

SYSTEMATIC POSITION OF *BASILISSOPSIS* AND *GUTTULA*, AND A DISCUSSION OF THE PHYLOGENY OF THE SEGUENZIOIDEA (GASTROPODA: PROSOBRANCHIA)

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ABSTRACT

The systematic position of the genera *Basilissopsis* Dautzenberg and Fischer, 1897, and *Guttula* Schepman, 1908, is discussed; both genera are confirmed to be members of the Seguenzioidea Verrill, 1884. A preliminary phylogenetic analysis of that superfamily, based principally on shell characters, is presented. The analysis suggests that two subfamilies (families) may be warranted: the Seguenziinae(idae) s.s., and the Guttulinae(idae) Goryachev, 1987. Three recent, major classifications of the Seguenzioidea are examined, with particular attention paid to the explicit or implicit characters on which those classifications were based. Assignment of the Seguenzioidea to the caenogastropod orders Littorinimorpha and Strombiformes is rejected. Placement of the superfamily, as a suborder, between the Vetigastropoda and Archaeotaenioglossa cannot be confirmed or rejected based on the available data. The pointed tip of the protoconch, presence of sensory micropapillae on cephalic and epipodial tentacles, and presence of a right subocular peduncle are suggested as potential synapomorphies with the Vetigastropoda. A compromise classification is proposed that would allow use of the taxa Archaeogastropoda and Vetigastropoda until more explicit statements of relationships among the included superfamilies can be made.

Recent discoveries of new gastropod taxa from deep-sea hydrothermal vent habitats, as well as re-examination and re-evaluation of previously known deep-sea taxa, have sparked renewed interest in the systematics, relationships, and phylogenies of "archaeogastropod" prosobranchs. In addition to the new animal morphologies, new, more comprehensive data sets and more stringent methodologies for estimating phylogenies are being used. These developments have presented systematists with exciting opportunities and challenges in determining relationships among archaeogastropods.

Hickman (1988) recently summarized the history of, and problems with, the concept of the order Archaeogastropoda Thiele, 1925. Most classifications since Thiele (1925) have used his concept, usually with a similar ordering of higher taxa (i.e., Pleurotomariina-Trochina-Patellina-Neritopsina) (Thiele, 1929; Wenz, 1938; Cox, 1960a; 1960b; Cox and Knight, 1960; Taylor and Sohl, 1962; Keen, 1971; Abbott, 1974; Boss, 1982; Vaught, 1989). With the exception of Yonge's (1947) proposal to exclude the Neritacea (Neritopsina) from the Archaeogastropoda, no formal assault on the constituency of the order was made until the mid-1970's. Golikov and Starobogatov (1975) proposed a radical and controversial classification of the prosobranch gastropods and totally abandoned the traditional Archaeogastropoda as a taxon. Not long after that classification was published, the deep-sea hydrothermal vents were discovered (Lonsdale, 1977), and the spectacular fauna associated with them sparked a frenzy of activity among systematists world wide (Fretter et al., 1981; McLean, 1981; 1988; 1989; 1990; Fretter, 1988; 1989; Haszprunar, 1989a; 1989b; McLean and Haszprunar, 1989; Warén and Bouchet, 1989). The many newly discovered anatomical ground plans of gastropods from the vents, as well as a better understanding of previously known groups (e.g., Seguenzioidea: Quinn, 1983b; Patelloidea: Lindberg, 1986; 1988; Cocculiniformia: Haszprunar, 1988c; Trochoidea: Hickman and McLean, 1990) have revealed an extraordinarily diverse and complex mosaic of "archaeogastropod"

evolution, particularly in the deep sea. Analyses of data derived from studies of these animals have resulted in at least one recent new classification of the Archaeogastropoda (Haszprunar, 1988a; 1988b). However, it is not within the purview of the present paper to deal in detail with relationships throughout the Archaeogastropoda, but rather to examine the phylogeny of the Seguenzioida Verrill, 1884, and to present an hypothesis of seguenzioid relationships (i.e., possible sister groups) within the Archaeogastropoda.

This paper is divided into three sections. The first section briefly examines the generic composition of the Seguenzioida, principally with respect to the systematic position of the genera *Basilissopsis* Dautzenberg and Fischer, 1897, and *Guttula* Schepman, 1908. The second section presents a brief, preliminary phylogenetic analysis of the relationships of the genera within the superfamily. The final section discusses the most recent classifications of the superfamily and the characters on which those classifications were based.

Relationships of *Basilissopsis* and *Guttula*

Prior to 1983, only six genera of seguenziids had been described: *Seguenzia* Jeffreys, 1876; *Basilissa* Watson, 1879a; *Ancistrobasis* Dall, 1889; *Basilissopsis* Dautzenberg and Fischer, 1897; *Guttula* Schepman, 1908; and *Thelyssa* Bayer, 1971 (Quinn, 1983a). Since that time, 11 additional genera have been described: *Carenzia* Quinn, 1983b; *Calliobasis* Marshall, 1983 (= *Ancistrobasis*; Quinn, in press); *Seguenziopsis* Marshall, 1983; *Thelyssina* Marshall, 1983; *Fluxinella* Marshall, 1983; *Asthelys* Quinn, 1987; *Hadroconus* Quinn, 1987; *Rotellenzia* Quinn, 1987; *Quinnia* Marshall, 1988a (replacement name for *Seguenziella* Marshall, 1983); *Halystes* Marshall, 1988a; and *Sericogyra* Marshall, 1988a. Recently, however, Goryachev (1987) excluded *Basilissopsis* and *Guttula* from the Seguenziidae, placing the former genus in the Trochidae and the latter in a new family, Guttulidae, assigned to the order Echinospirida (Caenogastropoda).

Dautzenberg and Fischer (1897) erected *Basilissopsis* for their new species *B. watsoni*, the shell of which they claimed was non-nacreous and lacked labral sinuses. These characteristics induced Dautzenberg and Fischer to place the genus near the Adeorbidae and induced Goryachev (1987) to assign it to the Trochidae. A specimen of *Basilissopsis* in the Natural History Museum, London (catalog number 1885.11.5.2598) conforms in all characters to those of *B. watsoni*, but is nacreous. The syntypes of *B. watsoni* are discolored and obviously long-dead, similar to many of the shells of *Basilissa* (*Ancistrobasis*) *rhyssa* Dall, 1927 (see below). Judging from Watson's (1879b, 1886) descriptions and illustrations, *Basilissa oxytropis* Watson, 1879, is a species that is certainly congeneric, if not conspecific, with *Basilissopsis watsoni* (Quinn, in press). Watson (1879b, 1886) stated that his species had nacreous shells (a contention that is borne out by the nacreous flakes that are all that remain of the syntypes [personal observation]) with labral sinuses. Dall (1927) described *Basilissa* (*Ancistrobasis*) *rhyssa* from the western Atlantic. This species has shells that are also very similar to those of *Basilissopsis watsoni*. Examination of Dall's specimens of *B. (A.) rhyssa* revealed that the shells are nacreous, and specimens with undamaged outer lips had shallow posterior and basal labral sinuses (Quinn, in press); one of those specimens is illustrated in Figure 1A-C. Most of the shells of *B. rhyssa* are discolored and have an opaque, porcelaneous surface obscuring the nacreous layer both externally and within the aperture, even when moistened. The opacity of these shell layers is probably a post-mortem mineralogical change. This condition also occurs in many specimens of *Ancistrobasis* (Quinn, in press) and *Seguenzia* (personal observation).

