

The influence of classification on the evolutionary interpretation of structure – a re-evaluation of the evolution of the pallial cavity of gastropod molluscs

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Abstract

The gastropod mantle, or pallial, cavity and its associated structures have served as a phylobase for studies of gastropod relationships for well over 100 years. We review C. M. Yonge's model for the evolution of the gastropod pallial cavity published a little more than 50 years ago, as well as its subsequent mutation by other authors. We then use a recently published (Ponder & Lindberg 1997) phylogenetic hypothesis of gastropod relationships to explore character transformations of attributes associated with the pallial cavity.

Significant features of the evolution of the gastropod pallial cavity are the reduction or loss of structures (gill, osphradium, hypobranchial gland) and associated neural and reno-vascular systems on the right side of the cavity, and mechanisms for coping with an increase in overall body size in many clades. The loss of pallial cavity structures has occurred independently in several major clades, the patellogastropods, neritopsines, cocculinoideans, and apogastropods, and probably more than once in the vetigastropods. Evolution of the pallial cavity and associated structures is discussed for each of the clades in which largely different solutions are found to enable the achievement of larger body size. A seeming contradiction – reduction of gills with increasing respiratory demand due to increasing body size – is a feature of the group. We also examine possible linkages between the evolution of the pallial cavity and other morphological characters that were not suspect as *a priori* correlates of one another.

The uncritical application of a current taxonomy to results obtained from applying the comparative method used to study form and function has been a significant hindrance to our understanding of evolution in the last several decades. C. M. Yonge's scenario published in 1947 was close to our phylogenetically based hypothesis. However, when it was later forced into agreement with the dominant classification of the last half-century (Thiele 1929–35), most of the points of agreement between the original scenario of Yonge and our phylogenetic hypothesis vanished, with four separate derivations reduced to a single event. This is an example of a Procrustean evolutionary scenario – fitting the data to a classification scheme, with taxonomy rather than phylogeny used as the bed.

Key words: Mollusca, Gastropoda, pallial cavity, mantle, cavity, evolution, function

Introduction

The era of comparative anatomy is giving way to a new era of functional morphology and comparative physiology, and we cannot afford to continue to be hindered by obscurities of terminology.

R. D. Purchon (1968: 515)

Since gastropod molluscs first appeared in the Cambrian over 550 million years ago, this clade has waxed

and waned through the entire Phanerozoic (Signor 1985; Erwin & Signor 1991). Living molluscan species diversity has been estimated at up to 200,000 species (ca.160,000 gastropod species) (Groombridge 1992; Heywood 1995), and they occupy niches in almost every known marine, freshwater, and terrestrial habitat and setting. The gastropod fossil record is one of the most complete and diverse “deep time” records available and has provided remarkable insights into the diversity of

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long extinct clades as well as putative ancestors of living taxa (Runnegar 1983; Yu 1990; Peel 1991; Wagner 1995). Given this diversity and record it is hard to identify a better taxon for temporal evolutionary studies.

Zoologists studying living taxa have also made substantial contributions to our understanding of gastropod evolution. Here the availability of anatomical data greatly increases the number of characters for observation and interpretation (Morton 1988; Haszprunar 1988a; Ponder & Lindberg 1997), and few organs or systems have escaped notice as a basis for gastropod classification and, by proxy, gastropod evolution.

Predilection for different organs and systems in early studies led to numerous competing classifications. The term taxobase has been used to recognize particular character(s) upon which classifications are built (Graham 1985; Fretter & Graham 1988). Gastropod examples include gills (Cuvier 1817; Gray 1821); reproductive strategies and structures (Blainville 1824; Latreille 1825); radula (Lovén 1848; Troschel & Thiele 1856–93; MacDonald 1880, 1881); heart and gill structure (Milne-Edwards 1848; Mörch 1865); nervous system (Ihering 1877; Spengel 1881; Bouvier 1887; Lacaze-Duthiers 1888); and renal organs (Perrier 1889). However, all of these competing classifications were ignored following the classification proposed by Thiele (1925) which rapidly gained authority after the publication of his *Handbuch* (1929–35). Thiele's classification, adopted by almost all subsequent major treatises and texts, had a profoundly dominating impact on gastropod phylogenetics for almost 75 years (Bieler 1992; Ponder & Lindberg 1996, 1997).

Thiele's major contribution was to incorporate many of the earlier classifications using different taxobases (i.e., emphasis on different characters) into a single classification. He did this by using the different taxobases at different levels (or ranks) in his classification. For example, his three primary gastropod groups – Prosobranchia, Opisthobranchia, and Pulmonata – reflected the evolution of respiratory structures. The Prosobranchia was divided into the Archaeogastropoda, Mesogastropoda and Stenoglossa (later called Neogastropoda by Wenz 1938–44). These groups were recognised on several character complexes including radula, gills, and heart structure. This arrangement also reflects the supposed geological age of the groups, with the Archaeogastropoda corresponding to a Palaeozoic radiation, Mesogastropoda to a Mesozoic origination and radiation, and Neogastropoda likewise in the Cenozoic.

As with the earlier classifications, Thiele's requires that some characters behave in ways not consistent with the overall scheme or substantially deviate from the pattern seen in the putative ancestor or descendent. Thus, caveats or special pleadings were needed to explain away inconsistencies such as the single auricle in the

Patellogastropoda – a condition unique among its reputed archaeogastropod brethren, or the untidy character conflicts that occur between radular, gill, and gut characters within some of the hydrothermal vent taxa (Ponder & Lindberg 1997). One such case led Fretter et al. (1981: 353) to conclude, when writing on the hydrothermal vent gastropod *Neomphalus*, that “it does not fit easily, moreover, into the customary division of prosobranchs into archaeogastropods and mesogastropods ... since according to the system used as a criterion, it falls clearly into one group or equally definitely into the other.” Similar examples are not uncommon in the gastropod literature because many workers have not only slavishly followed Thiele's classification, but have confused his classification with a phylogeny (e.g., Purchon 1968 on the feeding methods in the Gastropoda). What was lacking was an independent phylogenetic hypothesis to test the classification as well as constrain and delimit the evolutionary narratives and scenarios. Unfortunately, the characters that served as taxobases in Thiele's classification became phylobases (Graham 1985) without assessment. Falsification of the general null model of evolutionary studies – a taxon has a particular attribute because its ancestor had it (O'Hara 1988) – was unattainable. For well over half a century Thiele's classification alone served as a Procrustean bed on which to test scenarios describing gastropod evolution and adaptive radiations.

Here we review Sir C. M. Yonge's (1947) studies of the evolution of the gastropod pallial cavity, and their influence on gastropod classification and vice versa. The pallial cavity is thought to be a hallmark of gastropod evolution and, together with its associated structures, has served as a phylobase for studies of gastropod relationships for over 100 years (e.g., Bernard 1890). Perhaps more importantly, evolutionary scenarios of pallial cavity evolution have served as the basis for teaching gastropod evolution in some invertebrate zoology textbooks [e.g., Barnes 1987: 356 (and earlier editions); Meglitsch 1972: 302; Russell-Hunter 1979: 368].

We begin by presenting a brief review of Yonge's (1947) original evolutionary scenario and its subsequent mutations (Yonge 1960; Morton & Yonge 1964). After comparing these scenarios with Ponder & Lindberg's (1997) cladogram of the relationships amongst the gastropod molluscs, we discuss pallial cavity character evolution within each major gastropod subclade. We also explore possible linkages between the evolution of the pallial cavity and other morphological characters not suspected *a priori* as possible correlatives of one another. Lastly, we construct an evolutionary scenario consistent with the hypothesised relationships and the character state changes, trends and patterns present in Gastropoda.

C. M. Yonge's model of the evolution of the gastropod pallial cavity and its subsequent distortion

Yonge's (1947) classic study of gastropod pallial organs reported on the configuration of the "aspidobranch" [having two bipectinate primary ctenidia (gills)] pallial cavity, its derivation within the Gastropoda, and then extended the model to include other Mollusca. Yonge argued that the primitive molluscan pallial cavity was shallow and contained a pair of ctenidia, osphradia, hypobranchial glands, renal pores and a median anus. The gills served the dual purpose of generating water flow through the cavity as well as being the primary respiratory sites. Following the advent of torsion, in which the visceral mass is rotated through 180° during development (see Haszprunar 1988a and Ponder & Lindberg 1997 for recent reviews), Yonge (following Garstang 1929) argued that the positioning of the anus over the head produced sanitation problems. These were alleviated, it was argued, by the formation of a median slit on the anterior surface of the shell that enabled the exhalant current to be directed through this slit rather than on to the snail's head. Elongation of the slit over the body whorl of the shell allowed a deepening of the pallial cavity. This ancestral condition, which Yonge assumed to be similar to the states in the extinct planispiral bellerophonitids, served as the starting point for Yonge's evolutionary scenario.

Yonge summarized his observations of the pallial cavity arrangements in the "prosobranch" Gastropoda in his fig. 31 (p. 490) modified here as Fig. 1, and used this diagram to show the "possible course of evolution within the Prosobranchia." Yonge's scenario independently derived the single ctenidium from the paired state on four occasions: (1) *Pleurotomaria* to *Calliostoma* and *Patelloida*, (2) *Bellerophon* to *Valvata* and pectinobranch (single monopectinate ctenidium - group now known as Caenogastropoda), (3) *Bellerophon* to Neritacea, and (4) *Bellerophon* to Cocculinacea.

Although the paper was submitted in 1945, Yonge did not use Thiele's (1925 1929-1935) classification to order or circumscribe his results and may not have had access to Thiele's (1929-1935) Handbuch. He only briefly noted that his groups agreed with Thiele's (1925) concept of Archaeogastropoda with two exceptions (Yonge 1947: 449). However, Yonge was explicit about the fact that he had no intention of dealing with Thiele's classification in his study. His own words at the bottom of the title page (pg. 443), were subsequently ignored by everyone (including himself, see below) who sought to use the pallial cavity as a phylobase for gastropods. Yonge wrote, "The aspidobranch condition has been retained in a diverse variety of Prosobranchia; its possession *does not* indicate close relationships" [emphasis added].

Yonge's statement required a phylogenetic context, and based on his implicit model of gastropod evolution

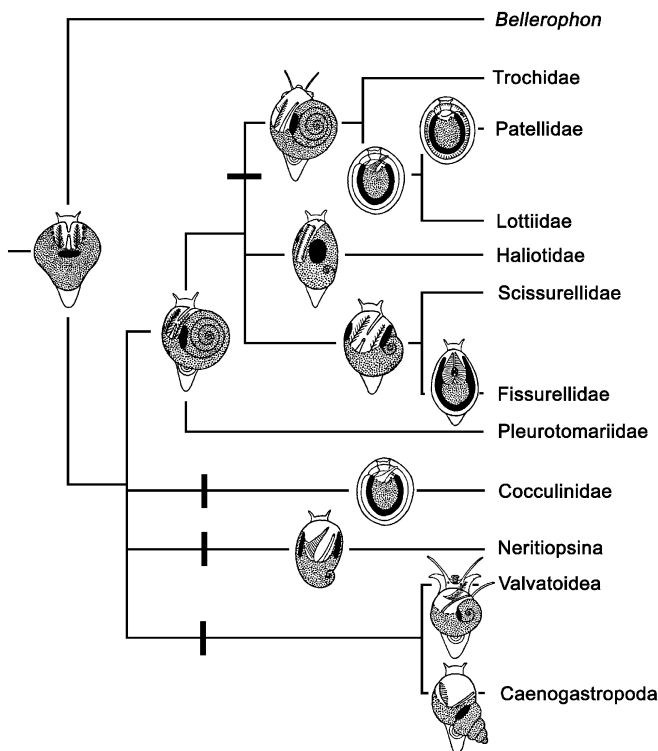


Fig. 1. Yonge's (1947) diagram of the evolution of the gastropod pallial cavity redrawn as a cladogram. Bars on branches indicate positions of loss of the aspidobranch (paired gills) condition.

he had discovered that the aspidobranch condition was plesiomorphic. Yonge's model of gastropod evolution appears to have come from Anna Meyer (1913), a work cited by Yonge, who published a schematic drawing of the renogenital systems of the "lower gastropods" (niedereren Gastropoden) and their "phylogenetic relationships" (phylogenetische Beziehungen). Yonge appears to have modified Meyer's diagram as his fig. 30 in the 1947 paper. In modifying her original figure, Yonge detorted Meyer's "Progastropoda", added the redundant trochid renogenital configuration (Yonge's fig. 30: G), placed arrows from Meyer's "Promonotocardia" to the taxa Cocculinacea and Valvatacea, and added the neritacean diagram (Yonge's fig. 30: I). The remaining eight diagrams, hypothetical ancestors, and purported relationships and transformations are identical to Meyer's phylogeny and figures. Yonge's pallial cavity drawings were then overlaid on his fig. 30 and reproduced as fig. 31.

