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Cover Photo: Dr. Lynn Margulis, Symposium Keynote Speaker, describes the structure and ecology of living stromatolites. Some, visible as grayish mounds near her feet, line the shore of Storrs Lake whereas others occur farther out in deep water. (See paper by D. C. Edwards, this volume).

Back Cover Photo: Group photo of the 6th Symposium participants and speakers.

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ANDREWS' ANATOMICAL STUDIES AND THEIR TAXONOMIC SIGNIFICANCE FOR THE SNAIL FAMILY NERITINIDAE

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ABSTRACT

Structure of the spermatophores and penis of the male and functional relationships among the vagina, oviduct, and rectum of the female were studied in the following species of Neritinidae: *Nerita (Nerita) peloronta, N. (N.) versicolor, N. (Amphinerita) polita, N. (Ritena) plicata, N. (Theliostyla) albicilla, N. (T.) tessellata, N. (T.) fulgurans, N. (T.) planospira, Puperita pupa, Neritina (Neritina) pulligera, N. (Clypeolum) latissima, N. (Neripteron) taitensis, N. (Vittina) parallela, N. (Vitta) virginea, Neritodryas cornea, Clithon (Clithon) retropictus, Clithon (Pictoneritina) oualaniensis, Neritilia succinea*, and *Septaria borbonica*. While traditional radula, shell, and operculum characters remain useful, these studies confirm that many of Andrews' 1937 anatomy-based proposals for the refinement of Baker's 1923 radula-based classification should be accepted.

INTRODUCTION

In spite of the abundance of Neritinidae, especially in the tropics and subtropics, their taxonomy remains in considerable confusion. Classical conchological approaches provided some meaningful distinctions (Sowerby, 1855; Reeve, 1855-1856; Martens, 1869, 1879, 1881, 1889; Tryon, 1888). Early anatomical studies providing useful data include Lenssen (1899a, 1899b) and Bourne (1908). Baker's (1923) extensive study of neritid radulae and Andrews' (1937a, 1937b) anatomical studies contributed a wealth of data. Fretter (1946, 1965, 1966), Starmühlner (1969), and Pace (1973) provided some specific anatomical information useful for comparative studies, while Komatsu (1986) added scanning electron micrographs of radulae.

Taxonomically, the studies of Baker and Andrews have contributed the most useful information. Baker's arrangement was based almost entirely on radular characteristics. Andrews, on the other hand, suggested groupings based on the structure of the spermatophore and penis of males and the functional relationships among the vagina, oviduct and rectum of females. Andrews' work has largely been ignored in favor of Baker's, as evidenced by the nearly universal acceptance of Baker's arrangement by Wenz (1938), Knight, et al., (1960), and Abbott and Boss (1989). While the first two are paleontological references and the latter classifies only living mollusks, all three are compendia of all molluscan groups and were not specifically monographs of neritinids. Even the most recent monograph (Komatsu, 1986) deals almost exclusively with radulae and ignores the possible significance of Andrews' anatomical findings.

The subfamily Smaragdiinae was characterized by Baker (1923) as having sessile eyes and several unique radular characters. To these features Andrews (1937a, 1937b) added the observations that *Smaragdia viridis* has the anus and oviduct openings widely separated and that spermatophores are simple slender tubes.

Baker (1923) separated the Neritiliinae on the basis of their lacking both a central radular tooth and a well developed lower, peg-like apophysis on the operculum. Andrews (1937a, 1937b) agreed with this separation and added the following traits: (1) absence of both the male (penis) and female (crescent-shaped ridge) head organs; (2) absence of the reinforcement sac; and (3) distinct separation of the anus and oviduct openings.

On the basis of their similar radulae, Baker (1923) united the rest of the neritinids

into the subfamily Neritininae (see Table 1), which he split into two tribes. The tribe Neritae contained the genus *Nerita* (including the subgenus *Puperita*) and the genus *Theodoxus* (including the subgenus *Clithon*). Sections of each subgenus were also named. The tribe Septariae contained the genera *Septaria*, *Neritina*, *Pseudonerita*, and *Neritodryas*. *Neritina* was further divided into five subgenera and ten sections. Various authors, often without explanation, have elevated many of the sections to subgenera or genera.

Andrews pointed out, however, that in the seven species of *Nerita* studied by him, all (1) lack a female ridge; (2) lack a functional association between the anus and oviduct; (3) have a reinforcement sac containing secreted spherulites (from the digestive gland); (4) have a simple verge extending forward; and (5) have a simple spermatophore sac.

