

## PHYLOGENY OF THE LIMACOIDEA *SENSU LATO* (GASTROPODA: STYLOMMATOPHORA)

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### ABSTRACT

There is hardly any agreement about relationships among the families of the Limacoidea *sensu lato* (Gastropoda: Stylommatophora) in modern classifications. The delimitation of this group and its systematic position within the Sigmurethra are discussed. A cladistic analysis of the families of the Limacoidea *sensu lato* is given, based on a detailed consideration of all relevant characters of the genitalia, nervous system, muscle system, lung, digestive system, external morphology and shell. The Sagdidae and the Helicoidea are included in the cladistic analysis as outgroups. The Helicoidea (including Arionoidea, Polygyridae, Camaenidae) proved to be the sister-group of the Limacoidea *sensu lato*. According to the strict consensus tree of 27 most parsimonious cladograms, the main groups of the Limacoidea *sensu lato* are shown to be related as follows: (Staffordiidae, ((Dyakiidae, Gastrodontoidea) (Parmacelloidea, ((Zonitoidea, Helicarionoidea), Limacoidea))))). The reliability of the individual clades and the subdivision of several families are discussed.

### INTRODUCTION

#### *Previous classifications of the Limacoidea sensu lato*

The Limacoidea *sensu lato* are a subgroup of the Sigmurethra (Gastropoda: Stylommatophora), which was already delimited by Pilsbry (1896) as group I of his Aulacopoda. All modern supra-generic classifications of this group are based on the revision of Baker (1941).

Five recent classifications of the Limacoidea *sensu lato* are compared in Table 1. These classifications are difficult to compare because of the extremely different degrees of splitting. There is an increasing tendency to split (super-) families in the sequence Boss (1982), Solem (1978), Tillier (1989), Nordsieck (1986), Schileyko (1979). Solem (1978) and Boss (1982) retained the Limacoidea *sensu lato* essentially in the sense of Baker (1941). Tillier (1989)

transferred the Vitrinidae and the Helicarionidae from the Limacoidea *sensu lato* (respectively his Zonitoidea) to the Helicoidea. Schileyko (1979) and Nordsieck (1986) split the Limacoidea *sensu lato* into several superfamilies, which Schileyko (1979) even included in different sub- and infraorders.

The classifications of Boss (1982), Nordsieck (1986), Schileyko (1979) and Solem (1978) are not based on detailed character analyses. Nordsieck (1986) and Solem (1978) explained only some points of their classifications, but did not give descriptions or definitions of the (super-) families. Schileyko (1979) described only his sub- and infraorders, while Boss (1982) also gave descriptions of the families and superfamilies. However, the descriptions of Boss (1982) and Schileyko (1979) are too vague to ascertain the systematic position of a given genus or family. All authors more-or-less implied that their classification is based on a phylogenetic system. Schileyko (1979) even presented a highly resolved phylogram of all families of the Stylommatophora. But none of the authors explained how he prepared his classification (or phylogram). Tillier (1989) was undoubtedly right when he called the classical classifications 'basically phenetic'.

Tillier (1989) was the first to carry out a detailed character analysis of most families of the Stylommatophora. He especially investigated characters of the digestive tract, the excretory system and the central nervous system. The search for additional taxonomic characters in insufficiently known organ systems is an important and meritorious task. However, Tillier (1989) excluded the classical characters of the external morphology and especially the genitalia because he could not define 'morphoclines' of these characters and because 'many more data may be found in the literature on these morphologies than on morphologies of other organ systems' (Tillier, 1989: 4). Of course, ignoring most of the characters which proved to be suit-

Table 1. Comparison of the proposed classification with five recent classifications of the families of the Limacoidea *sensu lato*.

present paper	Solem, 1978	Schileyko, 1979	Boss, 1982	Nordsieck, 1986	Tillier, 1989
Staffordioidea Staffordiidae	included in the Helicarionidae	included in the Ariophantidae	included in the Helicarionidae	included in the Helicarionidae	included in the Helicarionidae
Dyakioidea Dyakiidae	included in the Helicarionidae	included in the Ariophantidae	included in the Helicarionidae	included in the Helicarionidae	included in the Helicarionidae
Gastrodontoidea Vitreidae	included in the Zonitidae	included in the Zonitidae	included in the Zonitidae	included in the Zonitidae	included in the Zonitidae
Chronidae	included in the Helicarionidae	included in the Ariophantidae	included in the Helicarionidae	included in the Helicarionidae	included in the Helicarionidae
Euconulidae	included in the Helicarionidae	Gastrodontoidea Helixinia	included in the Helicarionidae	Helicarionoidea	Zonitoidea
Trochomorphaeidae	included in the Zonitidae	Vitrinoidea Helixinia	included in the Zonitidae	included in the Helicarionidae	Zonitoidea
Gastrodontoidea Gastrodontiidae	included in the Zonitidae	Gastrodontoidea Helixinia	included in the Zonitidae	Gastrodontoidea	included in the Zonitidae
Daudebardidae	included in the Zonitidae	Zonitoidea Zonitina (partly included in the Zonitidae)	included in the Zonitidae	Vitrinoidea (partly included in the Zonitidae)	included in the Zonitidae
Parmacelloidea Trigonochlamydoidea	Limacacea group B	Trigonochlamydoidea Trigonochlamydnia	Limacacea	Trigonochlamydoidea	Zonitoidea
Parmacellidae	Limacacea group B	Parmacelloidea Zonitina	included in the Limacidae	Vitrinoidea	Zonitoidea
Milacidae	included in the Limacidae	Parmacelloidea Zonitina	included in the Limacidae	Vitrinoidea	Zonitoidea
Zonitoidea Zonitidae	Limacacea group B	Zonitoidea Zonitina	Limacacea	Vitrinoidea	Zonitoidea

Table 1. (continued)

present paper	Solem, 1978	Schileyko, 1979	Boss, 1982	Nordsieck, 1986	Tillier, 1989
Helicarionoidea Helicarionidae	Limacacea group A	Vitrinoidea Helixinia	Limacacea	Helicarionoidea	Helicoidea
Ariophantidae	included in the Helicarionidae	Vitrinoidea Helixinia	included in the Helicarionidae	included in the Helicarionidae	included in the Helicarionidae
Urocyclidae	Limacacea group A	Vitrinoidea Helixinia	Limacacea	Helicarionoidea	included in the Helicarionidae
Limacoidea Vitrinidae	included in the Zonitidae	Vitrinoidea Helixinia	included in the Zonitidae	Vitrinoidea	Helicoidea
Boettgeriillidae	included in the Paramacellidae	Limacoidea Limaxinia	included in the Limacidae	Limacoidea	?
Limacidae	Limacacea group B	Limacoidea Limaxinia	Limacacea	Limacoidea	Zonitoidea
Agriolimacidae	included in the Limacidae	Limacoidea Limaxinia	included in the Limacidae	Limacoidea	included in the Limacidae
families not belonging to the Limacoidea <i>sensu lato</i>					
Aillyidae	Limacacea group A	Aillyida	Heterurethra	Aillyoidea	included in the Helicarionidae
Arionidae	Arionacea	Arionoidea Helixinia	Arionacea	Arionoidea	Zonitoidea
Cystopeltidae	included in the Helicarionidae	?	included in the Helicarionidae	Helicarionoidea	included in the Punctidae
Discidae	Arionacea	?	included in the Endodontoidea	Punctoidea	Zonitoidea
Systrophiiidae	Rhytidacea	Punctoidea Endodontinia	Limacacea	Rhytidoidea	Endodontoidea
Testacellidae	Limacacea ? group B	Testacelloidea Oleacinina	Testacellacea	Oleacinoidea	included in the Oleacinaidae
Thyrophorellidae	Limacacea ? group B	Thyrophorelloidea Endodontinia	Arionacea	?Achatinoidea	?

able for the investigation of the phylogenetic relationships of the stylommatophoran families in previous analyses cannot be justified by such arguments. On the other hand the variability of almost all characters used by Tillier (1989) is at least as large within the families as between them (see Tillier, 1989: 296 ff., appendix E). Therefore, most of these characters are not suitable for an analysis of the phylogenetic relationships among the families. Moreover, the value of Tillier's (1989) work is reduced by his inconsistent methods of analysis. Tillier (1989) mainly used a new algorithm, which presupposes the irreversibility of the characters used. Tillier (1989) did not present any evidence that this assumption holds true. Besides, this algorithm does not necessarily find the shortest tree (Tillier, 1989). Even more enigmatic than the algorithm is the fact that Tillier (1989) did not accept the results of his algorithm after all. After the detailed discussion of the trees computed with the algorithm, he changed some of the branching patterns arbitrarily. Tillier (1989) also presupposed that the families, in his delimitation, are monophyletic, and did not try to substantiate their monophyly by investigating their potential autapomorphies. Actually, some of the families considered by Tillier (1989) are not monophyletic. For example, the Helicarionidae *sensu* Tillier are polyphyletic: they include the Dyakiidae on the one hand and the Helicarionidae, Ariophantidae and Urocyclidae on the other. Because of these deficiencies, it is not surprising that Tillier's (1989) analysis resulted in artificial phylograms and a classification that is even more artificial than the previous (phenetic) classifications. For example, in the cladogram of Tillier (1989: text-fig. 24), all Palaearctic slug families (Arionidae, Parmacellidae, Milacidae and Limacidae *sensu lato*) form a monophylum, which is mainly supported by the shortening of the kidney. However, the shortening of the kidney is a consequence of limacisation. It has been previously shown by Likharev & Wiktor (1980) that the above-mentioned slug groups stem from three different snail groups. Emberton & Tillier (1995) published a clarification and evaluation of Tillier's (1989) paper in which they objected to many points which are also criticized here, and in which they pointed out errors and inconsistencies in defining and scoring characters.

The first strictly cladistic analysis of several families of the Stylommatophora has been carried out by Emberton (1991), while searching for the sister-group of the Polygyridae. Unfortunately, Emberton (1991) did not in-

clude any family of the Limacoidea *sensu lato* in his analysis.

The aim of the present investigation is to compile the available data about phylogenetically informative characters of the Limacoidea *sensu lato* and to reconstruct the phylogeny of the Limacoidea *sensu lato* in a cladistic analysis. This should moreover uncover deficiencies in our knowledge so that this analysis can serve as basis for further investigations. Finally, the cladistic analysis of the Limacoidea *sensu lato* will be used as the basis for an analysis of their historical biogeography (in prep.).