The first hint of acquiescence of this evolutionary scenario to the dictums of Thiele's (1925) classification came in Yonge (1960). In his chapter on "General Characters of Mollusca" Yonge reproduced his modified Meyer phylogeny of the renogenital system, only dropping the arrow to the Valvatacea. Perhaps surprisingly, there is no diagram of the evolution of the pallial cavity. Instead, Yonge's pallial cavity evolutionary scenario is weakly folded into Thiele's classification. Within the Archaeogastropoda Yonge (1960: 116–117) denotes four (*i–iv*) aspidobranch conditions. Statements of relationships are vague (e.g., "achieved independently", "arising presumably from ancestors in which ..."). The strong statements and arrows of transformation from the 1947 paper are missing. Moreover, while pallial cavity morphologies in the Meso- and Neogastropoda, Opisthobranchia, and Pulmonata are described, possible evolutionary scenarios are not suggested. Although Yonge

treated all of the major or "class rank" molluscan taxa in this chapter, it was only for the Gastropoda that a classification was inserted into the treatment. This action, by Yonge writing alone, is a harbinger of the future nullification of his 1947 evolutionary scenario. Fretter & Graham (1962: 618) follow a similar line of reasoning stating that the "monotocardians have evolved from a diotocardian ancestry with trochoid relationships", arguing that "alone of the diotocardians are the trochids sufficiently unspecialized to be regarded in this light".

The final recanting came in a paper coauthored with John E. Morton (Morton & Yonge 1964). Restating Fretter & Graham's (1962) position, Morton & Yonge argued that the primitive molluscan pallial cavity was deepened to accommodate the enlarged foot of the "protogastropod". The ancestral pallial cavity still contained a pair of ctenidia, osphradia, hypobranchial glands, renal pores and a median anus, and supposed sanitation problems were met with the evolution of the antero-dorsal shell slit in the first gastropods. However, their scenario for the evolution of the pallial cavity (redrawn here as Fig. 2) was substantially modified from Yonge's original (1947) scheme, as well as the 1960 treatment. Moreover, the new diagram clearly shows the effects of re-interpreting Yonge's earlier scenario within the constraints of Thiele's classification. The terms Archaeo-, Meso-, and Neogastropoda, scarcely or not mentioned in the original work (1947), were prominently defined in the opening pages of Morton & Yonge (1964), their use precisely establishing the taxonomic (not phylogenetic) mold that shaped the evolution of the gastropod pallial cavity. The vague language of Yonge (1960) is absent, and the arrows and transformation series are once again explicit. Meyer's (1913) diagram of the evolution of the gastropod renogenital system is absent from this paper, but five of her renogenital character state diagrams float among the pallial cavity cartoons in juxtaposition of the

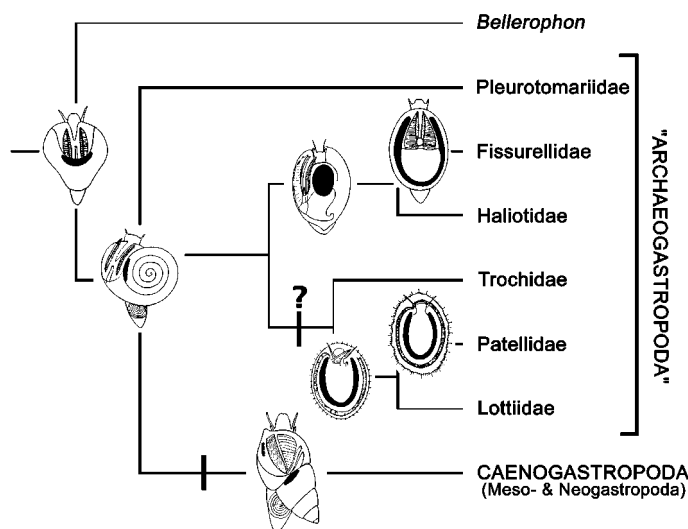


Fig. 2. Morton & Yonge's (1964) diagram of the evolution of the gastropod pallial cavity redrawn as a cladogram. Bars on branches indicate positions of loss of the aspidobranch (paired gills) condition.

corresponding pallial cavity morphology (Morton & Yonge 1964: fig. 6).

Of Morton and Yonge's seven pallial cavity figures, five (D–H) dealt solely with pallial cavity states found in the "Archaeogastropoda." Only about half of the taxa used in Yonge's original work would have been referable to this group. The remaining two cartoons illustrated the pallial cavity state in the supposedly ancestral bellerophonid (C) that gave rise to the archaeogastropods, while the last one (I) represents the condition in "Mesogastropoda and Neogastropoda" (equivalent to Yonge's Pectinobranchia and Meyer's Monocardia). The reduction from paired to single ctenidium now occurs twice in a lineage from *Pleurotomaria* to *Buccinum*, and *Pleurotomaria* (coming from trochids according to the figure caption) to *Lottia* (Morton & Yonge 1964: fig. 6 – modified and reproduced here as Fig. 2). There are not completely explicit statements in the text about the evolutionary relationships of the "proso-branch" gastropods, but the following quotes (p. 15) suggest the authors had in mind that the loss of the right gill was a single evolutionary event: "Thus this transformation to a single (left) ctenidium accounts for the states seen in both *Lottia* (Patellogastropoda) and meso- and neogastropods"; and "The now restricted inhalant current, created by the solitary aspidobranch ctenidium [of trochids] ... Final simplification and completed efficiency is attained by loss of the left filaments and fusion of the ctenidial axis to the left pallial wall, producing the pectinibranch ctenidium of the higher Prosobranchia". The only exception, and a significant one, to Thiele's (1925 and subsequent) classification in the classification presented by Morton & Yonge (1964) is that "Neritacea" are excluded from the Archaeogastropoda by the authors, and given equal rank (order) to archaeo, meso and neogastropods. However, neritoideans are not included in their diagram. This confusion is perhaps explained by the influence of Morton's evolutionary vision imposed on that of Yonge. Morton earlier (1958b: 70 and in subsequent editions) stated that "An archaeogastropod like *Trochus* is posed [*sic!*] for the evolution of all the later prosobranchs, with a single gill and auricle". Thirty years later, Morton (1988: 260) still espoused the same view by concluding "Thus the monocardian archaeogastropods and all later Prosobranchia have reorganized the pallial cavity with the dominance of the left side." Morton suggested that this "efficient single-gilled asymmetry" has been avoided only by the adaptation of the limpet habitat. First in the Scissurellidae and Fissurellidae where "the paired pallial complex was re-prieved before the completion of left-sidedness", and in the Patellogastropoda where the Acmaeidae maintain the single bipectinate ctenidium, which has been entirely lost in the Patellacea.

The hypothesis of the independent origin of pallial cavity states in the Gastropoda was laid to rest, replaced by a scenario largely consistent with Thiele's classifica-

tion and concordant with a well-ordered ladder of increasing proficiency and complexity ultimately becoming "a mechanism of beautiful efficiency" (Morton & Yonge 1964: 12). The noisy, confusing patterns of homoplasy and symplesiomorphy had been overcome.

Phylogenetic hypothesis

Our cladistic analysis of gastropod phylogeny (Ponder & Lindberg 1997) used 117 morphological characters for 40 molluscan taxa. Five of the taxa were outgroups used to estimate ancestral character states. The remaining 35 taxa were members of the ingroup Gastropoda. Analyses were conducted using PAUP 3.1.1 (Swofford & Begle 1993). Six analyses were done using different weighting and encoding schemes, and complete descriptions of character states, ontogeny, and polarity are presented by Ponder & Lindberg (1997), as are the full details of our previous analysis. The phylogenetic hypothesis presented here (Fig. 3) is based on a strict consensus tree of three trees (for details and statistics see Ponder & Lindberg 1997: table 2; fig. 3b).

The results of our analysis support the following major clades within the Gastropoda, and for the following discussion we define them as follows. The Patellogastropoda and their presumed coiled ancestors (Eogastropoda) are recognised as the sister taxon of all other living gastropod taxa (Orthogastropoda). The Vetigastropoda include most of the taxa formerly assigned to Thiele's "Archaeogastropoda" which is readily discernible as a grade in gastropod evolution (see also Graham 1985; Hickman 1988; Haszprunar 1988a, 1993; Ponder & Lindberg 1996). Many of the gastropods (see above) described from hydrothermal vents in the deep sea during the last 15 years are members of this clade, although their position remains equivocal (Ponder & Lindberg 1997). Three of these hydrothermal vent taxa (Neomphalidae, Peltospiridae and *Melanodrymia*) form a clade (Neomphaloidea) in some of our analyses and may possibly be independent of the Vetigastropoda, as suggested also by molecular data (Tillier et al. 1994), although unpublished molecular data (MacArthur, in litt.; Colgan et al. 2000) show this group as having affinities with the Vetigastropoda. The Neritopsina were shown to be a distinct clade by Bourne (1909, 1911) but were subsumed in the Archaeogastropoda by Thiele (1925). This was accepted by most subsequent workers with few exceptions (notably Morton & Yonge 1964) until Haszprunar's (1988a) seminal reassessment of gastropod phylogeny. In our previous analyses (Ponder & Lindberg 1996, 1997), they were grouped with the Cocculinoidea (see Ponder & Lindberg 1997 for details), albeit tentatively. More recent studies (Harasewych et al. 1997; Colgan et al. 2000; Haszprunar, pers. comm.) in-

dicate that there is not a sister group relationship between cocculinids and neritopsines as also suspected by Ponder & Lindberg (1997: 223) despite the results of their analysis. The sister-group relationships of the Cocculinoidea remain unresolved, and it is thus unclear as to whether or not the reduction in the ctenidium in this group is independent of that in other gastropod groups. We have modified our original tree to reflect their uncertain position (Fig. 3). The Apogastropoda is a major clade comprising the majority of extant gastropods, comprising Caenogastropoda [most of Thiele's Mesogastropoda + Stenoglossa (= Neogastropoda)] and the Heterobranchia, the latter comprising the paraphyletic Heterostropha (sensu Ponder & Warén 1988, not Bandel 1990, 1991) plus the Euthyneura – a group comprising the previously recognised “subclasses” Opisthobranchia and Pulmonata. The Architaenioglossa (comprising the enigmatic non-marine Cyclophoroidea and Ampullarioidea) is the sister taxon of all other caenogastropods (including Neogastropoda). Of Thiele's original tripartite division of the “Prosobranchia” only the Neogastropoda were found to be monophyletic.

Evolution of the gastropod pallial cavity

Recent reviews of the organs of the gastropod pallial cavity can be found in Haszprunar (1988a) and Ponder

& Lindberg (1997). Based on outgroup comparison and gastropod synapomorphies (e.g., operculum) we agree with Yonge (1947) and Fretter & Graham (1962) that the ancestral gastropod was coiled and its pallial cavity contained a median anus, and a pair of bipectinate ctenidia, renal openings and osphradia (Ponder & Lindberg 1997). Hypobranchial glands may also have been present, but their absence in all but one outgroup makes their distribution on the tree equivocal below the Eogastropoda (Fig. 3). With the exception of the anus, all of these structures are plesiomorphic, but only four of our 35 ingroup taxa retain the plesiomorphic structures. Thus, an important aspect of gastropod evolution is written in the history of the transformation of the pallial cavity from symmetrical to non-symmetrical states.