By contrast, Andrews found that in the species of *Puperita*, *Neritina*, *Theodoxus* (including *Clithon*), *Septaria*, and *Neritodryas* studied, all shared the following traits: (1) a crescent-shaped ridge lateral to the right tentacle of the female; (2) a functional terminal fusion of the anus and oviduct opening; (3) a reinforcement sac filled with sand, diatoms, sponge spicules and other foreign solids diverted from the rectum; (4) an elongated, complex penis carried under the right tentacle of the male; and (5) a specialized (female) spermatophore sac that retains and digests the spermatophores. This finding displaced *Puperita*, *Theodoxus* and *Clithon* from the tribe Neritae of the type genus (*Nerita*) to the tribe Septariae (Table 1).

Many authors have treated *Clithon* as no more than a subgenus of either *Neritina* (Martens, 1879; Tryon, 1888) or *Theodoxus* (Baker, 1923; Andrews, 1937a, 1937b; Kuroda, 1938). Most authors who have separated *Clithon* as a separate genus have either done so on the basis of shell characters (having spines) or have given no specific reason for doing so. Bourne (1908) provided some evidence that distinguishes *Theodoxus* from *Neritina*. He found a coelomic funnel in *Septaria*, *Neritina*, and *Nerita*, but not in *Theodoxus*. Also, *Septaria* and *Neritina* were found to possess a "ductus enigmaticus" which was lacking in *Nerita* and *Theodoxus*. Furthermore, Andrews' (1937a) work showed that members of the genus *Clithon* may be distinguished from those of *Theodoxus* and *Neritina* by the more complex penis in males and the vaginal spout in females. Both Starmühlner (1969) and Pace (1973) supplied anatomical illustrations supporting this separation. Long known opercular differences (Martens, 1879) were also noted and illustrated by Pace (1973). On the basis of these differences, Pace (1973) supported Andrews' separation of *Clithon* as a distinct genus.

The conservative nature of variation in reproductive structures and their utility in identifying species and their relationships has

Table 1 Comparison of the classifications of Baker and Andrews

Subfamily/Tribe	Baker's Classification	Andrews' Classification
Neritiliinae	Neritilia	Neritilia
Smaragdiinae	*Smaragdia*	*Smaragdia*
Neritininae		
Tribe Neritae	*Nerita* ***(Puperita)***, ***Theodoxus (Clithon)***	*Nerita*
Tribe Septariae	*Septaria, Neritina, Neritodryas, Pseudonerita*	*Septaria, Neritina, Neritodryas, Pseudonerita,* ***Puperita, Theodoxus, Clithon***

been demonstrated in many groups of organisms from plants to insects and mollusks. The major points of disagreement between Baker and Andrews are in the compositions of the tribes Neritae and Septariae of the subfamily Neritininae. The purpose of this study was to determine if Andrews' anatomical work could be verified and if his classification should be accepted.

MATERIALS AND METHODS

Table 2 lists the species dissected. For each species at least six specimens of each sex were dissected and drawn using a Wild M5 Stereomicroscope w/Camera Lucida. Alcohol-preserved specimens were provided by the Mollusk Division, Museum of Zoology, The University of Michigan and the Department of Invertebrate Zoology, Division of Mollusks, National Museum of Natural History, Smithsonian Institution. Personal collections from San Salvador, Bahamas, were made through the cooperation of the Bahamian Field Station and the Bahamian Government.

RESULTS

My dissections of specimens of eight species of the genus *Nerita*, including the type species of four subgenera (Table 2), confirm all five of Andrews' (1937a, 1937b) findings. While his drawings adequately illustrate the reproductive characteristics of the genus *Nerita*, Figure 1 shows the simple, forward-extended penis (P) and Figure 2 the relatively great distance (i.e., "lack of functional association") between the anus (A)

Table 2 Specimens dissected in this study
(*=Type species of the genus or subgenus)

Neritiliinae

Neritilia sp. (USNM 723802; Jamaica)

Smaragdiinae

None dissected; see Andrews (1937a)

