

Accounts on the phylogeny of the Risssooidea (=Hydrobioidea) and Littorinoidea, based on some American representatives, as base for a future taxonomic revaluation (Mollusca, Caenogastropoda).

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Abstract

This paper is developed based on descriptive studies published elsewhere. It aims to analyze the morphological data on a set of littorinoidans and risssooideans looking for the understanding their phylogeny and their relationships with remaining Caenogastropoda taxa. The examined set of species is relatively small, but considered sufficient for above mentioned analysis. The phylogenetic study revealed the monophyly of the Risssooidea, being the littorinoideans a paraphyletic arrangement of basal branches. A total of 44 morphological characters (59 states) is analyzed. Its analysis resulted in the following cladogram: (*Littorina flava* (*Annularia* sp (*Amphithalamus glabrus* (*Potamolithus ribeirensis* (*P. karsticus* – *P. troglobius*))))). A set of 14 morphological synapomorphies supports this monophyly.

Key words: Littorinoidea, Risssooidea, Caenogastropoda, Morphology, Phylogeny.

Resumo

Este estudo é desenvolvido baseado em estudos descritivos publicados em outros artigos. O objetivo é analisar os dados de um conjunto de Littorinoidea e Risssooidea, na procura do entendimento de sua filogenia e seu relacionamento com os restantes Caenogastropoda. O conjunto de espécies analisadas é relativamente pequeno, mas considerado suficiente para a supracitada análise. O estudo filogenético revelou a monofilia de Risssooidea, sendo Littorinoidea um arranjo parafilético de ramos basais. Um total de 44 caracteres morfológicos (59 estados) é analisado. Sua análise resultou no seguinte cladograma (*Littorina flava* (*Annularia* sp (*Amphithalamus glabrus* (*Potamolithus ribeirensis* (*P. karsticus* – *P. troglobius*))))). Um conjunto de 14 sinapomorfias morfológicas suporta esta monofilia.

Palavras-chave: Littorinoidea, Risssooidea, Caenogastropoda, Morfologia, Filogenia.

Introduction

The superfamily Risssooidea, also called Risssoidea, Hydrobioidea and Truncatelloidea, encompasses at least 27 families (Vaught, 1989). Most of them assemble minute sized species, with representatives having some millimeters in length. They are one of the more diverse and adaptable animals, occurring in practically all environments suitable for a mollusk. There are representatives in thermal founts, in phreatic pools, in caves, in marine, freshwater and terrestrial habitats, etc.

The superfamily Littorinoidea encompasses about 5 families (Vaught, 1989), presenting close relationship with the Risssooidea, with same widespread range of environment. No sure separation between Risssooidea and Littorinoidea had been pointed up to date, except that the littorinoideans generally present species with larger size, having about 1 – 2 cm.

A phylogenetic approach, regarded as preliminary, had been published by Ponder (1988), giving base for an on going larger project encompassing more representatives. This project is still being performed, based mainly on molecular data (Ponder, personal communication). The author has obtained the monophyly of the Risssooidea, but did not consider the littorinoideans.

As part of a larger project on phylogenetic relationship of the order Caenogastropoda, at the superfamily level, three features of each superfamily has been examined: 1) their monophyly; 2) the fact in being really an independent taxon, i.e., separated from the others; and 3) the ground plan. The three features are only reached by means of phylogenetic analysis. Representing the Superfamilies Risssooidea and Littorinoidea, species were selected for detailed morphological study and to base a comparative and cladistic analysis. The morphological study on each

species has been published elsewhere. The present study is a preliminary approach, necessary in the main project. Although the paper of Ponder (1988) is very important, and has been used in the present project, it has not aims to some important data for this (e.g., the odontophore muscles) and also does not analyze the littorinoideans. These facts imply in additional studies. However, in a so diverse and rich taxon, a full analysis would demand more time and effort than the analysis of the remaining caenogastropods together. Thus, it was idealized to analyze, at the moment, a small sample, very away from the ideal number of species for representing the group, but at least sufficient for a preliminary study on the relationship between the risssoideans and littorinoideans, and these with remainder caenogastropods. This study will serve as base and scenario for future studies.

