

A REVISION OF THE SEGUENZIACEA VERRILL,  
1884 (GASTROPODA: PROSOBRANCHIA). I.  
SUMMARY AND EVALUATION OF THE SUPERFAMILY

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*Abstract.*—A summary of the superfamily Seguenziacea is compiled from the literature and unpublished observations, and a complete bibliography is presented. A taxonomic resumé of seguenziacean genera is given. A preliminary classification of the superfamily includes 74 nominal species and subspecies in seven genera and four species-groups within *Seguenzia*. The known characters of the shells and anatomy are reviewed. The superfamily Seguenziacea is shown to be distinct from any other known archaeogastropod or mesogastropod superfamily. This superfamily is characterized by: nacreous shells of archaeogastropod ultrastructure, often complexly sculptured with 0–3 (usually 2 or 3) labral sinuses; modified rhipidoglossate radula (formula 12-4.1.1.1.4-12); paucispiral corneous operculum; epipodial tentacles; monopectinate ctenidium; long intestine with an anterior loop; specialized structures in the reproductive tract (e.g., a well developed penis); and modification of the mantle edge to form distinct incurrent and excurrent siphons. Contents of the intestine of *Seguenzia* sp. cf. *S. eritima* Verrill indicate that *Seguenzia* is a detritivore.

*Ancistrobasis* is known from the Eocene, Pliocene, and Recent; *Seguenzia* occurs from the Miocene to the Recent; all other genera are unknown as fossils. Although probably derived from the Trochacea, no direct link with any known fossil or living prosobranch group has yet been established. The superfamily Seguenziacea is here considered to be an isolated offshoot of the Trochacea, independently acquiring advanced anatomical features of a mesogastropod nature as a consequence of extremely small body size and in response to a deep-water habitat.

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The enigmatic superfamily Seguenziacea comprises a group of very small (usually 5 mm or less in height), trochoid-like prosobranchs of world-wide distribution. Although a few species have been recorded from outer continental shelf or abyssal plain depths, by far the majority of known species have been described from the continental slopes. Because of their deep-water habitats, information concerning seguenziacean species has been largely confined to original species descriptions and records published in reports of major national exploratory expeditions. Very few species are represented in collections by large series of specimens, and even fewer have been collected alive. As a result, the taxonomy and systematic position of the Seguenziacea have remained in states of confusion and debate. As a first step towards resolving the status and relationships of this group, a review of all information in the literature is presented, augmented by original observations.

The observations summarized here suggest that seguenziaceans are archaeogastropods which have acquired anatomical specializations more typical of a mesogastropod organization. Archaeogastropod affinity is indicated by the nacreous shell, protoconch, epipodial tentacles, anterior loop of the intestine, and

modified rhipidoglossate radula. Features in common principally with mesogastropods include a monopectinate ctenidium, specialized reproductive system including development of a penis, and functional modification of the mantle edge to form distinct incurrent and excurrent siphons. A similar combination of characteristics is not found in any other known gastropod group, and the argument for a separate superfamily, the Seguenziacea, as suggested by Keen (1971), Golikov and Starobogatov (1975), Goryachev (1979), Quinn (1981, 1983a, b), McLean (1981), and Marshall (in press), is supported. Although a probable origin within the Trochacea is postulated, phylogenetic relationships of the Seguenziacea are still unclear.

Seventy-four nominal species are here assigned to seven genera plus four species-groups within *Seguenzia* within the Seguenziacea and a preliminary classification is presented (Table 1). No attempt to determine species synonymies was made since that task is properly the province of a full monographic review. Such a monograph will be published as time and material permit. However, consideration of shell morphology and radular characters indicates that several rather discrete species-groups exist within *Seguenzia* sensu lato. These species-groups, not formally defined here, are referred to in the text and Table 1 as *Seguenzia* Groups I–IV, designations used here for convenience of discussion and as an indication of areas requiring close attention in future studies. Species names are used in the text without citation of date of description as this information may be found in Table 1. A synopsis of the history of the supraspecific taxa is presented and a complete bibliography is included in the Literature Cited.

### Taxonomic Resumé

*Seguenzia* was proposed almost simultaneously in 1876 by the British malacologist J. G. Jeffreys and the Italian paleontologist G. Seguenza. It appears that Jeffreys' paper (15 June 1876) was published prior to Seguenza's (May–June 1876), but there is still some doubt as I have been unable to determine an exact date of publication for Seguenza's paper; therefore, pending acquisition of further information, Jeffreys is here considered the author of *Seguenzia*. Although Jeffreys and Seguenza agreed on the name for the genus, they disagreed strongly on its supposed systematic position. Seguenza (1876) assigned the group to the Trochidae. Jeffreys (1876), on the other hand, thought that *Seguenzia* was most closely related to the Solariidae (=Architectonicidae) and later emphatically restated that opinion (Jeffreys 1879) after Watson (1879a) erected the second seguenziacean genus, *Basilissa*, and allocated it, along with *Seguenzia*, to the Trochidae on the basis of the nacreous shells.

Verrill (1884) was the first to examine the radula of *Seguenzia*, which he described as taenioglossate. On that evidence he erected the family Seguenziidae, included both *Seguenzia* and *Basilissa*, and placed the family near *Aporrhais* (Strombidae). Based on specimens from the collections of the Blake Expedition, Dall (1889b) defined *Ancistrobasis* as a subgenus of *Basilissa*, and placed both in the Trochidae. Dall assigned *Fluxina discula* to the Solariidae (=Architectonicidae) and placed the Seguenziidae near the Trichotropidae, approximating Tryon's (1887) allocation of *Seguenzia*. Dautzenberg and Fischer (1897a) defined *Basi-*

*lissopsis* for a small, distinctively shaped seguenziacean which they included in the Trochidae.

Schepman (1908, 1909) contributed perhaps the most information of any author to date to the understanding of the Seguenziacea. In his 1908 report, Schepman described and illustrated radulae of *Basilissa* and his new genus, *Guttula*, and although he retained these two genera in the Trochidae, he commented on the uniqueness of their radular formulae. In the second part of his report (1909), he illustrated the radula of *Seguenzia melvilli*, the first accurate description and clear illustration of a radula of *Seguenzia*. He speculated that *Seguenzia* would eventually be recognized as belonging to a rhipidoglossate group also encompassing *Basilissa*, although he followed Tryon (1887), Dall (1889b), and explicitly Pelsener (1906), in placing the Seguenziidae near the Trichotropidae. Dall (1925) included his new subgenus, *Orectospira*, in *Basilissa*, but Habe (1955a, b) has shown that *Orectospira* is turritellid rather than seguenziid.

Reflecting the hiatus in research on the deep sea, it was not until 1971 that another generic taxon was established. *Thelyssa* Bayer, 1971, was erected for a species described from University of Miami collections of deep-water Caribbean molluscs. *Thelyssa* is very similar to, and may eventually be considered a subgenus of, *Basilissa*. The most recently defined genus, *Mioseguenzia* Nordsieck, 1973, was introduced for *Janthina cimbrica* Sorgenfrei, a Miocene fossil from Denmark, and two new taxa, *M. cimbrica recens* and *M. conica*. Dr. Philippe Bouchet (in litt.) has informed me that his examination of Nordsieck's specimens revealed them to be larval shells of the Cypraeacea. From Sorgenfrei's illustration, it appears that *M. cimbrica* is also a larval form, thus excluding *Mioseguenzia* from the Seguenziacea.

The genus *Fluxina* Dall, 1881, has been used for a number of seguenziaceans (Dall 1889b; Schepman 1909; Bayer 1971) and recently included in a list of seguenziacean genera (Boss 1982); however, Merrill (1970a) has shown that the type-species of *Fluxina*, *F. brunnea* Dall, is a *Calliostoma* (Trochidae). *Fluxiella* (Okutani, 1968, 1974) is a nomen nudum, and *F. vitrea* Okutani, is here assigned to *Seguenzia* Group IV. Quinn (1983b) recently erected *Carenzia* for the *Seguenzia carinata* species-group, and Marshall (in press) is treating the species-groups referred to herein as *Seguenzia* Groups II and IV, as well as three other new genera.

### Shell Morphology

Species of the Seguenziacea, although not uncommon in collections of deep-water molluscs, are rarely represented by large suites of shells, and even fewer by live-collected specimens. Resulting identifications and classifications have been based almost solely on shell characters. The taxonomic value of shell characters has not been critically evaluated, and authors have labored under considerable uncertainty as to which variations are merely intraspecific, and which actually represent specific differences. This inadequacy is perhaps best illustrated by the following comments of W. H. Dall (1889b:269): "In examining the specimens of *Seguenzia* . . . I find myself in a dilemma. Either each separate individual is to be regarded as a species or the variability of the shells is very great. Persistent

Table 1.—Preliminary classification of the Seguenziaceae.

## Seguenziaceae Verrill, 1884

## Seguenziidae Verrill, 1884

*Seguenzia* Jeffreys, 1876Type-species.—*Seguenzia formosa* Jeffreys, 1876; by monotypy.Group I (*Seguenzia* s.s.)

<i>S. formosa</i> Jeffreys, 1876	NE Atlantic Ocean
<i>S. formosa</i> var. <i>lineata</i> Watson, 1879	W Atlantic Ocean
<i>S. formosa</i> var. <i>nitida</i> Verrill, 1884	NW Atlantic Ocean
† <i>S. moncingulata</i> Seguenza, 1876	Pliocene, Italy
† <i>S. moncingulata</i> var. <i>elegans</i> Seguenza, 1876	Pliocene, Italy
† <i>S. moncingulata</i> var. <i>elata</i> Seguenza, 1876	Pliocene, Italy
<i>S. eritima</i> Verrill, 1884	NW Atlantic Ocean
<i>S. elegans</i> Jeffreys, 1885	NE Atlantic Ocean
<i>S. elegans</i> var. <i>bicarinata</i> Locard, 1898	NE Atlantic Ocean
<i>S. occidentalis</i> Dall, 1908	NE Pacific Ocean
<i>S. stephanica</i> Dall, 1908	NE Pacific Ocean
<i>S. costulifera</i> Schepman, 1909	Celebes, Indonesia
<i>S. dautzenbergi</i> Schepman, 1909	Celebes, Indonesia
<i>S. melvillii</i> Schepman, 1909	Celebes, Indonesia
<i>S. certoma</i> Dall, 1919	NE Pacific Ocean
<i>S. giovia</i> Dall, 1919	NE Pacific Ocean
<i>S. cervola</i> Dall, 1919	NE Pacific Ocean
<i>S. caliana</i> Dall, 1919	NE Pacific Ocean
<i>S. antarctica</i> Thiele, 1925	S of Kerguelen, Southern Ocean
<i>S. sumatrensis</i> Thiele, 1925	SW of Sumatra, Indian Ocean
<i>S. orientalis</i> Thiele, 1925	E of Kenya, Indian Ocean
<i>S. floridana</i> Dall, 1927	W Atlantic Ocean
† <i>S. hapala</i> Woodring, 1928	Miocene-Recent, W Atlantic Ocean
<i>S. hosyu</i> Habe, 1953	Tosa Bay, Shikoku, Japan
<i>S. louiseae</i> Clarke, 1961	SE Atlantic Ocean
? <i>S. fatigans</i> Barnard, 1963	S of Madagascar, SW Indian Ocean
<i>S. soyoeae</i> (Okutani, 1964)	Off Torishima Is., Japan
<i>S. mirabilis</i> Okutani, 1964	Off Aoga-shima Is., Japan
<i>S. nipponica</i> Okutani, 1964	Sea of Enshu-Nada, Japan
<i>S. megaloncha</i> Rokop, 1972	NE Pacific Ocean
† <i>S. donaldi</i> Ladd, 1982	Pleistocene, New Hebrides