Neritininae

Neritae

Nerita (Nerita) peloronta Linné, 1758 (van der Schalie, Pace; Florida, Bahamas) *
Nerita (Nerita) versicolor Gmelin, 1791 (van der Schalie, Pace; Florida, Bahamas)
Nerita (Theliostyla) albicilla Linné, 1758 (USNM 616111; Caroline Is.)*
Nerita (Theliostyla) tessellata Gmelin, 1791 (Pace; Bahamas)
Nerita (Theliostyla) fulgurans Gmelin, 1791 (USNM 734704; Panama)
Nerita (Theliostyla) planospira Anton, 1839 (USNM 700999; Fiji Is.)
Nerita (Ritena) plicata Linné, 1758 (USNM 685036; Cook Is.)*
Nerita (Amphinerita) polita Linné, 1758 (USNM 763298; Johnston Is.)*

Septariae

Puperita (Puperita) pupa (Linné, 1767) (Pace; Bahamas)*
Theodoxus fluviatilis (Linné, 1758) (None dissected; see Fretter, 1946)*
Clithon (Clithon) retropictus (Martens, 1879) (Pace, 1973; Taiwan)
Clithon (Pictoneritina) oualaniensis (Lesson, 1830) (USNM 543939; Guam)*
Septaria borbonica (St. Vincent, 1803) (USNM 674386; Tahiti)*
Neritodryas cornea (Linné, 1758) (USNM 664319; Palau Is.)*
Neritina (Neritina) pulligera (Linné, 1767) (Pace, 1973; Taiwan)*
Neritina (Neripteron) taitensis Lesson, 1830 (USNM 668536; Tahiti)*
Neritina (Clypeolum) latissima Broderip, 1833 (USNM 681888; El Salvador)*
Neritina (Vittina) parallela (Röding, 1798) (USNM 674385; Tahiti)
Neritina (Vitta) virginea (Linné, 1758) (USNM 709905; Florida)*

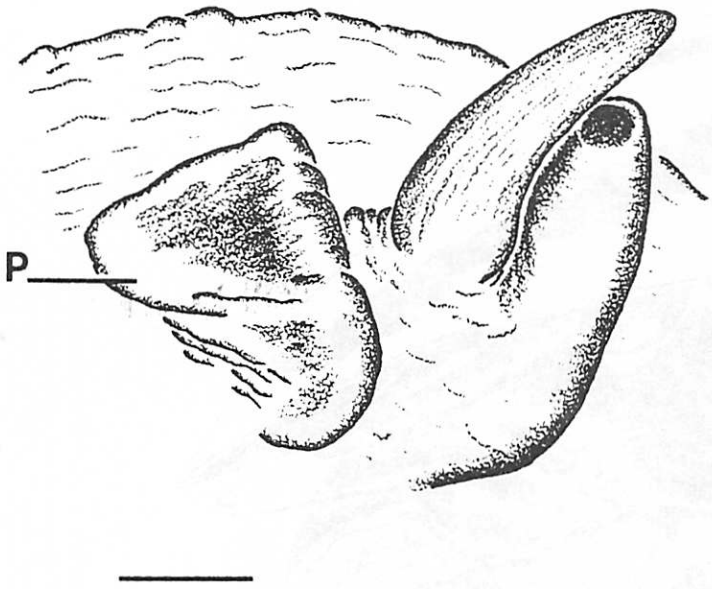

Figure 1 Penis (P) of *Nerita peloronta* L. View shows forward position just left of right tentacle. Scale line = 1 mm.

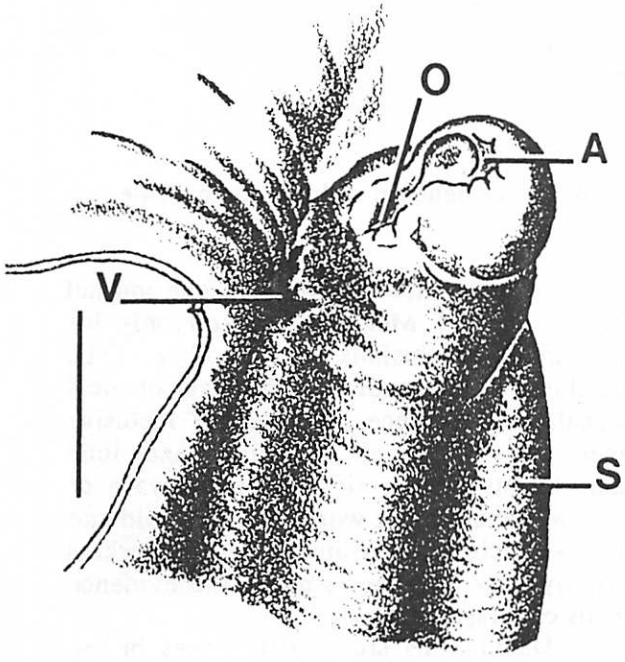

Figure 2 Terminal portions of female reproductive and digestive systems of *Nerita peloronta* L. visible when mantle is reflected. Vagina (V), Oviduct (O), Anus (A), Reinforcement Sac (S). Scale line = 1 mm.