#### *Delimitation of the Limacoidea sensu lato*

There are several characters which are more-or-less typical of the Limacoidea *sensu lato*, for example, the elongate radular marginals without entocones (Pilsbry, 1896; Baker, 1941), the external gland around oviduct or vagina (see character analysis, character 23), the oxygnath jaw, the aulacopod foot. However, there are also groups which are not related to the Limacoidea *sensu lato*, but which have elongate radular marginals without entocones, an oxygnath jaw or an aulacopod foot. There are also some groups which belong to the Limacoidea *sensu lato*, but do not have an external gland around the oviduct or the vagina, an oxygnath jaw or an aulacopod foot. In the present analysis all classical limacoid groups are included, whereas some families which were only assigned to the Limacoidea *sensu lato* in a few of the previously discussed classifications (Table 1) are excluded. None of these families, namely the Aillyidae, Arionidae, Cystopeltidae, Discidae, Testacellidae, Systrophiidae and Thyrophorellidae, has an oxygnath jaw. However, the jaw is completely absent in the Testacellidae and strongly reduced in the Systrophiidae due to their carnivorous diet. These two are the only of the mentioned families which have elongate radular marginals without entocones. As with the reduction of the jaw, this is due to their carnivorous diet and does not point to phylogenetic relations with the Limacoidea *sensu lato*. In the other families mentioned, the radular marginals are not elongate (the Arionidae, Discidae and Thyrophorellidae) or are elongate, but have entocones (the Aillyidae and Cystopeltidae). None of the families mentioned has a distinct external gland around the oviduct or the vagina. As long as the actual phylogenetic relationships of these families have not been clarified, one cannot definitively rule out the possibility that they are very aberrant Lima-

coidea *sensu lato*. But none of these families shows any features which would unambiguously justify their classification with the Limacoidea *sensu lato* at present.

There is one doubtful reason which might justify the classification of the Systrophiidae with the Limacoidea *sensu lato*, namely a structure at the vagina of *Systrophia lutea* (see Tillier, 1980: fig. 77) which resembles a rudimentary (or atavistic?) perivaginal gland. However, this structure is absent in all other anatomically known species of this family. Tillier (1980) considered the Systrophiidae to be close relatives of the Gastrodontidae because there are cords between the penis and the female genitalia in both families. However, these cords differ in structure and position. Whereas in the Gastrodontidae there is a true duct that connects the distal section of the penis with the distal section of the bursa copulatrix or the free oviduct, in the Systrophiidae there are only cords of connective tissue (and possibly muscles) between different parts of the genitalia: between epiphallus and atrium, between epiphallus and free oviduct, between the proximal section of the penis and an atrial caecum and between the proximal section of the penis and the base of the bursa copulatrix, but never between the distal section of the penis and the bursa copulatrix (or the free oviduct). Therefore, the homology of these structures is dubious. According to Tillier (1989), *Systrophia* (Systrophiidae) and *Ventridens* (Gastrodontidae) have a character in common not found in any other group, i.e. the position of the anterior duct of the digestive gland distinctly in front of the concave angle of the gastric pouch. But in *Tamayoa* (Systrophiidae) and *Gastrodonta* and *Zonitoides sensu stricto* (Gastrodontidae) the position of this duct is normal (Tillier, 1989). Therefore, the position of this duct in *Systrophia* and *Ventridens* is probably not a synapomorphy but a convergence. Despite the similarities between the Systrophiidae and the Gastrodontidae emphasized by Tillier (1980, 1989), Tillier (1989) even placed the two families in different suborders.

Some authors (e.g. Solem, 1978; Nordsieck, 1986) have placed the aulacopod Systrophiidae near the holopod Haplotrematidae, which have a somewhat similar shell and an adjacent distribution. Both groups are carnivorous and hence show similar adaptations, e.g. reduced jaw and usually unicuspid radular teeth. The Haplotrematidae are usually included in the Rhytidoidea (Solem, 1978; Schileyko, 1979;

Boss, 1982; Nordsieck, 1986). But the sequence of some short regions of the 28 S rRNA analysed by Emberton, Kuncio, Davis, Phillips, Monderewicz & Guo (1990) points to a closer relationship between the Haplotrematidae and the Limacoidea *sensu lato*. More morphological and molecular data will be necessary for a careful re-examination of the phylogenetic relationships of the Haplotrematidae and Systrophiidae.

#### *Systematic position of the Limacoidea sensu lato*

For the cladistic analysis of the Limacoidea *sensu lato* a suitable outgroup is necessary. The Limacoidea *sensu lato* belong to the Sigmurethra. Therefore, the proposed subdivisions of the Sigmurethra should be discussed.

The Pilsbry-Baker school (e.g. Pilsbry, 1896; Baker, 1955, 1962; Solem, 1978; Boss, 1982) divides the Sigmurethra (*sensu stricto*, i.e., excluding Mesurethra and Heterurethra) into the Holopodopes, the Aulacopoda and the Holopoda. The Aulacopoda and the Holopoda will be discussed in the following character analysis (character 27). Neither of these two groups is monophyletic. The Holopodopes were separated from the Holopoda by Baker (1962) without any clear reasons being given. Solem (1978) and Boss (1982) retained this classification without further substantiation.

Schileyko (1979) rejected any subdivision of the Stylommatophora based on the morphology of the excretory system. He divided the Geophila into five suborders with vague definitions. None of these suborders is substantiated by true autapomorphies and none has been recognized by any other author. At least the Achatinina, Pupillina, Helixina and Limaxina are polyphyletic (subgroups of the last two suborders belong to the Limacoidea *sensu lato* and will be discussed below).

Nordsieck (1985, 1986, 1992) divided the Sigmurethra (*sensu lato*, i.e., including Mesurethra and Heterurethra) into four infraorders, namely the Clausilioinei, Succineoinei, Achatinoinei and Arionoinei. The Achatinoinei and Arionoinei have to be discussed with respect to the phylogenetic relationship of the Limacoidea *sensu lato*. Both infraorders are based on the structure of the stimulator. The stimulator is 'mostly reduced, [and] if present inserted on the penis' in the Achatinoinei and 'frequently present, inserted mostly on the genital atrium or vagina' in the Arionoinei (Nordsieck, 1992). However, these co-called 'apomorphies'

cannot be accepted as autapomorphies of these groups. Within the scope of a cladistic analysis the statement 'mostly' has no meaning. The reduction of the stimulator can only be regarded as an autapomorphy of the Achatinoinei, if the stimulator has been reduced in the ancestor of this group. But if there are Achatinoinei with a primary complete stimulator, the reduction of this organ cannot be an autapomorphy of this group. However, I do not know of any Achatinoinei with a complete stimulator. On the other hand, the stimulator has also been reduced in many Arionoinei. The insertion of the stimulator on the penis in the Achatinoinei is a symplesiomorphy, because the stimulator also inserts on the penis in the Orthurethra. The 'frequent' presence of the stimulator in the Arionoinei is of course also a symplesiomorphy. The shift of the stimulator from the penis to the atrium is not an autapomorphy of the Arionoinei, because the stimulator inserts primarily on the penis in the Sagdidae. The shift of the stimulator to the vagina is an autapomorphy of subgroups of the Helicoidea and the Limacoidea *sensu lato*. Consequently, neither the Achatinoinei nor the Arionoinei in the sense of Nordsieck are substantiated by autapomorphies. The monophyly of both groups is dubious.

As a result of his analysis, Tillier (1989) divided the Sigmurethra (*sensu lato*) into the Dolichonephra and the Brachynephra. The Dolichonephra are characterized by an at least partly closed secondary ureter (the part of the ureter running to the mantle collar along the hindgut), the Brachynephra are characterized by the shortening of the kidney. However, as can be seen from Tillier's (1989: appendix E) data matrix, both of these characters, especially the relative length of the kidney, are variable within several families. The partial closing of the secondary ureter seems to be an autapomorphy of a group distinctly larger than assumed by Tillier (1989). Actually, the Dolichonephra and the Brachynephra are artificial groups generated by Tillier's (1989) unusual algorithm and his biased character selection (see section Previous classifications of the Limacoidea *sensu lato*). Both Nordsieck (1992) and Emberton in Emberton & Tillier (1995), therefore, rejected these groups.

To sum up, and in accordance with Emberton and Tillier (1995), there is no sufficiently substantiated subdivision of the Sigmurethra at present. Therefore, suitable outgroups for the phylogenetic analysis of the Limacoidea *sensu lato* have to be chosen on the basis of other

criteria. As will be shown, the stimulator is one of the most important character complexes for the reconstruction of the phylogeny of the Limacoidea *sensu lato*. Therefore, those Sigmurethra in which the stimulator is not reduced, namely the Sagdidae and the Helicoidea, have been chosen as outgroups for the cladistic analysis. The Sphincterochilidae and the Cepoliidae have been treated separately from the other Helicoidea, because they have generally an oxygnath jaw like the Limacoidea *sensu lato*. Therefore, Schileyko (1991) even affiliated the Sphincterochilidae to the aonitina *sensu* Schileyko, which include only groups of the Limacoidea *sensu lato* and the Sphincterochilidae.

## MATERIAL AND METHODS

### Data

The phylogenetic analysis of the Limacoidea *sensu lato* is based on my own investigations, which are restricted to Palaearctic groups, and an extensive evaluation of the relevant literature, of which the most important papers are listed in Table 2. Many more papers have been checked, but they do not contain additional information about the characters and taxa considered.

The commonly accepted families (see Table 1) were used as operational taxonomic units. The delimitation of some of these families differs from that of earlier authors in a few cases. These deviations are substantiated in the section Phylogenetic system. In the case of the Zonitidae *sensu auct.* the analysis was carried out on the level of subfamilies, because it was suspected that the Zonitidae *sensu auct.* are polyphyletic. The Zonitinae *sensu auct.* has been split in the Zonitidae *sensu stricto* and the Godwiniinae. By the exclusion of the Staffordiidae, Dyakiidae and Chronidae the delimitation of the Helicarionidae and the Ariophantidae differs essentially from that of earlier authors.

### Parsimony analysis

For the cladistic analysis of the character matrix the program PAUP 3.1.1 (Swofford, 1993) was used. All characters were treated as undirected and unordered. Therefore, the character polarity is determined by the rooting. If there are two or more character states in a taxon and if the ancestral character state of that taxon could be determined by an outgroup comparison or by a cladistic analysis of the subgroups of that taxon, this character state was used for the phylogenetic analysis. If the ancestral character state could not be determined, the character was scored as unknown for that family.