## Group II

<i>S. ionica</i> Watson, 1879	NW Atlantic Ocean
<i>S. lampra</i> (Watson, 1879)	E of Japan, NW Pacific Ocean
<i>S. polita</i> Verco, 1906	S of South Australia
<i>S. sykesi</i> Schepman, 1909	Banda Sea, Indonesia
<i>S. cazioti</i> Dautzenberg, 1925	NE Atlantic Ocean
<i>S. rushi</i> Dall, 1927	NW Atlantic Ocean

## Group III

<i>S. siberutensis</i> Thiele, 1925	SW of Sumatra, Indian Ocean
<i>S. simplex</i> Barnard, 1963	Off Cape Point, South Africa

## Group IV

<i>S. discula</i> (Dall, 1889)	NW Atlantic Ocean
? <i>S. dalliana</i> (Melvill and Standen, 1903)	N Indian Ocean
<i>S. marginata</i> (Schepman, 1909)	Banda Sea, Indonesia

Table 1.—Continued.

<i>S. trochiformis</i> (Schepman, 1909)	Ceram Sea, Indonesia
<i>S. stenomphala</i> (Melvill, 1910)	N Indian Ocean
<i>S. gelida</i> (Barnard, 1963)	W of Cape Point, South Africa
? <i>S. solarium</i> (Barnard, 1963)	S of Madagascar, SW Indian Ocean
<i>S. vitrea</i> (Okutani, 1968)	S of Boso Peninsula, Honshu, Japan
<i>Carenzia</i> Quinn, 1983	
Type-species.— <i>Seguenzia carinata</i> Jeffreys, 1877; by original designation.	
<i>C. carinata</i> (Jeffreys, 1877)	W and NE Atlantic Ocean
<i>C. trispinosa</i> (Watson, 1879)	W Atlantic Ocean
<i>C. inermis</i> (Quinn, 1983)	NE Pacific Ocean
<i>Basilissa</i> Watson, 1879	
Type-species.— <i>Basilissa superba</i> Watson, 1879; by subsequent designation, Cossmann, 1888.	
<i>B. alta</i> Watson, 1879	NW Atlantic Ocean
<i>B. alta</i> var. <i>oxytoma</i> Watson, 1879	NW Atlantic Ocean
<i>B. simplex</i> Watson, 1879	SW Atlantic Ocean
<i>B. munda</i> Watson, 1879	E Atlantic Ocean
<i>B. superba</i> Watson, 1879	N of Australia, SW Pacific Ocean
<i>B. sibogae</i> Schepman, 1908	Celebes, Indonesia
<i>B. watsoni</i> Dall, 1927	NW Atlantic
<i>Ancistrobasis</i> Dall, 1889	
Type-species.— <i>Basilissa costulata</i> Watson, 1879; by subsequent designation, Dall, 1927.	
† <i>A. reticulata</i> (Philippi, 1844)	Pliocene, Italy; ?Recent, NE Atlantic
<i>A. costulata</i> (Watson, 1879)	NW Atlantic Ocean
<i>A. lusitanica</i> (Fischer, 1882)	NE Atlantic Ocean
<i>A. depressa</i> Dall, 1889	NW Atlantic Ocean
?† <i>A. radialis</i> (Tate, 1890)	Eocene of South Australia
† <i>A. cossmanni</i> (Tate, 1894)	Eocene of South Australia
<i>A. compsa</i> Melvill, 1904	N Indian Ocean
?† <i>A. bilix</i> (Hedley, 1905)	E of Australia, SW Pacific Ocean
<i>A. bombax</i> (Cotton and Godfrey, 1938)	S of Australia
† <i>A. pacifica</i> Ladd, 1970	Eocene of Tonga, SW Pacific Ocean
<i>Basilissopsis</i> Dautzenberg and Fisher, 1897	
Type-species.— <i>Basilissopsis watsoni</i> Dautzenberg and Fisher, 1897; by monotypy.	
<i>B. oxytropis</i> (Watson, 1879)	S Atlantic Ocean
<i>B. watsoni</i> Dautzenberg and Fisher, 1897	NE Atlantic Ocean
<i>B. rhyssa</i> (Dall, 1927)	NW Atlantic Ocean
<i>Thelyssa</i> Bayer, 1971	
Type-species.— <i>Thelyssa callisto</i> Bayer, 1971; by original designation.	
<i>T. callisto</i> Bayer, 1971	NW Atlantic Ocean
<i>Guttula</i> Schepman, 1908	
Type-species.— <i>Guttula sibogae</i> Schepman, 1908; by monotypy.	
<i>G. sibogae</i> Schepman, 1908	N of New Guinea, W Pacific Ocean
<i>G. blanda</i> Barnard, 1963	Off Cape Point, S. Africa
<i>G. galathea</i> Knudsen, 1964	Kermadec Trench, SW Pacific Ocean

† = species described from fossil material.

? = provisional placement.

study of the specimens has convinced me that the latter is the true solution, and that the most evident characters, such as the umbilicus (in some adult specimens) may be present or absent; that the number of spiral threads, their strength and sharpness on the basal disk, are entirely inconstant, and, while in the typical *formosa* the ridge next to the suture is waved or granulate, in many it is perfectly plain."

Indeed, this is the impression obtained when only a few specimens are examined, especially within *Seguenzia* Group I. However, my examination and comparison of a large number of specimens and species indicate that shell characters are not as variable as thought; indeed, several appear to be of considerable importance in separating species.

*Shell shape.*—Shell shapes may be trochoid, turbate, conoid, or lenticular. Outlines of some major species-groups are given in Figs. 1–14. All seguenziacean groups except *Seguenzia* Group III, *Ancistrobasis*, and *Guttula* are distinctly carinate, at least at the periphery. *Carenzia* and *Basilissopsis* often have a mid-whorl ridge or angulation marking the abapical edge of the posterior labral sinus (Figs. 4, 12), which may approach the strength of the corresponding carina of *Seguenzia* Groups I and II (Figs. 1–3, 5, 6). The latter two species-groups, in addition to peripheral and medial carinae, have a basal, and often a subsutural, carina. Major intraspecific variation in shell shape is conferred by changes in height-width ratio with a concomitant increase or decrease in relative spire height.

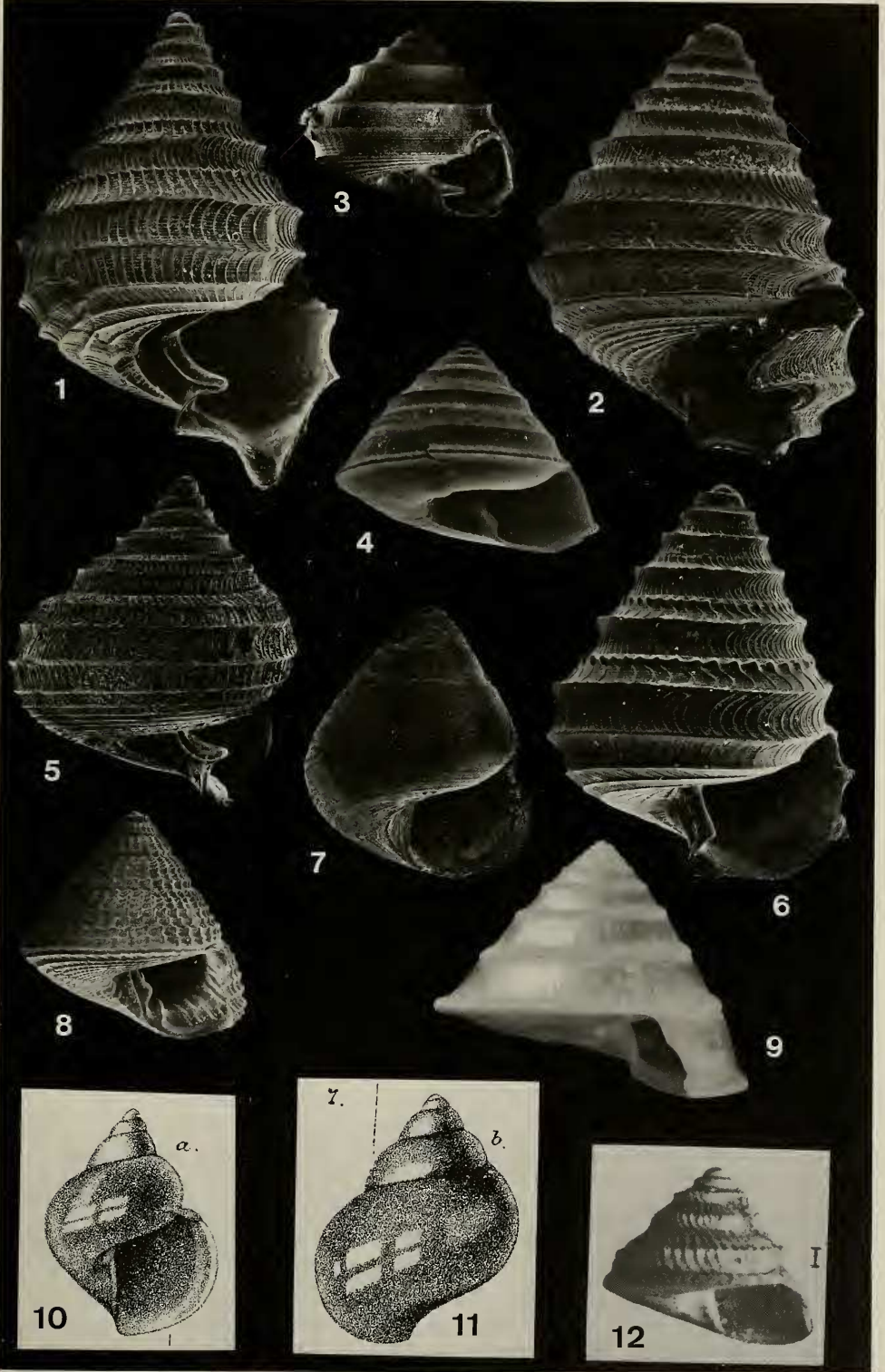
*Sculpture.*—*Guttula* and *Seguenzia* Groups III and IV, and *Carenzia* are almost devoid of sculpture, having at most fine spiral striae (Figs. 4, 7, 10, 11, 14). *Basilissa*, *Thelyssa*, and *Basilissopsis* usually have collabral growth lines slightly thickened at regular intervals, producing weak, sigmoid, axial riblets, often crossed by fine spiral threads (Figs. 9, 12, 13). Continuation of axial sculpture onto the peripheral carina often produces a crenulated or scalloped periphery. *Seguenzia* Group II species usually have rather strong spiral basal cords in addition to carinae and fine spiral striae (Fig. 3).