Reduction and even subsequent loss of the structures located on the right side of the pallial cavity is evident throughout the clade. Ctenidia transform from paired to single or loss, and bi- to monopectinate condition; auricles from paired to single; osphradia from paired to single and sometimes loss; and hypobranchial glands from paired to single or loss (Haszprunar 1988a; Ponder & Lindberg 1996, 1997). Our hypothesis of relationships does not support Morton's (1958a) scenario for the derivation of the monopectinate condition of the pallial cavity. In the opposite extreme, Graham (1985) suggested the possibility of multiple derivations of caenogastropods from archaeogastropods. We conclude that loss

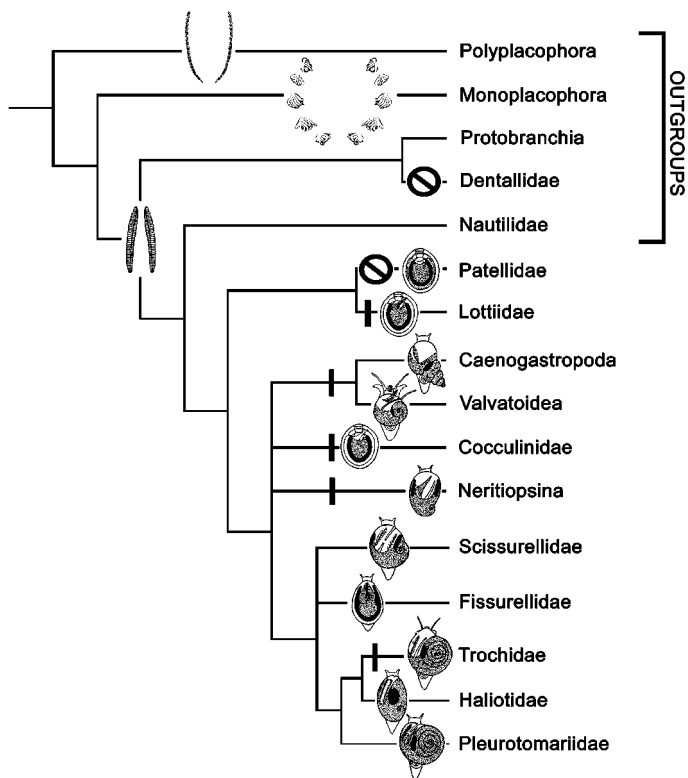


Fig. 3. Strict consensus tree of 3 equally parsimonious trees from PAUP analysis with all characters unordered and multi-state characters scaled (x1000). Gastropod taxa not treated by Yonge (1947) or Morton & Yonge (1964) have been pruned from the tree. See Ponder & Lindberg (1997: table 2) for further information. Bars on branches indicate positions of loss of the aspidobranch (paired gills) condition. Neritopsina and Cocculinidae have been redrawn as a polytomy. **X** = loss of gills.

of pallial cavity structures on the right side has occurred *at least* four times, in: (1) patellogastropods, (2) vetigastropods (with a probable separate derivation in the Neomphaloidea), (3) neritopsines and cocculinoideans, and (4) apogastropods (Caenogastropoda + Heterobranchia) (see also Ponder & Lindberg 1996: fig. 11.1). Within the vetigastropods the right ctenidium has been lost in more than one subclade (e.g., lepetodrioleans, trochoideans). In addition, the reduction or loss of each pallial structure does not necessarily track changes in other pallial structures, suggesting some independence (Haszprunar 1988a: table 1, 1993: table 1; Ponder & Lindberg 1996: fig. 11.1). Thus, the neat and orderly evolution of the pallial cavity inherent in Morton & Yonge's scenario and dictated by Thiele's classification is not present in our cladogram (Fig. 3).

When pallial cavity depth (i.e., external to maximum internal extent) is overlain on our cladogram (Fig. 3), an interesting trend is seen. Unlike Yonge's (1947) plesiomorphic deep pallial cavity in gastropods, our phylogeny suggests an initially shallow pallial cavity, as also suggested by Fretter & Graham (1962), Salvini-Plawen & Haszprunar (1987), and Haszprunar (1988a, 1992b), albeit on different grounds. In agreement with Yonge and Morton, the plesiomorphic pallial cavity would be outfitted with a full compliment of organs – a pair of bipectinate ctenidia, auricles, osphradia, and (possibly) hypobranchial glands – and the ctenidia would initially function as both ventilators and respiratory sites. In addition, the ancestor possessing this pallial cavity was probably coiled (cf. Haszprunar 1988a) and small (Chaffee & Lindberg 1986; Haszprunar 1988a, 1992b; Ponder & Lindberg 1997). From this starting point, we examine below how the gastropod pallial cavity has been modified in the major gastropod clades.

Patellogastropoda

In some members of the Patellogastropoda (Patellidae, Nacellidae, Lepetidae, Neolepetopsidae) both ctenidia are lost (Fig. 4A) (Lindberg 1988). In another patellogastropod clade (Acmaeoidea) members have only a single left gill that we only tentatively accept as homologous with the left ctenidium (see Eertman 1996 for a recent account of its structure) because this homology requires further testing. The distribution of the osphradium and associated sensory structures is much more varied. In the Patellidae at least four distinct sensory structures are associated with the pallial (i.e., nuchal) cavity. A pair of subpallial streaks extending from in front of the shell muscles along the sides of foot in Patellidae and Nacellidae are absent in the Acmaeoidea (Thiele 1892; Thiem 1917; Yonge 1947; Haszprunar 1985a). Based on TEM studies Haszprunar (1985a) concluded that these subpal-

lial streaks house mechanoreceptors. Confusion also exists regarding the homology of pallial sensory structures (osphradia, "wart organs" or tubercles, and sensory streaks; Thiele 1892; Thiem 1917; Yonge 1947; Stützel 1984; Haszprunar 1985a) between different patellogastropod taxa. In most Patellidae and Nacellidae, a single pair of osphradia and associated wart organs lie on either side of the neck near the shell attachment muscles (Stützel 1984; Haszprunar 1985a). In most Acmaeoidea two tubercles are located in similar positions, and an additional anterior sensory tubercle lies on the left side (Yonge 1947). In both of these groups, a sensory streak

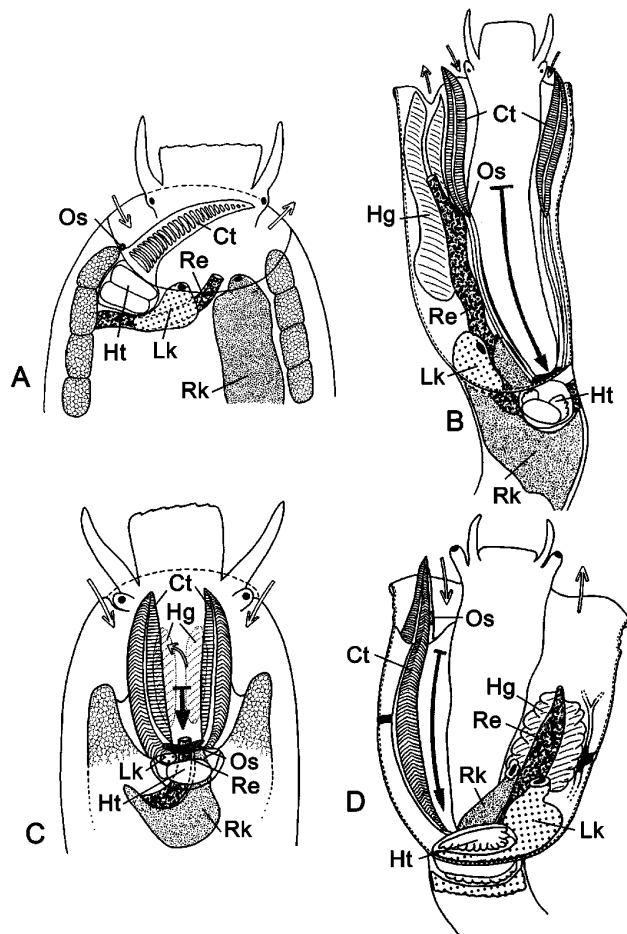


Fig. 4. Pallial cavities of patellogastropod (A) and vetigastropod (B–D) molluscs. A. *Tectura virginea* (Lottiidae), redrawn from Fretter & Graham (1962: fig. 259); B. *Perotrochus beyrichii* (Pleurotomiidae), redrawn from Woodward (1901); C. *Diodora apertura* (Fissurellidae), redrawn from Fretter & Graham (1962: fig. 257); D. *Monodonta lineata* (Trochidae), redrawn from Fretter & Graham (1962: fig. 53). Solid arrows with crossbar show the probable direction of pallial cavity elongation; crossbar indicates the likely approximate position of the original pallial cavity posterior wall in common ancestor. Open arrows show direction of water movement(s) through pallial cavity. Ct = ctenidium, Hg = hypobranchial gland, Ht = heart, Lk = left kidney, Os = osphradium, Re = rectum, Rk = right kidney.

is also located on the ventral mantle surface along the left shell muscle (Haszprunar 1985a). All four of these structures are lacking in the Lepetidae (Angerer & Haszprunar 1996), whereas species of *Acmaea* and *Pectinodonta* have only the ventral mantle sensory streak (Thiele 1883; Haszprunar 1985a). The osphradial ganglia or branches of them innervate all of these structures. We (Ponder & Lindberg 1997) have previously considered that the wart organs in patellogastropods may represent, in part, a pair of gill rudiments, as suggested by Stützel (1984), but based on new data collected by R. Guralnick (pers. comm. 1997) they appear to be sensory structures. We now concur with Yonge (1947) and regard the paired tubercles of Acmaeoidae to be wart organs and homologous with those found in patellids and nacellids.

Wart organs are a mixture of haemal lacunae and nervous and connective tissues (Haszprunar 1985a). Some workers (e.g., Fretter & Graham 1962; Walker 1968) have regarded them as osphradia. Neuro-lymphoid tissue is also found in two anteriolateral sensory streaks in the pallial cavity of lepetids (Angerer & Haszprunar 1996), but unlike the wart organs these structures are innervated by the pallial nerve rather than via the osphradial ganglia. Also like Yonge, we presume the "true" acmaeoidan osphradium to be single and located on the left side of the pallial cavity in juxtaposition with the left wart organ and near the base of the ctenidium (Yonge 1947: fig. 46). The ventral mantle sensory streaks appear to be apomorphic for patellogastropods, while the presence of subpallial streaks is an apomorphy for patellids and nacellids. Various combinations of loss produce a mosaic of character combinations of these four pallial cavity sensory structures.

In some lottiids the secondary acquisition of gills converged with those in the Patellidae (Lindberg 1986, 1988). Pallial cavity depth remains unchanged in these clades – although patelloideans tend to be shallower than acmaeoidans (Yonge 1947) – and is therefore independent of pallial cavity organ loss in the Patellogastropoda. The surfaces of both the ctenidial and secondary gill filaments bear concentrations of cilia; organised into bands or clusters (Yonge 1947; Nuwayhid et al. 1978). Unorganised cilia are also found in the pallial groove and pallial cavity (Yonge 1947; Fretter & Graham 1962) as well as over the body surface (Voltzow 1994). Ciliated epithelium is not associated with the osphradium (Haszprunar 1985a).

In addition to the ctenidium and secondary gills of the pallial groove, respiration probably occurs on the roof of the pallial cavity (Fleure 1904), and has been experimentally demonstrated on the surfaces of the pallial groove (Kingston 1968). Moreover, the presence of counter-current relationships between the ciliary water currents and the direction of blood flow in their pallial

cavity and pallial groove led Kingston (1968) to propose that the "cleansing currents" of Yonge (1947, 1962) might also have a respiratory role.

In those patellogastropods with a ctenidium, or secondary gill, these structures serve both as a ventilator and a respiratory surface. However, the surfaces of the pallial groove and pallial cavity appear to remain important sites of respiration as well with the limpet morphology greatly enhancing the available respiratory surface area, even resulting in a change in growth parameters (Ponder & Lindberg 1997). In those taxa that have neither ctenidium nor secondary gill (Lepetidae, Neolepetopsidae) the exposed mantle surfaces are probably the primary sites of respiration.

Ultrastructural characters of the patellogastropod osphradial cells are not shared with any other gastropod group (Haszprunar 1985a), thus, with the exception of their location and innervation by the osphradial ganglia, there is no evidence for homology between the osphradial structures of the patellogastropods and those of other gastropods. Wart organs and sensory streaks are apomorphic. There is no support in our (Ponder & Lindberg 1997) analysis for either Yonge's (1947) or Morton & Yonge's (1964) derivation of patellogastropods from a trochid-like ancestor, nor for the clade to be included with other groups in a taxon "Archaeogastropoda".

Vetigastropoda

The plesiomorphic pallial cavity condition in the Vetigastropoda is hypothesized as conforming with our plesiomorphic gastropod pallial cavity – a rather shallow cavity with a pair of bipectinate ctenidia (and associated auricles), osphradia, and hypobranchial glands (Ponder & Lindberg 1997). The presence of skeletal rods in the ctenidial filaments is the only significant difference between this ancestral condition and that of the supposed ancestral patellogastropod. The basic arrangement of pallial structures is present in some extant subclades (e.g., haliotids, scissurellids, pleurotomariids, and fissurellids). Several apparently independent losses of structures from the right side of the pallial cavity have occurred as well as the loss of the right shell muscle in others (e.g., trochoideans and several of the hydrothermal vent taxa).

The vetigastropod osphradial epithelium has sensory cells organised into a central zone, a character shared with all other gastropods except patellogastropods (Haszprunar 1985a,c). The osphradia are located at the free part of the efferent edge of each gill axis, with the osphradial ganglion inside the efferent membrane. As in patellogastropods the osphradium lacks a prominent ciliated epithelium (Haszprunar 1985a). A recent account of ctenidial ultrastructure in a trochid, *Austrocochlea*, is given by Eertman (1996).

The plesiomorphic, shallow pallial cavity has been deepened in vetigastropods at least three times by three different mechanisms: (1) Elongation of the posterior end of the pallial cavity not accompanied by gill elongation; both ctenidia present; kidneys in the pallial roof (as in Pleurotomariidae) (Fig. 4B); (2) some elongation of the posterior part of the gill (transverse vein posterior, gill membranes long); kidneys largely lying behind the generally rather short cavity (as in Fissurellidae) (Fig. 4C); (3) elongation of the posterior end of the gill (including elongation of the gill membranes) with the gill extended well behind the transverse vein (transverse vein in middle of gill); right ctenidium lost; kidneys in pallial roof (i.e., the cavity has extended beneath the kidneys) (e.g., Trochidae) (Fig. 4D).