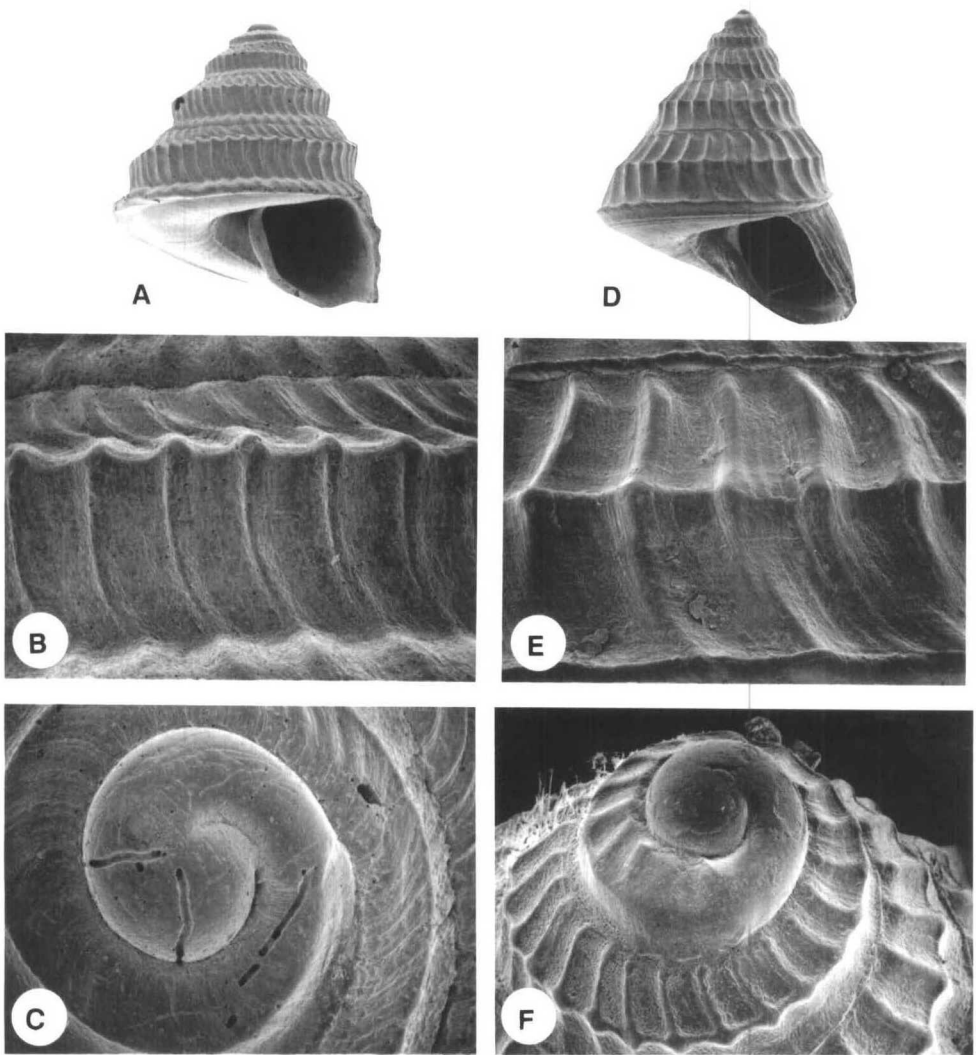


Figure 1. SEM micrographs of western Atlantic species of *Basilissopsis*. A–C, *B. rhyssa* (Dall, 1927) from off northeastern Florida, USNM 108395; A, apertural view of shell, 17 \times ; B, surface sculpture of same, 85 \times ; C, protoconch of another specimen, 114 \times ; D–F, *Basilissopsis* n. sp. from the Yucatán Channel, USNM 168769; D, apertural view of shell, 20 \times ; E, surface sculpture of same, 85 \times ; F, protoconch of same, oblique view, 114 \times .

collected with *B. rhyssa*. Because of this, Dall (1927), and probably Dautzenberg and Fischer (1897), considered their shells to be non-nacreous. Another western Atlantic species of *Basilissopsis* (Fig. 1D–F) also has nacreous shells with shallow labral sinuses and is currently being described (Quinn, in press). Nothing is known about the anatomy of *Basilissopsis* species, but the presence of nacre and labral sinuses supports inclusion of the genus in the Seguenzioidea as I have proposed elsewhere (Quinn 1983b; in press), rather than in the Trochidae (Watson, 1879b; 1886; Goryachev, 1987) or near a caenogastropod family such as the Adeorbidae (Dautzenberg and Fischer, 1897; Dautzenberg, 1927) or Strombidae (Golikov and Starobogatov, 1975; 1988).

Schepman (1908) erected the genus *Guttula* for his new species, *G. sibogae*. Two additional species, *G. blanda* Barnard, 1963, and *G. galathea* Knudsen, 1964, were described subsequently. Schepman (1908: 61) described the shells of *G. sibogae* as "pearly"; Barnard (1963: 266) described that of *G. blanda* as "iridescent"; and Knudsen (1964: 128), although not explicitly mentioning nacreous shells, implied that shells of *G. galathea* are nacreous by including the genus in the trochid subfamily Margaritinae, which is characterized by nacreous shells (Keen and Cox, 1960; Hickman and McLean, 1990). Therefore, Goryachev's (1987: 23) assertion that *Guttula* shells lack nacre is clearly erroneous.

Radulae of all three *Guttula* species have been described and figured (Schepman, 1908: 61, pl. 9, fig. 11; Barnard, 1963: 266, fig. 17; Knudsen, 1964: 128, fig. 4b-d; all reproduced in Quinn, 1983b: figs. 42-44). If we accept Barnard's (1963: 266) contention that the inner two marginal teeth in Schepman's drawing were transposed, all three radulae are extremely similar. All have a cusped rhachidian tooth flanked by a single pair of subrectangular lateral plates that may or may not have a weak cusp; the inner marginal teeth are long and blade-like, and are weakly denticulate near the tip; and the outer marginal teeth are long, slender, edentate, and have enlarged bases. This radular morphology is found, with relatively minor variations, in all seguenzioid genera for which radulae are known (e.g., see Marshall, 1983; 1988a; Quinn, 1983b; 1987; in press). Most recent authors agree that the radula of the Seguenzioida is of a reduced rhipidoglossan pattern (Boss, 1982; Marshall, 1983; 1988a; Quinn, 1983b; 1987; in press; Haszprunar, 1988a; 1988b; see also discussion below). Only Golikov and Starobogatov (1975; 1988) and Goryachev (1979; 1987) continue to consider the seguenzioid radular pattern to be taenioglossate, but explicit reasons for doing so have not been presented in any of their papers.

Characters of the external anatomy of *Guttula galathea*, a paratype of which was kindly loaned by Dr. Jorgen Knudsen (Zoologisk Museum, University of Copenhagen), provide further evidence supporting an hypothesis of close relationship of *Guttula* with the Seguenzioidae. The most obvious feature is the intentine (Fig. 2, i), which is very long, convoluted, and follows a course like that of *Seguenzia* (Quinn, 1983b), *Fluxinella*, *Hadroconus*, and *Ancistrobasis* (Quinn, 1987; in press). The fecal string is also similar to that of *Seguenzia*, *Fluxinella*, and *Hadroconus* (Quinn, 1983b; 1987; in press) in being continuous and in having a longitudinal stripe (or weak groove) that is darker and composed of coarser particles than the bulk of the feces. This probably represents the liver string found in some trochids (Fretter and Graham, 1962; personal observations) and, possibly, in the Peltospiridae (Warén and Bouchet, 1989: figs. 42-44, 52). Characters of the head-foot are as described by Knudsen (1964: 128) except that the penis and pallial tentacle are absent in the specimen I examined (Fig. 2); the cephalic and epipodial tentacles are micropapillate (personal observation). The external anatomy of *Guttula galathea* agrees quite well with that described for *Sericogyra periglenes* Marshall, 1988a (Marshall, 1988a: 246). Therefore, the presence of nacreous shells in *Guttula*; the strong similarities of radulae of this genus to those of *Seguenzia*, *Carenzia*, *Rotellenzia*, *Halystes*, *Quinnia*, *Hadroconus*, *Fluxinella*, *Ancistrobasis*, and *Sericogyra* (Marshall, 1983; 1988a; Quinn, 1983b; 1987; in press); and the similarity of the external anatomy of *Guttula galathea* to that of *Seguenzia*, *Fluxinella*, *Hadroconus*, *Asthelys*, and *Sericogyra* (Quinn, 1983b; 1987; in press; Marshall, 1988a) strongly suggest inclusion of *Guttula* in the Seguenzioidae.

Recent Russian authors have claimed that the relationships of *Guttula* are with the order Echinospirida (Goryachev, 1987) and, more specifically, with the sub-

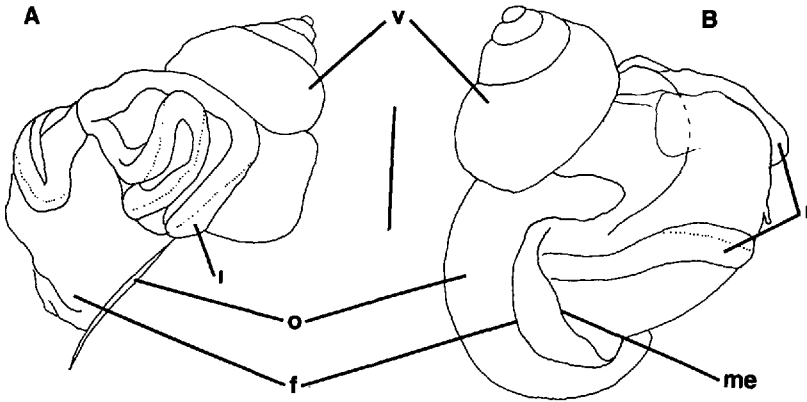


Figure 2. Diagrammatic sketches of the external anatomy of *Guttula galathea* Knudsen, 1964. A, Left side; B, right dorsal view. Scale bar = 1 mm. f, foot; i, intestine; me, mantle edge; o, operculum; v, visceral coils.

order Xenophoroidei (Golikov and Starobogatov, 1988). Goryachev cited three characters as reasons for his placement of *Guttula* in the Echinospirida: 1) lack of a nacreous layer of the shell, 2) lack of labral sinuses, and 3) unspecified radular characters. Reason 1 was shown above to be in error: shells of *Guttula* species are nacreous. The lack of labral sinuses is here considered a plesiomorphy within the superfamily because of the similarities of external anatomy and radula of *Guttula* species to those of "typical" seguenzioids. Because Goryachev's account did not specify what radular characters he considered important or why he suggested a relationship of *Guttula* with the Echinospirida, I cannot address individual points; however, he did imply that the radula of *Guttula* is taenioglossate, an interpretation I cannot accept (see discussion below). The nacreous shells, multispiral operculum with central nucleus, micropapillate cephalic and epipodial tentacles, continuous fecal rod with liver string, and reduced rhipidoglossate radula of *Guttula* species contrast with the non-nacreous shells, fan-shaped operculum with lateral nucleus, lack of micropapillae on the cephalic tentacles, no epipodial tentacles, fecal rod broken up into pellets, and true taenioglossate radula of *Xenophora* species (Morton, 1958; Ponder, 1983) and suggest that the two genera are not closely related as claimed by Golikov and Starobogatov (1988). Thus, I continue to consider *Guttula* to be a member of the Seguenzioidea, although more comprehensive anatomical examinations need to be completed.

