COMPARATIVE MORPHOLOGICAL STUDY AND PHYLOGENY OF REPRESENTATIVES OF THE SUPERFAMILY CALYPTRAEOIDEA (INCLUDING HIPPONICOIDEA) (MOLLUSCA, CAENOGASTROPODA).

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Abstract – With the objective of testing the monophyly of the Calyptraeoida and of searching for its ground plan, a detailed morphological analysis was conducted for the following species: a) Family Calyptraeidae, 1) Bostryxcalpus aculeatus (Gmelin) (formerly Crepidula); 2) Crepidula aff. plana Say; 3) C. protea Orbigny (these from Brazil); 4) C. aff. protea (from Argentina) (published elsewhere); 5) C. convexa Say (from Venezuela); 6) C. fornicata (L.) (from Europe); 7) Calyptraea centralis (Conrad) (from Brazil); 8) Cruciulium auricula (Gmelin) (from Venezuela); 9) Cr. quiriquinae (Lesson) (from Chile); 10) Trochita trochoformis (Born) (from Chile); 11) Sigapetella calyptraeformis (Lam.) (from New Zealand, formerly Calyptraea); b) Family Hipponicidae, 12) Hipponix costellatus Carpenter (formerly H. granyanus); 13) H. subrufus (Lam.); 14) H. incurvus (Gmelin) (formerly Calyptra incurvatus) (these 3 from NE Brazil); 15) H. granyanus Menke (from Mexico and Ecuador); 16) H. leptus n. sp. (N.E. Brazil); 17) Sabha conica (Schumacher); 18) Mallaviun devotus ( Hedley) (both Australia); 19) Cheilea equestris (L.) (N.E. Brazil); c) Family Capulidae, 20) Capulus yawchona Garrard (Australia); d) Family Trichotropidae, 21) Trichotropis cancellata Hinds (W. USA); e) Family Vanikoridae, 24) Vanikoro sp. (Australia). A phylogenetic analysis of 112 characters (177 states) from morphology of all systems and organs results in the following single most parsimonious tree: (((Bostryxcalpus aculeatus (Vaniorko sp (Cheilea equestris (Sabia conica (Mallaviun devotus (Hipponix granyanus – H. leptus) (H. incurvus (H. costellatus – H. subrufus))))))))))) Length: 267, CI: 67, RI: 88. Outgroups from other caenogastropod superfamilies were used as well as some archaeogastropod groups. The main result is the monophyly of Calyptraeoida supported by 27 synapomorphies with basal Caenogastropoda as the outgroup (Cerithioidea, Hydrobioidea), and 21 synapomorphies when Stromboidea and Cypraeoidea were used as outgroups. Calyptraeoida includes, successively along the tree, the following monophyletic families: Trichotropidae, Capulidae, Vanikoridae, Hipponicoide and Calyptraeidae. The hipparcoid affinity of Cheilea is confirmed. Some taxonomic problems found in the sampled representatives (as mentioned above), were partially resolved.

Key words - Caenogastropoda, Calyptraeoida phylogeny, morphology, cladistic analysis, Hipponicoide, Capulidae.

