Evolutionary relationships of euthyneuran gastropods (Mollusca): a cladistic re-evaluation of morphological characters

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Morphological characters of the Euthyneura available from the literature were re-evaluated in terms of terminology and primary homology. A total of 77 characters and 75 taxa were retained in a data matrix. Several assumptions on character weights and types were tested. In the cladistic analyses, it appeared that the data matrix was highly homoplastic, and only robust nodes (those which were little modified by variations in weight and coding of characters) were retained in a concensus tree. The evolutionary histories of all characters and monophylies of higher euthyneuran taxa were discussed. The following interrelationships of the taxa were obtained in a consensus tree: the clade Heterobranchia includes paraphyletic allogastropod taxa which emerge basally, and the clade Euthyneura. The latter includes the clade Pulmonata and at least 10 opisthobranch clades of unresolved relationship (Thecosomata, Gymnosomata, Acochlidioidea, Pyramidelloidea, Runcinoidea, Cephalaspidea, Sacoglossa, Umbraculoidea, Pleurobranchoidea, Nudibranchia). The Pulmonata include basommatophoran paraphyletic taxa and the clade Geophila (Onchidiidae, Soleolifera, Stylommatophora). The position of the Sacoglossa and the monophyly of the Notaspidea are also discussed. © 2002 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2002, **135**, 403–470.

ADDITIONAL KEYWORDS: character sampling – character variation – Heterobranchia – Opisthobranchia – phylogeny – Pulmonata

INTRODUCTION

EUTHYNEURA IN THE CLASSIFICATION AND PHYLOGENY OF GASTROPODS

When establishing the Gastropoda, Cuvier (1795) grouped them on the basis of their locomotory organs. He did not include the Pteropoda (which he established in 1804) in the Gastropoda but included chitons (called Polyplaxyphora by Blainville in 1816 and Polyplacophora by Gray in 1821). Agassiz (1866), however, included Pteropoda and von Ihering (1876) excluded Polyplacophora from Gastropoda. Numerous other systems were designed to classify gastropod taxa (see Bronn, 1862) during the first half of the nine-

teenth century. Milne-Edwards (1846) introduced a most important innovation by dividing the Gastropoda into three subtaxa: Prosobranchia, Opisthobranchia and Cuvier's (1817) Pulmonata. During the second half of the nineteenth century, many new names were proposed for the group composed by Milne-Edwards' Opisthobranchia and Pulmonata. Mörch (1865), in an often overlooked paper, used hermaphroditism as a diagnostic character for the group constituted by the Opisthobranchia, Pulmonata and Pteropoda under the name Androgyna. von Ihering (1876) renamed the same group Ichnopoda and merged it with the Pteropoda into the the Platymalakia, which he believed to be not closely related to his Cochlidae (= Prosobranchia). Nevertheless, using the anatomical work of Lacaze-Duthiers (1870), von Ihering (1876) asserted that torsion of the nervous system of gastropods was an important character and consequently divided the Cochlidae (= Prosobranchia) into

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Orthoneura (prosobranchs with a non-torted visceral commissure), Chiastoneura (prosobranchs with a torted visceral commissure) and Heteropoda (pelagic prosobranchs). Spengel (1881), using torsion of the nervous system as a key character, created the Euthyneura (= Androgyna), which he contrasted to the Streptoneura (= Prosobranchia), because he interpreted orthoneury as a hidden chiastoneury. Finally, Lacaze-Duthiers (1888) introduced the name Strepsineura as a synonym of Streptoneura, and Astrepsineura as a synonym of Euthyneura. The last years of the nineteenth century were crucial. In 1892, Pelseneer proposed the Euthyneura as the valid taxon grouping the Opisthobranchia, Pulmonata and Pteropoda, but did not mention Mörch's work. Using previous ideas (Spengel, 1881; Lacaze-Duthiers, 1888), he proposed a phylogram according to which the Streptoneura and the Euthyneura were two independent and basally separated lines of gastropods. Pelseneer (1894), using developmental studies, proposed streptoneury as the primitive condition from which euthyneury originated. Finally, Plate (1895) proposed the first phylogram of gastropods with the Euthyneura having a line of descent originating in the Streptoneura, in contrast to the conclusions of von Ihering (1891) and Haller (1894), who did not accept the value of embryological data.

Even though during the twentieth century a lot of excellent anatomical, histological and developmental studies accumulated for the Opisthobranchia and Pulmonata, and many of their characters were frequently discussed, phylogenetic studies on these two groups remained largely unconnected (Guiart, 1901; Pelseneer, 1901; Fretter, 1939; Hoffmann, 1939; Boettger, 1954; Johansson, 1954; Duncan, 1960a, b; Ghiselin, 1966; Minichev, 1967; Brace, 1977a, 1983; Hubendick, 1978; Solem, 1978; Gosliner, 1981a, 1991, 1994; Gosliner & Ghiselin, 1984; Robertson, 1985; Haszprunar & Huber, 1990; Huber, 1993). Although streptoneuran phylogeny has recently been re-evaluated (Haszprunar, 1988; Ponder & Lindberg, 1997) and many phylogenetic studies of subtaxa of Opisthobranchia and Pulmonata have been published (Willan, 1987; Tillier, 1989; Nordsieck, 1993; Jensen, 1996a, b; Mikkelsen, 1996; Hausdorf, 1998), only one cladistic analysis of the Euthyneura is available (Salvini-Plawen & Steiner, 1996; see Fig. 1).

REASSESSMENT OF THE RELATIONSHIPS OF THE EUTHYNEURA

Several potential synapomorphies have been proposed for the Euthyneura by Haszprunar (1988) and Salvini-Plawen & Steiner (1996). According to Robertson (1985), however, these characters should be discussed in detail before being coded in a data matrix. The
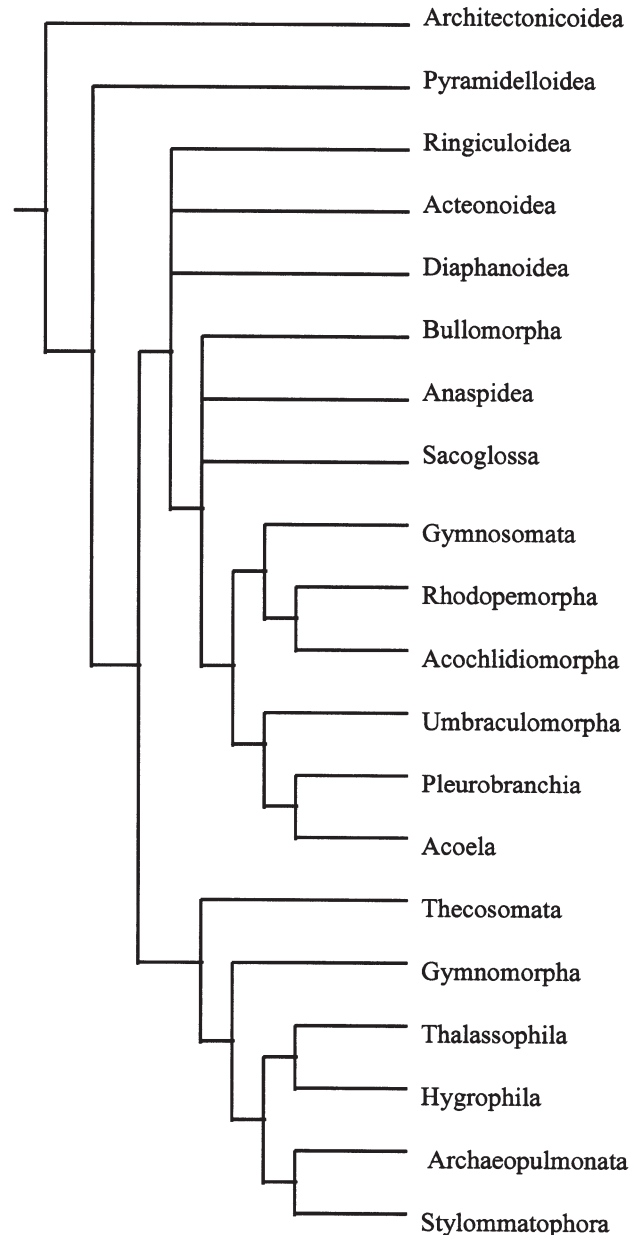

Figure 1. Phylogeny of Euthyneura proposed by Salvini-Plawen & Steiner (1996) according to anatomical characters.

narrow scope of the euthyneuran taxonomic sample (only four families) used by Ponder & Lindberg (1997) prevented them from re-evaluating these characters and taxa. A new coding of characters was thus necessary to evaluate the monophyly and synapomorphies of the Euthyneura and of their subtaxa. In accordance with previous work on gastropods (Haszprunar, 1988; Salvini-Plawen & Steiner, 1996; Ponder & Lindberg, 1997), Apogastropoda, and particularly Heterobranchia, have been taken into consideration in

the present work to: (1) test the monophyly of the Euthyneura and identify their sister group, and (2) propose an evolutionary history for every character. One objective has been to question and try to resolve monophylies and the phylogenetic positions of the main euthyneuran taxa. Surprisingly, the definition, monophyly, and relationships of the Pulmonata and Opisthobranchia have almost never been questioned, even though their similarities have often been discussed (Fretter, 1939; Johansson, 1954; Duncan, 1960a, b; Gosliner, 1981a; Robertson, 1985; Nordsieck, 1993). Taxa such as Tectibranchia, Cephalaspidea, Pteropoda, Notaspidea and Basommatophora equally require further analysis.

MATERIALS AND METHODS

INTERRELATIONSHIPS OF TAXONOMIC SAMPLING AND CHARACTER SAMPLING

In a preliminary step, taxa of familial or superfamilial rank were sampled, and a list of morphological characters was established. These primary taxa were subsequently divided into subtaxa in order to manage and control the polymorphism of numerous characters, and the use of generalization (Dayrat & Tillier, 2000). Because all characters were not described in all genera belonging to taxa of higher rank, it was necessary to use the exact domain of definition of the data set to appreciate their variability in heterobranch taxa. However, it was impossible to include all the euthyneuran taxa of generic rank in the data matrix, because of the lack of data and computing limitations. Only generic taxa for which morphological data were available were retained (see Appendices 1 and 2).

Initially, analysis of literature and observations led to a matrix containing 100 characters and 120 species belonging to as many genera. This matrix was too large to be analysed, and further reduction was achieved by removal of characters and taxa exhibiting only minor variation. This allowed reduction of the matrix to 75 taxa and 77 characters.

The generalizations to suprageneric taxa leading to proposals of phylogenetic relationships for suprageneric taxa was applied *a posteriori*.

CHARACTERS

Most hypotheses on phylogeny of Euthyneura, and of organisms in general, rely on assumptions of homology and homoplasy of characters. In addition to a discussion of their primary homology, made necessary by the wealth of data and terminology which accumulated over two centuries, we estimated that the only way to avoid bias was to accept as few assumptions as possible on the reliability of characters as phylogenetic markers. In order to fulfil this condition, a primary list of characters available from the literature was established (Pelseneer, 1894, 1901; Van Mol, 1967; Willan, 1987; Haszprunar, 1988; Tillier, 1989; Gosliner, 1994; Jensen, 1996a, b; Mikkelsen, 1996; Salvini-Plawen & Steiner, 1996; Ponder & Lindberg, 1997), attempting to avoid any preconceived ideas about their relative phylogenetic importance. In the course of the coding process, many of these characters were suppressed from the primary data matrix for the following reasons: (1) unsufficient description; (2) no variation known or observed; (3) variation continuous and character states consequently too variable and numerous to be coded as discrete forms; (4) highly problematic character homology; (5) supposed analogy.

The 77 remaining characters remained in our data set (see below) are listed in Appendices 1 and 2. A problem resulting from our decision not to make *a priori* choices among characters was that many had a low Consistency Index (CI).

CODING PRINCIPLES

In addition to the difficulty of defining homologous characters, the wealth of malacological terminology is a source of confusion in phylogenetic analysis, and was revised before coding. Numerous terms are used to homologous organs, these often being different in pulmonates and opisthobranchs. This problem has only been occasionally discussed for the Euthyneura (Johansson, 1954; Robertson, 1985; Huber, 1993).

As far as possible we tried to avoid generalization: if data were not available for a character for a particular taxon, they were not coded *a priori* based on their occurrence in another taxon, even though the latter seemed to be closely related to the first one. We coded only what was previously described (sometimes checked by us) and when a structure was missing in a taxon, we did not code it as present on the basis of its presupposed secondary loss, but as an absence. Such losses should be proposed *a posteriori*, after analysis.

When two or more codings were possible for a single character state because of ambiguity of observations (as in contradictory or confuse observations, variation between two or an intermediate condition character states, etc.), we coded them as alternative states in the data matrix (e.g. 0/1 or 0/1/2, etc.). Inapplicable characters were coded by question marks (see Appendix 2).

We decided to code character complexes in single characters. In the analysis VIII (Table 1), we tried to test the influence of a different coding in which character complexes were broken up into two or three characters, in order to distinguish things such as 'number', 'position' and 'shape' of a structure. In this supplementary analysis, the following characters were

Table 1. List of analyses

	I	II	III	IV	V	VI	VII	VIII
Procedure option completed or aborted	Heuristic general completed	Heuristic general aborted	Heuristic general aborted	Heuristic general aborted	Heuristic general aborted	Heuristic general aborted	Heuristic general aborted	Heuristic general aborted
Number of characters	77	77	77	77	77	77	77	87
Character weight (Char: weight)	no	(33:3)	(33:4)	(1:4)	(9, 19:33:4)	(17:0-1-2)	no	no
Character types	no	no	no	no	no	(17:0-1-2-)	no	no
State coded for character (23)	0/1	0/1	0/1	0/1	0/1	0/1	1	0/1
Number of trees retained	3446	10 000	10 000	10 000	10 000	10 000	10 000	10 000
Length of shortest trees	336	341	341	340	347	342	341	370
Length of strict consensus	354	455	393	342	379	430	373	399
Consistency Index (CI)	0.395	0.312	0.356	0.409	0.369	0.326	0.375	0.328
Homoplasy Index (HI)	0.605	0.688	0.644	0.591	0.631	0.674	0.625	0.672
Retention Index (RI)	0.747	0.634	0.701	0.762	0.718	0.681	0.726	0.723
Rescaled consistency (RC)	0.296	0.198	0.205	0.312	0.265	0.214	0.273	0.237

broken up: pedal gland (4), pallial cavity (11), jaws (30), oesophageal gizzard (36), albumen gland (54), membrane gland (56), mucous gland (57), extrapallial duct or groove (58) and prostate (59); a total of 87 characters were retained in this new data matrix (obtained from data matrix given in the Appendix 1).

PARSIMONY ANALYSIS

The programs PAUP 3.1.1 and PAUP 4.0b.2 (Swofford, 1993, 1997) were using a Power Mac 7300/166 and G4. All the characters were unordered, undirected and unweighted, at least in the first analysis (analysis I in Table 1). Diverse heuristic search options (General, Starting trees, Stepwise addition, Branch swapping) were employed.

We performed many analyses, by weighting characters differentially (analyses II–VI in Table 1) or by imposing a particular condition in the case of alternative character states (see character (23); analysis VII in Table 1), to test the homology of characters in terms of consistency within the tree and in terms of influence on the monophyly of higher taxa. Under particular conditions, it was not possible to complete the analysis because the number of trees increased asymptotically. Because prolonging the analyses did not seem to modify the results, we interrupted such analyses when 10 000 trees had been retained. We never observed a decrease in tree length after the 10 000th tree, even after one week of continuous computing.

All characters exhibit a very low CI, of which the amplitude of variation is itself low (Appendix 3). As shown by successive analyses I–VIII (Table 1, Appendix 3) and others not reproduced here, minor variations in character weighting induced important variations in tree topology and consequently we exam-

ined congruence amongst these trees. Successive weighting (Farris, 1969) was used to emphasize the influence of those characters with a higher CI.

We also examined possible tree spaces to avoid being trapped in islands of trees with analyses saving only subsets of all possible trees. One hundred random replications were undertaken from each of which 12 trees were saved, and then each of these 1200 trees has been swapped. We followed this procedure for our eight separate analyses.

CHARACTERS

In the following list, the plesiomorphic character states of undirected and unordered characters are determined by the analysis. The polarity is consequently not shown in the present character list, which consists of *a priori* data only. The numbers are the same as those used in the appendices and figures. 'D' denotes characters that were rejected from the analysis, for reasons explained in the text.

LARVAL SHELL

1. Orthostrophic/heterostrophic shell
The shell of gastropods includes an apical protoconch (embryonic and larval shells) and a teleoconch (adult shell). The protoconch and the teleoconch of the caenogastropod gastropods, are coiled in the same direction around a single axis (generally dextral) and the shell is thus called 'orthostrophic'. Plate (1895) introduced the term 'heterostrophic' to describe the pyramidellid shell in which the protoconch and the teleoconch are coiled in two different directions, often around two different axes (sinistral protoconch and dextral teleoconch). Plate explained the heterostrophy

by the mechanical pressure of adult whorls on the first whorls. This hypothesis, which was accepted by Simroth (1896, 1897–1907) and Hoffmann (1939), was later refuted by Lemche (1948). Causes of heterostrophy remain unknown. In this paper, occurrence of heterostrophy often results from interpretation rather than from observation, when the adult shell is absent (shell-less sacoglossans and nudibranchs) or symmetrical (as in *Tylodina* and *Umbraculum*), but the protoconch is sinistral and the adult anatomy is dextral. In stylommatophorans, where the development is direct, the embryonic and adult shells are always coiled in the same direction, so heterostrophy was coded as absent.

2. Protococonchs I & II
This character is related to planktotrophy, because only planktotrophic gastropods potentially possess a double protoconch. The evolutionary history of planktotrophy remains unclear, even though it seems that it has been independently acquired; either twice (Haszprunar, 1988) or three times (Ponder, 1991; Ponder & Lindberg, 1997). A secondary distinct protoconch (or protoconch II) occurs only among Caenogastropoda (Bouchet, 1987). We could not use the character 'presence/absence of planktotrophy' here because our taxon sampling did not correspond to its domain of definition. Here, we considered only absence (0) or presence (1) of a double protoconch.

FOOT

3. Operculum
The operculum occurs in all the gastropod embryos that have been studied, but not in all adults, where it can be present (0) or absent (1). Some opercula (e.g. the clausilium of many clausilids, the enlarged peristome of *Thyrophorella* (Stylommatophora), the membrane of planorbids) are convergent neoformations, and were not considered here as true opercula on the basis of their structure and/or ontogeny.

4. Pedal gland
Various types of pedal glands were homologized in spite of structural and topological differences. Two types of pedal glands seem to be apomorphic character states: the postero-ventral pedal gland of pleurobranchomorphs (Willan, 1987) and the stylommatophoran pedal gland are tongue-shaped, located on the floor of the visceral cavity but isolated from the latter by a membrane. They open into a groove between the anterior end of the foot and the mouth. In veronicellids and onchidiids the pedal gland is similar to that of the Stylommatophora, but lies free in the visceral cavity. The suprapedal gland of many

ellobiids (Morton, 1955b) can be considered homologous with the long pedal gland of stylommatophorans. It can be compact and anteriorly located, or a simple glandular area as in other gastropods. The pedal gland is coded: (0) various glandular areas (unicellular and/or pluricellular) distributed in the pedal mass and opening into the foot sole; (1) presence of a postero-ventral pedal gland; (2) presence of a long anterior pedal gland, lying free upon the floor of the visceral cavity and opening into a groove between the foot and the mouth; (3) like (2) but beneath a membrane; (4) like (2) and (3) but embedded within the pedal mass. The embryonic ectodermic invagination of the long pedal gland described in *Achatina* (Stylommatophora) by Ghose (1963d) occurs in the same position as in the ellobiids (Morton, 1955b), which suggests that the elongated pedal gland could be derived from the ellobiid arrangement. To test this hypothesis the pedal gland of ellobiids is coded alternatively (0) or (4).

5. Thecosomatous pedal wings
The pedal wings of the Thecosomata are located around the mouth and are joined at their base. In Euthecosomata, they are symmetrical and distinct, whereas in Pseudothecosomata only one wing occurs and is interpreted as resulting from fusion of two wings. The thecosomatous wings are absent (0), paired (1) or fused (2).

CEPHALIC APPENDAGES
Cephalic appendages are too diverse in morphology to be used in the present analysis. Distinction between the posterior tentacles of Pulmonata and the rhinophores of Opisthobranchia results partly from the traditional usage and partly from interpretation in terms of homology. The ocular tentacles of pulmonates have always been homologized with the tentacles of non-euthyneuran gastropods (Franc, 1968), whereas the rhinophores of opisthobranchs have been interpreted as secondary structures (Hoffmann, 1939; Gosliner, 1994). Whether secondary or not, diversity of their shapes prevents their use in our phylogenetic analysis. The rhinophores of non-cephalaspideans have often been homologized with the Hancock's organs of cephalaspidean gastropods (Hoffmann, 1939; Huber, 1993; Gosliner, 1994). Huber (1993) supported this homology because Hancock's organs and rhinophores seem to be innervated by supposedly homologous nerves (rhinophoral nerve). The innervation by homologous nerves, however, does not necessarily imply homology of organs: the oral appendages of *Aplysia rosea* and the anterior tentacles of *Cepaea hortensis* are innervated by the same nerves (Leyon, 1947), although they are probably not homologous.

Moreover, nerves are homologized according to their ganglionic origin, which is often too difficult to recognize to be used as a criterion for homology (e.g. nerve n1 in Fig. 5 and Fig. 8, Leyon, 1947).

6. Cephalic shield

A cephalic shield occurs in many cephalaspidean gastropods and seems to be related to a burrowing mode of life. It is absent (0) or present (1).

7. Hancock's organ

Hancock's organs are located under the edge of the cephalic shield, one on each side, and consist of rows of leaves. Their function is unknown. They are absent (0) or present (1).

8. Retractile tentacles

Stylommatophora have two pairs of cylindrical, retractile tentacles. The tentacles of the veronicellids and onchidiids (two pairs) are similar because of the apical position of the eyes at the tip of posterior tentacles, but are contractile (Runham & Hunter, 1970). Retractile tentacles are absent (0) or present (1). The particular and autapomorphic mode of tentacle retraction in athoracophorid slugs (Burch, 1968) is not considered here because the taxon has not been retained in data matrix.

9. Position of the eyes

The eyes are located in the cephalic tegument, at the base of the cephalic appendages (0) or at the tip of posterior tentacles (1). Exceptionally the eyes are absent (2).

10. Cerata filled with cnidocysts

Cerata are occasionally present on shell-less gastropods but their shape is too variable to be used here. Nevertheless, cerata filled with cnidocysts are only found in eolids and are coded absent (0) or present (1). Cnidocysts in cerata were interpreted by early workers as an endogenous product of the digestive gland of eolids (Vayssière, 1888; Hecht, 1896), but are actually ingested from Cnidaria (Cuénot, 1907; Edmunds, 1966). In addition to cnidocysts, cerata may also be filled with blood vessels and digestive diverticles.

PALLIAL CAVITY

The pallial cavity contains essential structures such as respiratory structures (gills or lung), reproductive structures (gonoducts and gonopores), digestive structures (rectum and anus), excretory structures (kidney and renal pore) and circulatory structures (pallial heart). Pallial organs are similarly arranged in caenogastropods, but exhibit a variety of arrangements in heterobranchs. The typical caenogastropod ctenidium is absent and replaced by secondary and analogous gills (Haszprunar, 1985a, 1988; Gosliner, 1994; Mikkelsen, 1996), or not replaced. The opening of the cavity may be reduced to a pneumostome. The cavity has been lost in minute gastropods (*Glacidorbis, Rissoella* and *Omalogyra*). Secondary gills are absent or convergently present in heterobranch taxa such as pyramidellids (Haszprunar, 1985a, 1988; Gosliner, 1994), architectonicids (Haszprunar, 1985a, b, c), thecosomes (Van der Spoel, 1967, 1976; Lalli & Gilmer, 1989), gymnosomes (Van der Spoel, 1976) and lymnaeid gastropods (Hubendick, 1978). These secondary gills are too variable to be used here. Whereas the longitudinal axis of the cavity and the direction of its opening are constant in caenogastropods, their variation in euthyneurans is such that they cannot be transposed into character states. In Cephalaspidea (Mikkelsen, 1996), for example, the opening varies from an anterior to a right posterior orientation.

11. Pallial cavity

The pulmonary cavity is homologous with the pallial cavity of non-pulmonate gastropods (Ruthensteiner, 1997). The cavity is coded as follows: present without pneumostome (0), present and opening through a pneumostome (1), absent (2). The pneumostome of Siphonariidae is not contractile (Dieuzeide, 1935; Hubendick, 1945b; Marcus & Marcus, 1960a) and may be not homologous to that of other pulmonates. It can therefore be coded either (1) or as an independent state (3).

12. Osphradium

The osphradium is located at the opening of the pallial cavity (Yonge, 1947; Fretter & Graham, 1994). It was first described by Spengel (1881) as an 'olfactory sense organ' and was consequently sometimes called 'Spengel's organ'. Haszprunar (1985d, e, 1988) described osphradial characters which have been used in phylogenetic investigations (Haszprunar, 1988; Ponder & Lindberg, 1997). An osphradium is present (0) or absent (1).

13. Si1 & Si2 cells

Si1 and Si2 cells occur in the osphradial ciliated ridges of many caenogastropods (Haszprunar, 1985d, e; 1988), and have been interpreted as a synapomorphic character of the Caenogastropoda (Haszprunar, 1988;

Ponder & Lindberg, 1997). Si1 & Si2 cells are absent (0) or present (1).

14. Si4 cells

Si4 cells occur in the osphradial ciliated ridges of many caenogastropods (Haszprunar, 1985d, e; 1988). They are absent (0) or present (1).

15. Pallial caecum

The pallial caecum is a posterior extension of the pallial cavity in which water circulates (Brace, 1977a; Mikkelsen, 1996). It is absent (0) or present (1).

16. Raphes

[Opposed ciliary tracts (Ponder & Lindberg, 1997)]. The inferior and superior raphes (Perrier & Fischer, 1909) are ciliated strips which create water currents in the pallial cavity. Raphes are absent (0) or present (1).

17. Plicatidium

The plicate gill of cephalaspideans (including shelled sacoglossans), also known as a plicatidium (Perrier & Fischer, 1911; Morton, 1972), is composed of two parallel rows of laminae (or leaflets) on each side of a membrane which functions as a blood space. It is attached to the roof of the mantle cavity by two folds. Afferent and efferent blood vessels run along the insertion of the folds on the suprapallium. The plicatidium is two-sided, except in sacoglossans where it is one-sided. The plicatidium is absent (0), present and two-sided (1), or present and one-sided (2).

18. Branchial circlet

A branchial circlet occurs on the notum of Doridoidea. It is either retractile (in cryptobranch dorids) or not (in phanerobranch dorids). A branchial circlet is absent (0) or present (1).

19. Pinnate gill

A pinnate gill is present on the right side of the visceral mass in pleurobranchomorphs (Willan, 1987). It consists of two parallel rows of pinnae originating from a membrane. The efferent blood vessel runs along the rachis (the exterior side of the membrane); the anus is located at the posterior end of the membrane, and the genital openings are located at its anterior extremity. It is absent (0) or present (1).

20. Prebranchial pocket

Leue (1813) described an aperture of a glandular pouch located in front of the anterior end of the pinnate gill of *Pleurobranchaea meckelli*. Lacaze-Duthiers (1859) asserted that this aperture corresponds to a communication between the circulatory system and the exterior, even though Delle Chiaje (1823) agreed with Leue. However, Pelseneer (1894) showed that the prebranchial aperture is the opening of an independent gland, often called 'prebranchial pocket' or 'prebranchial gland'. It does not communicate with the circulatory system. Its function remains unknown. It is present (1) or absent (0).

