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EDITORIAL COMMENT

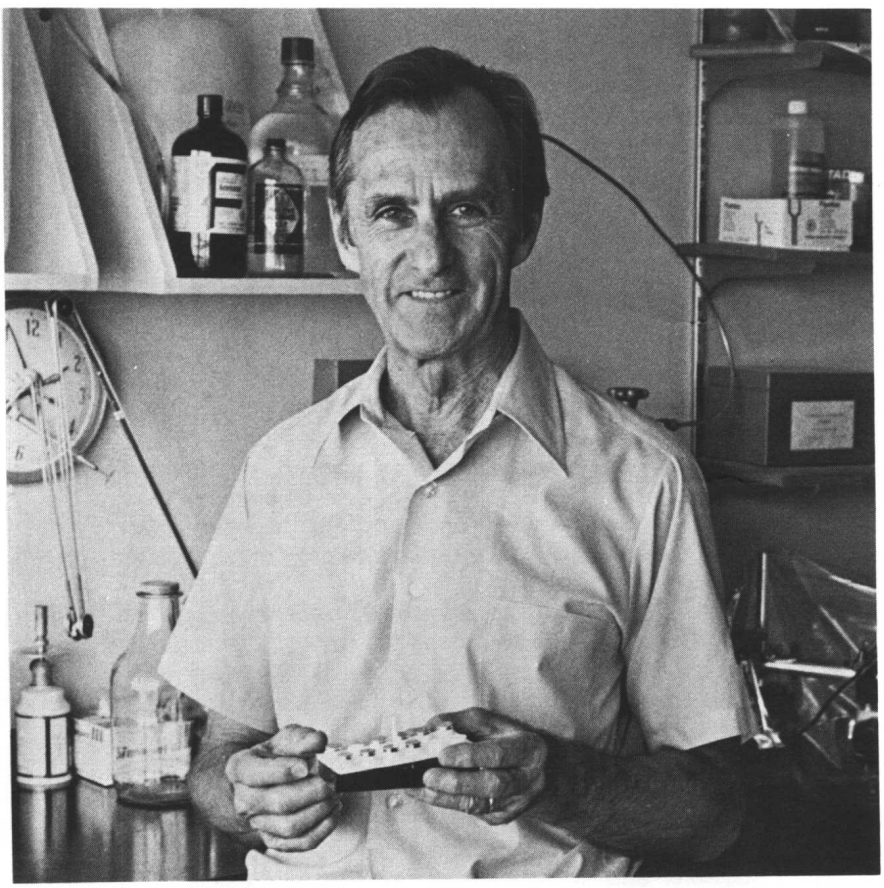
With the publication of *Perspectives in Malacology*, the *American Malacological Bulletin* embarks upon another new phase of its development. Through the publication of special editions, such as this and the forthcoming *Proceedings of the Second International Corbicula Symposium*, and *Entrainment of Larval Oysters*, we hope the *American Malacological Bulletin* will continue to serve as an outlet for timely and important communications of advances in Malacology.

These Special Editions will highlight recent malacological events and symposia. This first edition honors Professor M. R. Carriker on the event of his nominal retirement. Each participant of this Symposium Proceedings has in one way or another been influenced by Professor Carriker as co-worker, student, friend, or with luck, all three. The Editors of this Special Publication have been among the lucky ones and are thus particularly honored to have this opportunity to pay homage to their mentor.

We also take this opportunity to acknowledge Dr. L. Leon Campbell, Provost of the University of Delaware, for his continued support of this endeavor. The University of Delaware has kindly financed this publication because of Dr. Campbell's support. Dr. Franklin C. Daiber also deserves special thanks for his adept organization and coordination of this Symposium.

We are pleased to have the chance to start a new series of special publications in honor of Professor Carriker and hope this and future special editions will prove to be strong additions to our growing stable of AMU publications.

Editors
Perspectives in Malacology



PROFESSOR MELBOURNE R. CARRIKER

PERSPECTIVES IN MALACOLOGY; A SYMPOSIUM TO HONOR M. R. CARRIKER

FOREWORD

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This special issue of the *American Malacological Bulletin* is dedicated to Melbourne Romaine Carriker. The papers that make up this issue result from a symposium held on Thursday, February 7, 1985 on the campus of the University of Delaware to honor the time of his retirement and to give recognition to his many acccomplishments.

Mel, as he is fondly called by friends and associates, was born 25 February 1915 at Santa Marta, Colombia, South America, where his family owned a coffee plantation. His introduction to zoological studies came at an early age. During 1934, he was a member of a nine month ornithological expedition to the eastern Andean slopes of Bolivia sponsored by the Academy of Natural Sciences of Philadelphia and led by his father, Melbourne A. Carriker, Jr.

Dr. Carriker received his Bachelor of Science degree at Rutgers University in 1939 and his Ph.D. in 1943 in invertebrate zoology and physiological chemistry from the University of Wisconsin. He was granted an honorary Doctor of Science degree from Beloit College, Wisconsin in 1968.

His scientific career was interrupted during the war years when he served as a U.S. Naval Reserve officer in the North Pacific (1943-1945). Following the war he became Assistant Professor of Zoology at Rutgers University where he rapidly established himself as a master of molluscan comparative anatomy and functional morphology. He began long term investigations of shell-boring mechanisms of predatory gastropods in general, but of *Urosalpinx* in particular, the published results of which have been highly acclaimed. Mel served as Associate Professor of Zoology at the University of North Carolina from 1954 to 1961 and during 1961-62 he was Program Director for the U.S. Bureau of Commercial Fisheries at the Biological Laboratory, Oxford, Maryland. Subsequently he spent a decade directing the ambitious and highly valued Systematics-Ecology Program at the Marine Biological Laboratory at Woods Hole, a program that resulted in numerous publications through which our knowledge of the marine flora and fauna of the Northeastern United States has been greatly increased. Mel has continually served from 1965 as editor for the manuals produced by the National Marine Fisheries Service on the Marine Flora and Fauna series. In 1973, he was appointed Professor of Marine Studies at the College of Marine Studies, University of Delaware, based at the Lewes Marine Studies Complex. It was here that Dr. Carriker reached full stride as a marine biologist, malacologist, teacher, editor, nationally and internationally involved leader.

Mel's career can be characterized as one of continual growth, diverse and multifaceted. It can be viewed through the eyes and with the minds of his students, and colleagues with whom he has interacted. Hallmarks of his career have been his dedication to students, mentor to associates, enthusiasm for science, outstanding service to his institutions and community, dedication to scientific excellence, organizer, editor, communicator, and international scientific ambassador of good will.

While he has officially retired, it is in name only. He continues to participate and to serve as he has for more than forty years.



PERSPECTIVES IN MALACOLOGY

SPECIAL EDITION NO. 1 OF THE *AMERICAN MALACOLOGICAL BULLETIN*
HONORING PROFESSOR MELBOURNE R. CARRIKER

SPECIAL EDITION NO. 1 JULY 1985

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FOUR CHARACTERS AND THE HIGHER CATEGORY SYSTEMATICS OF GASTROPODS

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ABSTRACT

Four characters are shown to have fairly similar patterns of taxonomic occurrence in a diverse array of mainly marine Gastropoda. These patterns and the morphological and presumably functional uniformity support the ideas that, within themselves, the characters are homologous and reflect phylogeny. The characters are: 1, *pigmented mantle organs* (PMOs) in the dorsal or right lateral mantle cavity wall of larvae and (in some taxa) postlarvae; 2, longitudinal *ciliated strips* (CSs) dorsal and ventral in the mantle cavity of postlarvae, merging posteriorly (commonly replacing ctenidia or other "gills" in creating the flow of water through the mantle cavity); 3, *chalazae* (CHae) connecting egg cocoons one to another in a gelatinous egg mass or capsule, and 4, hyperstrophically coiled larval shells *(heterostrophy* [HET]).