Resumo – Com o objetivo de testar a monofilia dos Calyptraeoida e obter seu “plano básico”, um estudo morfológico detalhado é desenvolvido nas seguintes espécies: a) Família Calyptraeidae, 1) Bostryxcalpus aculeatus (Gmelin) (previamente Crepidula); 2) Crepidula aff. plana Say; 3) C. protea Orbigny (todos do Brasil); 4) C. aff. protea (da Argentina) (publicado em outro artigo); 5) C. convexa Say (da Venezuela); 6) C. fornicata (L.) (da Europa); 7) Calyptraea centralis (Conrad) (do Brasil); 8) Cruciulium auricula (Gmelin) (da Venezuela); 9) Cr. quiriquinae (Lesson) (do Chile); 10) Trochita trochoformis (Born) (do Chile); 11) Sigapetella calyptraeformis (Lam.) (do Novo Zelândia, previamente Calyptraea); b) Família Hipponicidae, 12) Hipponix costellatus Carpenter (previamente H. granyanus); 13) H. subrufus (Lam.); 14) H. incurvus (Gmelin) (previamente Calyptra incurvatus) (estes 3 do NE Brasil); 15) H. granyanus Menke (do México e Equador); 16) H. leptus n. sp. (N.E. Brasil); 17) Sabha conica (Schumacher); 18) Mallaviun devotus ( Hedley) (ambos da Austrália); 19) Cheilea equestris (L.) (N.E. Brasil); c) Família Capulidae, 20) Capulus yawchona Garrard (Austrália); d) Família Trichotropidae, 21) Trichotropis cancellata Hinds (W. USA); 22) T. borealis Broderip & Sowerby (N. Atlântico); 23) T. sp. (Alaska); e) Família Vanikoridae, 24) Vanikoro sp. (Austrália). Uma análise filogenética fundamentada em 112 caracteres (177 estados) é realizada, baseada na morfologia de todos os órgãos e sistemas. A única árvore obtida é a seguinte: (((Bostryxcalpus aculeatus – T. borealis) (Capulus yawchona (Vaniorko sp (Cheilea equestris (Sabia conica (Mallaviun devotus (Hipponix granyanus – H. leptus) (H. incurvus (H. costellatus – H. subrufus))))))))))) Length: 267, CI: 67, RI: 88. Outgroups de outros superfilmes caenogastropodos foram usados assim como alguns arqueogastropodos. O resultado principal destaca-se a monofilia de Calyptraeoida, suportada por 27 sinapomorfias com Caenogastropoda como grupo externo (Cerithioidea, Hydrobioidea), e 21 sinapomorfias quando Stromboidea e Cypraeoidea foram usados como grupos externos. Calyptraeoida inclui successivamente ao longo da árvore as seguintes famílias monofiléticas: Trichotropidae, Capulidae, Vanikoridae, Hipponicoide e Calyptraeidae. A afinidade com Hipponicoide de Cheilea é confirmada, dentre alguns problemas taxonômicos encontrados nos representantes amostrados (como mencionados acima), foram parcialmente resolvidos.

Palavras-chave: Caenogastropoda, Calyptraeoida filogenia morfologia análise cladística Hipponicoide, Capulidae.

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INTRODUCTION

The Calyptraeoidea (= Crepiduloidea) and the Hipponicoidea are very modified caenogastropods. They tend to modify their shells to a dorso-ventrally flattened, limpet or limpet-like morphology. They also tend to an almost sessile habit and to protandric hermaphroditism. The filter-feeding habit of the Calyptraeidae, in particular, has been the subject of some detailed studies of the movement of water and particles in the pallial cavity currents (Orton, 1912; Werner, 1953). Anatomical studies, however, are relatively scant in the literature (Kleinsteuber, 1913; Heath, 1916; Moritz, 1938, 1939; Ishiki, 1939; Coe, 1942; Werner & Grell, 1950; Werner, 1951, 1955), as are studies of the relationships within both superfamilies. The Capulidae, moreover, have enjoyed little taxonomical stability, and they have been considered to be in the Calyptraeoidea (Younge, 1962; Vaught, 1989), the Hipponicoidea (Abbott, 1974), as well as in the Capuloidea (Bandel & Riedel, 1994).

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 separation from the other taxa; and 3) the ground plan. These three features can only be examined using phylogenetic analysis. Species representing the Superfamily Calyptraeoidea and Hipponicoidea were selected for detailed morphological study to form the base of a comparative cladistic analysis.

A previous phylogeny of the Calyptraeoidea had been presented by Bandel & Riedel (1994). Although the authors applied no orthodox methodology, 2 interesting trees were obtained by the intuitive method. In the first tree (fig. 5), the authors united in a single branch the Calyptraeidae and the Hipponicidae as Calyptraeoidea, supported by 2 synapomorphies: 1) teleoconch limpet-shaped and 2) breeding stalked egg capsules. In the second tree (fig. 6), of the Neomesogastropoda Bandel, 1991, the Calyptraeidae appeared in a branch with the Capulidae (grouping, according to authors, Capulidae plus Trichotropidae, on the basis of a shared echinospira larva). The branch Calyptraeoida-Capuloidea is supported by the synapomorphy: facultative filter-feeding.

Hoagland (1977: 408-411, fig. 28) also gave a phylogenetic scenario for the group (except vanikorids and hipponicoids). She stated that the family arose from a protandrous mesogastropod ancestor, with a gill modified for. The first branch led to the trichotropids in cold waters. The remainder is united by a shell flattened for sedentary life and lack of operculum. The basal taxon in this group is represented by *Trochita*, with a limpet-like foot and large shell aperture. From this taxon arose the capulid stock with high patelliform shell plus modification for proboscis feeding, and the remaining calyptraeids, sharing the increased whorl expansion rate. The so-called calyptraeid stock, with a patelliform shell that retains some remains of spiral coiling, is represented by *Calyptraea*, which has the septum modified into a curved plate. From this taxon, a branch marked by further modified shell and mantle growth gave risen to 2 branches: 1) *Crucibulum*, possessing curved septal plate fused into a cup and secondary external radial symmetry and 2) early *Crepidula* stock which were characterized by having an unwound columella with muscle still attached to it, asymmetric growth, and a flattened septum.