The main objective of the present paper is to perform a phylogenetic analysis of a sample of risssoideans and littorinoideans, attempting for analyzing them in the study on the Caenogastropoda as a whole.

Material and Methods

The morphological study, including the list of examined species, was, or has been submitted to be, published. Although the several species anatomically known in the literature have been consulted, the present analysis only considers the following species: 1) *Amphithalamus glabrus* Simone, 1995a (Barleeidae), from São Paulo coast, Brazil. 2) *Littorina flava* (King & Broderip, 1832) (Simone, 1998) (Littorinidae), from coast of Venezuela and Brazil. 3) *Annularia* sp (Simone, 2004b) (Annulariidae), terrestrial species from Mexico; 4) *Potamolithus ribeirensis* (Pilsbry, 1911). 5) *P. troglobius* (Simone & Moracchioli, 1994). 6) *P. karsticus* (Simone & Moracchioli, 1994), these 3 species belonging to the freshwater family Hydrobiidae, collected in rivers and caves of south São Paulo (see Simone & Moracchioli, 1994).

The following section of comparative morphology is organized as a phylogenetic analysis, the account on each character begins with abbreviated descriptive sentence followed by plesiomorphic and derived conditions(s); also included CI and RI (consistency and retention indices, respectively), values for the character under the most parsimonious hypothesis. Following the apomorphic state(s), a list of terminal taxa with the apomorphic condition is presented. Hundreds of characters were selected, based on the examined sample. Those that resulted autapomorphic, highly variable, or overlapping, were selected but not included in the cladistic analysis. The remainder characters were organized in states, coded, polarized comparing with outgroups, and a cladistic analysis was performed.

As outgroups, the other Caenogastropoda up to now studied in the project were selected. They are mainly the following: Cerithioidea (Simone, 2001); Architaenioglossa (Simone, 2004b); Stromboidea (Simone, 2005); Cypraeoidea (Simone, 2004a); Calyptraeidea (Simone, 2002); Tonnoidea (Simone, 1995c); Muricoidea (Simone, 1995d on *Thala crassa*; Simone, 1996a on *Buccinanops* spp); Conoidea (Simone, 1999, 2000 on Terebridae). As more distant outgroups, some archaeogastropods were also analyzed (e.g., Simone, 1996b; 1997; Leal & Simone, 1998, 2000). In the discussion, some specific outgroup taxa are mentioned, based upon own observed or on literature data. On the other hand, in the matrix of characters (Table 1) only the ground plan of the Cerithioidea (Simone, 2001). The ground plan of this superfamily is chosen in the sense of being more representative, however, the final result is the same if the ground plan was substituted by anyone of the 19 (terminal) species present in that paper. Each character, state, and polarization is justified in the following section in such, if necessary, a concise explanation or discussion is presented.

The discussion of each character is also based on the analysis of the obtained tree (Fig. 1). Although the matrix of characters (Table 1) and the subsequent cladogram (Fig. 1) are shown only in section following.

The synapomorphies of the ingroup, (superfamily autapomorphies) are preserved in present paper, just because they are the main concern as referred in the introduction. The ingroup autapomorphies are the base for a better establishment a still imprecise taxon. They confirm the internal position of some possible "outgroups" such as littorioideans. They will be useful in the on going phylogenetic study of the entire order Caenogastropoda as the ground plan of the superfamily. Additionally, they are in agreement with some phylogenetic approach of studies on other groups (e.g., Yeates, 1992; Pinna, 1996).

Some multistate characters are here analyzed under an additive (ordered) approach. In each case, the additive concept is justified in the discussion and is always based on the ontogeny or on the fact in being each state a clear modification of the preceding one. Moreover, each additive multistate character was also analyzed as non-addictive, and any fortuitous change in the result and/or indices are also reported.

The cladistic analysis was performed with the aid of the computer program "Tree Gardner 2.2" (Ramos, 1997), which basically works as an interface of the Hennig86 (Farris, 1988). The used algorithm was "ie". The computer program PAUP was also used. Both programs presented the same result.