Correlated with, and overlaying, the deepening of the pallial cavity has been (1) the evolution of shell elaborations to entrain the exhalant current, (2) increasing whorl expansion rates to become limpet-shaped (patelliform), and (3) the reduction and loss of shell muscles and pallial organs from the right side of the pallial cavity. These features occur individually, and in most combinations, in different taxa.

In dibranchiate vetigastropods, the exhalant flow is commonly constrained with modifications to the shell that direct water currents dorsally or even posteriorly (e.g., *Macroschima africana*; Herbert 1988). In contrast, the monobranchiate Trochoidea have direct water flow from left to right and constrain pallial cavity flow solely with soft part morphology (i.e., neck lobes). Thus, hardware (shell modifications) control is replaced with software (tissue modifications) control.

Shells with slits (selenizones) or emarginations (sinuses) are common features of Palaeozoic gastropods and are often regarded as diagnostic of the most "primitive" vetigastropods (e.g., Signor 1985), and Yonge (1947) began his evolutionary scenario with a slotted "Bellerophon?" However, in several alternative hypotheses (Fretter & Graham 1962; Runnegar & Pojeta 1974; Runnegar 1981; Yu 1990), the earliest putative gastropods completely lack these structures (e.g., *Aldanella*), and slits and emarginations are derived multiple times from slitless ancestors (Wagner 1995; Bandel & Geldmacher 1996). Moreover, living representatives of some of the earliest fissurelloideans (e.g., Emarginulinae) have poorly developed, or lack, exhalant shell elaborations.

Given the small (1–2 mm) body size of most of these earliest gastropods (Runnegar 1981; Yu 1990; Peel 1991), and the presence of a shallow pallial cavity as the plesiomorphic state, deep invaginations of the shell would probably have decreased respiratory surface with little or no increase in respiratory efficiency or effectiveness. Most scissurellids are 0.5 to 2–3 mm in size and have holes or slits. A few that tend towards limpet shape

have lost or markedly reduced the slit (e.g., *Incissura* which lives in high-energy, oxygen-rich environments in New Zealand).

With size increase and deepening of the pallial cavity (as evidenced by the movement of muscle scars further into the shell), slits, tremata (holes), and sinuses undoubtedly provided increased ventilation of the larger, deeper cavities. Moreover, the evolution of the shell modifications (slits or holes) with the deepening of the pallial cavity brought control of pallial cavity water flow to the gastropods for the first, but not last, time.

Typically, the exhalant slit or holes in the shell of the vetigastropods is associated with an (as yet undemonstrated) need for sanitation (e.g., Garstang 1929; Yonge 1947; Fretter & Graham 1962; Morton & Yonge 1964). However, these shell openings could be a mechanism to enable more direct and controlled flow (and therefore gain greater efficiency) of the respiratory current through the pallial cavity. For example, in pleurotomariids and other slit-bearing vetigastropods the position of the exhalant flow is adjustable along the slit (R. Linsley, pers. comm.), thereby providing variable ventilation of the deepest pallial cavities. In taxa such as fissurellids and haliotids, with small holes providing the openings, the exhalant flow(s) can either be controlled through multiple openings (Voltzow 1983; Tissot 1992), or if a single opening is present it is located near the apex of the shell thereby enhancing flow through the cavity by induced flow (Murdock & Vogel 1978). Control of the size of the exhalant aperture through associated mantle tissue also can vary residence time of water in the pallial cavity.

Limpet-like forms evolved at least six times in the vetigastropods. In the Clypeosectidae, Fissurellidae, and Haliotidae limpet-like forms are associated with deepened pallial cavities, and their shells have slits, holes or sinuses. In some fissurellids such shell elaborations may be absent (e.g., in the intertidal fissurellid limpet *Montfortula*); and most of these taxa are relatively small (<20 mm). Many large fissurellid taxa (such as *Scutus*) have reduced, sometimes internal, shells covered by an expansive mantle (and potential secondary respiratory surface). In the hydrothermal vent limpet-shaped Lepetodriolea, slits or holes are absent but the large, long, single bipectinate ctenidium is expanded across the roof of a long, wide pallial cavity.

In the Lepetelloidea, a mainly deep-sea group of small-sized limpets, the shallow pallial cavity contains only a single (left) ctenidium displaced to the right (Haszprunar 1988b). Thus, in becoming patelliform this group has coopted the pallial groove between the side of the foot and the edge of the mantle along the shell. This strategy has enabled lepetelloideans to increase the extent of their pallial cavities in a way analogous to the development of the secondary gill in the pallial groove of some patellogastropods. Water flow through the shallow lepetel-

loidean pallial cavity is assumed to be left to right, as in Patellogastropods. In one group of lepetelloideans, the pseudococculinids, a single (or sometimes more than one) gill leaflet may be present immediately in front of the left shell muscle (Haszprunar 1988b,c). Respiratory surfaces on these gill leaflets are typically lacking or quite small; only in those species with multiple leaflets are respiratory surfaces developed, and the left kidney extends into the posterior pallial roof in most taxa (Haszprunar 1988b,c). In taxa that lack gills, ciliary spots may be present in the pallial cavity to provide ventilation (Haszprunar 1988c). Choristellids, the only coiled members of this subclade investigated anatomically, also have a rather shallow pallial cavity and have lost the pallial organs on the right side (Haszprunar 1992a).

As with lepetelloideans and lepetodriloides, water flow in the trochoidean pallial cavity is also from left to right. The ctenidium and osphradium on the right side of the pallial cavity have been lost. However, they have a deepened pallial cavity, are not patelliform, and have gained control over pallial cavity water flow by using neck lobes. Neck lobes are thin, highly innervated extensions of epipodial tissue that can form grates, flaps, and tubes on either side of the head at the openings to the pallial cavity (Hickman & McLean 1990). In some taxa, neck lobes are poorly developed or absent. However, in two separate clades (Tricoliidae, and Trochidae s.l.), neck lobes, primarily on the inhalant (left) side, are often large and digitate (Hickman & McLean 1990), and, in some trochids (s.l.), can even be rolled into tubular siphons (Robertson 1985; Hickman & McLean 1990). The most digitate of these structures are typically found in suspension feeders (McLean 1986; Hickman 1985a,b; Hickman & McLean 1990), and have been interpreted solely as filters, particularly in the burrowing taxa (Hickman 1985a; Hickman & McLean 1990; but see also Robertson 1985). Several lines of evidence, however, suggest additional or alternative functions. Taxa that suspension-feed using a modified gill are presumably placing an additional load on the ctenidium that is already functioning both as a respirator and ventilator. Thin, ramified extensions of epipodial tissue placed directly in the inhalant flow provide additional potential respiratory surface in these taxa, and the placement of the smooth, rolled exhalant (right) neck lobe above the substrate would increase flow through the pallial cavity via induced flow (Murdock & Vogel 1978). The presence of digitated neck lobes (albeit reduced) on the exhalant (right) side of some taxa calls into question the usefulness of “filters” that would trap particles within the pallial cavity (e.g., see Robertson 1985: pl. 9), and the pattern of stronger elaboration of neck lobes on the inhalant (left) side throughout the Trochoidea is also consistent with the idea that these are increased respiratory surfaces. In contrast, not all taxa that suspension-

feed are burrowers (e.g., Lirularines), yet their inhalant left neck lobes are finely digitate (Hickman & McLean 1990). In addition, the trochid *Gaza*, considered by Hickman & McLean (1990) to be a putative burrower with “distinctly siphonal-like” neck lobes, lacks a filter, but neither is it a suspected suspension feeder.

In summary, vetigastropod pallial cavities retain ctenidia that function as both respirators and ventilators. In several clades the cavities have deepened, but in different ways. In coiled taxa, this deepening has been accompanied by elaborations of the shell to increase ventilation, or the loss of the right pallial structures, and the adoption of the left-to-right current flow. Other clades have evolved patelliform shells with or without their further elaboration. Only the patelliform lepetelloideans have a shallow pallial cavity. In taxa with shell elaborations or neck lobes, flow out of (and sometimes into) the pallial cavity can be mediated, and highly branched inhalant neck lobes may also function as respiratory sites.

Vetigastropods possess an impressive array of sensory structures (Crisp 1981; Salvini-Plawen & Haszprunar 1987; Haszprunar 1988a; Ponder & Lindberg 1997). In addition to the small osphradia(um), there are the external cephalic and epipodial tentacles and epipodial sense organs as well as synapomorphic bursicles associated with the ctenidium (Szal 1971; Haszprunar 1987b) that are apparently associated with predator detection (see also discussion).

When the taxa not considered by, or known to, Yonge (1947) and Morton & Yonge (1964) are removed from consideration, good consensus between their derivations of the pallial states in this clade and our phylogeny is obtained, with the exception of their recognition of the deepened pallial cavity as the plesiomorphic state. There is also relatively good concordance between this clade and Thiele's Archaeogastropoda, when the Patellogastropoda and Neritopsina are excluded (see also Hickman 1988, and Haszprunar 1993).

Neomphaloidea

The relationships of members of this taxon are problematic. In some analyses, members of this group are paraphyletic stem taxa within the vetigastropods, while in other analyses they form a clade both within (Ponder & Lindberg 1997 and some molecular analyses – see above) and outside the vetigastropods (Ponder & Lindberg 1996; Tillier et al. 1994). We treat them as a single clade here, but we suspect that the taxon resides within the Vetigastropoda.

Members of the Neomphaloidea are known only from hydrothermal vents. The plesiomorphic state for members of this group appears to be a coiled shell with a relatively shallow pallial cavity, and although both left and right shell muscle are present there is only a single left

ctenidium, auricle, osphradium and hypobranchial gland (e.g., *Melanodrymia* – see Haszprunar 1989). From this initial morphology, we see three trends, two of them in parallel. Although the minute *Melanodrymia* and the larger *Pachydermia* (Israelsson 1998) lack skeletal rods, all other examined taxa in this group possess them.

The parallel trends involve patelliform morphologies. The peltospirids have become limpet-like, but retain a pair of shell muscles. The pallial cavity is substantially deepened, extending along almost the entire length of the right side of the animal (Fretter 1989). Some Neomphaloidea (e.g., *Neomphalus*) have also become limpet-like, but the expansion of the pallial cavity in this taxon is achieved by rotating the viscera counter-clockwise to deepen the cavity along the left side of the shell (Fretter et al. 1981). Although the final pallial cavity morphologies of *Neomphalus* and peltospirids appear nearly identical (except for the lack of the left shell muscle in *Neomphalus*), they are achieved by very different mechanisms – elongation versus rotation.

Patelliform Neomphaloidea probably do not share a most recent common ancestor with either peltospirids or *Melanodrymia*. Instead, the single muscle condition in neomphalids is found in a common ancestor probably shared with coiled taxa such as *Cyathermia* (Warén & Bouchet 1989) and *Pachydermia* (Israelsson 1998) (neither taxon included in our analysis). Both these taxa are relatively small, coiled gastropods found at hydrothermal vent sites. The pallial cavity is deepened and contains a single left ctenidium. The shell has a median sinus in *Cyathermia* (up to 6.6 mm in length) but not *Pachydermia* (up to 4.6 mm in length) (Warén & Bouchet 1989), and the gill is relatively smaller in *Pachydermia* and confined to the posterior half of the pallial cavity whereas it extends the length of the pallial cavity in *Cyathermia*. Warén & Bouchet (1989) suggest that *Cyathermia* is a filter-feeder based on the gill morphology shared with *Neomphalus*, but there is no additional evidence to support this supposition. No food groove is present, and gut contents contain thin membranes thought to originate from the worm tubes on which the snails live.

The convergent and extensive elongation of the pallial cavity and ctenidium in the limpet-like vent taxa may be a response to the reduced oxygen tension of the hydrothermal vent environments and the need for increased respiratory surfaces. A similar selective pressure would probably not be felt by small coiled taxa such as *Melanodrymia*, but in the larger *Cyathermia* a deepened pallial cavity (with sinus) and enlarged ctenidium are congruent with increased respiratory proficiency in this habitat. However, this relationship between size and the modification of respiratory surfaces in the vent fauna is obviously more complicated because *Pachydermia* is only slightly smaller than *Cyathermia* and has a relatively short gill, is more tightly coiled and has no shell in-

dentation. Moreover, that peltospirids, *Pachydermia* and probably *Cyathermia*, have increased pallial cavity depth and gill size independent of becoming filter-feeders suggests that the modifications made for low oxygen tensions served as an exaptation (Gould & Vrba 1982) for the evolution of filter-feeding in *Neomphalus*.