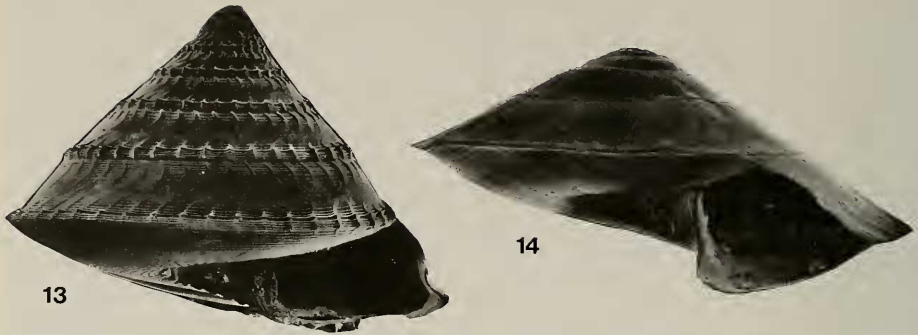
Only *Seguenzia* Group I and *Ancistrobasis* exhibit strong sculptural patterns (Figs. 1, 2, 5, 6, 8). *Ancistrobasis* has reticulate sculpture of subequal axial and spiral cords with nodules produced at the intersections, and the base bears strong, obscurely nodulous or undulate spiral cords. The intricate sculpture of *Seguenzia* Group I is by far the most striking of all seguenziaceans. In addition to the three or four spiral carinae previously described, the shell bears strong basal cords, fine spiral threads between carinae, and collabral riblets. The abrupt changes in di-

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Figs. 1–12. Seguenziacean shells: 1, 2, 5, 6, *Seguenzia* Group I; 3, *S.* Group III; 4, *Carenzia*; 7, *S.* Group IV; 8, *Ancistrobasis*; 9, *Thelyssa*; 10, 11, *Guttula*; 12, *Basilissopsis*. 1, *Seguenzia* n. sp., Philippines, USNM, SEM, 20×; 2, *S. hapala*, off West Florida, FDNR, SEM, 33.5×; 3, *S. rushi*, off Puerto Rico, USNM, SEM, 13.4×; 4, *Carenzia carinata*, Straits of Florida, UMML, SEM, 13.4×; 5, *Seguenzia* sp. cf. *S. elegans*, off Yucatan, UMML, SEM, 13.4×; 6, *S. lineata*, off Yucatan, UMML, SEM, 20×; 7, *S. siberutensis*, Philippines, USNM, SEM, 13.4×; 8, *Ancistrobasis* n. sp., off West Florida, FDNR, SEM, 13.4×; 9, *Thelyssa callisto*, W of Great Inagua Is., Bahamas, USNM, height 5.8 mm; 10, 11, *Guttula sibogae* (from Schepman 1908, pl. II, fig. 7); 12, *Basilissopsis watsoni* (from Dautzenberg 1927, pl. VI, fig. 36). (USNM = U.S. National Museum of Natural History; FDNR = Florida Department of Natural Resources, Marine Research Laboratory; UMML = Rosenstiel School of Marine and Atmospheric Science, University of Miami.)



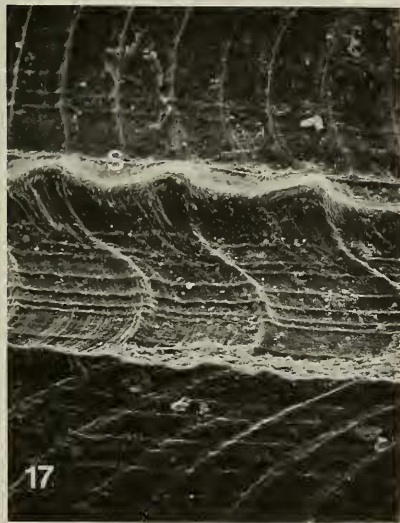
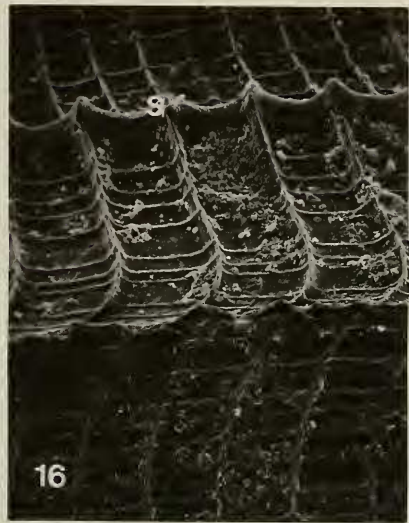
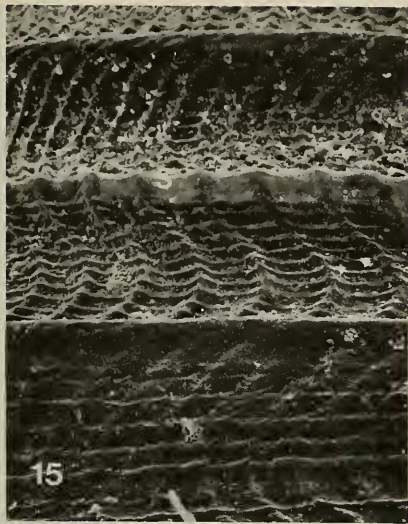


Figs. 13, 14. Seguenziacean shells: 13, *Basilissa alta*, Straits of Florida, UMML, SEM, 6.5 $\times$ ; 14, *Seguenzia* Group IV, *Seguenzia discula*, Straits of Florida, UMML, SEM, 6.5 $\times$ . (UMML = Rosenstiel School of Marine and Atmospheric Science, University of Miami).

rection of the collabral lirae reflect the positions of the three labral sinuses characteristic of this group.

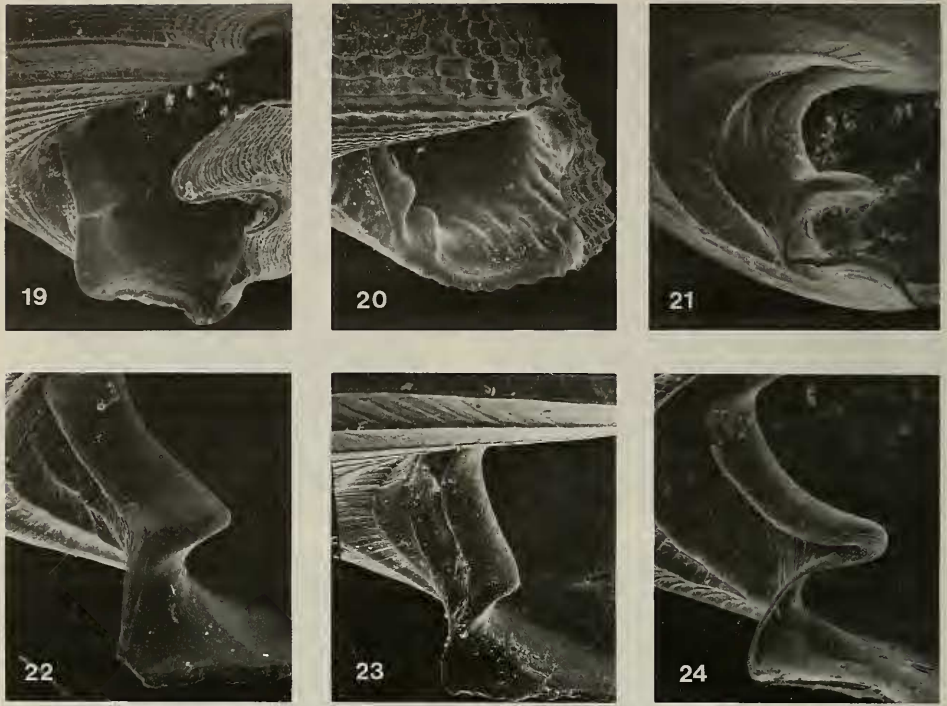
*Labral sinuses.*—Reminiscent of many Pleurotomariacea and Turridae, almost all Seguenziacea are characterized by the presence of usually two, often three, sinuses in the outer lip. *Guttula* alone exhibits an entire lip (Fig. 10). All other groups have a shallow to deep subsutural (=anal) sinus and a shallow sinus in the peripheral part of the basal lip. A third, very narrow sinus occurs in the anterolateral part of the lip of *Seguenzia* Group I, corresponding to the peripheral carina, and has been reported to occur in *Seguenzia* Group II (Watson 1879a; 1886). In groups with a strong, flange-like peripheral carina (*Seguenzia* Group IV and *Caranzia*, *Basilissa*, *Basilissopsis*, and *Thelyssa*), the anterolateral sinus is represented by a channel corresponding to the carina. The outer lip descends from the suture, defining the edge of the subsutural sinus which may be J- (Figs. 15, 17), reversed L- (Fig. 16), or V- or U-shaped (Fig. 18), then abruptly swings forward perpendicular to the axis of coiling (as far as  $\frac{1}{4}$  whorl in some species of *Seguenzia* Group I), retreats to the anterolateral sinus, advances again for a short distance, retreats again to form the basal sinus, and finally arcs forward slightly to the columellar region. In undamaged specimens of species of *Seguenzia* so far examined, the edges of the three sinuses are usually distinctly flared and often strongly produced into a spout-like process, especially the anal sinus. The "sinus" at the base of the columella may be more an artifact of development of the columellar tooth rather than primarily of functional significance, although there is a shallow, papillate embayment of the mantle edge in *Seguenzia* sp. cf. *S. eritima* (see *Anatomy* section). The basal sinus is analogous to the anterior (inhalent) siphonal canal of many higher gastropods, and the subsutural sinus corresponds to the anal, or excurrent, sinus of many prosobranchs, most notably the pleurotomariaceans and the Turridae. The subsutural sinus apparently appears immediately after termination of the protoconch (Figs. 25–29 herein; see also Bandel 1979, pl. 1, Figs. 2, 4). The slightly sinuous or straight subsutural riblets descend almost perpendicularly before abruptly swinging forward to become confluent with the mid-whorl carina. This configuration is very similar to that seen in adult shells (Figs. 15–17), and seems to contradict Bandel's statement that no subsutural sinus is present prior to the third teleoconch whorl (Bandel 1979:52).