Discussion of characters

1. Shell

1. Size: 0= about 30 mm; 1: about 10 mm (*Littorina flava*, *Annularia sp*); 2=less than 5 mm (*Potamolithus* spp. *Amphithalamus*) (CI= 100; RI= 100, additive).

The character denotes a clear tendency for miniaturization, maybe the more remarkable character of the ingroup. In the present sample, two different states are possible to be considered, however it is recognized that this is a more difficult task in a more complete sample.

2. Aperture: 0= orthocone; 1= prosocline (*Potamolithus* spp) (CI= 100; RI= 100).
3. Protoconch: 0= smooth; 1= with series of minutes pits (*Amphithalamus*); 2= lost (*Annularia sp*) (CI= 100; RI= 100; not additive).
4. Teleoconch sculpture: 0= smooth; 1= strong axial ribs (*Annularia sp*); 2= spiral ribs (*Littorina flava*, *Amphithalamus*) (CI= 66; RI= 0; not additive).

The state 2 has 2 equally parsimonious optimizations: appearing in node 1 with reversion in node 4, or convergence between *Littorina flava* and *Amphithalamus*. The first hypothesis is shown in the cladogram.

5. Determinate growth: 0= present; 1= absent (all except *Annularia sp*) (CI= 50; RI= 0).

The determinate growth is the presence of a differentiated peristome in the shell aperture when the specimen finishes the development. The presentation of the character and a further discussion is found in Vermeij & Signor (1992). It is absent in the archaeogastropods and architaenioglossans, but remarkably present in remainder caenogastropods, such as cerithioideans and stromboideans. For this reason, the presence of determinate growth is considered plesiomorphic, having the *Annularia* reverted the condition.

The shell (characters 1-5) is the main structure analyzed in the current literature, and it is the commonest structure that the malacologist has in hands for analyzing. With these facts in mind, special attention was paid for searching conchological characters, and several ones were obtained. However, most of them were deleted by virtue to the autapomorphic result. Even though, from the 5 shell characters presented herein, only 2 (characters 1 and 2) resulted non-homoplastic, while the states of the character 3 resulted autapomorphic. It was maintained due to interest in future discussion in the main project.

2. Head-foot

6. Ommatophore: 0= absent; 1= present (*Littorina flava*, *Annularia sp*) (CI= 50; RI= 50).

The ommatophore is herein defined as a small stalk of the eyes, keeping them slightly distant from the main tentacle axis. In caenogastropods, the ommatophore is part of the tentacles. There are 2 equally parsimonious optimizations: appearing in node 1 with reversion in node 3, or convergence between *Littorina flava* and *Annularia sp* (first is shown in the cladogram).

7. Snout anterior region: 0= rounded; 1= somewhat bifid (*Potamolithus* spp, *Amphithalamus*); 2= with lateral expansions (*Annularia sp*) (CI= 100; RI= 100; not additive).

8. Posterior furrow of pedal glands in foot sole: 0= absent; 1= present (*Annularia sp*, *Amphithalamus*, *Potamolithus* spp) (CI= 100; RI= 100).

The posterior furrow of pedal glands is normally associated with miniaturization. This is convergent with other miniaturized gastropods, such as Cerithioidea node 13 (of Simone, 2001) and some minute heterobranchs (e.g., *Rissoella*, see Simone, 1995b)

9. Operculum: 0= central nucleus; 1= nucleus situated close to inferior and inner quadrant (all) (CI= 100; RI= 100).

The operculum of most archaeogastropods and the basal cerithioideans (Simone, 2001) is multispiral or palcispical, rounded, with a central nucleus. The ingroup species possess a similar shaped operculum, palcispical, rounded or elliptical, but with an excentric nucleus. The nucleus is situated as explained in the state 1, resulting as an ingroup synapomorphy.

3. Mantle organs

10. Mantle border type: 0= thick; 1= thin (*Amphithalamus*, *Potamolithus* spp) (CI= 100; RI= 100).

The mantle border is very thin, long and broad in *Amphithalamus* and *Potamolithus* spp. This condition differs from the normal fashion of the gastropods, which is shorter and thicker.

