillariinae, which may constitute good families in their own right (Houbrick, 1984:1-2). While members of the Potamidinae differ considerably from the planaxids, those of Batillariinae share many anatomical traits in common with the planaxids. The central radular tooth is morphologically the same as in the planaxids and the osphradium corresponds closely with that of planaxids. Healy (1983:63-65) has suggested a close relationship between the Batallariinae and the Planaxidae on the basis of sperm ultrastructure studies. Some *Batillaria* species are anatomically well known (Bright, 1958, 1960; Driscoll, 1972) and I have had first hand experience with the anatomy of several species. For these reasons, *Batillaria* was considered the best choice for outgroup comparison (Table 5).

DISCUSSION OF CHARACTERS

The specific characters used with both outgroups are discussed below:

SHELL.—Several of the characters, such as shell shape and sculpture are, at best, undesirable and may be polarized only by outgroup comparison. Shells with apertures less than one-half the shell length were termed "narrow". A short, wide, or decollate shell is presumed to be derived from the more common, tall, narrow shells seen in most cerithiids, batillariids, and thiarids. The presence of a sinusigeral notch on the protoconch is also an unstable character for cladistic analysis as prosobranchs may have several developmental types within the same genus.

PERIOSTRACUM.—Planaxids generally have a moderately thick or hispid periostracum. If the outgroup is a batilariid, a thickened periostracum in the planaxids would be considered apomorphic, whereas a thickened periostracum would be considered plesiomorphic if the outgroup were a thiarid, in which a thick periostracum is the rule (personal observation).

RADULA.—One of the distinctive characteristics of the planaxid radula is a rachidian tooth with basal cusps. This condition also exists in members of the Batillariinae (Thiele, 1929:208) but not in thiarids (Starmühlner, 1974, 1976). The cusps are basally placed in these groups, but in some planaxids they are medianly placed and this is considered an apomorphy. Most other cerithiaceans have a rachidian tooth with a multi-cusped cutting edge; thus, a single-cusped rachidian is a derived condition in planaxids. The flanges on the marginal teeth of some planaxids also occur in some potamidids (Houbrick, 1986) and may represent a plesiomorphic trait. The unusual bifurcated tips of the marginal teeth also occur in modulids (Houbrick, 1980:126). The number of cusps on the rachidian cutting edge, the shape of the rachidian basal plate, and the convexity or concavity of the top of the rachidian tooth, are unordered character traits that may only be polarized by outgroup comparison and may be regarded as unstable characters for phylogenetic analysis.

OPERCULUM.—The position of the opercular nucleus is important only in separating the Planaxidae from the Batillariinae but is not useful for defining planaxid taxa or for outgroup comparison with the Thiaridae.

EXTERNAL ANATOMY.—The broad, flared snout is unique to the planaxids and is clearly apomorphic. A smooth mantle edge is an apomorphy not found in the Batillariinae (personal observation) or in *Melanoides* (Abbott, 1948:290; personal observation). Other thiarids have smooth mantle edges (Abbott, 1948:286). The presence of a luminescent mantle organ is an apomorphy not recorded in any other prosobranch, and occurs only in *Angiola*. The ciliated egg groove on the right side of the foot is deep and well defined in all planaxid taxa except *Hinea* and *Angiola*, where it is lacking. A ciliated egg groove occurs in many cerithiacean groups (Houbrick, 1984:10), including the two outgroups used in this analysis; consequently, its presence in planaxids is regarded as plesiomorphic.

MANTLE CAVITY.—A long ctenidium, comprised of long tapering filaments, is a primitive trait shared in common with most other cerithiaceans. Reduction of the ctenidium resulting in low, broad ctenidial filaments is considered a derived condition correlated with long periods of exposure. This has also occurred in the amphibious *Cerithidea*, family Potamididae (Houbrick, 1984:11).

ALIMENTARY TRACT.—The salivary glands are simple, convoluted tubes in the Batillariinae (Driscoll, 1972:378) and in the Thiaridae (Starmühlner, 1974:136). This state contrasts with the mass-like, tightly coiled apomorphic condition of the salivary glands seen in some planaxids. A long style sac, extending anteriorly to the pericardium, is the primitive condition in prosobranch herbivores and detritivores (Fretter and Graham, 1962:223-225). A shortened style sac, extending anteriorly only a short distance beyond the stomach, is thus apomorphic.