In veligers, PMOs have almost invariably been thought to be excretory (larval kidneys). They are retained through metamorphosis into adulthood in the Epitoniacea, Architectonicidae, and Pyramidellidae. Also, they are retained sporadically in some young postlarval Bullomorpha. In postlarvae, PMOs have often been called hypobranchial glands. PMOs have not been shown to be excretory or hypobranchial in structure or function, and it seems highly unlikely that they change either of these at metamorphosis. PMOs release fine particles in suspension when the animal metamorphoses or is stressed. A PMO is thus unlike the purple-secreting true hypobranchial gland of muricaceans, the prey-anesthetizing dye of which is released in solution and becomes purple only after exposure to oxygen and light. The colors of the PMO pigments, which range from black, purple and brown to yellow, are in some cases genus- or species-specific. A histological cross-section of the mantle cavity, PMO, and two CSs of postlarval *Fargoa bartschi*, a pyramidellid, is illustrated as a basis for future comparisons.

Data on the taxonomic occurrences of the four characters (with larval and postlarval PMOs distinguished) are tabulated and summarized. The characters occur doubtfully in a few "primitive" mesogastropods. They occur definitely in some or all Epitoniacea, Architectonicacea, Pyramidellidae, Bullomorpha, Thecosomata, Aplysiomorpha, Pleurobranchomorpha, Ascoglossa, and Basommatophora, *i.e.* taxa in all three subclasses of the Gastropoda. It is well-established that "primitive" Opisthobranchia and "primitive" Pulmonata (Euthyneura) are related, being similar to one another anatomically and functionally. Hitherto, it was believed that the Euthyneura were derived from archaeogastropods or "primitive" mesogastropods (cerithiaceans, rissoaceans, or littorinaceans). This paper shows that the ancestor or ancestors of euthyneurans probably also had some characters retained in living prosobranchs primarily in the Epitoniacea, Architectonicacea, and Pyramidellacea — which are now (and always have been?) far too specialized to be ancestral to gastropod higher taxa, which should be characterized by *combinations* of many more than four characters.

Over twenty years ago I began intermittent study of the natural history of the Epitoniidae, Architectonicidae, and Pyramidellidae. Aspects of particular interest to me are their feeding, reproductive biology, larvae, and systematics (including higher categories). The three families are of phylogenetic interest because they combine prosobranch and opisthobranch traits (Robertson, 1974). This paper presents and reviews certain data from the egg masses, veligers, larval shells, and postlarval anatomies of the three families and what I believe to be their closest living relatives (in different superfamilies, orders, and even subclasses). Four characters are shown to be relevant to an overall understanding of gastropod higher category relationships, and of the evolutionary origins of the extraordinary diversity in gastropod form and function.

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Studying the veligers of all three families, I noted the consistent presence of a conspicuous pigmented organ. This is variously colored (commonly black, brown, purple, or yellow) or two- or even three-colored, and is located in the dorsal or right lateral mantle cavity wall under the shell near the anus. In the literature, these organs have been called larval excretory organs (kidneys). Having doubts that this is their function, since 1973 I have noncommittally been calling them *pigmented mantle organs* (PMOs).

My own (partly unpublished) and several other studies have shown that in epitoniids, architectonicids, and pyramidellids, PMOs in the veligers are retained with little or no change through metamorphosis and throughout postlarval life, maintaining approximately the same relative size. In the literature, the PMOs of adults have been called, among other things, hypobranchial glands. A larval kidney can hardly transform at metamorphosis into a hypobranchial gland!

The PMO has not been shown to have the histology or functions of an excretory organ or a hypobranchial gland. The idea that the PMO is hypobranchial in postlarval epitoniids, architectonicids, and pyramidellids derives from its release of pigment that in some cases is purple. At least two more crucial differences between hypobranchial and PMO colors have been overlooked. In muricids, for example, the true hypobranchial gland secretes an indigo-like dye in solution that is first greenish yellow and then becomes purple upon exposure to oxygen and light (Fretter and Graham, 1962). The PMO, by contrast, consists of a thin-walled, easily-ruptured sac full of paste-like material that does not change color (except rarely during ontogeny). This pigment is released as a cloud of fine particles in suspension. These particles have yet to be characterized chemically (but see Comfort, 1961). The second difference is that the purple of muricaceans is used to anesthetize prey. In the Bahamas, I have observed *Purpura patula* (Linné) using its purple to attack the chiton *Acanthopleura granulata* (Gmelin). By contrast, repeated observations have shown that the PMO of postlarval epitoniids does not release pigment before or while the animal feeds (*e.g.*, Robertson, 1983a,b). Pigment is released when the animal metamorphoses, or is molested, nearly drying out, dying, or dropped into alcohol. Further discussion of a possible repugnatorial role of the PMO is beyond the scope of this paper.

(Parenthetically, it should be mentioned that there is a third major kind of purple dye released by gastropods, aplysiopurpurin, coming from postlarval *Aplysia*. This is released in solution and does not change color. Its chemistry has been shown to differ radically from that of muricid purple. Judging by Comfort (1961), aplysiopurpurin is not the same as a PMO pigment (ianthinine, from *Janthina*). *Aplysia* does, however, release its dye when it is stressed.)

Thorson (1946) was struck by the similarity between the PMOs of larval pyramidellids and tectibranchs. These and other data led to Fretter and Graham's (1949) transfer of the Pyramidellidae from the Prosobranchia to the Opisthobranchia. Thus PMOs have already been used to infer phylogenetic relationships. Thorson later (1957) noted that larval epitoniids also have pyramidellid- and tectibranch-like PMOs.

In the mantle cavities of adult architectonicids and pyramidellids, there are paired and juxtaposed longitudinal *ciliated strips* (CSs) that join posteriorly. When ctenidia or other "gills" are reduced in size or absent, CSs create the left to right flow of water through the mantle cavity. CSs are beside and below the (shorter) PMO, and they help to stir the particles into suspension when the PMO is ruptured. CSs seem not to be present in any veligers or epitoniids of any age.

Similar (homologous?) PMOs and CSs also occur in a wide array of mainly opisthobranch gastropods, the PMOs primarily in veligers and the CSs in postlarvae. CSs also occur in certain postlarval basommatophorans. I became intrigued by the possibility that the pattern of taxonomic occurrence of each of these characters might yield evidence on whether there are homologies from taxonomic group to group. This would support the idea that these characters are relevant to an understanding of higher category relationships. I therefore assembled the data in Tables 1-3 from my own work and the literature.

Two characters are obviously too small a sample to achieve the desired ends, so two more characters already familiar to me were added to this study. These are *chalazae* (CHae), connecting egg cocoons end to end within an egg mass or capsule (Table 4), and *heterostrophy* (HET), larval hyperstrophy (Table 5).

