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A proposal to improve the resolution of the high phylogeny and taxonomy of the Neogastropoda

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Abstract

Based on a series of papers dealing with detailed anatomy and phylogeny of several neogastropod representatives, a dichotomy between the Order Neogastropoda (28 synapomorphies) and its superfamilies is proposed and discussed herein. The suborder **Toxoglossa** (61 synapomorphies) is suggested to include the Conoidea, mainly characterized by the development of a venom apparatus. The suborder **Rachiglossa** (26 synapomorphies) is suggested to include the remaining superfamilies, and is characterized by the loss of the marginal radular teeth and by the valve of Leiblein. Proper discussion and justifications are provided.

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Introduction

The recent publication of a phylogeny mostly focusing the buccinoidean neogastropods based on phenotypic features by Pastorino & Simone (2021), brought into attention the possibility of a division of the Order Neogastropoda.

Neogastropoda has traditionally been considered an order-level taxon, it has a complex and unstable taxonomic history as usual for molluscan taxa. Perform a complete historic report is an impractical task at best, thus, only few of the most expressive papers are addressed herein. Thiele (1929-1935) referred to the taxon as Order Stenoglossa, subdivided into stirps Muricacea, Buccinacea, Volutacea, and Toxoglossa. Ponder (1974) divided the Neogastropoda into Muricacea, Cancellariacea and Conacea, based on internal organization, mostly on radular features. Ponder's Muricacea (which was later named Muricoidea) encompassed all neogastropod families, except for Cancellariidae and the then conoidean trio Turridae-Conidae-Terebridae. Most subsequent works usually follow one of these authors, adopting the superfamily suffix -oidea. In my papers, in particular, Ponder's view was preferred. The organization of the Neogastropoda was further modified, with the inclusion of molecular data. Presently, the Order Neogastropoda (= Stenoglossa) is subdivided into Buccinoidea, Conoidea, Mitroidea, Muricoidea, Olivoidea, Pholidotomoidea, Turbinelloidea, and Volutoidea (alphabetical order – MolluscaBase, 2021), with no accepted divisions between order and superfamily levels.

Considering the present status of the molluscan taxonomy and phylogeny, one can notice that higher classification hypotheses, which have been quite fluid, is far for including data on every single species of each taxon. The alternative has been to select samples, representatives, analyze their relationships using a phylogenetic approach, and then extrapolate the results to the entire taxon. This is a usual method in biology, as science of samples and representatives, including systematics. Over the years, the detailed anatomy of a considerable sample of representatives of several neogastropod main branches has been studied. Some examples are papers with rich data on muricids and conoideans (Simone, 2011), marginellids (Souza & Simone, 2019), fasciolariids (Couto et al., 2016; Couto & Simone, 2019), terebrids (Simone, 2000), and other representatives (Simone, 2007; Abbate & Simone, 2015, etc.). The above-mentioned study (Pastorino & Simone, 2021), in particular, included a wide sampling of buccinoideans.