Neritopsina

Our analysis suggests that the common ancestor of the Neritopsina and apogastropods had a shallow pallial cavity with a pair of bipectinate ctenidia, auricles, hypobranchial glands and osphradia. While the number and position of the pallial structures appear to be plesiomorphic in the neritopsines, instances of pallial cavity elongation are few and are associated with the acquisition of limpet-like shapes. This is in strong contrast to the Vetigastropoda which exhibit numerous patterns of pallial cavity elongation. In addition, the neritopsines – unlike the vetigastropods, most neomphaloideans and caenogastropods – have ctenidial filaments that lack skeletal rods. Assuming homology of ctenidial skeletal rods within gastropods (Haszprunar 1988a; Ponder & Lindberg 1997), their absence in neritopsines is assumed to be secondary. No living neritopsine has two functional ctenidia, but at least some neritids possess a vestigial right gill (Fretter 1965). A recent account of the structure of a neritid gill is given by Eertman (1996). Only the left osphradium exists in living species.

Marine neritopsines show pallial cavity modifications similar to those seen in vetigastropod clades. For example, some deep sea neritopsines from hydrothermal vents with low oxygen tensions are patelliform and convergent with the vetigastropod Lepetodrilioidea and the neomphaloid Peltospiridae discussed above in having deepened pallial cavities with single ctenidia extending posteriorly along the course of the left shell muscle (Beck 1992). In the shallow-water, limpet-like taxa *Phenacolepas* and *Septaria*, the pallial cavity is deepened by the posterior movement of the entire visceral mass and shell muscles (Fretter 1984). The pallial organs in these taxa consist of a single ctenidium, osphradium, and auricle on the left side of the chamber (Fretter 1984). In contrast, the relatively unmodified *Nerita* and *Theodoxus* have a shallower pallial cavity and smaller ctenidium. The osphradium remains relatively small, but has distinct ciliated epithelia on either side of the nervous tissue (Haszprunar 1985a). There are no obvious auxiliary ventilating surfaces present.

Terrestrial neritopsines (e.g., Helicinidae) have modified the pallial cavity through the loss of the pallial organs into a lung (Bourne 1911; Baker 1925). Bourne argues that elongation of the cavity in these terrestrial neritopsines is accomplished by the rotation of the visceral mass, analogous to that seen in *Neomphalus* (see above).

Modifications to increase respiratory surfaces in the Neritidae are limited and include the evolution of the globose shell and elongation of the pallial cavity. The posterior movement of the shell muscles has elongated the pallial cavity (Fig. 5A). This elongation is tracked by the visceral nerve, which further suggests that, in this group, the ganglia are concentrated prior (either ontogenetically or phylogenetically) to the extension of the pallial cavity. The possible plesiomorphic condition is seen in the Cocculinoidea (see below) where the pallial cavity remains shallow and the visceral nerve is not elongate. Although somewhat elongate (Fig. 5A), the nerite pallial cavity remains relatively shallow compared to veti- and caenogastropods. This apparent failure to increase pallial cavity depth or ventilation has left the coiled nerites with their conservative globose shell morphology.

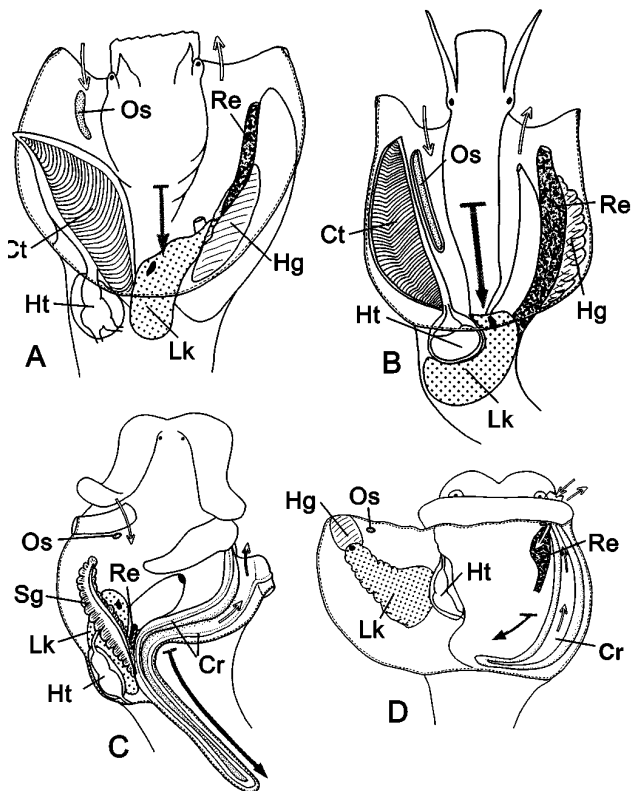


Fig. 5. Pallial cavities of neritopsine (A), caenogastropod (B), and heterobranch (C–D) molluscs. A. *Theodoxus fluviatilis* (Neritidae), redrawn from Fretter & Graham (1962: fig. 52); B. Generalized sorbeoconch caenogastropod; C. Generalized acteonid gastropod (Acteonidae - Opisthobranchia), based on Rudman (1972a). D. *Amphibola crenata* (Amphibolidae - Pulmonata), modified from Pilkington et al. (1984). Solid arrows with crossbar show the probable direction of pallial cavity elongation; crossbar indicates the likely approximate position of the original pallial cavity posterior wall in common ancestor. Open arrows show direction of water movement(s) through pallial cavity. Cr = ciliated ridges, Ct = ctenidium, Hg = hypobranchial gland, Ht = heart, Lk = left kidney, Os = osphradium, Re = rectum, Rk = right kidney, Sg = secondary gill.

Moreover, despite considerable habitat diversification in this group, there is not a single filter-feeding taxon; a feeding mode that taxes the respiratory/ventilator functions of the ctenidium. Thus, with the exception of the patelliform taxa, the Neritopsina appear to retain the plesiomorphic pallial cavity states, with a slight elongation of the cavity in the apparently derived Neritidae.

Although diverse in habitat and pallial cavity morphology (through elongation, rotation and development of a lung), in terrestrial taxa, Neritopsina are more constrained than Vetigastropoda. No special secondary respiratory surfaces (other than extended mantle surfaces as a result of some taxa adopting a limpet shape) or flow control mechanisms appear to have evolved, and instead the Neritopsina possess simple left to right flow within a relatively shallow pallial cavity outfitted with a ctenidium that still functions as both a respirator and ventilator.

The results of our (Ponder & Lindberg 1997) analysis support Yonge's (1947) independent derivation of the "Neritacea" from the plesiomorphic state of the pallial cavity, and falsify Morton & Yonge's (1964) contention of a single derivation via a lineage leading to the caenogastropod condition. The inclusion of this clade in a taxon "Archaeogastropoda" is unwarranted, as also argued by Morton & Yonge (1964) and Graham (1985).

Cocculinoidea

Although this taxon is shown as the sister of the neritopsines in our analysis (Ponder & Lindberg 1997), this is not supported by recent molecular work or morphological data (see above chapter 'Phylogenetic hypothesis'). The plesiomorphic conditions discussed above were probably also present in the Cocculinoidea, although substantially modified in living cocculinoideans, which may be secondarily limpet-like. As in other patelliform species, they have expanded the pallial cavity by making it continuous with the pallial groove. The single (left) bipectinate ctenidium has shifted to the right side of the cavity as in lepetelloideans (see above). They also possess a single left auricle, a single left osphradium, and the hypobranchial glands are lost (Haszprunar 1987a). The cocculinids show a much greater degree of reduction and loss of pallial cavity structures than the neritopsines, but the latter group shows more variation in the ways in which the elongation of the pallial cavity has occurred.

Apogastropoda

We discuss pallial cavity evolution in three clades of apogastropods (Fig. 3). These are: (1) the Heterobranchia ("Heterostropha" + Opisthobranchia + Pulmonata), (2) the Architaenioglossa, and (3) the Sorbeo-

concha (Ponder & Lindberg 1997). These last two clades are collectively the Caenogastropoda.

Pallial cavity character states for the assumed common ancestor of the heterobranchs and caenogastropods are difficult to determine, because of the parallel pallial cavity evolution taking place in the vetigastropods, neomphaloideans, and neritopsines (see above). Some heterobranchs possess a ctenidium-like gill which is thought to be secondary (e.g., Haszprunar 1985b, 1988a; Rath 1988; Ponder & Lindberg 1997). Schaefer (1996) has concluded that the heterobranch pigmented mantle organ or anal gland, a supposed synapomorphy of heterobranchs (Haszprunar 1985b, 1988a), is probably homologous with the hypobranchial gland. A single osphradium and hypobranchial gland are present in basal heterobranchs and in caenogastropods, and caenogastropods also have a single (left) ctenidium.

The depth of the pallial cavity in the apogastropod ancestor is equivocal. Under straight parsimony, and ignoring the aforementioned parallel evolutionary trends, it would be elongated, but other character states likely associated with the deepening of the cavity (renal organs, neck lobes, ciliated ridges, see below) suggest that the pallial cavity was deepened independently in the heterobranchs and in caenogastropods as in the clades discussed above.

Caenogastropoda. The plesiomorphic pallial cavity states in the Caenogastropoda are difficult to hypothesise because of the numerous autapomorphic features of the pallial cavities in the Heterobranchia.

Architaenioglossa. The cyclophorids, an entirely terrestrial group, provide little information as they have lost the ctenidium, osphradium (present in *Cyclophorus* – Kretschmar 1919), and modified the pallial cavity as a lung. They possess a single hypobranchial gland, and the single left auricle suggests that the assumed common ancestor shared with the freshwater ampullariids (and viviparids) had lost the right ctenidium, osphradium and hypobranchial gland. The Ampullariidae have a single left ctenidium (and associated left auricle) as well as a new structure serving as a lung. The lung resides on the left side of the pallial cavity whereas the left ctenidium has moved to the right side. The pallial cavity is extremely deep and a ciliated ridge, the epitaenia – first described by Cuvier (1817) – lies along the right floor of the pallial cavity and produces the exhalant current (Demian 1965; Andrews 1965) (Fig. 5B). This structure is typically considered autapomorphic in the ampullariids, but may be homologous with the food groove in viviparids.

The osphradium of the freshwater *Architaenioglossa* is proportionally larger than that of the vetigastropods and neritopsines (Ponder & Lindberg 1997). In am-

pullariids it is situated at the base of the siphon (Prashad 1925; Haszprunar 1985a), in viviparids it is located on the left side of the gill. Thus, in both taxa it is situated in the inhalant current of the pallial cavity.

An exhalant (right) neck lobe is present in the Viviparidae, but ampullariids have both left and right “neck” lobes, somewhat similar to those seen in the higher vetigastropod Trochidae, located on either side of the neck (Fig. 5B). The left lobe is capable of being rolled into a siphon-like tube and is used to fill the lung with air during aerial respiration. The right neck lobe directs the current exiting the pallial cavity away from the animal, is smaller and siphonate, comparable with the exhalant siphon in viviparids (Andrews 1965). The lobes are composed of mantle tissue and innervated by the pleural ganglia (Prashad 1925; Brown & Berthold 1990). In the Trochidae the tissue that forms the neck lobes is derived from the epipodium, and the lobes are innervated by the pedal ganglia (Randles 1904). Because neck lobes are an autapomorphy in the higher vetigastropods and innervated differently, the presence of neck lobes in these two groups is due to convergence rather than common ancestry (Ponder & Lindberg 1997).

Although highly autapomorphic the *Architaenioglossa* provide a preview of coming attractions in the Sorbeoconcha. Enlarged osphradia in close juxtaposition with the gill suggest the first signs of separation of ventilation and respiration within the pallial cavity while reinvention of neck lobes provides flow control out of the pallial cavity.

Sorbeoconcha. Neither Yonge (1947) nor Morton & Yonge (1964) directly address the question of the evolution of Sorbeoconcha. Morton (1988) considered the modification of pallial cavity structures in this group to be driven by the predatory nature of many of these taxa and their dependence on chemodetection in locating prey – particularly the enlargement of the osphradium.

In the Sorbeoconcha pallial water flow for respiration and ventilation is driven by the large, ciliated osphradium, as well as the ctenidium. There is also the formation of an anterior (inhalant) notch or siphon in the shell and the mantle in many taxa. Some taxa also have a posterior notch in the shell that is associated with the exhalant current (e.g., Turridae, Bursidae), and in some this is elaborated into a shelly tube (e.g., some Triphoridae and Bursidae).

In many basal caenogastropods there is a long, narrow osphradium that tracts along the gill (Fig. 5C), but this becomes shorter and broader in many littoriniforms and all neogastropods. In some, particularly carnivorous groups (Taylor & Miller 1989), including all the neogastropods, a marked increase in the ciliated (and sensory) osphradial surface is achieved by folding one

or more edges into folds or lamella. This modification is often associated with the development of a long, sometimes mobile inhalant siphon. In some minute neotaenioglossans (e.g., Caecidae, Rastodontidae), the ctenidium is reduced or absent and the ciliated ridge surrounding the sensory area of the osphradium generates the inhalant current (e.g., Ponder 1966).