SEGUENZIOID PHYLOGENY

Relationships within the Seguenzioidea

Data on shells, radulae, and external anatomy of the 16 genera considered valid here (see preceding section) were gathered from descriptions and illustrations published by Quinn (1983a; 1983b; 1987; in press) and Marshall (1983; 1988a). Twenty-two characters were chosen, of which 14 are conchological, 4 are radular, and 4 are anatomical. Data on shell characters are incomplete for *Basilissa*, the radulae of five genera are unknown, and the external anatomies of nine genera are incompletely described or unknown. The following discussion is necessarily preliminary and less detailed than that for an analysis using more complete data, yet I believe that the results do reflect the broader relationships within the su-

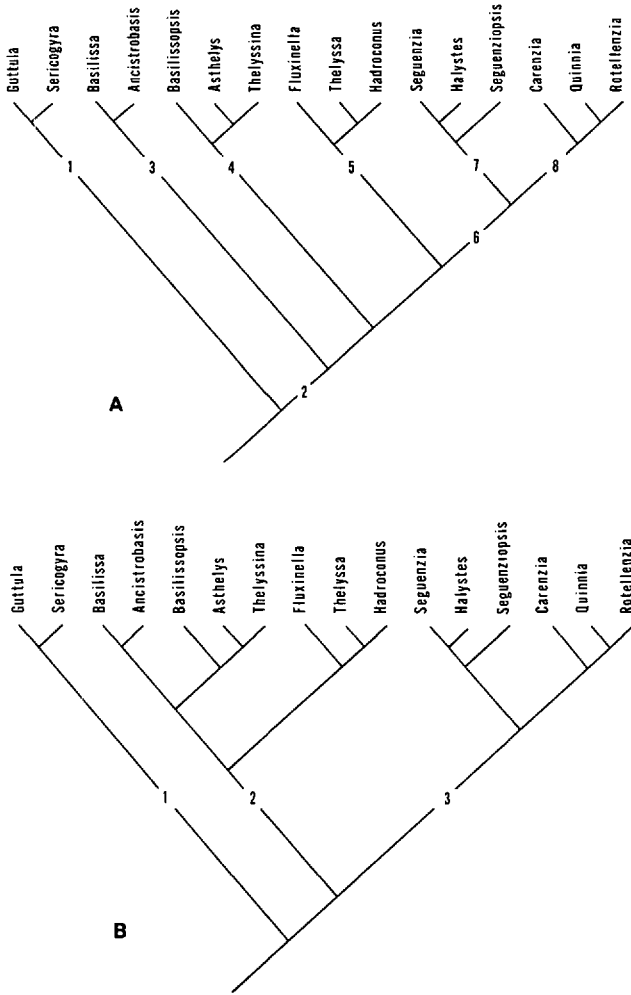


Figure 3. Cladograms representing the most probable relationships of seguenzioid genera.

perfamily. Adjustments in generic relationships and branching sequences will probably occur principally in the *Basilissa* "clade" (branch 2 in Fig. 3B).

Character states and their presumed transformation series are presented in Table 1; character-state transformations were determined by outgroup comparison with the Trochoidea. Transformation series analysis of multistate characters (Michevich, 1982) was performed after the initial computer analysis. Presence of an umbilical septum (Character 13) and absence of a cusp on the lateral tooth (Character 17) were both determined to be convergences and were recoded accordingly (Tables 1, 2). The resulting data matrix for this superfamily is presented in Table 2. The data were analyzed using the FACTOR and MIX options in PHYLIP (Felsenstein, 1989; compiled version for the Macintosh microcomputer provided by W. Ellis, Institute of Taxonomic Zoology, Amsterdam) and the resulting trees were manipulated (i.e., branch swapping and rotation) using MacCLADE (Madison and Maddison, 1987).

Seven shortest trees were produced, each requiring 74 steps and having a con-

Table 1. Character states used for analysis of generic relationships with the Seguenzioidea (hypotheses of character transformations in parentheses)

1. Shell shape: (a) turbinate (b) conical (c) conicoturbinate (d) lenticular (a : b; a : c; b : d).
2. Peripheral carina: (a) absent (b) present, single (c) present, double (a : b; b : c).
3. Axial riblets: (a) absent (b) collabral, rounded (c) collabral, sharp (d) not collabral (b : a; b : c; b : d).
4. Midwhorl angulation: (a) absent (b) initially absent, present on later whorls (c) initially present, becoming weak or absent on later whorls (d) present on all whorls (a : b; a : d; d : c).
5. Spiral lirae: (a) absent (b) present on some whorls (c) present on all whorls (c : b; c : a).
6. Posterior sinus depth: (a) absent (b) shallow (c) deep (a : b; b : c).
7. Posterior sinus shape: (a) absent (b) U (c) V (d) J (a : b; a : c; b : c; b : d).
8. Anterolateral sinus: (a) absent (b) channel (c) sinus (a : b; b : c).
9. Basal sinus: (a) absent (b) present (a : b).
10. Columellar sinus: (a) absent (b) present (a : b).
11. Apertural shape: (a) circular (b) rhomboidal (c) ovate (a : b; a : c; b : c).
12. Columellar tooth: (a) absent (b) Type I (c) Types II + III (a : b; b : c).
13. Umbilical septum: (a) absent (b) present (*Thelyssa*) (c) present (*Basilissa*) (a : b; a : c).
14. Microsculpture: (a) absent (b) punctate (c) granular (d) pustulate (e) dendritic (a : b; a : c; a : d; a : e).
15. Rachidian tooth: (a) broader than high (b) higher than broad (a : b).
16. Rachidian tooth: (a) lateral wings prominent (b) lateral wings reduced or absent (a : b).
17. Lateral tooth cusp: (a) broad (b) narrow, proximal (c) rudimentary or lacking (d) broad to absent (*Guttula* + *Sericogyra*) (a : b; b : c; a : d).
18. Marginal tooth pairs: (a) > 10 (b) ≤ 10 (a : b).
19. Accessory cephalic process: (a) absent (b) present (a : b).
20. Eyes: (a) present (b) absent (a : b).
21. Oral lappets: (a) present (b) absent (a : b).
22. Snout: (a) indented (b) more or less bifid (a : b).

sistency index of 0.57. The low consistency index reflects the ambiguities caused by the missing data. All trees had four stable generic groupings: (1) *Guttula* + *Sericogyra*; (2) *Thelyssa* + *Hadroconus* + *Fluxinella*; (3) *Seguenzia* + *Halystes* + *Seguenziopsis*; and (4) *Carenzia* + *Rotellenzia* + *Quinnia*. A fifth group, *Asthe-lyls* + *Thelyssina* + *Basilissopsis*, was distinguished in six of the seven trees. Branching sequences were similar in all trees. *Basilissa* clustered once with group (5) and once with *Ancistrobasis*, undoubtedly the result of lack of knowledge not only of the animal but also of the apical whorls and shell microsculpture. I consider *Basilissa* and *Ancistrobasis* to be closely related, based on most shell characters (Quinn, in press), and therefore, the tree illustrated in Figure 3A is preferred.