The different characters evolve at different rates

**Table 2.** Papers evaluated for the compilation of Table 3.

	References
Sagdidae	Baker (1940); Goodfriend (1986)
Sphincterochilidae	Forcart (1972, 1974); Hesse (1931)
Cepolidae	Baker (1943); Moreno (1950)
odontognath Helicoidea	Hesse (1931); Pilsbry (1939, 1948); Schileyko (1978); Wurtz (1955)
Staffordiidae	Blanford & Godwin-Austen (1908)
Dyakiidae	Baker (1941); Hausdorf (1996)
Vitreidae	Baker (1931); Mermod (1926); Riedel (1980)
Chronidae	Azuma (1982); Baker (1941); Burne (1910)
Euconulidae	Baker (1928, 1938, 1941); Tillier & Bouchet (1988)
Trochomorphidae	Baker (1941); Stoliczka (1873)
Gastrododontidae	Baker (1928, 1930); Riedel (1980)
Godwiniinae	Baker (1941); Riedel (1980); Wiegmann (1893)
Oxychilinae	Riedel (1980, 1989); Wiegmann (1893)
Daudebardinae	Plate (1891); Riedel (1980); Schileyko (1986a)
Trigonochlamydidae	Hesse (1926); Likharev & Wiktor (1980)
Parmacellidae	Hesse (1926); Likharev & Wiktor (1980)
Milacidae	Hesse (1926); Wiktor (1987)
Zonitidae	Riedel (1960, 1980, 1982); Riedel & Radja (1983); Sicard (1874)
Helicarionidae	Baker (1941); Blanford & Godwin-Austen (1908); Solem (1966); Van Mol (1973)
Ariophantidae	Baker (1941); Blanford & Godwin-Austen (1908); Dasen (1933); Hoffmann (1940); Van Mol (1968); Wiegmann (1898); Woldt (1932)
Urocyclidae	Ortiz de Zárate López (1951); Van Mol (1970); Watson (1920)
Vitrinidae	Eckardt (1914); Schileyko (1986b)
Boettgerillidae	Jungbluth, Likharev & Wiktor (1981); Likharev & Wiktor (1980)
Limacidae	Hesse (1926); Likharev & Wiktor (1980)
Agriolimacidae	Hesse (1926); Likharev & Wiktor (1980)

and consequently have different 'cladistic reliabilities'. Equal weighting of characters with high rates of evolution and therefore high chance of homoplasies and characters with low rate of evolution leads to artifacts in the phylogenetic analysis. These artifacts can be avoided by a higher weighting of characters with low rates of evolution. According to Kluge & Farris (1969), the variation within OTU's (operational taxonomic units) can be used as an index to the relative evolutionary rates of characters. In the cladistic analysis the characters were weighted inversely according to their variation within the OTU's as proposed by Kluge & Farris (1969). For the calculation of the weights the following formula was used:  $1/(1+n)$  ( $n$  = number of OTU's in which a character varies).

The autapomorphies of the individual clades were calculated with the delayed transformation (DELTRAN) character state optimization as well as with the accelerated transformation (ACCTRAN) optimization. For the discussion of the phylogenetic system, the autapomorphies were taken from the list of apomorphies calculated with the DELTRAN optimization which prefers parallelisms to reversals, whereas the ACCTRAN optimization prefers reversals to parallelisms.

## RESULTS

### *Character analysis*

The characters used for the phylogenetic analysis and their states in the families under consideration are compiled in Table 3. In this character matrix all character states found in a taxon are listed. If there are two or more character states in a taxon and if the ancestral character state of the respective taxon could be determined with high certainty (for many taxa preliminary phylogenetic analysis at the intra-familial level have been carried out; data partly shown in the section Phylogenetic system), this character state is stated first and the other character states are enclosed in brackets. If the ancestral character state could not be ascertained, all character states are enclosed in brackets. The characters are explained in the following (the numbering refers to Table 3 and to the cladogram in Figure 5):

1. The so-called 'stimulator' is one of the most important characters for the systematics of the Stylommatophora. Its actual function is unknown in

**Table 3.** Character matrix used for the phylogenetic analysis.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
Sagdidae	0(1)	0	0	0	1	0	0	0	1	1
Sphincterochilidae	0	1	0	1	1	1	0(1)	(0,1)	1	1
Cepoliidae	0	1	0	1	1	1	1	0	0	1
odontognath Helicoidea	0(1)	1	0(1)	1(0)	1	1	1	0(1)	0(1)	1
Staffordiidae	0	1	0	1	1	0	0	0	0	1
Dyakiidae	0	1	0(1)	1	1	0(2)	0(1)	0	0	1
Vitreidae	(0,1)	1	1	?	?	?	?	1	1	1
Chronidae	0(1)	0	1	?	?	?	?	1	1	1
Euconulidae	0(1)	0	1(0)	0	1	0	0	1	1	1
Trochomorphidae	1	?	?	?	?	?	?	?	?	?
Gastrodontidae	0(1)	(0,1)	0(1)	0	1	1	1	0(1)	0	0(1)
Godwiniinae	1	?	?	?	?	?	?	?	?	?
Oxychilinae	(0,1)	0	1	?	?	?	?	?	0	0
Daudebardiinae	1	?	?	?	?	?	?	?	?	?
Trigonochlamydidae	1	?	?	?	?	?	?	?	?	?
Parmacellidae	0	1	0	1	1	3	?	1	1	1
Milacidae	0	1	0	1	1	0	0	0	1	1
Zonitidae	(0,1)	1	0	1	0(1)	2	?	(0,1)	1	1
Helicarionidae	0(1)	1	0	1	0	2	?	0	1	1
Ariophantidae	0(1)	1	0	1	0	2	?	0	1(0)	1
Urocyclidae	0(1)	1(0)	1	?	?	?	?	0(1)	1(0)	1
Vitrinidae	0(1)	1	0(1)	1	1	2	?	0	1	1
Boettgerillidae	1	?	?	?	?	?	?	?	?	?
Limacidae	1	?	?	?	?	?	?	?	?	?
Agriolimacidae	1	?	?	?	?	?	?	?	?	?

**Table 3.** (continued)

	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.
Sagdidae	1	?	0(1)	0	0	1	0	0	0(1)	1
Sphincterochilidae	1	?	1	0	0	1	0	0	0(1)	1
Cepoliidae	1(0)	0	0	?	0(1)	1	0	0	0(1)	1
odontognath Helicoidea	(0,1)	0	(0,1)	0(1)	0	1	0	0	0(1)	1
Staffordiidae	?	?	?	?	0	1	?	?	1	?
Dyakiidae	1	?	1	(0,1)	0	1	?	?	1	?
Vitreidae	(0,1)	0	?	0	(0,1)	1	0	0	1	?
Chronidae	0	0(1)	(0,1)	(0,1)	0	1	0	0	0(1)	?
Euconulidae	0	0	(0,1)	1	0	1	0	1(0)	1(0)	1
Trochomorphidae	1	?	(0,1)	0	0	1	0	1	1	?
Gastrodontidae	0	(0,1)	(0,1)	1	0	1	0	0	1	?
Godwiniinae	1	?	(0,1)	1	0(1)	1	(0,1)	0	1	?
Oxychilinae	0(1)	0	1	0	0	1(0)	0	0	1	?
Daudebardiinae	0	0	1(0)	0	0(1)	1	?	?	1	?
Trigonochlamydidae	0(1)	0	1	?	0	1	0	0	1	?
Parmacellidae	1	?	(0,1)	?	0	1	0	0	1	?
Milacidae	1	?	0	1	0	1	0	0	1	?
Zonitidae	0	0	(0,1)	0	(0,1)	1	(0,1)	0	1	?
Helicarionidae	0	0	(0,1)	(0,1)	0	0(1)	0	0	0(1)	0
Ariophantidae	0	1	(0,1)	1	0	0(1)	0	0	0(1)	0
Urocyclidae	0	1	0(1)	0	0	0(1)	0(1)	0	0(1)	0(1)
Vitrinidae	0(1)	?	1	1	1	?	1	?	?	?
Boettgerillidae	1	?	0	0	1	?	1	?	?	?
Limacidae	1	?	1	0	1	?	1	?	?	?
Agriolimacidae	(0,1)	?	1	0	1	?	1	?	?	?



Table 3. (continued)

	21.	22.	23.	24.	25.	26.	27.	28.	29.	30.
Sagdidae	?	0	1	?	0	0	1	1	1	0(1)
Sphincterochilidae	?	0	1	?	0	(0,1)	1	1	1	0
Cepoliidae	0	0	1	?	0	0(1)	1	1	1	0
odontognath Helicoidea	(0,1)	0	1	?	0	0(1)	1(0)	1(0)	1(0)	0(1,2)
Staffordiidae	?	0	?	?	?	?	1	1	1	0
Dyakiidae	?	0	0(1)	0	0	0(1)	0	1	0	0
Vitreidae	1	0	0(1)	(0,1)	0	0	0	1	0	0
Chronidae	0	0	0(1)	0	0	0	0	(0,1)	0	0
Euconulidae	0(1)	0(1)	0(1)	0	0	0	0	0	0	0(1)
Trochomorphidae	?	0(1)	0	0	0	0	0	1	0(1)	0
Gastrodontidae	0	0	(0,1)	0	(0,1)	1	(0,1)	1	(0,1)	0
Godwiniinae	?	0	(0,1)	1	1	1	0	(0,1)	0(1)	0(1)
Oxychilinae	(0,1)	0	0	1(0)	1	0	0	0(1)	(0,1)	0
Daudebardiinae	1(0)	0	0	1(0)	1	1	0	0	0	1
Trigonochlamydidae	1	0	1	?	0(1)	0	0	0	1	2
Parmacellidae	?	0	1	?	0	0	0	0	1	2
Milacidae	?	0	1	?	1	1	0	0	1	2
Zonitidae	(0,1)	0	0(1)	1	(0,1)	(0,1)	0	0	0	0
Helicarionidae	0	0	0	0	0	0	0	0	0	0(1,2)
Ariophantidae	0	0	0	0	0	0	0	0(1)	0	0(1,2)
Urocyclidae	0	0	0	0	0	0(1)	0	0	0	0(1,2)
Vitrinidae	2	0(1)	1	?	0	0(1)	0	0	1	1(2)
Boettgerillidae	?	0	1	?	0	0	0	0	1	2
Limacidae	?	1(0)	1	?	0	0(1)	0	0	1	2
Agriolimacidae	2	1(0)	1	?	0	0(1)	0	0	1	2

Table 3. (continued)