NERVOUS SYSTEM.—The RPG ratio of Davis et al. (1976) is an index of the concentration of the nervous system. A high RPG ratio indicates a loose condition that is considered plesiomorphic, whereas a low RPG ratio represents a tight, more advanced, condition. The long extensions of the pedal ganglia do not occur in other cerithiaceans and are here considered an apomorphic trait. The close proximity of the subesophageal ganglion to the left pleural ganglion is also seen in the Cerithiidae, Potamididae, and Thiaridae (Bouvier, 1887, pl. 6: fig. 24).

REPRODUCTIVE SYSTEM.—If the Batillariinae is used as the outgroup, a cephalic brood pouch would have to be regarded as derived. In contrast, the brood pouch is a

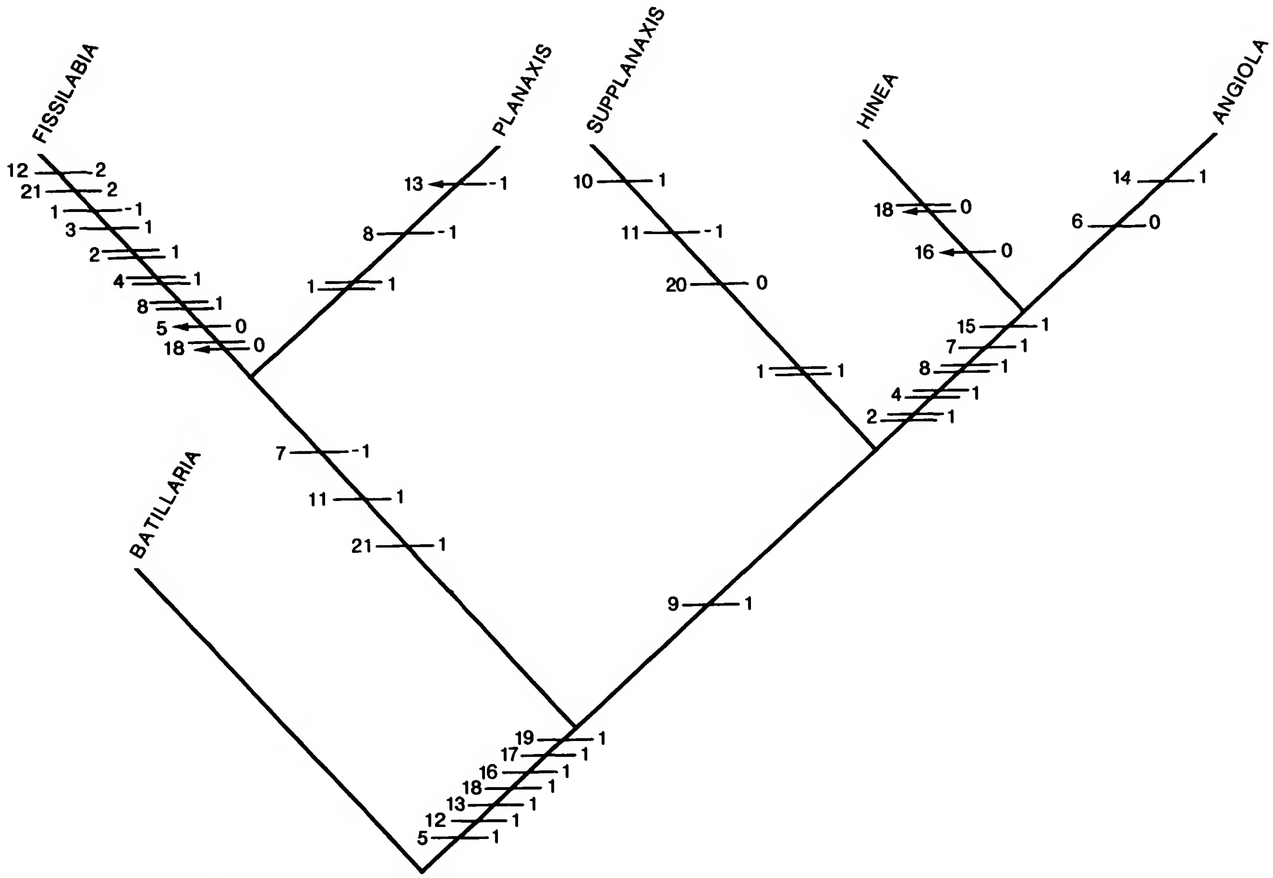

Figure 26.—Cladogram using *Batillaria* as outgroup. Nodes represent hypothetical ancestors. Numbers on left of tree branches represent characters and those on right indicate character states. Single bars across tree branches indicate changes in character states. Double bars signify character transformations that occur more than once (parallelisms and convergences). Arrows represent reversals. Characters used listed in Table 5.