The ctenidium is remarkably uniform in the great majority of Sorbeoconcha (see Eertman 1996 for a recent description of two taxa), with the main development being in the elongation of the filaments, particularly in filter-feeders (see below).

Neck lobes are usually absent in the Sorbeoconcha, although they are found in a few groups. However, pallial tentacles and neck lobes are found in some taxa that lack a siphon and are small in size. In some rissosoideans and cingulopsoideans, nearly all of which lack an anterior apertural notch, the neck lobe-like structures are sometimes found and, when present, are strongly ciliated and may assist in generating inhalant and exhalant water flow (Ponder 1966, 1988). Similarly, strongly ciliated pallial tentacles that also assist in generating exhalant water currents are found in many rissosoideans, and ciliation on cephalic tentacles may direct water towards the pallial cavity (Ponder 1988). Hypertrophied ciliated ridges lie on the proximal part of the left cephalic tentacle of some rissosoideans (e.g., Davis et al. 1982; Ponder & Clark 1988) and these may assist in increasing inhalant flow. Neck lobe-like structures that form short siphons are found in some filter-feeding taxa (e.g., *Turritella* (right side only) – Fretter & Graham 1962: fig. 57; *Bithynia* (right side only) – Fretter & Graham 1962: fig. 55; *Calyptrea* (both sides) – Werner 1953, Fretter & Graham 1962: fig. 63) where they are involved in food collection, suggesting that these structures may also have evolved (probably independently) to assist with the management of pallial waste rejection currents rather than ventilation.

Filter-feeding groups increase the ctenidial surface in different ways. All elongate the ctenidial filaments (e.g., Yonge 1938). Fretter (1972) has documented the limpet-like expansion of the calyptraeid shell, with the broad expansion of the pallial cavity and the gill. This converges on the body plan seen in the vent taxa Lepetodrioloidea and *Neomphalus*. In contrast, turritellids and siliquariids (Morton 1951b) markedly increase the length of their narrow pallial cavities. Most turritellids have a posterior apertural sinus, and some siliquariids even have slit/holes like vetigastropods (Morton 1951b). Other filter-feeders such as *Struthiolaria* (Morton 1951a) have more normally coiled shells but have a sinuate aperture, a broad, rather long, pallial cavity, and a large gill.

Two special modifications associated with filter-feeding include the development, in some groups, of an en-

dostyle (Orton 1913) and a food channel on the left and right side of the gill, respectively (Yonge 1938; Werner 1952, 1959; Fretter & Graham 1962). The homology of each of these two structures across the filter-feeding groups (Turritellidae and Siliquariidae [Cerithioidea], Struthiolariidae [Stromboidea], Vermetidae [Vermetoidea], and Calyptraeidae [Calyptraeidea]) is uncertain given their superficial documentation and the poorly resolved phylogenetic relationships within the Sorbeoconcha.

Heterobranchia. The ctenidium has been lost in all living heterobranchs (Haszprunar 1985b, 1988a; Ponder & Lindberg 1997), but many have a secondary gill (plicatidium, Morton 1972) that has sometimes been considered a ctenidial homologue (e.g., Gosliner 1981, 1991, 1994; Schmekel 1985). The gill of some heterostrophes (a paraphyletic grouping of lower heterobranchs), opisthobranchs and pulmonates somewhat resembles a ctenidium, but the detailed structure of these gills differs considerably (Porvaznik et al. 1979; Rath 1988). Despite this, Gosliner (1994) argues that the plicatidium and ctenidium are homologues because “associated blood vessels and positional relationships of the heart and kidney are identical in opisthobranchs and other monotocardian gastropods”. Even more surprisingly, Gosliner (1994) also favours the homology of the posterior gills of dorid nudibranchs with ctenidia because of their “proximity to the anus and general structure”. Hughes & Morgan (1973) have shown that secondary gills often have similar nervous, muscular and vascular connections in widely divergent groups of animals. In addition, the plicatidium lacks any of the synapomorphic characters of ctenidia (Haszprunar 1985b, 1988a; Ponder & Lindberg 1997). The osphradial ultrastructure of heterobranchs differs markedly from that of caenogastropods (Haszprunar 1985c).

The evolution of the heterobranch pallial cavity has been discussed by several workers including Franc (1968); Haszprunar (1985b, 1988a) and Morton (1988). Ponder & Lindberg (1997) suggest that the pallial cavity in this group is characterised by heterochrony and a reversion from sinistral (hypostrophic) coiling in the juvenile to dextral adult coiling. Heterostrophes, as well as many lower opisthobranchs and pulmonates, have opposed ciliated ridges within the pallial cavity. One ridge lies on the pallial roof, the other on the floor below, and they create an exhalant current. In some shelled opisthobranchs the ridges are extended posteriorly into a long, narrow caecum to increase their efficiency (e.g., Fretter & Graham 1954) (Fig. 5D). The homology of the ciliated ridges between the various groups of heterobranchs has been questioned by Ponder (1991), whereas Haszprunar (1985b, 1988a) has argued for their homology. Exhalant currents are also assisted in valvatoideans,

which have less well developed opposed ciliated ridges, by a long ciliated pallial tentacle analogous with those seen in rissooideans.

The Euthyneura (Opisthobranchia + Pulmonata) have undergone varying degrees of detorsion affecting the placement of the pallial cavity. Most shelled opisthobranchs have an elongate aperture typically resulting in the "bubble shell" form. The posterior placement of the exhalant part of the aperture is also paralleled in some caenogastropods (e.g., Cypraeidae, Olividae, Volutidae) and is essentially, as far as the position of the anus is concerned, a detorting mechanism. In most shelled opisthobranchs the posterior part of the mantle is extended as a siphon and in a few this is also mirrored in the shell (e.g., *Volutella*).

In the pulmonates the pallial cavity has moved back along the right side to open mid-laterally via a restricted pneumostome to the pallial cavity which has been modified as a lung (Ruthensteiner 1991, 1997). Brace (1977a,b, 1983) and Tillier (1989) (see also Emberton & Tillier 1995) give detailed descriptions of pallial characters in pulmonates. In opisthobranchs the pallial cavity has also moved along the right side in some taxa but, as it does so, it becomes smaller (e.g., Aplysiidae) or is effectively absent (e.g., Notaspidea). There is no pallial cavity in the nudibranchs that are secondarily bilaterally symmetrical, some even with a medially located anus (see Thompson 1976 for a detailed discussion of these structures in opisthobranchs).

Discussion

The plesiomorphic gastropod pallial complex

Outgroup analysis provides the following pallial cavity organization in the common ancestor of the gastropods: (1) a pair of ctenidia with semi-circular filaments; (2) filaments with (a) lateral ciliary bands (ventilation) and (b) frontal cilia along perimeter (cleansing); (3) each ctenidium with an adjacent auricle; (4) a pair of small osphradia; (5) openings from a pair of kidneys; and (6) a median anus (Table 1).

While this configuration is not unconventional, attributing much of the subsequent modification of the gastropod pallial cavity to a conflict between ventilation and respiratory function is. However, patterns of character transformations along our tree clearly argue for this antagonism. The existence of this functional dichotomy is well-documented in fishes (e.g., see Hughes & Morgan 1973), and alternative solutions to ctenidial duality are readily apparent in the molluscan outgroups. Of our four ctenidial-bearing outgroups, only two (*Bivalvia* and *Polyplacophora*) have ctenidia that function as both ventilators and respirators. However, while these functions

are clear in protobranch bivalves, in the eulamelli-branches the patterns are muddled because the gills are highly modified for filter-feeding (Ghiretti 1966). In the Cephalopoda the respiratory currents are produced by muscular contraction of the mantle or funnel (Ghiretti 1966), and in living Monoplacophora the respiratory currents appear to be generated by the ctenidia, while the pallial groove serves as the respiratory surface (Lindberg & Ponder 1996; Haszprunar & Schaefer 1997).

Previously, scenarios of pallial cavity evolution have been driven almost exclusively by envisioned sanitation problems that arose after torsion – the swinging forward of the pallial cavity (complete with excretory orifices) over the head (Garstang 1929). Such a model required little data, the image being worth a thousand words. However, this scenario is now being tested for its relevance in adults, both experimentally (Voltzow & Collin 1995) and phylogenetically (this paper), and many of the new data do not support the traditional scenario.

Voltzow & Collin (1995) examined natural and manipulated blockages of the exhalant aperture of the vetigastropod *Diodora aspera* and found no evidence of damage to the pallial cavity or associated organs, nor an accumulation of faeces in the course of their four-week study. Instead of a sanitation imperative, they concluded that the dorsal opening in the shell was necessary to induce passive flow to increase the rate of ventilation of the pallial cavity.

As noted above, the plesiomorphic shape for molluscan ctenidial filaments is approximately semicircular (Fig. 6A–C). Semicircular gill filaments are also found in the secondary gills of patellogastropods, neritopsines and valvatids, and are typical of fish gill filaments as well (Hughes & Morgon 1973). However, the presence of triangular gill filaments is a previously unrecognised synapomorphy of the Orthogastropoda (*Neritopsina* excepted) (Fig. 6F–G). This change in shape is enigmatic because triangular filaments have less surface area per unit dimension than semi-circular filaments.

For filaments with a 1:1 ratio between their base (diameter) and height (radius), the triangular filament has

Table 1. Plesiomorphic states for respiratory structures in the gastropod pallial cavity. Data from Yonge (1947) and Ponder & Lindberg (1997).

Character	C. M. Yonge	This study
Pallial cavity	deep	shallow
Ctenidia	paired	paired
Afferent & efferent membranes	present	absent
Skeletal rods	present	absent
Filament shape	triangular	semi-circular
Lateral & frontal cilia	present	present
Terminal cilia	absent	absent

only 64% of the surface area of a semi-circular one. Triangular filaments fare best in surface area comparisons when they are equilateral in shape (a common and possibly plesiomorphic shape in the orthogastropods), and as triangular filaments elongate their surface area quickly converges to a little more than 50% of the surface area of semi-oval filaments of the same dimensions. What then might select for a change that would seemingly reduce the amount of respiratory surface area?

A triangular filament, unlike a semi-circular one, forms an acute angle at its apex, and it is at this point that long, terminal cilia are positioned. Terminal cilia provide strong rejection currents for the removal of sediment (Yonge 1947; Morton 1951a) from individual filaments, and in some vetigastropods they provide an inter-

lock device between ctenidia (Yonge 1947). The importance of reducing fouling of the gill filaments appears to be reflected in apomorphic triangular filaments having three ciliary fields that handle fine particulate matter (abfrontal, frontal, and terminal cilia), whereas only one ciliary field, albeit a major one, provides ventilation (lateral cilia) (cf. Yonge 1947: fig. 4). This arrangement has been shown experimentally to work equally well throughout the orthogastropods (Gilinsky 1984) despite a huge range of environmental and life-style differences.

The history of gastropod evolution demonstrates that increases in body size, activity levels, exposure to aerial conditions, exposure to lower oxygen tensions, filter-feeding, etc., are typically coupled with an increase in size of the pallial cavity regardless of ancestry. Enlarg-

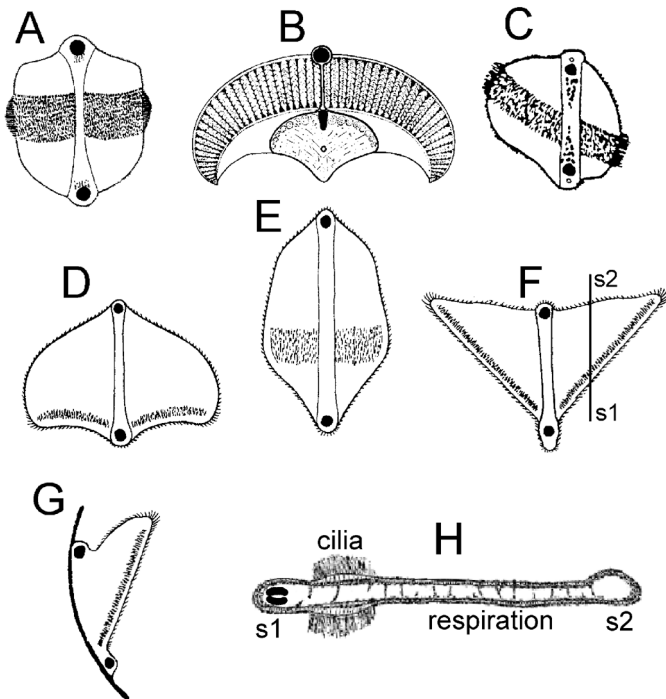


Fig. 6. Gill filament morphologies of molluscs. A–C Outgroups: A. Polyplacophora, modified from Salvini-Plawen (1985); B. Cephalopoda (*Nautilus*), redrawn from Naef (1921–23); C. Aplacophora, modified from Salvini-Plawen (1985). D–G Gastropod Ingroup, redrawn from Yonge (1947): D. Patellogastropoda; E. Neritopsina; F. Vetigastropoda; G. Caenogastropoda. H. Cross-section (F: s1–s2) through gastropod gill filament illustrating respiratory and ventilation surfaces, redrawn from Righi (1966).