	31.	32.	33.	34.	35.	36.	37.	38.
Sagdidae	0	1	?	(0,1)	0	0	1	?
Sphincterochilidae	1	1	?	0	1	0	1(0)	?
Cepoliidae	(0,1)	1	?	0	1(2)	0	1(0)	?
odontognath Helicoidea	1(0)	1(0)	1	0(1)	2(1)	0	1(0)	21-31
Staffordiidae	0	0	?	?	1	1	2	?
Dyakiidae	0	1	?	0	1	1	2(1)	28
Vitreidae	0	1	?	1	(0,1)	1	2	20
Chronidae	0(1)	1	?	0	1	1	(0,1,2)	?
Euconulidae	0	(0,1)	?	1	1	1	(0,1,2)	?
Trochomorphidae	0(1)	1	?	1	1	1	(0,1,2)	28-30
Gastrodontidae	0	1	?	(0,1)	1	1	2	ca. 30
Godwiniinae	0	1	?	1	1	1	2	31
Oxychilinae	0(1)	1(0)	?	(0,1)	1	1	2	24-30
Daudebardiinae	0	1	?	1	3	1	2	?
Trigonochlamydidae	?	?	0	(0,1)	3	1	2	?
Parmacellidae	?	?	0	0	1	1	2	?
Milacidae	?	?	0	0	1	1	2(1)	33-34
Zonitidae	0	1	?	(0,1)	1	1	2	?
Helicarionidae	0(1)	0	1	(0,1)	1	1	(0,1,2)	25-28
Ariophantidae	0(1)	0(1)	1	0	1	1	(1,2)	27-32
Urocyclidae	0	(0,1)	1	0	1	1	(0,1,2)	?
Vitrinidae	0	0(1)	1	0	1	1	2(0,1)	31
Boettgerillidae	?	?	1	1	1	1	(0,2)	?
Limacidae	?	?	1	0	1	1	(0,1,2)	24-31
Agriolimacidae	?	?	1	0	1	1	2(1)	30

**Table 3.** Character matrix used for the phylogenetic analysis.

1. Stimulator: 0 = present; 1 = absent.
2. Insertion site of the stimulator: 0 = on the penis; 1 = on the atrium (or vagina); ? = not applicable because stimulator is absent (see character 1).
3. Stimulator section  $A_5$ : 0 = present; 1 = absent; ? = not applicable because stimulator is absent (see character 1).
4. Stimulator section  $A_5$ : 0 = bursa-like; 1 = acinose gland; ? = not applicable because stimulator or its section  $A_5$  is absent (see character 1 and 3).
5. Stimulator section  $A_5$ : 0 = with retractor muscles; 1 = without retractor muscles; ? = not applicable because stimulator or its section  $A_5$  is absent (see characters 1 and 3).
6. Stimulator section  $A_4$ : 0 = inserts terminally at section  $A_2$ ; 1 = inserts laterally on section  $A_2$ ; 2 = absent, because section  $A_5$  fused with  $A_2$ ; 3 = absent, because section  $A_5$  inserts at the vagina; ? = not applicable because stimulator or its section  $A_5$  is absent (see characters 1 and 3).
7. Stimulator section  $A_4$ : 0 = longer than  $\frac{1}{3}$  of the sections  $A_1 + A_2$ ; 1 = shorter than  $\frac{1}{3}$  of the sections  $A_1 + A_2$ ; ? = not applicable because stimulator or its sections  $A_2$ ,  $A_4$  or  $A_5$  are absent (see characters 1, 3 and 6).
8. Stimulator section  $A_2$ : 0 = with papilla; 1 = without papilla; ? = unknown or not applicable because stimulator is absent (see character 1).
9. Stimulator sections  $A_2$ : 0 = with dart; 1 = without dart; ? = not applicable because stimulator is absent (see character 1).
10. Stimulator sections  $A_2$ : 0 = with a retractor muscle inserting at a different part of the genitalia; 1 = without retractor muscle; ? = not applicable because stimulator is absent (see character 1).
11. Penial tunica: 0 = present; 1 = absent or rudimentary; ? = unknown.
12. Penial tunica: 0 = not attached to the epiphallus; 1 = attached to the epiphallus; ? = unknown or not applicable because penial tunica or epiphallus is absent (see character 11 and 15).
13. Penial papilla: 0 = present; 1 = absent or rudimentary.
14. Fibres of the penial nerve: 0 = run through the cerebral ganglion; 1 = do not run through the cerebral ganglion; ? = unknown.
15. Epiphallus: 0 = present; 1 = absent.
16. Epiphallic caecum: 0 = present; 1 = absent; ? = not applicable because epiphallus is absent (see character 15).
17. Spermatophore: 0 = present; 1 = absent; ? = unknown.
18. Spermatophore: 0 = thick walled; 1 = thin walled; ? = unknown or not applicable because spermatophore is absent (see character 17).
19. Flagellum: 0 = present; 1 = absent; ? = not applicable because epiphallus is absent (see character 15).
20. Flagellum: 0 = with axial filament; 1 = without axial filament; ? = unknown or not applicable because flagellum is absent (see character 19).
21. Vas deferens: 0 = not connected with the penial tunica; 1 = attached to the proximal end of the penial tunica; 2 = runs along the inside of the penial tunica; ? = not applicable because penial tunica is absent or unknown (see character 11).
22. Insertion site of the bursa copulatrix: 0 = vagina or atrium; 1 = penis.
23. (External) Capsular gland: 0 = present; 1 = absent; ? = unknown.
24. (External) Capsular gland: 0 = only around oviduct; 1 = at least partly around vagina or atrium; ? = not applicable because external capsular gland is absent or unknown (see character 23).
25. Genital orifice: 0 = in the anteriormost third of the anterior part of the cephalopodium (anterior to the visceral stalk or the mantle); 1 = shifted posteriorwards (in the posterior two thirds of the anterior part of the cephalopodium); ? = unknown.
26. Right ommatophoral retractor muscle: 0 = passes between penis and vagina; 1 = passes to the left of the genitalia; ? = unknown.
27. Pedal grooves: 0 = distinct; 1 = indistinct.
28. Sole furrows: 0 = distinct; 1 = indistinct.
29. Caudal pit: 0 = present; 1 = absent.
30. Shell: 0 = heliciform; 1 = vitriniform; 2 = subdermal.
31. Peristome: 0 =  $\pm$  sharp, 1 = distinctly thickened; ? = not applicable because slugs (see character 30).
32. Shell lobes: 0 = present; 1 = absent; ? = not applicable because slugs (see character 30).
33. Mantle of slugs: 0 = with a horseshoe-shaped groove; 1 = without a horseshoe-shaped groove; ? = not applicable because no slugs (see character 30).
34. Lung: 0 = with distinct minor venation; 1 = without distinct minor venation; ? = unknown.
35. Jaw: 0 = stegognath; 1 = oxygnath (or almost smooth); 2 = odontognath (or striated); 3 = reduced.
36. Radular marginals: 0 = short, generally with entocones; 1 = elongate, without entocones.
37. Radular marginals: 0 = with several ectocones; 1 = with one ectocone; 2 = without ectocone.
38. Haploid chromosome numbers.

most Stylommatophora. However, in a helioid, it has been shown that it produces and transfers a pheromone that increases the size of the recipient's genital eversion and decreases courtship duration (Adamo & Chase, 1990). Thus, the stimulator is apparently an adaptation to reciprocal copulation. Chung (1987) has discussed possible additional functions of the stimulator and hypotheses about its adaptive significance. Whereas some authors (e.g. Thiele, 1935; Solem, 1978; Emberton, 1991) thought that the different stimulator types evolved independently several times, Schileyko (1979, 1986) supposed that the different types evolved several times from non-specialized glandular tissue and other authors (e.g. Ihering, 1892; Simroth (in Simroth & Hoffmann), 1912; Nordsieck, 1985) thought all types or at least a part of them to be homologous. However, even among the last mentioned authors there are great differences of opinion about which stimulator types are homologous and which are not. Nordsieck (1985) has substantiated the hypothesis that most of the different stimulator types are homologous in detail. Furthermore, this hypothesis is supported by the unique transformation series between some of the extreme stimulator types in the Dyakiidae (Hausdorf, 1996) which can serve as a model for the understanding of such transformations. Therefore, it is assumed here that most stimulator types are homologous. But there are several structures which were homologized with the stimulator by Nordsieck (1985) or other authors, which have nothing to do with this organ. The appearance of stimulator-like structures in addition to the 'true' stimulator in some Hygromiidae shows that a *de novo* origin of such structures is possible. For example, *Trochoidea* and *Xeropicta* have evolved stimulator-like appendages at the atrium in addition to the dart apparatus which can be homologized with the 'true' stimulator by its structure and by connecting links in other Helicoidea. Therefore, a critical examination of stimulator-like appendages is necessary, before they can be homologized with the stimulator. The homology can easily be recognized as long as an appendage shows the typical structure of the stimulator (Fig. 1), consisting of a terminal bursa or gland which is connected with a basal shaft through a papilla. Some derived stimulator types can be homologized by means of connecting links (e.g. the transformation series in the Dyakiidae). But the homology of many more-or-less strongly reduced stimulator-like structures will remain doubtful and can only be indicated by phylogenetic evidence based on other characters.

In the present paper the terminology for the stimulator sections introduced for the Orthurethra by Schileyko (1984: 39, fig. 18) is used for all stimulator types (Fig. 1). In all groups considered the stimulator section  $A_3$  is absent, whereas the sections  $A_1$ ,  $A_2$ ,  $A_4$  and  $A_5$  can easily be homologized.

A stimulator, or a rudiment of it, is present in the ancestral state of many families of the Limacoidea *sensu lato* (Fig. 2), but the stimulator has been repeatedly lost in some members of all these families.

In the Vitreidae only *Ogaridiscus* (Fig. 2G) has

a tubular appendage at the vagina with an internal process which might be a rudiment of the stimulator section  $A_1$  ( $+A_2?$ ).

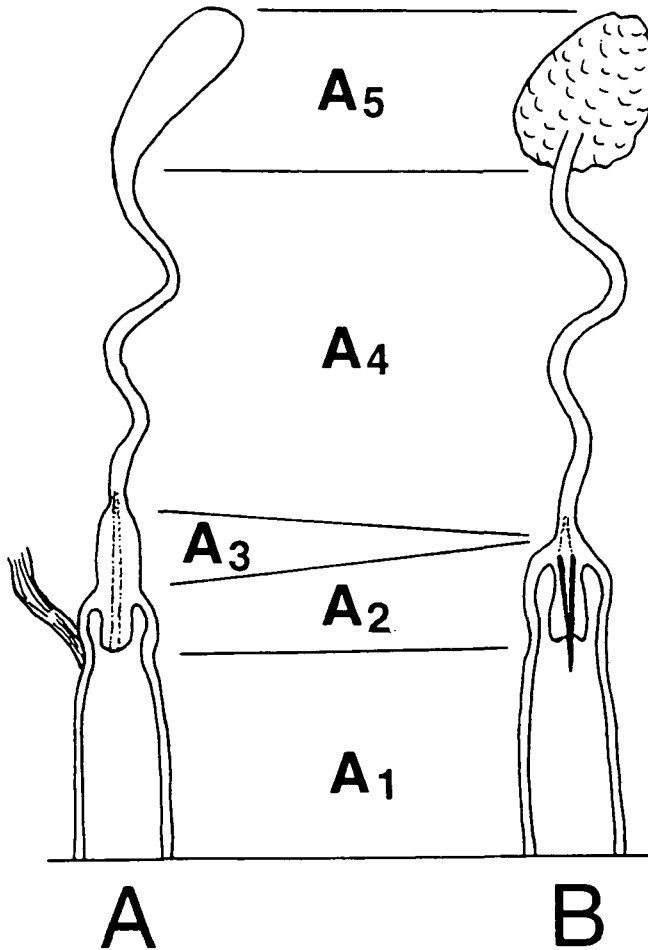
In some groups of the Euconulidae and Chronidae there is an appendage at the penis which is probably a rudiment of the stimulator section  $A_1$  (and  $A_2?$ ). This hypothesis is supported by the presence of a bursa-like terminal section at the rudiment in some individuals of *Gunongia gregaria* (Euconulidae, Fig. 2H; Tillier & Bouchet, 1988). This structure resembles the stimulator sections  $A_4 + A_5$  of the Orthurethra and the Sagdidae and is obviously an atavism. In some Trochomorphidae there are inner structures in the penis which resemble the basal structures of the penial appendage of the Euconulidae. Therefore, these structures might also be rudiments of the stimulator.