Explanation is needed as to why pyramidellids are here classified as prosobranchs. After transferring the family to the opisthobranchs in 1949, Fretter and Graham treated it extensively in their classic 1962 book on British *prosobranchs*, tabulating some of the prosobranch, transitional, and opisthobranch traits of pyramidellids on p. 639. Grouping pyramidellids as opisthobranchs separates them from their closest living (prosobranch?) relatives, *i.e.* architectonicids and more distantly epitoniids. Morton (1963:56) wrote: "In their totality of characters, the Pyramidellidae are somewhat unlike any classical opisthobranch." Fretter (1980) stated that no family but pyramidellids "has evolved a mosaic of opisthobranch-prosobranch characters ...," and that this family is the only one to have "turned ... the balance towards opisthobranchs ..." Fretter (1980) divided the Opisthobranchia into the Pyramidellimorpha and Euopisthobranchomorpha, thereby implicitly acknowledging differences. Most recently, Gosliner (1981), a student primarily of opisthobranchs, gave reasons for excluding pyramidellids from the subclass. I concur, but the question is not so much "Which subclass does this family belong in?" as "Where should the line be drawn between the two intergrading subclasses?"

Explanation is also needed as to why the order (or suborder) Heterogastropoda does not appear in the tables. The taxon was named and defined in an illustrated popular shell book in Japanese by Habe and Kosuge

(1966) and further discussed in a scientific paper in English by Kosuge (1966). Recently, some other malacologists (*e.g.* Climo, 1975; Fretter and Graham, 1982) have, formally or informally, been recognizing the Heterogastropoda. I quote from Robertson (1974:215):

> [Habe and Kosuge] grouped the Architectonicidae, Mathildidae, Epitoniidae, Janthinidae and Triphoridae in ... the Heterogastropoda, which they placed between the Neogastropoda and Basommatophora; they dispensed with subclasses and placed the Entomotaeniata (Pyramidellidae) and Cephalaspidea [Bullomorpha] after the Basommatophora. This classification is unsatisfactory because the relationships between Triphoridae and the other 4 families seem highly tenuous and because the other families are separated from their nearest relatives (mesogastropods, pyramidellids and cephalaspids).

In 1980, Fretter did not consider the heterogastropods "to be a valid group of gastropods, but a convenient descriptive term for those which may have followed some initial steps towards the opisthobranch grade." Fretter and Graham (1982) extended the concept of the 'Heterogastropoda' to include the Cerithiopsacea and Eulimacea, but they persisted in excluding the Pyramidellidae. Boss (1982) did include the Pyramidellidae in the Heterogastropoda provisionally, but he excluded the Cerithiopsidae, Epitoniacea, Aclididae and Eulimacea (all six taxa were grouped as prosobranchs).

In a paper mainly on one character (osphradial fine morphology), the Architectonicidae and Pyramidellidae were grouped by Haszprunar (1985b) in a new higher taxon (order?) Allogastropoda, which he placed in the subclass (?) Heterobranchia (=Euthyneura). He did not characterize these or (Haszprunar, 1985a) the suborder Heteroglossa (his new name for the Heterogastropoda), but referred for supporting evidence to two of his papers still in press. As these are not yet available to me, I pass judgment on the need for these higher taxa. It seems improbable, though, that a good case can be made for the Architectonicidae and Pyramidellidae being "the most primitive members of recent Heterobranchia [=Euthyneura]" (Haszprunar, 1985b:504).

Organismic nomenclature in the tables in many cases is updated. Taxa are identified only down to genera except in the case of previously unpublished data, for which species names are given. The classification and nomenclature of prosobranchs mainly follow Taylor and Sohl (1962), of opisthobranchs Thompson (1976), and of basommatophorans Hubendick (1978). Tillier's (1984) reclassification of the lower pulmonates arrived too late

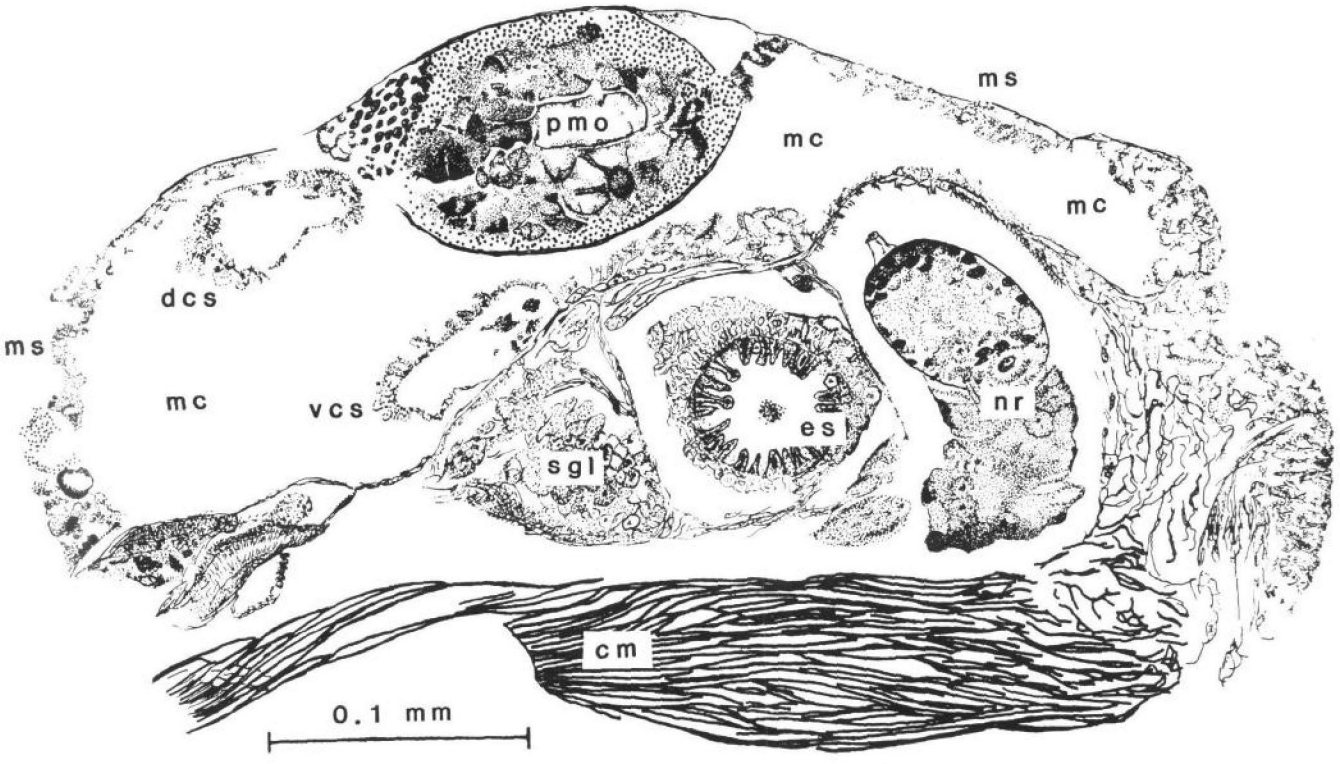


Fig. 1. Histological cross section through the mantle cavity (mc) of an adult odostomioid pyramidellid, *Fargoa bartschi*, showing the pigmented mantle organ (pmo) and the nearby dorsal and ventral ciliated strips (dcs, vcs), which are shown to be hollow crests that are attached weakly to the mantle cavity walls. The animal's left and right are transposed. In this species the periphery of the PMO is yellow and the interior purple. Other abbreviations: cm, columellar muscle; es, esophagus; ms, mantle skirt; nr, nerve ring; sgl, salivary gland.