11. Pallial cavity: 0= long (about 2 whorls); 1= short (about half whorl) (all) (CI= 100; RI= 100).

12. Osphradium form: 0= long; 1= short, somewhat elliptical (*Amphithalamus*, *Potamolithus* spp) (CI= 100; RI= 100).

The normal fashion of the basal caenogastropod osphradium is long, ridge-like. The osphradium of the

indicated species becomes shorter, in a form of an elliptical node.

13. Osphradium situation in relation to gill: 0= anterior; 1= middle (*Potamolithus* spp) (CI= 100; RI= 100).

This character refers to the normal situation of the anterior end of the osphradium, just anterior or in the same level of that of gill. In hydrobiids, on the other hand, the organ is dislocated towards posterior, in middle level of the gill.

14. Gill filaments: 0= triangular; 1= rounded and low (*Potamolithus* spp, *Amphithalamus*); 2= absent (*Annularia* sp) (CI= 100; RI= 100; not additive).

The gill responds to the animal adaptations with morphological singularities. In the miniaturized species, as those listed in state 1, the gill is reduced, most probably due to the space economy and gas diffusion provided by the integument. In the terrestrial form, *Annularia*, the gill disappeared totally, replaced by a richly vascular surface called lung. However, in *Annularia* the circulation fashion shows vestige of gill, as well as remains of the osphradium.

4. Circulatory and excretory systems

15. Pericardium situation: 0= most in visceral mass; 1= most exposed in pallial cavity roof (all) (CI= 100; RI= 100).

The pericardium and the heart of the ingroup species are of a small size. Besides, they are situated in the roof of the pallial cavity, mostly exposed within this cavity. The normal fashion of the caenogastropods, on the contrary, is bearing the pericardium mostly situated inside the visceral mass, having only a membrane as posterior edge of the cavity.

16. Kidney: 0= most solid-glandular; 1= with a posterior hollow chamber (*Annularia* sp); 2= thin, most exposed in pallial cavity (*Potamolithus* spp, *Amphithalamus*) (CI= 100; RI= 100; not additive).

The modification of the kidney is expected in non-marine species, working in the extra effort economizing electrolytes (freshwater) and water (terrestrial forms). The modifications are reflected in the morphology, explored in the present character. However, the *Amphithalamus* is an exception, since it is a marine form.

17. Intestinal loop passing through kidney: 0= almost straight; 1= several looped (*Annularia* sp) (CI= 100; RI= 100).

There is always an enigmatic relation between kidney and intestine in the mollusks. The increasing of the renal intestinal looks is observed in some species, e.g., stromboideans (Simone, 2005). However, it is in the non-marine forms that sometimes several looped

intestines are found in kidney, as, e.g., ampullariids (Simone, 2004b). The same feature is found in the terrestrial *Annularia*.

5. Digestive system

18. Oral tube: 0= short; 1= relatively long (*Amphithalamus*, *Potamolithus* spp) (CI= 100; RI= 100).

The oral tube is the connection between the mouth and the buccal mass. Normally it is short, mainly in basal caenogastropods. Although the oral tube is exceptionally long in the above listed species.

19. Jaws: 0= well-developed pair; 1= weak pair of plates (*Potamolithus* spp, *Amphithalamus*); 2= missing (*Annularia* sp, *Littorina flava*) (CI= 66; RI= 66; additive).

There are 2 equally parsimonious optimizations of the state 2, appearing in node 1 with reversion in node 3, or convergence between *Annularia* and *L. flava*. The first is shown in the cladogram. The additive optimization is based on ontogeny, since a weak pair precedes the disappearance of the jaws during the early development. However, nothing changes if the character is considered non additive.

20. Narrow dorsal folds of buccal mass: 0= absent; 1= present (all) (CI= 100; RI= 100).

The dorsal folds are a pair situated in buccal mass just in the level of the exposed portion of the radula. Normally it is continuous running along the anterior esophagus. The ingroup species possess this pair of folds relatively narrow. This character is used for organizing the outgroups, since the state 1 is shared with the stromboideans.