Table 5.—Comparison of characters and character states of five major genera of Planaxidae using *Batillaria* as the outgroup (A = *Planaxis*; B = *Fissilabia*; C = *Hinea*; D = *Angiola*; E = *Supplanaxis*; F = *Batillaria*).

Character	A	B	C	D	E	F
SHELL						
1. Shell shape	1	−1	0	0	1	0
turreted narrow (0)						
turreted wide (1)						
turreted, decollate (−1)						
2. Shell sculpture	0	1	1	1	0	0
strongly sculptured (0)						
weakly sculptured (1)						
3. Columellar fold	0	1	0	0	0	0
present (1)						
absent (0)						
4. Outer lip placement	0	1	1	1	0	0
extended on penultimate whorl (1)						
only moderately extended (0)						
5. Deep sinusigeral notch in protoconch	1	0	1	1	1	0
present (1)						
absent (0)						
6. Thick periostracum	1	1	1	0	1	0
absent (0)						
present (1)						

Table 5.—Continued

Character	A	B	C	D	E	F
RADULA						
7. Rachidian cutting edge large central cusp, 3–4 denticles (0) single large blunt cusp (−1) large triangular saw-edged cusp (1)	−1	−1	1	1	0	0
8. Rachidian basal plate squarish tall (−1) rectangular tall (0) semilunar, narrow (1)	−1	1	1	1	0	0
9. Rachidian top edge concave (1) convex (0)	0	0	1	1	1	0
10. Rachidian basal cusps basal placement (0) median placement (1)	0	0	0	0	1	0
11. Lateral teeth sharp long cusps (0) large wide blunt cusps (1) large blunt outwardly turned (−1)	1	1	0	0	−1	0
ANIMAL						
12. Operculum multispiral, central nucleus (0) paucispiral, eccentric nucleus (1)	1	1	1	1	1	0
13. Mantle edge fringed (0) smooth (1) scalloped (−1)	−1	1	1	1	1	0
14. Luminescent mantle organ absent (0) present (1)	0	0	0	1	0	0
15. Ciliated groove on head-foot weak (1) strong (0)	0	0	1	1	0	0
16. Salivary glands tightly coiled (1) relatively uncoiled (0)	1	1	0	1	1	0
17. Style sac long (0) short (1)	1	1	1	1	1	0
NERVOUS SYSTEM						
18. Nervous system concentration RPG below 59 (1) RPG above 60 (0)	1	0	0	1	1	0
REPRODUCTIVE SYSTEM						
19. Brood pouch present (1) absent (0)	1	1	1	1	1	0
20. Placement of seminal receptacle sr proximal to sb (0) sr adjacent to sb (1)	1	1	0	0	0	0
LARVAE						
21. Type of development lecithotrophy (2) planktotrophy (0) mixed (1)	1	2	0	0	0	0