Table 1. Systematic list of gastropods hypothesized to have homologous pigmented mantle organs (PMOs) either in veligers or postlarvae.

Taxon	Observed in veliger (V) or postlarva (PL)	Term applied	Color	Reference
PROSOBRANCHIA				
Mesogastropoda				
Superfamily?				
Rissoellidae?	PL	blotches	dark	[Note 1]
Epitoniacea ("Ptenoglossa")				
Epitoniidae	PL	Manteldrüse	purple-like	Thiele, 1928
Epitoniidae	PL	hypobranchial gland	purple	Robertson, 1963
Epitoniidae	PL	pigmented mantle organ	?	Robertson, 1974
Epitoniidae	V	pigmented mantle ("excretory") organ	?	Robertson, 1976
Couthouyella [Note 2]	PL	hypobranchial gland	purplish	Warén, 1980a
Epitonium	V	excretory organ	bluish-purple	Thorson, 1946 [in part as *Aclis*; Note 3]; Thorson, 1957
Epitonium, *Amaea, etc.*	PL	purple gland	ashy brown	Taki, 1956, 1957
Epitonium	PL	hypobranchial gland	purple	Fretter and Graham, 1962
Epitonium	PL	hypobranchial gland area	purple	Salo, 1977
Epitonium	V & PL	purple gland (V); hypobranchial gland (PL)	dark purple	McDermott, 1981
Epitonium	PL	hypobranchial gland	purple	Fretter and Graham, 1982
Janthinidae	V	pigmented mantle ("excretory" organ)	?	Robertson, 1976
Janthina	V	pigment mass	violet	Haddon, 1882
Janthina	PL	Hypobranchialdrüse; Manteldrüse; Farbdrüse	purple-like	Thiele, 1897
Janthina	V	Farbdrüse	?	Fraenkel, 1927
Janthina	PL	hypobranchial gland	purple; violet	Fretter and Graham, 1962, 1982
Architectonicacea				
Architectonicidae	V	pigmented mantle ("excretory") organ	?	Robertson, 1976
Heliacus spp.	V & PL	PMO	black; pink; yellow; violet	Robertson, unpublished
Philippia	V & PL	(opisthobranch-like) larval excretory organ	black	Robertson *et al.*, 1970
Mathildidae?				
Gegania?	PL	sac-like organ [Note 4]	dark	Climo, 1975
Pyramidellacea				
Pyramidellidae (including Cyclostremellidae [Note 5])		pigmented hypobranchial gland	?	Fretter and Graham, 1962
Pyramidellidae	V & PL	PMO	usually dark	Robertson, 1974
Pyramidellidae	V	pigmented mantle ("excretory") organ	?	Robertson, 1976
Boonea 3 spp.	V & PL	PMO	yellow and brown	Robertson, unpublished
Cyclostremella	PL	PMO (?hypobranchial gland)	greenish white, bright yellow, and brown	Robertson, 1973
Ebala	V	larval kidney	reddish-yellowish	Rasmussen, 1944
Ebala	V	excretory organ	sealing-wax red; brownish; dark reddish purple	Thorson, 1946
Fargoa bartschi	PL	PMO	yellow-brown (juv.); dark brick red (adults)	Robertson, 1978
Fargoa 3 spp.	PL	PMO	yellow and brown	Robertson, unpublished
Odostomia	V	glande anale	?	Pelseneer, 1914
Odostomia	V	anal gland	nearly black	Lebour, 1932
Odostomia	V	larval kidney	grey	Rasmussen, 1944
Odostomia	V	excretory organ		Thorson, 1946
Odostomia	V & PL	pigmented gland	brown-orange or pink	Fretter and Graham, 1949
"Odostomia"	V	excretory organ	black	Amio, 1959
Odostomia	PL	Excretionsorgan	orange-red	Ankel, 1959

Table 1. (continued)

Taxon	Observed in veliger (V) or postlarva (PL)	Term applied	Color	Reference
Odostomia	PL	Larvenniere	orange-red	Maas, 1965
"Odostomia"	V	[larval kidney]	dark	Minichev, 1971
Pseudoskenella	PL	[colored] region of hypobranchial gland	yellowish orange	Ponder, 1974
Pyramidella crenulata		PMO	pale yellow	Robertson, unpublished
Turbonilla	PL	protein cells of hypobranchial gland	?	Fretter and Graham, 1962
Turbonilla sp.	PL	PMO	pale greenish yellow and pale brown	Robertson, unpublished
Turbonilla vineae	PL	PMO	pale greenish yellow	Robertson, unpublished
OPISTHOBRANCHIA ("Euthyneura" in part)				
Bullomorpha ("Cephalaspidea")				
Many families	V	excretory organ (kidney)	orange-red; black; carmine (V); purple; red	various, e.g. Thorson, 1946; Hurst, 1967
Diaphanidae	PL	pigmented hypobranchial gland	?	Fretter and Graham, 1962
Retusidae				
Retusa	V & PL	larval (secondary) kidney	black	Smith, 1967
Aglajidae				
Aglaja	V	[PMO]	brown-black	Fasulo *et al.*, 1982
Philinidae				
Philine	V	spot (excretory organ)	red, later black	Amio, 1963
Philine	V & PL	larval kidney	jet black	Horikoshi, 1967
Philinoglossidae				
Philinoglossa [Note 6]	V	larval kidney	black	Swedmark, 1968
Pleurobranchomorpha ("Notaspidea")				
Umbraculidae				
Umbraculum	V	Exkretionsorgan	brown	Heymons, 1893
Umbraculum	V	large . . . spot	brown	Ostergaard, 1950
Pleurobranchidae				
Berthella	V	anal cells	dark	Usuki, 1969
Berthellina	V	larval kidney	dark reddish	Gohar and Abul Ela, 1957
Pleurobranchus	V	excretory organ	pink	Rao and Alagarswami, 1962
Ascoglossa ("Sacoglossa")				
Several families	V	excretory organ (kidney)	black	various, e.g. Thorson, 1946; Hurst, 1967
PULMONATA? ("Euthyneura" in part)				
Basommatophora?				
Amphibolidae?				
Amphibola?	V	larval kidney	black	Pilkington and Pilkington, 1982 [Note 7]

for consideration here.

MATERIALS AND METHODS

The main places where epitoniids, janthinids, architectonicids, and pyramidellids were studied alive are listed in the Acknowledgments. The species are listed in the tables.

Several North American east and Gulf coast odostomioid pyramidellids were studied histologically. The most instructive section was from *Fargoa bartschi* (Winkley, 1909), a "rare" ectoparasite on the serpulid polychaete *Hydroides dianthus* (Verrill, 1873). For information on the systematics, spermatophores, and feeding of *Fargoa* and *Boonea*, see Robertson (1978) and Robertson and Mau-Lastovicka (1979). The specimen of *F. bartschi* came from less than 1 m below low tide mark on the shore adjacent to Flume Pond, S of Gunning Point, 4 km NNE of Woods Hole, and was collected on July 13, 1978. The animal was relaxed with a solution of $MgCl_2$ isotonic with sea water, and fixed in Ciaccio (as suggested by Dr. Vera Fretter). Sections were cut 7 μm thick, and stained with hematoxylin and eosin.