21. M2: 0= present; 1= absent (*Littorina flava*, *Annularia* sp) (CI= 50; RI= 0).

The m2, or retractor pair of muscles of the buccal mass, is expected in all caenogastropods, except the architaenioglossans (Simone, 2004b). The absence of the m2 in the littorinid and annulariid is regarded as a reversion. There are 2 equally parsimonious optimizations: 1) the state 1 in the node 1, with reversion to the plesiomorphic state (0) in the node 3; or 2) convergence between *Littorina* and *Annularia*. The first hypothesis is shown in the cladogram.

22. M11: 0= present; 1= absent (all) (CI= 100; RI= 100).

The odontophore muscle pair m11 is the ventral tensor of the radula. Generally this pair is originated in the floor of the haemocoel, in the level of the odontophore, penetrates inside it by side of radular sac, and inserts in subradular membrane in its end after this exposed, in use region. The m11 pair is normally

narrow and thin in caenogastropods, and remarkably absent in the ingroup species.

23. Radular sac: 0= about double of buccal mass length; 1= extending little beyond buccal mass (*Potamolithus* spp, *Amphithalamus*); 2= several times longer than buccal mass (*Littorina flava*, *Annularia* sp) (CI= 100; RI= 100; not additive).

The length of radular sac, which stores the radular teeth that will replace the lost or eroded ones, is proportional to how intensely the teeth are used. The longer is the radular sac, the more intense usage is expected. The contrary appears to be also applicable. Both conditions are found in the ingroup as extremes of variation from the basic model of the caenogastropods, which is a radular sac with about same length of that of the odontophore. According to the obtained cladogram, the long fashion is the basal one, becoming very short in the node 3.

24. Rachidian basal cusp: 0= absent; 1= single pair (*Amphithalamus*); 2= several pairs (*Potamolithus*) (CI= 100; RI= 100; additive).

25. Rachidian central cusp: 0= small; 0= large (most of cusp edge) (*Littorina flava*, *Annularia* sp, *Amphithalamus*) (CI= 50; RI= 50).

The radular characters have succeeded those of the shell in importance in gastropod systematics. Then, several radular characters were searched. However, except those above (characters 24, 25) they resulted autapomorphic and were omitted.

26. Salivary glands: 0= clustering posterior to nerve ring; 1= as 2 separated masses (*Annularia* sp, *Potamolithus* spp, *Amphithalamus*) (CI= 100; RI= 100).

27. Esophageal gland; 0= present; 1= absent (*Annularia* sp, *Potamolithus*, *Amphithalamus*); 2= with transversal folds (*Littorina flava*) (CI= 100; RI= 100; not additive).

The normal fashion of the gastropod esophagus is having a gland in its middle, ventral portion, called esophageal gland. This feature is remarkably absent in the specimens listed in state 1. The *Littorina*, on the other hand, possesses an esophageal gland with transversal septa, very similar to those of higher caenogastropods, such as naticoideans, cypraeoideans and tonnoideans (Simone, 2004a). The loss of the esophageal gland resulted as an ingroup synapomorphy, while the modified gland is a *Littorina* autapomorphy. However, the outgroup Stromboidea (Simone, 2005) also presents the state 1 in its ground plan, then the state served for organizing the outgroups in the cladogram.

28. Stomach: 0= occupying about half of space of visceral mass adjacent to it; 1= occupying about entire space of visceral mass adjacent to it (*Potamolithus*, *Amphithalamus*) (CI= 100; RI= 100).

The stomach of the hydrobiids and linked families is notably large, almost separating completely the posterior and anterior portions of the animal.

29. Style sac: 0= united to intestine; 1= separated from intestine (*Amphithalamus*, *Potamolithus*) (CI= 100; RI= 100).

30. Gastric ducts to digestive gland: 0= a separated pair; 1= a pair close with each other (*Littorina flava*); 2= single (*Annularia* sp, *Potamolithus*, *Amphithalamus*) (CI= 100; RI= 100; additive).

The state 1 has 2 equally parsimonious optimizations, in the node 1 or as *L. flava* autapomorphy, first is shown in the cladogram.

31. Intestinal loop contouring style sac: 0= present; 1= absent (*Amphithalamus*, *Potamolithus*) (CI= 100; RI= 100).

The characters of the stomach (28-31) reflect the importance of the organ in ingroup comparison, mainly due to its complexity and enlargement. A high complexity of the midgut is normally expected in herbivore and microphage animals, as the ingroup species are.