In contrast to the opinion of Schileyko (1979, 1986) and Nordsieck (1985), the 'perivaginal gland' of the Zonitidae *sensu auct.* is not homologous to the stimulator, because it is also present in the Zonitidae (*Troglagopsis*; Fig. 2M), Oxychilinae (*Nastia*; Fig. 2J), Gastrodontidae and many other families of the Limacoidea *sensu lato* which possess a well-developed stimulator (see also character 23).

The glands and appendages of the Parmacellidae (Fig. 2K) are difficult to homologize. There are usually one or two tubular appendages on the vagina or the atrium and there is an acinose gland on the vagina. The tubular appendages might be (duplicated) rudiments of the stimulator section  $A_1$  ( $+A_2?$ ). The gland at the vagina might be homologous to the stimulator section  $A_5$  which was shifted to the vagina, as in most Helicoidea. It is certainly not homologous to the perivaginal gland (see character 23), because it never surrounds the vagina evenly, but is distinctly detached from the vagina or is associated with the base of the tubular appendage.

In the Boettgeriidae, Limacidae and Agriolimacidae the stimulator is absent. Simroth (in Simroth & Hoffmann, 1912) and Nordsieck (1985) supposed that the stimulator is fused with the penis in these families. As examples of transition states of such fusion, both authors mentioned *Lehmannia* (Limacidae) and *Deroceas* (Agriolimacidae). However, the structures in or on the penis of these taxa are respectively differentiations of the inner penis wall or rather simple caeca similar to those also present in many groups with a true stimulator. Moreover, *Lehmannia* and *Deroceas* are highly derived genera. There are no indications of a fusion between stimulator and penis in the more primitive subfamilies and genera of the Limacidae and Agriolimacidae. Finally, the structures of *Lehmannia* and *Deroceas* are different. Consequently, the appendages and inner structures of the penis of *Lehmannia*, *Deroceas* and other limacoid taxa are most probably *de novo* developments.

2. The stimulator inserts on the penis in the Orthurethra, the Heterurethra, the Sagdidae and some families of the Limacoidea *sensu lato*, whereas it inserts at the atrium or the vagina in some other families of the Limacoidea *sensu lato* and in the



**Figure 1.** Structure of the stimulator. **A.** Generalized Orthurethra type (modified after Schileyko, 1984). **B.** Ancestral state of the Limacoidea *sensu lato*.

Helicoidea. The shift of the stimulator was probably connected with changes in the mating behaviour. One can suppose that such coordinate changes of morphology and behaviour have not happened frequently. Actually, there are only two families containing groups with different insertion sites of the stimulator.

3. The stimulator section  $A_5$  is absent in all Vitreidae, Chronidae, Oxychilinae and Urocyclidae. This section is present at least in some taxa of all other families in which there are groups possessing a stimulator.

4. The stimulator section  $A_5$  is bursa-like in the Orthurethra (Fig. 1A) and the Sagdidae (Fig. 2A). A similar character state is present in the Gastrodontidae (Fig. 2I; 'coronal gland') and as an atavism in the Euconulidae (Fig. 2H; see character 1). On the contrary, the stimulator section  $A_5$  is an acinose gland in

the Sphincterochilidae (Fig. 2B), Cepoliidae (Fig. 2C), in the ancestral state of the Helicoidea (Fig. 2D), in the Staffordiidae (Fig. 2E), Dyakiidae (Fig. 2F), Parmacellidae (Fig. 2K), Milacidae (Fig. 2L), Zonitidae (Fig. 2M), Helicarionidae (Fig. 2N), Ariophantidae (Fig. 2N) and Vitrinidae (Fig. 2P).

5. There are retractor muscles at the stimulator section  $A_5$  in those Helicarionidae and Ariophantidae (Fig. 2N) and Zonitidae (Fig. 2M) in which the stimulator is not reduced. In the Helicarionidae and Ariophantidae these muscles form a cord that inserts on the columellar retractor muscle, whereas in the Zonitidae there are some smaller muscles which insert on the body wall. Therefore the homologization of these muscles is questionable.

6. In the Orthurethra (Fig. 1A), the Sagdidae (Fig. 2A), and the Staffordiidae (Fig. 2E), in the ancestral states of the Dyakiidae (Fig. 2F) and the Milacidae

(Fig. 2L), and as an atavism in the Euconulidae (Fig. 2H) the stimulator section  $A_4$  inserts terminally at the section  $A_2$ . In the Sphincterochilidae (Fig. 2B), Cepoliidae (Fig. 2C), odontognath Helicoidea (Fig. 2D) and the Gastrodontidae (Fig. 2I) the stimulator section  $A_4$  inserts laterally at the section  $A_2$ . In the Zonitidae (Fig. 2M), Helicarionidae (Fig. 2N), Ariophantidae (Fig. 2N), Vitrinidae (Fig. 2P) and some Dyakiidae the stimulator section  $A_4$  is absent, because the glandular section  $A_5$  is fused with the section  $A_2$ . In the Parmacellidae (Fig. 2K) the stimulator section  $A_4$  is absent, because the section  $A_5$  inserts directly at the vagina.

7. In the Orthurethra (Fig. 1A), in the Sagdidae (Fig. 2A), in the Staffordiidae (Fig. 2E), in the ancestral state of the Sphincterochilidae (Fig. 2B), the Dyakiidae (Fig. 2F) and the Milacidae (Fig. 2L) and as an atavism in the Euconulidae (Fig. 2H) the stimulator section  $A_4$  is longer than 1/3 of the sections  $A_1 + A_2$ , whereas it is shorter than 1/3 of the sections  $A_1 + A_2$  in the Cepoliidae (Fig. 2C), odontognath Helicoidea (Fig. 2D), Gastrodontidae (Fig. 2I) and some Sphincterochilidae and Dyakiidae.

8. In the Orthurethra (Fig. 1A) and the Sagdidae (Fig. 2A), in the ancestral state of the Helicoidea (Figs 2B, C, D) and in many families of the Limacoidea *sensu lato* (Figs 2E, F, I, L, M, N, O, P) there is a papilla in the stimulator section  $A_2$ . This papilla is absent in the strongly reduced stimulators of the Vitreidae (Fig. 2G), Chronidae, Euconulidae (Fig. 2H) and Parmacellidae (Fig. 2K) and in some Sphincterochilidae, odontognath Helicoidea, Gastrodontidae, Zonitidae and Urocyclidae.

9. In the Cepoliidae (Fig. 2C), in the ancestral state of the odontognath Helicoidea (Fig. 2D), the Staffordiidae (Fig. 2E), Dyakiidae (Fig. 2F), Gastrodontidae (Fig. 2I), Oxychilinae (Fig. 2J; *Nastia*, see character 1), Parmarioninae (Ariophantidae) and some Urocyclidae the stimulator section  $A_2$  is provided with a dart, which is absent in the Orthurethra (Fig. 1A), the Sagdidae (Fig. 2A), the Sphincterochilidae (Fig. 2B) and the other Limacoidea *sensu lato* (Figs 2G, H, K, L, M, N, O, P).

10. In the Gastrodontidae (Fig. 2I) and the Oxychilinae (Fig. 2J) there is a retractor muscle at the stimulator section  $A_2$ , which inserts at a different part of the genitalia. Such a muscle is absent in all other taxa considered.

11. The cover of muscular tissue around the penis (Fig. 3) has often been called penial sheath (= Penisscheide = fourreau pénien). However, this term is ambiguous, because it has also been used for the penial wall. Therefore, the term penial tunica (Van Goethem, 1977) is used here. Our knowledge of the penial tunica is rather fragmentary, because many anatomists have ignored or removed this tissue cover. In most Orthurethra (except the Cerastuidae; see Mordan, 1992) a penial tunica is absent. In several 'achatimid' Sigmurethra (e.g. Orthalicidae, Streptaxidae, Systrophidae, Haplotrematidae) tunica-like structures have developed. There is no penial tunica in the Sagdidae, but there is a sheath around the epiphallus which might be homologous to the

penial tunica. Some Helicoidea and most Limacoidea *sensu lato* have a penial tunica.

12. In the Helicoidea and most Limacoidea *sensu lato* the penial tunica is proximally free. In the Ariophantidae, Urocyclidae and in a few Chronidae (*Ryssota sensu stricto*) and Gastrodontidae the penial tunica is proximally attached to the epiphallus (Fig. 3).

13. In the Sagdidae, the Helicoidea and many families of Limacoidea *sensu lato* there are also groups without penial papilla (= verge) (Fig. 3). This character is therefore not very useful for the phylogenetic analysis of the Limacoidea *sensu lato* and its evolution can hardly be reconstructed unequivocally.

14. The penial nerve originates from the pedal ganglion (de Nabias, 1894), but in many taxa fibres of the penial nerve run through the cerebral ganglion. The course of the penial nerve is not a very useful character for the phylogenetic analysis of the Limacoidea *sensu lato* families, since it changed several times within the families.

15. Most Stylommatophora possess an epiphallus (Fig. 3). In the Limacoidea *sensu lato* it is absent only in the Vitrinidae, Boettgerillidae, Limacidae, Agriolimacidae, and some Vitreidae, Godwiniinae, Daudebardiinae and Zonitidae. The epiphallus takes part in the production of the spermatophore (see character 17).