RESULTS

PIGMENTED MANTLE ORGANS (PMOs)

These are here defined as nearly spherical to elongate, thin-walled, vacuole-containing sacs, each in a dorsal or right lateral mantle cavity wall, near the anus and under the shell (often visible in transparency). The sac

contains paste-like pigment particles (on their colors see later). When the sac ruptures, particles are released in a cloudy suspension. Care has to be taken not to identify as PMOs pigment markings having other attributes and positions.

Figure 1 illustrates a histological cross section of the mantle cavity (mc) of the odostomioid pyramidellid *Fargoa bartschi*, showing its PMO and nearby CSs (see later). The section is anterior to the anus, at the level of the nerve ring (nr) and salivary gland (sg). Fretter and Graham's (1962: fig. 79, pc) cross section of the mantle cavity of a *Turbonilla* (Pyramidellidae) is one of the few published histological portrayals of a PMO. Their figure shows more discrete cell outlines, and they identify them as "protein cell[s] of [the] hypobranchial gland." Farther to the animal's right, above the dorsal CS, they show "mucous cell[s] of the hypobranchial gland." Fretter and Graham also show something else not seen in *Fargoa*: "hypertrophied gland cells on [the] floor of [the] mantle cavity."

The "purple gland" (PMO) in postlarval Epitoniidae is long and cylindrical and lies to the right of the ctenidium and to the left of the oviduct ("vagina") and (posteriorly) the rectum ("intestine") (Taki, 1956, 1957). The purple-secreting "hypobranchial gland" of *Janthina janthina* (Linné) is a broad band in the region between the "vas efferens" and the rectum; that of *J. exigua* Lamarck lies above the anterior end of the "uterus," which is anterior to the rectum (Thiele, 1897:647-648). In adult *Heliacus* (Architectonicidae), the PMO is fragmented by transverse folds of the mantle (a "gill"?) and extends between the dorsal CS and rectum (Robertson, unpublished). Generally, though, a PMO remains cohesive.

PMOs occur in many veligers of taxa in the meso-gastropod - lower euthyneuran grade (Table 1). Histologically, the PMO of a larval *Retusa* (Bullomorpha) is like that of postlarval *Janthina, Fargoa,* and *Turbonilla* (Smith, 1967). In larval *Philine* (also Bullomorpha), however, the pigment appears to surround the PMO cells (Brown, 1934), but perhaps these had ruptured.

PMOs are retained through metamorphosis and throughout life in four or five prosobranch families: the Epitoniidae, Janthinidae, Mathildidae, Architectonicidae, and Pyramidellidae. Unfortunately, the relevant observations on metamorphoses showing that this is definitely the case remain largely unpublished (I am the principal culprit). Dr. Jane B. Taylor (unpublished) has made such observations on *Epitonium* (Epitoniidae) and *Janthina* (Janthinidae), and I have on *Heliacus* (unpublished) and *Philippia* (both Architectonicidae) (Robertson *et al.*, 1970); I have also on *Boonea* (Pyramidellidae) (unpublished). McDermott (1981:70) remarked that the "dark purple mass" in an *Epitonium* veliger "is probably the rudiment of the pigmented hypobranchial gland of the adult."

PMOs also occur in the young postlarvae (rarely adults) of at least two opisthobranch families, the Retusidae and Philinidae (Table 1). In the prosobranchs in which it occurs, the PMO maintains approximately the same size relative to the shell, although it often elongates after metamorphosis. In the few opisthobranchs that retain the PMO into the young postlarva, the PMO decreases in relative size and in most species disappears (see Thorson, 1946). Thus the prosobranch PMO condition seems more "primitive" than the opisthobranch one.

In *Philine*, a remnant of the "larval kidney" is visible in the postlarval juveniles of at least four species, and it is retained in the adults of one or more of these (Horikoshi, 1967). In *Retusa*, "the embryonic kidney degenerates ... after hatching" (Smith, 1967:751).

PMO pigments occur in nearly all colors in the spectrum: black, purple, violet, blue, greenish, yellow, grey, brown, orange, pink, and red. Commonly, one PMO is two- or even three-colored, one color partly masking another. The colors are usually genus- or species-specific (Table 1) so they are, in many cases, good taxonomic characters at the levels of species and genera. Only in *Philine* has a PMO color been reported to change during ontogeny. Combining all the available color information about the Pyramidellidae and all the other PMO-bearing taxa combined, it can be seen (Table 2) that there is about the same color diversity within this family as in all the others combined. Thus there is no basis for a claim that the color diversity reflects non-homology. There are taxonomic trends: yellow is commonest in the Pyramidellidae, purple in the Epitoniacea, black in the Architectonicacea and Bullomorpha, etc. *Janthina* is the PMO-bearing gastropod yielding the most copious quantities of PMO pigment. This happens to be purple or violet. Comfort (1961) did well to choose this animal for his preliminary biochemical study.

Table 2. PMO colors (from Table 1): approximate numbers of occurrences in different species or genera.

	Occurrences	
	Pyramidellidae	Non-Pyramidellidae
Yellow/orange	13	2
Red/pink	7	7
Brown	7	4
Black/grey	3	10
Greenish white	3	0
Purple/violet/blue	1	14

"Larval or secondary kidneys" are well known in aplysiomorph, nudibranch, and onchidiid veligers. These organs are like PMOs in being near the anus, but they mostly are colorless; occasionally, though, they have some pigmented inclusions. Heymons (1893), Mazzarelli (1904), Saunders and Poole (1910), Smith (1967), Thompson (1976:81), and Bonar (1978), among others, believed that these "larval kidneys" are homologous with PMOs, but this seems questionable. Fioroni (1966) provisionally distinguished between primary larval kidneys, cephalic larval kidneys, anal or pallial larval kidneys, and other larval excretory organs. PMOs belong in the third

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category, but Fioroni also included in it some possibly extraneous transparent or even paired structures. The best recent papers on the confused subject of opisthobranch "larval kidneys" are by Bonar and Hadfield (1974), and Bickell and Chia (1979). Hurst (1967) was the first to emphasize the absence of pigment in the "kidneys" of most larval "higher" opisthobranchs.

CILIATED STRIPS (CSs)

These are here defined as paired dorsal and ventral longitudinal tracts of strongly beating cilia extending from near the mouth of the mantle cavity to its posterior, near or at which the strips join. Figure 1 shows that, along part of their lengths, *Fargoa* CSs are close to the PMO. (The PMO is differently positioned in some other taxa.) The figure also shows that lumina underly some CSs. In *Heliacus*, the ventral CS lumen is the pedal gland that passes through the nerve ring and secretes the tough, elastic mucous thread emerging from the ventral pedal pore (Dr. George M. Davis, unpublished). In other taxa, the lumina may be blood sinuses. These strips and their posterior termination are present even in the extraordinarily long pallial cecum of *Acteon*, which coils to the tip of the viscera (Fretter and Graham, 1954). CSs commonly aid or replace ctenidia or "gills" in creating the left to right flow of water through the mantle cavity. In taxa with post-larval PMOs, CSs help to stir the PMO pigment particles into suspension. It is noteworthy that the taxon with the most copious PMO pigment (Epitoniacea) lacks CSs that would help to disperse it.