6. Genital system

6.1. Male

32. Coiled seminal vesicle: 0= absent; 1= present (all) (CI= 100; RI= 100).

A coiled seminal vesicle appears to be also present in other higher caenogastropods, being absent in the cerithioideans and architaenioglossans. The homology among the caenogastropod seminal vesicles is subject under analysis, but in the present sense, it is considered homologue with the outgroup Stromboidea, helping in the organization of the outgroups.

33. Pallial prostate: 0= absent; 1= long and narrow (*Annularia* sp, *Littorina flava*); 2= broad and elliptical (*Amphithalamus*, *Potamolithus*) (CI= 100; RI= 100; additive).

34. Pallial prostate situation relative to rectum: 0= ventral; 1= dorsal (*P. karsticus*, *P. troglobius*) (CI= 100; RI= 100).

The prostate gland (characters 33-34) situated along pallial spermduct is maybe a modification for making the spermatophore. No information on the presence of spermatophores in the ingroup species is

available; however, all them possess a well-developed prostate, remarkably useful comparative analysis.

35. Pallial spermducts: 0= opened (a groove); 1= closed (a tube) (all) (CI= 100; RI= 100).

Most basal and higher caenogastropods bears an opened pallial spermduct. The closure of this duct, becoming a tube, is a distinguished feature of the ingroup species.

36. Exophalic penis: 0= absent; 1= present (all) (CI= 100; RI= 100).

The exophalic penis is most probably homologue with those of remaining caenogastropods that possess one. As the cerithioideans do not have the structure, it is maintained provisionally as an ingroup plus stromboidean synapomorphy.

37. Penis situation: 0= just posterior to right tentacle; 1= far removed towards posterior (*Annularia sp*, *Potamolithus*, *Amphithalamus*.); 2= at right from right tentacle (*Littorina flava*) (CI= 100; RI= 100; not additive).

38. Penis fashion: 0= simple; 1= very long, slightly sinuous (*Annularia sp*); 2= divided by a middle constriction (*Littorina flava*); 3= with a terminal papilla (*P. ribeirensis*); 4= intensely coiled (*Amphithalamus*) (CI= 100; RI= 100; not additive).

The penis of the hydrobioideans and littorinoideans is normally complex and very useful for comparative analyses. However, except the characters above (36-38), they resulted autapomorphic in the present sample and were omitted.

6.2. Female

39. Gonopericardial duct: 0= present (*Littorina flava*); 1= absent (remainder) (CI= 100; RI= 100).

40. Pallial oviduct: 0= opened (a groove); 1= closed (a glandular tube) (all) (CI= 100; RI= 100).

The closure of the pallial oviduct is another remarkable feature of the ingroup if compared with the cerithioideans, but it is known as occurring in most caenogastropods (except the cerithioideans). The homology of the closure of the pallial oviduct between the ingroup and outgroups is under investigation, but in the present paper it is considered homologue with the outgroup Stromboidea (Simone, 2005), helping in the organization of the cladogram.

41. Posterior situated seminal receptacle: 0= absent (*Annularia sp*); 1= present (*Littorina flava*, *Potamolithus*, *Amphithalamus*) (CI= 50; RI= 60).

There are 2 equally parsimonious optimizations, appearing in node 1 with reversion in

Annularia, or convergence between *L. flava* and node 3, the first is shown in the cladogram.

42. Posterior situated bursa copulatrix: 0= absent; 1= present (*Amphithalamus*, *Potamolithus*) (CI= 100; RI= 100).

43. Albumen and capsule glands: 0= mixed glands; 1= individualizable glands (all except *P. ribeirensis*) (CI= 50; RI= 50).

The characters of the pallial oviduct (39-43) are of particular importance in the analysis of the ingroup species, mostly due to its complexity and high development. Most of pallial oviduct structures are not investigated in histological details, keeping the nomenclature still suggestive, based on topology or on comparisons. Certainly some concepts can change with further studies, as well as the considerations of homologies. The polarization is mainly based on the analysis of the condition of the cerithioideans (Simone, 2001).