16. An epiphallic caecum (Fig. 3) is known only in some *Oxychilus* species (Oxychilinae), the Helicarionidae, Ariophantidae and Urocyclidae. There are also taxa without epiphallic caecum in the last three above-mentioned families. However, these are highly derived taxa in which the epiphallic caecum is apparently reduced secondarily. In these families the caecum serves to turn over the spermatophore, or at least its distal section (Dasen, 1933; Van Goethem, 1977). This probably eases the transfer of the spermatophore, which usually carries serrated appendages at its proximal section in groups with an epiphallic caecum. Moreover, in these families the epiphallic caecum originally served as the insertion site of the penis retractor. In the ancestral state of the families which do not possess an epiphallic caecum, the penis retractor inserts directly at the epiphallus or the penis. The penis retractor shifted back to the epiphallus in several groups which lost the epiphallic caecum secondarily and even in some groups which still possess a caecum, e.g. the Urocyclidae except *Trochozonites*. In contrast to the Helicarionidae, Ariophantidae and Urocyclidae, a part of the spermatophore is formed in the epiphallic caecum of *Oxychilus* species (Riedel, 1980).

17. Lind (1973) found that the spermatophore has, at least in the Helicidae, no function in protecting the enclosed sperm during the transference from one individual to another, but it ensures that a number of spermatozoa can escape into the oviduct without coming into contact with the digesting bursa copulatrix. Accordingly, one would not expect a correlation between the presence of a spermatophore and environmental factors. However, the spermatophore has only been reduced or lost in groups restricted to

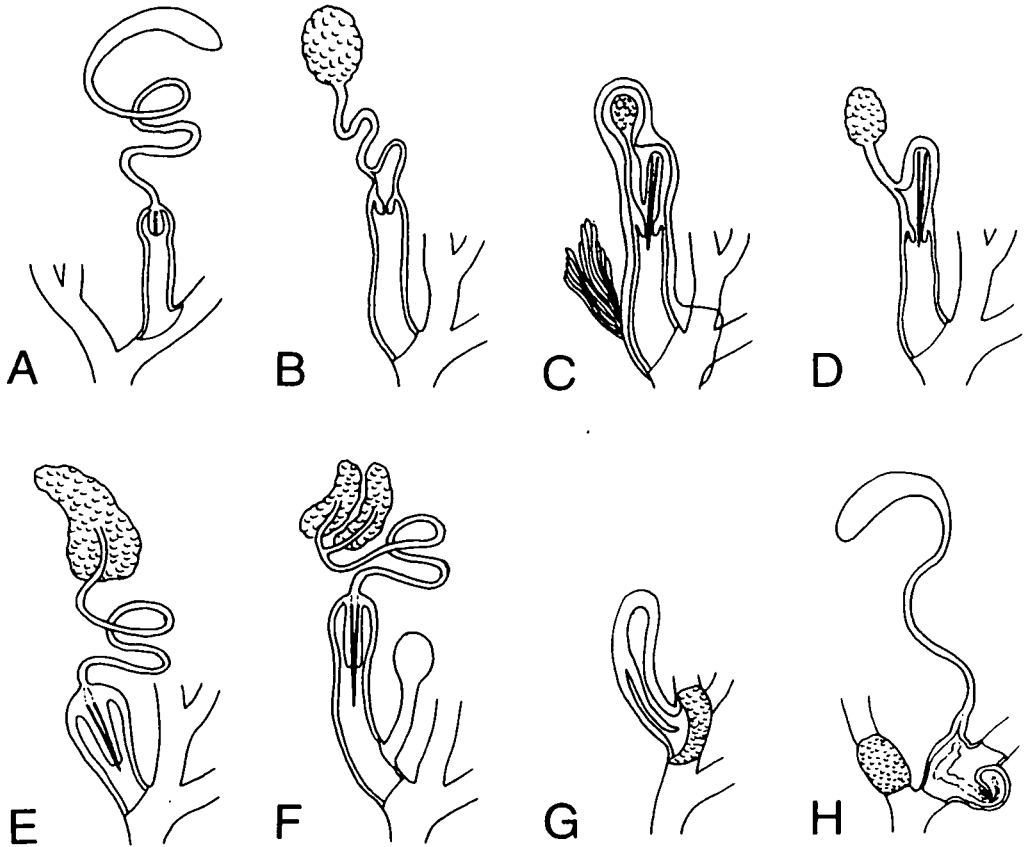


Figure 2. Stimulator types. **A.** Ancestral state of the Sagdidae. **B.** Ancestral state of the Sphincterochilidae. **C.** Ancestral state of the Cepoliidae. **D.** Ancestral state of the odontognath Helicoidea. **E.** Staffordiidae. **F.** Ancestral state of the Dyakiidae. **G.** *Ogaridiscus* (Vitreidae). **H.** Atavistic stimulator of *Gunongia gregaria* (Euconulidae). **I.** Ancestral state of the Gastrodontidae. **J.** *Nastia* (Daudebaridiidae). **K.** Ancestral state of the Parmacellidae. **L.** Ancestral state of the Milacidae. **M.** Ancestral state of the Zonitidae. **N.** Ancestral state of the Helicarionidae and Ariophantidae. **O.** Ancestral state of the Urocyclidae. **P.** Ancestral state of the Vitrinidae. Combined and modified from various references listed in Table 2.

rather moist biotops, like the Vitrinidae and the limacid slugs.

18. The spermatophores of most Stylommatophora have thick, horny walls, whereas the spermatophores of the Euconulidae and Trochomorphidae are simplified and usually thin walled (with a few exceptions; see Baker, 1938). In most Euconulidae the bursa copulatrix, which digests and absorbs the received spermatophore, is reduced. This is probably a consequence of the simplification of the spermatophore.

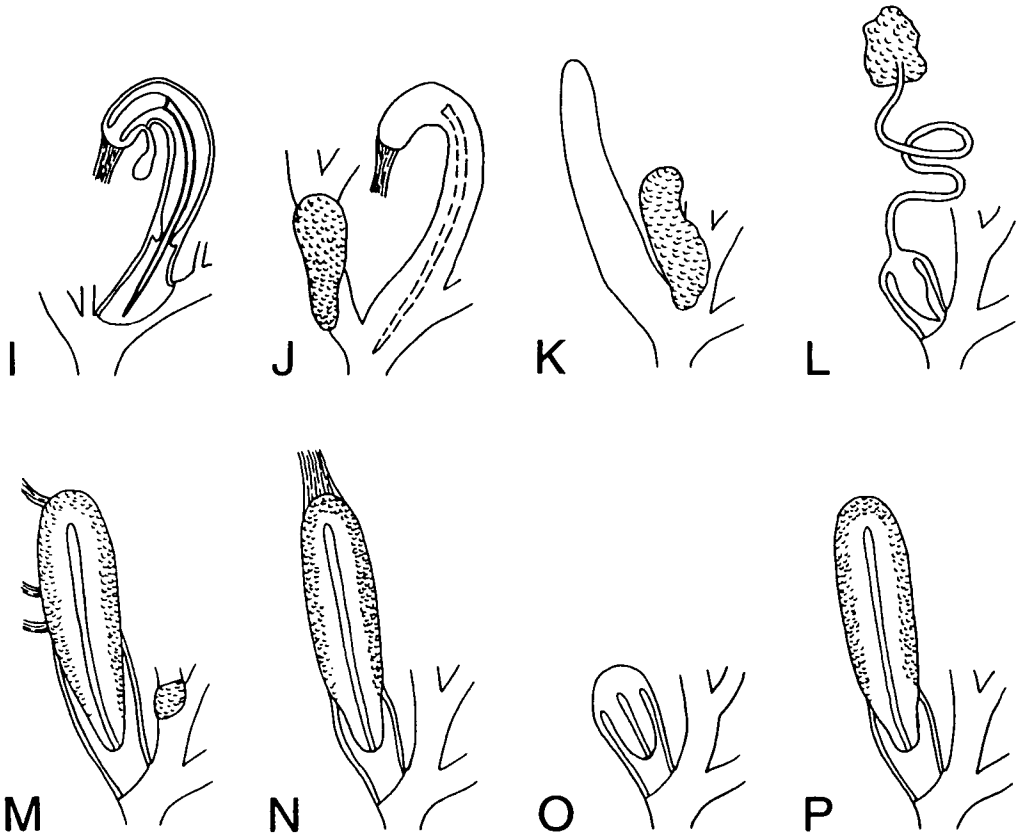
19. There are taxa with and taxa without a flagellum (Fig. 3) in almost all major subgroups of the Stylommatophora as well as in several families of the Limacoidea *sensu lato*. This character is therefore not very useful for the phylogenetic analysis of the Limacoidea *sensu lato* at family level and its evolu-

tion would be difficult to reconstruct unequivocally.

20. In the ancestral state of the Helicarionidae, Ariophantidae and Urocyclidae there is an axial filament (Fig. 3) in the flagellum, which is absent in the other groups considered.

21. The vas deferens (Fig. 3) of many Stylommatophora is not connected with the penial tunica (if one is present). In several taxa the vas deferens is attached to the proximal end of the penial tunica. Only in the Vitrinidae and in *Mesolimax* (Agriolimacidae), the only limacoid slug with a penial tunica, the vas deferens runs at the inside of the penial tunica.

22. The bursa copulatrix inserts at the proximal end of the vagina in most Stylommatophora. In the ancestral state of the Limacidae and Agriolimacidae and in subgroups of the Vitrinidae, Euconulidae and

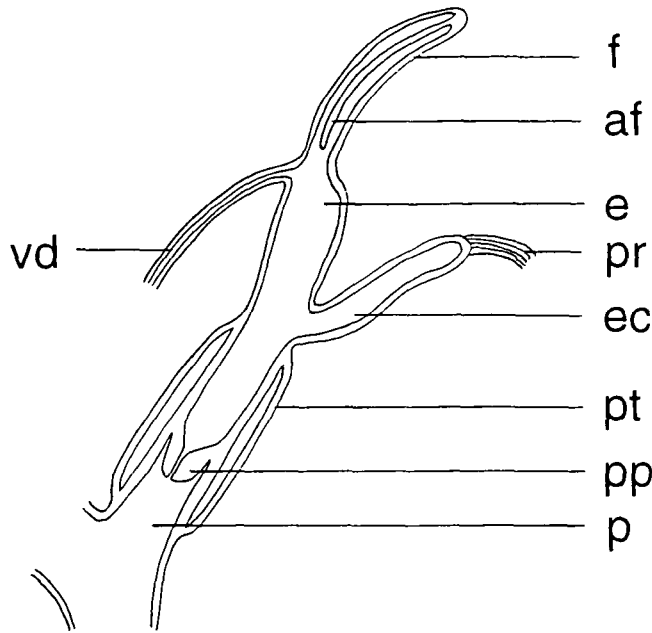


Trochomorphidae the vagina is absent and the bursa copulatrix inserts at the base of the penis.