21. Pulmonary vessels

The suprapallium of the pallial cavity can be hypervascularized when respiratory exchange between air and blood occurs in the cavity. It is consequently called a 'lung'. The pulmonary vessels of the suprapallium are absent (0) or present (1). The pulmonary vessels which are restricted to the mantle ridges (e.g. *Carychium* and *Otina*) or which are rudimentary (e.g. *Amphibola* and *Gadinia*) are considered to be present.

EXTERNAL AND PALLIAL GLANDS

The homology of the pigmented mantle organ (PMO) with other glandular structures of gastropods has often been discussed. The PMO has been homologized with many other glandular structures of gastropods and in relation with the occurrence of pigments (Robertson, 1985): larval kidney, excretory organ, pigmented gland, anal gland, pigmented hypobranchial gland, hypobranchial gland. Schaefer (1996) considers the PMO homologous with the anal glands, larval kidneys, black larval kidneys, but not with the hypobranchial gland. Here we code the hypobranchial gland and the PMO as two distinct characters because: (1) the PMO and the hypobranchial gland may be both present as in the pyramidellid *Amathina* (Ponder, 1991); (2) the coloured secretion of the hypobranchial gland differs from the pigmented and crystalline concretions of the PMO; (3) the development of the PMO (called 'larval kidney') and that of the hypobranchial gland are distinct (Bickell & Chia, 1979); (4) the coloured secretions of hypobranchial gland occur in numerous species belonging to various genera and are probably convergent. Histological studies of the glandular cells are needed to determine the homology of various pallial glands (Perrier & Fischer, 1911; Van der Spoel, 1967; Hunt, 1973). Here we consider four distinct glands: hypobranchial, pallial, purple, and opaline glands. Defensive glands ('repugnatorial gland' in Fretter & Graham, 1954), of which the homology has been questioned (Gosliner, 1994), are not retained for phylogeny here because they were

only described in three genera and their taxonomic distribution and homology are dubious: 'glandes semilunaires' in *Scaphander* (Pelseneer, 1894), defensive glands in *Ringicula* (Fretter, 1960) and *Haminoea* (Rudman, 1971).

22. Hypobranchial gland

In monopectinate caenogastropods, the hypobranchial gland is an elongate glandular region, located between the rectum and the ctenidium. It secretes mucus in the pallial cavity. The mucus contains mucopolysaccharids and glycoproteins (Woltzow, 1994) to agglutinate debris in the pallial cavity. The pallial gland of Thecosomata (also called 'mantle gland'), which secretes a web for food collecting, has been homologized with the hypobranchial gland (Van der Spoel, 1967). The 'adult and pigmented anal gland' of Euthecosomata has also been homologized with the hypobranchial gland (Van der Spoel, 1967). Here we code the hypobranchial gland as: present (0), absent (1), or a mantle gland secreting a web (2). The homology of the pigmented anal gland of the Euthecosomata with the PMO is not accepted *a priori*.

23. Pigmented mantle organ (PMO)

The PMO is a vacuolated and pigmented organ which is located on the roof of the mantle cavity close to the anus. It appears in veliger or postveliger stages and generally disappears at metamorphosis. In many pyramidellids, however, the PMO is retained in adults (Schander, 1997). In Nudibranchia it is considered absent by Hurst (1967) or 'probably absent' by Robertson (1985); it has nevertheless been described by Pelseneer (1901) in many genera such as *Goniodoris*, *Acanthodoris*, *Onchidoris*, *Facelina*, *Cuthona*, *Tergipes*, *Doto* and *Dendronotus*. It was described as colourless in *Doridella steinbergae* by Bickell & Chia (1979). We code it present (1) where it has been described, and absent (0) elsewhere.

24. Purple gland

[Gland of Blochmann (Perrier & Fischer, 1911)]. The purple ink of *Aplysia limacina* and *Aplysia californica* is aplysioviolin, a derivative of phycoerythrin (Chapman *et al.*, 1967, 1968; Rudiger, 1967a, b, 1968; Chapman & Fox, 1969). Purple secretions are known in many caenogastropods. The secretion of muricids is the best known, and is an indigoid derivate (Bouchilloux & Roche in Franc, 1968). The purple gland has been considered either as a distinct gland, according to histological and anatomical studies (Mazzarelli, 1890; Perrier & Fischer, 1911), or as a gland homologous to the hypobranchial gland of non-euthyneuran gastropods (Guiart, 1901). Although the first assumption is accepted here, 'glands of Blochmann' have been described in *Scaphander* and 'other bullomorph gastropods' (Perrier & Fischer, 1911), in *Cylichna* (Lemche, 1956) and in *Siphonaria* (Dieuzeide, 1935). Rudman (1971a) homologized the yellow defensive secretions of aglajids with the aplysid purple ink. These glands cannot be reasonably considered as purple glands because they differ in position and secretion from the gland found in Aplysiidae. The purple gland is absent (0) or present (1).

25. Opaline gland

[Gland of Bohadsch (Mazzarelli, 1889)] The opaline gland (Vayssière, 1885) is present in *Aplysia*. Perrier & Fisher (1911) described in detail the gland of Bohadsch in *Akera* and considered that it is analogous with the purple gland of aplysids, because these two types of glands are simultaneously present. It is absent (0) or present (1). Its function is unknown.

CIRCULATORY AND EXCRETORY SYSTEMS

The auricle of the monotocardian gastropods pumps the blood from afferent vessels and sinuses through the posterior aorta into the ventricle, which pulses blood into the anterior aorta, the efferent vessels and lacunae. This topology is constant among the genera studied here, except those that have no heart (*Microhedyle*, *Alderia*, Marcus & Marcus, 1957; Rankin, 1979) or in which the heart is simple (*Hedylopsis*, Rankin, 1979). The kidney communicates with the pericardial cavity by a ciliated renopericardial canal (Hecht, 1896). Some characters are not used here because their variation is continuous: position of pericardial cavity, kidney, and renal pore.

26. Blood gland

[Glandular body (Alder & Hancock, 1845–1855); glande orangée (Lacaze-Duthiers, 1859); glande lymphatique (Cuénot, 1891)]. The term 'blood gland', which is used for glands producing blood pigments (such as haemocyanin or haemoglobin) and blood cells, has been introduced in gastropod terminology by Bergh (1884) for the spongy gland on the anterior aorta of dorids. The 'crista aortae' (Cuénot, 1891; Lemche, 1956) has been homologized with other blood glands even though it occurs in a distinct position. The crista aortae is included in the pericardial cavity, whereas the other blood glands are independent from it. Following Cuénot (1891), Schmekel & Weichter

(1973) confirmed that one of the functions of the blood gland of *Archidoris pseudoargus* is the production of haemocyanin. The lung of stylommatophorans could function as a blood gland (Cuénot, 1891). This character has been poorly described in Euthyneura because the observation of the blood gland seems to be very difficult in preserved specimens. The blood gland is absent (0) or present (1).

27. Renopericardial duct
Except in taxa without a pericardium, the renopericardial duct is always present. It is a simple duct (0), a structure called a 'syrinx' (1), or absent (2). The syrinx is found in nudibranchs only.

28. Secondary ureter
The kidney, which originates from mesoderm, plesiomorphically opens through a simple aperture into the pallial cavity or into the outside as a result of a reduction of the pallial cavity. In Stylommatophora the nephropore may be prolongated by a tubular ureter originating from ectoderm and called a 'secondary ureter' exhibiting two cell types (Delhaye & Bouillon, 1972a, b, c; Tillier, 1989). In many basommatophoran pulmonates (Delhaye & Bouillon, 1972c), in *Valvata* (Bernard, 1890; Andrews, 1988) and in the orthurethran Stylommatophora (Delhaye & Bouillon, 1972c), a tubular ureter exhibits only one cell type. It was originally called a primary ureter but it originates from mesoderm and is therefore a renal structure *sensu stricto*. The embryological origin of the ureter of the veronicellids (Delhaye & Bouillon, 1972c) and *Onchidella* (Fretter, 1943) remains unknown. The secondary ureter is absent (0) or present (1).

29. Nephridial gland
A nephridial gland has been described in monotocardian gastropods (Perrier, 1889; Fretter & Graham, 1994). It is located between the kidney and the left auricle. It allows reabsorbtion of ions and water from blood. It can be present (0) or absent (1). The nephridial gland seems to be absent in Euthyneura for which the kidney has been precisely described.

D. Podocytes
Podocytes are epicardial cells that filtrate blood (Andrews, 1988; Gosliner, 1994). They have been described in a few non-euthyneuran species by Andrews (1976a, 1976b, 1981, 1988) and are absent in *Cylichna* (Lemche, 1956) and in the Pseudothecosomata (Van der Spoel, 1967). More data are needed to use this character in phylogenetic analyses.

DIGESTIVE SYSTEM
The terminology used by Fretter & Graham (1994) for the description of the digestive apparatus of *Littorina littorea* (Linné, 1758) is adopted here. Radular characters were not used because they are too variable at the level considered here.

30. Jaws
A pair of lateral jaws can be present (0) or absent (1). The epithelium, which is cuticularized (in cylindrobullids, onchidids, and *Scaphander*, *Philine*, *Gastropteron*, *Archidoris*, *Glacidorbis*…), is coded as an absence of jaws. An unpaired dorsal jaw can occur in many taxa. Consequently, there may be either three jaws (2) or only one unpaired dorsal jaw (3).

31. Evaginable proboscis
The pyramidellid proboscis functions as a muscular pump by which the buccal mass, which includes no radula, is extruded from the buccal cavity (Fretter, 1951). It is anatomically distinct from the other long prosboces as in Eulimidae and Architectonicoidea. Short evaginable buccal masses have been described in many cephalaspidean species (Hurst, 1965) and notaspidean species (Willan, 1984) but they are not considered homologous with the pyramidellid proboscis. The latter is absent (0) or present (1).

32. Acid gland
The acid gland only occurs in Pleurobranchoidea. It consists of a duct, medially opening into the roof of the buccal cavity, and by tubules which originate from this duct and which fill the visceral cavity between the visceral organs. Glandular cells in the tubules produce an acid fluid (pH = 1) which could be used in feeding (Thompson & Slinn, 1959; Willan, 1987). This gland was first described by Leue (1813) and was later called 'acid gland' by Thompson & Slinn (1959). It is absent (0) or present (1).

33. Ascus and descending limb of radular apparatus
Bergh (1878) distinguished the Ascoglossen (taxon which he named in 1876 for the shell-less ascoglossans) in the order Nudibranchia, because of a unique radular character. The worn radular teeth are collected in a pouch, the ascus, located at the posteroventral side of the odontophore, whereas in other gastropods the teeth are lost as they are used by rasping (Jensen, 1991, 1996a, b). In all gastropods the radular ribbon extends in an ascending limb located upon the dorsal side of the odontophore but in

Ascoglossa the radula includes an additional descending limb under the odontophore. It is delineated by an epithelium and emerges into the ascus (Jensen, 1989, 1993, 1996a, b). The descending limb and ascus are present (0) or absent (1). It seems that at least one species of the genus *Acochlidium* (Rankin, 1979) and one species of the nudibranch genus *Cuthona* (Baba, 1963) exhibit radular topology similar to that of the Ascoglossa, but without an ascus. This should be reinvestigated.

34. Odontophoral cartilage

The odontophoral cartilage (Gabe & Prenant, 1955; Voltzow, 1994) seems to be absent in several heterobranch taxa (Haszprunar, 1988), but this requires further investigation. It is present (0) or absent (1).

35. Odontoblasts

The odontoblasts are the cells which produce the radula. Former data have been summarized by Schnabel (1903) and re-evaluated by Prenant (1924, 1925, 1926) and Pruvot-Fol (1925, 1926). The odontoblasts are generally considered to be narrow in non-euthyneuran gastropods and wide in Euthyneura (Sharp, 1883; Schnabel, 1903; Hoffmann, 1932, 1939; Gabe & Prenant, 1951, 1952a, b; Lemche, 1956; Franc, 1968; Salvini-Plawen & Steiner, 1996). The term 'odontophytes' (Prenant, 1926; Pruvot-Fol, 1926) has been abandoned to designate large odontoblasts. According to Gabe & Prenant (1951, 1952a, b), the large odontoblasts can occur either in a subterminal position (upon the underside of the radular sac, as in Euthyneura except cephalaspideans) or in a terminal position (at the extremity of the radular sac, as in cephalaspideans). The odontoblasts are: narrow, high cells (0), wide cells in a subterminal position (1), wide cells in a terminal position (2), undifferentiated (neither narrow nor wide) cells (3).

D. Oesophageal appendages

Paired oesophageal pouches opening into the dorsal side of the oesophagus have been described in *Cerithium*, *Campanile*, *Triphora*, *Coriandria*, *Littorina*, *Diaphana*, *Colpodaspis* and Thecosomata. An unpaired pharyngeal pouch, called oesophageal diverticule by Burn (1966), has been described in many ascoglossan species (Jensen, 1996a, b; Mikkelsen, 1996) and in *Bulla* (Rudman, 1971). These oesophageal appendages are assumed here to be convergent because of the high adaptability of the oesophagus. More histological data are needed to use this character in phylogenetic analyses.

D. Crop

The definition and delimitation of the crop, which is often observable as a dilatation of the oesophagus, is not clear. It is often difficult to distinguish the crop from other oesophageal regions, although its presence is obvious when it is well developed (Tillier, 1989). Runham & Hunter (1970) considered that the absence of ridges distinguished the crop from the oesophageal part in the stylommatophoran slugs *Arion* and *Agriolimax*; Lemche (1956) described the thin-walled epithelia of the crop and oesophagus as morphologically similar but histologically distinct in *Cylichna*. The crop therefore may correspond either to gross morphological or to histological differentiation, or possibly to both. Its presence or absence cannot be defined simply. More data are needed to investigate the homology of the oesophagus and crops.

36. Oesophageal gizzard

In the cephalaspideans and thecosomes, the oesophagus can be differentiated into a muscular gizzard bearing internal plates or spines. It is considered to be analogous to the gastric gizzard on the basis of anatomical differences (Fretter, 1943; Fretter & Graham, 1994; Gosliner, 1994; Mikkelsen, 1996). It can be absent (0) or present. The plates vary in shape and composition: (1) chitinous plates (2) chitinous spines (3) calcified plates (4) calcified plates and chitinous spines.

37. Pouch of gastric gizzard

The stomach can always be easily located in relation to the ducts of the digestive gland. Its anatomy is complex in non-euthyneuran gastropods (Fretter & Graham, 1949, 1994) and seems to be more simple in several euthyneuran taxa (eolids, notaspids, *Veronicella*, Stylommatophora). This simplification, which is continuous, is nevertheless difficult to transpose into character states and cannot be used in this analysis. In several basommatophoran pulmonates (Runham, 1975), the stomach is characterized by a gizzard that is independent of the stomach cavity. The pouch of the gizzard is absent (0) or present (1).

38. Gastric caecum

Here the gastric caecum, which is supposedly analogous to the caecum found in several vetigastropods (Fretter & Graham, 1994), occurs in the stomach of *Akera*, *Aplysia* and basommatophoran genera. It is absent (0) or present (1).

39. Shape of faeces

The morphology of faeces has been fully described by Arakawa (1963, 1965, 1968, 1972) and has been used

in a phylogenetic analysis by Moore (1931) and Ponder & Lindberg (1997). In gastropods, the faeces either form rods (0) or pellets (1).

NERVOUS SYSTEM

The nervous system has been discussed in detail by Dayrat & Tillier (2000). Here we adopt the terminology of Fretter & Graham (1994) and Hoffmann (1939). The circumoesophageal nerve ring includes three pairs of ganglia (two cerebral, two pleural and two pedal ganglia). Three connectives join, respectively, the pleural and pedal, the pedal and cerebral, and the cerebral and pleural ganglia on each side. The cerebral and pedal ganglia are joined, respectively, by the transversal cerebral and pedal commissures. A long visceral loop, joining the left and right pleural ganglia, can include either three ganglia (one left suboesophageal, one abdominal and one right supraoesophageal ganglia) or more (with one supplementary left parietal, located between the left pleural and the suboesophageal one, and with one right parietal, located between the right pleural and the supraoesophageal one). The abdominal ganglion of gastropods is called 'visceral ganglion' by many authors. In order to avoid confusion, we use the term 'visceral ganglia' to designate all the ganglia of the visceral loop, and the term 'abdominal ganglion' for the unpaired posterior ganglion of the visceral loop. To describe the anatomical composition of the visceral loop in a simple way, we use the diagram proposed by Mikkelsen (1996), slightly modified: {Pl-PaSb-(AbSp)-Pa-Pl} is the formula for a pentaganglionate visceral loop with left parietal, suboesophageal, abdominal, supraoesophageal, right parietal and two pleural ganglia. {...} denotes the limits of the visceral chain, pleural ganglia included. Hyphens indicate occurrence of a visible connective, and brackets indicate apparent fusion of ganglia into a single 'nervous mass'.

40. Streptoneuran/euthyneuran visceral loop
Spengel (1881), following Lacaze-Duthiers (1870) and von Ihering (1876), distinguished the streptoneurous (twisted) and euthyneurous (not twisted) conditions of the visceral loop of gastropods. Several hypotheses, in relation to the processes of detorsion and concentration of the visceral loop, were proposed to explain euthyneury (Pelseneer, 1901; Naef, 1913; Merker, 1913; Krull, 1934; Régondaud et al., 1974; Haszprunar, 1988; Gosliner, 1994). Haszprunar (1985a, 1988) distinguished three types of euthyneurous nervous systems, resulting from: (1) detorsion of the visceral mass and visceral commissure; (2) concentration of the visceral commissure close to the anterior circumœsophageal nerve ring; (3) concentration and detorsion. Haszprunar (1988) did not define precisely the type of euthyneury that occurs in allogastropods and euthyneuran groups, but concluded that euthyneury by detorsion is 'principally present in detorted animals (most opisthobranchs, all pulmonates . . .)'. He considered euthyneury too convergent to use in his phylogenetic analysis. Moreover, 'euthyneury in pulmonates and opisthobranchs always is a result of detorsion', according to Gosliner (1994). The relationship between euthyneury, detorsion and concentration is also problematic because a concentrated nervous system occurs in most Euthyneura. It is consequently necessary to define the stage at which concentration occurs in relation to the torsion and detorsion processes during development. Concentration can take place at the streptoneuran stage (after torsion but before detorsion), or it occurs in the euthyneuran stage (after torsion and detorsion), its occurrence thus being diverse and complex. Concentration may clearly occur: (1) in a pretorsionnal stage as in *Aplysia californica* (Kandel, 1979); (2) after slight torsion, as in *Achatina* (Ghose, 1962); (3) before torsion without a modification of the visceral loop because it is short (i.e. the Naef's theory), as in *Lymnæa* (Régondaud et al., 1974), *Limax* (Henchmann, 1890), *Æolidiella* (Tardy, 1970) and *Phestilla* (Bonar & Hadfield, 1974); (4) without either torsion or detorsion, as in *Retusa* (Smith, 1967), *Adalaria* (Thompson, 1958) and *Tritonia* (Thompson, 1962). Thompson (1962) explained the 'evolutionary detorsion' proposed by Pelseneer (1901) as a 'decreased developmental torsion instead of an increased detorsion in the young stages'. The relationship between topology of the visceral loop and the processes of concentration and detorsion is still unresolved. The visceral loop is: streptoneurous (0), concentrated and close to the circumœsophageal nerve ring or reduced to a very short loop (1); slightly streptoneurous with a loop in the dorso-ventral axis restricted at the posterior end (2); euthyneurous (3); absent (4).

41. Hypoathroid/epiathroid circumoesophageal nerve ring
The circumoesophageal nerve ring is hypoathroid when the pleural ganglia are closer to the pedal ganglia than to the cerebral ganglia. It is called epiathroid elsewhere. The hypo-epiathroid condition cannot be defined when all ganglia are aggregated or are equidistant, which is the case in many taxa. The distance between cerebral and pleural ganglia used by Mikkelsen (1996) seems to be too subjective and is not used here.

The circumœsophageal nerve ring is: hypoathroid with separated ganglia (0); epiathroid (1). Assymmetry in hypo-epiathroidy, known in a few Stylommatophora (Tillier, 1989), is not considered here because it does not occur in taxa in the present data matrix. Ghose (1962) described the nervous system of *Achatina* as hypoathroid in the first ontogenetic stages and secondarily epiathroid.

42. Circumœsophageal nerve ring
The circumœsophageal nerve ring can be prepharyngeal (0) or postpharyngeal (1).

Polarity. In *Adalaria*, Thompson (1958) described a primary prepharyngeal nerve ring which secondarily moves to a posterior position, whereas in *Marisa* (Ampullarioidea) Demian & Youssif (1975) described a primary postpharyngeal nerve ring. Gosliner (1994) asserted that the postpharyngeal condition is secondary in Heterobranchia.

43 & 44. Left and right parietal ganglia
These characters have been discussed in detail in terms of terminology, hypotheses of fusion, and homology (Dayrat & Tillier, 2000). Here the left and right parietal ganglia are coded as two separate characters because they occur independently in the visceral loops. They are absent (0) or present (1).

45. Subcerebral commissure
The left and right cerebral ganglia are joined by a cerebral commissure of varying length, and can be also joined by an additional subcerebral commissure which is homologous among Gastropoda (Bouvier, 1887c). It has been described in Pulmonata by Van Mol (1967). It can be absent (0) or present (1).

46. Parapedal commissure
Pedal ganglia are joined by a pedal commissure of varying length or joined by a parapedal commissure. It is absent (0) or present (1).

D. Length of the cerebral and pedal commissures
The lengths of the cerebral and pedal commissures depend on the location of the ganglia in relation to the œsophagus (dorsal, lateral or ventral) and reflect in part the concentration of the anterior nerve ring. These lengths vary continuously from short to long, and are not used here for this reason even though they have been used by Mikkelsen (1996), and even though long commissures seem to be plesiomorphic (Henchmann, 1890; Thompson, 1958, 1962; Ghose, 1962; Demian & Youssif, 1975).

47 & 48. Position of the subœsophageal and supraœsophageal ganglia
The homology of subœsophageal and supraoesophageal ganglia has been discussed by Haszprunar (1988) and Dayrat & Tillier, 2000). In fused nervous masses, suboesophageal and supraoesophageal ganglia are located by observation of the origin of the nerves; they occur during ontogeny, as far as known, except in many nudibranchs (Thompson, 1958, 1962). They are: (0) free on the visceral commissure, separated from other ganglia by a cord of varying length; (1) close to the left/right pleural ganglia (or pleurocerebral mass), no commissure being visible; (2) fused to the left/right pleural; (3) close to the abdominal ganglion, no commissure visible; (4) fused with the abdominal; (5) close to the left/right pleural and the abdominal (and sometimes the parietal) and possibly fused with one of these ganglia in a concentrated nervous system, or in a same nervous mass; (6) close to the right/left pleural ganglion (with shortening of the right/left anastomosis); (7) vestigial ganglia on a vestigial visceral loop; (8) absent.

CEREBRAL LOBES
Cerebral lobes were first described by Lacaze-Duthiers (1872) in the freshwater snails *Planorbis*, *Physa* and *Lymnaea*. They occur in pulmonates and were studied in the last decades of the nineteenth century (Böhmig, 1883; Schmidt, 1891; De Nabias, 1899; Pelseneer, 1901) and since the 1950s (Geraerts & Algera, 1976; Lever, 1958a, b; Lever *et al*., 1959; Joosse, 1964; Van Mol, 1967; Geraerts & Joosse, 1975; Wijdenes & Runham, 1976). Dorsal lobes are called 'medio-dorsal bodies' (Lever, 1958a, b) and lateral lobes the 'procerebrum' (Van Mol, 1967).

49. Procerebrum
[Lobes latéraux (Pelseneer, 1901); lobules de la sensibilité spéciale (Lacaze-Duthiers, 1872)]. The procerebrum contains a follicle gland (Geraerts & Joosse, 1975) and appears in dissection as a kind of basal tentacular ganglion. It can be absent (0) or present (1).

50. Medio-dorsal bodies
Medio-dorsal bodies are endocrine organs located on the dorsal side of the cerebral ganglia, close to the insertion of the cerebral commissure. Isolated neurosecretory cells were found in few opisthobranch species (Franc, 1968). They are not considered to be homologous with the dorsal bodies here because: (1) they are variously located in the cerebral, pleural, parietal and abdominal ganglia, and (2) they do not

constitute a distinct organ. The medio-dorsal bodies are absent (0) or present (1).

GENITAL APPARATUS

The genital apparatus of gastropods are considered as homologous but their respective terminologies are often different. We have standardized terminology in order to propose hypotheses of homology by using Fretter & Graham (1994) for non-euthyneuran gastropods, and Thompson & Bebbington (1969) and Duncan (1960a, 1960b) for Euthyneura, as standard references.

The terminology for non-euthyneuran gastropods has been defined by Fretter (1980), Fretter & Graham (1994) and Reid (1989) in the gonochoric *Littorina littorea* (Linné, 1758). The gametes (oocytes and sperm) are produced in the acini of follicles adpressed together in a gonad. The ovary or testis are embedded within the digestive gland in the apical whorls. A simple gonadial duct conveys the gametes to the carrefour. Even though this term is not used in noneuthyneuran taxa – mainly because this functional region is not differenciated in morphology – it can be defined as the site where the receptaculum seminis opens. The auto-sperm can be stored during the non-breeding season in the testicular duct. The male and female gonoducts differ from each other distally from the carrefour. The spermiduct (traditionally called male duct for non-euthyneuran gastropods) is surrounded by the prostate, which secretes a product involved in maturation of sperm. A receptaculum seminis opens into the female carrefour and can release exo-sperm for fertilization of the oocytes. The fertilized oocytes (eggs) are transported in the oviduct, which includes three female glands: (1) the albumen gland secreting albumen (galactogen) which surrounds each egg; (2) the membrane gland secreting a covering capsular membrane which surrounds every albuminate egg (consequently called 'capsules'); (3) the mucous gland secreting a gelatinous mass, in which the capsules are embedded. The external wall of the gelatinous mass (called 'outer-capsular-wall') is the external wall of the spawn. The male aperture is located on the right side of the pallial floor, close to the anus. A bursa copulatrix, which stores exo-sperm deposited during copulation, opens into the proximal part of the oviduct close to the female aperture. A ventral channel in the oviduct carries the exo-sperm from the bursa copulatrix into the receptaculum seminis, from which it will be used for fertilization. The auto-sperm is transported to the penis (located under the right cephalic tentacle) by an external ciliated groove in *Littorina littorea* but in many related taxa this groove is closed and a duct (vas deferens) transfers the sperm to the penis. Eggs about to be laid run along the ovipositor, on the right side of the foot. The penis is not retractile and the sperm groove is opened to its tip in this species. Here the capsules are released and larvae are planktonic until metamorphosis, when, owing to lack of a velum, they fall to the bottom.

The terminology is more complex for hermaphroditic gastropods. Here we follow that of *Aplysia* as described by Thompson & Bebbington (1969). The gametes (oocytes and autosperm) are produced in the ovotestis and transported by a little hermaphroditic duct (LHD) into the carrefour. The median region of LHD is inflated into an ampulla in which autosperm is stored. In *Aplysia*, the female glands are located in a female gland mass opening into the carrefour. Fertilization occurs in a fertilization chamber opening into the carrefour. The large hermaphroditic duct (HD), which carries gametes from the carrefour to the common genital aperture, is divided into three fold-separated grooves: one for the encapsulated eggs, another for the autosperm, and the last one for the exosperm. The prostate runs along the autosperm groove. The bursa copulatrix opens into the vestibule (at the distal end of the HD). Autosperm and eggs are discharged through the common genital aperture (CGA) into the external ciliated groove. The penis is retractile into an internal penial sheath, which is located behind the right tentacle. In several euthyneurans the autosperm is carried in a duct independent from the CGA or from the carrefour into the penis by a vas deferens (Duncan, 1960a, b).