The first branching point separates the holostomatous *Guttula* + *Sericogyra* clade from all other seguenzioids, which all have posterior and basal labral sinuses (branch 2). Branches 3–5 are not well supported by synapomorphies, and the relationships of most of these genera would probably be better represented as a polychotomy; however, all genera in these groups are similar in having shallow, U-shaped posterior sinuses, and in the five genera for which radulae are known, all have a broad lateral tooth cusp. The clade above branch 6 is defined by the presence of a narrow lateral tooth cusp (except *Carenzia*, which lacks a lateral tooth cusp). The *Seguenzia* clade (branch 7) has conicoturbinate to turbinate shells (reversal to the plesiomorphic state), J-shaped posterior sinuses, and usually a distinct anterolateral sinus. The *Carenzia* clade (branch 8) includes genera with conical or lenticular shells lacking distinct anterolateral sinuses, and with shallow, V-shaped posterior sinuses. More detailed analyses of this cladogram are unjustified because of the missing data and the great degree of homoplasy. An alternative tree (Fig. 3B) had the same consistency index and number of steps as the tree in Fig. 3A, but the three main branches are better defined. Branch 1 again contains

Table 2. Character states data matrix for seguenzioid genera

	1	2	3	4	5	6	7	8	9	0	1	2
<i>Gutula</i>	a	a	a	a	a	a	a	a	a	a	a	a
<i>Sericogyra</i>	a	a	c	a	c	a	a	a	a	a	b	b
<i>Basilissa</i>	b	b	b	b	?	b	b	a	b	a	?	?
<i>Ancistrobasis</i>	b	b	b	d	c	b	b	a	b	b	?	?
<i>Basilissopsis</i>	b	b	b	d	a	b	b	a	b	a	?	?
<i>Hadrocomus</i>	b	b	d	c	c	b	b	a	b	a	?	?
<i>Thelyssa</i>	b	b	d	c	c	b	b	b	b	a	?	?
<i>Asthelys</i>	b	b	a	b	a	b	b	a	b	a	a	a
<i>Thelyssina</i>	b	b	a	b	a	b	b	b	b	a	?	?
<i>Fluxinella</i>	d	b	a	c	a	b	b	b	b	a	?	?
<i>Seguenzia</i>	c	a	c	d	c	c	d	c	b	a	b	a
<i>Halysetes</i>	c	a	c	d	c	b	d	a	b	a	b	a
<i>Carenzia</i>	b	b	c	d	b	b	c	b	b	a	?	?
<i>Quinnia</i>	b	b	c	d	b	b	c	b	b	a	?	?
<i>Rotellenzia</i>	d	c	c	d	b	b	c	b	b	a	?	?
<i>Seguenziopsis</i>	a	c	c	d	a	c	d	c	?	a	?	?

the two genera that lack labral sinuses; branch 2 contains all the genera that have U-shaped posterior labral sinuses and broad lateral tooth cusps; and branch 3 includes the genera with narrow lateral tooth cusps. All cladograms seem to suggest that the family Seguenziidae could be divided into two family-group taxa: the Seguenziidae(inae) sensu stricto, and the Guttulidae(inae) Goryachev, 1987; however, I do not advocate doing so until more anatomical data are available.

Systematic Position of Seguenzioidea

Most pre-1979 classifications of members of the Seguenzioidea placed the group, in whole or part, either in the Archaeogastropoda near the Trochoidea or in the Caenogastropoda near the Stromboidea (see Quinn, 1983b, for summary). Goryachev (1979) concluded that the family Seguenziidae should be included in the caenogastropod order Protopoda (sensu Golikov and Starobogatov, 1975), but he provided no specific data to support that claim. I (Quinn, 1981; 1983b) concluded that the family should be treated as a superfamily, citing apomorphies of the shell, radula, and external anatomy; however, I rejected Goryachev's (1979) hypothesis of seguenzoid relationships and placed the superfamily in the Archaeogastropoda near the Trochoidea based on similarities of shell, radular, and anatomical morphologies. This scenario has been accepted by some subsequent authors (Boss, 1982; Ponder and Warén, 1988; Vaught, 1989).

Salvini-Plawén and Haszprunar (1987) decided that the Seguenzioidea were sufficiently distinct from the superfamilies included in the suborder Vetigastropoda, Salvini-Plawén, 1980, to elevate the former to subordinal status, the Seguenziina, which they hypothesized to be intermediate between the "rhipidoglossate" and "taenioglossate" gastropods. Their exclusion of the Seguenzioidea from the Vetigastropoda was based on the seguenzioidean radular formula, and some characters of the external and internal anatomy, principally that of *Carenzia* (see discussion below); Haszprunar (1988a; 1988b) reaffirmed that position. Hickman (1988) did not challenge that classification, but she did not necessarily endorse it either (Hickman, pers. comm.). Golikov and Starobogatov (1988) also considered the Seguenzioidea to be a separate suborder (as Seguenzioidei), but they referred this taxon to the caenogastropod order Strombiformes for unspecified reasons.

At about the same time as the Salvini-Plawén and Haszprunar (1987) paper was published, Goryachev (1987) published an abstract in which he emphatically declared that the Seguenzioidea are "taenioglossal" gastropods; moreover, he elevated the superfamily to ordinal status, the Seguenziiformes, and assigned the order to the superorder Littorinimorpha (sensu Golikov and Starobogatov, 1975). Goryachev cited as evidence the presence of a taenioglossate radula and some anatomical characters (see discussion below). Several factors have contributed to these discordant classifications: 1) a dramatic increase in the knowledge of gastropod anatomies, many new and from specialized deep-sea habitats; 2) differing interpretations of available characters and character sets (included in this are the problems of estimations of homology, polarity, and interpretation of absence of characters); and 3) novel ways of creating and analyzing suites of characters, as well as an evolution of the theoretical framework within which these analyses are performed. Here I will attempt to discuss the characters of the Seguenzioidea as understood now and as used in recent classificatory efforts. However, because the anatomy of the Seguenzioidea is still largely undescribed and comparable data for many other archaeogastropod families are incomplete or ambiguous, the following discussion of the systematic position of seguenzioids is necessarily preliminary and restricted.

Shell Characters.—Seguenzioid shells have an interior nacreous layer and a “trochoid” protoconch, and usually have labral sinuses. A nacreous layer is widely acknowledged as a plesiomorphic character within the Gastropoda because of its presence in the Monoplacophora and in primitive members of the Cephalopoda and Bivalvia. However, it is interesting to note that only five, possibly six, extant families of gastropods (Pleurotomariidae, Haliotidae, Turbinidae, Trochidae, Seguenziidae, and possibly Skeneidae [see Marshall, 1988b]) retain this character (Bandel, 1979). Protoconchs with an apical fold similar to those of seguenzioids are found in the Trochidae, Turbinidae, Skeneidae, Scissurellidae, and Fissurellidae, and perhaps the Peltospiridae (see figs. 87 and 90 in Warén and Bouchet, 1989). Whether this type of protoconch is a useful phylogenetic character is uncertain, and further research is required; however, it should be considered as a potential character in future phylogenetic studies. One or more labral sinuses of various conformations and locations are found in shells of such disparate groups as the Neomphaloidea (Warén and Bouchet, 1989); the vetigastropod superfamilies Pleurotomarioidea, Fissurelloidea, and Scissurellidea; the cerithioidean Siliquariidae; and the conoidean Turridae. Therefore, the labral sinuses of seguenzioids are considered to be autapomorphic for the superfamily.

Radular Characters.—Much attention has been directed to considerations of the pattern or “formula” of the seguenzioid radula. Most discussions have centered on whether the seguenzioid radula is rhipidoglossate or taenioglossate (see Quinn, 1983b, for summary; Marshall, 1983; 1988a; Goryachev, 1987; Golikov and Starobogatov, 1988; Haszprunar, 1988a; 1988b). The seguenzioid radula has a well-developed central tooth that usually has a well-developed, denticulate cusp. Adjacent to and interlocking with each rhachidian tooth are two broadly triangular lateral plates. Distal to each lateral plate lies an enlarged, ensiform, distally denticulate tooth that usually has been interpreted to be an inner marginal tooth (Quinn, 1983b; Marshall, 1983; 1988a). An alternative interpretation is suggested by the work of Herbert (1987) on the trochid subfamily Solariellinae. He found that the solarielline “inner marginal” tooth, which is very similar in morphology and position to that of seguenzioids, occurs proximal to the lateromarginal plate (when present), and thus is the outer lateral tooth. However, rhipidoglossan archaeogastropods have developed either the outer lateral tooth (e.g., Solariellinae) or inner marginal tooth (e.g., Calliostomatinae) in various related or unrelated taxa, and in the absence of a lateromarginal plate, there is no way at present to decide whether the seguenzioid ensiform tooth represents a lateral or marginal tooth. The slender, falcate outer marginal teeth number from about 3 to about 20 pairs per tooth row (Marshall, 1983; 1988a; Quinn, 1983b), with most genera having fewer than 10 pairs.

Reduction in the number of elements in the lateral marginal and tooth fields has occurred several times, although no other rhipidoglossate archaeogastropod group has such a reduced number of teeth in both fields as have some seguenzioids. Thus, some skeneids have only a single pair of lateral teeth (Marshall, 1988a) but retain numerous marginal tooth pairs, whereas the trochid subfamily Solariellinae has the number of marginal tooth pairs reduced to 6–10 but retains 4 lateral tooth pairs. The seguenzioid radular pattern is unique, but the underlying ground plan is clearly rhipidoglossate.

Anatomy.—Seguenzioid anatomy remains rather poorly known. Recent accounts have described the external anatomy of several genera (Knudsen, 1964; Quinn, 1983b; 1987; in press; Marshall, 1988a), and some data are available for the internal anatomy of a species of *Carenzia* (Salvini-Plawén and Haszprunar, 1987;

Haszprunar, 1988a; 1988b). The combination of plesiomorphic "archaeogastropod" characteristics and autapomorphies, many of which are convergent on those of other groups, has produced a distinctive anatomical ground plan.