23. There is an externally visible gland around the oviduct or the vagina (Figs 2G, H, J, M) in most Limacoidea *sensu lato*, which is absent in the other Stylommatophora. There are also glandular elements in the oviduct of other Stylommatophora (e.g. in the Streptaxidae ('shell gland', see Visser, 1973) and in the Aillyidae (Van Mol, 1978)), which are, however, not externally visible. The homology of these glandular elements and the gland around the oviduct or the vagina of the Limacoidea *sensu lato* is unclear. This gland has been called either the oviducal or the perivaginal gland, according to its position. But if it is the same homologous structure, it is desirable to have only one name. Van Mol (1968) has proposed the term uterus. Previously Baker (1928, 1938, 1941) has used this designation for the 'sacculate region of the oviduct, regardless of its function'. In any case the term uterus is inappropriate, because both structures mentioned are neither homologous nor analogous to the vertebrate uterus. Dasen (1933) has demonstrated that at least in the Ariophantidae the function of the oviducal gland is to secrete a capsule around the eggs. Therefore, he called this gland the

capsular gland and this term is also used here.

Based on a note of Van Mol & Van Bruggen (1971), Nordsieck (1985) maintained that the structure of the perivaginal gland of the Zonitidae *sensu auct.* and the oviducal gland of the helicarionid families is different and that the perivaginal gland is not homologous with the oviducal gland, but instead with the stimulator. The only difference between the two gland types mentioned by Van Mol & Van Bruggen (1971) is the presence of a subepithelial muscular layer between the gland cells and the lumen of the vagina in the Zonitidae *sensu auct.*, which apparently is absent in the Euconulidae, Helicarionidae and Urocyclidae, but there are usually also muscle fibres in the oviducal glands of these families. They can also be found in the connective tissue around the gland in the Urocyclidae (Van Mol, 1970), Helicarionidae (Hoffmann, 1931) and Ariophantidae (Van Mol, 1968). According to Dasen (1933), they can be found even between the glandular cells in *Cryptozona* (Ariophantidae). The data about the position of the circular muscles of the capsular gland are too fragmentary to decide how constant the position of these muscles is and whether it is useful for the phylogenetic analysis of the Limacoidea *sensu lato*. Based



**Figure 3.** Scheme of the male genitalia. Abbreviations: af, axial filament; e, epiphallus; ec, epiphallic caecum; f, flagellum; p, penis; pp, penial papilla; pr, penis retractor; pt, penial tunica; vd, vas deferens.

on the structure of the perivaginal and the oviducal gland, there is no reason to reject the homology of these glands. An argument for the hypothesis that both glands are homologous is that even in the Zonitidae *sensu auct.*, the position of the 'perivaginal' gland is not constant. In some Vitreidae, Oxychilinae and Daudebardiinae it is not around the vagina but only around the oviduct. On the other hand the perivaginal gland cannot be homologous with the stimulator, because it is also present in some Zonitidae (*Troglaeogopsis*), Oxychilinae (*Nastia*), Gastrodontidae and many other families of the Limacoidea *sensu lato* which possess a well-developed stimulator (see also character 1).

24. The capsular gland only surrounds the oviduct in most Limacoidea *sensu lato*. However, in some Vitreidae and in the ancestral state of the Godwiniinae, Oxychiliinae, Daudebardiinae and Zonitidae it at least partly surrounds the vagina.

25. In most Stylommatophora the genital orifice is near the tentacles in the anteriormost third of the anterior part of the cephalopodium (anterior to the visceral stalk or the mantle). In some Gastrodontidae, Trigonochlamyidae, Zonitidae and in all Godwiniinae, Oxychilinae, Daudebardiinae and Milacidae it is shifted posteriorwards.

26. In most Stylommatophora the right ommatophoral retractor passes between penis and vagina. But in several families of the Helicoidea and Limacoidea *sensu lato* there are also groups in which the retractor passes left to the genitalia. Only this character state

has been found in the Gastrodontidae, Godwiniinae, Daudebardiinae and Milacidae.

27. Wächtler (1935) has shown that the pedal grooves, on which Pilsbry (1896) based the Aulacopoda, are present in all Stylommatophora. The only difference between the Aulacopoda and the Holopoda is the distinctness of the pedal grooves. In the Sigmurethra the plesiomorphous character state is the holopod foot with indistinct pedal grooves as in the Orthurethra. Baker (1955) supposed that the aulacopod foot is an autapomorphy of the Sigmurethra, but has not given any arguments for this hypothesis. The aulacopod foot probably evolved several times in the Sigmurethra (Schileyko, 1979). It is present e.g. in the Systrophiidae, the Punctoidea, the Arionoidea and in all Limacoidea *sensu lato* except the Staffordiidae and *Poecilozonites* (Gastrodontidae). The holopod foot of *Poecilozonites* is obviously a secondary reduction of the aulacopod foot of the other Gastrodontidae. Therefore, the Aulacopoda as well as the Holopoda are polyphyletic.

28. Many authors distinguish an 'undivided' and a 'tripartite' sole. Wächtler (1935) has shown, however, that the sole of almost all Stylommatophora is tripartite. But only in several groups of the Limacoidea *sensu lato* and in some American Arionidae distinct sole furrows have developed, so that the three sole fields can easily be discerned. In contrast to Schileyko's (1979) opinion, the lower pedal incisions of *Cecilioides* (Ferussaciidae) are not homologous to



the sole furrows but with the lower pedal furrows (Wächtler, 1935).

29. A caudal pit (this structure should not be called caudal gland, caudal pore, etc.; see Wächtler, 1935) is present only in *Sigmurethra* with distinct pedal grooves, namely in many *Punctoidea*, *Arionoidea* and *Limacoidea sensu lato*. The original function of the caudal pit is possibly the gathering of the slime which is moved posteriorly along the pedal grooves (Climo, 1969). Therefore, it probably evolved several times in the *Sigmurethra* just as the distinct pedal grooves (see character 27).

In the *Dyakiidae*, *Helicarionidae*, *Ariophantidae*, *Urocyclidae*, *Chironidae* and *Euconulidae* the tail is more or less truncated and the vertical caudal pit is generally overhung by a process ('horn'). This process might serve to guide the slime from the pedal grooves into the caudal pit (Climo, 1969). A similar process is also present in some *Punctoidea*. On the contrary, in the *Gastrodontidae* and *Zonitidae* the caudal pit is a slit in the sloping foot margin, which is not overhung by a process. According to Stoliczka (1873) and Tillier & Bouchet (1988), there is at least a rudimentary slit in some *Trochomorphidae*.

30. I define shells with generally more than three whorls into which the animal can withdraw (almost) completely as heliciform. A vitriniform shell has usually less than three whorls and the animal is relatively too large to withdraw into the shell. The shell has been reduced in several families of the *Limacoidea sensu lato*.

31. In the *Sagdidae* and most *Limacoidea sensu lato* (except some genera in a few families) the peristome is more-or-less sharp, whereas it is distinctly thickened in the *Sphincterochilidae* and most *Cepoliidae* and odontognath *Helicoidea* (and many other *Stylommatophora*).

32. Shell lobes are present in many groups of several families of the *Limacoidea sensu lato*, especially in those with reduced shells. Whereas all *Staffordiidae* and *Helicarionidae* and many *Ariophantidae*, *Urocyclidae*, *Vitrinidae* and *Euconulidae* have shell lobes, they are present rarely in the *Oxychilinae* (*Vitrinoxychilus*) and absent in some other families.

33. There is a horseshoe-shaped groove on the mantle in three families of slugs, namely the *Trigonochlamyidae*, *Parmacellidae* and *Milacidae*. In all other slugs such a groove is lacking. However, *Krynickyllus* (*Agriolimacidae*) has a crescent-like groove on the mantle and the *Boettgerillidae* have a groove along the left margin of the mantle.

34. The macroscopically visible minor venation of the lung has been reduced in many groups of several families of the *Limacoidea sensu lato*.

35. Like many primitive 'achatimid' *Sigmurethra* the *Sagdidae* have an stegognath jaw (composed of fused platelets; Fig. 4A). This character state has been found in *Limacoidea sensu lato* only in *Pristiloma* and *Ogaridiscus* (*Vitreidae*). The other *Limacoidea sensu lato* and the *Sphincterochilidae* and most *Cepoliidae* have an oxygnath (smooth) jaw (Fig. 4B). Most other *Helicoidea* have an odontognath (ribbed or striated) jaw (Fig. 4C). In the *Limacoidea sensu lato* the jaw has been reduced in the two exclusively carnivorous groups, *Daudebardiinae* and *Trigonochlamyidae* (Fig. 4D).

In contrast to Schileyko's (1991) opinion, there are many *Limacoidea sensu lato* in which the jaw has no distinct median projection at the concave edge (see, e.g., Baker, 1928, 1938; Blandford & Godwin-Austen, 1908; Hesse, 1926; Van Goethem, 1977). On the other hand, the jaw of the *Cepoliidae* has a median projection just as the jaw of most *Sphincterochilidae*. Therefore, the median projection of the jaw is a variable character which is not important for the analysis of the phylogenetic relationships of the families of the *Limacoidea sensu lato*.

36. Whereas the radular marginals of the *Sagdidae* and *Helicoidea* are short and generally with entocones, the radular marginals of the *Limacoidea sensu lato* are elongate and almost always without entocones. Among the *Limacoidea sensu lato* *Dendrolimax* (*Urocyclidae*; see Van Goethem, 1977) is the only exception in which the radular marginals are provided with entocones.

37. The number of the ectocones of the radular marginals varies in most families of the *Limacoidea sensu lato*. It varies even within single species (onto-

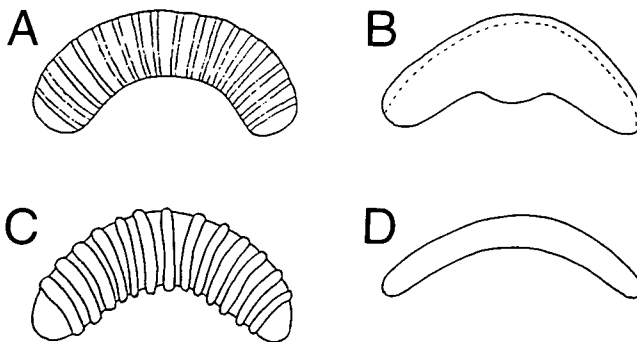


Figure 4. Jaw types. A. Stegognath. B. Oxygnath. C. Odontognath. D. Reduced jaw of carnivorous snails.

genetically regulated?). For example, most authors (e.g. Likharev & Wiktor, 1980) stated that *Boettgerilla pallens* has unicuspid radular marginals, whereas Jungbluth, Likharev & Wiktor (1981) have shown that this species has multicuspid radular marginals. Therefore, this character is not very useful for the phylogenetic analysis of the Limacoidea *sensu lato* and its evolution can hardly be unequivocally reconstructed.