7. Nervous system

44. Statocyst: 0= with several statoconia; 1= with single statolith (all) (CI= 100; RI= 100).

Other caenogastropods also possess statolith, such as the stromboideans. The homology is still under investigation, anyway, this is an important feature of the ingroup species.

The remaining characters of the central nervous system were not searched under details, mostly due to preservation problems and small size of the specimens. However, they look very uniform among the studied species.

Cladistic analysis

Table 1: matrix of characters of ingroup and 2 outgroups (last rows).

Taxon \ character	1		2		3		4		1234
	12345	67890	12345	67890	12345	67890	12345	67890	
<i>Littorina flava</i>	10020	10010	10001	00021	11201	02001	01101	12201	1011
<i>Annularia</i> sp	10211	10110	10021	11021	11201	11002	01101	11111	0011
<i>Amphithal. glabrus</i>	20120	01111	11011	20111	01111	11112	11201	11411	1111
<i>P. ribeirensis</i>	21000	01111	11111	20111	01120	11112	11201	11311	1101
<i>P. karsticus</i>	21000	01111	11111	20111	01120	11112	11211	11011	1111
<i>P. troglobius</i>	21000	01111	11111	20111	01120	11112	11211	11011	1111
Stromboidea	00001	10000	00000	00001	00000	01000	01000	10001	0011
Cerithioidea	00000	00000	00000	00000	00000	00000	00000	00000	0000

Abbreviations: Amphithal: *Amphithalamus*; P.: *Potamolithus*.

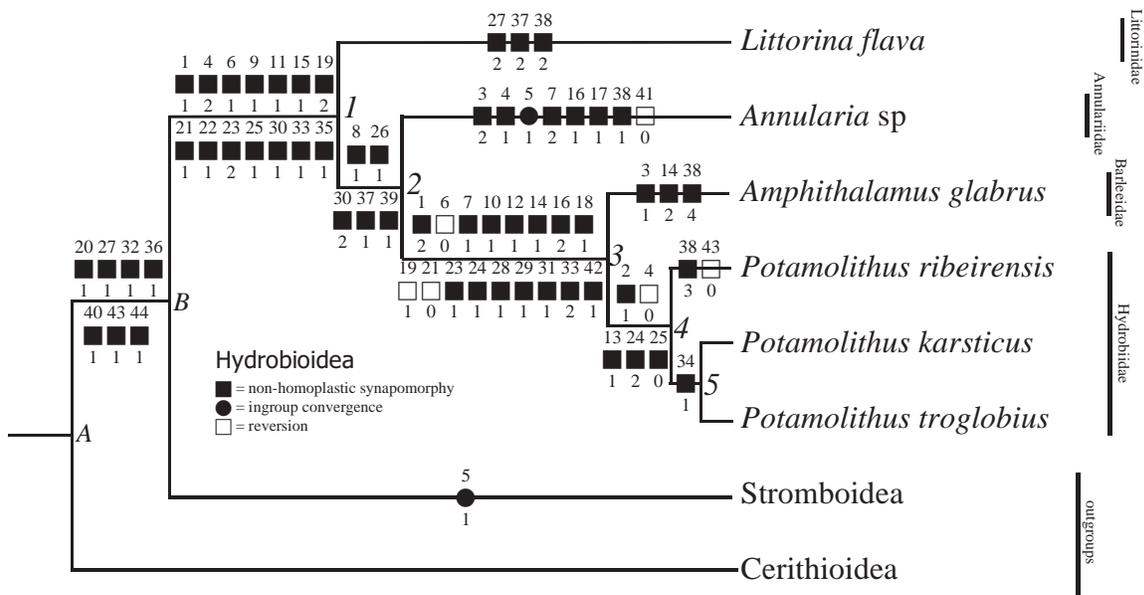


Figure 1. Single obtained cladogram, based on 6 ingroup and 2 outgroup taxa. Each node named in italics (outgroups with letters, ingroup with numbers). Synapomorphies of each node shown, number superior to each symbol means the character, the inferior means the state. Symbols: black square = non-homoplastic synapomorphy; white square = reversion; black circle = convergence. Families in such each species belongs indicated at right. Length: 255; CI: 76; RI: 91.