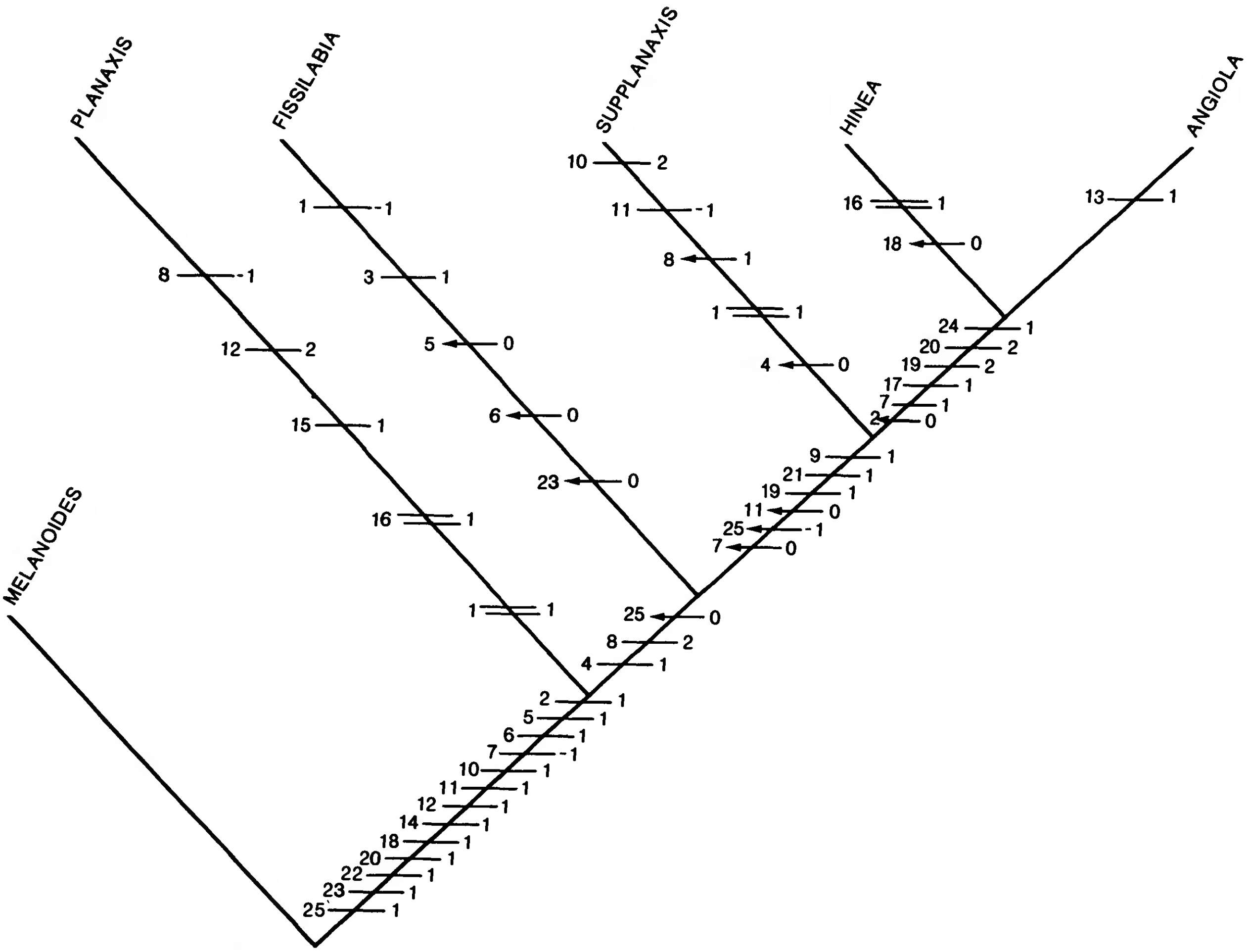

FIGURE 27.—Cladogram using *Melanoides* as outgroup. Nodes represent hypothetical ancestors. Numbers to left of tree branches represent characters and those on right indicate character states. Single bars across tree branches indicate changes in character states. Double bars signify character transformations that occur more than once (parallelisms and convergences). Arrows represent reversals. Characters used listed in Table 6.

TABLE 6.—Comparison of characters and character states of five major genera of Planaxidae using *Melanoides* as the outgroup (A = *Planaxis*; B = *Fissilabia*; C = *Hinea*; D = *Angiola*; E = *Supplanaxis*; F = *Melanoides*).

Character	A	B	C	D	E	F
SHELL						
1. Shell shape turreted narrow (0) turreted wide (1) turreted decollate (−1)	1	−1	0	0	1	0
2. Shell sculpture strongly sculptured (1) weakly sculptured (0)	1	1	0	0	1	0
3. Columellar fold present (1) absent (0)	0	1	0	0	0	0