Among Euthyneura, only *Microhedyle*, *Strubellia* (Acochlidioidea) and *Thalassopterus* (Gymnosomata) are known to be gonochoric. Here we follow Haszprunar (1988), who rejected the use of hermaphroditism because of its convergence in several non-euthyneuran taxa (Haszprunar, 1988; see the 'gonoducts' in the present paper).

51. Ampulla

[Ampulla = seminal vesicle = bursa seminis (Van der Spoel, 1967)]. The ampulla varies in shape and stores autosperm. The autosperm may be stored either in the gonadial duct (testicular duct in gonochoric snails, and LHD for hermaphroditic snails) or in the ampulla, except in *Cylichna* (Lemche, 1956), in which there seems to be no ampulla nor sperm storage. Another possible function of the ampulla is sperm absorption, which only has been described in *Acteon*, *Helix* and *Limax*. The shape of the ampulla cannot be used in the present analysis because: (1) it is too diverse; (2) several other shapes probably exist and are not represented in the present data set; (3) it certainly depends on various other conditions such as

seasonal reproduction. The ampulla is absent (0) or present (1).

GENITAL APPARATUS: CARREFOUR

D. Receptaculum seminis and bursa copulatrix

The receptaculum seminis (RS) and bursa copulatrix (BC) are pouches in which the exosperm is stored (Ghiselin, 1966; Tardy, 1970; Gosliner, 1981a; Hadfield & Switzer-Dunlap, 1984; Fretter & Graham, 1994). The RS opens into the carrefour (in the proximal part of the gonoduct), whereas the BC opens into the distal part of the gonoduct, close to the female (or common) genital aperture. Unused gametes can be destroyed in the BC but not in the RS after fertilization, which explains why the BC is also often called 'gametolytic gland'. The internal epithelium of the RS bears spermatozoa fixed by their head, but this is not the case in the BC. In spite of these criteria, two major problems complicate recognition of homology of sperm pouches: it is complicated by the use of overly diverse terminologies, and by their variable and ambiguous position and function.

The receptaculum seminis has been also called the accessory bursa (Morton, 1955b); exogenous sperm sac (Rudman, 1971a, 1972a), spermatocyst (Lemche, 1956; Edmunds, 1963; Burn, 1966; Marcus, 1972a; Marcus & Gosliner, 1984), poche séminale (Moquin-Tandon, 1870), talon (Baker, 1938; Breckenridge & Fallil, 1973) and caecum (Reynell, 1906); the bursa copulatrix has also been called the gametolytic gland (Thompson & Bebbington, 1969; Rudman, 1972e; Brown, 1979), spermatheca (Brown, 1934; Baker, 1938; Lemche, 1956; Edmunds, 1963; Harry, 1964; Burn, 1966; MacFarland, 1966; Marcus, 1972a, b; Stears, 1974; Hubendick, 1978), gametolytic sac (Rudman, 1971a, 1974), vesicola di Swammerdam (Mazzarelli, 1894; Eales, 1946), receptaculum seminis (Laidlaw, 1940; Meyer, 1955; Van der Spoel, 1967), spermathecal sac (Cooke & Kondo, 1960), poche copulatrice (Moquin-Tandon, 1870; Vayssière, 1898) and sperm bursa (Houbrick, 1993). A sperm pouch can be interpreted as a RS or as a BC in many taxa, such as the proximal and gametolytic pouch found in *Acteon* (Fretter & Graham, 1954; Johansson, 1954; Duncan, 1960a, b; Gosliner, 1981a; Mikkelsen, 1996), which is simultaneously coded by Mikkelsen (1996) as a present proximal RS and as a present distal BC, in two distinct characters. In *Tritonia* the exosperm pouch opening into the distal vestibule seems to be a BC in which the sperm is orientated as in a RS (Thompson, 1961a, 1976); this has also been described in *Armina* (Marcus & Marcus, 1967; Miller & Willan, 1986), in *Cymbulia* (Pelseneer, 1887b; Van der Spoel, 1967), in *Omalogyra* (Fretter, 1948; Haszprunar, 1985a; Fretter & Graham, 1994), in shell-less Ascoglossa (Gascoigne,

1978; Schmekel & Portmann, 1982; Jensen, 1996a, b) and in *Valvata* (Garnault, 1889; Fretter & Graham, 1994). Moreover, coding spermatic pouches is complicated by the observation that some characters of BC and RS seem to 'depend on the amounts of sperm present' (Warén, 1983). The exospermatic pouches are not used in the present analysis, because histological and physiological data are needed in order to have operational criteria for the definition of their homologies.

52. Sphincter of the carrefour

In many taxa, a sphincter allows separation of the male and female gametes in the carrefour. The character is not applicable when the pallial gonoducts are opened. The sphincter is absent (0) or present (1). It has been described by Duncan (1958) in *Physa*, *Planorbis*, *Lymnaea* and *Ancylus*. A valve is also present in the carrefour of the genital system of many nudibranchs such as *Tritonia*, *Doto*, *Archidoris* and *Glaucus*.

53. Fertilization pouch

The fertilization pouch opens into the carrefour by a distinct duct. Here it is distinguished from a fertilization chamber, homologous with the carrefour, and which does not have any duct. Following this definition, the 'talon' described in many pulmonate gastropods (Baker, 1938; Hubendick, 1978; Solem, 1978) is coded as a fertilization chamber only. The fertilization pouch is absent (0) or present (1).

FEMALE GLANDS

[Glandes nidamentaires (Guiart, 1901)]. Three types of glands are recognized in the oviducal apparatus where internal fertilization occurs: the albumen, the membrane, and the mucous (or jelly) glands (Ghiselin, 1966; Tardy, 1970; Els, 1978; Hadfield & Switzer-Dunlap, 1984). Although the homology of the albumen gland, which is always present, seems to be unambiguous, those of the membrane and mucous glands are more problematic. The membrane gland and the mucous gland are contained in the 'capsule gland' (Beeman, 1977; Fretter, 1980).

54. Albumen gland

The albumen gland is always pouch-like except when it surrounds the oviduct or the large hermaphroditic duct (0). The gland is coded as an unpaired gland (1) or a pair of glands (6) opening into the carrefour; a gland in a proximal (2), distal (7) or median (8) female gland mass; a gland opening into the vestibule of a common aperture (3), or into the distal end of the

pallial oviduct close to the female aperture (4). It is leaflet-like in *Campanile (*5).

55. Course of the eggs
The eggs must either cross the albumen gland in the inner glandular folds for covering (0), or not (1). In the latter case, the albumen gland discharges its secretion into a lumen (carrefour or oviduct).

56. Membrane gland
[Posterior mucous gland (Berry *et al.*, 1967; Rudman, 1972a, b; Brown, 1979); glande contournée (Guiart, 1901); winding gland (Lemche, 1956; Thompson & Bebbington, 1969; Kandel, 1979)]. The membrane gland may be fused with the mucous gland in the capsule gland, in a unique glandular area (0) or be independent of the mucous gland. In the latter case it can open into the pallial gonoduct through a separate duct (1) or by the duct of the albumen gland (2), surround the pallial gonoduct (3), open into the vestibule (4), located in a distal (6) or a proximal (8) female gland mass, open into the carrefour (7), or be absent (5).

57. Mucous gland
[Glandular part of the inner lamina (Houbrick, 1981); anterior mucous gland (Berry *et al.*, 1967); glande de la glaire (Guiart, 1901); nidamental gland (Lemche, 1956); uterus (Kress, 1992)]. The mucous gland is pear-shaped, except in cases where it surrounds the pallial oviduct or large hermaphrodite duct (0). It may consists of: one pouch opening into the carrefour (1); a pair of pouches opening into the carrefour (5); one pouch opening into a vestibule (8); one gland opening into the distal end of the oviduct, close to the female aperture (4); divided into a portion opening into the carrefour, and a portion surrounding the pallial gonoduct (6); forming part of a female gland mass opening proximally into the gonoduct (2); included in a female gland mass opening distally into the gonoduct (7); included in a female gland mass opening into the middle of the gonoduct (9); J-shaped mucous gland opening into the vestibule (3). In Stylommatophora (except Succineidae), the female gland is in a unique uterine glandular area, and seems to be (0), but secretes jelly and a calcified layer that consists of calcium carbonate crystals (Bayne, 1968; Tompa, 1984). The calcification of the egg wall is coded in the character (64).

GONODUCTS
The origin of the genital system is traditionally considered to be mesodermic for the gonads and gonadial ducts, and ectodermic for the pallial gonoducts (Duncan, 1960a; Ghiselin, 1966; Tardy, 1970; Beeman, 1977; Hadfield & Switzer-Dunlap, 1984; Mikkelsen, 1996). However, homology in these structures is not clear and this needs to be reviewed (Beeman, 1977; Brisson & Régondaud, 1977). Nevertheless we have no new data and consequently accept the separation between the mesodermic (also called coelomic or pallial) part, and the ectodermic (also called extrapallial) part of the gonoducts.

The classification of the gonoducts has been introduced by Ghiselin (1966) to establish character states in Opisthobranchia. The gonoduct is called monaulic when the oocytes (and/or eggs), autosperm and exosperm are carried in a unique duct, oodiaulic when the oocytes (and/or eggs) and sperms are transported in two separate ducts, androdiaulic when the autosperm and exosperm are carried in two separate ducts, and triaulic when oocytes (and/or eggs), exosperm and autosperm are transported in three separate ducts. These character states have been used some time (Gosliner, 1994) but have been recently criticized by Mikkelsen (1996). We do not use the gonoduct type as a character because (1) it is a condition and not a discrete character (Mikkelsen, 1996), (2) the frequent ignorance of the courses of gametes and of the site of fertilization often prevents its recognition, and (3) it may be more complex than stated in definitions when analysed in detail (the gonoduct can be apparently monaulic but physiologically triaulic owing to the occurrence of sperm carrying grooves, as in *Aplysia*).

Exospermatic transport is too diverse to be used in the present analysis. Several topologies seem to be autapomorphic conditions: *Cerithium* (Houbrick, 1971; Houston, 1985), *Triphora* (Houston, 1985), *Coriandria* (Fretter & Patil, 1958), *Valvata* (Cleland, 1954), *Rissoella* (Fretter, 1948) and *Cornirostra* (Ponder, 1990). In *Limapontia*, *Cyerce*, *Hermaea* and *Elysia*, the exosperm is carried in different ways, although these genera are closely related (Schmekel & Portmann, 1982; Jensen, 1996a, b). All topologies certainly cannot be represented in our data matrix. Moreover, the site of fertilization and the courses of gametes are rarely well known, preventing the definition and use of exospermatic transport as a character that can be scored for the majority of taxa.

An external ciliated groove (ECG) transports the sperm from the male aperture to the cephalic penis in the male *Littorina littorea*. In the female, an unpigmented pedal ovipositor is present but it can be absent outside the spawning season (Reid, 1989; Fretter & Graham, 1994). Reid (1989) and Fretter & Graham (1994) considered the male ECG to be analogous with the female ovipositor. The occurrence of an ovipositor varies too much in the Littorinidae (Reid, 1989) to be

used in the present analysis. The pedal exhalant strip of Cerithioidea (Marcus & Marcus, 1964; Houbrick, 1988, 1993; Reid, 1989; Fretter & Graham, 1994) transports waste and eggs and is another analogous structure. The external ciliated groove, which transports autosperm (and/or eggs) from the common genital aperture to the penial complex in many hermaphroditic gastropods (such as cephalaspideans, basommatophorans), is considered to be homologous with the ECG here. All positions are found when a variety of taxa is considered, preventing the distinction made by Mikkelsen (1996) between the dorsal ciliated groove of caenogastropods and the lateral ECG of cephalaspids.

58. Extrapallial duct or groove
[External ciliated groove; ciliated tract (Warén, 1983); seminal groove (Rudman, 1971, 1972, 1974); ciliated sperm groove (Lalli & Gilmer, 1989); sperm groove (Morse, 1976)]. The extrapallial transport structure of sperm (duct or groove) is absent (0) or present. If present, it is an embedded extrapallial spermiduct (also called 'pars proximalis') (1), or an extrapallial sperm groove running on the body wall (2), an external ciliated groove and an embedded duct occurring simultaneously as observed in several shelled ascoglossans (6), a hermaphroditic pars proximalis owing to migration of the posterior female genital aperture forward leading to fusion with the male anterior opening (3), extrapallial duct/groove absent, because of anterior fusion (or only migration, as in *Oxynoe*) of the female aperture with the male genital aperture in a common genital aperture (4), and functionally replaced by a vas deferens located in the visceral cavity, and extrapallial duct/groove absent because of a migration of the male genital aperture to a posterior position close to the female genital aperture (5). The open groove of *Littorina littorea* is autapomorphic (Reid, 1989) in this analysis.

D. Genital apertures
The female aperture of *Littorina littorea* is located on the right side of the pallial floor, the male aperture at the tip of the penis under the right cephalic tentacle. Owing to their position, the posterior female aperture of the gonochoristic gastropods is here considered homologous with the posterior common genital aperture of the hermaphroditic gastropods. The subtentacular male apertures (or anterior apertures) of hermaphroditic and gonochoristic gastropods are homologous. In many hermaphroditic gastropods, posterior and anterior apertures are fused into an anterior or posterior vestibule or atrium. The migration of the anterior penial aperture posteriorly to form the

common genital aperture together with the female aperture has been described in nudibranchs by Tardy (1970). These conditions have already been coded in the preceding character.

59. Prostate
The shape and location of the prostate are diverse. The prostate is elongated, and it may surround either the vas deferens (or a large hermaphrodite duct), or the prostatic channel of the hermaphroditic duct (0). It may be independent of these ducts and open into the carrefour (1), or open close to the dorso-cephalic penis as a penial gland (2) or open into the pallial gonoduct (3). It may be elongated along the pallial spermiduct and composed of many digitate follicles (or evaginations) (4). It may run along the extrapallial spermiduct (5) or open into the proximal portion of the pallial autospermiduct (7) or finally may be absent (6).

60. Male copulatory organ
The copulatory organ is absent (0), present and always exterior even in the non-breeding period and/or folded on itself in the pallial cavity (1), retractile into an internal haemocoelic penial sheath and everted for copulation (2).

61. Ejaculatory duct
The autosperm is carried to the tip of the penis along an ejaculatory groove (0) or in a closed ejaculatory duct (1).

62. Spermatophore
A spermatophore is a defined mass of sperm which is enclosed in a soft or cuticular membrane, and which is transferred to the partner during copulation. Spermatophore is absent (0) or present (1).

SPAWN
The structure of the spawn cannot be used in the present analysis because it is too diverse, and because several other shapes and structures probably exist that are not represented in the present data set. Only the calcified egg wall, which seems to occur universally in land snails, will be considered here.

63. Chalazae
The occurrence of chalazae has been considered a synapomorphic character by Haszprunar (1988) and Salvini-Plawen & Steiner (1996). Nevertheless, it appears that its taxonomic distribution may be not so simple (Houbrick, 1981; Robertson, 1985; Ponder,

1990), in part because of doubtful homology. Chalazae unite capsules (albuminate eggs embedded in a capsular wall) and not the eggs themselves (Fretter & Graham, 1994). This distinction is often complicated by confusions in terminology (see *Campanile*, *Valvata*, in Appendix 1). Moreover, chalazae are considered to be absent only if capsules are close to each other, as described by Bandel (1976) in *Aglaja*. The 'chalazae' of veronicellids, which are made up of filaments of mucus, are not here considered homologous with other chalazae. The chalazae are absent (0) or present (1).

64. Calcified egg wall

In land snails except Succineidae, each egg is individually released with a calcified membrane. The latter is absent (0) or present (1).

DEVELOPMENT

65. Polar lobes

Polar lobes appear during the first stages of development of many caenogastropods, where they induce acceleration of embryological mechanisms such as cellular division (Verdonk, 1979; Freeman & Lundelius, 1992). The occurrence of polar lobes has been described and discussed by Fol (1879), Pelseneer (1911), Verdonk & Van der Biggelaar (1983) and Van der Biggelaar (1996), and has been used for phylogenetic analysis by Ponder & Lindberg (1997), who interpreted the occurrence of polar lobes as a synapomorphy of a new taxon, Sorbeoconcha. The polar lobes are absent (0) or present (1).

MORPHOLOGY OF SPERMATOZOA

The morphology of spermatozoa has been reviewed by Healy (1988, 1993) and Koike (1985). Ponder & Lindberg (1997) included these characters in their phylogenetic analysis of Gastropoda. Plesiomorphic spermatozoa are found in externally fertilizing gastropods, whereas modified spermatozoa are found in internally fertilizing gastropods such as neritimorphs, the vetigastropod genus *Zalipais* (Healy, 1990a) and Apogastropoda. The characters used here have been taken from the studies of Thompson (1973b), Healy (1983a, b, 1986a, b, c, 1987, 1988, 1990a, b, 1991, 1993), Healy & Willan (1984, 1991), Koike (1985), Healy & Jamieson, 1989, 1991) and Ponder & Lindberg (1997).

66. Granules of the glycogen piece

Few distinct morphologies of glycogen granules occur in the sperm tail. The glycogen piece is short (0), long with granules arranged as nine tracts (1), or long with granules arranged as a continuous sheath (2).

67. Acrosomal vesicle

The vesicle located at the apex of the acrosome is conical (0), rounded (1), or irregular or absent (2).

68. Accessory membrane of acrosomal vesicle

An accessory membrane is present in several caenogastropods. It is absent (0) or present (1).

69. Subacrosomal material

Subacrosomal material occurs in the apogastropods. It is absent (0), curved dish-shaped (2), conical (3), columnar (4), or occurs as a basal plate (1).

70. Mitochondria in sperm midpiece

The midpiece is very short and contains only few discrete mitochondria in vetigastropods (0); it is long with many mitochondria (1) or it forms a continuous sheath (2).

71. Paracrystalline material in sperm midpiece

Paracrystalline material is is absent (0) or present (1).

72. Cristae

Cristae in mitochondria are easily recognizable (0) or reduced or lost (1).

73. Coarse fibres

Periaxonemal coarse fibres are absent (0) or present (1).

74. Intra-axonemal dense granules

They are absent (0) or present (1).

75. Paraspermatozoa

Paraspermatozoa are absent (0) or present (1).

76. Temporary support cylinders

The apogastropod spermatids seem to be associated with temporary support cylinders (1) or none (0).

77. Microtubular sheath

The spermatid midpiece and nucleus development seems to associated with a microtubular sheath in apogastropods (1) which may be absent (0).

RESULTS

DATA ANALYSES

In a first step all the characters were unordered, undirected and equally weighted 1 (analysis I in Table 1; Fig. 2). To test the consistency of this result we tested several assumptions of character weights and types, either as alternative hypotheses of coding or different weights were given to characters formerly considered to be key characters in the phylogeny of the Euthyneura. Only eight out of many resulting trees were selected, as representing *a posteriori* the minimum sample to test the consistency of our phylogenetic results (analyses II–VIII in Table 1). For each analysis, all heuristic options provided similar results (General, starting trees, stepwise addition, branch
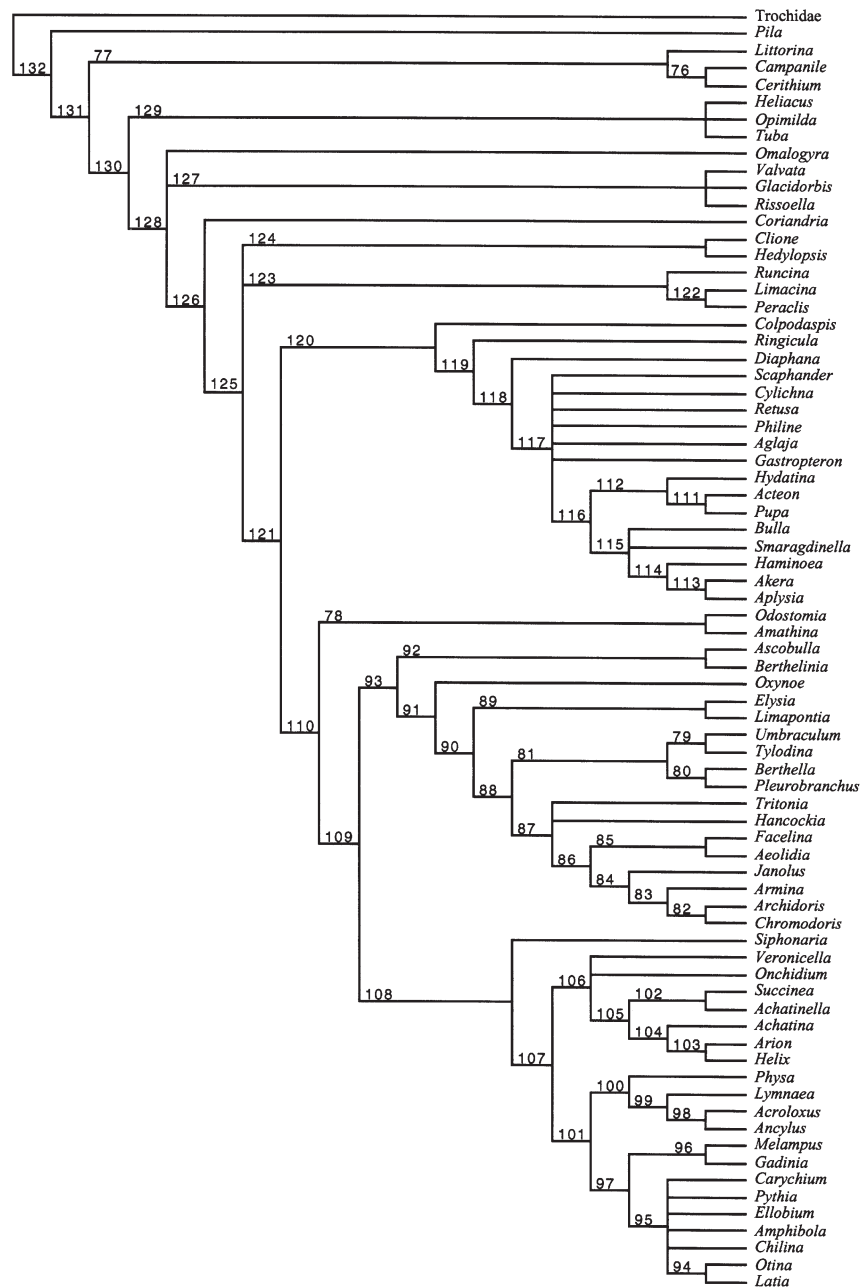

Figure 2. Strict consensus tree of 3446 equally parsimonious trees, for analysis I (all the characters unordered, undirected and unweighted; see Table 1). Data matrix is shown in Appendix I. Node numbers are those used in Appendix 4 where character changes at each node are listed.

swapping). Random addition sequence (reps = 10) option was not completed (the second replicate had to be stopped), but provided trees 337 steps length, instead of 336 in the former options. Consequently, we only provide the general option results. Similar results were obtained with the ACCTRAN and DELTRAN assumptions (Swofford & Maddison, 1987). We show only the default ACCTRAN. Equiparsimonious trees (always a few thousands) were condensed in a strict consensus tree (not shown here). Consistency indices of all characters in all analyses are listed in Appendix 3. Character change lists of analysis I are shown in Appendix 4.

The fact that extremely contradictory results were obtained from the various analyses I–VIII although few changes in characters were tested, suggesting that data are very inconsistent, and include a very high proportion of homoplastic states. Stable characters were very rare in our dataset, as shown by the induction of important topological modifications in trees and in character histories by slight modifications in characters. For example: (a) only analysis I could be completed, although it differed from the other analyses shown here only by weight of a single character weight or type; (b) analyses II and III differed by the weight of the ascus only (character 33, weight 3 and 4, respectively), and provided two highly incongruent topologies. This may indicate that the present dataset could easily provide any phylogenetic assumption through differential character weighting. In the discussion of characters below, we try to establish which appear to be phylogenetically informative.

The technique employed to test the influence of multiple random replications on topology gives the same phylogenetic results for every analysis.

HOMOLOGY A POSTERIORI AND EVOLUTION OF CHARACTERS

1. Orthostrophic/heterostrophic shell
The acquisition of heterostrophy is a unique event only with this character weighted 4 (analysis IV) instead of 1 (other analyses). In the consensus tree of the analysis IV, heterostrophy is acquired before the Architectonicoidea split. In the other analyses, it is acquired at least twice. It is always secondarily lost in the taxon (Stylommatophora + Systellommatophora).

2. Protoconchs I & II
This character is a synapomorphy of Sorbeoconcha (Ponder & Lindberg, 1997).

3. Operculum
In spite of a low CI and variable evolutionary history, our analyses show that the occurrence of an operculum could be secondary even though this organ has always been interpreted as 'primitive', as in *Amphibola* or Acteonoidea (it is particularly clear in analysis I, in which the loss of the operculum is unique).

4. Pedal gland
This character supplies three crucial synapomorphies: the acquisition of a postero-ventral gland in Pleurobranchoidea, the acquisition of an anterior pedal gland lying free on the floor of visceral cavity in Geophila, and its transformation into a gland lying beneath a membrane (as in Stylommatophora). The ellobiid pedal gland is not interpreted as a distinct apomorphic character state (4) here, but as plesiomorphic (0).

5. Thecosomatous pedal wings
The occurrence of thecosomatous wings is a synapomorphy of Thecosomata.

6. Cephalic shield
The occurrence of a cephalic shield has been interpreted as a synapomorphy of diverse taxa, such as the Euthyneura by Haszprunar (1988), Opisthobranchia by Huber (1993) and Salvini-Plawen & Steiner (1996), and Sacoglossa by Jensen (1996a, b). These interpretations imply that the head shield has been acquired only once but secondarily lost several times. According to our coding and results, the cephalic shield has only been lost in Aplysioidea. In all analyses its absence can be interpreted as plesiomorphic in taxa such as the Nudibranchia, Notaspidea and Pulmonata. The ambiguous relative position of the Sacoglossa implies that its acquisition is convergent in this taxon and in the Cephalaspidea.

7. Hancock's organs
The co-occurrence of paired Hancock's organs, and of a cephalic shield, has been formerly interpreted as correlated synapomorphies (Salvini-Plawen & Steiner, 1996). Our present analysis shows Hancock's organs as a synapomorphy of the Cephalaspidea only, secondarily lost in the Aplysioidea.

8. Retractile tentacles
The occurrence of retractile tentacles is a synapomorphy of Stylommatophora.

9. Position of the eyes
The occurrence of the eyes at the tip of posterior tentacles is always interpreted as a synapomorphy of the whole (Stylommatophora + Systellommatophora).

10. Cerata filled with cnidocysts

The occurrence of cerata filled with cnidocysts is a synapomorphy of Aeolidoidea.

11. Pallial cavity

Acquisition of a pneumostome is generally considered to be a synapomorphy of Pulmonata (Salvini-Plawen & Steiner, 1996) and this is in agreement with our results, with the non-contractile pneumostomes of *Gadinia* and *Siphonaria* being homologous with true contractile pneumostomes.

12. Osphradium

The history of this character, which has been repeatedly lost and found according to all analyses, can hardly be traced. This result is not totally satisfying, because the evolution of this character could be less complex (Ponder & Lindberg, 1997).