and the oviduct (O) of the type species *Nerita (Nerita) peloronta.*

Of Andrews' Tribe Septariae, I also dissected specimens of ten species representing five subgenera of the genus *Neritina*, two subgenera of the genus *Clithon*, and three other genera. Again, Andrews' illustrations demonstrate the basic differences between these two tribes. Supporting illustrations may be found in Bourne (1908), Starmühlner (1969), and Pace (1973). The anatomy of *Theodoxus fluviatilis* has been beautifully illustrated by Fretter (1946, 1965, 1966). Examples shown here are of *Puperita (Puperita) pupa*, the type species of this genus. Figure 3 shows a lateral view of the male carrying its penis (P) beneath the right tentacle. The female ridge (R), just to the right of the right eye and tentacle is illustrated in Figure 4, while Figure 5 shows the close, functional relationship of the anus (A) and oviduct (O). Andrews (1935, 1937a, 1937b) and others have explained the functional relationship of these structures to the reinforcement sac (S) during egg laying. Materials (sand, spicules, etc.) from the rectum are carried by ciliary tracts to the reinforcement sac for storage. During oviposition these materials are delivered to the surface of the egg.

Table 3 summarizes differences between members of the two tribes of the subfamily Neritininae.

CONCLUSIONS

Baker (1923) proposed three subfamilies: Smaragdiinae, Neritiliinae, and Neritininae. He divided the latter subfamily into two tribes, Septariae and Neritae. Andrews (1937a, 1937b) added anatomical characteristics to the definitions of the first two subfamilies, but disagreed as to the relative placement of certain taxa within Baker's tribes of the Neritininae. The present study confirms Andrews' findings. Specifically, Andrews' definitions of the tribes Neritae and Septariae should be accepted. *Puperita, Theodoxus,* and *Clithon* were correctly removed from subordinate status under *Nerita* and should be considered separate genera in the tribe Septariae. *Septaria* remains a genus in the tribe Septariae, and is

Figure 3 Lateral view of male *Puperita pupa* (L.) carrying penis (P) beneath right tentacle. Scale line = 1 mm.

not considered to represent a separate family as was done by Abbott & Boss (1989).

Curiously, Andrews' anatomical studies and his taxonomic conclusions have not received wide acceptance. This family has many nominal species distributed all over the world in marine (*Nerita, Puperita*), brackish (*Neritina*), freshwater (*Septaria*), and even terrestrial habitats (*Neritodryas*). Few individual scientists would have wide enough interests or access to such a broad range of specimens to attempt a thorough examination of this family. Also, Baker was a world renowned malacologist working at The Philadelphia Academy of Natural Sciences with H.A. Pilsbry. While Andrews' work appears excellent and he was working out of Johns Hopkins University, he unfortunately published his anatomical work in one journal (The Journal of Morphology) and only his taxonomic conclusions in another (The Nautilus). Furthermore, in the malacological journal, no reference to the more inclusive paper can be found. Thus, taxonomic malacologists of the time were unaware of Andrews' anatomical work and so could not take his conclusions seriously. Recent workers similarly may have not studied the evidence for his conclusions.

During this study differences in the terminal portion of the vagina and its positional relationship to the oviduct and anus were discovered among many taxa. These differences suggest that further revisions within the tribe Septariae may be necessary, particularly within the genus *Neritina* (as