A new phylogenetic analysis is performed here, using an orthodox methodology to analyse holistic morphology of organs and structures never analyzed before.

MATERIAL AND METHODS

Specimens examined for this study either belong to institutional collections or were collected especially for this study. The specimens were dissected using standard techniques, under a stereo-microscope, with the specimens immerse in water. Some organs such as the oviduct and foro-regut were processed using standard histological technique for serial sections of 5 µm with Mallory stain. Hard structures, such as shells, radulae and jaws were examined using SEM in the “Laboratório de Microscopia Eletrônica do Instituto de Biociências da Universidade de São Paulo” and in the MZSP. Some specimens were collected and examined alive in the laboratories of CEBIMar (Centro de Biologia Marina, Universidade de São Paulo). The descriptive part of this paper provides a complete description of the first species. The remaining species are described in comparison to the first species and most of the similar features are omitted. This measure is adopted to decrease the length of this contribution, and for highlighting the informative characters. The same approach is adopted in the figures. A detailed list of specimens examined follows each species description.

The section of comparative morphology is organized as a phylogenetic analysis. The account of each character begins with an abbreviated descriptive sentence followed by plesiomorphic and derived condition(s) and the 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 examined but those that resulted autapomorphic, highly variable, or overlapping, were not
Figures 1-4, shells: 1, *Bostryxocapulus aculeatus*, dorsal view of a spiny specimen; 2, same, ventral view; 3, same, specimen with weak spines; 4, *Crepidula aff plana*, dorsal view. Scales = 30 mm.
Figures 10-16. Shells: **10-11. Crepidula fornicata**, dorsal and ventral views, scale = 3 mm; **12-13. Calyptraea centralis**, SEM, ventral and dorsal views, scales 1 and 0.5 mm respectively; **14.** same, detail of apex, scale = 0.1 mm; **15-16. Crucibulum auricula**, ventral and dorsal views, scale = 3 mm.
Figures 24-29, shells in SEM: 24-25, *Hipponix subrufus*, dorsal and ventral views, scales = 1 mm; 26, same, frontal and dorsal view of 2 young specimens extracted from capsules, scale = 0.2 mm; 27, *Hipponix incurvus*, ventral view, scale = 1 mm; 28, same, detail of apex, scale = 0.5 mm; 29, same, dorsal view, scale = 0.5 mm.
Figures 30-38, shells: 30, *Hipponix grayanus*, SEM, dorsal view; 31-32, same, SEM, dorsal and frontal views of young specimens extracted from capsules, spire of specimen of fig 32 partially broken, with part of dry soft parts and operculum shown; 33-34, *Hipponix leptus*, holotype, dorsal and ventral views; 35, same species, a in situ colony of 6 specimens; 36-38, *Sabia conica*, lateral-left, ventral and dorsal views, fig 37 with specimen still in shell. Scales = 5 mm, except 31-32 = 30 µm.
Figures 49-53, shells: **49-50**, *Hipponix costellatus*, holotype, SEM, lateral-right and dorsal views, scale = 0.5 mm; **51-53**, Vanikoro sp., frontal, dorsal and profile views, scales = 5 mm.
Figures 71-79, Radulae in SEM: **71**, *Crepidula fornicata*, scale = 40µm; **72-73**, *Trochita trochiformis*, scales = 200µm; **74-75**, *Sigapatella calyptraeformis*, scales = 50µm; **76**, *Hipponix grayanus*, scale = 50µm; **77**, *Hipponix subrufus*, scale = 20µm; **78-79**, *Hipponix incurvus*, scales = 20 and 10µm respectively.
included in the cladistic analysis. The remaining characters were organized in states, coded, polarized by outgroup comparison, and a cladistic analysis was performed.

The other Caenogastropoda already studied in this project were selected as outgroups. They are mainly the following: Cerithioidea (Simone, 2001); Littorinoidea - Hydrobioidea (Simone & Moracchioli, 1994; Simone 1995c, 1998); Stromboidea (Simone, in press); Cypraeoidea (Simone, submitted); Tonnoidea (Simone, 1995a); Muricoidea (Simone, 1995b on Thula crassa; Simone, 1996a on Bucinanalops spp); Conoidea (Simone, 1999, on Terebridae).