Figs. 15–18. SEM micrographs of surface sculpture of *Seguenzia* and *Carenzia* species, 134 $\times$  (s = suture): 15, *S. hapala*; 16, *Seguenzia* n. sp.; 17, *S. lineata*; 18, *C. carinata*.

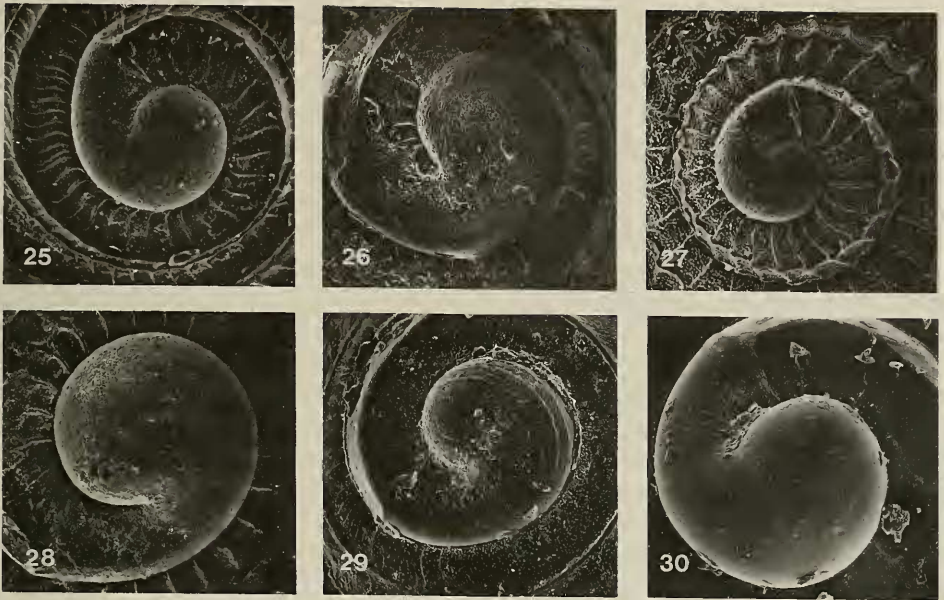
*Columellar tooth*.—Although the columellae of several seguenziacean groups end in blunt, obscure denticles, only *Seguenzia* Groups I and II, and some *Ancistrobasis* species, have prominent tooth development. The teeth in these groups are basically of three types. The Type I tooth, present in *Ancistrobasis* and a few *Seguenzia* Group I species (Figs. 19, 20), appears as a low to moderate ridge or swelling midway down the columella. This ridge may represent the true termination of the columella, with the vertical part of the basal lip thickened to form an effective continuation of the columellar structure. The Type II, or patulous, tooth (Fig. 21) occurs in *Seguenzia* Group II and occasionally in Group I. It forms a very strong, tongue-like projection extending into the aperture and terminating a strongly concave columella. In some species the projection is not so pronounced



Figs. 19–24. SEM micrographs of apertures of *Seguenzia* and *Ancistrobasis*: 19, *S. hapala*, 50 $\times$ ; 20, *Ancistrobasis* n. sp., 25 $\times$ ; 21, *S. floridana*, 25 $\times$ ; 22, *Seguenzia* sp., 50 $\times$ ; 23, *S. lineata*, 50 $\times$ ; 24, *Seguenzia* n. sp., 50 $\times$ .

(Figs. 22, 23). The basal lip descends from the outer edge of the tooth well back from the tip (Fig. 21). The Type III tooth (Fig. 24) is also strongly projecting, but forms a fairly acute tooth rather than a broad shelf. In this type, the basal lip joins along the inner side of the tip. Although usually easily distinguishable in specimens in which they are fully developed, teeth of Types II and III are often indistinguishable during ontogeny. In addition, the tooth may appear at different times within the same species, or even within the same population. This usually presents little problem in identification; however, it does pose problems in making accurate and consistent measurements of shell height, since the collumellar tooth is more often preserved than any part of the fragile basal lip.

*Protoconch*.—The seguenziacean protoconch is perhaps the most conservative shell feature within the group, varying only in size and relative prominence. It is very similar to the trochacean protoconch, consisting of about one whorl, sometimes smooth, but usually sculptured with microscopic granules that usually coalesce into irregular ridges, and ending in a slightly thickened rim (Bandel 1979; Figs. 25–30 herein). Bandel (1979) also showed that the mineralogical ultrastructure of the protoconch was typically archaeogastropodan (see discussion of shell structure below). Size (between 275  $\mu\text{m}$  and 400  $\mu\text{m}$  in all specimens so far examined) and morphology of the seguenziacean protoconch indicate direct or lecithotrophic development (see Bouchet 1976; Bouchet and Warén 1979). Size



Figs. 25–30. SEM micrographs of protoconchs of *Seguenzia*, *Carenzia*, *Ancistrobasis*, and *Basilissa*, 100 $\times$ : 25, *S. hapala*; 26, *Seguenzia* sp. cf. *S. elegans*; 27, *Ancistrobasis* n. sp.; 28, *B. alta*; 29, *C. carinata*; 30, *C. trispinosa*.

of the protoconch is very consistent within a species, and may be used with some confidence to distinguish between morphologically similar species.

*Shell structure.*—Two studies of the ultrastructural organization of *Seguenzia* have been published recently (Bandel 1979; Barskov et al. 1980). Bandel's study investigated all aspects of shell structure from all parts of the shells of *S. megaloncha* Rokop and *S. floridana* Dall (as *S. monocingulata* Seguenza), while Barskov *et al.* concentrated on the nacreous layer near the aperture of a shell of *Seguenzia* "sp. 3" from the Pacific [possibly the species cited as *S. elegans* (sic) in Barsanova (1966)].

Protoconchs of *S. megaloncha* and *S. floridana* have a very thin periostracum through which crystallites of the outer acicular prismatic layer protrude, forming nodules and irregular ridges, an organization typical of most archaeogastropods (except the Neritacea), but not found in mesogastropods or neogastropods (Bandel 1979). Beneath the acicular prismatic layer are added, in order from outer to inner: granular, dendritic, dissected crossed acicular, and blocky prismatic layers. The granular and dendritic layers disappear in the post-protoconch shell, with the dissected crossed acicular layer forming the entire outer prismatic structure beneath the outer acicular layer in *S. floridana*; in *S. megaloncha* the dissected crossed acicular organization is replaced by "spherulite sectors with marginal needles dissecting each other" (Bandel 1979:51).

The nacreous layer appears only after the first two post-protoconch whorls, and is sandwiched between the outer dissected crossed acicular (or spherulitic) and inner blocky prismatic layers, except in the last whorl of actively growing indi-

viduals where the inner blocky prismatic layer is absent. The nacreous layer comprises numerous lamellae of closely packed, generally rhomboidal tablets (Bandel 1979; Barskov et al. 1980), and forms the major structural unit of the adult shell (Barskov et al. 1980). Insertion of the nacre tablets into the outer prismatic layer may be of two types: a stair-step arrangement found in the whorl walls, and columnar stacks of tablets found on the columellar wall (Bandel 1979). Fully developed nacre, however, is the columnar nacre typical of the Pleurotomariacea and Trochacea (Bandel 1979).

Barskov et al. (1980) reported that the shell of *Seguenzia* "sp. 3," which from their Fig. 1 appears very similar to *S. megalaconcha*, was constructed in two layers: 1) an outer prismatic layer with a thickness of about 0.02 mm, the structure of which they did not describe, and 2) an inner nacreous layer about 0.20 mm thick. Absence of an inner prismatic layer indicates that the specimen was not fully grown because the last whorl of actively growing specimens examined by Bandel (1979:52) also lacked the inner layer. Barskov et al. (1980) described in some detail the structural arrangement of the nacreous layer: generally rhomboidal tablets, 20–30  $\mu\text{m}$  long, 15–20  $\mu\text{m}$  wide, and 4–6  $\mu\text{m}$  high, closely packed into lamellae, with the edges of a tablet offset from those above and below it. This arrangement results in a stair-step, or "brickwork," pattern of tablet stacking which is similar to that characteristic of some bivalves, but not previously known in gastropods (Barskov et al. 1980; also see Wise 1970, and Erben 1972). Barskov et al. interpreted this as distinguishing *Seguenzia* from all other known gastropods. However, the "brickwork" pattern described and figured by Barskov et al. appears virtually identical to the transitional stair-step nacre described and illustrated by Bandel (1979:51, pl. 3, fig. 7) which he found near the edge of the aperture. Since the shell chip examined by Barskov et al. was taken from near the outer lip of their specimen, it seems more probable that they only observed Bandel's transition nacre and missed the typical gastropod type of nacre found by Bandel. Also, if the fracture plane is not just right, it is very difficult to distinguish between the different types of nacre constructions (Dr. Roger Batten, pers. comm.). Therefore, rather than *Seguenzia* being totally different in shell structure from all other gastropod groups, as claimed by Barskov et al., it bears strong similarity to the shell structures of the Pleurotomariacea and Trochacea as demonstrated by Bandel (1979).

*Aperture.*—The aperture in *Seguenzia* Group I is roughly auriculate, that of *Guttula* ovate, and in the other seguenziacean genera more or less quadrate. The basic shape of the aperture is often distorted by relative development of, or lack of, a columellar tooth, and by the claw-like extension of the outer lip, especially in *Seguenzia*. *Ancistrobasis* is the only defined seguenziacean group which develops apertural lirae, consisting of a thickened ridge crenulated by several short, low, rounded ridges, and located at the abapertural edge of the posterior labral sinus (Fig. 20). However, several species of *Seguenzia* develop a ridge similar to that in *Ancistrobasis*, but without the crenulations.