Discussion of the cladogram

The littorinoideans (*Littorina* and *Annularia*) and the rissooideans (*Amphithalamus* and *Potamolithus*) resulted in a single branch that can be called simply as Rissooidea (node 1). The monophyly of the Rissooidea (*sensu lato*, including Littorinoidea) is supported by a set of 14 synapomorphies. From those,

the more remarkable are: tendency for miniaturization (character 1); protoconch with spiral ribs (4); ommatophore (6); operculum with nucleus closer to inferior-inner quadrant (9); shortness of the pallial cavity (11); the exposition of the pericardium in the pallial cavity (15); decreasing jaw plates (19); the loss of odontophore muscles m2 (retractor of buccal mass) and the m11 (ventral tensor muscle of radula) (21, 22);

diminution of ducts to digestive gland (30); pallial prostate (33); closure of pallial spermducts, inclusive of the penis (35).

The node 2 encompasses the ingroup except *Littorina*, being supported by 5 synapomorphies. From those, the more important are: the posterior furrow of pedal glands (character 8); the salivary glands separated from each other (26); the single duct to digestive gland (30); the posterior situation of the penis (37); and the absence of the gonopericardial duct (39).

The disposition of the littorinoideans (*Littorina* and *Annularia*) on the cladogram indicates that the taxon is paraphyletic.

The node 3 reunites the “true” rissooideans, being supported by 17 synapomorphies. The more notable synapomorphies are: the extreme miniaturization (character 1); the somewhat bifid anterior region of the snout (7); the broad mantle border (10); the shortness of the osphradium (12); kidney protruding inside pallial cavity (16); the large size of stomach (28), with style sac separated from the intestine (29); special arrangement of the intestine contouring the style sac (31); the prostate very large, similar sized than the oviduct (33); and the posterior situation of the bursa copulatrix (42).

The node 4 comprises the *Potamolithus* species, representing the freshwater family Hydrobiidae, separated from the marine *Amphithalamus*, representing the Barleeidae. The node is supported by 5 synapomorphies, being the more important: the prosocline aperture (character 2), i.e., the aperture is inclined, and not in the plane of the shell axis; the middle position of the osphradium in relation to the gill (13); and the several pairs of basal cusps in the radular rachidian tooth (24).

The node 5, supported by a single synapomorphy (character 34, the dorsal position of the prostate gland in relation to rectum), separates *Potamolithus karsticus* and *P. troglobius* from *P. ribeirensis*.

The node B comprises the ingroup, i.e., the Rissooidea, and the outgroup Stromboidea (its ground plan as defined by Simone, 2005). The node is supported by 7 synapomorphies and shows that the rissooideans are closer to stromboideans than the cerithioideans. From the synapomorphies, the outstandingly ones are: the narrow pair of buccal mass dorsal folds (character 20); the loss of the esophageal gland (27); the coiled seminal vesicle (32); the exophalic penis (36); the closed (tubular) situation of the pallial oviduct (40); the statocyst with single statolith (44).

The present study is not to be considered as “the phylogeny of the Rissooidea”, but so another step in that direction, associated to Ponder (1988) data. The ground plan here obtained is considered sufficient for a study on the relationship of the taxon with remaining caenogastropods, being this the main objective of this

study, associated with the results of other studies, such as Ponder (1988). However, it is recognized that further studies are certainly necessary. As referred in the Introduction, the present study was developed just for fulfill the lack of the knowledge on some structures, e.g., the odontophore, and to help in the analysis of the relationship of the littorinoideans.

Conclusions

- 1) The superfamily Rissooidea is a monophyletic taxon, encompassing also the previously considered Littorinoidea.
- 2) A set of 14 morphological synapomorphies supports the monophyly of the Rissooidea, being considered its group plan.
- 3) These conclusions are considered sufficient for a previous analysis of the Rissooidea with remaining Caenogastropods. It is recognized, however, that the utilized sample is small. Certainly studies on further samples are necessary for refining the knowledge on the taxon.

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Received: June 27, 2006. Accepted: September 16, 2006