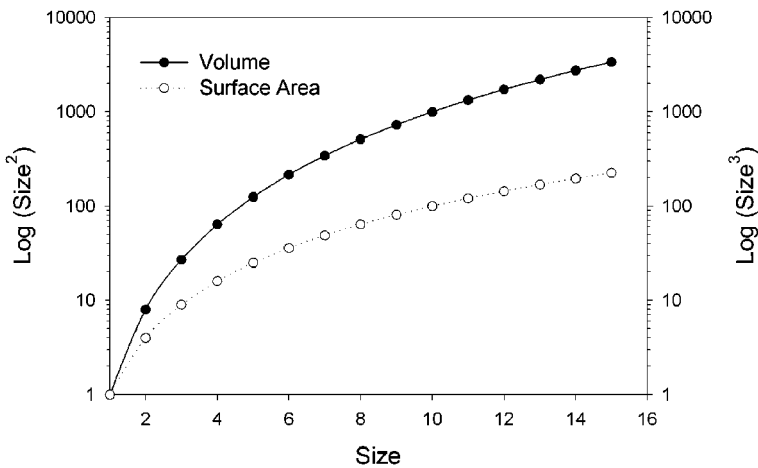


Fig. 7. Scatterplot of surface area and volumetric changes relative to standardized size.

ing the pallial cavity increases its volume (a cube function), while adding or enlarging filaments can only increase respiratory and ventilating surfaces as a square function (Fig. 7, see also Mill 1972). With increasing pallial cavity volume the conflict between the respiration and ventilation functions appears unavoidable, and the gastropod solution to this conflict appears to be moving all or part of the ventilation and/or respiratory functions somewhere else.

From these patterns and their distribution on the gastropod tree, we hypothesise that:

- a. The evolution of a cleansing and sediment rejection system of the ctenidia selected for filaments with angular apices with concentrations of rejection cilia.
- b. This in turn reduced surface area (respiratory and ventilation) of the filaments.
- c. The reduction of respiratory surface area necessitated that:
 - 1 more filaments be added to the ctenidium, and/or
 - 2 the enlargement of the filaments.
 - 3 More or bigger filaments required enlargement of the pallial cavity to accommodate the larger ctenidia.
 - 4 Concordant with the lengthening of the filaments was the appearance of skeletal support rods within the filaments that provide:
 - i. more efficient respiratory flow between the rigid gill filaments, and
 - ii. allowed more organised rejection cilia on the filaments and on the pallial roof and floor.

Previously such speculation in pallial cavity evolutionary scenarios involved stories of increasing efficiency as the evolutionary ladder was climbed (e.g., Yonge 1947, Morton & Yonge 1964, Yonge & Thompson 1976). Our scenario is not one of them. Instead we propose that the initial selection for more effective cleansing of the gills produced a cascade of events in the evolution of the pallial cavity that are actually the consequences of intertwined ventilation and respiration problems produced by that initial change and, as we will show below, sensory structures also reflect these changes.

Ventilation. We propose that changes in ventilation are reflected in controlling the flow through the pallial cavity, producing passive flow enhancement and providing additional ventilating surfaces. The patellogastropods and neritopsines retain the plesiomorphic condition with semicircular filaments and a shallow pallial cavity. Ventilation is driven solely by the lateral cilia of the ctenidial filaments (and/or secondary gill filaments when present) (Yonge 1962). While flow through the pallial cavity is similar between groups, water currents in the pallial groove vary from group to group (e.g., Yonge 1947, 1962), and inhalant or exhalant control is

not favoured. Similarly in Neritopsina, there are no significant modifications of either the inhalant or exhalant parts of the pallial cavity. However, in vetigastropods and heterobranchs, the primary control over pallial water currents is exhalant.

The deep pallial cavity, shell slit and venturi involved in exhalant control are the hallmarks of several vetigastropod groups, but others have lost these "hardware" solutions. Pallial cavity flow became left to right rather than lateral to anterior and dorsal in the groups in which the right pallial organs are reduced or lost. In the major group of vetigastropods in which this happened, the trochoideans, exhalant control of flow through the pallial cavity was again achieved with the development of a new structure on the right side of the head, a "neck" lobe apparently formed from a modified anterior epipodium. Furthermore, similar lobes on the left side of the neck could also provide inhalant control as well.

The basal caenogastropods (the architaenioglossan Ampullarioidea) also primarily have exhalant control and some Sorbeoconcha (rissooideans and cingulopsoides) have neck lobes, these being markedly ciliated in some (Ponder 1966). Many of these taxa have anterior and/or posterior pallial tentacles, never anterior tentacles alone. These tentacles are ciliated, the posterior tentacles with currents beating out of the pallial cavity suggesting a partial adoption of exhalant control. Similarly, notches or even short siphons or rarely tubes are often associated with the exhalant corner of the aperture in sorbeoconchs. Exhalant enhancement also appears present in *Struthiolaria* where a ciliated pallial tentacle provides an exhalant current (Morton 1951a) and is convergent with some rissooideans and valvatoideans. While all these modifications suggest some control over exhalant currents, the predominant control in the Sorbeoconcha appears to be inhalant (see also Morton 1958b, 1988).

In the Heterobranchia an anterior siphon is uniquely formed in the burrowing *Ringicula* (Fretter 1960) but not in other burrowing bullomorphs (Fretter & Graham 1954; Rudman 1972b). However, the shelled bullomorphs all have well-developed posterior "siphons" (Fretter & Graham 1954; Fretter 1960; Rudman 1972a,b) indicating that they, like the vetigastropods, concentrate on exhalant, not inhalant control.

Additional ventilating surfaces appear less varied than flow control devices. The osphradia, originally mistaken for secondary gills (see Williams 1856), have long been recognized for their sensory importance (see below), however they are also capable of providing and enhancing ventilation in the pallial cavity (Haszprunar 1988a). Several events on our tree suggest this as well. Osphradial size increases as one moves "up" the gastropod tree and into the caenogastropods, and this increase in size correlates well with increased occurrence of carnivorous taxa (Haszprunar 1985a; Taylor & Miller

Table 2. Morphological and functional characteristics of gastropod osphradium structures by taxon.

Taxon	Size	Position	Function
Patellogastropoda	osphradium small	on anterior pallial roof	Arnold (1957) showed that the osphradium had no role in responding to freshwater.
Vetigastropoda	osphradium small	located on efferent edges of free ends of ctenidia	Burke (1964) confounded olfactory responses between osphradium and bursicles.
Neritopsina	osphradium rather small	located on left anterior floor of pallial cavity in aquatic members	There are no studies on function.
Caenogastropoda		located on left side of pallial floor	
Architaenioglossa	osphradium small to medium-sized		Wölper (1950): <i>Viviparus</i> (chemoreception, including response to members of opposite sex).
Sorbeoconcha			
Littorinimorpha	osphradium medium to large, sometimes mono- or bipectinate		Surprisingly, there do not appear to be any studies on osphradial function in any member of the Littorinimorpha.
Neogastropoda	osphradium large, bipectinate		Copeland (1918): <i>Nassarius</i> and <i>Busycon</i> (chemoreception). Kohn (1961): <i>Busycon</i> and <i>Pleuroploca</i> (chemoreception; but data not conclusive). Bailey & Benjamin (1968) and Bailey & Laverack (1963, 1966): <i>Buccinum</i> (chemoreception, response to food extracts but not to mechanical stimuli or changes in pH or osmolarity). Brown & Noble (1960): <i>Bulla</i> (chemoreception in food detection). Ikuta & Nakahara (1986): <i>Volutharpa</i> (uptake of manganese). Bryan et al. (1993): <i>Nucella</i> (uptake of tributyltin).
Heterobranchia		on pallial floor when present	
Heterostropha	osphradium moderate size in Valvatoidea and Architectonicoidea, small or absent in other groups		There are no studies on function.
Opisthobranchia	small when present, lost in detorted taxa		Downey & Jahan-Parvar (1972) and Jahan-Parvar et al. (1969): <i>Aplysia</i> (chemoreception). There have also been several studies on the osmodetection and regulation role of the osphradium in <i>Aplysia</i> (e.g., Stinnacre & Tauc 1966, 1969; Kupfermann & Weiss 1976; Skinner & Peretz 1989); but not found in <i>Aplysia brasiliiana</i> (Scemes et al. 1991). Jahan-Parvar (1976) has shown that the osphradium plays a role in detecting the aggregation pheromone from the egg mass in <i>Aplysia</i> , and how neurosecretion is activated by osphradial stimulation following stimulation by dilute extracts of seaweed, oyster and shrimp (Jahan-Parvar et al. 1969). However, Frings & Frings (1965) and Preston & Lee (1973) found no evidence for behavioural change following contact of food with the osphradium.
Pulmonata		near inner edge of pulmonary opening when present	
Archaeopulmonata	osphradium small		Kamardin (1988): <i>Siphonaria</i> (possible role of osphradium in homing).

Table 2. (Continued).

Taxon	Size	Position	Function
Basommatophora	small ciliated channel or pit		Kamardin (1976): <i>Lymnaea</i> (response to oxygen concentration). Sokolov & Kamardin (1977): <i>Lymnaea</i> (response to oxygen and inulin concentration). Townsend (1973a, b): <i>Biomphalaria</i> (osphradium NOT involved in chemoreception and food location; cf. earlier results of Michelson 1960). Nezlin et al. (1994): <i>Lymnaea</i> (distribution of neuroactive substances). Nezlin (1997): <i>Lymnaea</i> (osphradium involved in the control of egg-laying). Wedemeyr & Schild (1995): <i>Lymnaea</i> (chemoreception, olfaction, and detection of CO ₂ levels).
Stylommatophora	osphradium absent		

1989; and below). As well as a general size increase we also see: (1) the elongation of the osphradium (beginning in the Neritopsina), (2) its repositioning in juxtaposition with the left side of the ctenidium (beginning in the Caenogastropoda), and (3) the development of ciliated filaments (some Sorbeoconcha). All may suggest additional morphological changes that may have contributed to enhanced ventilation of the pallial cavity.

The role of the osphradium in ventilation in sorbeoconchs is most convincingly demonstrated in some small caenogastropods where an enlarged osphradium is the main pallial cavity ventilator when the ctenidium is absent or reduced (Götze 1938; Ponder 1966). There is also the seemingly problematic osphradium of *Crepidula fornicata*, that lies across the inhalant aperture and has well-developed right leaflets whereas the left leaflets are presumed lost. This species is a sedentary filter-feeder with its potential mates stacked on its back (Fretter & Graham 1962). The traditional roles for the osphradium appear redundant here, and we suggest that the cilia on the right leaflets enhance flow into the pallial cavity, whereas the left leaflets have atrophied. Taylor & Miller (1989) also illustrate enlarged right leaflets for *Polinices tumidus* and *Nassarius reticulatus*. Clearly, studies of the strength and direction(s) of water movement by the osphradia in the caenogastropods are needed.

Inhalant flow control is the hallmark of the Sorbeoconcha. This switch places the narrowed inhalant water current where it can be sampled by the osphradium that lies in a position over which the incoming stream flows. The suggestion that an early advantage of torsion was bringing the pallial cavity to the anterior end of the animal, enabling the animal to “sniff” the incoming water currents (Morton 1958a), may well be justified at least in part, although Morton’s use of an exemplar based on a sorbeoconch caenogastropod is inappropriate because the first sorbeoconchs appeared in the fossil record about 100 million years after the first torped gastropods. However, the anterior placement of the osphradium may

well provide some chemosensory advantages in post-larval individuals, even in patellogastropods.

In heterobranchs, the ctenidium is lost and opposed ciliated ridges on the pallial roof and floor have taken over the ventilation role. In those taxa with a deep pallial cavity, these ridges are extended into a long pallial caecum (Fig. 5D). However, the inherent inefficiency of the heterobranch pallial cavity has resulted, presumably with increasing size, in several trends including reduction of the pallial cavity, largely through detorsion and the development of accessory respiratory structures independent of pallial water currents (external gills, pulmonary cavity). Of the “heterostrophe” groups, the architectonicids are unusual in being of large size. This group differs from other heterostrophes (except omalogyrids) in having the opposed ciliated ridges located on the left side, not the right as in other heterobranchs. This shift in position of the opposed ridges (questionable homology with those in other heterobranchs, Ponder 1991; Ponder & Lindberg 1997) might be related to its predatory habits and the advantage of an inhalant water flow to assist in prey (coelenterates) detection. Moreover, the rather large osphradium in this group might also be correlated with this habit. However, this apparently convenient scenario is unacceptable because of their similar position in the small algae-sucking omalogyrids, and observations on the architectonicid *Philippea* by one of us (W.F.P.) show that the opposed ridges have an exhalant flow as in other heterobranchs.