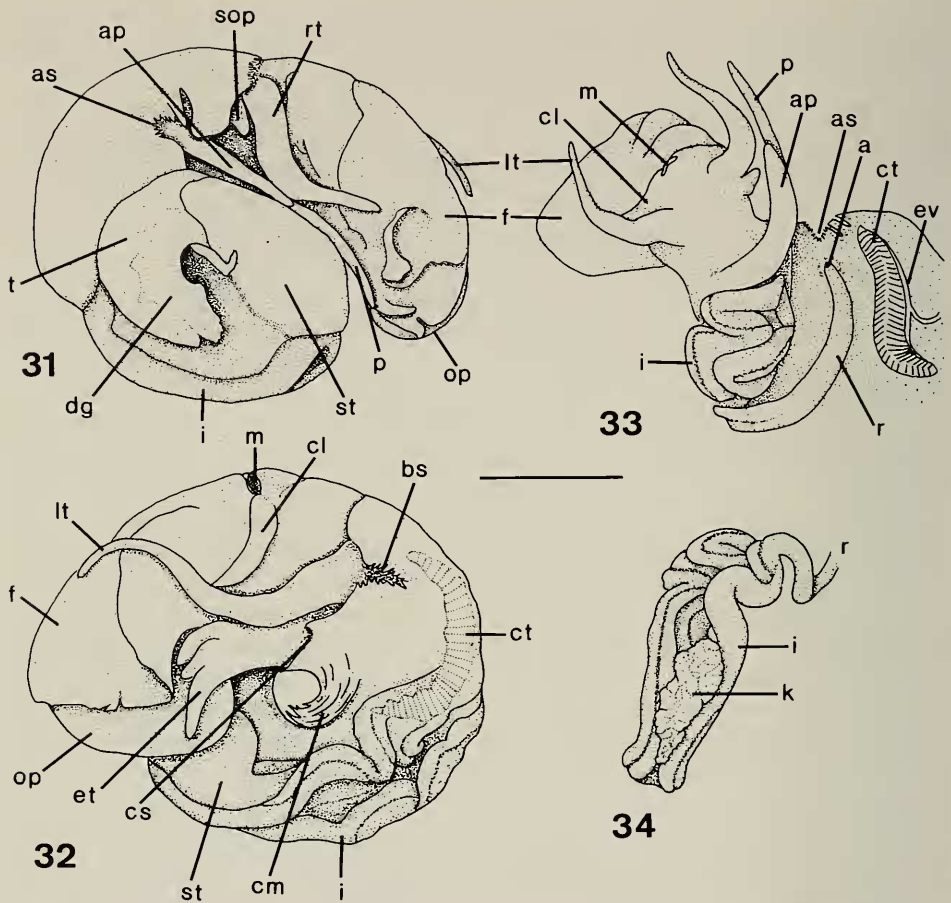
#### Operculum and Anatomy

*Operculum.*—In all species for which the operculum has been described (e.g., Bayer 1971: 124, 126, Fig. 7A), it has been characterized as thin, corneous,

paucispiral with subcentral nucleus, and auriculiform. Figure 35 shows the operculum of an undescribed *Seguenzia* species. Superficially, it appears more similar to many mesogastropod opercula than to the multispiral opercula of most operculiferous archaeogastropods. However, it is perhaps unwise to attribute phylogenetic significance to this structure since there are some archaeogastropods with similar opercula (e.g., *Euchelus Philippi*), and mesogastropods with multispiral opercula (e.g., *Echininus* Clench and Abbott). Moreover, the oligogyrous condition may be the result of the extremely small size of seguenziaceans.

*Anatomy.*—Although most shell characters of apparent phylogenetic significance (e.g., nacreous layer, protoconch) indicate that seguenziaceans are archaeogastropod in affinity, the incompletely known anatomy of these animals shows an intriguing combination of characters often used to distinguish archaeogastropods from mesogastropods. There is only one published account of the anatomy of a seguenziacean (*Guttula galathea*; Knudsen 1964); however, Dr. Philippe Bouchet (in litt.) has informed me that anatomical work on *Carenzia carinata* (Jeffreys) is in progress. To Knudsen's remarks, Dr. James McLean has generously allowed me to add observations he made on a partial dissection of *Seguenzia megaloncha* Rokop from the eastern Pacific, and I have added a commentary on my own dissection of *Seguenzia* sp. cf. *S. eritima* Verrill (hereafter *S. "eritima"*). Knudsen's description of the external anatomy is as follows (Knudsen 1964:128): "The foot is broad and has a distinct median ridge. A well developed propodium is present. The posterior part of the foot is rounded. An epipodium is present, having 3–4 tentacles. The cephalic tentacles are well developed, and pointed. No eyes could be observed. The mantle edge has a finger-shaped tentacle located on the right side. The anus is situated on a rounded lobe projecting from the extreme right side of the mantle edge. The penis is extremely well developed." McLean adds the following commentary on *Seguenzia megaloncha*: "The foot is contracted so that its shape cannot be described nor the epipodial tentacles counted, though there seem to be six on the right and at least three, probably 6, on the left. In the terminology of Crisp (1981) the epipodial tentacles are papillate like the cephalic tentacles. The foot is too contracted to tell whether or not there are epipodial sense organs. Eyes and optic tentacles are lacking; the cephalic tentacles are long, papillate, and evenly tapered, the greatest diameter at the base 4 times broader than the blunt tips, the attachment to the head constricted to half the maximum basal diameter. The right cephalic tentacle has the right subocular peduncle projecting from the thickened basal area. There are no neck lobes or cephalic lappets. The penis is longer than the cephalic tentacles, not papillate, evenly tapered, the tip narrower in diameter than the tips of the cephalic tentacles, the basal diameter exceeding the diameter of the bases of the cephalic tentacles. The snout is  $\frac{1}{3}$  the length of the cephalic tentacles, the mouth a vertical slit under an upper lip. The gill is attached to the mantle skirt and is pectinibranch with about 30 triangular filaments, with no evidence of a free bipectinate tip or the transverse pallial vein of the Trochacea. The edge of the mantle skirt is finely fringed, but the pallial tentacle on the right side of the mantle skirt is relatively small."

The following description is based on my study of a male specimen of *S. "eritima"*: Although strongly contracted, the foot appears to be truncated anteriorly, tapering gradually to a broadly rounded, possibly bilobed, posterior; there



Figs. 31–34. Animal of *Seguenzia "eritima"*: 31, animal removed from shell, right side; 32, same, left side; 33, mantle reflected to right showing head and anterior portion of pallial cavity; 34, dorsal view of intestine and kidney. Scale bar = 1 mm for Figs. 31, 32; 1.5 mm for Figs. 33, 34. Abbreviations: a, anus; ap, accessory cephalic process; as, anal sinus; bs, basal sinus; cl, lateral processes of snout; cm, columellar muscle; cs, columellar sinus; ct, ctenidium; dg, digestive gland; et, epipodial tentacle; ev, efferent branchial vein; f, foot; i, intestine; k, kidney; lt, left cephalic tentacle; m, mouth; op, operculum; p, penis; r, rectum; rt, right cephalic tentacle; sop, subocular peduncle; st, stomach; t, testis.

is a small, short tentacle at each anterolateral corner. There appear to be four pairs of epipodial tentacles which increase in size from anterior to posterior. Epipodial sense organs appear to be lacking. Epipodial tentacles (Fig. 32, et) are like those described by Crisp (1981). The operculum is very thin, corneous, with a subcentral nucleus and about four or five rapidly expanding whorls.

The snout is very short, but provided with long, triangular, lateral extensions (oral lappets?; Figs. 32, 33, cl). The mouth is transversely elongate, surrounded by an outer lip which is interrupted mid-ventrally. The cephalic tentacles (Figs. 31–33, rt, lt) are long, papillate, and tapered from a broad base to a blunt tip. The right tentacle bears a prominent subocular peduncle (Figs. 31, 33, sop) on

the base. There are no eyes or optic tentacles. A very long, slender penis (Figs. 31, 33, p) arises from the right side of the head lateral and posterior to the right cephalic tentacle; a ciliated sperm groove runs along the ventral side of the free part of the penis, becoming lateral at the base where the seminal duct opens into the groove. Two small accessory tentacles are situated just posterior to the base of the penis. A large cephalic process (Figs. 31, 33, ap) arises dorsal and posterior to the left cephalic tentacle, crosses the head obliquely to the right, and curves forward to the right of the right cephalic tentacle. It is attached to the head for about half its length, becomes free behind the right tentacle and projects forward between the tentacle and penis.

The mantle edge bears two deep and two shallow papillate embayments, or mantle sinuses, which correspond in position to the shell sinuses. One of the major embayments, corresponding to the basal sinus of the shell, is located over the base of the left cephalic tentacle and undoubtedly acts as the primary incurrent siphon (Fig. 32, bs). This embayment is papillate along the entire edge, and a ridge of muscle is located just back of the edge, indicating that this area can be expanded to some extent. The other large embayment functions as the excurrent, or anal, siphon, and is in the extreme right part of the mantle edge (Figs. 31, 33, as). It too is papillate, but only along the posteriormost edge. The medial edge of this mantle sinus is strongly folded, indicating that considerable extension is possible, forming a baffle or pseudosiphon directing the exhalent current to the right. The two smaller embayments, one located on the extreme left (Fig. 32, cs) and the other mid-dorsally, are both papillate; the other areas of the mantle edge are smooth. There are no pallial tentacles.

The ctenidium (Figs. 32, 33, ct) is monopectinate, with about 30 triangular lamellae, extending in a curve from a posterolateral position medially and anteriorly to end just to the right of the large left mantle sinus. Neither osphradium nor hypobranchial gland was observed. The intestine (Figs. 31–34, i) is prominent, convoluted, arising from the style sac of the stomach, running forward to about the accessory cephalic process, turning to the left and running back to the middle part of the stomach, and finally turning forward along the right to the anus which is on a small papilla. The intestine was filled with fine detrital material (mostly mud, foraminiferan tests, and diatom frustules) which was consolidated into a continuous fecal string which had an ovoidal cross section and a generally dorsal longitudinal groove. The preservation of the large, thin-walled stomach (Figs. 31, 32, st) was not adequate for detailed study of the internal morphology. The left kidney (Fig. 34, k) is located above the stomach, above and within the posterior bight of the intestine. There appears to be no right kidney. The circulatory system is apparently of monotocardian layout. The heart is located dorsolaterally to the right of the anterior end of the stomach. The single auricle receives the long efferent branchial vein and the ventricle is not penetrated by the intestine. The aortae emerge and run along the right side of the body.

The above descriptions, although of differing completeness, have several elements in common. The epipodium, epipodial tentacles, and penis are shared by all three species. A pallial tentacle is present in both *Guttula galathea* and *Seguenzia megaloncha*. Although by no means conclusive, these similarities, along with radula and shell characters, tend to support my inclusion of *Guttula* in the Seguenziacea.