13. Si1 & Si2 cells

The occurrence of Si1 & Si2 cells has been interpreted as homoplastic by Ponder & Lindberg (1997), being independently acquired in Cerithiidae and Hypsogastropoda. It cannot be interpreted here because of unsufficient data.

14. Si4 cells

In agreement with Haszprunar (1988) and Ponder & Lindberg (1997), occurrence of Si4 cells is a synapomorphy of Sorbeoconcha.

15. Pallial caecum

The evolutionary history of this character remains uncertain, except that the pallial caecum has been secondarily lost in Aplysioidea and the pallial caecum of *Chilina* is convergent with that of cephalaspideans.

16. Raphes

Raphes of *Chilina*, Architectonicoidea and cephalaspideans should be considered as analogous structures and reinvestigated.

17. Plicatidium

According to analyses I–V, the gills of *Runcina* and shelled sacoglossans (*Ascobulla* and *Berthelinia*) should be considered as convergent with that of cephalaspideans. Even in analysis VI (in which the transformation of this character is ordered and directed as '0–1-2'), the gill of the shelled sacoglossans is never derived from that of cephalaspideans. The plicatidium cannot be considered as a synapomorphy of the Opisthobranchia but could be considered as a synapomorphy of the Cephalaspidea (with or without *Runcina*). The hypothesis of two convergent acquisitions is supported by the presence of a one-sided plicate gill, morphologically similar to that of *Ascobulla* and *Berthelinia*, in *Siphonaria*. Gill folds of *Tuba* (coded as 0/2), are also shown to be a convergent structure. Further studies on the histology and ontogeny of these gills are needed, in order to elucidate character homology.

18. Branchial circlet

The occurrence of a branchial circlet is a synapomorphy of Doridoidea, as it has always been hypothetized.

19. Pinnate gill

The occurrence of a pinnate gill has previously been interpreted as an important synapomorphy of the Notaspidea (Willan, 1987). However, notaspidean monophyly is not supported by any other strong character, and the evolutionary history of the pinnate gill could be different. From analyses III and IV, the pinnate gill is acquired before the notaspideans and secondarily lost before the Nudibranchia. More detailed investigations of these gills are needed to at least determine their homology.

20. Prebranchial pocket

The occurrence of prebranchial pocket is a synapomorphy of the Pleurobranchoidea.

21. Pulmonary vessels

The acquisition of pulmonary vessels is interpreted as a synapomorphy of Pulmonata. The absence of vessels in Onchidiidae has always been interpreted as secondary and is not surprising, given the reduction of their lung. The absence of pulmonary vessels in *Siphonaria* is also secondary (III, V, VI) or not (I, IV, VI).

22. Hypobranchial gland

The evolutionary history of this character is too variable, except for the acquisition of a gland secreting a web being a synapomorphy of the Thecosomata. Its interpreted occurrence in *Runcina* (which lacks a gland) in analysis I, results from its coding as (?).

23. PMO

The occurrence of a PMO has been considered as an important synapomorphy of Heterobranchia (less Val-

vatidae; *sensu* Haszprunar) by Haszprunar (1988) and by Salvini-Plawen & Steiner (1996). In the analysis VII, the pigmented blotches occurring in Rissoella and Omalogyra (Fretter, 1948) have been unambiguously considered as homologous with a PMO (Haszprunar, 1985a; Ponder, pers. comm.). In all other analyses, they have been coded as an ambiguous PMO alternatively absent or present (Robertson, 1985). Variable and contradictory evolutionary character histories were obtained. The number of acquisitions varies from one (for Euthyneura (including Pyramidelloidea) + Architectonicoidea, as in analysis I, and for Euthyneura (excluding Thecosomata and Gymnososmata) + Rissoella + Omalogyra + Valvata, as in analysis (VII), to three (as in analysis V). The number of losses of the PMO is also highly variable. A reason for this was that coding was ambiguous for many taxa, resulting in the PMO being interpreted as present or absent in taxa such as *Coriandria*, *Omalogyra*, *Rissoella*, *Limacina* and *Peraclis*. The history of the PMO is consequently considered unresolved here, in part as a result of ambiguous descriptions and coding.

24. Purple gland
The acquisition of a purple gland is a synapomorphy of Aplysioidea (including *Akera*). The glands of *Scaphander* and *Cylichna*, coded (0/1), were not subsequently interpreted as purple glands.

25. Opaline gland
The acquisition of an opaline gland is a synapomorphy of Aplysioidea (including *Akera*). The gland of *Runcina*, coded (0/1), was not subsequently interpreted as a opaline gland.

26. Blood gland
A blood gland is primarily acquired for all opisthobranchs (except Acteonoidea and pteropods, but including the Pyramidelloidea) in analyses III and IV. This result, however, implies that a blood gland occurs in all the opisthobranchs in which this character is principally coded as uncertain. In other analyses, at least three distinct acquisitions of a blood gland are inferred, and in our opinion, blood glands should be considered analogous structures. Further comparative studies are needed to establish if these glands can be interpreted as three synapomorphies (for the cephalaspideans, notaspideans and, in part, nudibranchs).

27. Renopericardial duct
The differenciation of the renopericardial duct into a syrinx may constitute a synapomorphy of Nudi-

branchia. This assumption needs to be tested by observations in more nudibranch taxa.

28. Secondary ureter
The occurrence of a secondary ureter is a synapomorphy of Stylommatophora. The ureter of *Veronicella* and that of *Achatinella* coded (0/1) can be, respectively, interpreted as primary and secondary ureter *a posteriori*.

29. Nephridial gland
Loss of the nephridial gland appears as a synapomorphy of Heterobranchia. Further studies are nevertheless needed because this character has been very poorly described.

30. Jaws
The evolutionary history of the jaws is chaotic, except in Geophila (Stylommatophora + Systellommatophora). In analyses where the latter are monophyletic (all except IV), the acquisition of an unpaired jaw is a unique event (this unpaired jaw is secondarily lost in Onchidiidae).

31. Evaginable proboscis
This character is a synapomorphy of Pyramidelloidea.

32. Acid gland
The occurrence of acid gland is a synapomorphy of Pleurobranchoidea, as suggested by Willan (1987).

33. Ascus
The presence of an ascus is a synapomorphy of the Ascoglossa in analyses III (where it is weighted 4) and V. In analyses I, IV and VI, the ascus is primarily acquired and secondarily lost; in analysis II, it is independantly acquired three times (see analyses I–VI in Table 1, and Appendix 3). In our view, the complexity of this structure, in conjonction with unique and complex biological characters such as suctorial feeding (Jensen, 1993) and symbiotic retention of functional chloroplasts (Clark & Busacca, 1978), justifies reweighting this character enough to imply monophyly of the Sacoglossa.

34. Odontophoral cartilage
Loss of odontophoral cartilage seems to be homoplastic. Insufficient data and descriptions prevent further intepretation.

35. Odontoblasts
The evolutionary history of odontoblasts is highly variable and contradictory between analyses, because

of inadequate descriptions, particularly in non-euthyneuran taxa. Consequently it is impossible to interpret character states as synapomorphies (see Salvini-Plawen & Steiner, 1996). Nevertheless, the undifferentiated odontoblasts occurring in *Acteon* and *Limacina* seem to be convergent.

36. Oesophageal gizzard
Evolutionary history of this character is complicated by (a) the variable position of the Acteonoidea among the Cephalaspidea in different analyses, and (b) multiple acquisitions and losses in all consensus trees.

37. Pouch of gastric gizzard
Acquisition of a gastric gizzard can be interpreted either as a synapomorphy of Pulmonata, if they are monophyletic (as in analyses III, IV and VI), or as a synapomorphy of the Basommatophora (except *Siphonaria*), if they are monophyletic (as in analysis I). In every case, the gastric gizzard can be lost secondarily. Here we interpret the numerous convergent acquisitions of a gastric gizzard in analysis II as a weighting artefact. In analysis I, monophyly of basommatophorans (except *Siphonaria*) is supported by only one character (40). The evolutionary history of this character in relation to the monophyly of basommatophorans remains unresolved.

38. Gastric caecum
It seems clear that gastric caeca have been independently acquired and lost in the course of euthyneuran evolution.

39. Shape of faeces
The occurrence of pellet-shaped faeces is here interpreted as a synapomorphy of Sorbeoconcha rather than Caenogastropoda (Ponder & Lindberg, 1997) because this character is undescribed in *Pila* (Ampullarioidea), although pellet-shaped faeces 'generally' occur in Ampullarioidea according to these authors.

40. Streptoneury/euthyneury
No transformation from one state to another can be interpreted as a synapomorphy because the evolutionary history of the visceral loop is too variable between analyses, as already concluded by Haszprunar (1988). Neverthelesss, streptoneury of the visceral loop of Acteonoidea is always interpreted being secondary in our analyses.

41. Hypoathroid/epiathroid circumoesophageal nerve ring
No transformation from one state to another can be interpreted as a synapomorphy because the evolutionary history of the visceral loop varies too much from one analysis to another. Acquisition of the epiathroid condition, which is a synapomorphy of Heterobranchia in analyses I and II only, cannot be reasonably taken into account.

42. Circumoesophageal nerve ring
No transformation from one state to another can be interpreted as a synapomorphy here because the evolutionary history of this character varies too much between analyses.

43. Left parietal ganglion
A left parietal ganglion always appears independently in three taxa (*Latia*, *Akera* and Acteonoidea) in all analyses. Note that all the *a priori* ambiguous codings have been *a posteriori* interpreted as (0) except in *Hydatina* (left parietal ganglion present).

44. Right parietal ganglion
No transformation from one state to another can be interpreted as a synapomorphy because the evolutionary history of the right parietal ganglion varies too much from one analysis to another. The synapomorphic acquisition of the right parietal ganglion in some cephalaspideans occurs in analysis I only. Moreover, *a priori* ambiguous codings are variously interpreted *a posteriori*. Consequently the evolutionary history of this character is uncertain.

45 & 46. Subcerebral & parapedal commissures, and 47 & 48 Position of the suboesophageal and supraoesophageal ganglia
These characters are very homoplastic in the analyses.

49. Procerebrum, and 50 Medio-dorsal bodies
Here the occurrence of a procerebrum and medio-dorsal bodies are synapomorphies of Pulmonata, except in analysis II because of what we consider to be a weighting artefact. All *a priori* unknown codings in Pulmonata have been interpreted as possessing a procerebrum and medio-dorsal bodies.

51. Ampulla
Ponder & Lindberg (1997) considered that the ampulla of hermaphroditic genital systems and the seminal

vesicle of gonochoric genital systems are analogous, whereas here we interpreted them as homologous organs. Consequently, the acquisition of an ampulla here is interpreted as a synapomorphic character of the taxon (Sorbeoconcha + Heterobranchia), whereas the acquisition of a seminal vesicle is interpreted as a synapomorphic character of Sorbeoconcha only by Ponder & Lindberg (1997). The homology of this character should be investigated in further phylogenetic studies of Gastropoda.

52. Sphincter of the carrefour

Our results suggest that the two types of sphincter should be considered analogous characters: one is a synapomorphy of Nudibranchia, and one occurs in *Physa* only. In analysis I, the Hygrophyla are monophyletic and the occurrence of a sphincter is *a posteriori* generalized from *Physa* to the whole taxon.

53. Fertilization pouch

The acquisition of a fertilization pouch is homoplastic. The pouches are probably not homologous organs.

54. Albumen gland

Two transformations are constant in all analyses: the occurrence of a pair of glands opening into the carrefour (state 6), which is a synapomorphy of the Elysioidea; and the occurrence of a median gland mass (state 8), which is a synapomorphy of (*Armina* + Doridoidea).

55. Course of the eggs

The evolutionary history of this character is highly variable among analyses, probably because of both ambiguous coding and homoplasy within Euthyneura.

56. Membrane gland

Only two autapomorphies occur in all analyses: the occurrence of the state (4) in *Aglaja* and the occurrence of state (6) in *Gastropteron*. The evolutionary history of other character states is uncertain.

57. Mucous gland

The acquisition of a mucous gland in two parts (the first opening into the vestibule and the second surrounding the pallial gonoduct, i.e. state 6) is interpreted here as a constant synapomorphy of the Bulloidea. The evolutionary history of other character states is highly variable.

58. Extrapallial duct or groove

This character provides two synapomorphies related to the position of the genital apertures. The anterior migration of the female aperture (state 4) is a synapomorphy of Stylommatophora, its occurrence within the shell-less Sacoglossa apparently convergent. The posterior migration of the male aperture (state 5) can be interpreted as a synapomorphy of Eleutherobranchia (Notaspidea + Nudibranchia), which would revert in Umbraculoidea (as in analysis I) or in the taxon (Pleurobranchoidea + Nudibranchia) as in analyses III and IV. This last case implies paraphyly of the notaspideans. The posterior migration of the male aperture appears to be convergent in *Otina*. Other character states are highly homoplastic and variable *a posteriori* (particularly the transformations between ducts and grooves), and it appears that coding the position of genital apertures only might have been more efficient.

59. Prostate

Character states are too homoplastic and induce too much variation in possible histories to be interpreted here.

60. Copulatory organ

Haszprunar (1988) already proposed synapomorphic acquisition of a 'retractile penis' for taxon (Euthyneura + *Glacidorbis*). No transformation can be interpreted unambiguously here because the evolutionary history of the copulatory organ varies too much from one analysis to another.

61. Ejaculatory duct

This character is too homoplastic in the analyses.

62. Spermatophore

Spermatophores seem to be analogous structures. This view is supported by the diverse shape and structure of these structures.

63. Chalazae

Chalazae were interpreted as a synapomorphy of (Heterobranchia + Campanilomorpha) by Haszprunar (1988), and of Heterobranchia only by Salvini-Plawen & Steiner (1996). The present analyses suggest that the chalazae are analogous. This interpretation is also supported by the existence of many other so-called 'adaptive chalazae' (see 'Characters' in the present paper), which were not taken into account *a priori*.

64. Calcified egg wall

The acquisition of a calcified egg wall is an unique event in all analyses here. It supports the monophyly of the taxon (*Achatina* + *Arion* + *Helix*) with a CI = 1, or of Stylommatophora with a CI = 0.5. In the latter case, the calcified egg wall has been lost in *Succinea* and *Achatinella* secondarily.

65. Polar lobes

In agreement with Ponder & Lindberg (1997), the acquisition of polar lobes is here interpreted as a synapomorphy of Sorbeoconcha.

66–77. Morphology of spermatozoa

These characters are crucial synapomorphies for phylogeny within Apogastropoda, as previously discussed by Haszprunar (1988), Salvini-Plawen & Steiner (1996) and Ponder & Lindberg (1997). We obtain similar results here. However, the evolutionary history of these characters can differ from that of preceding works, because in our analyses the position of Architectonicoidea differs from that found by Ponder & Lindberg (1997), and the taxon (Architaenioglossa + Sorbeoconcha) is found to be paraphyletic. In agreement with Haszprunar (1988), the absence of paraspermatozoa in Heterobranchia is here interpreted as a secondary loss, whereas Ponder & Lindberg (1997) interpreted this absence as plesiomorphic in relation to the monophyly of Caenogastropoda (i.e. including Architaenioglossa).

PHYLOGENETIC AND TAXONOMIC ANALYSES

Classification cannot be extensively discussed here because of numerous unresolved relationships (and the taxonomic sample should probably be expanded). However, the present lack of resolution is an important result for the future of Euthyneuran classification, as many characters formerly considered important appear to be of little or no utility. Conversely, the few monophyletic taxa and their relative synapomorphies that have been obtained from analyses must be emphasized, although results need to be tested by further studies. This is particularly important in the case of characters that remain undescribed in several taxa, although they represent potentially crucial synapomorphies (e.g. character 29 for Heterobranchia, or character 27 for Nudibranchia). The relationships that can be inferred from the present results are shown in Fig. 3, a consensus of the nodes retained in the various analyses. The unambiguous synapomorphies which support these relationships are also shown.

Heterobranchia include allogastropod taxa of unresolved relationships, but which emerge basally, and the clade Euthyneura. Monophyly of the Heterobranchia is supported by the loss of the nephridial gland (character 29). Phylogeny within allogastropod taxa (Architectonicoidea, Omalogyridae, Valvatidae, *Glacidorbis*, Rissoellidae, Cingulopsidae) remains unresolved. The Heterobranchia do not include Valvatidae according to Haszprunar (1988), whereas we conclude the contrary, in agreement with Ponder & Lindberg (1997). Nevertheless, the Architectonicoidea seem to be the most basal heterobranch taxon and the Cingulopsidae could be the sister group of the Euthyneura (analyses I, II and VI). Note that *a priori* the analogous gills and analogous hermaphroditic genital apparatus of Heterobranchia are so different that they cannot be coded as a single character, even though a single change can be inferred *a posteriori* from the trees for both gills and hermaphroditism. Even if we cannot trace the precise evolutionary history of these sets of characters, the loss of the caenogastropod pallial gill has no exceptions, and the loss of gonochorism has only very few exceptions. Further studies (developmental, anatomical, ecological) are needed to elucidate the complex evolutionary pattern of the gills and genital systems in Euthyneura.

The basal emergence of the Architectonicoidea and the monophyly of the taxon (Heterobranchia except Architectonicoidea) are supported by sperm characters: occurrence of a long glycogen piece with granules arranged as a continuous sheath (state 2 of character 66); transformation of a curved dish-shaped subacrosomal material (state 2 of character 69) into a columnar material (state 4); occurrence of a paracrystalline material in sperm midpiece (character 71); and loss of mitochondrial cristae (character 72). Nevertheless, this position is contradicted by analysis IV (in which character (1) is weighted 4 instead of (1)), in which the Architectonicoidea is the sister group of the Euthyneura (including Pyramidelloidea). The position of the Architectonicoidea therefore depends on the relative importance of sperm characters and heterostrophy.

The position of the Cingulopsidae as the sister group of the Euthyneura is only supported by variable characters, such as the osphradium (character 12), the visceral loop condition (character 40), and the position of the suboesophageal and supraoesophageal ganglia (characters 47 & 48). Consequently, our results do not resolve the phylogenetic position of Cingulopsidae, which is traditionally considered to be a caenogastropod taxon (Ponder & Yoo, 1980). The problematic position of this family in our results is probably a consequence of the lack of other typical caenogastropod taxa and characters in our data matrix.

One possible synapomorphy of Euthyneura is the loss of the operculum (character 3). Euthyneura
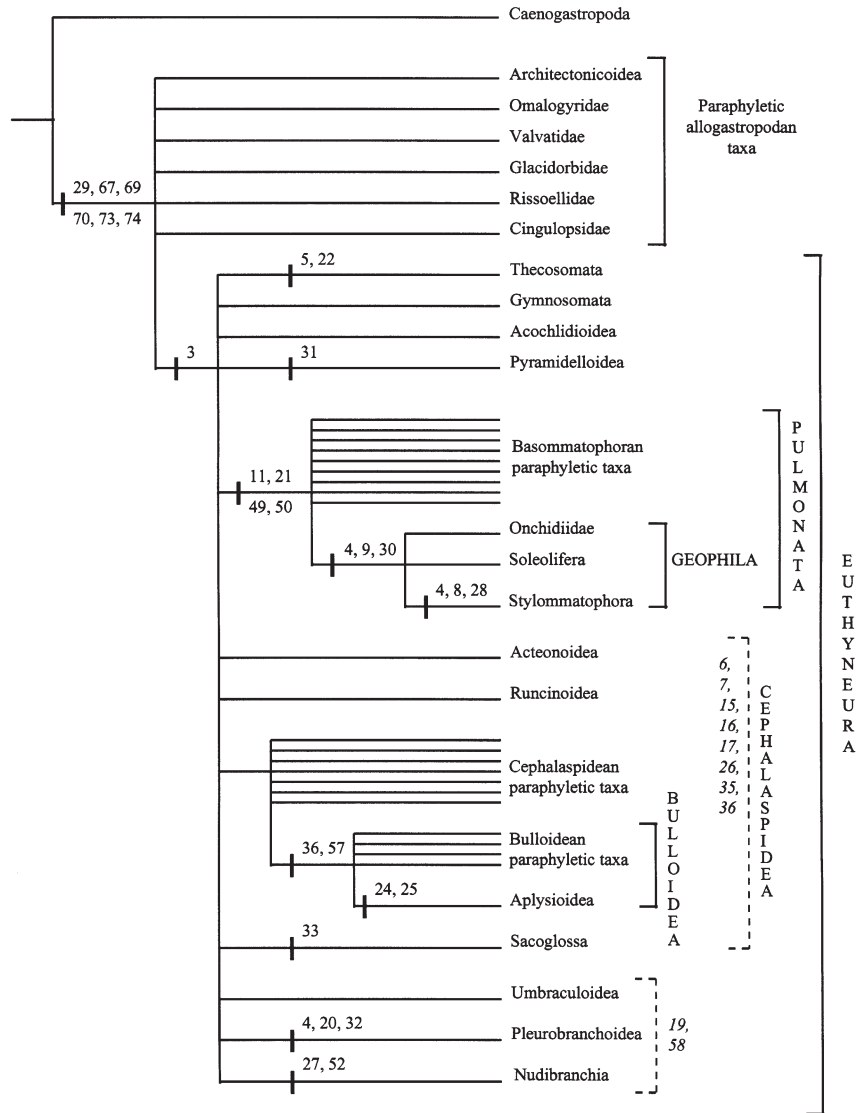
Figure 3. Proposition of a phylogeny of Heterobranchia. Here well supported nodes according to present results and character discussions are shown only. Interrupted lines indicate possible phylogenetic relationships. Unambiguous synapomorphies supporting the phylogenetic relationships of euthyneuran taxa are shown by character numbers such as listed in the text. The character numbers in italics are potentially important but require further analysis and discussion (see phylogenetic and taxonomic results).

includes several clades for which it would be illusive to propose phylogenetic relationships from the present results: paraphyletic taxa of opisthobranch (Thecosomata, Gymnosomata, Acochlidioidea, Pyramidelloidea, Runcinoidea, Acteonoidea, Cephalaspidea, Sacoglossa, Umbraculoidea, Pleurobranchoidea and Nudibranchia) and Pulmonata.

Monophyly of the Pulmonata is supported by several or few characters: acquisition of a pneumostome (11), acquisition of pulmonary vessels (21), presence of a procerebrum (49) and dorsal bodies (50). Pulmonata

includes paraphyletic basommatophoran taxa and the monophyletic taxon Geophila. The latter name was introduced by Férussac, 1819) to designate the grouping of Onchidiidae, Soleolifera and Stylommatophora (even though these subtaxa were not so named by him). The synapomorphies that we found supporting the monophyly of the Geophila are: eyes located at the tip of posterior tentacles (9), acquisition of a long pedal gland located upon the floor of the visceral cavity (4), and acquisition of an additional unpaired jaw (30). Although we did not find any synapomorphy for Sys-

tellommatophora (Soleolifera + Onchidiidae), several synapomorphies support monophyly of the Stylommatophora: a long pedal gland placed beneath a membrane (4), the occurrence of retractile tentacles (8), and the acquisition of a secondary ureter (28).

Several characters unambiguously support the monophyly of clades within Euthyneura. Thecosomata: thecosomatous wings (5) and hypobranchial gland secreting a web (22); Pyramidelloidea: evaginable proboscis (31); Aplysioidea: purple gland (24), opaline gland (25); Pleurobranchoidea: postero-ventral pedal gland (4), prebranchial pocket (20), and acid gland (32); and Nudibranchia: renopericardial duct differentiated into a syrinx (27) and carrefour sphincter (52).

The occurrence of an ascus (character 33) is interpreted as a strong synapomorphy of the Sacoglossa, even though their relationships with euthyneuran taxa remain unresolved. According to Mikkelsen (1996) and Jensen (1996a, b), the sister group of Sacoglossa could be a cephalaspidean taxon, but this relationship is shown in our analysis.

The monophyly of Cephalaspidea is supported by the presence of a cephalic shield (6), Hancock's organs (7), pallial caecum (15), raphes (16), plicatidium (17), blood gland (26), and odontoblasts (35). Their inferred evolutionary history varies in relation to the inclusion of the Acteonoidea (represented here by the genera *Hydatina*, *Acteon* and *Pupa*), Sacoglossa and Runcinoidea *(*represented here only by the genus *Runcina*).

Acteonoidea is: (1) the sister group of Bulloidea (as in analyses I, II and V) and thus terminally included within the Cephalaspidea, (2) the sister group of Cephalaspidea and thus basally included in this taxon (analysis VI) or (3) excluded from the Cephalaspidea (analyses III and IV). No character constantly supports monophyly of the Acteonoidea, although the group was monophyletic in all analyses. The following characters were synapomorphies for the group in the various analyses (see Appendix 4 for details): odontoblasts (35), visceral loop condition (40), left parietal ganglion (43), extrapallial part of the genital duct (58), prostate (59), copulatory organ (60) and ejaculatory duct (61).

Runcina, because of its highly simplified anatomy, has a very variable position in our various analyses. Cephalaspidea (with or without Runcinoidea and Sacoglossa) include paraphyletic taxa (*Scaphander*, *Cylichna*, *Retusa*), and Bulloidea represents one clade whose phylogenetic position does not vary. Monophyly of the Bulloidea is supported by the occurrence of an oseophageal gizzard bearing calcified plates and chitinous spines (36) and by a mucous gland where the first part opens into the vestibule, and the second surrounds the pallial gonoduct (57).

Relationships between Nudibranchia, Pleurobranchoidea and Umbraculoidea are not clearly resolved, even though it seems that these taxa are closely related (analyses I, III–VI). Two characters particularly influence inferred relationships between these three taxa (see also discussion of characters): a pinnate gill (19) and the posterior migration of the male aperture close to the female aperture (58). The Eleutherobranchia was named by Haszprunar (1985a) to group Nudibranchia, Anthobranchia (= Phyllidiidae) and Notaspidea, but it has never been demonstrated that Phyllidiidae should be excluded from Nudibranchia. Three assumptions can be formulated on the phylogeny of Eleutherobranchia: (1) Notaspidea are monophyletic and the sister group of Nudibranchia, (2) Notaspidea are paraphyletic and Pleurobranchoidea are the sister group of Nudibranchia and (3) Notaspidea are paraphyletic and the sister group of Nudibranchia remains unknown. The first hypothesis (analyses I and VI) is supported by the unique presence of a pinnate gill (19) for Notaspidea, and a primary posterior migration of the male aperture (58) in Eleutherobranchia, secondarily reverted in Umbraculoidea. The second hypothesis (analyses III and IV) is supported by the unique posterior migration of the male aperture in (Pleurobranchoidea + Nudibranchia). The third hypothesis implies the same evolutionary history of character (58) as in the first hypothesis, plus independent acquisitions of pinnate gills. We consider the migration of the male aperture as a stronger phylogenetic signal than the occurrence of a pinnate gill, which can be easily lost. Therefore we favour Pleurobranchoidea as the sister group of Nudibranchia, because they share a posterior position of the male aperture. The monophyletic group including Pleurobranchoidea and Nudibranchia has been recently called Nudipleura (Wägele & Willan, 2000). The Umbraculoidea would then be the sister group of the latter taxon (Pleurobranchoidea + Nudibranchia), as proposed by Salvini-Plawen & Steiner (1996).

CONCLUSION

We aimed to assess the variability of characters as precisely as possible utilizing several coding principles, and attempting to avoid the use of preconceived interpretations or generalizations in the construction of the data matrix. This method has allowed the identification of gaps and imprecisions in descriptions, which led in turn to the re-evaluation of previously accepted synapomorphies and the proposal of previously unconsidered characters.