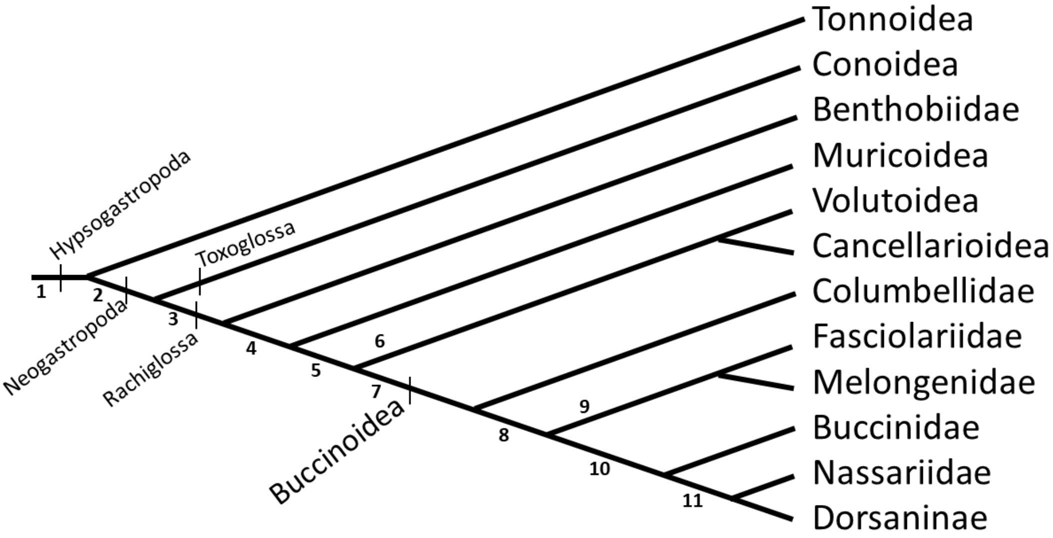
In the present paper, hypothesis proposing the division of the Neogastropoda into two subordinal branches – Toxoglossa and Rachiglossa – is presented. This is a refinement of the taxonomy and phylogeny of the order, introducing a step between order and superfamily levels. This argumentation was present in the original draft of Pastorino & Simone (2021) during its publication saga under 4 high profile scientific journals. The manuscript was finally accepted for publication in the fourth submission, provided that this phylogenetic inference was removed from the text. This demand has become common in molluscan systematics. The main criticism is that morphology-based analyses are not congruent with results from molecular-based approaches. This practice, in fact unscientific and dogmatic, deprives the scientific community of additional viewpoints that could raise and enrich discussions, bring new ideas, insights, and should be something inherent to the scientific method. In this paper, therefore, that phylogenetic discussion excluded from Pastorino & Simone (2021) is presented, which was carried out with the expected scientific rigor and supported by crystal-clear arguments, most of them already previously published.

Material and methods

Data from several papers describing the detailed anatomy of neogastropods published in recent years were added to the phenotype-based phylogeny by Simone (2011). That paper brought an initial analysis of 305 molluscan taxa. Some subsequent papers resulted in the addition of more taxa, characters, and character-states to the initial matrix (Simone, 2011: 267-308). That paper (Simone, 2011) already included 77 neogastropod taxa (fig. 20: node 178) and showed a basal dichotomy (fig. 20, pg. 216) at node 179 (conoideans), and node 210 (muricoideans-cancellarioideans sensu Ponder, 1974), both discussed below. Some examples of additional character-states included in Simone's (2011) matrix are explained in Pastorino & Simone (2021: 3, item 2.1). The new enriched matrix was re-analyzed using the same parameters and methodology by Simone (2011). The resulting cladogram was, thus, presented (Pastorino & Simone, 2021: 39, fig. 35), focusing only on the branch including the inserted taxa – the buccinoideans, node 215 – in which the new insertions merged with those already present in Simone (2011). This paper is still more focused in the subdivisions below Neogastropoda (node 178) (Figs. 1-2). Providing argumentations basing its division in suborder level.

Discussion and argumentation

Although a phylogeny of the Neogastropoda is far from being well-established and uncontroversial, accounts on it can be inferred here based on the data already present in Simone (2011) Pastorino & Simone (2021), and others (e.g., Simone, 1999, 2003, 2007, 2017, 2019). Fig. 1 is, thus, a synopsis of the phylogenies involving neogastropods.



1. Cladogram summarizing a suggestive relationship of the hypsogastropods, with special reference to the main neogastropod groups. It is mostly based on data from Simone (2011), Pastorino & Simone, 2021, and others.

Fig. 1 focuses on the Hypsogastropoda (Tonnoidea + Neogastropoda) (node 1), which corresponds to node 148 in Simone (2011: fig. 20; see set of 18 synapomorphies on pg. 314 supporting this node). Hypsogastropods are mostly an evolutionary frame of active hunters, with different predatory strategies, mainly using the foot, the long proboscis, and a glandular torpidity or predigestive capacity provided by the complex glandular apparatus of the foregut.