Of the four characters treated in this paper, CSs are the one most likely not to be homologous in all the animals in which they are here recorded (Table 3). Molluscan skin is commonly ciliated, and ciliary tracts might evolve convergently in places where there is a functional "need" for them. The "ciliated strips" of the minute prosobranchs *Omalogyra* and *Rissoella* may well be convergent with the other CSs in Table 3 (Note 8).

CHALAZAE (CHae)

The chalazae in a hen's egg are different from gastropod chalazae, the latter being a misnomer well entrenched in the literature. Gastropod chalazae are here defined as threads connecting egg cocoons (Thorson's 1946 term) end to end in a continuous string in the order in which they are laid, inside a gelatinous egg mass or capsule. There are one or more egg cells or embryos in a cocoon (they are most numerous in *Aplysia*). CHae help maintain the integrity of an egg mass, and they may also tether each cocoon to facilitate hatching of its contained larva(e).

A chalaza is continuous with the wall of the cocoon. According to Pelseneer (1914: fig. 5), chalazae of a European *Odostomia* (Pyramidellidae) have inner and outer layers, the inner one terminating at the *inner* end of the cocoon, interrupting the inner layer of the cocoon (shown black in Pelseneer's figure). The outer layer of the chalaza is continuous with the outer layer of the cocoon. Morton (1955c) made similar observations on the egg cocoons and CHae of *Ovatella* (Ellobiidae), except that he did not distinguish two layers in the cocoon walls, only fine concentric laminae. CHae are commonly thin and overlooked.

CHae occur almost exclusively in taxa of the "higher" mesogastropod - lower euthyneuran grade (Table 4). However, they have also been reported in *Valvata* (Valvatidae), an enigmatic group generally classified somewhere among "lower" mesogastropods, and *Campanile* (Campanilidae), a cerithiacean also in the "lower" mesogastropods.

The best published work on *Valvata* "chalazae" is by Kruglov and Frolenkova (1981), who did not realize their phylogenetic interest. *Valvata* lays its cocoons in egg capsules, which by my definition have hardened flexible outer walls. All other CHae recorded in Table 4 are from gelatinous egg masses. A capsule necessitates the presence of a preformed exit hole or slit through which the young can hatch. A slit is present on a *Valvata* capsule. CHae connecting the cocoons are attached inside the base and apex of the capsule. Oddly, the oval egg cell occupies nearly all the space in a cocoon, leaving little if any room for albumen therein (it may be extra-cocoonal). According to Kruglov and Frolenkova (1981), *Valvata* "chalazae" have species-specific morphologies (grooves, swellings, etc.) — which is not the case with any other CHae known to me. Houbrick (1981) observed and reported but did not illustrate *Campanile* "chalazae". He expressed doubts about their being true CHae. Thus the homologies of both *Valvata* and *Campanile* "chalazae" are uncertain.

CHae-like structures occur in some of the freshwater ("higher limnic") Basommatophora. Bondesen (1950) reported "egg strings (*fila ovi*)" in egg masses of the Physidae and Lymnaeidae; Régondaud (1973) reported them also in the Chilinidae. In Bondesen's complex terminology, these strings are extensions of the tertiary envelope of the 2nd order, or the external membrane, and are "built up of several layers of fine lamellae" (Bondesen, 1950:78). The egg strings described and illustrated by Bondesen are indistinct, and he seems wrongly to have homologized them with CHae. The differences are best seen by comparing Bondesen's figure 35A and C, showing *Radix* (lymnaeid) egg cocoons with egg strings (f.o.) and Pelseneer (1914: fig. 5).

HETEROSTROPHY (HET)

Heterostrophy is hyperstrophic coiling of just the larval shell. Hyperstrophy has been defined, illustrated, and discussed most clearly by Knight (1952). Gastropod coiling can be likened to a spiral spring before and after it has been pulled through itself. Before, it is called orthostrophic; after, it is hyperstrophic; planispirality (coiling almost in one plane) is the intermediate condition. The direction of coiling *around* the axis and anatomical asymmetry are unreversed; it is the *polarity* of the axis that

Table 3. Systematic list of gastropods hypothesized to have homologous ciliated strips (CSs) in their mantle cavities.

Taxon	Term applied (key words)	Reference
PROSOBRANCHIA		
Mesogastropoda		
Superfamily uncertain		
Omalogyridae?		
Omalogyra? [Note 8]	strips of ciliated columnar cells (epithelium)	Fretter, 1948
Rissoellidae?		
Rissoella? [Note 8]	strips of columnar ciliated cells (epithelium)	Fretter, 1948
Architectonicacea		
Architectonicidae		
Heliacus	ciliated tracts (dorsal crest)	Robertson, 1974
Heliacus	ciliary tracts	Haszprunar, 1985b
Pyramidellacea		
Pyramidellidae	ciliated ridges; strips	Fretter and Graham, 1962
Boonea	ciliated tracts	Robertson, 1974
"Chrysallida"	strip of ciliated epithelium (cells)	Fretter and Graham, 1949
Odostomia	ciliated strips on ridges	Fretter and Graham, 1949
Pyramidella	CSs	Robertson, unpublished
Turbonilla	strip of ciliated columnar epithelium	Fretter, 1951
Turbonilla	ciliated strip	Fretter and Graham, 1962
Turbonilla 3 spp.	CSs	Robertson, unpublished
OPISTHOBRANCHIA ("*Euthyneura*" *in part*)		
Bullomorpha ("Cephalaspidea")		
Acteonidae		
Acteon	raphé; bande ciliée; bandelette ciliée	Perrier and Fischer, 1911
Acteon	ciliated ridge	Fretter and Graham, 1954
Acteon	dorsal and ventral ciliated bands	Fretter, 1975
Acteon	ridges	Brace, 1977
Maxacteon	raphae	Rudman, 1972c
Pupa	ciliated ridges; raphae	Rudman, 1972c
Bullinidae		
Bullina	ciliated ridges; raphae	Rudman, 1972a
Hydatinidae		
Hydatina	raphé; bande ciliée	Perrier and Fischer, 1911
Hydatina	raphae	Rudman, 1972b
Micromelo	ciliated ridges; raphae	Rudman 1972a
Ringiculidae		
Ringicula	ciliated band	Fretter, 1960
Bullidae		
Bulla	ciliated bands; ridge	Brace, 1977
Atyidae		
Haminoea	raphés palléaux; bande épithéliale ciliée	Perrier and Fischer, 1910
Haminoea	ciliated ridges; raphae	Rudman, 1971
Haminoea	ciliated bands; ridge	Brace, 1977
Phanerophthalmus	raphae	Rudman, 1972e
Smaragdinella	raphae	Rudman, 1972e
Scaphandridae		
Cylichna	raphae	Lemche, 1956
Scaphander	raphé; bande épithéliale, etc.	Perrier and Fischer, 1911
Scaphander	superior raphe	Thompson, 1976
Scaphander	ciliated bands, ridge	Brace, 1977
Akeridae		
Akera	raphés palléaux, etc.	Perrier and Fischer, 1911
Akera	raphes; tracts	Morton, 1972
Akera	ciliated bands; ridge	Brace, 1977
Aglajidae		
Aglaja	ciliated bands; ridge	Brace, 1977
Chelidonura	dorsal and ventral ciliated stripe	Marcus, 1955