The lack of adequate descriptions prevented the use of several characters in the data matrices, such as the occurrence of podocytes. It also prevented the precise

tracing of evolutionary histories of some characters, or the confirmation of some previously proposed synapomorphies. For example, the occurrence of odontoblasts (character 35) was previously interpreted as a synapomorphy of Euthyneura by Salvini-Plawen & Steiner (1996), and that of a PMO (character 23) was previously interpreted as a synapomorphy of Heterobranchia (less Valvatoidea *sensu* Haszprunar) by Haszprunar (1988) and Salvini-Plawen & Steiner (1996), but it was not possible to trace their evolutionary history here.

The present codings and results have allowed a re-evaluation of characters. Even though several synapomorphies were confirmed (such as those defining Pulmonata and Stylommatophora), and some new synapomorphies were proposed (the occurrence of a syrinx for the Nudibranchia), the evolutionary history of many characters appears to be more complicated than formerly thought. Several characters previously interpreted as synapomorphies are interpreted as highly homoplastic. Examples are the occurrence of chalazae (character 63), previously interpreted as a synapomorphy of Heterobranchia (*sensu* Haszprunar) by Haszprunar (1988) and Salvini-Plawen & Steiner (1996), the occurrence of parietal ganglia (characters 43 & 44), which was interpreted as a synapomorphy of Euthyneura by these authors, and the occurrence of a subcerebral commissure (character 45), which was interpreted by Salvini-Plawen & Steiner (1996) as a synapomorphy of the Euthyneura. The evolutionary histories of other characters, such as the occurrence of a cephalic shield (character 6), ascus (character 33) or the posterior migration of male aperture (character 58), require further investigation.

The present phylogenetic results can be considered as unsatisfactory owing to the absence of a fully resolved Euthyneuran phylogeny, even though monophyly of the Heterobranchia and of the Euthyneura plus some subtaxa are confirmed. Nevertheless, the low phylogenetic resolution obtained is a worthwhile conclusion. Indeed, any phylogenetic study has a limit of resolution that fundamentally relates to the variability of the characters. In taking this variability into account as objectively and precisely as possible in the construction of our dataset, the low resolution reflects the high variability of euthyneuran anatomical characters. Establishing the degree of phylogenetic resolution that characters can actually provide is just as important as resolving the tree. We have showed elsewhere (Dayrat & Tillier, 2000) how gradist presuppositions, which result in use of generalization, and *a priori* interpretation for coding, can influence the coding of characters in a data matrix. The present work shows how coding and weighting directly influence phylogenetic results in terms of topology and the evolutionary history of characters. Such an unresolved phylogeny emphasizes the need for additional research and description of morphological characters. Finally, as emphasized in molecular studies, the absence of resolution can indicate some biological or evolutionary phenomenon such as rapidly occurring cladogenetic events, which may result in a scarcity of synapomorphies.

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APPENDIX 1

Data matrix. See character descriptions detailed in the text, and Appendix 2 for the list of bibliographic sources. – indicates unknown data, ? indicates inapplicable character or a problematic coding,/indicates contradictory codings following the sources, & indicates polymorphic character.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Trochidae	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0
Pila	0	?	0	0	0	0	0	0	0	?	0	0	0	–	0	0	0	?	0	0	0	0	0	0	0	0/1
Campanile	0	1	0	0	0	0	0	0	0	?	0	0	0	1	0	0	0	?	0	0	0	0	0	0	0	0
Cerithium	0	1	0	0	0	0	0	0	0	?	0	0	–	–	0	0	0	?	0	0	0	0	0	0	0	–
Coriandria	0	–	0	0	0	0	0	0	0	?	0	0	–	–	0	0	0	?	0	0	0	0	0	0	0	–
Littorina	0	1	0	0	0	0	0	0	0	?	0	0	1	1	0	0	0	?	0	0	0	0	0	0	0	0
Valvata	?	?	0	0	0	0	0	0	0	?	0	0	0	1	0	0	0	?	0	0	0	0	0	0	0	–
Glacidorbis	0	0	0	0/4	0	0	0	0	0	?	0	1	?	0	0	0/1	0	?	0	0	0	1	0	0	0	–
Rissoella	0	0	0	0	0	0	0	0	0	?	0	1	?	?	0	0/1	0	?	0	0	0	0	0/1	0	0	–
Omalogyra	0	0	0	0	0	0	0	0	0	?	0	1	?	?	0	0/1	0	?	0	0	0	0	0/1	0	0	–
Odostomia	1	0	0	0	0	0	0	0	0	?	0	0	0	?	0	1	0	?	0	0	0	0	1	0	0	–
Amathina	1	0	1	0	0	0	0	0	0	?	0	0	–	0	0	1	0	?	0	0	0	1	1	0	0	–
Heliacus	1	0	0	0	0	0	0	0	0	?	0	0	0	–	0	1	0	?	0	0	0	0	0	0	0	–
Opimilda	1	0	0	0	0	0	0	0	0	?	0	0	0	0	0	1	0	?	0	0	0	0	1	0	0	–
Tuba	1	0	0	–	0	1	0	0	0	?	0	0	0	0	0	1	0/2	?	0	0	0	0	1	0	0	–
Acteon	1	0	0	0	0	1	1	0	0	?	0	0	–	0	1	1	1	?	0	0	0	0	–	0	0	–
Pupa	?	–	0	–	0	1	1	0	0	?	0	–	–	–	1	1	1	?	0	0	0	0	–	0	0	–
Ringicula	?	–	1	–	0	1	–	0	0	?	0	–	–	–	1	1	1	?	0	0	0	0	–	0	0	–
Hydatina	?	–	1	–	0	1	1	0	0	?	0	–	–	–	1	1	1	?	0	0	0	0	–	0	0	–
Scaphander	1	0	1	0	0	1	1	0	0	?	0	0	0	0	1	1	1	?	0	0	0	0	–	0/1	0	0/1
Cylichna	1	0	1	0	0	1	1	0	0	?	0	0	0	0	1	1	1	?	0	0	0	0	1	0/1	0	1
Retusa	1	0	1	–	0	1	1	0	0	?	0	0	–	–	1	1	1	?	0	0	0	0	1	0	0	–
Philine	1	0	1	0	0	1	1	0	0	0	0	0	–	–	1	1	1	?	0	0	0	0	1	0	0	1
Aglaja	–	–	1	0	0	1	1	0	0	0	0	0	–	–	1	1	1	?	0	0	0	0	1	0	0	1
Gastropteron	–	–	1	0	0	0	1	0	0	0	0	0	–	–	1	1	1	?	0	0	0	0	–	0	0	–
Runcina	–	–	1	0	0	1	0	0	0	0	0	–	–	–	0	0	1	0	0	0	0	?	–	0	0/1	–
Diaphana	1	0	1	–	0	0	1	0	0	0	0	–	–	–	0	1	1	?	0	0	0	0	–	–	0	–
Colpodaspis	1	0	1	0	0	1	0/1	0	0	0	0	1	?	?	1	1	1	?	0	0	0	0	–	0	0	–
Bulla	–	–	1	–	0	1	1	0	0	?	0	0	–	–	1	1	1	?	0	0	0	0	–	0	0	–
Haminoea	1	0	1	0	0	1	1	0	0	?	0	0	–	–	1	1	1	?	0	0	0	1	1	0	0	–
Smaragdinella	–	–	1	–	0	0	1	0	0	?	0	0	–	–	1	1	1	?	0	0	0	–	–	–	0	–
Limacina	0	0	0	–	1	0	0	0	0	?	2	0	–	–	0	0	0	?	0	0	0	2	0/1	0	0	0
Peraclis	0	0	0	–	1	0	0	0	0	?	2	0	–	–	0	0	–	?	0	0	0	2	–	0	0	–
Clione	0	0	1	–	0	0	0	0	0	0	2	0	–	–	?	?	?	0	0	0	?	0	0	0	0	–
Hedylopsis	–	–	1	–	0	1	0	0	0	0	2	–	–	–	?	?	?	0	0	0	?	0/1	1	0	0	–
Akera	1	0	1	0	0	0	1	0	0	?	0	0	–	–	1	1	0	?	0	0	0	0	–	1	1	1
Aplysia	1	0	1	0	0	0	0	0	0	0	0	1	?	?	0	0	0	?	0	0	0	1	0	1	1	1
Umbraculum	1	0	1	–	0	0	0	0	0	?	2	1	?	?	0	0	?	?	1	0	?	1	1	0	0	–

APPENDIX 1 (*Continued*)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Tylodina	1	0	1	–	0	0	0	0	0	?	2	0	–	–	0	0	?	?	1	0	?	1	–	0	0	1
Berthella	0/1	0	1	1	0	0	0	0	0	0	2	1	?	?	0	0	?	?	1	1	?	1	1	0	0	1
Pleurobranchus	0/1	0	1	1	0	0	0	0	0	0	2	1	?	?	0	0	?	?	1	1	?	1	1	0	0	1
Ascobulla	1	0	1	0	0	1	0	0	0	?	0	–	–	–	0	1	2	?	0	0	0	0/1	–	0	0	–
Oxynoe	1	0	1	0	0	0	0	0	0	?	0	–	–	–	0	1	–	?	0	0	0	0	–	0	0	–
Berthelinia	1	0	1	0	0	0	0	0	0	?	0	0	–	–	0	1	2	?	0	0	0	0	–	0	0	–
Elysia	1	0	1	0	0	0	0	0	0	0	2	1	?	?	?	?	?	0	0	0	?	1	1	0	0	–
Limapontia	1	0	1	–	0	0	0	0	0	0	2	1	?	?	?	?	?	0	0	0	?	1	1	0	0	0
Tritonia	1	0	1	0	0	0	0	0	0	0	2	1	?	?	?	?	?	0	0	0	?	1	1	0	0	–
Hancockia	–	–	1	0	0	0	0	0	0	0	2	1	?	?	?	?	?	0	0	0	?	1	1	0	0	–
Archidoris	–	–	1	0	0	0	0	0	0	0	2	1	?	?	?	?	?	0	0	0	?	1	–	0	0	1
Chromodoris	1	0	1	0	0	0	0	0	0	0	2	1	?	?	?	?	?	1	0	0	?	1	0	0	0	1
Armina	1	0	1	0	0	0	0	0	0	0	2	1	?	?	?	?	?	0	0	0	?	1	1	0	0	1
Janolus	–	–	1	0	0	0	0	0	0	0	2	1	?	?	?	?	?	0	0	0	?	1	–	0	0	–
Facelina	1	0	1	0	0	0	0	0	0	1	2	1	?	?	?	?	?	0	0	0	?	1	1	0	0	0
Aeolidia	1	0	1	0	0	0	0	0	0	1	2	1	?	?	?	?	?	0	0	0	?	1	–	0	0	0
Otina	1	0	1	0	0	0	0	0	0	?	1	1	?	?	0	0	0	?	0	0	?	1	0	0	0	0
Carychium	1	?	1	0/4	0	0	0	0	0	?	1	1	–	–	0	0	0	?	0	0	1	0	0	0	0	–
Pythia	1	?	1	–	0	0	0	0	0	?	1	1	–	–	–	–	0	?	0	0	–	1	–	–	1	–
Melampus	1	?	1	0/4	0	0	0	0	0	?	1	1	?	?	0	0	0	?	0	0	1	0	0	0	0	–
Ellobium	1	?	1	0/4	0	0	0	0	0	?	1	1	?	?	0	0	0	?	0	0	1	1	–	0	0	–
Gadinia	1	0	1	0	0	0	0	0	0	?	1/3	–	–	–	0	0	0	?	0	0	1	1	–	0	0	0
Siphonaria	1	0	1	0	0	0	0	0	0	?	1/3	0	–	–	0	1	0/2	?	0	0	0	1	0	0	0	0
Amphibola	1	0	0	0	0	0	0	0	0	?	1	0	–	–	1	0	0	?	0	0	1	0	0	0	0	0
Chilina	1	?	1	0	0	0	0	0	0	?	1	0	–	–	1	1	0	?	0	0	1	1	0	0	0	0
Latia	0/1	?	1	–	0	0	0	0	0	?	1	–	–	–	0	0	0	?	0	0	–	1	0	0	0	–
Physa	–	?	1	–	0	0	0	0	0	?	1	1	?	?	0	0	0	?	0	0	1	1	–	0	0	–
Lymnaea	–	?	1	–	0	0	0	0	0	?	1	1	?	?	0	0	0	?	0	0	1	1	–	0	0	–
Acroloxus	–	?	1	0	0	0	0	0	0	?	2	1	?	?	0	0	?	?	0	0	?	1	–	0	0	–
Ancylus	–	?	1	–	0	0	0	0	0	?	2	0	–	–	?	?	?	?	0	0	?	1	–	0	0	–
Veronicella	?	?	1	2	0	0	0	0	1	0	2	1	?	?	?	?	?	?	0	0	1	1	–	0	0	1
Onchidiella	0	0	1	2	0	0	0	0	1	0	1	1	?	?	0	0	0	?	0	0	0	1	–	0	0	0
Succinea	–	?	1	3	0	0	0	1	1	?	1	1	?	?	0	0	0	?	0	1	1	1	–	0	0	–
Achatinella	0	?	1	–	0	0	0	1	1	?	1	1	?	?	1	1	0	?	0	1	1	1	–	0	0	–
Achatina	0/1	?	1	3	0	0	0	1	1	0	1	1	?	?	0	0	0	?	0	1	1	1	0/1	0	0	–
Arion	–	?	1	3	0	0	0	1	1	1	1	1	?	?	0	0	0	?	0	1	1	1	–	0	0	–
Helix	0	?	1	3	0	0	0	1	1	?	1	1	?	?	0	0	0	?	0	1	1	1	0/1	0	0	–

	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
Trochidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pila	0	0	0	0	0	0	0	0	–	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	–
Campanile	0	0	0	0	0	0	0	–	–	0	0	0	–	0	1	0	0	0	0	0	6	0	0	0	0	–
Cerithium	0	0	0	0	0	0	0	–	–	0	0	0	–	0	1	0	0	0	0	0	6	0	0	0	1	–
Coriandria	–	0	1	1	0	0	0	–	–	0	0	0	1	1	?	0	0	0	0	0	6	0	0	0	1	0
Littorina	0	0	0	0	0	0	0	0	–	0	0	0	–	1	1	0	0	0	0	0	1	5	0	0	1	0
Valvata	0	0	0	0	0	0	0	–	–	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0
Glacidorbis	–	0	–	1	0	0	0	–	–	0	0	0	0	1	1	1	0	0/1	0	0	1	1	0	0	1	0
Rissoella	–	0	–	0	0	0	0	–	–	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0
Omalogyra	–	0	–	1	0	0	0	–	–	0	0	0	–	1	?	–	0	0	0	0	0	0	0	0	–	0
Odostomia	–	0	–	1	1	0	?	?	–	0	0	0	–	0	?	–	0	0	0	0	–	0	0	0	1	0
Amathina	–	0	–	1	1	0	?	?	–	0	0	0	–	0	?	0	0	0	0	0	5	5	0	0	1	0
Heliacus	–	0	–	1	0	0	0	–	–	0	0	0	–	1	1	1	0	1	0	1	5	5	0	0	1	0
Opimilda	–	0	–	1	0	0	0	–	–	0	0	0	–	1	1	1	0/1	1	0	1	0	0	0	0	1	0
Tuba	0	0	–	0	0	0	0	–	–	0	0	0	–	0	?	1	0	1	0	1	1	0	0	0	1	0
Acteon	0	0	–	1	0	0	0	1	3	0	0	0	–	0	?	1	1	1	0	1	0	0	0	0	1	0
Pupa	–	0	–	0	–	0	0	1	–	0	0	0	–	0	?	1	1	1	0	1	1	0	0	0	1	0
Ringicula	–	0	–	1	–	0	0	1	–	0	0	0	–	0	?	–	1	1	–	–	0	0	0	0	1	0
Hydatina	–	0	–	0	0	0	0	1	–	0	0	0	–	0 & 3	?	1	0 & 1	0 & 1	1	1	3	1	0	0	1	0
Scaphander	0	0	1	1	0	0	0	–	2	3	0	0	0	2	?	1	0	1	1	1	3	0	0	0	1	0
Cylichna	0	0	1	0	0	0	0	1	2	3	0	0	–	2	?	1	0	1	0	1	3	0	0	0	0	0
Retusa	–	0	–	1	0	0	?	?	–	3	0	0	–	2	?	1	0	1	–	–	–	0	0	0	1	0
Philine	0	0	1	1	0	0	–	–	2	3	0	0	–	2	?	1	0 & 1	0 & 1	1	1	3	1	0	0	1	0
Aglaja	0	0	–	1	0	0	?	?	–	0	0	0	–	3	?	0	0	0	1	1	3	1	0	0	1	0
Gastropteron	0	0	–	1	0	0	0	–	–	3	0	0	–	0	?	0	0	0	1	1	1	1	0	0	1	0
Runcina	–	0	–	0	–	0	0	–	2	0	0	0	0	1	1	?	0	0	0	0	5	5	0	0	1	0
Diaphana	–	–	–	1	–	0	0	–	–	3	0	0	0	3	?	1	0	0	0	–	5	1	0	0	1	0
Colpodaspis	–	0	–	1	0	0	0	0	–	0	0	0	–	3	?	1	0	0	–	0	0	0	0	0	1	0
Bulla	0	0	0	0	0	0	0	0	–	4	0	0	–	2	?	1	0/1	0/1	0	1	3	3	0	0	1	0
Haminoea	0	0	0	0	0	0	0	0	2	4	0	0	–	2	1	0 & 1	0 & 1	0 & 1	1	1	3	0	0	0	1	0
Smaragdinella	–	–	–	0	0	0	0	–	–	4	0	0	–	3	?	0	0	1	–	–	3	1	0	0	–	0
Limacina	0	0	0	0	0	0	–	–	3	1	0	0	0	1	?	0	0	0	0	–	–	4	0	0	1	0
Peraclis	–	0	0	0	0	0	0	–	–	1	0	0	–	1	?	0	0	0	0	–	4	4	0	–	–	–
Clione	–	0	0	1	0	0	0	1	–	0	0	1	–	1	?	0	0	0	–	1	3/4	3/4	0	0	1	–
Hedylopsis	0	0	0	1	0	0	–	–	–	0	1	0	–	2	?	1	0	0	0	–	5	5	–	0	1	–
Akera	0	0	–	0	0	0	0	–	2	2	0	0	1	0	0	0	1	1	1	1	3	0	0	0	1	–
Aplysia	0	0	0	0	0	0	0	–	–	2	1	0	0	2	0	0	0	0	0	1	3/4	3/4	0	0	1	0
Umbraculum	0	0	1	0	0	0	0	–	–	0	0	0	–	1	?	0	0	0	0	1	5	5	0	0	1	0
Tylodina	0	0	–	0	0	0	0	–	–	0	0	0	–	1	?	0	0	0	0	1	5	5	0	0	1	–

APPENDIX 1 (*Continued*)

	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
Berthella	0	0	–	0	0	1	–	–	1	0	0	0	–	1	?	1	0	0	0	1	5	7/8	0	0	1	–
Pleurobranchus	0	0	1	0	0	1	0	–	–	0	0	0	–	1	?	1	0	0	0	1	5	7/8	0	0	1	–
Ascobulla	–	–	–	1	0	0	1	–	–	0	0	0	–	2	?	0	0	0	–	–	0	0	0	0	1	–
Oxynoe	–	–	–	1	0	0	1	–	–	0	0	0	–	1	?	0	0	0	0	–	5	5	0	0	1	–
Berthelinia	–	–	–	1	0	0	1	–	–	0	0	0	–	2	?	0	0	0	0	1	0	5	0	0	1	–
Elysia	0	0	–	1	0	0	1	–	–	0	0	0	0	–	?	0	0	0	0	1	5	5	0	0	1	–
Limapontia	0	0	–	1	0	0	1	–	–	0	0	0	–	1	?	?	0	0	0	–	4/8	5	0	0	1	1
Tritonia	1	0	1	0	0	0	–	–	–	0	0	0	–	1	?	?	0	0	0 & 1	1	8	8	0	0	1	1
Hancockia	–	0	–	0	0	0	–	–	–	0	0	0	–	1	?	0	0	–	1	1	8	8	0	0	1	1
Archidoris	1	0	1	1	0	0	–	–	1	0	0	0	–	4	?	0	0	–	0	0	8	8	0	0	1	1
Chromodoris	1	0	1	0	0	0	–	–	–	0	0	0	–	4	–	–	–	–	–	–	–	–	–	–	1	–
Armina	–	0	–	0	0	0	–	–	–	0	0	0	–	4	?	0	0	0	0	–	8	8	0	0	1	–
Janolus	1	0	–	0	0	0	–	–	–	0	0	0	–	1	?	0	0	0	1	0	8	8	0	0	1	–
Facelina	1	0	1	0	0	0	–	–	–	0	0	0	–	1	?	0	0	0	1	1	8	8	0	0	1	–
Aeolidia	1	0	1	0	0	0	–	–	–	0	0	0	–	1	?	0	0	0	0	1	8	8	0	0	1	–
Otina	–	0	–	0	0	0	0	0	–	0	0	0	–	3	1	1	0	0	–	–	1	1	1	–	1	0
Carychium	0	0	1	2	0	0	0	–	–	0	1	0	–	1	?	–	0	0	–	0	0	0	–	1	1	0
Pythia	–	0	–	2	–	0	0	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0
Melampus	0	0	1	2	0	0	0	–	–	0	1	1	–	1	0	0	0	0	0	1	0	5	1	1	1	0
Ellobium	0	0	–	2	0	0	0	–	–	0	1	1	–	1 & 2	0	1	0	0	0	0	0	0	–	–	1	0
Gadinia	0	0	1	2	0	0	0	–	–	0	1	1	–	1	0	–	0	0	0	1	4	2	1	1	1	0
Siphonaria	0	0	1	2	0	0	0	–	–	0	0	1	0	1	?	–	0	0	0	1	4	3	1	1	1	0
Amphibola	0	0	1	1	0	0	0	–	–	0	1	0	–	1	?	–	0	0	1	1	0	0	1	1	1	0
Chilina	0	0	–	2	0	0	0	0	–	0	1	0	–	3	1	1	0 & 1	0 & 1	0	1	0	0	1	1	1	–
Latia	0	0	1	2	0	0	0	–	–	0	1	0	–	3	1	1	1	0	–	1	3	0	1	1	1	0
Physa	0	0	1	2	0	0	0	–	1	0	1	1	0	1	?	0	0	0	0	1	5	5	1	1	1	1
Lymnaea	0	0	1	2	0	0	0	0	–	0	1	1	0	1	?	0	0/1	0/1	1	1	5	5	1	1	1	0/1
Acroloxus	0	0	1	2	0	0	0	0	–	0	0	1	0	1	?	0	0	0	0	1	2	2	1	1	1	–
Ancylus	0	0	–	2	0	0	0	0	1	0	1	1	–	1	?	0	0	0	0	1	2	2	1	1	1	0/1
Veronicella	0	0/1	1	3	0	0	0	–	–	0	0	0	–	1	?	0	0	0	0	1	5	5	1	1	1	–
Onchidiella	0	0	1	1	0	0	0	–	–	0	0	0	–	1	?	0	0	0	1	1	5	2/5	–	0/1	1	0
Succinea	0	1	1	3	0	0	0	–	1	0	0	1	0	1	?	0	0	0	1	0	4	4	1	1	1	0
Achatinella	0	0/1	1	3	0	0	0	–	–	0	0	0	1	1	?	0	0	0	1	–	5	4	–	–	1	0
Achatina	0	1	1	3	0	0	0	–	–	0	0	0	0	2	1	0	0	0	1	0	5	5	1	–	1	0
Arion	0	1	1	3	0	0	0	–	–	0	0	1	1	1	0	0	0	0	0	0	5	5	1	–	?	–
Helix	0	1	1	3	0	0	0	0	1	0	0	0	–	1	0	0	0	0	1	0	5	5	1	–	1	0

	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77
Trochidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pila	0	0	0	0	0	0	0	1	0	0	0	0	–	1	0	0	1	1	0	0	0	0	1	1	1
Campanile	0	5	0	0	0	0	0	0	?	?	1	0	–	1	0	1	1	1	0	0	0	0	1	1	1
Cerithium	0	0	0	0	0	0	0	0	?	0 & 1	0	0	–	1	0	1	1	1	0	0	0	0	1	1	1
Coriandria	0	0	0	0	0	0	0	0	?	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Littorina	0	0	0	0	0	2	0	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	1	1	1
Valvata	0/1	4	0/1	0	4	1	3	1	1	0	1	0	0	2	2	0	3	2	1	1	1	1	0	1	1
Glacidorbis	0	0	0	0/1	?	1	2	1	–	0	0	0	–	–	1	–	–	–	–	–	–	1	–	–	1
Rissoella	0	0	0	0	0	1	5	1	1	0	0	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Omalogyra	0	0	0	0	0	0	0	0	?	0	0	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Odostomia	0	1	1	7	1/5	2	0	2	0	0/1	1	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Amathina	0	?	?	?	?	1 & 2	–	1	0	0	0/1	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Heliacus	0	0	0	0	0	0	0	0	?	1	1	0	–	1	1	0	2	2	0	0	1	1	0	1	1
Opimilda	0	0	0	0	0	0	0	0	?	1	0/1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tuba	0	0	0	0	0	0	0	0	?	1	0/1	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Acteon	0	0/1	0/1	0	0	1	0	1	1	0	0	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Pupa	0	1	1	2	0	0	0	1	1	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Ringicula	0	0	–	0	0	1/2	2	1	0/1	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hydatina	0	1	1	2	0	1	0	1	1	0	0	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Scaphander	0	3	–	0/5	3	2	2	2	–	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cylichna	0	0	0	3	0	2	2	2	0	0	0	–	–	2	1	0	4	2	1	1	1	1	0	1	1
Retusa	0	0	0	3	3	2	2	2	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Philine	0	3	–	0/4/5	3	2	2	2	1	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–
Aglaja	0	3	–	4	3	2	2	2	0	0	0/1	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Gastropteron	0	7	–	6	7	2	2	2	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Runcina	0	1	0	3	6	2	2	2	1	1	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Diaphana	0	1	0	0	0	2	2	2	0	0	–	–	–	2	1	0	4	2	1	1	1	1	0	1	1
Colpodaspis	0	1	–	7	8	2	2	2	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bulla	0	1	1	2/7	3	2	2	2	0	0 & 1	0/1	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Haminoea	1	1	–	2	6	2	2	2	0	0	0	0	0	2	1	0	4	2	1	1	1	1	0	1	1
Smaragdinella	0	1	–	2	6	2	2	2	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Limacina	0	0	0	3/7	0	2	2	2	–	1	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Peraclis	0	4	–	–	0/7	2	2	2	–	–	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Clione	0	0	–	0	1	2	2	2	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Hedylopsis	0	0 & 3	–	0	0 & 8	2	–	0 & 2	?	0/1	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Akera	?	2	?	8	2	2	?	2	0	0	0	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Aplysia	1	2	1	8	2	2	0	2	0	0	0	0	0	2	1	0	4	2	1	1	1	1	0	1	1
Umbraculum	0	?	–	?	?	2	0/6	1	0	0	0	0	0	2	1	0	4	2	1	1	1	1	0	1	1
Tylodina	0	2	–	8	2	2	–	1	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

APPENDIX 1 (*Continued*)

	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77
Berthella	0	7	–	0/6	7	5	0 & 6	2	1	0	0	0	0	2	1	0	4	2	1	1	1	1	0	1	1
Pleurobranchus	0	7	–	0/6	7	5	1 & 6	2	1	0	0	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Ascobulla	0	–	–	–	7	6	4	2	1	0	–	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Oxynoe	0	7	–	0	7	4	4	2	1	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Berthelinia	0	7	–	0	7	1	4	2	1	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Elysia	0	6	1	0	0	4	6	2	1	0	0	0	0	2	1	0	4	2	1	1	1	1	0	1	1
Limapontia	0	6	1	0	0	4	6	2	1	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Tritonia	0	7	1	0	7	5	0	2	1	0	0	0	0	2	1	0	4	2	1	1	1	1	0	1	1
Hancockia	0	7	1	0	7	5	0	2	1	0	–	–	–	2	1	0	4	2	1	1	1	1	0	1	1
Archidoris	0	8	0	0	9	5	0	2	1	0	0	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Chromodoris	0	8	0	0	9	5	0	2	1	0	–	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Armina	0	7/8	0	0	7/9	5	0	2	1	–	–	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Janolus	0	7	–	0	7	5	0	2	1	0	–	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Facelina	0	7/8	0	0	7/9	5	0	2	1	0	–	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Aeolidia	0	7/8	0	0	7/9	5	0	2	1	0	–	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Otina	0	1	0	7	0	5	3	2	1	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Carychium	0	1	1	7	0	1	0	2	1	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Pythia	0/1	1	–	7	0	2	0	2	1	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Melampus	0	1	1	0	1	1	1	2	1	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Ellobium	0	1	–	7	0	1	0	2	1	0	1	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Gadinia	0	1	–	0	0	1	0	2	1	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Siphonaria	0	1	–	0	0	3	0	0	?	0 & 1	0	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Amphibola	0	1	–	0	0	3	0/2	2	1	0 & 1	–	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Chilina	0	1	–	–	0	1	0	2	1	0	–	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Latia	0	1	–	–	0	1	3	2	1	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Physa	0	1	0/1	3	0	1	4	2	1	0	0	0	0	2	1	0	4	2	1	1	1	1	0	1	1
Lymnaea	0	1	1	3	0	1	4	2	1	0	0 & 1	0	0	2	1	0	4	2	1	1	1	1	0	1	1
Acroloxus	0	1	1	3	0	1	3	2	1	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Ancylus	0 & 1	1	1	3	0	1	4	2	1	0	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–
Veronicella	0	1	1	0	0	1	7	2	1	0	0/1	0	–	–	–	–	–	–	–	–	–	–	–	–	–
Onchidiella	0	1	–	0	0	1	7	2	1	0	0/1	0	–	2	1	0	4	2	1	1	1	1	0	1	1
Succinea	1	1	0 & 1	0	0	4	3	2	1	0	–	0	0	2	1	0	4	2	1	1	1	1	0	1	1
Achatinella	0	1	0/1	0	0	4	1	2	1	0	?	?	–	2	1	0	4	2	1	1	1	1	0	1	1
Achatina	0	1	1	0	0	4	4	2	1	0	0	1	1	2	1	0	4	2	1	1	1	1	0	1	1
Arion	–	1	1	0	0	4	0	2	1	1	0	1	0	2	1	0	4	2	1	1	1	1	0	1	1
Helix	0	1	1	0	0	4	0	2	1	1	0	1	0	2	1	0	4	2	1	1	1	1	0	1	1

APPENDIX 2

LIST OF BIBLIOGRAPHIC SOURCES FOR EACH TAXON

Because descriptions of taxa are often ambiguous, coding many characters requires discussion and justification, which are provided here, taxon by taxon. Character numbers in brackets are those used in the text and in Appendices 3 and 4. For each taxon, references on which coding was based are listed and discussed when necessary.