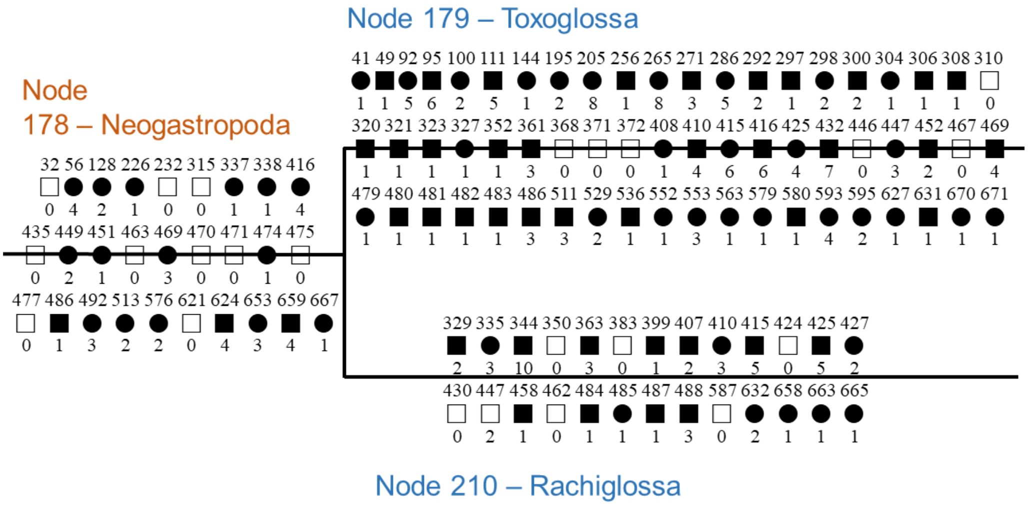
Neogastropoda is another well-established node (Fig. 1: node 2) corresponding to node 178 by Simone (2011, see set of 28 synapomorphies on page 315) (Fig. 2). However, no order-status subdivision of the Neogastropoda has been unanimously accepted. MolluscaBase (2021) database gives only eight superfamilies as direct children taxa. However, based on the above-mentioned bulk of papers, some taxa used, e.g., by Thiele (1929-1935) can be taxonomically resurrected. One of these taxa is **Toxoglossa** Troschel, 1848, presently considered a synonym of Conoidea Fleming,

1822. The toxoglossans are an evolutive branch of poison inoculators that bear modified foregut structures, such as the poison gland and barbed radula. The conoideans are suffering a modern profusion of taxonomic changes, currently with no clear view on how many divisions should be accepted at superfamily, or even family ranks. In any event, Toxoglossa could encompass them. It is represented by node 179 by Simone (2011) (Fig. 2). Toxoglossa is supported by no less than 61 morphological synapomorphies (Simone, 2011: 315) (Fig. 2).

The other neogastropod subdivision can be called **Rachiglossa** Gray, 1853 (Fig. 1: node 3), which would reunite the remaining neogastropod superfamilies listed by MolluscaBase (2021) excluding Conoidea. This taxon is represented by node 210 by Simone (2011) (Fig. 2), supported by 26 synapomorphies (Simone, 2011: 316). Stenoglossa would be an excellent alternative name, as it denotes the unusual radula of the non-conoidean neogastropods, but it is officially considered a synonym of Neogastropoda Wenz, 1938, despite no stenoglossate taxon has been recorded amongst the conoideans. The stenoglossate radula, i.e., a radula with only 3 teeth per row (rachidian and a pair of lateral teeth), appears to be the base of all rachiglossan branches, and, as such, the most common modification in this group is the loss of the lateral tooth (e.g., cancellariids, marginellids, and volutids), and, more rarely, the reduction of the rachidian (e.g., columbellids).

The remaining nodes in Fig. 1 (4 to 11) are subdivisions of Rachiglossa, including some sampled superfamilies and families. The first branch represents the Benthobiidae (node 211 by Simone, 2011; 16 synapomorphies), which MolluscaBase (2021) includes within the Olivoidea. However, this deep-water group has shown to be one of the most basal neogastropod group (Simone, 2003), nothing related to the olivids and allies. It represents the first rachiglossan branch, in having, e.g., a mesogastropod-like odontophore. The following node 4 has the Muricoidea as a branch (Simone, 2011: node 230 – 9 synapomorphies) and node 5. The muricoideans usually inhabit consolidated substrate and have a relatively small foot, adapted to that environment. The main and more specious family – Muricidae – have most representatives with a dwelling ABO (accessory boring organ) used for killing shelled prey.

Node 5 (Fig. 1) has two branches: node 6, with representatives of the Volutoidea, Cancellarioidea, Olivoidea, and Mitroidea in MolluscaBase (2021), i.e., taxa usually with weak to strong columellar folds, and are represented by node 218 by Simone (2011, 3 synapomorphies); a branch in which most taxa are adapted to unconsolidated substrates, with a wide foot, and a plow-like anterior region. The other is node 7 – the **Buccinoidea** (nodes 215 and A in fig. 35 by Pastorino & Simone, 2021 – 15 synapomorphies).