TABLE 6.—Continued

Character	A	B	C	D	E	F
4. Outer lip placement extended on penultimate whorl (1) only moderately extended (0)	0	1	1	1	0	0
5. Protoconch sculpture no sculpture (0) sculptured (1)	1	0	1	1	1	0
6. Sinusigera notch in protoconch present (1) absent (0)	1	0	1	1	1	0
RADULA						
7. Rachidian cutting edge large central cusp, 2–4 denticles (0) single large blunt cusp (−1) large triangular saw-edged cusp (1)	−1	−1	1	1	0	0
8. Rachidian basal plate squarish tall (−1) rectangular narrow (0) rectangular tall (1) semilunar narrow (2)	−1	2	2	2	1	0
9. Rachidian top edge concave (1) convex (0)	0	0	1	1	1	0
10. Rachidian basal cusps absent (0) basal placement (1) median placement (2)	1	1	1	1	2	0
11. Lateral teeth sharp long cusps (0) large wide blunt cusps (1) large blunt, outwardly turned (−1)	1	1	0	0	−1	0
ANIMAL						
12. Mantle edge fringed (0) smooth (1) scalloped (2)	2	1	1	1	1	0
13. Luminescent mantle organ present (1) absent (0)	0	0	0	1	0	0
14. Snout tip narrow bilobed, highly extensible (0) moderately extensible (1)	1	1	1	1	1	0
15. Ctenidium long triangular leaflets (0) broad shallow leaflets (1)	1	0	0	0	0	0
16. Hypobranchial gland thick pad near anus (1) absent (0)	1	0	1	0	0	0
17. Ciliated groove on head-foot absent (1) present (0)	0	0	1	1	0	0
18. Salivary glands tightly coiled (1) relatively uncoiled (0)	1	1	0	1	1	0

TABLE 6.—Continued

Character	A	B	C	D	E	F
REPRODUCTIVE SYSTEM						
19. Brood pouch size large, 4 rounded chambers (1) large, many lamellar chambers (0) single small chamber (2)	0	0	2	2	1	0
20. Brood pouch location dorsal part of head-foot (0) right side of head-foot (2) both sides of head-foot (1)	1	1	2	2	1	0
21. Brood pouch relationship to esophagus under esophagus (1) over esophagus and into upper neck (0)	0	0	1	1	1	0
22. Pallial oviduct closed (0) open (1)	1	1	1	1	1	0
LARVAE						
23. Larval size small (1) large (0)	1	0	1	1	1	0
24. Number of larvae brooded many (1) few (0)	0	0	1	1	0	0
25. Type of development lecithotrophic (0) planktotrophic (−1) ovoviviparity (2) mixed (1)	1	0	−1	−1	−1	2

common, plesiomorphic character if the Thiaridae is the outgroup. A brood pouch with internal lamellae is the common kind seen in thiarids (Starmühlner, 1969:240) and is considered to be plesiomorphic in planaxids. A transformation series analysis based on structural complexity of the brood pouch was used in comparing the Planaxidae to the Thiaridae. The evolution of a single chamber in the right side of the head-foot from a more complex lamellar median chamber seems a logical, parsimonious progression. A long sperm gutter in the medial lamina of the pallial oviduct seems to be the primitive condition in most planaxids, cerithiids, and potamidids, but a shorter gutter sometimes occurs in thiarids. In most cerithiaceans, the seminal receptacle is distal and beneath the spermatophore bursa (bursa copulatrix) (personal observation). Thus, a location differing from this is regarded as apomorphic.

LARVAE.—Most workers regard planktotrophy as the primitive larval condition of prosobranchs (Jablonsky and Lutz, 1983:55). Transformation of this state through mixed development to lecithotrophy seems to be a logical progression.

CLADISTIC ANALYSIS

Polarization of binary character status was supported by evidence derived from morphological homology and ontogeny where possible, as described above, but was mainly achieved by out-group comparison. Multi-state characters were arranged in transformation series according to structural complexity or by the process of reciprocal illumination (Cairns, 1984:41), resulting from generation of trees derived from only binary characters. The characters used in the two analyses were chosen from shell, radula, soft anatomy and reproductive biology. In many cases, the characters are not completely comparable between outgroups. For example, *Batillaria* does not have a brood pouch and thus lacks the suite of characters associated with that structure.

Two analyses were made using the characters listed in Tables 5 and 6 and employing *Batillaria* and *Melanoides* as outgroups. By reshuffling the taxa five times, a total of five identical trees per outgroup were generated. A discussion of the two cladograms based on the two different data sets and two outgroups follows:

OUTGROUP *BATILLARIA*.—An analysis of 21 characters comprising 48 character states (Table 5) produced the cladogram in Figure 26. This tree had a consistency index of 0.75, and showed 5 reversals, and 8 character transformations that occurred more than once. There are seven changes in character states near the root of the cladogram between the outgroup and the Planaxidae. Character 18, the RPG ratio, is an index of the state of concentration of the nervous system and was particularly homoplastic. It underwent 2 reversals, 2 convergences, and had a consistency index of 0.25. The low consistency index of this character indicates that it is not a particularly discriminating one. This may be due to the narrow range of the RPG ratio among planaxid genera and the arbitrary division of the two character states between 59–60. Thus, the RPG ratio may not be conservative at the generic level. The three other characters that were homoplastic and showed low consistency indices were all derived from the shell (characters 1, 2, 4). This is not surprising because the shell is frequently subject to convergence in molluscan evolution (Davis, 1979:35; Gosliner and Ghiselin, 1984:261; Harasewych, 1984:23). Only one apomorphy defines the stem between the branch of the cladogram supporting *Fissilabia* and *Planaxis* and that branch defining the three taxa, *Supplanaxis, Hinea,* and *Angiola*. This is character 9, a relatively weak character, which defines the convexity of the rachidian tooth top. If this character were not considered, the separation would collapse into a trichotomy.