VETIGASTROPODA

Trochidae (Bouvier, 1887c; Risbec, 1939; Gabe & Prenant, 1952b; Hickman & MacLean, 1990; Hodgson et al., 1990; Hodgson & Forster, 1992;Fretter & Graham, 1994; Hickman, 1996; Ponder & Lindberg, 1997).

CAENOGASTROPODA (INCLUDING ARCHITAENIOGLOSSA)

Pila Röding, 1798 (Bouvier, 1886b, 1887b, c, 1888; Ranjah, 1942; Andrews, 1964, 1965a, b, 1976a, b; Lutfy & Demian, 1966, 1967; Berthold, 1991; Bieler, 1993). (24) Hypobranchial gland reduced but here considered present. (28) Blood gland surrounding the posterior aorta, and not the anterior one, doubtfully homologized here with euthyneuran blood glands. (31) The nephridial gland is absent in *Pila* but it is present in other freshwater caenogastropods (Franc, 1968; Andrews, 1976a, b). We code the nephridial gland present because of the occurrence of a vein interpreted as a remnant of the efferent vein of this gland. (32–42) Digestive system similar to that of *Marisa cornuarietis* (Andrews, 1965b; Lutfy & Demian, 1967; Berthold, 1991). (43–51) A left anastomosis joins the supraœsophageal and left pleural ganglia; a short right anastomosis joins the subœsophageal to the right pleural side by side: {lPl-Sb[rPl]-Abd-Sp[-lPl]-rPl}.

Campanile Bayle, 1884 (Bouvier, 1887a; Houbrick, 1981, 1989). (43–51) Right anastomosis joining the right pleural ganglion and the subœsophageal ganglion (Bouvier, 1887a; Houbrick, 1981, 1989). (60) Glandular part of the inner lamina of the pallial oviduct homologized here with the mucous gland because of its position and its gelatinous secretion (Houbrick, 1981, 1989). (66) Spermatophore probably present (Houbrick, 1989). (67) The spawn is a crescent-shaped mass which includes many capsules surrounded by gelatinous fluid homologous with mucus (Houbrick, 1981). Robertson (1985) coded the chalaze of *Campanile* as a (?), whereas Haszprunar (1988) considered it present in Campanilimorpha. The capsules, which contain 1–5 eggs, are joined by a chalaze-like structure which we consider homologous with a true chalaze because it clearly joins capsules and not eggs. The intracapsular fluid is considered to be albumen here, even though it has not been described as such owing of the anatomy of the pallial female glands (Houbrick, 1981).

Cerithium Bruguière, 1789 (Bouvier, 1887c; Johansson, 1953; Marcus & Marcus, 1964; Houbrick, 1971, 1973, 1974a, b, 1988, 1992; Delhaye, 1975; Houston, 1985). (43–51) Nervous system similar to that of *Pila* except for the very short left visceral cord between the left pleural and the suboesophageal: {lPlSb[-rPl]-Abd-Sp[-lPl]-rPl}. (66) Spermatophores, which are plesiomorphically present in cerithioids (Houbrick, 1971, 1973), are either considered as probably present in the genus *Cerithium* (Houbrick, 1973), or exceptionally present in *Cerithium muscarum* (Houston, 1985).

Littorina Linné, 1758 (Bouvier, 1887c; Fretter, 1980; Guyomarch-Cousin, 1976; Andrews, 1981, 1988; Reid, 1989, 1996; Fretter & Graham, 1994). (43–51) {Pl-Sb-Abd-Sp-Pl} (Bouvier, 1887c; Fretter & Graham, 1994).

Coriandria Tomlin, 1917 [The genus *Cingulopsis* Fretter & Patil (1958) has been synonymized to *Coriandria* by Lebour (1937), Fretter (1953), Fretter & Patil, 1958, and Ponder & Yoo, 1980]. (43–51) {PlSb-AbdSpPl} (Fretter & Patil, 1958). (66) Males aphallic, internal fertilization allowed by a pallial water flow largely created by a ciliated osphradium and a muscular duct from the posterior part of the pallial cavity to the carrefour (Fretter & Patil, 1958).

ALLOGASTROPODS

Valvata O.F. Müller, 1774 (Moquin-Tandon, 1852; Bouvier, 1887c; Garnault, 1889; Bernard, 1890; Yonge, 1947; Cleland, 1954; Johansson, 1955; Kruglov & Frolenkova, 1981; Rath, 1988; Ponder, 1990, 1991; Fretter & Graham, 1994). (1) Heterostrophy uncertain (Robertson, 1985) or absent (Ponder, 1991). (30) Duct called 'uretère' by Bernard (1890) considered here as analogous with that of stylommatophoran pulmonates, because of its distinct position and anatomy. (43–51) {PlSb-Abd-SpPl} (Bouvier, 1887c; Bernard, 1890). (63) the terminology and interpretation of Fretter & Graham (1994) is adopted here for the spawn, rather than that of Cleland (1954). The spawn is a spherical sac incorrectly called a capsule (Cleland, 1954; Fretter & Graham, 1994), which contains from 4 to 60 capsules joined by a chalaze. The latter is interpreted as present here, even though Robertson (1985) coded it as a (?).

Glacidorbis Iredale, 1943 (Bunn & Stoddart, 1983; Ponder, 1986; Haszprunar, 1988). (17) Posterior pallial ciliated ridge (Ponder, 1986; Haszprunar, 1988) probably homologous with the pallial raphes of opistho-

branchs. (43–51) Ponder (1986) described a tetraganglionate commissure as {Pl-Pa-Abd-Acc-Pa-Pl} but he used the pulmonate terminology, according to which the suboesophageal and supraoesophageal ganglia are called 'parietal ganglia' because he classified *Glacidorbis* in the Basommatophora; consequently this visceral lopp should be interpreted as {Pl-Sb-Abd-Acc-Sp-Pl}. Haszprunar (1988) mentioned the occurrence of an osphradial ganglion but did not define its origin (i.e. 'accessory' or 'right parietal ganglion'). Three interpretations of the visceral loop can be stated: (a) {Pl-Sb-Abd-Acc-Sp-Pl}, according to which the Ponder's 'right parietal' is the supraœsophageal ganglion and the 'accessory' is a true accessory ganglion; (b) {Pl-Sb-Abd-Sp-Pa-Pl} with Ponder's 'accessory ganglion' the supraœsophageal ganglion and the 'right parietal' really a parietal ganglion; (c) {Pl-Sb-Abd1-Abd2-Sp-Pl}, according to which there is no homologue to the right parietal ganglion and the 'accessory' ganglion is in fact a second part of the visceral ganglion – as has been described, for example, in *Litttorina* by Fretter & Graham (1994) or in *Ampullaria* by Bouvier (1887b, c). (44) Circumoesophageal nervous system highly concentrated (Ponder, 1986; Haszprunar, 1988). (60) Egg capsules individually brooded in the pallial cavity and mucous gland probably absent.

Rissoella Gray, 1847 (Lebour, 1937; Fretter, 1948; Ponder & Yoo, 1977; Rodriguez, 1982; Robertson, 1985; Haszprunar, 1985a; Huber, 1993; Fretter & Graham, 1994). (16) Ciliated strips present on the right side of the pallial cavity, either homologized by Fretter & Graham (1949) or only tentatively homologized by Robertson (1985) with the raphes of opisthobranchs. (23) Pigmented blotches (Fretter, 1948) either homologized with the PMO (Haszprunar, 1985a; Ponder, pers. comm.) or not (Robertson, 1985). (43–51) Subœsophageal ganglion on left (left visceral cord not twisted as in euthyneuran nervous systems) and supraoesophageal ganglion on the left (right visceral cord twisted as in streptoneuran nervous systems). We code the visceral loop as: {(CPl)-Sb-Abd-Sp-(PlC)} following Huber (1993).

Omalogyra Jeffreys, 1860 (Fretter, 1948, 1953; Robertson, 1985; Haszprunar, 1985a, 1988; Huber, 1993; Fretter & Graham, 1994). (16) Ciliated strips (Fretter, 1948) homologized by Robertson (1985) to opisthobranch raphes. (23) Homology between the 'pigmented hypobranchial gland' (Fretter & Graham, 1994) with the PMO accepted (Haszprunar, 1988) or not (Robertson, 1985). (30) Jaws absent, with only cuticularized walls of the buccal cavity present. (56) The carrefour is called a 'fertilization chamber' by Fretter (1948). (43–51) The nervous system is similar to that of *Ammonicera* according to Huber (1993), but there is only one probable parietal ganglion described in the visceral commissure of the latter. (45) Circum-

oesophageal nerve ring located around the buccal mass (Haszprunar, 1985a).

Odostomia Fleming, 1817 (Thorson, 1946; Fretter & Graham, 1949, 1994; Fretter, 1951; Maas, 1965; Robertson, 1966; Thompson, 1976; Haszprunar, 1985a; Huber, 1993; Wise, 1996). (12) Osphradium absent (Fretter & Graham, 1949) or present (Wise, 1996). (43–51) {PlSb-Abd-SpPl} (Huber, 1993; Fretter & Graham, 1994). (57–60) Homologies of the upper and lower capsule glands (also called 'mucous glands' by Haszprunar and by Fretter & Graham) unknown (probably a membrane gland and a mucous gland, but the lower one is located proximal to the albumen gland, i.e. an exceptional position raising doubt on homology). (66) Spermatophores described in two American species (Robertson, 1966; Wise, 1996).

Amathina Gray, 1842 (Ponder, 1987). (1) Just a 'little sign of heterostrophy' described. (17) two ciliated ridges originate from the anus, located in the posterior part of the pallial cavity, and are considered as homologous with opisthobranch raphes (Ponder, 1987). The homology of the gill is unknown. (25) The glandular area of the pallial cavity is homologized with the PMO by Ponder. (43–51) The nervous system is similar to that of other pyramidellids, and is highly concentrated: {PlSbAbdSpPl}. (57–60) Homologies of the posterior and anterior mucous glands questionnable. (62) Prostatic glandular area probably absent. (67) 'indistinct chalaze' coded here as (?).

Heliacus Orbigny, 1842 (Bouvier, 1886a; Robertson, 1967, 1973; Haszprunar, 1985a, b, c, 1988; Bieler, 1988). (43–51) {Pl-Sb-Abd-Sp-Pl} (Haszprunar, 1985b). (66) Spermatolytic gland of the visceral sac has been homologized with a spermatophoral bursa by Haszprunar (1985b) even though spermatophores have been observed in only one species (Robertson, 1973). (75) Paracrystalline material absent (Healy, 1993) or present (Ponder & Lindberg, 1997).

Opimilda Iredale, 1929 (Haszprunar, 1985c). (18) Lamellate gill considered as secondary because of the fine structure of lamellae (which are only pallial folds, lacking skeletal rods and ciliary bands). (43–51) Nervous system similar to that of *Gegania* except for epiathroid/hypoathroid condition (Haszprunar, 1985c). The 'accessory ganglion', which has been described by Haszprunar (1985c) on the visceral commissure between the subœsophageal and the left pleural is coded either as a probable parietal ganglion or as a secondary part of the abdominal ganglion: {Pl-Sb-Abd-Sp-(PlC)} or {Pl-Par-Sb-Abd-Sp-(PlC)}. (67) Haszprunar (1985c) described a chalaze but did not describe eggs nor spawn: chalaze considered to be probably present here.

Tuba Lea, 1833 (Robertson, 1973, 1985; Climo, 1975, Haszprunar, 1985a, c, 1988; as *Gegania*; Bieler, 1988; Mikkelsen, 1996). (18) Pallial leaflets were homolo-

gized with a one-sided plicatidium (Mikkelsen, 1996) but we do not accept this interpretation because: (a) leaflets are not plicated (Haszprunar, 1985c) as in a true plicatidium, (b) the leaflets are each divided into a posterior and anterior part, and (c) distinct secondary branchial leaflets occur in other architectonicoids (Haszprunar, 1985c). (43–51) Visceral loop coded {Pl-Sb-Abd-Sp-Pl}, following Haszprunar (1985c). (67) Chalazae were described by Climo (1975) and were accepted by Haszprunar (1985a, c, 1988) but not by Robertson (1985).

CEPHALASPIDEANS (WITHOUT SACOGLOSSA AND APLYSIOIDEA)

Acteon Montfort, 1810 (Bouvier, 1893; Pelseneer, 1894; Guiart, 1901; Perrier & Fisher, 1911; Hoffman, 1939; Leyon, 1947; Lemche, 1948; Gabe & Prenant, 1952a, b, c, 1953; Fretter & Graham, 1954; Johannson, 1954; Duncan, 1960a, b; Rudman, 1972b, f; Brace, 1977a, b; Edlinger, 1980a, b; Gosliner, 1981a; Robertson, 1985; Huber, 1993; Mikkelsen, 1996). (43–51) In *Acteon solidulus,* Bouvier (1893) described a double pedal commissure, a subcerebral commissure and the absence of a parapedal commissure, while in *Acteon tornatilis,* Pelseneer (1894) described a simple pedal commissure, the absence of a subcerebral commissure and the occurrence of a parapedal commissure. The simple pedal and parapedal commissures of *A. tornatilis* are coded here as a double pedal commissure, but the presence and absence of the subcerebral commissure is considered here as a case of polymorphism. We have coded the visceral loop as {(CPl)-Pa-Sb-Abd-Sp-Pa-(PlC)}.

Ringicula Deshayes, 1838 (Pelseneer, 1924; Fretter, 1960; Minichev, 1967; Schiro, 1980; Gosliner, 1981a, 1994; Ciccone & Savona, 1982; Thompson *et al.*, 1985; Mikkelsen, 1996). (32) Jaws are considered to be present (Fretter, 1960), contrary to Mikkelsen's interpretation (1996). (46–47) Mikkelsen (1996) coded the presence of a parietal ganglion in *Ringicula*, whereas the latter have never been described by Pelseneer (1924), nor by Fretter (1960) {PlSb-AbdSp-Pl}. (61) Whereas Fretter (1960) was unable to locate an the extrapallial tract in *R. buccinea*, Gosliner (1994) described a extrapallial groove in *R. nitida*, and Pelseneer (1924) described a closed spermiduct in *R. conformis*.

Hydatina Schumacher, 1817 (Vayssière, 1906; Eales, 1938; Rudman, 1972a; Gosliner, 1981a; Winner, 1984). (43–51) The nervous system is described as either euthyneuran (Eales, 1938) or streptoneuran (Rudman, 1972a) in different species. According to Vayssière (1906) in *H. velum,* and Hoffman (1939) in *H. albeocincta,* the pleural and parietal ganglia are distinct but joined side by side, whereas according to

Eales (1938), in *H. velum* these ganglia are fused into a single mass. Moreover, according to Rudman (1972a) there are no parietal ganglia in *H. physis*. Using Rudman's data, Mikkelsen (1996) regarded the parietal ganglia as being fused to the corresponding pleurals. Only Rudman (1972a) described a complete visceral commissure and Hoffman (1939) proposed the homologies of ganglia as hypothetical. Nevertheless, Vayssière (1906) described parietal ganglia. We code the visceral loop as {(PlPa)-SbAbd-Sp-(PaPl)}, {PlPa-SbAbd-Sp-PaPl} or {Pl-SbAbd-Sp-Pl}. (57) Posterior mucous gland (Rudman, 1972a) interpreted as a membrane gland here.

Scaphander Montfort, 1810 (Vayssière, 1880; Cuénot, 1891; Guiart, 1901; Perrier & Fisher, 1911; Fretter, 1939; Gabe & Prenant, 1952b; Hurst, 1965; Marcus & Marcus, 1967a; Thompson, 1976; Brace, 1977a, b). (26) The gland of Blochmann (Perrier & Fischer, 1911) is considered here as a repugnatorial gland and not as a purple gland because of the colour of the secretion. (28) The blood gland is either present (Vayssière, 1880) or absent (Cuénot, 1891). (43–51) According to Guiart (1901), many cells could represent a left vestigial parietal ganglia which has been fused (because for Guiart, the 'primitive condition' is the visceral commissure of *Acteon*) with the subœsophageal and abdominal ganglia at the posterior end of the visceral commissure. After Brace (1977b) '. . . small somata at the point of origin of the pallial nerve may represent a vestige . . . of . . . the left-pallial-ganglion supposedly incorporated within the pleural . . .'. Mikkelsen (1996) considered the 'vestigial somata' as a free parietal ganglion. Histological or developmental studies are clearly necessary to resolve these issues. The left parietal ganglion is considered here absent because vestigial somata are not a ganglion. All authors recognized a right parietal ganglion close to the right pleural ganglion. We code the visceral loop as {Pl-SbAbd-Sp-PaPl}.

Cylichna Lovén, 1846 (Cuénot, 1891; Lemche, 1956). The crista aortae is homologous with the blood gland (Cuénot, 1891). (46–47) Lemche (1956), who described the anatomy of *Cylichna* in detail, reported that '. . . it has not been possible to find any indisputable remains of the left parietal ganglion in this genus . . .' but Mikkelsen (1996) – using Lemche's data – coded a left parietal ganglion because of the occurrence of a pallial nerve which usually originates from parietal ganglion. We code the visceral loop as {Pl-SbAbd-Sp-PaPl}. (57–61) The winding and nidamental glands (Lemche, 1956) are, respectively, considered to be membrane and mucous glands.

Retusa T. Brown, 1827 (Vayssière, 1893; Rasmussen, 1944; Thorson, 1946; Hurst, 1965; Smith, 1967; Burn & Bell, 1974a, b; Thompson, 1976; Edlinger, 1980a, b; Berry, 1989; Berry *et al.*, 1992;

Huber, 1993; Mikkelsen, 1996). (43–51) According to Mikkelsen (1996), the topology of the visceral commissure is {Pl-SbAbd-Sp-(PaPl)} in *R. obtusa* and *R. truncatula*, whereas according to Huber (1993), the topology is {(PlPa)-SbAbd-SpPa-Pl} in *R. semisulcata.* According to Smith (1967), the topology is {Pl-SbAbd-Sp-Pl} in *R. obtusa* and, finally, Hurst (1965) described a parietal ganglion but in a wrong location (between the supraœsophageal and the subœsophageal). The cerebral and pleural ganglia are fused from the beginning of development in *R. obtusa* (Smith, 1967), and no parietal ganglion has been observed.

Philine Ascanius, 1772 (Guiart, 1901; Pruvot-Fol, 1930, 1960; Si, 1931; Brown, 1934; Thorson, 1946; Gabe & Prenant, 1952b; Hurst, 1965; Horikoshi, 1967; Challis, 1969; Rudman, 1970, 1971b, 1972d, g; Thompson, 1976; Seager, 1978; Gosliner, 1988b). (28) A blood gland is present (Cuénot, 1891). (43–51) There are no parietal ganglia in *P. aperta* (Vayssière, 1880; Guiart, 1901; Brown, 1934; Hoffman, 1939) nor in *P. gibba* (Rudman, 1972d). In *P. falklandica*, Rudman (1972d) described a free left parietal on the visceral commissure and a right parietal which is fused with the supraœsophageal ganglion; in *P. powelli* and *P. quadrata*, he described a right parietal only and, finally, in *P. angasi*, he described a left parietal only. Moreover, Mikkelsen (1996) confirmed the lack of a left parietal ganglion in *P. aperta* but coded it as present because of 'the generally plesiomorphic nature of *P. falklandica*'. Many hypotheses should be considered for coding the left parietal ganglion: {Pl-SbAbd-SpPl}, {Pl-Pa-SbAbd-(SpPa)Pl}, {Pl-Pa-SbAbd-SpPl}, {Pl-SbAbd-(SpPa)Pl}. (59–60) A mucous gland was described by Brown (1934) but Rudman (1970) considered that both mucous and membrane glands were present.

Aglaja Renier, 1804 (Guiart, 1901; White, 1945; Marcus & Marcus, 1966; Rudman, 1972c, h, 1974; Bandel, 1976; Brace, 1977a, b; Edlinger, 1980a, b; Gosliner, 1980; Vayssière, 1880). We code the visceral loop as {Pl-SbAbd-SpPl}. (67) A string between the egg-capsules, which are deposited in rows, has been described by Bandel (1976). It seems that this 'string' is only due to a sort of 'touching between the sides of the eggs', and it is not considered as a real chalaze here.

Gastropteron Kosse, 1813 (Vayssière, 1880, 1885; Guiart, 1901; Baba & Tokioka, 1965; Gosliner, 1988, 1989). (16) The gastropterid flagellum is homologous with the pallial caecum (Gosliner, 1989). (43–51) On the left side of the visceral commissure, Vayssière (1880) described 'un renflement du connectif cérébro-pédieux', a subœsophageal and a visceral ganglion close to the left pleural ganglion. Guiart (1901) described a left parietal ganglion fused to the subœsophageal ganglion only. On the right side of the vis-

ceral commissure, Guiart (1901) and Vayssière (1880) described three ganglia (pleural, parietal and supraœsophageal) fused into a single mass. Finally, Hoffman (1939) used Vayssière's and Guiart's data but interpreted the 'renflement du connectif cérébro-pédieux' as fused pleural and parietal ganglia on the left side. Moreover, Gosliner (1989) described no parietal ganglia in any species of *Gastropteron* and we consider these ganglia to be absent: {PlSbAbd-SpPl}. Nerve ring location prepharyngeal (Guiart, 1901) or postpharyngeal (Vayssière, 1880).

Runcina Forbes, 1853 (Vayssière, 1883; Mazzarelli, 1894; Colosi, 1915; Gabe & Prenant, 1952b; Baba & Hamatani, 1959; Ghiselin, 1963; Miller & Rudman, 1968; Thompson, 1976, 1980; Kress, 1977, 1985a, b, 1986; Thompson & Brodie, 1988; Cervera *et al.*, 1991; Gosliner, 1991; Kress & Schmekel, 1992; Kress *et al.*, 1994). (27) The 'opaline gland' described by Ghiselin (1963) is probably the kidney. The gill is reduced to few leaflets but is homologous with the plicatidium (Mazzarelli, 1894; Ghiselin, 1963; Thompson, 1976) and not with a pinnate gill (Vayssière, 1883). (43–51) Nervous system highly concentrated, and visceral loop unganglionate. Ghiselin (1963) supposed that parietal ganglia occur in the two pleural nervous masses but noted that '…the present account should be considered provisional until verified by serial sections'. We code the visceral loop as {(PlSb)-(AbdSpPl)}.

Diaphana T. Brown, 1837 (Hoffman, 1939; Thompson, 1976; Jensen, 1996a, b). We consider only *Diaphana s.str.* (*Diaphana minuta, D. candida, D. expansa*), excluding *Toledonia* and *Newnesia* (Jensen, 1996a; Odhner, 1926; Marcus, 1976). (43–51) {Pl-SbAbdSp-Pl}.

Colpodaspis N. Sars, 1870 (Brown, 1979). (8) The supposed homology of the cephalic sense organs with the organs of Hancock, suggested by Brown (1979), is doubtful because of their unusual structure. (43–51) {Pl-SbAbd-Sp-Pl}. (59–60) The posterior and anterior mucous glands described by Brown (1979) are, respectively, homologized with the membrane and the mucous gland.

Bulla Linné, 1758 (Vayssière, 1885; Pelseneer, 1894; Si, 1931; Eales, 1938; Risbec, 1951; Gabe & Prenant, 1952b; Marcus, 1957; Rudman, 1971b; Robles, 1975; Brace, 1977a, b; Winner, 1985, 1992). (43–51) In *Bulla striata*, left and right parietal ganglia are present (Marcus, 1957; Brace, 1977b) or absent (Hoffman, 1939): {Pl-Pa-SbAbd-Sp-PaPl} or {Pl-SbAbd-Sp-Pl}. (67) The 'narrow thread' joining eggs (Robles, 1975) is considered as a probable chalaze here, even though it is considered to be absent by Robertson (1985).