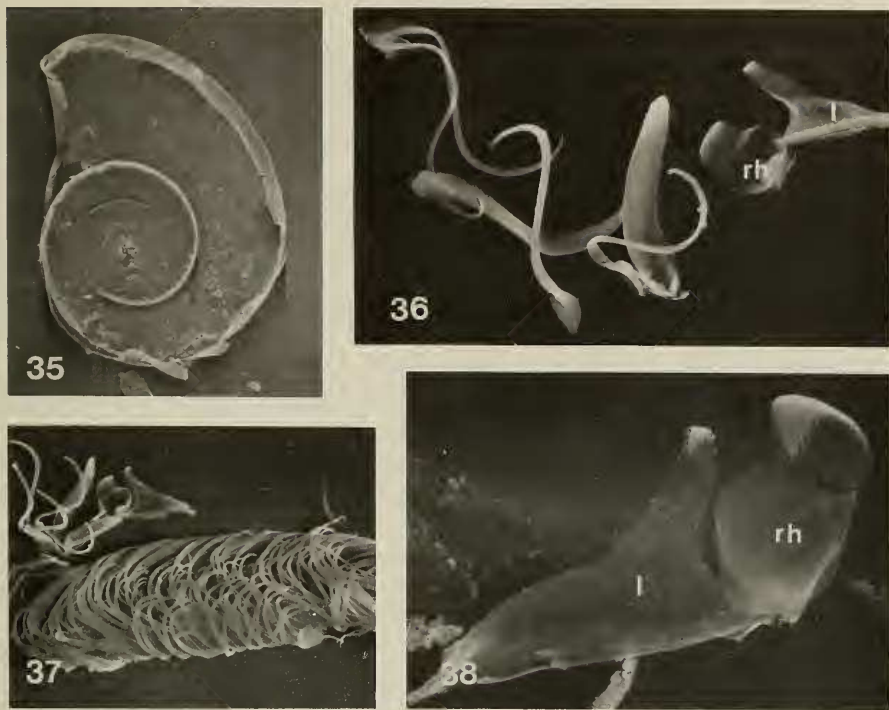
The descriptions of *Seguenzia megaloncha* and *S. "eritima"* agree in most respects, but there are a few obvious differences in external morphology between the two species. The pallial tentacle of *S. megaloncha* is absent in *S. "eritima,"* and there is no basal constriction of the cephalic tentacles in *S. "eritima."* Presence of pallial tentacles in one and not another species of the same genus is also seen in the rissoacean genera *Cingula* and *Onoba* (Fretter and Graham 1978b). This situation may also be found in individuals of the same species (e.g., *Onoba semicostata*; Fretter and Graham 1978b:165). The basal constriction of the cephalic tentacles in *S. megaloncha* may not have any significance but bears investigation in other species. The lateral extensions of the snout in *S. "eritima,"* not found in *S. megaloncha*, are of functional importance but are of unknown taxonomic significance at present. The extensions are probably primarily sensory in nature, supplementing the cephalic tentacles, but may be used in feeding, either by stirring up the substrate, or by aiding in the movement of food into the mouth.

The most striking difference between *S. megaloncha* and *S. "eritima"* is the large accessory cephalic process which lies obliquely across the head of *S. "eritima,"* but is totally absent in *S. megaloncha*. It is a conspicuous structure, arising from the head behind the left tentacle, remaining attached to the dorsum behind the right tentacle, and finally projecting forward as a finger-like process to the right of the right tentacle. The internal structure of this process has not yet been determined, although it appears to be solid and muscular; its function is not immediately evident, and I have not been able to locate any reference in the literature to a similar structure occurring in any other prosobranch. The penes of *S. megaloncha* and *S. "eritima"* originate at different positions. That of *S. megaloncha* arises from the dorsum of the head near the midline, and that of *S. "eritima"* arises from the right side. The significance of this difference is unclear to me. The location of the anterior and posterior aortae, on the right side of the animal, is apparently unique among coiled gastropods. All accounts I have been able to locate have described the aortae being on the left side. Knowledge of the anatomy of other seguenziacean species is needed before the systematic significance of these anatomical structures can be inferred.

#### Radula

The distinctive seguenziacean radula combines features of rhipidoglossate and taenioglossate radular types, but fits neither type. All seguenziaceans for which radulae have been illustrated (Figs. 39–48) have the central part of the radula comprised of a rhachidian (Figs. 37, 38, rh) flanked by a single pair of laterals (Figs. 37, 38, l), and the outer part of 4–12 pairs of marginals which completely cover the central portion in the folded, non-working condition (Fig. 36). It thus appears to be a modification of the rhipidoglossate radula, derived by reduction of number of laterals and marginals to the point where, in *Seguenzia* Group I, the radula bears a strong superficial similarity to the taenioglossate state (Fig. 46). In fact, many of the species in the family Triphoridae have radular formulae (Triphorinae, 30-9.1.1.1.9-30; Mastoniinae, 8-5.1.1.1.5-8; see Kosuge 1966) which are similar to that of the seguenziaceans (12-4.1.1.1.4-12). However, the teeth of the two radular types are totally different structurally, and there is little resemblance in shell or anatomy between triphorids and seguenziaceans. There is little





Figs. 35–38. SEM micrographs of operculum and radula of *Seguenzia* sp.: 35, operculum, 47 $\times$ ; 36, intact radular ribbon with marginals folded over central part, 268 $\times$ ; 37, individual teeth teased out of ribbon, 570 $\times$ ; 38, rhachidian and lateral teeth, 1340 $\times$ .

doubt that these two groups are unrelated, and further comparisons are unnecessary. There are a large number of modified radular types in the archaeogastropods, especially in deep-water groups, and use of this structure to infer relationships should be made with care.

*Seguenzia*.—(Figs. 36–38, 46–48). The *Seguenzia* radula consists of the rhachidian, a single pair of laterals, and (as far as is known) four pairs of marginals per row. The rhachidian is pyriform with a basal attachment process and a single, denticulate cusp. The lateral has a broad, rather triangular base with a long, slender, finely denticulate cusp near the proximal corner. The first marginal is larger than the rest, blade-like, and denticulate on both sides near the tip. The remaining marginals are long, very slender, with a few fine, spinular teeth slightly removed from the tip, and a rhomboidal base. Both Schepman (1909) and Barnard (1963c) illustrated *Seguenzia* radulae (*S. melvilli* and *S. simplex*; Figs. 47 and 48, respectively) showing rhachidians without the basal process and cusplless laterals. In *S. melvilli*, Schepman may have simply missed the basal process of the rhachidian, and the cusp of the lateral may have been worn or broken off. Barnard's species, *S. simplex*, may not be congeneric with *Seguenzia* sensu stricto, although the same considerations as those mentioned for *S. melvilli* may also apply here. Scanning electron micrographs presented by Bandel (1979) and Hickman (1980) of the radula of *S. megaloncha* are almost indistinguishable from those pre-

sented here (Figs. 36–38, 46) of the radula of an undescribed species from the Philippines. Schepman (1908) also described the radula from a syntype of *Basilissa lampra* Watson, which he mistakenly considered the type of *Basilissa*. However, that radula (Fig. 45) is more similar to those described for *Seguenzia* (Figs. 46–48) than to those of true *Basilissa* (Figs. 40, 41). The shell shape of *B. lampra* is similar to those of *Seguenzia* Group III, so it is probable that this species is a *Seguenzia* sensu lato rather than a *Basilissa*. Thiele (1925) described the radula of *Fluxina trochiformis* Schepman, in which he found a single, broad lateral, a single, rather wide inner marginal, and five outer marginals denticulate on the distal edges. Thiele therefore transferred *F. trochiformis* to *Basilissa*. This species bears a strong conchological resemblance to *F. discula* Dall, which has recently been assigned to *Basilissa* (Merrill 1970b; Quinn 1979). However, *F. discula* and *F. trochiformis* are here referred to *Seguenzia* Group IV pending description of that group as a new genus by Marshall (in press).

*Basilissa*.—(Figs. 40, 41). The radula of *Basilissa* differs from that of *Seguenzia* sensu stricto in having 6–7 marginal teeth (Bayer 1971) and a larger, more triangular cusp on the lateral tooth.

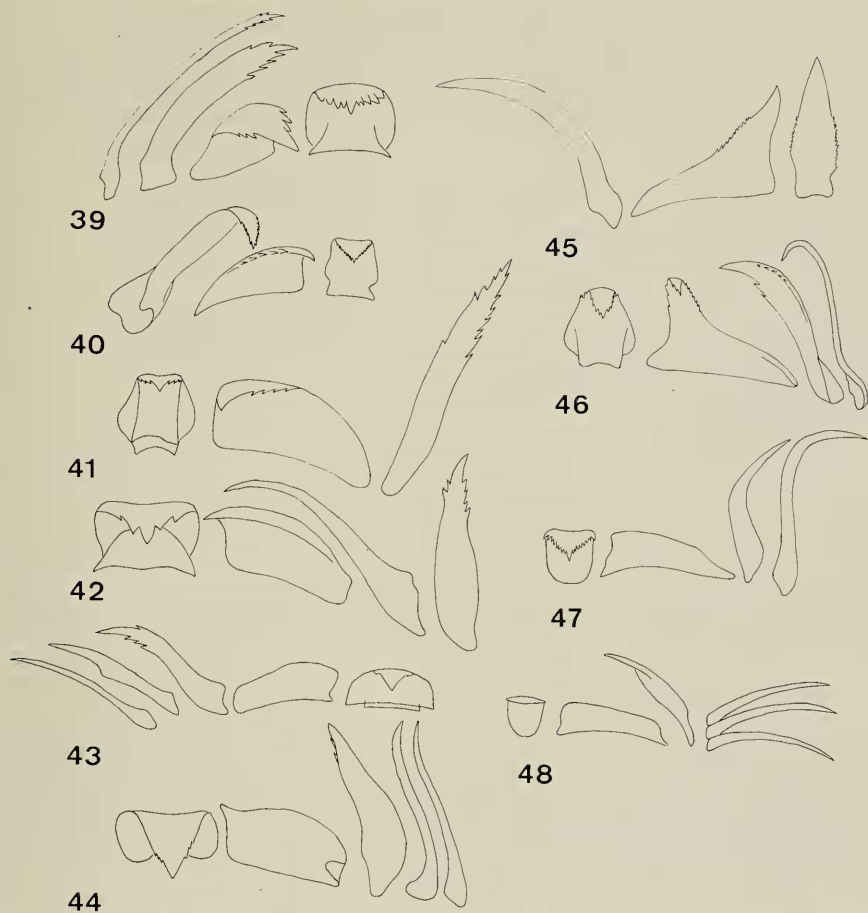
*Ancistrobasis*.—(Fig. 39). The radula of *Ancistrobasis* has not been previously illustrated or described. It is more trochoid than that of either *Seguenzia* or *Basilissa*, having a rather large, rectangular rhachidian with denticulate cusp, a large, subquadrate lateral with an inwardly directed cusp denticulate on both sides, and twelve slender marginals finely denticulate near the tip.

*Guttula*.—(Figs. 42–44). The radulae of all three nominal species of *Guttula* have been described and illustrated, and indicate an affinity with more typical seguenziaceans. The rhachidian is broad, rather rectangular, with a denticulate cusp. The lateral is large, broad, and rectangular, with or without a cusp. There are a “few” marginals (no one has given a specific number, although Barnard (1963c:266) states “not more than ten”). The length of the radula of *G. sibogae* Schepman is about 1 mm and its width about 0.3 mm (Schepman 1908). Schepman counted about 20 rows of teeth, Barnard (1963c) about 22.