The epipodium bears 1–10 epipodial tentacles on each side (Quinn, 1983b; 1987; Goryachev, 1987; Marshall, 1988a) but lacks epipodial sense organs (Salvini-Plawén and Haszprunar, 1987; Haszprunar, 1988a; 1988b; personal observations); the epipodial tentacles are distinctly ciliated (micropapillate) in *Fluxinella* and *Guttula* (personal observations). Cephalic lappets and neck lobes are lacking, but *Sericogyra metallica*, *S. periglenes*, *Asthelys antarctica*, and *Halystes chimaera* (all Marshall, 1988a) have a cluster of small tentacles near the base of the left cephalic tentacle (Marshall, 1988a) that could represent a vestigial left neck lobe. The cephalic tentacles are long, tapered, and conspicuously micropapillate, and the right tentacle sometimes has a subocular peduncle at the base (Quinn, 1983b; Marshall, 1988a). In males, a long, slender copulatory organ with an open sperm groove is located near the base of the right cephalic tentacle (Quinn, 1983b; Marshall, 1988a), and the copulatory organ is innervated from the cerebral ganglion (Haszprunar, 1988a; in litt.), indicating an epipodial origin (Goryachev, 1987). Eyes are known in two genera, *Asthelys* (Marshall, 1988a) and *Ancistrobasis* (Quinn, in press), and are placed at the bases of the cephalic tentacles, not on separate eyestalks; the eye structure is unknown.

The single (left) ctenidium is monopectinate (Quinn, 1983b; Haszprunar, 1988a) and has skeletal rods but lacks bursicles (sensory pockets) (Salvini-Plawén and Haszprunar, 1987); there is no transverse pallial vein (Quinn, 1983b). The heart has only a single auricle (monotocardian) (Quinn, 1983b; Haszprunar, 1988b). The excretory system includes both left and right kidneys, but the genital tract is separated from the right kidney (Haszprunar, 1988b); the fine structure of the kidneys has not been described. The nervous system is hypoathroid with pedal cords (Haszprunar, 1988b).

The anterior part of the alimentary tract lacks a subradular organ (Haszprunar, 1988b), is roughly circular in cross section, has large dorsal folds and a single ventral fold, lacks a ventral ciliated tract and a specialized lateral (high) epithelium, and has close-set oesophageal glands (Salvini-Plawén and Haszprunar, 1987; Haszprunar, 1988b; Salvini-Plawén, 1988). However, contrary to published reports (Salvini-Plawén and Haszprunar, 1987; Haszprunar, 1988b), the figures published in the former paper (fig. 2e) for *Carenzia* and those in a subsequent work for *Seguenzia* (Salvini-Plawén, 1988: fig. 14e) show vestigial esophageal pouches, an interpretation confirmed by Haszprunar (in litt.). The posterior portion of the esophagus is rather simple (Salvini-Plawén and Haszprunar, 1987). The statement by Goryachev (1987: 22) that there is a "blind sac with a crystal rod" opening into the stomach is not supported by Haszprunar (in litt.), who did not find such features in *Carenzia*. The intestine is very long and convoluted and has an anterior loop (Quinn, 1983b; 1987; in press). The fecal rod is continuous with a shallow groove along one side (Quinn, 1983b; 1987).

DISCUSSION

In the last decade numerous papers have detailed the anatomies of many archaeogastropod families, both new and old. This dramatic increase in our knowledge of archaeogastropod organization has allowed introduction of many new higher-level taxa and has forced reconsiderations of relationships among taxa throughout the traditional order Archaeogastropoda. As a result, the following major clades have been confirmed and are generally accepted in most recent

classifications (Graham, 1985; Salvini-Plawén and Haszprunar, 1987; Golikov and Starobogatov, 1988 [in part]; Haszprunar, 1988a; 1988b): patelloideans (Lindberg, 1986; 1988), cocculiniforms (Haszprunar, 1988a; 1988b; 1988c), neritiforms (Yonge, 1947; Fretter, 1965), and vetigastropods (Salvini-Plawén, 1980; Salvini-Plawén and Haszprunar, 1987; Haszprunar, 1988a; 1988b; but see Ponder and Warén, 1988). This is not to say that there is agreement on nomenclature, taxonomic rank, or phylogenetic interrelationships of these major groups.

Several archaeogastropod taxa have been described that cannot be assigned with any confidence to any of the major groups mentioned above: Neomphalidae McLean, 1981; Cyathermiidae McLean, 1990; Peltospiridae McLean, 1989; *Melanodrymia* Hickman, 1984b (the preceding taxa united in Neomphaloidea by Warén and Bouchet, 1989, but see Haszprunar, 1989b; and McLean, 1990); Lepetodrilidae and Gorgoleptidae (both McLean, 1988, as Lepetodriloidea; placed in Vetigastropoda by Haszprunar [1988a; 1988b]); Seguenziidae Verrill, 1884; and Pelyciidae Ponder and Hall, 1983 (anatomy unknown). All groups except the last are known to have many archaeogastropod characters, but also have one or more organ systems modified to resemble conditions once thought restricted to mesogastropods.

The distinctive body and radular plans of seguenzioids have prompted several recent attempts to determine the phylogenetic relationships of these animals (Goryachev, 1979; 1987; Quinn, 1983b; Salvini-Plawén and Haszprunar, 1987; Golikov and Starobogatov, 1988; Haszprunar, 1988a; 1988b). Goryachev (1979) originally assigned the Seguenziidae to the littorinimorph order Protopoda, although he suggested that a separate order might be needed; these claims were made on the basis of the radular pattern and unspecified anatomical characters. Later, Goryachev (1987) fulfilled his own prediction by elevating the family to the order Seguenziiformes, retaining it at the base of the superorder Littorinimorpha. As evidence for this conclusion he noted the "archaic" features (nacreous shells; multispiral, conchiolin operculum; labral sinuses [this last has been shown above to be an autapomorphy of the Seguenziidae]), but he emphasized the following "progressive" features: the radula that he interpreted as taenioglossate, a single ctenidium, a single kidney, an epipodial penis with open sperm groove, a monotocardian heart, a "crystal rod" (?=crystalline style) in the stomach, and a rectum not passing through the "stomach" (sic, error for ventricle). As discussed above, the seguenzioid radula is best interpreted as reduced rhipidoglossate. Loss of the right ctenidium is a widespread trend within the archaeogastropod grade (see Haszprunar, 1988b: table 1, and references therein); most of these same groups have also lost the right auricle (Haszprunar, 1988b: table 1). The reported absence of a right kidney (Quinn, 1983b; Goryachev, 1987; Salvini-Plawén and Haszprunar, 1987) has been shown to be erroneous (Haszprunar, 1988b); a right kidney is present, but does not share a duct or opening with the gonad (Haszprunar, 1988b: fig. 2Q). Gastropods have been remarkably facile in the elaboration of copulatory organs. Archaeogastropods have co-opted the left cephalic tentacle (Neomphaloidea: Fretter et al., 1981; Warén and Bouchet, 1989; McLean, 1990), a process on the left of the snout (Gorgoleptidae: Fretter, 1988), the right cephalic tentacle (Lepetelloidea: Haszprunar, 1988c), both cephalic tentacles (*Melanodrymia*; Haszprunar, 1989b), the right neck lobe (Trochidae: Warén and Bouchet, 1989), and various epipodial structures near the right cephalic tentacle (Cocculinoidea: Haszprunar, 1988c; Neritimorpha: Fretter and Graham, 1962; 1978; Fretter, 1965; Lepetodrilidae: Fretter, 1988; Clypeosectidae: Haszprunar, 1989a; Seguenziidae: Quinn, 1983b; 1987; Marshall, 1988a). All of these structures are innervated from a cerebral ganglion, but all are probably autapomorphic for each

group (Haszprunar, 1988b). Copulatory structures, when present, of caenogastropods are usually innervated from the pleural or pedal ganglia (Fretter and Graham, 1962; Haszprunar, 1988b), but in the truncatelloid families Anabathridae and Emblandidae the penial innervation is from the cerebral ganglion (Ponder, 1988). Therefore, homology of copulatory structures between the Seguenzioidea and littorinimorph superfamilies is highly unlikely. Two families of archaeogastropod affinity but unresolved relationships (Neomphalidae: Fretter et al., 1981; Warén and Bouchet, 1989; Peltospiridae: Fretter, 1989; Warén and Bouchet, 1989) have an intestine like that of the Seguenziidae; in all three groups the intestine has an anterior loop, bypasses the pericardium, and contains similar fecal strings. The anterior loop and type of fecal string are archaeogastropod characters, and to use separation of intestine from the pericardium as a homology indicating direct relationship of any of these families with caenogastropods (or with each other) is unwarranted at present. The only anomalous character cited by Goryachev (1987) was a "blind sac with a crystal rod" opening into the stomach. If this is a reference to presence of a crystalline style, as it seems to be, it has not been corroborated for *Carenzia* (Haszprunar, in litt.) or *Seguenzia* (personal observation); however, this apparent conflict cannot be resolved now on the basis of available data. Because none of the characters mentioned by Goryachev (1987) can be considered synapomorphies of the Seguenzioidea and members of the Littorinimorpha (sensu Golikov and Starobogatov, 1975), his assignment of the superfamily to the Littorinimorpha (1979; 1987) cannot be accepted.