Haminoea Gray, 1847 (Guiart, 1901; Eliot, 1906; Perrier & Fisher, 1914; Berrill, 1931; Si, 1931; Fretter, 1939; Gabe & Prenant, 1952b; Marcus, 1956, 1958; Inaba, 1959; Marcus & Burch, 1965; Hurst, 1967;

Rudman, 1971a; Bandel, 1976; Thompson, 1976; Harrigan & Alkon, 1978; Edlinger, 1980a, b; Gibson & Chia, 1989; Schaefer, 1996). (43–51) The accessory ganglion described by Rudman (1971a) is homologized here with the parietal ganglion, because of its position. The nerve ring is either prepharyngeal (Rudman, 1971a) or postpharyngeal (Mikkelsen, 1996). There are either no parietal ganglia at all (Marcus, 1956), or a right accessory (= parietal) ganglion (Rudman, 1971a), or two parietal ganglia (personal observation): {Pl-SbAbd-Sp-PaPl} (Rudman), {Pl-Pa-Sb-Abd-Sp-PaPl} (pers.obs.), or {Pl-SbAbd-Sp-Pl} (Marcus). (57–61) The homologies of the female glands are complicated because of different terminologies employed (Guiart, 1901; Rudman, 1971a; Thompson, 1976). We recognize here a posterior mucous gland opening in the carrefour, the capsule gland and the albumen gland fused into a single 'genital glandular mass' opening into the carrefour, and an anterior mucous gland surrounding the pallial gonoduct from the carrefour to the vestibule. (65) The penial complex is innervated by the right pedal ganglion (pers. obs.). (66) Spermatophores are produced by the penial complex (Perrier & Fisher, 1914) and not by a spermatophore gland.

Smaragdinella A. Adams, 1848 (Marcus & Burch, 1965; Rudman, 1972e). (43–51) {Pl-SbAbd-Sp-PaPl}.

THECOSOMATA

Limacina Lamarck, 1819 (Pelseneer, 1887b (*Limacina = Spiratella*); Meisenheimer, 1905; Vayssière, 1915; Lebour, 1932; Hoffman, 1939; Gabe & Prenant, 1951, 1952b; Morton, 1954; Van der Spoel, 1967; Lalli & Wells, 1978; Lalli & Gilmer, 1989). (43–51) The highly concentrated nervous system (Pelseneer, 1887b) has two symmetrical pairs of cerebral and pedal nervous masses and one asymmetrical pair of visceral nervous masses, in which histological sections (Meisenheimer, 1905) did not allow identification of fused ganglia. We accept the hypothesis of Hoffmann (1939) here for the visceral loop ganglia {PlSb(AbdSp)Pl}.

Peraclis Forbes, 1844 (Van der Spoel, 1976; Pelseneer, 1887b; Meisenheimer, 1905; Vayssière, 1915; Lalli & Gilmer, 1989). (18) In accordance with Pelseneer (1887b) and Van der Spoel (1967), gill lamellae are considered here analogous with that of cephalaspideans. (43–51) The visceral loop of the highly concentrated nervous system is coded: {PlSbAbdSpPl} (Pelseneer, 1887b; Meisenheimer, 1905).

GYMNOSOMATA

Hydromyles Gistel, 1848 (Pelseneer, 1887a; Meisenheimer, 1905; Van der Spoel, 1967, 1976; Robertson, 1985; Lalli & Gilmer, 1989). (11) A pallial cavity is absent. (31) The proboscis is considered here analogous with that of pyramidellids (presence of the radula and hook-sacs in relation with occurrence of a proboscis). (43–51) Meisenheimer (1905) described fused suboesophageal and pleural ganglia even though his serial sections are not convincing: the visceral loop is coded {(PlSb)Abd(SpPl)}. (44) The circumoesophageal ganglia are aggregated together.

Clione Pallas, 1774 (Pelseneer, 1887a; Meisenheimer, 1905; Tesch, 1950; Morton, 1958; Van der Spoel, 1967, 1976; Lalli & Gilmer, 1989). (1) The heterostrophic condition cannot be ascertained because the protoconch is uncoiled and the teleoconch is absent (Lalli & Conover, 1976). (43–51) The visceral loop is coded {Pl-(SbAb)Sp-Pl} or {Pl-Sb(AbSp)-Pl} (Pelseneer, 1887a).

ACOCHLIDIOIDEA

Hedylopsis Thiele, 1931 (Kowalevsky, 1901; Odhner, 1937; Challis, 1970; Salvini-Plawen, 1973; Morse, 1976; Rankin, 1979; Wawra, 1989; *H. cornuta* has been placed in the genus *Pseudunela* Salvini-Plawen, 1973 by Rankin (1979) and is consequently not included here). (46–47) The visceral loop topology {Pl(PaAb)(AbPa)Pl} of Rankin (1979) is interpreted here as: {Pl(SbAb)SpPl} or {PlSb(AbSp)Pl}. (57–61) Albumen and mucous glands either open in the distal portion of the pallial gonoduct (*Hedylopsis suecica*: Wawra, 1989) or surround the proximal portion of the pallial gonoduct (*Hedylopsis riseri*: Morse, 1976). (61) The common genital aperture opens into a cloaca into which the anus also opens. (63–66) Penial complex and spermatophore absent or present (Morse, 1976).

APLYSIOIDEA

Akera O.F. Müller, 1776 (Pelseneer, 1894; Guiart, 1901; Thorson, 1946; Gabe & Prenant, 1952b; Morton & Holme, 1955; Marcus & Marcus, 1967a; Marcus, 1970; Morton, 1972; Thompson, 1976; Brace, 1977a, b; Mikkelsen, 1996). (7) Cephalic shield reduced but considered here as present. (24) The 'cellules mucipares' described by Perrier & Fisher (1911) are probably homologous with the hypobranchial gland. (43–51) The visceral loop described by Brace (1977a) and Pelseneer (1894) seems to be euthyneurous because they depicted a detorted – and not *in situ* – nervous system, whereas it is considered here as slightly streptoneurous (Mikkelsen, 1996): the visceral loop is coded {Pl-Pa-SbAb-SpPa-Pl}. (62) The prostate gland is either in the penial complex (Marcus & Marcus, 1967a) or in the common genital duct (Thompson, 1976).

Aplysia Linné, 1767 (Cuénot, 1891; Guiart, 1901; Eales, 1921; Marcus & Marcus, 1957; Hugues & Tauc,

1963; Ghiselin, 1966; MacFarland, 1966; Thompson & Bebbington, 1969; Beeman, 1968; Coggeshall, 1972; Marcus, 1972b; Brandriff & Beeman, 1973; Bebbington, 1974; Kriegstein *et al*., 1974; Bridges, 1975; Thompson, 1976; Brace, 1977c; Kriegstein, 1977a, b; Strenth & Blankenship, 1978; Kandel, 1979). (7) The absence of cephalic shield is coded here as a secondary loss or as a primary absence. (28) Crista aortae (Cuénot, 1891) are homologous with the blood gland. (43–51) Kriegstein *et al*. (1974) described in *Aplysia californica*: (a) the fusion of three ganglia (subœsophageal, supraœsophageal and abdominal) into a single visceral ganglionic mass, and (b) development without any appearence – and thus fusion – of parietal ganglia. In accordance to Kriegstein *et al*. the visceral loop topology is {Pl-(SbAbSp)-Pl}. The hypothesis of fusion supposed by Guiart (1901) and Eales (1921), who described the following topology {Pl-(PaSbAb)-(SpPa)-Pl}, is not accepted, and we interpret their observations as {Pl-(Sb-Ab)-Sp-Pl}. (62) The prostate gland is located along the exospermatic groove in the large hermaphroditic duct (Ghiselin, 1966; Thompson, 1976).

NOTASPIDEA

Umbraculum Schumacher, 1817 (Moquin-Tandon, 1870; Vayssière, 1885; Heymons, 1893; Guiart, 1901; O'Donoghue, 1929; Ostergaard, 1950; Marcus & Marcus, 1967a; Thompson, 1970; Marcus, 1985; Robertson, 1985; Willan, 1987). (43–51) One left and one right visceral nerve mass is present and the position of the pleural ganglia is unknown (Moquin-Tandon, 1870; Vayssière, 1885). The topology {(PlPaSb)-(AbSpPaPl)} (Hoffman, 1939) is not accepted here: we have coded the visceral loop as {(PlSb)-(AbSpPl)} or {(CPl)Sb-(AbSp)(PlC)}.

Tylodina Rafinesque, 1819 (Vayssière, 1883; Odhner, 1939; Burn, 1960; MacFarland, 1966; Thompson, 1970; Gosliner, 1981a; Willan, 1983, 1987; Marcus, 1985). (1) Protoconch sinistral, teleoconch patelliform, and adult anatomy dextral: heterostrophy is thus coded here as present. (13) Osphradium described by Pelseneer (1894) only and has not been observed since (MacFarland, 1966; Gosliner, 1981a; Willan, 1987), and is thus considered absent. (43–51) We do not accept here the topology of the visceral loop {(PlPaSb)Ab(SpPaPl)} described by Hoffmann (1939), but use the following: {(CPl)SbAbSp(CPl)} (Vayssière, 1885; Pelseneer, 1894). (64–67) Exact homologies of the genital system are unknown, even though the latter has been macroscopically described (MacFarland, 1966; Gosliner, 1981a). Female glands are coded here as a proximal 'female gland mass'.

Berthella Blainville, 1825 (Vayssière, 1898; Guiart, 1901; Prenant, 1925; O'Donoghue, 1929; Hirase,

1937; Odhner, 1939; Thorson, 1946; Burn, 1962; MacFarland, 1966; Bandel, 1976; Heller & Thompson, 1983; Willan, 1983, 1984, 1987; Marcus, 1984; Marcus & Gosliner, 1984; Robertson, 1985; Gosliner & Bertsch, 1988). (1) Heterostrophy has been treated as absent (Willan, 1983) or present (Thorson, 1946; Robertson, 1985); the two assumptions are retained here because of the ambiguity in protoconch morphology (pers. obs. on *Berthella plumula*). (28) The gland of Lacaze-Duthiers is present (pers. obs. on *Berthella plumula*). (43–51) One pair of cerebral and one of pedal masses, and many aggregated cells are located on the visceral loop (Vayssière, 1898; Guiart, 1901). The topology {(CPlPaSb)-(AbSp)-(PaPlC)} proposed by Hoffmann (1939) is not accepted, but the topology {(CPlSb)-(AbSp)-(PlC)} is retained because parietal ganglia have not been anatomically observed. (59) The position of the membrane gland is unknown; the eggs being encapsulated, we suppose the membrane gland is probably present and thus code it as ?. (62) A prostate gland is polymorphically present (Willan, 1983, 1984; Marcus, 1984) or absent (Burn, 1962; Willan, 1984), this latter condition possibly due to the immaturity of the specimens.

Pleurobranchus Cuvier, 1805 (Lacaze-Duthiers, 1859; Pelseneer, 1894; Bergh, 1897; Vayssière, 1898; Guiart, 1901; Thompson & Slinn, 1959; MacFarland, 1966; Thompson, 1970; Baba & Hamatani, 1971; Marcus, 1984; Marcus & Gosliner, 1984; Willan, 1987; Cervera *et al.*, 1996). (43–51) Similar to that of *Berthella* (Vayssière, 1898; Guiart, 1901).

SACOGLOSSA

Ascobulla Marcus, 1972 (Marcus & Marcus, 1956, 1970; Taylor & Sohl, 1962; Hamatani, 1969; 1971; Marcus, 1972a; De Freese, 1987; Jensen, 1989, 1990, 1991, 1996a, b; Jensen & Wells, 1990). (1) Even though the protoconch (Marcus, 1970; Jensen & Wells, 1990) is ambiguous, the shell has been intrepreted as heterostrophic (Robertson, 1985; Jensen, 1996a, b) and this assumption is accepted here. (24) A hypobranchial gland is probably present (Jensen & Wells, 1990). (43–51) We code the visceral loop as {(CPl)-Sb-Ab-Sp-(CPl)} (Jensen & Wells, 1990). (57–60) The homologies of the female glands (except the mucous gland) are unknown (Marcus, 1972a).

Oxynoe Rafinesque, 1819 (von Ihering, 1892; Eliot, 1906; Hoffman, 1939; Haefelfinger, 1960; Burn, 1966; Marcus & Marcus, 1970; Hamatani, 1980; Jensen, 1980, 1996b; Jensen & Wells, 1990; Schmekel & Portmann, 1982]. (43–51) similar to that of *Elysia*, we code the visceral loop as {(CPl)SbAbSp(CPl)} (Burn, 1966; Jensen, 1980).

Berthelinia Crosse, 1875 (Kawaguti & Baba, 1959; Kawaguti & Yamasu, 1960a, b, 1961, 1966, 1967;

Baba, 1961; Keen & Smith, 1961; Edmunds, 1963; Warmke, 1966; Yamasu, 1969; Sarma, 1975; Jensen, 1993a, b, c, 1996b; Kay, 1964, 1968; Schmekel & Portmann, 1982; Sanders-Esser, 1984). (43–51) We code the visceral loop as {(Cpl)-Sb-Ab-Sp-(CPl)} (Baba, 1961; Edmunds, 1963; Kay, 1968).

Elysia Risso, 1818 (Pelseneer, 1894; Russell, 1929; Thorson, 1946; Marcus, 1956, 1957; Baba, 1957; Pruvot-Fol, 1960; Reid, 1964; Thompson, 1973a, 1988; Carlson & Hoff, 1977, 1978; Marcus, 1980; Schmekel & Portmann, 1982; Sanders-Esser, 1984; Jensen, 1985, 1990, 1992, 1993a, b, c, 1996a, b; Thompson & Jaklin, 1988; Jensen & Wells, 1990). (1) Protoconch senestral (Thorson, 1946) and anatomy dextral: heterostrophy considered to be present here. (29) Few renopericardial apertures are present and this is coded as plesiomorphic state. (43–51) We code the visceral loop as {(CPl)SbAbSp(CPl)} (Russell, 1929).

Limapontia Johnston, 1836 (Pelseneer, 1894, 1934; Kevan, 1934, 1939; Vesteergaard & Thorson, 1938; Quick, 1950; Gascoigne, 1956, 1974, 1978, 1985). (1) The larval shell (Thorson, 1946) is similar to that of *Elysia*. (43–51) We code the visceral loop as {(CPl)(SbAb)Sp(CPl)} (Jensen, 1993). The topology {(CPl)AbSp(CPl)} proposed by Pelseneer (1894) is not accepted here.

NUDIBRANCHIA

Tritonia Cuvier, 1803 (Pelseneer, 1894; Odhner, 1936; Alder & Hancock, 1845–1855; Vestergaard & Thorson, 1938; Marcus, 1959, 1961; Thompson, 1961a, 1962, 1976; Marcus & Marcus, 1967b, c; Schmekel, 1970; Gosliner & Ghiselin, 1987). (43–51) The suboesophageal, supraoesophageal and abdominal ganglia are absent (Hoffmann, 1939) and do not appear during development (Thompson, 1962). We code the visceral loop as {(CPl)-(PlC)}. (48) The subcerebral commissure (Hoffmann, 1939) is either present (in *Tritonia hombergi*) or absent (in *Tritonia plebeja*).

Hancockia Gosse, 1877 (Hoffmann, 1939; Marcus, 1957; Schmekel, 1970). We code the visceral loop as {(CPl)-(PlC)}.

Archidoris Bergh, 1878 (Alder & Hancock, 1855; Eliot, 1910; Prenant, 1925; Pruvot-Fol, 1934; Hoffmann, 1939; MacGowan & Pratt, 1954; Thompson, 1966a; b, 1976; Kay & Young, 1969; Edmunds, 1971; Kress, 1971; Schmekel & Weichter, 1973; Schmekel & Portmann, 1982). (28) The blood gland on the anterior aorta is probably homologous with that of other euthyneurans (Eliot, 1910; Schmekel & Weichter, 1973). (43–51) We code the interrupted visceral loop as {(CPl)...(PlC)} (Alder & Embleton, in Alder & Hancock, 1855; Eliot, 1910; Hoffman, 1939).

Chromodoris Alder & Hancock, 1855 (Schmekel, 1970; Rudman, 1973, 1977, 1984; Bertsch, 1978;

Schmekel & Portmann, 1982). (1) The shell is considered here as heterostrophic (Thompson, 1961b). (28) The blood gland (Rudman, 1978) is probably homologous with that of other euthyneurans.

Armina Rafinesque, 1814 (Bergh, 1866; Eales, 1938; Marcus & Marcus, 1960b, 1966, 1967b, c; Schmekel & Portmann, 1982; Miller & Willan, 1986). (1) The shell is considered here as heterostrophic (Hurst, 1967). (43–51) {(CPl)...(PlC)} (Bergh, 1866). (59–60) The albumen and mucous glands either surround the pallial oviduct (Marcus & Marcus, 1967b, c) or lie in the female gland mass (Miller & Willan, 1986).

Janolus Bergh, 1884 (Marcus, 1958; MacFarland, 1966; Miller, 1971; Gosliner, 1981b, 1982; Miller & Willan, 1986; Schrödl, 1996). (43–51) We code the visceral loop as {(CPl)-(PlC)} (Hoffmann, 1939).

Facelina Alder & Hancock, 1855 (Pelseneer, 1901; Loyning, 1922; Odhner, 1939; Thorson, 1946; Macnae, 1954; Marcus, 1958; Edmunds, 1969, 1970; Gosliner, 1979; Schmekel & Portmann, 1982). (1) The shell is considered here as heterostrophic (Pelseneer, 1901; Thorson, 1946). (43–51) {(CPl)-(PlC)} (Hoffmann, 1939). (57–60) The distal female gland mass is ambiguous (Macnae, 1954; Marcus, 1958; Schmekel & Portmann, 1982).

Aeolidia Cuvier, 1798 (*Aeolidia papillosa* = *Aeolis papillosa*) (Alder & Hancock, 1845–1855; Pelseneer, 1894; Hecht, 1896; Eliot, 1910; Russell, 1929; Hoffmann, 1939). (1) The shell is considered here as heterostrophic (Pelseneer, 1911). (43–51) We code the visceral loop as {(CPl)-(PlC)} (Russell, 1929).

PULMONATA, BASOMMATOPHORAN TAXA

Otina Gray, 1847 (Pelseneer, 1911; Morton, 1955b; Duncan, 1975; Berry, 1977; Geraerts & Joose, 1984; Robertson, 1985). (1) The shell is considered here as heterostrophic (Pelseneer, 1911; Morton, 1955b; Robertson, 1985). (43–51) We code the visceral loop as {PlSb-Ab-SpPl} (Pelseneer, 1901).

Carychium O.F. Müller, 1774 (Morton, 1955a, c, d). (1) Heterostrophy is considered as present here (Doll & Sander, 1985; Harbeck, 1996). (43–51) We code the visceral loop as {Pl-Sb-Ab-Sp-Pl} (Pelseneer, 1901; Bargmann, 1930; Lever, 1958b). (57) The shell gland (Morton, 1955a, c, d) is homologous with the albumen gland.

Pythia Röding, 1798 (Plate, 1897; Harry, 1951; Morton, 1955a, c; Berry *et al.*, 1967; Berry, 1977; Hubendick, 1978; Geraerts & Joosse, 1984). (1) The shell is considered here as heterostrophic (Harbeck, 1996).

Melampus Montfort, 1810 (Koslowsky, 1933; Meyer, 1955; Morton, 1955a; Knipper & Meyer, 1956; Marcus & Marcus, 1965b; Apley, 1970; Russell-Hunter *et al.*, 1972). (25) The PMO is considered here as absent

(Russell-Hunter *et al*., 1972). (43–51) We code the visceral loop as {PlSbAbSpPl} (Meyer, 1955; Van Mol, 1967). (59) The posterior mucous gland (Apley, 1970) is homologous with the capsule gland, because the eggs are embedded in the capsular membrane.

Ellobium Röding, 1798 (Pelseneer, 1894, 1901; Odhner, 1925; Morton, 1955a, c; Knipper & Meyer, 1956; Marcus & Marcus, 1965b; Berry *et al.* 1967; Hubendick, 1978). (43–51) We code the visceral loop as {Pl-Sb-Ab-Sp-Pl} (Pelseneer, 1901; Marcus & Marcus, 1965b).

Gadinia Gray, 1824 (Pelseneer, 1901; Schumann, 1911; Dieuzeide, 1935; Hubendick, 1946, 1978; Yonge, 1958; Van Mol, 1967; Haven, 1973; Berry, 1977; Harbeck, 1996). (43–51) We code the visceral loop as {Pl-(SbAb)-(SpPl)} (Schumann, 1911; Van Mol, 1967).

Siphonaria G.B. Sowerby, 1824 (Pelseneer, 1894, 1901; Dieuzeide, 1935; Abe, 1940; Hubendick, 1943, 1945a, 1946, 1947a, b, 1978; Yonge, 1952; Marcus & Marcus, 1960a; Berry, 1977; Mapstone, 1978). (12) The pallial cavity opens through a pneumostome (also called 'orifice respiratoire' by Dieuzeide, 1935), which is not retractile as in other pulmonates. (18) The gill is either homologized with the plicatidium (Dieuzeide, 1935; Marcus & Marcus, 1960a) or not (Yonge, 1952). (25) A PMO is considered here as absent (Dieuzeide, 1935). (43–51) here we accept the topology of the visceral loop as {(Pl-(SbAb)Sp-Pl)} (Hubendick, 1978); Marcus & Marcus (1960a) proposed the topology {(PlPa)-(SbAb)-(SpPa)-Pl} but arbitrarily called the right visceral ganglion a 'parieto-supraintestinal ganglion' using Hæckel's terminology (1911). (66) The epiphallus gland probably secretes spermatophores (Hubendick, 1947a, b).

Amphibola Schumacher, 1817 (Bouvier, 1892; Pelseneer, 1894; Farnie, 1919, 1924; Hubendick, 1945b, 1978; Van Mol, 1967; Berry, 1977; Pilkington & Pilkington, 1982; Geraerts & Joose, 1984; Little *et al.*, 1985). (1) The shell is considered here as heterostrophic (Little *et al.*, 1985). (25) The larval kidney is red-pigmented (Little *et al.*, 1985) and homologous with the PMO. (43–51) Here we accept the topology of the visceral loop as {(Pl-Sb-Ab-Sp-Pl)} (Hubendick, 1945b). (62) The flagellum (Hubendick, 1945b, 1978) is considered as homologous with the prostate (Farnie, 1919; Berry, 1977).

Chilina Gray, 1828 (Pelseneer, 1894; Plate, 1894; Haeckel, 1911; Harry, 1964; Régondaud, 1973; Hubendick, 1978; Brace, 1983; Ituarte, 1997). (1) The shell is considered here as heterostrophic (Régondaud, 1973). (16) Pallial caecum and ciliated ridges (homologized here with the raphes) are considered here as present (Harry, 1964; Brace, 1983; Robertson, 1985). (25) A PMO is considered here as absent (Régondaud, 1973). (43–51) Many topologies of the visceral loop have been proposed, in distinct species: {PlSb-

Uncalled-Ab-Sp-Pl} (Pelseneer, 1894), {PlPa-Sb-Ab-Sp-Pl} (Pelseneer, 1901), {Pl-Pa(=Sb)-Ab-Pa(=Sp)-Pl} (Harry, 1964), {Pl-Sb-Ab-Sp-Pl} (Hubendick, 1978). (66) Spermatophores are either present or absent (Harry, 1964).

Physa Draparnaud, 1801 (Lacaze-Duthiers, 1872; Fol, 1879; Pelseneer, 1901; Bondesen, 1950; Duncan, 1958, 1975; Van Mol, 1967). (43–51) We code the visceral loop as {PlSpAbSbPl} (Lacaze-Duthiers, 1872; Fol, 1879; Pelseneer, 1901).

Lymnaea Lamarck, 1799 (Lacaze-Duthiers, 1872; Fol, 1879; Schnabel, 1903; Crabb, 1927; Hoffmann, 1932–39; Carriker, 1943, 1947; Hubendick, 1945c, d, 1951; Carriker & Bistad, 1946; Fraser, 1946; Holm, 1946; MacCraw, 1957; Itagaki, 1959; Demian, 1962; Joose & Reitz, 1969; Walter, 1969; Régondaud *et al.*, 1974; Brisson & Besse, 1975; Brisson & Régondaud, 1977; Swiderski, 1990). (43–51) We code the visceral loop as {PlSbAbSpPl} (Lacaze-Duthiers, 1872; Fol, 1879; Carriker, 1947; MacCraw, 1957; Walter, 1969); we do not accept here the pulmonate terminology (one left and one right parietal ganglia instead of one suboesophageal and one supraoesophageal) that has been used by every author (except Lacaze-Duthiers who introduced his own terminology). (59–60) The posterior mucous gland (Duncan, 1960b) is homologized here with the membrane gland because of its secretion.

Acroloxus Beck, 1837 (Bondesen, 1950; Lever, 1958a, b; Lever *et al.*, 1959; Hubendick, 1962, 1978; Brisson, 1964; Van Mol, 1967). (43–51) We code the visceral loop as {(PlSp)Ab(SbPl)} (Hubendick, 1978). We reject his other assumption {(PlPa)Ab(PaPl)} (Hubendick, 1962) because of an erroneous terminology of ganglia.

Ancylus O.F. Müller, 1774 (Sharp, 1883; Lacaze-Duthiers, 1899; Bondesen, 1950; Lever, 1958a, b; Lever *et al.*, 1959; Duncan, 1960b; Van Mol, 1967). (43–51) We code the visceral loop as {Pl(SbAb)(SpPl)} (Lever, 1958a, b; Lever *et al.*, 1959; Van Mol, 1967).

PULMONATA, SOLEOLIFERA

Veronicella Blainville, 1817 (Simroth, 1891; Sarasin & Sarasin, 1899; Pelseneer, 1901; Robbins & Cockerell, 1909; Colosi, 1922; Baker, 1925a, b, 1926, 1931; Grimpe & Hoffmann, 1925; Hoffmann, 1925; Coifmann, 1934a, b, 1935, 1938; Lanza & Quatrini, 1964a, b; Simroth, 1913; Thomé, 1975; Tillier, 1980, 1984) (According to Thiele: *Vaginula = Vaginulus = Meisenheimera = Veronicella*). (1) The shell is probably not heterostrophic (Robertson, 1985). (43–51) We accept here the topology of the visceral loop {Pl(SbAbSp)Pl} (Coifmann, 1934a, b; Van Mol, 1967) and we do not accept here the topology which has been described by Hoffmann (1939): {Pl(Pa(SbAb)Sp)Pl}

because parietal ganglia have not been anatomically observed. (52–53) Dorsal bodies that cannot be observed externally (Pelseneer, 1901; Van Mol, 1967) are supposed to be present here. (56) Fertilization pouch either present (Lanza & Quattrini, 1964a, b) or absent (Baker, 1925a, b; 1926; 1931). (67) Eggs of the spawn are joined by a 'filamento mucozo' (Lanza & Quatrini, 1964a, b), which is analogous with a chalaze, because of a distinct anatomy.

PULMONATA, ONCHIDIIDAE

Onchidium Buchanan, 1800 (Awati & Karandikar, 1948; Ruthensteiner, 1997). Anatomy similar to that of *Onchidiella* for all characters (except few characters of the nervous system). Spermatic characters described on *Onchidium* only.

Onchidiella Gray, 1850 (Semper, 1880, 1882; Joyeux-Laffuie, 1882; Plate, 1893; Pelseneer, 1901; Watson, 1925; Labbé 1933a, b, c, 1934a; Tuzet, 1940; Fretter, 1943, 1975; Awati & Karandikar, 1948; Boettger, 1954; Marcus, 1959; Solem, 1959; Ghiselin, 1966; Oberzeller, 1969; Marcus & Marcus, 1970; Gosliner, 1981a; Tillier, 1984; Robertson, 1985; Young *et al.*, 1986). (1) The shell is probably not heterostrophic (Robertson, 1985); moreover, the veliger shell and adult anatomy are dextral (Joyeux-Laffuie, 1882; Fretter, 1943). (25) The larval kidney (Joyeux-Laffuie, 1882) is probably homologous with the PMO, but Robertson (1985) considered that the PMO is probably absent in Onchidiidae. (43–51) Many assumptions should be tested according to studies of Joyeux-Laffuie (1882) and Van Mol (1967) because they used an ambiguous terminology for the visceral loop: {Pl(SbAb)(SpPl)}, {(PlSb)Ab(SpPl)} or {SbAbSp}. (53) Dorsal bodies are either considered as absent (Lever, 1958b) or present (Van Mol, 1967). (67) The gelatinous coating that joins the albuminate eggs of the spawn is probably homologous with a chalaze (Awati & Karandikar, 1948).