Table 3 (continued)

Taxon	Term applied (key words)	Reference
Philinidae		
Philine	raphae	Rudman, 1972d
Philine	ciliated bands; ridge	Brace, 1977
Aplysiomorpha ("Anaspidea")		
Aplysiidae?		
Aplysia? [Note 9]	patch of long cilia	Marcus and Marcus, 1957
Ascoglossa ("Sacoglossa")		
Juliidae		
Berthelinia	ciliated ridges	Kay, 1968
Volvatellidae		
Volvatella	ciliated ridges	Kay, 1968
Oxynoidae		
Oxynoe	ciliated ridges	Kay, 1968
Cylindrobullidae		
Cylindrobulla	ciliated ridges	Marcus and Marcus, 1956
PULMONATA ("Euthyneura" in part)		
Basommatophora		
Amphibolidae		
Amphibola	ciliated band	Pilkington *et al.*, 1984
Salinator	Flimmerband; Cilienband	Hubendick, 1945
Siphonariidae		
Siphonaria	bandelettes ciliées	Dieuzeide, 1935
Siphonaria	Flimmerband; Cilienband	Hubendick, 1945
Siphonaria	ridge	Yonge, 1952
Siphonaria	ciliated pallial ridges; etc.	Marcus and Marcus, 1960
Siphonaria	dorsal and ventral ciliated bands	Fretter, 1975
Siphonaria	ciliated ridge	Hubendick, 1978
Williamia	Cilienband; Flimmerband	Hubendick, 1945
Chilinidae		
Chilina	Flimmerleiste	Haeckel, 1911
Chilina	Flimmerband; Cilienband	Hubendick, 1945
Chilina	pulmonary cavity lamella	Harry, 1964
Chilina	dorsal and ventral ciliated bands	Fretter, 1975
Chilina	ciliated bands	Brace, 1983
[Latiidae? *Latia?* Note 10]		
[Planorbidae? Note 11]		

changes. Thus the base of the shell grows into a false spire, and *vice versa*. Dextral and hyperstrophic shells, with the false spire directed upwards, have left-handed shells that commonly are called sinistral (e.g. Vermeij, 1975, who did not distinguish the five gastropod coiling types). I prefer to use the term "sinistral" for *anatomical* mirror image reversals of symmetry, *i.e.* reversals in the direction of coiling *around* the axis. Anatomical sinistrality is already established early in embryology (Crampton, 1894) and cannot be reversed during the life of a gastropod. Thus a sinistral gastropod cannot suddenly become dextral, but a hyperstrophic (HETic) one can, and commonly does, become orthostrophic. This happens at metamorphosis in many of the taxa listed in Table 5. The functional significance of HET is unknown, and its presence in so many disparate taxa is remarkable.

As can be seen from Table 5, HET is common in many groups of opisthobranchs and their presumed prosobranch and pulmonate relatives. Strictly speaking, though, they are not all HETic. One usually thinks of a HETic protoconch at the tip of a teleoconch. The thecosome families Limacinidae and Peraclidae are hyperstrophic and remain so throughout life. They are holoplanktonic and do not really metamorphose; essentially, they are neotenous larvae (Bandel *et al.*, 1984). There are also the ascoglossan and nudibranch slugs, which discard their larval shells soon after metamorphosis and do not grow a teleoconch. By extension, these cases are grouped with HET in this paper. Another taxon interesting from the standpoint of coiling is *Blauneria* (Ellobiidae), which is anatomically sinistral and has a HETic (right-handed) protoconch.

"Anastrophie" and "co-axial heterostrophy" are terms introduced, respectively, by Dautzenberg and Fischer (1896) and Minichev and Starobogatov (1971) for the kind of HET seen in low-spired, widely umbilicate shell forms such as architectonicids and *Cyclostremella*,

Table 4. Systematic list of gastropods hypothesized to have homologous chalazae (CHae) in their egg capsules and masses.

Taxon	Term applied (key words)	Reference
PROSOBRANCHIA		
Mesogastropoda		
Valvatacea?		
Valvatidae?		
Valvata?	Chalazen; Faden	Nekrassow, 1928a, b
Valvata?	thread; string; cord	Cleland, 1954
Valvata?	chalaza	Fretter and Graham, 1962
Valvata? [see text]	[chalazae]	Kruglov and Frolenkova, 1981
Cerithiacea?		
Campanilidae?		
Campanile? [see text]	chalazae	Houbrick, 1981
Architectonicacea		
Architectonicidae		
Architectonica	string	Bandel, 1976a
Heliacus cylindricus, H. perrieri	CHae	Robertson, unpublished
Philippia	chalazae	Robertson, 1970
Mathildidae?		
Gegania?	chalazae [Note 12]	Climo, 1975
Pyramidellacea		
Pyramidellidae		
Odostomia	mucus string	Rasmussen, 1944
Odostomia	mucus string; chalaza	Rasmussen, 1951
"Odostomia"	fine canal	Amio, 1959
"Odostomia"	[thin flagellate appendage]	Minichev, 1971
Odostomia	[thick cord-chalaza]	Minichev, 1971
Odostomia	chalazae	Robertson, 1976
OPISTHOBRANCHIA ("Euthyneura" in part)		
Bullomorpha ("Cephalaspidea")		
"Acteocinidae"		
Acteocina	chalazal material	Mikkelsen and Mikkelsen, 1984
Aglajidae		
Aglaja	connections . . . ; string	Bandel, 1976b
Aglaja	[CH]	Fasulo *et al.*, 1982
Philinidae		
Philine	threads	Horikoshi, 1967
Aplysiomorpha ("Anaspidea")		
Aplysiidae		
Aplysia	thin thread	Fujita, 1904
Aplysia	fine filaments	Amio, 1955
Pleurobranchomorpha? ("Notaspidea")		
Pleurobranchidae?		
Berthellina?	short tube or tiny capsule [Note 13]	Bandel, 1976b
PULMONATA ("Euthyneura" in part)		
Basommatophora		
Ellobiidae		
Ellobium	gelatinous threads	Ewald, 1963
Ellobium	[CHae]	Marcus and Marcus, 1963
Ellobium	chalaziform filaments	Berry *et al.*, 1967
Ellobium	mucoid threads	Sumikawa, 1983
Melampus	allochalazal strand	Russell-Hunter *et al.*, 1972
Ovatella	chalaziform filament	Morton, 1955c
Amphibolidae		
Salinator	[CHae]	Tanaka, 1959
Siphonariidae		
Siphonaria	fine string	Hutton, 1882
Siphonaria	[CHae]	Fujita, 1895

Table 4 (continued)