In my previous attempt to assess relationships of the Seguenzioidea (Quinn, 1983b) I recognized the significant contributions of archaeogastropod plesiomorphies and seguenzioid autapomorphies to the superfamily's unique organization of shell, radular, and anatomical characters. My conclusion, which presented the scenario that the Seguenzioidea most probably were derived from a trochoid-like ancestor, was based on my perception that the modified seguenzioid characters could be derived most easily from those present in trochoids. In addition, I cited the trochoid-like fecal string, the cephalic tentacles with brush organs (micropapillae), and the presence of a right suboptic tentacle as possible evidence of close relationship between the two superfamilies. However, those characters have not been confirmed to be synapomorphies of the two groups (but see discussion below), and current knowledge of other archaeogastropod groups has complicated the process of phylogenetic reconstruction of relationships.

Golikov and Starobogatov (1988) presented a classification of the Seguenzioidea that is essentially the same as that of their earlier (Golikov and Starobogatov, 1975) classification. Their proposed relationship of the Seguenzioidea with the Stromboidea was based on unspecified characters of the shell and radula in 1975 and on additional, unspecified characters of the genital system in 1988. Because of their lack of specific data, these classifications cannot be addressed on a point-by-point basis; however, the same critiques presented above for Goryachev's (1979; 1987) classifications may be applied to the implied homologies of Golikov and Starobogatov (1975; 1988) of stromboid radulae and penis with those of the Seguenzioidea. Therefore, I cannot accept Golikov and Starobogatov's (1975; 1988) hypothesis of a relationship between the stromboids and seguenzioids.

The new anatomical data on the Seguenzioidea has been presented by Salvini-Plawén and Haszprunar (1987) and Haszprunar (1988a; 1988b) and, combined with previously described characters, induced these authors to present the hypothesis that the Seguenzioidea are not closely related to any other archaeogastropod group and represent an isolated suborder placed between their Vetigastropoda and the Architaenioglossa. As most other authors have done, Salvini-Plawén

and Haszprunar (1987) and Haszprunar (1988a; 1988b) emphasized the distinctiveness of seguenzioid anatomy. Here I will address the phylogeny and classification presented by Haszprunar (1988b) because they are the most complete and are virtually identical to his earlier efforts (Salvini-Plawén and Haszprunar, 1987; Haszprunar, 1988a). Characters considered plesiomorphic were the nacreous shell with trochoid-like protoconch, hypoathroid nervous system with pedal cords, simple tentacular nerve, epipodium with tentacles, "interior" (sic, error for anterior) intestinal loop, and presence of two kidneys. Advanced characters were the reduced marginal field of the radula; lack of a radular diverticulum and subradular organ; lack of esophageal pouches, anterior ventral folds, and posterior esophageal folds; absence of the right ctenidium, osphradium, hypobranchial gland, and auricle; monopectinate left ctenidium with skeletal rods but lacking sensory pockets (bursicles); lack of epipodial sense organs; presence of a copulatory organ innervated from the cerebral ganglion; separation of the female gonoduct from the right kidney; reduction of the labial commissure and ganglia; and reduction of the distance between the cerebral ganglia. Of the advanced characters, conditions of the radula, right pallial organs and auricle, and copulatory organ have been discussed above. In aggregate these characters help produce a distinctive body plan, but all have analogues within the archaeogastropod grade and are not phylogenetically informative in determining relationships. Haszprunar's (1988b) mention of reduced labial ganglia and commissure and of a "concentrated" nerve ring (i.e., the cerebral commissure is shortened) is interesting, but he notes that the former condition is also found in the Cocculiniformia and in *Melanodrymia* Hickman, 1984b (also see Haszprunar, 1989b), and the latter condition is found in the Cocculiniformia and in the Viviparidae; thus, the phylogenetic significance of these characters is unclear.

The seguenzioid alimentary system is greatly simplified compared to those of most other archaeogastropods (Salvini-Plawén and Haszprunar, 1987; Haszprunar, 1988b). The radular diverticulum and subradular organ are absent, but the latter character is also absent in the Cocculiniformia, *Melanodrymia*, and *Neomphalus* (Fretter et al., 1981; Haszprunar, 1988b; 1988c; 1989b). Contrary to statements made by Salvini-Plawén and Haszprunar (1987) and Haszprunar (1988b), the figures presented by Salvini-Plawén and Haszprunar (1987: fig. 2e left) for *Carenzia* and by Salvini-Plawén (1988: fig. 14e left) for *Seguenzia* indicate the presence of vestigial esophageal pouches; this has been confirmed by Haszprunar (in litt.). The esophageal pouches of *Melanodrymia* are distinct but reduced relative to other archaeogastropods (Haszprunar, 1989b). Those figures also depict a pair of low, longitudinal ridges along the lateroventral floor of the esophagus; I interpret these ridges as vestigial ventral folds. Ventral mucous pockets are present in the anterior esophagus (Salvini-Plawén and Haszprunar, 1987). However, it is not clear that the seguenzioid mucous pockets are homologous with those shown for *Diodora* (Salvini-Plawén and Haszprunar, 1987: fig. 2d) or the Neritidae (Salvini-Plawén and Haszprunar, 1987: fig. 2b); this question should receive further consideration. Posterior to this anterior portion a well-developed ventral fold appears, and farther back both dorsal and ventral folds are lacking. Seguenzioids ingest copious quantities of fine particulate matter swept from the sediment surface (Quinn, 1983b), and the reduction of most esophageal structures except enlarged mucous pockets suggests that the esophagus serves only as a conduit between the mouth and stomach. I also suggest that either one or both of the anterior esophagus and middle esophagus may be foreshortened and that the cross sections shown by Salvini-Plawén and Haszprunar (1987: fig. 2e right) and Salvini-Plawén (1988: fig. 14e right) are the posterior esophagus. An analogue to this condition is found

in the esophagus of the peltospirid limpets, in which the anterior esophagus cannot be recognized (Fretter, 1989). Therefore, the "characteristic stages" (i.e., homologous cross sections?) figured by Salvini-Plawén and Haszprunar (1987: fig. 2) and Salvini-Plawén (1988: fig. 14) may not represent all homologous portions of the esophagus; this is supported by the traditional definition that the mid-esophagus is "typically identified as the area to which the esophageal glands open" (Fretter, 1989: 131). This problem must be examined more critically in future studies.

The seguenzioid reproductive system is unique in having the oviduct separate from the right renal duct (Haszprunar, 1988b: fig. 2Q). However, in lepetodriloids, the renal portion of the gonoduct is separated from the right kidney by a septum (Fretter, 1988; 1989), and it would seem to be a simple advance for the genital duct to split off from the kidney completely.

Salvini-Plawén and Haszprunar (1987) and Haszprunar (1988a; 1988b) used two characters, presence of ctenidial bursicles and epipodial sense organs (hereafter bursicles and ESO's, respectively), as synapomorphies of the Vetigastropoda (Fissurelloidea + Scissurelloidea + Haliotoidea + Pleurotomarioidea + Trochoidea + Lepetodrilioidea). Presence of bursicles does seem to be a synapomorphy for the first five taxa, but I am uncertain about the lepetodriloid condition. Haszprunar (1988b: 414) stated that he had observed bursicles in lepetodriloids, but Fretter (1988) did not mention them in her extensive account and discussion of lepetodriloid anatomy. *Melanodrymia* ctenidial leaflets also have "sensory pockets" (Haszprunar, 1988b; 1989b). Hickman and McLean (1990) report lack of bursicles in some Skeneidae. ESO's at the bases of epipodial tentacles in "archaeogastropods" were noted by Fretter and Graham (1962: 314), and those of trochids were described by Crisp (1981). Of the superfamilies included in the Vetigastropoda (Salvini-Plawén and Haszprunar, 1987; Haszprunar, 1988a; 1988b), only the Pleurotomarioidea seemingly lack ESO's (Fretter, 1964; 1966; Fretter and Graham, 1976; Salvini-Plawén and Haszprunar, 1987; Haszprunar, 1988b), a condition probably the result of secondary loss. Peltospirid limpets are also known to have sensory processes at the tips of the epipodial tentacles (Fretter, 1989); however, these structures were not reported to occur in coiled gastropods assigned to the Peltospiridae (Warén and Bouchet, 1989). Two considerations have not been addressed: 1) homology of these sensory organs has been assumed but not formally proven, and the varying placements of these organs (near base of tentacle, side of tentacle, tip of tentacle) (Fretter and Graham, 1962; 1976; 1977; Fretter, 1988; 1989; Haszprunar 1989a) and the presence of a similar structure on the mantle edge of *Acmaea* (Fretter and Graham, 1962) raise the possibility of convergence; 2) absence of ESO's has been interpreted as a symplesiomorphy of all other archaeogastropods (Salvini-Plawén and Haszprunar, 1987), but absence of ESO's in otherwise highly derived animals such as those of the Seguenzioidea could as easily be interpreted as a secondary loss (autapomorphy). The trochoid family Skeneidae has not been reported to have ESO's (Fretter and Graham, 1977; Marshall, 1988b; Hickman and McLean, 1990). Thus, like most other characters of archaeogastropods, bursicles and ESO's have a mosaic distribution that has not been satisfactorily explained, except by ad hoc hypotheses. As most papers have emphasized, the seguenzioid anatomy, in aggregate, is distinctive, but perhaps not as distinctive as the classifications of Salvini-Plawén and Haszprunar (1987) and Haszprunar (1988a; 1988b) indicate.