2. Portion of the cladogram by Simone (2011: 213-216, fig. 20) focusing the Neogastropoda branch (node 178) and its immediate subdivision (nodes 179 and 210), which has been named herein Toxoglossa (179) and Rachiglossa (210), with the synapomorphies supporting them shown. Symbols: ■ = non-homoplastic synapomorphy; □ = reversion; ● = convergence with any internal branch of entire cladogram. Superior number of each symbol as character, inferior number as state as specified by Simone (2011: 238-266).

Buccinoidea appears to have the Columbellidae at the base, followed by node 8. This node has the Fasciolariidae-Melongenidae in a branch (Pastorino & Simone, 2021: fig. 35: node B; Fig. 1: node 9), and node 10 (Pastorino & Simone, 2021: node E in fig. 35). Node 10 groups the Buccinidae with a branch of Nassariidae including Dorsaninae (sensu Allmon, 1990) (Pastorino & Simone, 2021: fig. 35: node F; Fig. 1: node 11). Buccinoideans are a well-recognized branch of neogastropods with very a long proboscis. The odontophore is very elongated, its cartilages are widely anteriorly fused, and they lack accessory salivary glands. Some branches tend to miniaturization, being the smallest neogastropods (e.g., some columbellids). Some branches exhibit a trend towards detritivory and even herbivory, such as, e.g., columbellids and nassariids. Buccinoideans are a very wide-ranging group regarding marine habitats. Usually, the larger representatives live on unconsolidated substrates, while the smaller ones live on hard substrates and even algae.

The classification summarized in Figs. 1-2 appears a step forward in relation to the polytomy presently considered in the MolluscaBase (2021) website, which lacks any subdivision between order and superfamily levels. The suggested division into Toxoglossa and Rachiglossa seems intuitive and well based on most classic analyses based on morphology. However, the internal organization of both is still under analyses, and will be more detailed in future papers.

Conclusions

1. The analysis of a wide sample of Neogastropoda has revealed that the order can be subdivided into 2 suborders, being **Toxoglossa** exclusive to Conoidea, and **Rachiglossa** encompassing the remaining superfamilies.
2. Taxonomic definition of **Toxoglossa** Troschel, 1848 (Simone, 2011: node 179; Figs. 1-2).

Diagnosis: Shell normally thick-walled. Reduction of odontophore and mid esophagus. Esophageal gland elongated (venom gland), with muscular bulb at distal end, inserted close to nerve ring. Rhynchodeal wall weakly muscular and not exteriorized. Additional main characters are the shell anal canal (Simone, 2011: character 41); the pointed proboscis tip (95); the small sized nephridial gland (286); the reduction of rhynchodeal wall musculature (292); rhynchostome with well-developed sphincter (297); reduction of the buccal mass (304), with long oral tube (306); buccal mass placed in proboscis base (320); the odontophore pair m4 connected with pair m2 forming a broad posterior muscular platform (352); the loss of pair m7 (371); the reduction of the radular rachidian tooth (415); the radular marginal teeth wishbone shaped in base, and tip sharp pointed (432); the pair of salivary gland as two semi-spherical masses (447); the gland of Leiblein modified in venom gland (469) positioned posterior to nerve ring (480), with posterior venom muscular bulb (482); the male ejaculatory duct (552); penis with papilla in tip (563), protected by a preputial fold (580); and the female terminal pouch (627).

List of included taxa: Conoidea.

3. Taxonomic definition of **Rachiglossa** Gray, 1853 (Simone, 2011: node 210; Figs. 1: node 3, 2)

Diagnosis: Loss of radular marginal teeth. Valve of Leiblein. Additional main characters are the modification of the odontophore pair mj (Simone, 2011 character 329); narrow and long pair m2 running attached to esophagus (335); the growth of odontophore pair of ventral tensors of radula (m11) (350); the modification of subradular cartilage at buccal cavity (407); the stenoglossan radular type (410); the hook-like lateral radular teeth (425); the loss of radular marginal teeth (430); the accessory salivary glands (458); the valve of Leiblein (484); and the supra-esophageal ganglion close to nerve ring (633).