### Fossil Record

As far as is known, the Seguenziacea are relatively young, possibly originating sometime during the late Cretaceous or early Tertiary, and at least one group (*Ancistrobasis*) attained its modern form by the Eocene. Over 20 fossil species have been described, most of which were assigned to *Basilissa*, but less than half of these taxa are true seguenziaceans (Tables 1, 2).

The earliest occurrences of the Seguenziacea in the geological record are *Seguenzia radialis* Tate (Tate 1888, 1890) and *Basilissa cossmanni* Tate (Tate 1894) from the Eocene of South Australia, and *Basilissa (Ancistrobasis) pacifica* Ladd (Ladd 1970) from the Eocene of Tonga. All three taxa are here considered *Ancistrobasis* species. *Ancistrobasis* also occurs in the Pliocene of Sicily (*Solarium reticulatum*; Philippi 1844; Jeffreys 1885). The first known occurrence of *Seguenzia* is *S. hapala* Woodring from the middle Miocene of southern Mexico (Perrilliat 1972). Specimens of this species have also been collected from the basal Pliocene of the Dominican Republic (Gurabo Formation; H. E. Vokes, in litt.), the upper Pliocene-basal Pleistocene of Jamaica (Bowden Formation; Woodring



Figs. 39–48. Diagrammatic sketches of seguenziacean radulae, not to scale: 39, *Ancistrobasis depressa*; 40, *Basilissa alta* (after Bayer 1971); 41, *B. sibogae* (after Schepman 1908); 42, *Gutula sibogae* (after Schepman 1908); 43, *G. blanda* (after Barnard 1963); 44, *G. galathea* (after Knudsen 1964); 45, *Seguenzia lampra* (after Schepman 1908); 46, *Seguenzia* sp.; 47, *S. melvilli* (after Schepman 1909); 48, *S. simplex* (after Barnard 1963).

1928), and the Recent throughout the Gulf of Mexico and Caribbean [Treece, 1977, 1980 (as *S. formosa*); Treece 1979 (as *S. monocingulata*); Quinn unpublished data]. Seguenza (1876, 1877, 1879) recorded *S. monocingulata* from the Pliocene of Italy. *Mioseguenzia* Nordsieck, 1973, described with a Miocene type-species, is cypraeacean (Bouchet, in litt.), not seguenziacean. Some members of the Paleozoic-Mesozoic family Omphalotrochidae Knight, 1945, bear a superficial resemblance to *Basilissa*, but, as discussed below, this similarity is probably convergent and not an indication of relationship.

Other allocations of fossil species to *Basilissa* (Cossmann 1888; Noetling 1901; Oppenheim 1906, 1923; Yokoyama 1922; Koperberg 1931; Riedel 1932; Ravn 1933, 1939) followed Cossmann's (1888) erroneous concept of the genus. Most of these species appear to be referable to the Trochidae (Table 2).

Table 2.—Taxa rejected from, or of doubtful inclusion in, the Seguenziacea.

ORIGINAL BINOMEN	
<i>Seguenzia tricarinata</i> Jeffreys, 1885	Nassariid protoconch
<i>S. laxa</i> Jeffreys, 1885	Indeterminate
† <i>Basilissa boutillieri</i> Cossmann, 1888	?
<i>B. patula</i> von Martens, 1901	<i>Calliotropis</i>
† <i>B. lorioliana</i> Noetling, 1901	?
<i>B. ottoi</i> var. <i>chuni</i> von Martens, 1903	<i>Calliotropis</i>
† <i>Trochus (Basilissa) libycus</i> Oppenheim, 1906	?
<i>B. babelica</i> Dall, 1907	<i>Orectospira</i>
<i>B. niceterium</i> Hedley and May, 1980	<i>Calliostoma</i>
† <i>B. ?laeviuscula</i> Yokoyama, 1922	<i>Proconulus?</i>
<i>Trochus (Basilissa) lukavatzensis</i> Oppenheim, 1923	?
† <i>B. lemoinei</i> Koperberg, 1931	?
† <i>B. antiqua</i> Riedel, 1932	?
† <i>B. tricincta</i> Ravn, 1933	cf. <i>Bathybembix</i>
† <i>B. odumi</i> Ravn, 1939	cf. <i>Bathybembix</i>
† <i>B. (Orectospira) nenokamiensis</i> Kanno, 1958	<i>Orectospira</i>
<i>B. bicarinata</i> Habe, 1961	<i>Calliotropis</i>
<i>Mioseguenzia</i> Nordsieck, 1973	
Type-species.— <i>Janthina cimbrica</i> Sorgenfrei, 1958; by original designation.	
† <i>M. cimbrica</i> (Sorgenfrei, 1958)	Cypraeacean larval shell
<i>M. cimbrica recens</i> Nordsieck, 1973	Cypraeacean larval shell
<i>M. conica</i> Nordsieck, 1973	Cypraeacean larval shell

† = species described from fossil material.

? = affinities uncertain.

### Relationships

Speculations on relationships of the Seguenziacea to other prosobranch groups have been, and remain, inconclusive. Jeffreys (1876, 1879) strongly advocated assignment of *Seguenzia* to the Solariidae (=Architectonicidae), but this view has never gained acceptance. Following Seguenza's (1876) lead, many authors have placed *Seguenzia* in the Trochidae (Watson 1879a, 1886; Thiele 1925, 1929; Wenz 1938; Cotton 1959; Keen and Cox 1960; Barnard 1963c; Knudsen 1964; Barsanova 1966; Bayer 1971; Abbott 1974). These authors also considered *Basilissa* and *Guttula* to be trochids. *Seguenzia* has also been included in the Pleurotomariidae (Tryon 1883), Haliotidae (von Martens 1881; Tate 1888), and Scissurellidae (Locard 1898), principally because of the posterior sinus in the outer lip. Verrill's (1884) establishment of the Seguenziidae, including *Seguenzia* and *Basilissa*, and placement in the Mesogastropoda near the genus *Aporrhais* was followed by Golikov and Starobogatov (1975). The Seguenziidae have also been placed near, or included in, the Trichotropidae (Tryon 1887; Dall 1889b, c; Tate 1890; provisionally by Schepman 1909), near the Triphoridae (Dall 1927; Woodring 1928; Taylor and Sohl 1962), between the Archaeogastropoda and Mesogastropoda (Keen 1971), and near the Trochidae (Clarke 1961, 1962; Bandel 1979; Quinn 1979, 1981; Boss 1982). Recently Goryachev (1979) proposed inclusion

Table 3.—Comparison of shell and anatomical features of the Trochacea, Seguenziacea, and Rissoacea. Characters of the Trochacea and Rissoacea taken from Fretter and Graham (1962).

Structure	Trochacea	Seguenziacea	Rissoacea
Shell	Nacreous or porcellaneous	Nacreous	Porcellaneous
Protoconch	Archaeogastropod	Archaeogastropod	Mesogastropod
Radula	Rhipidoglossate	Modified rhipidoglossate	Taenioglossate
Epipodium	Present, with tentacles and sense organs	Present, with tentacles	Absent
Reproductive system	No copulatory organs; gametes shed through right kidney; fertilization external	Penis and closed gonoduct present; fertilization internal	Penis present; glandular gonoducts with accessory structures in female; fertilization internal
Ctenidium	Bipectinate (rarely monopectinate)	Monopectinate	Monopectinate
Pallial tentacles	Absent	Present in at least 2 species	Often present
Circulatory system	Diotocardian, with transverse pallial vein	Monotocardian (?), without transverse pallial vein	Monotocardian
Kidneys	Both right and left present	Right kidney lost (?)	Right kidney lost
Intestine	Long, with anterior loop; rectum passing through ventricle	Long, with anterior loop; rectum free of ventricle	Short, without anterior loop; rectum free of ventricle

of the Seguenziidae in the Protopoda Fisher, 1884 [sensu Golikov and Starobogatov (1975) = Turritellacea + Vermetacea] or possibly in a separate order. In view of data presented here, both proposals seem very unlikely. These assignments were made principally on the evidence of shell and, occasionally, radular characters. Therefore, features of the anatomy and shell morphology detailed in this paper permit a more critical examination of the possible affinities of the Seguenziacea than has yet been possible.

The first problem in assessing the probable relationships of the Seguenziacea is to determine the proper prosobranch suborder, Archaeogastropoda or Mesogastropoda, to which the group should be assigned. Table 3 presents a summary of the known characters of the Seguenziacea in comparison with corresponding traits of the Trochacea and Rissoacea, as representatives of the Archaeogastropoda and Mesogastropoda, respectively. If the use of the term "mesogastropod" is restricted to describe a certain level of anatomical organization rather than as a discrete taxonomic entity (Fretter et al. 1981), the Seguenziacea must be interpreted as mesogastropodan. However, as will be argued below, most of the *Seguenzia*-mesogastropod (the taxon) similarities are probably convergent, and may not be indicative of any phylogenetic relationship. Therefore, I propose that the Seguenziacea are highly modified and specialized archaeogastropods whose an-

atomical advances are consequences of extremely small body size and adaptation to life in the deep-sea.

Two seguenziacean characters which are the most indicative of archaeogastropod affinity are the shell and radula. Nacreous shells are known in the Monoplacophora and some lower groups of the Bivalvia, Cephalopoda, and Gastropoda, leading to the assumption that nacre is a primitive character within the Mollusca. Besides the Seguenziacea only two groups of living gastropods, the Pleurotomariacea and most Trochacea (both archaeogastropod), have nacreous shells. Nacre has not been noted in any mesogastropod or higher group. The seguenziacean radula seems to be a modification of the rhipidoglossate radula. Verrill's (1884) description of the radula of *S. eritima* as taenioglossate has induced many authors to assign *Seguenzia* to the Mesogastropoda. The seguenziacean radula does resemble the taenioglossate radula superficially, principally in having only a single lateral and a reduced number of marginals in each radula half-row. Of the mesogastropod families discussed by Boss (1982), only two were recorded as having more than two marginal teeth, the Turritellidae (3-0.1.1.1.0-3) and the Triphoridae (30-9.1.1.1.9-30 or 8-5.1.1.1.5-8), and neither family is in any way similar to seguenziaceans in shell or anatomy. Moreover, the two marginals of the typical taenioglossate radula are very similar to each other in shape and size. Seguenziacean marginals are morphologically different, the innermost tooth being rather large and robust and the outer whisker-like, a situation reminiscent of several rhipidoglossate ground plans in which the marginals may be divided into two or more distinct morphological groups, with the innermost usually much stronger than the outer. It has been suggested to me that the multiple marginals of the seguenziacean radula might have been produced by repeated splitting of the taenioglossan marginals. While this remains a possibility, especially in view of the observations of Shimek and Kohn (1981) on the Turritidae, the apparent affinity of the Seguenziacea with archaeogastropods such as the Trochacea (discussed below) suggests that the seguenziacean radula is merely a modification of the rhipidoglossate radula, and is adapted for sweeping particulate matter from the bottom and conveying it to the esophagus.