Taxon	Term applied (key words)	Reference
Siphonariidae (continued)		
Siphonaria	fine threads	Fujita, 1904
Siphonaria	fine threads	Abe, 1940
Siphonaria	cord of gelatinous substance	Abe, 1941
Siphonaria	strings	Borland, 1950
Siphonaria	fine filaments	Amio, 1955
Siphonaria	fine canal	Amio, 1959
Siphonaria	fine thread	Voss, 1959
Siphonaria	[CHae]	Marcus and Marcus, 1960
Siphonaria	fino ligamento	Olivier and Penchaszadeh, 1968
Systellommatophora		
Onchidiidae		
Onchidella	funicule	Joyeux-Laffuie, 1882
Onchidella	fine strand	Fretter, 1943
Onchidium	cordon	Serène, 1937
Onchidium	gelatinous knot; cords	Awati and Karandikar, 1948
Veronicellidae	processus chalaziformes	Franc, 1968 [Note 14]

a near planispiral pyramidellid. These authors mistakenly believed that the axes of protoconch and teleoconch coiling coincide. Except in architectonicids with planispiral larval shells, the axes do not coincide: see my drawing of this (Robertson, 1976). In pyramidellids there can be suppressed HET, with the larval shell consisting of only about one nearly planispiral whorl, in which case the protoconch and teleoconch axes probably do coincide approximately. But the direction in which the false spire of a *several-whorled* HETic protoconch projects correlates with (is determined by?) the shape of the teleoconch, specifically whether it has a wide umbilicus. If there is no wide umbilicus (as in mathildids, and nearly all pyramidellids) the false spire has to project transversely (protoconch resorption seeming not to occur). Since they intergrade with transverse HET, the terms anastrophy and its synonym co-axial HET seem superfluous.

The three other characters are usually constant in their presence or absence in a genus or family. HET, on the other hand, commonly is sporadic within a genus (or species?). In certain European species of *Odostomia*, Thorson (1946) and Rodriguez Babio and Thiriot-Quiévreaux (1975) believed that planktotrophy correlates with HET, and lecithotrophy with reduced or wholly suppressed HET. This generality is not true of certain east North American species of *Fargoa (Odostomia, sensu lato)* that combine planktotrophy and suppressed HET (Robertson, unpublished). Suppressed HET may relate more to phylogeny than larval ecology. In the two genera in the Amphibolidae, both of which are planktotrophic, monotypic *Amphibola* is HETic while at least one species of *Salinator* is wholly orthostrophic (Pilkington and Pilkington, 1982; Tanaka, 1959). These examples show that HET cannot safely be predicted from planktotrophy in HET-prone taxa, and *vice versa*. However, it is possible that HET and lecithotrophy never go together.

HET has been reported in various prosobranchs not in Table 5. Minichev (1971) wrote that HET is apparently a widespread phenomenon among Prosobranchia. I disagree. The supposedly HETic taxa include the Trochidae, Docoglossa, Cyclophoridae, Rissoidae, Turritellidae, Aclididae, Eulimidae, Epitoniidae (Note 15), Janthinidae, Calyptraeidae, and Muricidae. It is beyond the scope of this paper to confirm or refute these mainly undocumented reports.

DISCUSSION AND CONCLUSIONS

The four characters treated herein co-occur in two families combining some prosobranch with some opisthobranch traits. These are the Architectonicidae and Pyramidellidae, both classified as prosobranchs in the present paper. Two more prosobranch families, also with some opisthobranch traits, the Epitoniidae and Janthinidae, have well-developed larval and postlarval PMOs, but lack CSs, CHae, and probably HET. The four characters are otherwise unknown in prosobranchs except for a few doubtful cases.

Among opisthobranchs, all four characters occur in the Bullomorpha, which is the most "primitive" order in this diverse subclass. In other opisthobranch orders, the four characters do not co-occur. Indeed, their patterns of taxonomic occurrence appear irregular. In the Aplysiomorpha and Ascoglossa, three of the characters are represented in each; in the Pleurobranchomorpha, two; in the Thecosomata, Acochlidiacea, and Nudibranchia, one each, and in the highly specialized Gymnosomata, none.

Larval PMOs are known in the Bullomorpha, Pleurobranchomorpha, and Ascoglossa. In the Bullomorpha, certain species of *Retusa* and *Philine* are the only opisthobranchs known to retain PMOs past me-

Table 5. Systematic list of Recent gastropods hypothesized to have homologous heterostrophy (HET), including hyperstrophy of some adult thecosomes, and hyperstrophy of some larval ascoglossan and nudibranch slugs.

Taxon	Term applied (key words)	Reference
PROSOBRANCHIA		
Mesogastropoda		
Epitoniacea? ("Ptenoglossa")		
Epitoniidae?		
Couthouyella? [Notes 2, 15]	HET	Gosliner, 1981
Architectonicacea		
Architectonicidae	HET [Note 16]	Robertson, 1963b
Architectonica	protoconch . . . sinistral	Hedley, 1903
Architectonica	sinistral	Bandel *et al.*, 1984
Heliacus	Protoconch . . . hyperstroph	Bieler, 1984c
Heliacus spp.	HET	Robertson, unpublished
Philippia	[HET]	Pelseneer, 1888a
Philippia	hyperstrophic larval shells	Robertson, 1964
Philippia	hyperstrophic protoconchs	Robertson, 1970
Philippia	hyperstrophically coiled larval shell	Robertson *et al.*, 1970
Philippia	hyperstrophically coiled protoconch	Robertson, 1976
Pseudomalaxis	[slight HET]	Hedley, 1903
Pseudomalaxis	hyperstropher Protoconch	Bieler, 1984a
Pseudomalaxis	Protoconch anastroph	Bieler, 1984b
Mathildidae		
Gegania	heterostrophe protoconch	Climo, 1975
Mathilda	heterostrophe . . . apex	Jeffreys, 1884
Mathilda	[HET]	Hedley, 1903
Pyramidellacea		
Pyramidellidae [incl. Cyclostremellidae; Note 5] [Note 17]		
Angustispira	nucléus sénestre	Pelseneer, 1912
Boonea	sinistral embryonic shell	Wells, 1959
Boonea	[HET]	Wells and Wells, 1961
Boonea	HET	Robertson, unpublished
Cyclostremella	heterostrophic protoconch	Moore, 1966
Cyclostremella	hyperstrophic protoconch	Robertson, 1973
Cyclostremella	coaxial heterostrophy	Hickman, 1980
Ebala	sinistral larval shell	Rasmussen, 1944
Myxa	heterostrophe apex	Hedley, 1903
"Odostomia"	nucléus sénestre	Pelseneer, 1912
Odostomia	sinistral	Rasmussen, 1944
Odostomia	sinistral	Rasmussen, 1951
Odostomia	hyperstrophically coiled protoconch	Robertson, 1976
Pseudoskenella	slight . . . heterostrophy	Ponder, 1974
Sayella [family?]	sinistral nucleus	Dall, 1885
Turbonilla	[HET]	Hedley, 1903
OPISTHOBRANCHIA		
Bullomorpha ("Cephalaspidea")		
Acteonidae		
Acteon	[HET]	Thorson, 1946
Acteon	heterostrophy	Lemche, 1948
Diaphanidae		
Diaphana	[HET]	Thorson, 1946
Diaphana	heterostrophy	Lemche, 1948
"Acteocinidae"		
Acteocina	nucléus . . . sénestre	Dautzenberg and Fischer, 1896
Acteocina	hyperstrophic . . . protoconch	Mikkelsen and Mikkelsen, 1984
Retusidae		
Retusa	*sinistral*	Rasmussen, 1944
Retusa	[HET]	Thorson, 1946
Retusa	heterostrophy	Lemche, 1948

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