As more distant outgroups, some archaeogastropods were also analyzed (e.g., Simone, 1996b; 1997). In the discussion, some specific outgroup taxa are mentioned, based on my own observations or on data from the literature. In the matrix of characters (Fig. 436) only 2 taxa are shown, the ground plan of the Stromboidea and Cypraeoidea (Simone, in press and submitted, respectively). The ground plan of these superfamilies were chosen as being more representative, however, the final result is the same if the ground plan was substituted by anyone of the 49 (terminal) species present in those papers. Two analyses were performed, 1) with the ground plan of the Cerithioidea (Simone, 2001) and a pool of hydrobioidean and archaeogastropod characters as outgroups, which represents an "all zero" row in the data matrix (omitted); and 2) including the ground plan of the Stromboidea and Cypraeoidea operationally as part of the ingroup. The topology of the ingroup cladogram is the same in both analyses. The distribution of synapomorphies and differences of the indices of both analyses are shown in the Fig. 438. Each character, state, and polarization is justified in the discussion section and, if necessary, a concise explanation is presented.

The discussion of each character is also based on the phylogenetic tree that was obtained (Figs. 437, 438). Although the matrix of characters (Fig. 436) and the subsequent tree (Figs. 437, 438) are shown only in the section following.

The synapomorphies of the ingroup. (superfamily autapomorphies) are preserved in the present paper, because they are the main concern as referred in the introduction. The ingroup autapomorphies are the basis to better establish a still imprecisely defined taxon. They confirm the internal position of some possible "outgroups" such as hippingicoideans and capuloideans. They can be used in the on-going phylogenetic study of the entire order Caenogastropoda as the ground plan of the superfamily (see, additionally, Yeates, 1992 and Pinna, 1996).

Some multistate characters are analyzed here with 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 that each state is a clear modification of the preceding one. Additionally, each additive multistate character was also analyzed as non-additive, and any 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 works as an interface of Hennig86 (Farris, 1988). The algorithm “ie” was used (which search for all trees). The computer program PAUP was also used, mainly to obtain bootstrap support values for each node. Both programs presented the same result.

Abbreviations: aa, anterior aorta; ab, auricle region beyond ventricles connection; ac, anterior extremity of gill on mantle border; ad, adrectal sinus; af, afferent gill vessel; ag, albumen gland; an, anus; au, auricle; bb, bulged part of br; bc, bursa copulatrix; bg, buccal ganglion; bm, buccal mass; bs, blood sinus; bv, mantle blood vessel inserting in kidney; cb, glandular concavity where capsules attach; cg, capsule gland; cm, columellar muscle; cp, capsules; cr, crossing muscles; cv, ctenidial vein; da, aperture of duct to digestive gland; dc, dorsal chamber of buccal mass; dd, duct to digestive gland; df, dorsal fold of buccal mass; dg, digestive gland; dm, dorsal shell muscle; dp, posterior duct to digestive gland; ea, esophageal aperture; en, endostyle; ep, esophageal pouch; es, esophagus; ey, eye; fd, foot dorsal surface; fg, food groove; fl, female papilla; fm, foot retractor muscle; fp, female pore; fs, foot (mesopodium) sole; ft, foot; ga, parietal ganglion; gc, cerebral ganglion; gd, gonopercardial duct; ge, supra-esophageal ganglion; gf, gastric fold; gi, gill; gp, pedal ganglion; gr, gill thicker apical region of filament rod; gs, gastric shield; hg, hypobranchial gland; hm, head muscle; ig, ingesting gland; in, intestine; ir, insertion of m4 in “br”; is, insertion of m5 in radular sac; ii, “U”-shaped loop of intestine on pallial roof; jw, jaw; kc, kidney chamber; kd, dorsal lobe of kidney; ki, kidney; km, membrane between kidney and pallial cavity; kv, ventral lobe of kidney attached to intestine; li, left lateral expansion (flap) of neck; lm, lateral shell muscle; m1 to m14, odontophore muscles; ma, accessory pair of muscles of jaws; mb, mantle border; mc, circular muscle (sphincter) of mouth; mj, muscles of jaws and mouth; ml, mantle region restricting pallial cavity; mo, mouth; mr, mantle reinforcement; ne, nephrostome; ng, nephridial gland; nr, nerve ring; ns, neck ventral surface; oc, odontophore cartilage; od, odontophore; om, odontophore superficial ventral membrane; op, operculum; os, osphradium; ov, pallial oviduct; oy, ovary; pc, pericar-