List of included taxa: Muricoidea + Cancellarioidea (sensu Ponder, 1974); OR Buccinoidea, Mitroidea, Muricoidea, Olivoidea, Pholidotomoidea, Turbinelloidea, Volutoidea (sensu MolluscaBase, 2021).

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References

Abbate, D & Simone, LRL, 2015. Review of *Pugilina* from the Atlantic, with description of a new species from Brazil (Neogastropoda, Melongenidae). African Invertebrates 56(3): 559-577.

Allmon, WD, 1990. A review of the *Bullia* group (Gastropoda: Nassariidae) with comments on its evolution, biogeography, and phylogeny. Bulletins of American Paleontology 99: 1-179.

Couto, DR & Simone, LRL, 2019. A morphology-based phylogenetic analysis of Fasciolariidae (Gastropoda: Buccinoidea). Zootaxa 4684(1): 1-65. doi.org/10.11646/zootaxa.4684.1.1

Couto, DR; Bouchet, P.; Kantor, YI; Simone, LRL & Giribet, G. 2016. A multilocus molecular phylogeny of Fasciolariidae (Neogastropoda: Buccinoidea). Molecular Phylogenetics and Evolution 99: 309-322. doi.org/10.1016/j.ympev.2016.03.025.

MolluscaBase eds. 2021. MolluscaBase. Neogastropoda. Accessed at: http://molluscabase.org/aphia.php?p=taxdetails&id=146 on 2021-06-06.

Pastorino, G & Simone, LRL, 2021. Revision of the genus *Buccinanops* (Mollusca: Neogastropoda: Nassariidae), an endemic group of gastropods from the Southwestern Atlantic, including a new genus and accounts on the Buccinanopsinae classification. Journal of Zoologic Systematics and Evolutionary Research 59: 1-46. https://doi.org/10.1111/jzs.12479.

Ponder, W.F. 1974. The origin and evolution of the Neogastropoda. Malacologia 12: 295-338.

Simone, LRL, 1999. Comparative morphology and systematics of Brazilian Terebridae (Mollusca, Gastropoda, Conoidea), with descriptions of three new species. Zoosystema 21(2): 199-248. http://www.moluscos.org/trabalhos/1999/Simone%201999%20Terebridae.pdf

Simone, LRL, 2000. A phylogenetic study of the Terebrinae (Mollusca, Caenogastropoda, Terebridae) based on species from the Western Atlantic. Journal of Comparative Biology 3(2): 137-150. http://www.moluscos.org/trabalhos/2000/Simone%202000%20Terebrinae%20phylogeny.pdf

Simone, LRL, 2003. Revision of the genus *Benthobia* (Caenogastropoda, Pseudolividae). Journal of Molluscan Studies 69: 243-261.

Simone, LRL, 2007. Family Pseudolividae (Caenogastropoda, Muricoidea): A polyphyletic taxon. American Malacological Bulletin 23: 43-78)

Simone, LRL, 2011. Phylogeny of the Caenogastropoda (Mollusca), based on comparative morphology. Arquivos de Zoologia 42(4): 161-323. http://www.moluscos.org/trabalhos/Caenogastro/Simone%202011a%20Caenogastropoda%20Phylogeny%20LIGHT.pdf

Simone, LRL, 2017. A new species of *Thaisella* (Neogastropoda: Muricidae) from Caribbean Guatemala, with accounts in the anatomy and taxonomy of the genus in the Western Atlantic. Archiv für Molluskenkunde 146(1): 111–120.

Simone, LRL, 2019. The proboscis of the Gastropoda 1: its evolution. Malacopedia 2(4): 22-29 http://www.moluscos.org/trabalhos/Malacopedia/02-04Simone%202019%20Malacopedia-Probosis.pdf

Souza Jr., PJS & Simone, LRL, 2019. Cladistic analysis of the family Marginellidae (Mollusca, Gastropoda) based on phenotypic features. Zootaxa 4648(2): 201-240. doi.org/10.11646/zootaxa.4648.2.1

Thiele, J, 1929-1935. Handbuch der systematischen. Weichtierkunde, 4 vols. [translation by Bhatti, JS, Rüdiger, B & Mikkelsen, PM, 1988. Smithsonian Institution Libraries. Pauls Press. New Delhi].