Three seguenzioid characters that may be useful in future phylogenetic studies are the protoconch, the specialized sensory structures of the cephalic and epipodial tentacles, and the presence of a right subocular peduncle. The seguenzioid pro-

toconch has an obscurely to distinctively pointed apex (Bandel, 1979; Marshall, 1983; 1988a; Quinn, 1983b; 1987; in press), a feature that is characteristic of most Trochoidea (Fretter and Graham, 1977; Marshall, 1979; Bandel, 1979; Herbert, 1987; Hickman and McLean, 1990) and some other vetigastropods (Herbert, 1986). Bandel (1979) has also shown that the ultrastructure of the seguenzioid protoconch is the same as that found in most vetigastropod families. The somewhat pointed protoconchs of some coiled neomphalids and peltospirids (Turner et al., 1985: figs. 13-16; Warén and Bouchet, 1989: figs. 79-90) are not here considered homologous, but further investigation is warranted.

The micropapillate (terminology of Hickman and McLean, 1990) cephalic and epipodial tentacles of trochids have long been known (Flemming, 1884) and were recently described in detail by Crisp (1981). These ciliated micropapillae are also present in the Fissurelloidea, Scissurelloidea, and Haliotoidea. Salvini-Plawén and Haszprunar (1987: 752) noted the presence of "fringed head tentacles . . . in certain Neritopsina and Cocculiniformia" and concluded that "this character" is symplesiomorphic [for archaeogastropods?]. Salvini-Plawén and Haszprunar (1987) and Haszprunar (1988c) stated that the Pseudococculinidae have sensory papillae on the cephalic tentacles. However, homology of the cephalic tentacle sensory papillae of the Neritopsina and the Pseudococculinidae with each other or with vetigastropods and seguenzioids has not been proven. Moreover, neither neritimorphs nor pseudococculinids have micropapillate epipodial tentacles, but neritopsins lack an epipodium (Boss, 1982), and only a single pair of epipodial tentacles is present in cocculinimorphs (Haszprunar, 1988c), so the comparisons may not be appropriate. At present, then, presence (or absence) of tentacular micropapillae is equivocal, although suggestive of potential synapomorphy between vetigastropods and seguenzioids.

The base of the right cephalic tentacle of many trochoids and some fissurelloids and seguenzioids has an associated process that has been termed a suboptic tentacle, postoptic tentacle, or suboptic peduncle (Hickman and McLean, 1990). Again, these are structures that should be evaluated further for their potential use as phylogenetic characters.

The seguenzioid shells, radulae, and anatomies present a complex pattern of presence or absence of characters that produces a distinctive animal. Presence of some characters is clearly plesiomorphic (e.g., nacre, right kidney), some are autapomorphic (e.g., copulatory organ), and others are of equivocal interpretation (e.g., micropapillate cephalic and epipodial tentacles). None of these characters has been determined to be an unequivocal synapomorphy with any other superfamily. Because of the lack of a synapomorphy, interpretation of absence of characters in seguenzioids as plesiomorphies or apomorphies is not possible at present. Detailed descriptions and discussions of the anatomy of seguenzioid species are needed.

Another problem that has influenced recent attempts to classify the Seguenzioidea is the tendency to emphasize the distinctiveness of the group (Golikov and Starobogatov, 1975; 1988; Goryachev, 1979; 1987; Quinn, 1983b; Salvini-Plawén and Haszprunar, 1987; Haszprunar, 1988a; 1988b). This tendency has resulted in a taxonomic inflation to a monotypic suborder (Salvini-Plawén and Haszprunar, 1987) and order (Goryachev, 1987). As presented and justified, these classifications have rendered the Seguenzioidea a phylogenetic orphan of gastropod systematics. I have tried here to show that the order Seguenziiformes (Goryachev, 1987) and the suborder Seguenzoidei (Golikov and Starobogatov, 1988) are based on insufficient or erroneous data, and interpretation of character states

(either explicit or implicit) is not supported by available data; therefore, these two classifications are rejected.

Obviously, I do not disagree with Salvini-Plawén and Haszprunar (1987) and Haszprunar (1988a; 1988b) in their assessment of the distinctiveness of the overall body plan of seguenzioids; however, I do disagree with their perception of the degree of separation from some other archaeogastropod groups that the distinctive anatomical organization suggests. Much of the argument presented by Salvini-Plawén and Haszprunar (1987) and Haszprunar (1988a; 1988b) depended largely on absence of characters. As discussed above, some statements were in error, and in the absence of known relationships based on synapomorphies, the absence of bursicles and ESO's cannot be shown to be either plesiomorphic or autapomorphic secondary loss of these structures. These issues, while not disproving those authors' thesis, certainly weakens it; therefore, the systematic position of the Seguenzioidea presented in the phylograms of Salvini-Plawén and Haszprunar (1987: fig. 4) and Haszprunar (1988b: fig. 5) is a phylogenetic scenario that cannot be accepted or rejected.

At present, I cannot present a phylogeny of the Seguenzioidea based on confirmed synapomorphies with other archaeogastropod superfamilies. As a prelude to writing this section of this paper, I attempted to develop a data matrix incorporating 43 characters in 27 families for computer-assisted phylogenetic analysis. I used Haszprunar's (1988b) paper as a starting point because it is the most extensive recent summary of gastropod characters. Bieler (1990: 372) noted that Haszprunar "frequently avoids clear statements about the distribution of a character state in the entire group. Is it not present in the other groups; is it not applicable because the character itself is not present; or are the data not yet available?" I encountered the same problems and attempted to resolve the uncertainties by referring to the primary descriptive literature. Some questions were resolved, particularly with respect to presence or absence of certain structures within individual groups, but even in the most complete accounts (Fretter, 1988; 1989; Haszprunar, 1988c; 1989a; 1989b), discussions center on the more interesting organ systems (e.g., reproductive, alimentary) and often do not mention other characters. This is not to say that the data presented in papers such as those cited above are incomplete—on the contrary, they are extraordinarily complete and plug many of the holes in our knowledge of gastropod organization and variation. However, the essence of phylogenetics is analysis of explicit statements of homology and polarity of characters (Eldredge and Cracraft, 1980; Wiley, 1981); such statements often cannot be unequivocally derived from published accounts. The data matrix I was able to compile from published accounts was too equivocal, and I abandoned my attempt to make a formal phylogenetic analysis.

As an alternative to the hypotheses of seguenzioid relationships discussed above, I offer the following scenario: the Seguenzioidea are a monophyletic group that is most closely related to the Vetigastropoda. I base this principally on my conviction that the micropapillae on both cephalic and epipodial tentacles, the presence of a right subocular peduncle, and, possibly, the presence of the pointed, slightly recurved tip of the protoconch will prove to be synapomorphies of the two groups. If this relationship is true, then the seguenzioid anatomy may have been derived by simplification of organ systems in response to small size and mode of feeding, and by adoption of a deep-sea habitat (Quinn, 1983b). In snails of very small size, elaboration of one organ system probably would result in reduction or loss of others (of course, reduction of some organ systems could allow elaboration of others). In all seguenzioids I have examined, the intestine is

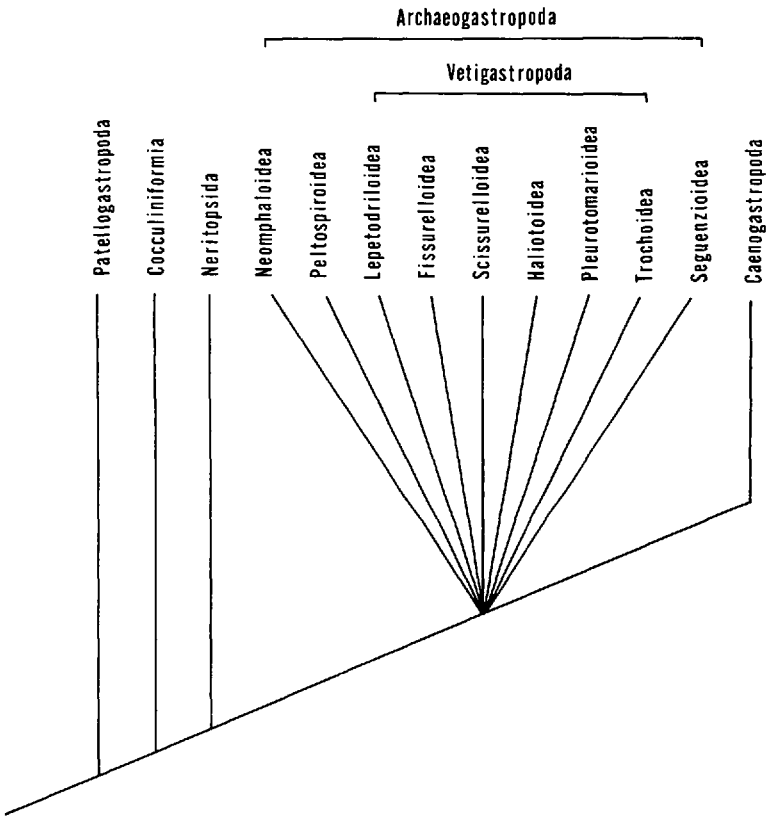


Figure 4. Hypothetical cladogram illustrating unresolved polychotomy of archaeogastropod superfamilies.