OUTGROUP *MELANOIDES*.—Analysis of 25 characters comprising 61 character states (Table 6) resulted in the cladogram shown in Figure 27. This tree had a consistency index of 0.73, with 11 reversals and 4 character transformations that occurred more than once. The total number of characters (25) and character states (61) used in this analysis was substantially greater than that in the *Batillaria* outgroup analysis, resulting in more homoplasy in this cladogram than in the other. The 13 steps at the root of the tree provide an adequate separation of the Thiaridae from the Planaxidae. Of the homoplasous characters, both character 1 and 16 show transformations that occurred more than once. Character 1 (shell shape) is particularly subject to evolutionary modification, as discussed above. Character 16 refers to a thickening of the hypobranchial gland near the anus that may be of a transitory nature and not suitable for cladistic analysis. This character needs to be reexamined more closely. Eleven characters underwent reversals. Of these, characters 2, 4, 5, and 6 refer to shell morphology, while characters 7, 8, and 11 are based on radular morphology. Reversals in these characters are not unexpected as both shell and radula are highly subject to modification, and changes in their morphology frequently represent adaptive shifts in taxa due to changing environments. Characters 23 and 25 concern the type of larval development, character 25 being more homoplastic than any other, having undergone 2 reversals. This is not surprising because it is not unusual for congeners of cerithiacean taxa to exhibit different kinds of development (Houbrick, 1973:898–899; 1974:33–34; 1980:139–140; 1985:6–8).

Both cladograms are essentially similar in their arrangement of taxa and support the hypothesis that the five planaxid taxa examined are valid and that the family is monophyletic. Although *Angiola* is given generic status herein, the case could be made that it is merely a subgenus of *Hinea*. The cladogram using the outgroup *Batillaria* (Figure 26) unites *Planaxis* and *Fissilabia* more closely and has a slightly higher consistency index than the one using outgroup *Melanoides* (Figure 27). The cladogram using *Melanoides* as the outgroup better defines the branch supporting *Supplanaxis, Hinea,* and *Angiola* from the other taxa than the cladogram employing *Batillaria* as the outgroup.

These same data produced identical trees when run on Felsenstein's PHYLIP package using the Wagner Network. For these reasons both cladograms are presented herein as suitable hypotheses of the phylogenetic relationships among planaxid genera. Although the genus *Holcostoma* was not used in the analysis, its shell and radular morphology suggest that it is closely related to the *Hinea–Angiola* lineage.

In summary, the Planaxidae is a small group of prosobranchs closely related to the freshwater Thiaridae and the subfamily Batillariinae of the Potamididae. They have a tight anatomical organization and have undergone moderate cladogenesis. The family represents a monophyletic radiation of the superfamily Cerithiacea into intertidal, hard substrate environments. They have adopted unusual brooding methods that are homologous or parallel to those commonly seen in the freshwater Thiaridae. *Angiola* species are unique in becoming bioluminescent, when disturbed.

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Formal tables (numbered, with captions, boxheads, stubs, rules) should be submitted as carefully typed, double-spaced copy separate from the text; they will be typeset unless otherwise requested. If camera-copy use is anticipated, do not draw rules on manuscript copy.

Taxonomic keys in natural history papers should use the aligned-couplet form for zoology and may use the multi-level indent form for botany. If cross referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa, using the same numbers with their corresponding heads in the text.

Synonymy in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

Text-reference system (author, year:page used within the text, with full citation in "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series: "(Jones. 1910:122)" or ". . . Jones (1910:122)." If bibliographic footnotes are required, use the short form (author, brief title, page) with the full citation in the bibliography.

Footnotes, when few in number, whether annotative or bibliographic, should be typed on separate sheets and inserted immediately after the text pages on which the references occur. Extensive notes must be gathered together and placed at the end of the text in a notes section.

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