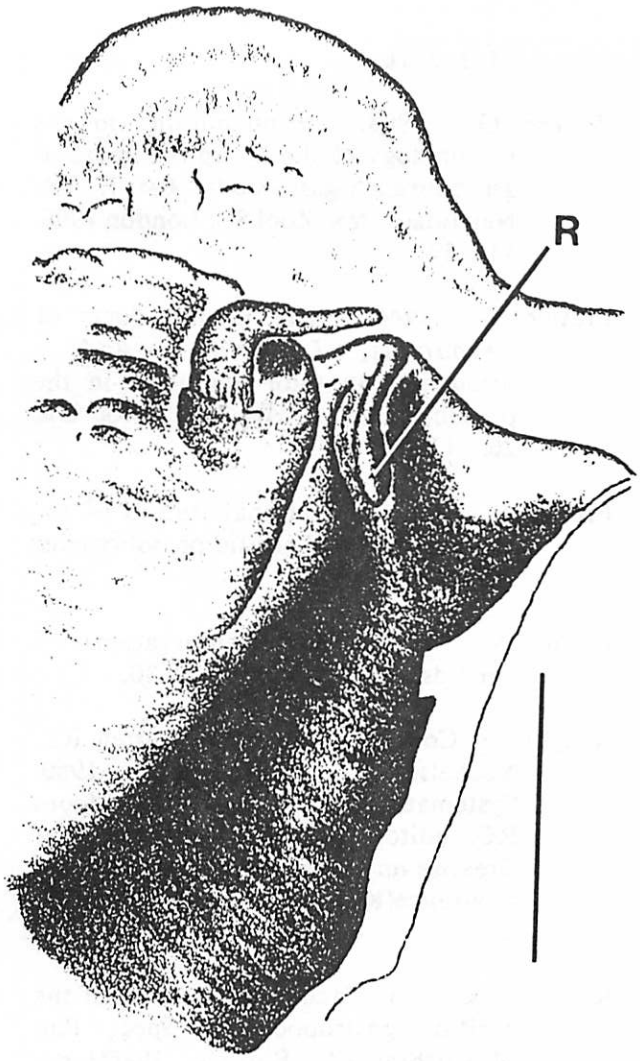

Figure 4 Dorsal view of female *Puperita pupa* (L.) showing female ridge (R) to right of right tentacle. Scale line = 1 mm.

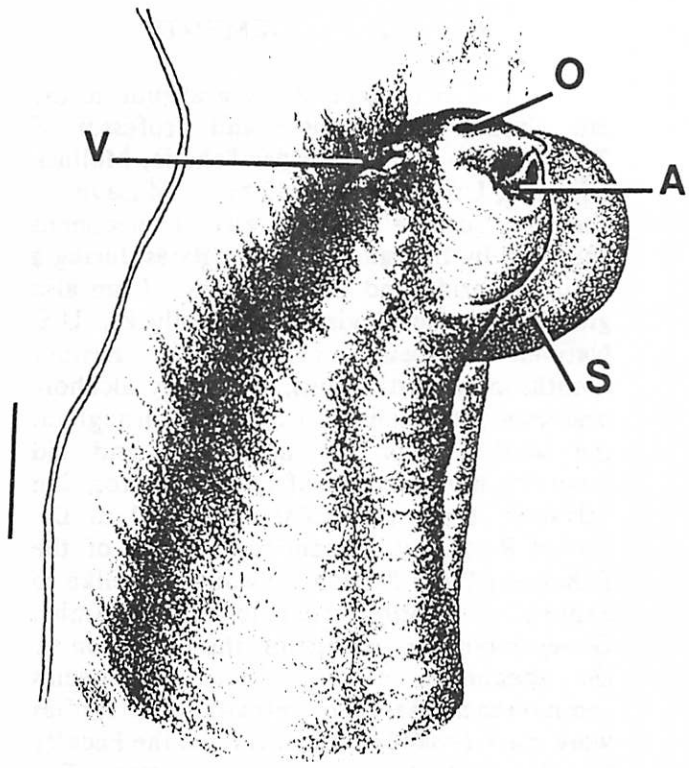

Figure 5 Terminal portions of female reproductive and digestive systems of *Puperita pupa* (L.) visible when mantle is reflected. Vagina (V), Oviduct (O), Anus (A), Reinforcement Sac (S). Scale line = 1 mm.

Table 3 Andrews' separation of the tribes Neritae and Septariae

Characteristic	Neritae	Septariae
Female Ridge	Absent	Present
Functional Oviduct-Anus Association	Absent	Present
Reinforcement Sac Contents	Secreted Spherulites	Sand, Diatoms, Sponge, Spicules
Penis (Verge)	Simple, Carried Foward	Complex, Carried Under Right Tentacle
Spermatophore Sac	Simple	Complex
Major Taxa	*Nerita*	*Septaria, Neritina, Neritodryas, Clithon, Pseudonerita, Puperita Theodoxus*

currently understood). These will be reported in a subsequent publication.

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Key words: Neritinidae, Neritidae, *Nerita*, *Neritina*, *Neritodryas*, *Neritilia*, *Theodoxus*, *Clithon*, *Puperita*, *Septaria*, *Smaragdia*, reproductive anatomy, taxonomy.