PULMONATA, STYLOMMATOPHORA

Succinea Draparnaud, 1801 (Baudon, 1877; Schnabel, 1903; Quick, 1933, 1939; Franzen, 1959; Duncan, 1961; Rigby, 1965; Cook, 1966; Delhaye & Bouillon, 1972c; Bayne, 1973; Solem, 1976; Visser, 1977, 1981). (43–51) We code the visceral loop as {(CPl)(SbAbSp)(PlC)} (Cook, 1966). (57) The albumen gland is ambiguous (Rigby, 1965).

Achatinella Swainson, 1828 (Pilsbry, 1900; Cooke & Kondo, 1960; Van Mol, 1967; Tillier, 1984, 1989). (32) The ureter of orthurethrans is interpreted either as secondary (Cooke & Kondo, 1960) or as primary (Delhaye & Bouillon, 1972c). (43–51) We code the visceral loop as {PlSb(AbSp)Pl} (Van Mol, 1967; Tillier, 1984, 1989). (57–60) The species of the genus *Achatinella* are ovoviviparous: eggs are stored in the oviduct and nidamental glands are consequently absent.

Achatina Lamarck, 1799 (Reynell, 1906; Mead, 1950; Ghose, 1962a, b, c, 1963a, b, c, d, e, 1964; Hyman, 1967; Van Mol, 1967; Brisson, 1968; Breckenbridge & Fallil, 1973; Tillier, 1989). (1) The embryological shell is dextral but seems to be senestral at the begining of development (Brisson, 1968). (25) A larval kidney (Brisson, 1968) is probably homologous with the PMO. (43–51) The topology of the visceral loop {PlPaAbPaPl} (Ghose, 1962; Tillier, 1989) is interpreted here as {PlSbAbSpPl}.

Arion Férussac, 1819 (Lamy, 1929; Van Mol, 1962; Smith, 1966; Van Mol *et al.*, 1970; Parivar, 1978). (43–51) We code the visceral loop as {(PlSb)Ab(SpPl)}, {Pl(SbAbSp)Pl} or {(PlSb)(AbSp)Pl} (Van Mol, 1962).

Helix Linné, 1758 (Schnabel, 1903; Prenant, 1924, 1926; Lamy, 1929; Duncan, 1960a; Lind, 1973; Kerkut & Walker, 1975; Visser, 1977; Godan, 1979; Enée & Griffond, 1983; Tillier, 1989). (1) The embryological shell is dextral (Godan, 1979). (43–51) We code the visceral loop as {PlSbAbSpPl} (Kerkut & Walker, 1975; Tillier, 1989). No parietal ganglia appear during development (Fol, 1879).

APPENDIX 3

Consistency Index of all characters in strict consensus trees of analyses I to VII.

Characters	CI (I)	CI (II)	CI (III)	CI (IV)	CI (V)	CI (VI)	CI (VII)
1	0.333	0.333	0.200	0.500	0.333	0.143	0.333
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000
3	0.200	0.200	0.167	0.167	0.200	0.100	0.167
4	1.000	1.000	1.000	1.000	1.000	1.000	1.000
5	1.000	1.000	1.000	1.000	1.000	1.000	1.000
6	0.333	0.333	0.250	0.250	0.333	0.250	0.250
7	0.500	0.500	0.333	0.333	0.500	0.500	0.333
8	1.000	1.000	1.000	1.000	1.000	1.000	1.000
9	1.000	1.000	1.000	1.000	1.000	1.000	1.000
10	1.000	0.500	0.500	1.000	1.000	1.000	0.500
11	0.400	0.154	0.286	0.333	0.286	0.333	0.333
12	0.100	0.077	0.091	0.125	0.091	0.091	0.091
13	1.000	1.000	1.000	1.000	1.000	1.000	1.000
14	1.000	1.000	1.000	1.000	1.000	1.000	1.000
15	0.333	0.333	0.250	0.250	0.333	0.250	0.250
16	0.167	0.111	0.143	0.200	0.143	0.111	0.125
17	0.667	0.667	0.667	0.667	0.667	0.667	0.667
18	1.000	1.000	1.000	1.000	1.000	1.000	1.000
19	1.000	0.333	0.500	0.500	1.000	1.000	0.500
20	1.000	1.000	1.000	1.000	1.000	1.000	1.000
21	0.500	0.143	0.333	0.500	0.250	0.333	0.333
22	0.222	0.200	0.222	0.222	0.200	0.222	0.222
23	0.200	0.100	0.250	0.250	0.167	0.167	0.200
24	1.000	1.000	1.000	1.000	1.000	1.000	1.000
25	1.000	1.000	1.000	1.000	1.000	1.000	1.000
26	0.333	0.250	0.333	0.333	0.333	0.333	0.333
27	1.000	1.000	1.000	1.000	1.000	1.000	1.000
28	1.000	1.000	1.000	1.000	1.000	1.000	1.000
29	1.000	1.000	1.000	1.000	1.000	1.000	1.000
30	0.214	0.136	0.231	0.231	0.200	0.214	0.214
31	1.000	0.500	1.000	1.000	0.500	1.000	1.000
32	1.000	1.000	1.000	1.000	1.000	1.000	1.000
33	0.500	0.333	1.000	0.500	1.000	0.500	0.500
34	0.333	0.333	0.333	0.333	0.333	0.333	0.333
35	0.750	0.750	0.750	1.000	0.750	0.600	1.000
36	0.500	0.500	0.800	0.800	0.500	0.571	0.800
37	0.500	0.111	0.250	0.333	0.200	0.250	0.250
38	0.125	0.100	0.111	0.125	0.125	0.100	0.100
39	1.000	1.000	1.000	1.000	1.000	1.000	1.000
40	0.286	0.286	0.286	0.333	0.286	0.235	0.364
41	0.200	0.167	0.167	0.200	0.200	0.167	0.167
42	0.143	0.111	0.100	0.167	0.111	0.091	0.125
43	0.333	0.333	0.333	0.333	0.333	0.333	0.333
44	0.250	0.250	0.333	0.333	0.250	0.200	0.333
45	0.091	0.091	0.100	0.100	0.091	0.091	0.100
46	0.125	0.100	0.091	0.143	0.125	0.077	0.111
47	0.318	0.269	0.292	0.333	0.280	0.269	0.304
48	0.273	0.231	0.250	0.316	0.240	0.214	0.250
49	1.000	0.125	1.000	1.000	0.500	1.000	1.000
50	1.000	0.111	1.000	1.000	0.500	1.000	1.000
51	0.500	0.500	0.500	0.500	0.500	0.500	0.500
52	0.500	0.500	0.500	0.500	0.500	0.500	0.500

APPENDIX 3 (*Continued*)

Characters	CI (I)	CI (II)	CI (III)	CI (IV)	CI (V)	CI (VI)	CI (VII)
53	0.250	0.250	0.250	0.250	0.250	0.250	0.250
54	0.500	0.421	0.533	0.533	0.500	0.444	0.533
55	0.250	0.167	0.125	0.167	0.250	0.167	0.143
56	0.429	0.375	0.333	0.429	0.375	0.333	0.333
57	0.500	0.444	0.533	0.533	0.500	0.500	0.533
58	0.429	0.333	0.353	0.429	0.400	0.286	0.429
59	0.368	0.350	0.318	0.412	0.368	0.304	0.350
60	0.222	0.200	0.167	0.222	0.222	0.143	0.222
61	0.167	0.111	0.167	0.200	0.167	0.167	0.200
62	0.333	0.333	0.250	0.250	0.333	0.200	0.250
63	0.200	0.200	0.200	0.200	0.200	0.200	0.200
64	1.000	0.500	0.500	1.000	1.000	0.500	0.500
65	1.000	1.000	1.000	1.000	1.000	1.000	1.000
66	1.000	1.000	0.667	0.667	1.000	0.667	1.000
67	1.000	1.000	1.000	1.000	1.000	1.000	1.000
68	1.000	1.000	1.000	1.000	1.000	1.000	1.000
69	1.000	1.000	1.000	1.000	1.000	1.000	1.000
70	1.000	1.000	1.000	1.000	1.000	1.000	1.000
71	1.000	1.000	0.500	0.500	1.000	0.500	1.000
72	1.000	1.000	0.500	0.500	1.000	0.500	1.000
73	1.000	1.000	1.000	1.000	1.000	1.000	1.000
74	1.000	1.000	1.000	1.000	1.000	1.000	1.000
75	0.500	0.500	0.500	0.500	0.500	0.500	0.500
76	1.000	1.000	1.000	1.000	1.000	1.000	1.000
77	1.000	1.000	1.000	1.000	1.000	1.000	1.000

APPENDIX 4

Character change lists of the strict consensus tree obtained from the analysis I. See Fig. 2 for node numbers. = = > indicates unambiguous change, −> indicates change which does not occur in all reconstructions, <−> indicates undirected transformation.

Character	CI	Changes
1. Heterostrophy	0.333	node 125 0 = = > 1 node 121
		node 107 1 = = > 0 node 106
		node 130 0 = = > 1 node 129
2. Protoconch	1.000	node 131 0 = = > 1 node 77
3. Operculum	0.200	node 126 0 = = > 1 node 125
		node 78 1 = = > 0 *Odostomia*
		node 95 1 = = > 0 *Amphibola*
		node 112 1 = = > 0 node 111
		node 123 1 = = > 0 node 122
4. Pedal gland	1.000	node 88 0 − > 1 node 81
		node 107 0 = = > 2 node 106
		node 106 2 = = > 3 node 105
5. Thecos.wings	1.000	node 123 0 = = > 1 node 122
6. Cephalic shield	0.333	node 92 0 = = > 1 *Ascobulla*
		node 120 0 = = > 1 node 119
		node 113 1 = = > 0 *Aplysia*
7. Hancock's organ	0.500	node 121 0 − > 1 node 120
		node 113 1 = = > 0 *Aplysia*

APPENDIX 4 (*Continued*)

Character	CI	Changes
8. Retractile tentacles	1.000	node 106 0 = = > 1 node 105
9. Position of eyes	1.000	node 107 0 = = > 1 node 106
10. Cerata	1.000	node 86 0 = = > 1 node 85
11. Pallial cavity	0.400	node 91 0 = = > 2 node 90
		node 109 0 = = > 1 node 108
		node 99 1 = = > 2 node 98
		node 106 1 = = > 2 *Veronicella*
		node 125 0 = = > 2 node 124
12. Osphradium	0.100	node 130 0 – > 1 node 128
		node 128 1 – > 0 node 126
		node 93 0 – > 1 node 91
		node 79 1 = = > 0 *Tylodina*
		node 108 0 = = > 1 node 107
		node 95 1 = = > 0 *Amphibola*
		node 95 1 = = > 0 *Chilina*
		node 98 1 = = > 0 *Ancylus*
		node 120 0 = = > 1 *Colpodaspis*
		node 127 1 – > 0 *Valvata*
13. Si1 & Si2 cells	1.000	node 77 0 = = > 1 *Littorina*
14. Si4 cells	1.000	node 131 0 = = > 1 node 77
15. Pallial caecum	0.333	node 95 0 = = > 1 *Chilina*
		node 118 0 = = > 1 node 117
		node 113 1 = = > 0 *Aplysia*
16. Raphes	0.167	node 125 0 = = > 1 node 121
		node 91 1 – > 0 node 90
		node 108 1 = = > 0 node 107
		node 95 0 = = > 1 *Chilina*
		node 113 1 = = > 0 *Aplysia*
		node 130 0 = = > 1 node 129
17. Plicatidium	0.667	node 109 0 – > 2 node 93
		node 121 0 = = > 1 node 120
		node 123 0 = = > 1 *Runcina*
18. Branchial circlet	1.000	node 83 0 = = > 1 node 82
19. Pinnate gill	1.000	node 88 0 = = > 1 node 81
20. Prebranchial pocket	1.000	node 81 0 = = > 1 node 80
21. Pulmonary vessels	0.500	node 108 0 – > 1 node 107
		node 106 1 – > 0 *Onchidium*
22. Hypobranchial gland	0.222	node 78 0 = = > 1 *Amathina*
		node 91 0 = = > 1 node 90
		node 109 0 = = > 1 node 108
		node 95 1 = = > 0 *Carychium*
		node 95 1 = = > 0 *Amphibola*
		node 96 1 = = > 0 *Melampus*
		node 115 0 = = > 1 *Smaragdinella*
		node 125 0 – > 2 node 123
		node 127 0 = = > 1 *Glacidorbis*
23. PMO	0.200	node 125 0 = = > 1 node 121
		node 86 1 – > 0 node 84
		node 109 1 = = > 0 node 108
		node 114 1 – > 0 node 113
		node 130 0 = = > 1 node 129
24. Purple gland	1.000	node 114 0 = = > 1 node 113
25. Opaline gland	1.000	node 114 0 = = > 1 node 113

APPENDIX 4 (*Continued*)

Character	CI	Changes
26. Blood gland	0.333	node 88 0 = = > 1 node 81
		node 86 0 – > 1 node 84
		node 121 0 – > 1 node 120
27. Renoperic. duct	1.000	node 88 0 = = > 1 node 87
28. Secondary ureter	1.000	node 106 0 = = > 1 node 105
29. Nephridial gland	1.000	node 131 0 – > 1 node 130
30. Jaws	0.214	node 131 0 = = > 1 node 130
		node 90 1 = = > 0 node 88
		node 82 0 = = > 1 *Archidoris*
		node 109 1 = = > 2 node 108
		node 95 2 = = > 1 *Amphibola*
		node 107 2 = = > 3 node 106
		node 106 3 = = > 1 *Onchidium*
		node 117 1 = = > 0 node 116
		node 111 0 = = > 1 *Acteon*
		node 117 1 = = > 0 *Cylichna*
		node 125 1 = = > 0 node 123
		node 128 1 – > 0 node 127
		node 127 0 – > 1 *Glacidorbis*
		node 129 1 = = > 0 *Tuba*
31. Evaginable proboscis	1.000	node 110 0 = = > 1 node 78
32. Acid gland	1.000	node 81 0 = = > 1 node 80
33. Ascus	0.500	node 109 0 = = > 1 node 93
		node 90 1 – > 0 node 88
34. Odont. cartilage	0.333	node 120 0 = = > 1 node 119
		node 116 1 = = > 0 node 115
		node 125 0 – > 1 node 124
35. Odontoblasts	0.750	node 132 2 < – > 0 Trochidae
		node 121 2 – > 1 node 110
		node 116 2 – > 3 node 112
		node 123 2 – > 3 node 122
36. Oesophageal gizzard	0500	node 118 0 – > 3 node 117
		node 117 3 – > 0 node 116
		node 116 0 – > 4 node 115
		node 114 4 = = > 2 node 113
		node 117 3 – > 0 *Aglaja*
		node 117 3 – > 0 *Gastropteron*
		node 125 0 – > 1 node 123
		node 123 1 – > 3 *Runcina*
37. Gastric gizzard	0500	node 107 0 = = > 1 node 101
		node 98 1 = = > 0 *Acroloxus*
38. Gastric caecum	0125	node 94 0 = = > 1 *Latia*
		node 95 0 = = > 1 *Ellobium*
		node 97 0 = = > 1 node 96
		node 100 0 = = > 1 node 99
		node 102 0 = = > 1 *Succinea*
		node 104 0 = = > 1 *Achatina*
		node 108 0 = = > 1 *Siphonaria*
		node 114 0 = = > 1 node 113
39. Shapes of faeces	1000	node 131 0 = = > 1 node 77
40. Visceral loop	0286	node 128 0 = = > 1 node 126
		node 84 1 = = > 4 node 83
		node 93 1 = = > 2 node 92

APPENDIX 4 (*Continued*)

Character	CI	Changes
		node 95 1 = = > 3 node 94
		node 95 1 = = > 3 *Chilina*
		node 121 1 = = > 3 node 120
		node 118 3 = = > 2 node 117
		node 116 2 = = > 0 node 112
		node 115 2 = = > 3 *Smaragdinella*
		node 117 2 = = > 3 *Aglaja*
		node 117 2 = = > 1 *Gastropteron*
		node 119 3 = = > 0 *Ringicula*
		node 127 0 = = > 1 *Glacidorbis*
41. Hypo./Epiathroidy	0200	node 132 0 = = > 1 node 131
		node 95 1 = = > 0 *Ellobium*
		node 97 1 = = > 0 node 96
		node 104 1 = = > 0 node 103
		node 114 1 = = > 0 node 113
42. Circumoesoph.	0143	node 81 0 = = > 1 node 80
		node 97 0 = = > 1 node 95
		node 121 0 = = > 1 node 120
		node 116 1 = = > 0 node 115
		node 124 0 = = > 1 *Hedylopsis*
		node 127 0 = = > 1 *Valvata*
		node 130 0 = = > 1 node 129
43. Left parietal gang.	0.333	node 94 0 = = > 1 *Latia*
		node 116 0 – > 1 node 112
		node 113 0 = = > 1 *Akera*
44. Right parietal gang.	0250	node 118 0 = = > 1 node 117
		node 113 1 = = > 0 *Aplysia*
		node 117 1 = = > 0 *Aglaja*
		node 117 1 = = > 0 *Gastropteron*
45. Subcerebral com.	0091	node 87 0 = = > 1 *Hancockia*
		node 85 0 = = > 1 *Facelina*
		node 95 0 = = > 1 *Amphibola*
		node 99 0 = = > 1 *Lymnaea*
		node 107 0 – > 1 node 106
		node 106 1 – > 0 *Veronicella*
		node 103 1 = = > 0 *Arion*
		node 114 0 = = > 1 *Haminoea*
		node 117 0 = = > 1 *Scaphander*
		node 117 0 = = > 1 *Gastropteron*
46. Parapedal com.	0125	node 110 0 = = > 1 node 109
		node 86 1 = = > 0 node 84
		node 95 1 = = > 0 *Carychium*
		node 95 1 = = > 0 *Ellobium*
		node 106 1 = = > 0 node 105
		node 120 0 – > 1 node 119
		node 125 0 – > 1 node 124
		node 130 0 = = > 1 node 129
47. Position of suboes.	0318	node 132 0 = = > 6 *Pila*
		node 77 0 = = > 6 node 76
		node 128 0 – > 1 node 126
		node 126 1 – > 5 node 125
		node 88 5 = = > 8 node 87
		node 89 5 = = > 48 *Limapontia*

APPENDIX 4 (*Continued*)

Character	CI	Changes
		node 93 5 = = > 0 node 92
		node 101 5 = = > 0 node 97
		node 95 0 – > 1 node 94
		node 94 1 – > 3 Latia
		node 96 0 = = > 4 *Gadinia*
		node 99 5 = = > 2 node 98
		node 102 5 = = > 4 *Succinea*
		node 108 5 = = > 4 *Siphonaria*
		node 121 5 = = > 3 node 120
		node 112 3 = = > 0 node 111
		node 117 3 = = > 5 *Gastropteron*
		node 118 3 = = > 0 *Diaphana*
		node 119 3 = = > 1 *Ringicula*
		node 123 5 = = > 4 node 122
		node 124 5 = = > 34 *Clione*
		node 127 0 = = > 1 *Valvata*
48. Position of supraoes.	0273	node 128 0 = = > 5 node 126
		node 90 5 – > 8 node 88
		node 81 8 – > 5 node 79
		node 93 5 = = > 0 node 92
		node 97 5 = = > 0 node 95
		node 95 0 = = > 1 node 94
		node 96 5 = = > 2 *Gadinia*
		node 99 5 = = > 2 node 98
		node 105 5 = = > 4 node 102
		node 108 5 = = > 3 *Siphonaria*
		node 121 5 = = > 0 node 120
		node 119 0 – > 1 node 118
		node 112 1 – > 0 node 111
		node 115 1 = = > 3 *Bulla*
		node 115 1 – > 0 node 114
		node 113 0 = = > 34 *Aplysia*
		node 117 1 – > 0 *Scaphander*
		node 117 1 – > 0 *Cylichna*
		node 117 1 – > 0 *Retusa*
		node 123 5 = = > 4 node 122
		node 124 5 = = > 34 *Clione*
		node 127 0 = = > 1 *Valvata*
49. Procerebrum	1000	node 109 0 = = > 1 node 108
50. Medio-dorsal bodies	1000	node 109 0 = = > 1 node 108
51. Ampulla	0500	node 132 0 = = > 1 node 131
		node 117 1 = = > 0 *Cylichna*
52. Sphincter	0500	node 88 0 = = > 1 node 87
		node 101 0 – > 1 node 100
53. Fertilization pouch	0250	node 94 0 = = > 1 *Otina*
		node 102 0 = = > 1 *Succinea*
		node 104 0 – > 1 node 103
		node 115 0 = = > 1 node 114
54. Albumen gland	0500	node 76 0 = = > 5 *Campanile*
		node 125 0 = = > 1 node 121
		node 109 1 = = > 7 node 93
		node 81 7 – > 2 node 79
		node 84 7 – > 8 node 83

APPENDIX 4 (*Continued*)

Character	CI	Changes
		node 90 7 = = > 6 node 89
		node 118 1 = = > 3 node 117
		node 117 3 = = > 1 node 116
		node 114 1 = = > 2 node 113
		node 117 3 = = > 0 *Cylichna*
		node 117 3 = = > 0 *Retusa*
		node 117 3 = = > 7 *Gastropteron*
		node 119 1 = = > 0 *Ringicula*
		node 123 0 = = > 1 *Runcina*
		node 122 0 = = > 4 *Peraclis*
		node 127 0 = = > 4 *Valvata*
55. Course of eggs	0250	node 121 0 = = > 1 node 110
		node 87 1 = = > 0 node 86
		node 95 1 – > 0 node 94
		node 117 0 = = > 1 node 116
56. Membrane gland	0429	node 110 0 – > 7 node 78
		node 81 0 – > 8 node 79
		node 97 0 = = > 7 node 95
		node 95 7 = = > 0 *Amphibola*
		node 101 0 = = > 3 node 100
		node 117 0 = = > 2 node 116
		node 111 2 = = > 0 *Acteon*
		node 114 2 = = > 8 node 113
		node 117 0 = = > 3 *Cylichna*
		node 117 0 = = > 3 *Retusa*
		node 117 0 = = > 4 *Aglaja*
		node 117 0 = = > 6 *Gastropteron*
		node 120 0 = = > 7 *Colpodaspis*
		node 125 0 = = > 3 node 123
57. Mucous gland	0500	node 110 0 – > 1 node 78
		node 109 0 = = > 7 node 93
		node 81 7 – > 2 node 79
		node 84 7 – > 9 node 83
		node 90 7 = = > 0 node 89
		node 96 0 = = > 1 *Melampus*
		node 116 0 = = > 6 node 115
		node 115 6 = = > 3 *Bulla*
		node 114 6 = = > 2 node 113
		node 117 0 = = > 3 *Scaphander*
		node 117 0 = = > 3 *Philine*
		node 117 0 = = > 3 *Aglaja*
		node 117 0 = = > 6 *Gastropteron*
		node 120 0 = = > 8 *Colpodaspis*
		node 124 0 = = > 1 *Clione*
		node 127 0 = = > 4 *Valvata*
58. Extrapallial tracts	0429	node 77 0 = = > 2 *Littorina*
		node 126 0 = = > 2 node 125
		node 110 2 = = > 1 node 109
		node 93 1 = = > 4 node 91
		node 90 4 = = > 5 node 88
		node 81 5 = = > 2 node 79
		node 92 1 = = > 6 *Ascobulla*
		node 94 1 = = > 5 *Otina*

APPENDIX 4 (*Continued*)

Character	CI	Changes
		node 95 1 = = > 2 *Pythia*
		node 95 1 = = > 3 *Amphibola*
		node 106 1 = = > 4 node 105
		node 108 1 = = > 3 *Siphonaria*
		node 116 2 = = > 1 node 112
		node 128 0 = = > 1 node 127
59. Prostate	0368	node 126 0 = = > 2 node 125
		node 121 2 = = > 0 node 110
		node 109 0 = = > 4 node 93
		node 91 4 = = > 6 node 90
		node 88 6 = = > 0 node 87
		node 95 0 = = > 3 node 94
		node 96 0 = = > 1 *Melampus*
		node 101 0 = = > 4 node 100
		node 98 4 = = > 3 *Acroloxus*
		node 107 0 – > 7 node 106
		node 106 7 – > 0 node 105
		node 105 0 – > 1 node 102
		node 102 1 – > 3 *Succinea*
		node 104 0 – > 4 *Achatina*
		node 116 2 = = > 0 node 112
		node 114 2 – > 0 node 113
		node 128 0 – > 2 node 127
		node 127 2 – > 3 *Valvata*
		node 127 2 – > 5 *Rissoella*
60. Copulatory organ	0222	node 132 0 = = > 1 Pila
		node 77 0 = = > 1 *Littorina*
		node 126 0 = = > 2 node 125
		node 78 2 = = > 1 *Amathina*
		node 81 2 = = > 1 node 79
		node 108 2 = = > 0 *Siphonaria*
		node 116 2 = = > 1 node 112
		node 119 2 = = > 1 *Ringicula*
		node 128 0 = = > 1 node 127
61. Ejaculatory duct	0167	node 110 0 = = > 1 node 109
		node 81 1 = = > 0 node 79
		node 116 0 = = > 1 node 112
		node 117 0 = = > 1 *Philine*
		node 125 0 – > 1 node 123
		node 128 0 = = > 1 node 127
62. Spermatophore	0.333	node 104 0 = = > 1 node 103
		node 125 0 = = > 1 node 123
		node 130 0 = = > 1 node 129
63. Chalazae	0200	node 76 0 = = > 1 *Campanile*
		node 110 0 – > 1 node 78
		node 95 0 = = > 1 *Ellobium*
		node 127 0 = = > 1 *Valvata*
		node 130 0 – > 1 node 129
64. Calcified egg wall	1000	node 105 0 = = > 1 node 104
65. Polar lobes	1000	node 131 0 – > 1 node 77
66. Granules	1000	node 132 1 < = > 0 Trochidae
		node 130 1 = = > 2 node 128

APPENDIX 4 (*Continued*)

Character	CI	Changes
67. Acrosomal vesicle	1000	node 131 0 = = > 1 node 130
		node 127 1 = = > 2 *Valvata*
68. Accessory memb.	1000	node 131 0 = = > 1 node 77
69. Subacros. material	1000	node 132 1 < = > 0 Trochidae
		node 131 1 – > 2 node 130
		node 130 2 – > 4 node 128
		node 127 4 = = > 3 *Valvata*
70. Mitochondria	1000	node 132 1 < = > 0 Trochidae
		node 131 1 = = > 2 node 130
71. Paracrystalline	1000	node 130 0 = = > 1 node 128
72. Cristae	1000	node 130 0 = = > 1 node 128
73. Coarse fibres	1000	node 131 0 = = > 1 node 130
74. Intar-axonemal	1000	node 131 0 = = > 1 node 130
75. Paraspermatozoa	0500	node 132 1 < – > 0 Trochidae
		node 131 1 – > 0 node 130
76. Temporary support	1000	node 132 1 < = > 0 Trochidae
77. Microtubular sheath	1000	node 132 1 < = > 0 Trochidae