Respiration. Like ventilation surfaces discussed above, respiratory changes appear to be intertwined with filter-feeding, aerial respiration, and low oxygen tensions.

Building new respiratory surfaces is apparently not as constrained as producing new ventilators. The entire epidermis of the gastropod is typically capable of cutaneous respiration (Ghiretti 1966), but three regions are of particular importance because of their intimate association

with the ctenidia and inhalant and exhalant water currents: (1) the roof of the pallial cavity, (2) the pallial groove, and (3) the epidermis of the head and foot.

Enlarging the pallial cavity for larger ctenidia also increases the surface area available for pallial respiration. However, the greatest increase in pallial respiratory space comes from becoming patelliform, or from shell reduction or loss. In patelliform taxa this additional mantle space can contain secondary gills or just provide a continuity of space with the pallial cavity. The plethora of patelliform taxa (regardless of ancestry) at hydrothermal vents most likely results from ancestral response to low oxygen tension and the homoplastic response of enlarging ctenidia for filter-feeding as well as secondary respiratory surfaces.

Increasing gill surface area for respiration also creates larger surfaces for potential filter-feeding. We agree with Yonge (1938, 1947) that the sediment cleansing currents of the ctenidial filaments are an exaptation for filter-feeding in gastropods and, furthermore, there is little conflict between ventilation and filter-feeding. Increase in ciliation to augment sorting and the movement of mucus involved in food capture are commensurate with ventilation. However, larger and denser cilia and mucous-bound particulate matter on the surface of the gill presumably reduce its respiratory potential, and the ventilation/respiratory conflict model would predict the addition of respiratory surfaces in filter-feeding taxa.

Filter-feeding trochoidean vetigastropods and the caenogastropod turrillids have large, highly branched structures across the inhalant aperture of the pallial cavity. These branched tentacles have been previously identified as filters or sieves (e.g., Hickman 1985a,b), but in *Turritella* these branched tentacles are richly supplied with blood and clearly have a respiratory role (W.F.P., pers. obs.). The same is probably true in the filter-feeding vetigastropods. In other filter-feeding caenogastropods a patelliform shell has evolved (*Capulus*, *Crepidula*, *Calyptraea*) providing a substantial increase in mantle respiratory surface; gill filaments are highly modified for filter-feeding and (as also in turrillids) probably have virtually no respiratory function (Orton 1915; Yonge 1947). The single vermetid species that is an obligate ctenidial filter-feeder, *Dendropoma maxima*, has no obvious additional respiratory structures (Morton 1965). However, this species has the largest and best-developed ctenidium, the largest shell and largest length/width ratio of shell (and animal) of any vermetid gastropod, and lives fully exposed to surf on the outermost barrier reefs (Yonge 1932; Morton 1965). Given these characteristics, additional respiratory sites may be unnecessary. *Struthiolaria*, another filter-feeder, is thought to use its mantle margin as a respiratory surface given the specialisation of the gill as a ventilator and feeding structure (Morton 1951a).

In addition to using the vascularised roof of the pallial cavity, respiratory effectiveness is also increased by the incorporation of the kidneys (with rich venous blood supplies) into the mantle skirt (see above). This modification is typically found in taxa in which the pallial cavity has been elongated posteriorly.

Attaining large size in opisthobranchs is often associated with the reduction and eventual loss of the pallial cavity. External respiratory surfaces have replaced internal ones, contributing to the internalization and loss of the shell early in opisthobranch evolution. Pulmonates have developed a lung but even this is much reduced in many species adopting a slug habit (e.g., Tillier 1989).

Sensory Structures. The cephalic and pallial tentacles, the osphradium, and various areas of the mouth, mantle and foot have all been shown to have a chemosensory function in at least some gastropods (Croll 1983). Such functions are vital, not only for food detection but for the detection of mates or the presence of eggs or sperm (in the case of free spawning taxa), the recognition of predators and, in some taxa, trail-following and homing behaviour. Crisp (1981) pointed out the amazing complement of mantle-related sense organs in vetigastropods. This array of non-pallial cavity sense organs may be associated with the general lack of inhalant control of pallial water flow. However, there is one set of vetigastropod sense organs, the bursicles, that have been shown to detect predatory starfishes (Szal 1971) by utilizing the diffuse inhalant water stream passing through the ctenidial filaments. The abundance of mantle-related sensory structures in the basal gastropod clades is particularly obvious when comparing vetigastropods with the sorbeoconch caenogastropods.

Sorbeoconch gastropods established inhalant control prior to the hypertrophy of the osphradium. An anterior siphon, sometimes long and mobile, is developed in most groups of sorbeoconchs, and may further enhance the detection of stimuli (location of predators, food and mates), not only at a distance but to determine the direction from which the stimuli are emanating (e.g., Henschel 1932; Carr 1967). Such changes to the sensory equipment of caenogastropods may have enabled them to utilize a much wider spectrum of resources than vetigastropods, notably by several lineages independently becoming active carnivores. In contrast, vetigastropods have had to rely to a much greater extent on direct contact with the body to assess the direction of stimuli (Burke 1964; Yarnall 1964).

In most aquatic gastropods the osphradium has generally been implicated as an important organ in chemoreception (e.g., Fretter & Graham 1962). Although there have been a number of seminal studies on the structure of the osphradium (e.g., Spengel 1881; Bernard 1887, 1890; Pelseneer 1893; Stork 1935; Storch 1972; Crisp

1973; Sokolov & Kamardin 1977; Maeda 1983; Haszprunar 1985a,b, 1986; Taylor & Miller 1989), remarkably few studies demonstrate osphradial function (see also reviews by Demal 1955; Kohn 1961; Charles 1966; Croll 1983; Dorsett 1986; Haszprunar 1987a; Nezhlin 1997).

Hulbert & Yonge (1937) proposed a mechanoreceptor function in which the osphradium was utilized primarily to detect sediment in inhalant water (see also Yonge 1947, Charles 1966). However, no evidence has been produced to date to support this function (Voltzow 1994). Studies that have provided experimental evidence of function are listed in Table 1 to emphasize the dearth of information for some of the major clades.

In summary, the osphradium has been demonstrated to be involved in chemosensory activity in several clades (Table 1). More specifically, it is involved in food detection in caenogastropods (including architae-nioglossans) and at least some aquatic heterobranchs, and in mate detection at least in *Viviparus* (Architae-nioglossa). However, we have no information regarding some major taxa, including the patellogastropods, vetigastropods and neritopsines, most work having been done on a very small number of highly specialised species. Clearly, more experimental work remains to be done before definitive statements can be made regarding any clade-specific traits in osphradial function.

In the outgroups, patellogastropods and vetigastropods, the osphradia are small, typically paired, and situated near the base of the ctenidia (Fig 4A-D). In the neritopsines the osphradium, like that of "primitive" heterobranchs (see below), is moderately well developed (Fig. 5A), and they show no obvious modification for either inhalant or exhalant control. Ampullarioideans have "neck" lobes and lack an inhalant notch in the aperture, having only exhalant control. In the caenogastropods the osphradium may have become hypertrophied (Fig. 5B) concordant with the need for increased sensory facility given the lack of other sense organs other than the eyes and cephalic tentacles (e.g., Crisp 1971). In heterostrophes, the osphradium reaches a reasonable size in orbitestellids (Ponder 1990), and architectonicids and mathildids (Haszprunar 1985d,e) both of which have deep, narrow pallial cavities. In some other heterostrophes (e.g., Omalogyridae, Rissoellidae – Fretter 1948), the osphradium is lost.

The osphradium may have been reduced in parallel in the two major heterobranch clades (opisthobranchs and pulmonates) (Fig. 5C & D) due to the marked decrease in importance of the pallial cavity in respiration in the opisthobranchs and the substitution of new external sensory organs such as the oral tentacles and Hancock's organ (Thompson 1976; Croll 1983; Dorsett 1986). In aquatic pulmonates, the restriction of the pulmonary opening to the small pneumostome resulted in the mor-

phological modification of the osphradium, its late ontogenetic development, and placement on the right.

Lateral ciliated ridges border the caenogastropod osphradium, and it is possible that caenogastropods may have initially developed a large osphradium to assist with producing a stronger inhalant current. Small-sized caenogastropod taxa also have large osphradia, but not all have anterior siphons and notches – for example members of the Littorinoidea, Cingulopsoidea and Rissoidea. Littorinoideans live mainly in the intertidal where desiccation is a problem, and while an anterior notch was possibly present in the ancestor(s) of these groups, no extant member has a true anterior siphon. Some larger muricids and other neogastropods that have colonised the intertidal also show notch reduction.

Attaining large size in opisthobranchs may be associated with the reduction and eventual loss of the mantle cavity in this group where external respiratory surfaces have replaced internal ones. Pulmonates have developed a relatively efficient lung derived from the pallial cavity (Ruthensteiner 1997), but even this is further reduced in many species adopting a slug habit.

General conclusions

Our evolutionary scenario for the pallial cavity and associated organs in the Gastropoda arose from character distributions seen in our phylogenetic hypotheses of gastropod relationships (Ponder & Lindberg 1996, 1997). The distribution of gill states mapped onto our cladogram (Fig. 3) is similar to Yonge's (1947) "course of evolution" (Fig. 1), while differing substantially from the later Yonge (1960) narrative and the Morton and Yonge (1964) evolutionary tree (Fig. 2). However, the actual observational data on which all are based have remained relatively unchanged with the exception of the discovery and addition of the hydrothermal vent taxa (1981-present). Our perspective has undoubtedly benefited from the countless new papers with ancillary data, many of which have been used to test these hypotheses, and we also occupy a retrospective position from which to gauge Yonge's and Morton's work. But most importantly, our scenario is not primarily functionally driven (Yonge 1947) nor based on the common misconception that function (or structure) + classification = evolution (Morton & Young 1964).

C. M. Yonge's original scenario was close to the phylogenetic hypothesis presented here only in its suggestion that the single-gill condition had evolved several times. Our plesiomorphic states differ (Table 2), as does causality. Moreover, when Yonge's original scenario was forced into agreement with Thiele's classification (Morton & Yonge 1964), the four separate derivations of the single gill were reduced to at most two events. This

classic Procrustean exercise of fitting data to a classification scheme is similar to “telling the tree” (O’Hara 1988), but classification rather than phylogeny is used as the framework.

Yonge’s (1947) and Morton & Yonge’s (1964) papers on the evolution of the pallial cavity reveal that these authors subscribed to the idea that the evolutionary history of a taxon can be revealed by understanding the function of select organ systems – in this case the pallial cavity (see also Trueman & Clarke 1988; Voltzow 1994). We could not disagree more (see Ponder & Lindberg 1996: 151). To the often quoted Vogel & Wainwright (1969) statement that “structure without function is a corpse; function sans structure is a ghost” we would add the caveat that evolutionary interpretation of structure and function without phylogeny is a grave mistake. And contrary to Purchon’s (1968) quote at the beginning of this paper we argue that classification is not an exercise in obscure terminology that hinders studies of functional morphology and comparative physiology. In modern comparative biology classification must correspond to a robust model of relationships, and these classifications are prerequisite for the construction of scenarios for the evolution of structure and function.

For example, the correlation of bilateral sensory structures with patterns of ventilation in the vetigastropods was not previously recognized because neither classification nor function could place these characters in juxtaposition. While it is well known that inhalant control (anterior siphon) is associated with osphradial morphologies and cell types (Haszprunar 1985a; Ponder & Lindberg 1997), the association of bilateral epipodial and ctenidial sensory structures with non-directional exhalant control could not be fully recognized in the vetigastropods while the paraphyletic archaeogastropods remained intact.

Moreover, not all models or hypotheses of relationships are equal. By heavily weighting pallial cavity characters in his general phylogenetic scheme, Thiele assumed that rampant parallelism in other characters was not a problem, and he basically produced the equivalent of a parsimony tree based on that system. However, analyses with equal weighting of all characters (e.g., Ponder & Lindberg 1997) say that the general pattern among pallial cavity features reflects something other than phylogeny, and clearly demonstrate how considering all available characters will generally overcome incorrect assumptions about single character systems.

We have attempted to use the somewhat scant available ancillary data that have the potential to falsify our scenario. For example, is the coopting of ctenidia for filter-feeding reflected in compensations for respiration? How does the deepening of the pallial cavity affect ventilation? In most cases the scenario is supported, but

there is also a dearth of important data, including histological studies of, and oxygen measurements from, suspected secondary respiratory surfaces such as neck lobes, measurements of water velocity and paths through osphradia as well as their sensory function, etc. As pointed out before (Ponder & Lindberg 1996), there remain substantial (and often surprising) gaps in our knowledge.

Additional tests should also come from the fossil record. Fossil taxa need to be included in the analysis of gastropod phylogeny, and while most “soft-part” morphology will not be recovered, data such as the depth of the pallial cavity, ventilation patterns as suggested by shell emarginations and holes, muscle scar patterns, overall size, etc. can easily be obtained and mapped. We look forward to all such tests.

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