extremely long, capacious, and filled with sediment (Quinn, 1983b; 1987; in press; this paper); this occupies a large portion of the volume provided by the conispiral shell, but whether this hypertrophy was the result or the cause of reduction of the pallial organs cannot be resolved. Feeding must be more-or-less continuous, as indicated by the full intestine and a similarly full esophagus (personal observations); the small, delicate radula probably sweeps the surface sediment selecting only the finest particle sizes (Hickman, 1980; 1984a). If this is so, then the sensory subradular organ and pouch would be unnecessary; furthermore, the elaboration of compact ventral mucous pouches would obviate the necessity for the capacious lateral esophageal pouches, thus conserving space. Seguenzioids are well-equipped with tactile sense organs (micropapillate cephalic and epipodial tentacles), and ESO's might be redundant luxuries. The chemosensory bursicles (Szal, 1971) of most vetigastropods (these are absent in the skeneid genera *Haplocochlias* and *Dillwynella* [Hickman and McLean, 1990]) may also have been lost. Therefore, it seems plausible that the seguenzioid anatomy was derived from that of a vetigastropod-like ancestor.

Undoubted seguenzioids are known from the Eocene (Tate, 1888; 1890; 1894; Ladd, 1970; Marshall, 1983) and a Cretaceous origin would not be out of the question. The most derived vetigastropod superfamily, the Trochoidea, are demonstrably the most labile with respect to anatomical modification and innovation (Hickman and McLean, 1990). Perhaps significantly, 14 (15?) of the 20 trochoid subfamilies accepted by Hickman and McLean (1990), including all the

Table 3. Provisional classification of "archaeogastropod" mollusks modified from Hickman's (1988) concept

Class Gastropoda Cuvier, 1797
Subclass Prosobranchia Milne-Edwards, 1848
Superorder unnamed
Order Patellogastropoda Lindberg, 1986
Order Cocculiniformia Haszprunar, 1987
Order Neritopsida Cox and Knight, 1960
Order Archaeogastropoda Thiele, 1925
Superfamily Neomphaloidea McLean, 1981
Superfamily Peltospiroidea McLean, 1989
*Superfamily Lepetodriloidea McLean, 1988
*Superfamily Fissurelloidea Fleming, 1822
*Superfamily Scissurelloidea Gray, 1847
*Superfamily Haliotoidea Rafinesque, 1815
*Superfamily Pleurotomarioidea Swainson, 1840
*Superfamily Trochoidea Rafinesque, 1815
Superfamily Seguenzioidea Verrill, 1884
Superorder Caenogastropoda Cox, 1959

* Superfamilies currently included in the order Vetigastropoda Salvini-Plawén, 1980.

subfamilies hypothesized to be most advanced (e.g., Calliostomatinae, Solariellinae, Umboniinae), are known only from Cretaceous or younger strata. Thus, a possible derivation of the Seguenzioidea from a trochoid ancestor would not be unreasonable as far as time of origin is concerned. However, Bandel (1988: 269) raised another set of problems by mentioning that he has identified possible seguenziid ancestors in the Triassic. If this assertion is substantiated, then the origin of seguenzioids within the Vetigastropoda, or even the Trochoidea, cannot be confirmed or denied, nor can the independent origin hypothesized by Haszprunar (1988b) be refuted. A Triassic (or earlier?) origin of the Seguenzioidea also resurrects the possibility that the group might have relationships with a group such as the Euomphaloidea (Quinn, 1981), although such a derivation is now considered improbable (McLean, 1981; Quinn, 1983b); further complicating such a scenario is the current controversy concerning whether euomphaloids are gastropods or coiled monoplacophorans (see summary in Signor, 1985). Until Bandel's (1988) assertion is confirmed and a method of distinguishing diagenetically altered nacre from normal crossed-lamellar shell structure is found, I prefer to consider seguenzioids an offshoot of the vetigastropod lineage.

Hickman (1988) reviewed the history and current status of the taxon Archaeogastropoda. She suggested retaining the taxon in a restricted sense: a clade comprising a subset of the traditional Archaeogastropoda defined by the common presence of skeletal rods in the ctenidium; however, she included only the "fissurelloid-pleurotomarioid-trochoid" clades, making Archaeogastropoda a synonym of, and therefore replacing, the Vetigastropoda. Fretter and Graham (1988) and Bieler (1990) also favor Hickman's solution. Using skeletal rods as a synapomorphy would also include, by definition, the Neomphaloidea, Peltospiroidea, Lepetodriloidea, and Seguenzioidea; only *Melanodrymia*, which lacks skeletal rods (Haszprunar, 1988b; 1989b), would be excluded, but the radula and gross anatomy of that genus suggest possible inclusion in the Peltospiridae (Warén and Bouchet, 1989; Haszprunar, 1989b). I therefore propose that Hickman's concept of the Archaeogastropoda be expanded to include those four superfamilies. This proposed expansion would have several advantages: 1) it "permits archaeogastropods to be clearly related to higher prosobranchs" (Hickman, 1988: 28); 2) "it is con-

Table 4. Alternative classification of "archaeogastropod" mollusks based on the traditional concept

Class Gastropoda Cuvier, 1797
Subclass Prosobranchia Milne-Edwards, 1848
Superorder Archaeogastropoda Thiele, 1925
Order Docoglossa Troschel, 1866 (=Patellogastropoda)
Order Rhipidoglossa Mörch, 1865
Suborder Cocculiniformia Haszprunar, 1987
Suborder Neritopsida Cox and Knight, 1960
Suborder unnamed
Superfamily Neomphaloidea McLean, 1981
Superfamily Peltospiroidea McLean, 1989
*Superfamily Lepetodrioloidea McLean, 1988
*Superfamily Fissurelloidea Fleming, 1822
*Superfamily Scissurelloidea Gray, 1847
*Superfamily Haliotoidea Rafinesque, 1815
*Superfamily Pleurotomarioidea Swainson, 1840
*Superfamily Trochoidea Rafinesque, 1815
Superfamily Seguenzioidea Verrill, 1884
Superorder Caenogastropoda

*These superfamilies could be grouped in an infraorder Vetigastropoda Salvini-Plawén, 1980.

sistent with recognizing other, former archaeogastropod, clades (e.g., Patellogastropoda, Neritopsina) at coordinate status" (Hickman, 1988: 28); 3) it "admits a large number of extinct taxa and a significant historical record" (Hickman, 1988: 28); 4) it admits the possibility that these groups constitute a clade; and, 5) it allows use of the taxon Vetigastropoda as a suborder by those who wish to recognize this subset of the Archaeogastropoda, but it reflects the current uncertainty regarding the relationships of the vetigastropod superfamilies among themselves and the group with other superfamilies (Haszprunar, 1988b: 413, fig. 5). This proposal may be expressed by the "phylogram" in Figure 4 and the classification in Table 3.

On the other hand, retention of the traditional scope of the Archaeogastropoda has advocates (Salvini-Plawén, 1980; Salvini-Plawén and Haszprunar, 1987; Haszprunar, 1988a; 1988b; McLean, 1990). A possible classification based on this concept is presented in Table 4. Clearly, further analyses of archaeogastropod anatomy, as well as publication of results from paleontological studies like those cited by Bandel (1988), are needed before any widely accepted phylogeny and associated classification is forthcoming; a commonly agreed upon nomenclature of groups above the superfamily level also requires a more considered and judicious approach than has prevailed during the last decade.

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Note added in proof: B. A. Marshall, 1991, *Mem. Mus. Natn. Hist. Nat. (A)* 150: 41–109, in a paper on the Seguenziidae of New Caledonia and the Loyalty Islands, formally recognized three subfamilies and two tribes, transferred one genus to the family from the Trochidae, and described two new genera and 50 new species. His conclusions as to the generic compositions (and the resulting cladogram) of the subfamilies are very similar to the arrangement presented in Fig. 3B of the present paper. The relatively minor differences between his arrangement and mine will be discussed in a future paper (Quinn, in press).