Other traits of the Seguenziacea which suggest archaeogastropod affinity are a long intestine with an anterior loop, a subocular peduncle on the base of the right cephalic tentacle, and an epipodium with epipodial tentacles. The intestine follows a course similar to that of the Trochacea, but the seguenziacean anterior loop (perhaps not homologous with that of the Trochacea?) is much longer, and the intestine does not penetrate the ventricle. The subocular peduncle has been noted in several species of Trochidae (Crisp 1981), but to my knowledge is not known in any other prosobranch group, except, perhaps, the Fissurellacea (McLean, in litt.). The epipodium and associated tentacles have been generally considered an archaeogastropod trait (Fretter and Graham 1962), but epipodial tentacles are also known in some mesogastropods [e.g., Litiopidae and Dialidae (Houbriek 1980; see also Thiele 1929)]. Even the fecal string of *Seguenzia* resembles that of the Trochacea, although there is no liver string (see Fretter and Graham 1962).

Several seguenziacean features show progression into an advanced grade of organization. However, most of the advancement may be attributed to adaptation to a small body size and for increased functional efficiency. The radula has already been discussed. The other principal modifications include the development of an

advanced reproductive tract, a monopectinate ctenidium, and functional inhalent and exhalent pallial siphons.

Although no in-depth anatomical examination of the seguenziacean reproductive system has yet been made, presence of a well-developed penis suggests other modifications of the tract, such as possible accessory structures in the female oviduct. I have not examined any females, but Dr. Anders Warén (pers. comm.) has indicated that such modifications may be present in female *Carenzia carinata* from the northeastern Atlantic. My examination of the male of *S. "eritima"* indicates a simple sperm duct, without prostate gland, which opens into a ciliated sperm groove on the penis. Penial structures, either as modifications of a cephalic tentacle or de novo structures, are rare, but not unknown in the archaeogastropods. Perhaps the best known situation is in the Neritacea, in which a true cephalic penis has been developed (see Fretter and Graham 1962; Fretter 1965). Several other archaeogastropod groups also have been reported to have a penis: Cocculinacea (*Cocculina* and *Addisonia*; see Dall 1889b, 1890); Trochidae [*Solariella* (= *Calliotropis*) and *Turricula* (= *Bathybembix*); Dall 1889a, b, 1890]; Fissurellacea (*Rimula* and *Fissurella*; Dall 1889b); and the recently described Neomphalacea (*Neomphalus*; McLean 1981; Fretter et al. 1981). The Cocculinacea and Neomphalacea each have a modified cephalic tentacle (the former the right, and the latter the left tentacle), but the function as a penis is undoubted. The "penis" described by Dall (1889b) in the Fissurellacea was found to be solid by Odhner (1932) who referred to the structure as a "sexual cirrus." The rudimentary "penis" reported in the Trochidae (Dall 1889a, b, 1890) has not been investigated subsequently. McLean (in litt.) considers the penis-like structures of the fissurellaceans and trochids to be the right subocular peduncle. Since all archaeogastropod groups with an undoubted penis except the Neritacea (Cocculinacea, Neomphalacea, and Seguenziacea) are principally deep-sea forms, and most are extremely small (less than 10 mm, except *Neomphalus fretterae* McLean, 1981, which may be as much as 30 mm in diameter and which lives in a unique situation, the Galápagos Rift), energy conservation is a primary concern. Internal fertilization severely reduces the wastage of gametic products, and evolution of copulatory structures would be the most efficient solution to that problem.

A monopectinate ctenidium is generally associated with a mesogastropod, or higher, grade of organization, and has not been reported previously in any archaeogastropod except *Umbonium* (Fretter 1975; McLean 1981). Presence of such a ctenidium in the Seguenziacea may well be an adaptation for economy of space in the pallial cavity of these small animals. A monopectinate ctenidium provides more efficient use of space and eliminates any circulatory dead spots which are found in most bipectinate ctenidia. However, the change from bipectinate to monopectinate conditions must require some compensation for the decrease in strength of the ciliary currents flowing through the pallial cavity caused by reduction of the number of ctenidial leaflets; therefore, the Seguenziacea, like many mesogastropods and virtually all neogastropods, have modified the mantle edge to form inhalent and exhalent siphons. However, seguenziacean siphons are papillate embayments in, rather than extensions of, the mantle edge. The papillae may augment the ctenidial cilia in producing the inhalent and exhalent currents, and the siphons undoubtedly enhance the efficiency and directionality of the currents. The seguenziacean siphons are apparently analogous to those of meso-

gastropods and neogastropods, but are de novo structures derived in conjunction with evolution of a monopectinate ctenidium. In addition, in at least one species (*S. "eritima"*), a cephalic process forms a baffle across the opening of the mantle cavity which probably prevents water from entering or exiting the mantle cavity except through the siphons.

Since the known features of the Seguenziacea are either clearly archaeogastropod in nature or can be derived from archaeogastropod structures as adaptations for small body size and life in the deep-sea, it seems most prudent to consider the Seguenziacea the end of a long-separated evolutionary lineage of archaeogastropod derivation, which has developed mesogastropod-like adaptations independent of any mesogastropod lineage. In this regard, the Seguenziacea are similar to the Neomphalacea (McLean 1981) and Neritacea (Fretter and Graham 1962; Fretter 1965).

If Seguenziacea are indeed archaeogastropods, as argued here, then which group might be considered seguenziacean precursors? Solely on the basis of shell shapes and position of anal sinuses, two possibilities exist. First is an origin in a euomphalacean group such as the Omphalotrochidae Knight, 1945, especially *Omphalotrochus* Knight, 1945, *Orecoptia* Knight, 1945, and *Babylonites* Yochelson, 1956. Earlier (Quinn 1981) I suggested that the Seguenziacea might have been derived from such omphalotrochids based on the subsutural sinus and channeled, claw-like extension of the outer lip, which are apparent homologues of the anal and basal sinuses of the seguenziacean shell. McLean (1981) has since pointed out that the Omphalotrochidae are not known to have nacreous shells, and that a reversion to the nacreous condition would be unlikely. In addition, there is a gap of about 200 million years between the extinction of the Omphalotrochidae (Middle Permian) and the earliest known seguenziacean (Eocene). Therefore, an Omphalotrochidae-Seguenziacea lineage is not supported.

The other, and more probable origin, involves a derivation from within the Pleurotomariacea-Trochonematacea-Trochacea lineage. It has been hypothesized that the Pleurotomariacea gave rise to the Trochonematacea (Knight et al. 1960), which in turn were ancestral to the Trochacea (Fretter and Graham 1962). All three superfamilies have nacreous shells and the Pleurotomariacea and Trochonematacea both have labral sinuses. We know the anatomy of living Pleurotomariacea and Trochacea from which we may infer possible relationship with the Seguenziacea, but inferences about the extinct Trochonematacea are purely speculative. The Pleurotomariacea are gastropods retaining such primitive conditions as paired pallial organs, simple reproductive system and intestine penetrating the ventricle [see Fretter and Graham (1962) and Fretter (1964, 1966) for summary of other features]. From the position of the shallow anal sinus or channel, the Trochonematacea were probably dibranchiate, with the right ctenidium possibly being lost in the later forms (Knight et al. 1960). The Trochacea have lost the right ctenidium and osphradium, but retain the other paired pallial structures, the intestine is long, with an anterior loop, but still penetrates the ventricle, and the reproductive system remains relatively unspecialized (Fretter and Graham 1962). The Pleurotomariacea and Trochacea have rhipidoglossate radulae, although comparatively reduced in the latter group, and, in most other anatomical regards, the Trochacea and Pleurotomariacea are also remarkably similar (Fretter and Graham 1962; Fretter 1964, 1966; Graham 1965). Although similar to the



Trochacea and Pleurotomariacea in having nacreous shells, rhipidoglossate radulae (although modified), epipodium and epipodial tentacles, and an anterior loop of the intestine, the Seguenziacea have highly modified reproductive and circulatory systems and a monopectinate ctenidium, which indicate a long-standing separation from the mainstream of archaeogastropod evolution. My contention that the seguenziaceans are more likely to have had their origin within the Trochacea rests primarily on the fact that it seems more plausible to derive the seguenziacean organization as modifications of a trochoid organization than of a zeugobranche condition, and secondarily on the radula, trochoid-like fecal-string, and cephalic tentacles, especially the presence of a subocular peduncle on the right tentacle. Admittedly, this is rather tenuous evidence from which to draw a conclusion, but may serve as a working hypothesis for further research.

Since the anatomy of no seguenziacean is fully known, only three having been partly described, and the fossil record is so scanty, no discussion of relationships within the superfamily is now possible, nor is it possible to determine whether the anal sinus is a primitive character which was inherited from some ancestor or an innovation of the seguenziaceans. In view of the tendency of many other prosobranchs to develop similar structures, I believe the latter to be true, thus reinforcing my belief that the seguenziaceans are derived from some holostomatous ancestor, i.e., a trochoid. It is probable that additional family-group taxa may be required as future systematic studies are completed. Indeed, the monophyly of the Seguenziacea may even now be questioned. For example, it could be argued that the genera with labral sinuses may have evolved from the Trochonematacea, *Guttula* may have arisen independently from the Trochacea, and the selective pressures of similar habitats subsequently produced similarly constructed organisms. However, the presence of a penis, epipodium and epipodial tentacles, and radulae and shells similar to some undoubted seguenziaceans, suggest that *Guttula* should be included in the Seguenziacea.

Therefore, the Seguenziacea, as here defined, comprise the genera *Seguenzia*, *Carenzia*, *Basilissa*, *Basilissopsis*, *Ancistrobasis*, *Thelyssa*, and *Guttula*. The superfamily is characterized by nacreous shells, generally with labral sinuses, modified rhipidoglossate radula, and an anatomy retaining some archaeogastropod traits (epipodium with tentacles, long anterior loop of the intestine, and subocular peduncle) but attaining several mesogastropod features (penis in males, monopectinate ctenidium, and monotocardian circulatory system). This combination is so different from other known prosobranchs that there can be little doubt that recognition of a separate superfamily as suggested by Keen (1971), Golikov and Starobogatov (1975), Goryachev (1979), Quinn (1981, 1983a, b), McLean (1981), and Marshall (in press) is necessary. The Seguenziacea are here retained within the Archaeogastropoda as an independent offshoot of the Pleurotomariacea-Trochonematacea-Trochacea lineage, with the Trochacea as the most probable ancestral stock.

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NOTE: While this paper was in press, the monograph cited as “Marshall in press” was published (New Zealand Journal of Zoology 10:235–262, September 1983). In that report, Marshall recognizes 22 new species in eight genera, five of which were new. Since Marshall provided names for *Seguenzia* Groups II and IV (*Seguenziella* and *Fluxinella*, respectively), and modified the composition of several other taxa of my Table I, the reader is urged to consult his paper for further information.