38. Another potentially phylogenetically informative character is the karyotype. Until now there are no studies about the evolution of the chromosome banding pattern in the Limacoidea *sensu lato*. Even the knowledge about the haploid chromosome numbers, which are compiled in Table 3 from Patterson (1969) and Kiauta & Butot (1969, 1973), are still fragmentary. Because of their high variability within the families the chromosome numbers are not useful for the present phylogenetic analysis. This character has not been used for the phylogenetic analysis with PAUP.

Tillier (1989) investigated several additional characters of the digestive tract, the excretory system and the central nervous system, and used them for the reconstruction of the phylogenetic relationships of the stylommatophoran families. An analysis of the data matrix of Tillier (1989: 296 ff., appendix E) shows that the variability of all characters used by him is at least as high within the families of the Limacoidea *sensu lato* as between these families (with the exception of the degree of the closure of the ureter, which is invariable in all examined Limacoidea *sensu lato*). Therefore, these characters are not useful for the phylogenetic analysis of the families of the Limacoidea *sensu lato*.

The topological relations of the ganglia of the visceral chain are the only character complex used by Tillier (1989) of which a detailed discussion is necessary here, because this character complex has also been used by Bargmann (1930) and Emberton (1991). However, it has already been recognized by Bishop (1978) that this character complex is not suitable for the reconstruction of phylogenetic relationships at higher levels, because of its high intrafamilial variability: 'To the extent that the shortening of connectives and the fusion of the ganglia of the visceral chain are processes which are likely to have occurred independently in many lineages, their application as key characters to construct a classification is clearly of no value'. Therefore, the statement of Emberton (1991) that Bishop (1978) 'recommended' the investigation of the ganglia of the visceral chain for stylommatophoran systematics is imprecise. Bishop (1978) rather was of the opinion that

the fusion of the ganglia of the visceral chain can provide 'information about the direction of evolution in lineages which may be identified by other means' 'given the assumption of irreversibility'. But exactly this assumption, which was also the basis of Tillier's (1989) analysis, must be questioned. The approach and fusion of the ganglia of the visceral chain are ontogenetic processes (Henchman, 1890). Therefore, apparently 'primitive' forms with unfused ganglia can originate from ancestors with fused ganglia by neoteny. The possibility of reversals reduces the value of the pattern of fusion of the ganglia of the visceral chain for phylogenetic studies considerably. The existence of reversals of ganglionic fusions has already been inferred by Emberton (1991) from his parsimony analysis. Moreover, there is a practical reason for the rejection of ganglionic fusions as phylogenetic informative characters in the present analysis: there are no objective non-histological criteria upon which to decide whether two ganglia are actually fused. This leads to differences between the investigators of the visceral chain concerning the character states of several taxa. Tillier (1989) maintained that 'Bargmann's observations lack precision', partly because she did not distinguish between the proximity and the fusion of ganglia. Emberton (1991) reproached Tillier (1989) with exactly the same. Until the pattern of ganglionic fusions is ascertained reproducibly using histological methods as recommended by Emberton & Tillier (1995), it is better to ignore this character complex in phylogenetic analysis, otherwise false character states can lead to wrong phylogenetic conclusions.

Emberton (1991) used some additional characters, especially of the pallial complex, for his cladistic analysis. Although Emberton investigated only a small number of genera, homoplasies in some of these characters were detected in his analysis. Nevertheless, the investigation of these and other additional characters is required to obtain more robust phylogenies with a higher resolution. However, the studies of Tillier (1989) and Emberton (1991) have shown that there are probably not too many additional gross morphological characters which are suitable for the analysis of phylogenetic relationships at higher taxonomic levels within the Stylommatophora, and that morphological homoplasies are rampant (Emberton & Tillier, 1995). As already discussed by Emberton (1991), the reasons for this may be that the stylommatophoran radiation into families was so ancient and rapid and the selective pressures

on the evolving families might have been very similar.

Therefore, DNA sequence data as obtained by Emberton *et al.* (1990), Tillier, Masselot, Philippe & Tillier (1992) and Tillier, Masselot & Tillier (1996) might improve the robustness and resolution of the phylogenetic hypothesis more easily than further morphological studies. However, to resolve the relationships within the Stylommatophora the data set must be essentially larger than those in these studies (Tillier *et al.*, 1992). On the other hand, the expectations with regard to DNA sequences should not be too high, because in the case of ancient and rapid radiations as in the Stylommatophora there are the same problems with DNA sequences as with morphological characters: during the rapid radiation rather few substitutions (= potential synapomorphies) happen, whereas in the comparatively long time after the radiation many convergent substitutions accumulate (Tillier *et al.*, 1996).

#### Phylogenetic system

A phylogenetic analysis using PAUP (see Material and Methods) has been carried out with the character matrix (Table 3) and the weighting method described in that section. In a heuristic search PAUP found 27 most parsimonious trees (consistency index CI = 0.60; retention index RI = 0.74), a strict consensus tree of which is shown in Figure 5. The low consistency and retention index indicate that homoplasies within the Limacoidea are just as rampant as within the Stylommatophora in general. Actually, the values of the indices are even overestimated, because the intrafamilial variation is not allowed for. Therefore, it must be admitted that the result of the present analysis is only tentative. It is the best possible interpretation of the available data, but several nodes in the tree are based on questionable autapomorphies and need further corroboration.

The resulting monophyla and in some cases their subdivisions are discussed below. The numbering of the autapomorphies, which are taken from the list of apomorphies calculated with the DELTRAN optimization of PAUP (see the section Material and Methods), refers to the character matrix (Table 3) and to the character analysis. If additional autapomorphies of the individual families are known, they are also listed. It has been preferred not to name all monophyla, because most of the names would be superfluous. The families are

arranged in superfamilies as usual to facilitate the survey.

#### Sagdidae Pilsbry, 1895

*Autapomorphies.* None known.

*Remarks.* The Sagdidae were included in the analysis only as an outgroup. No synapomorphies between the Sagdidae and the other groups considered have been found.

#### Helicoidea + Limacoidea *sensu lato*

*Autapomorphies.* 2(1); 4(1); 35(1).

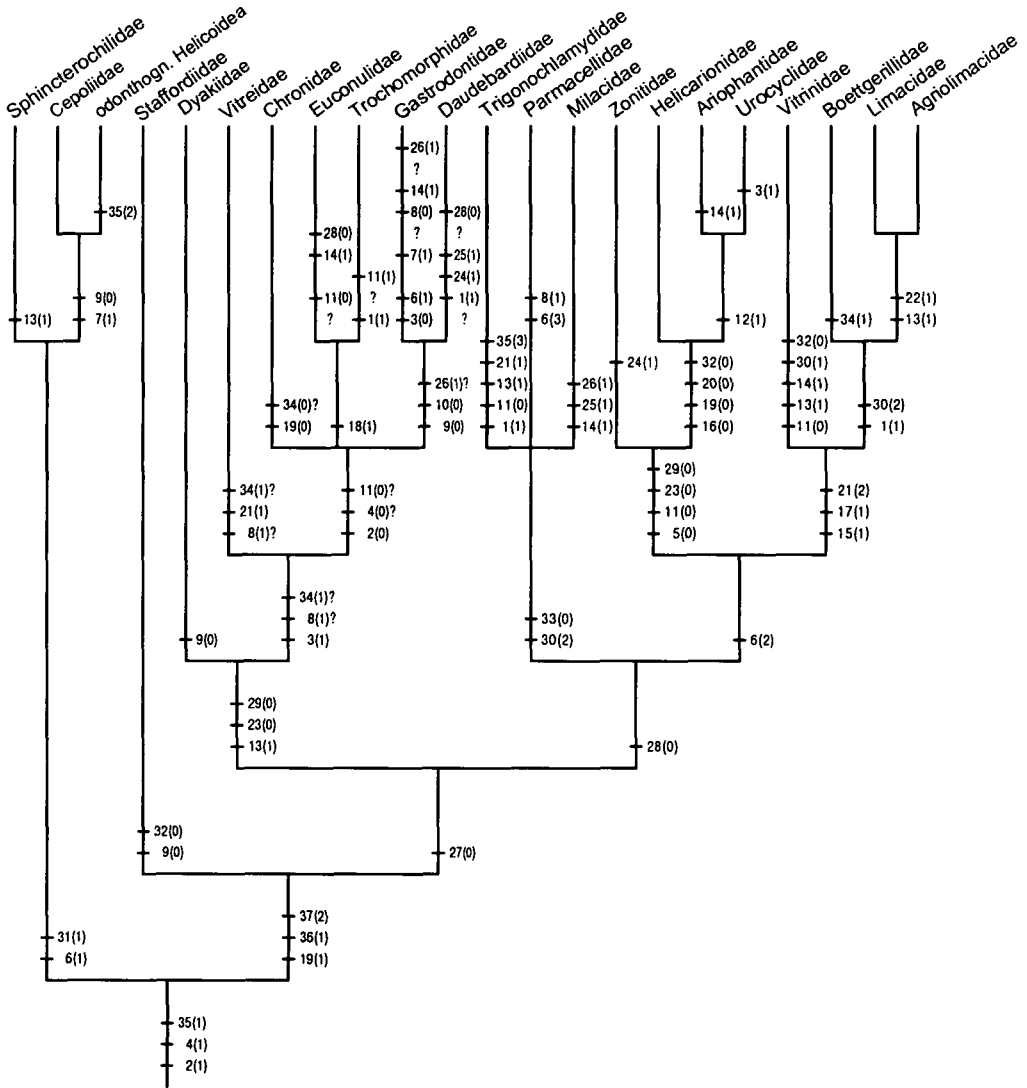
*Remarks.* The Helicoidea were included as an additional outgroup. The analysis revealed three potential synapomorphies between the Helicoidea *sensu lato* and the Limacoidea *sensu lato*. The insertion site of the stimulator at the atrium and the transformation of the stimulator section A<sub>5</sub> to an acinose gland are synapomorphies of these two groups because in the Sagdidae as well as in the Orthurethra the stimulator inserts on the penis and the stimulator section A<sub>5</sub> is bursa-like. Furthermore, the analysis implies that the ancestor of the Helicoidea *sensu lato* and the Limacoidea *sensu lato* had an oxygnath jaw.

#### Helicoidea Rafinesque, 1815

*Autapomorphies.* 6(1); 31(1).

*Remarks.* According to the present analysis, the Helicoidea are characterized by the lateral insertion of the stimulator section A<sub>4</sub> on the section A<sub>2</sub> and the thickened peristome. The thickened peristome is considered to be an autapomorphy of the Helicoidea, because the Sagdidae which have a sharp peristome, are used as outgroup. However, there are also many outgroups with a thickened peristome. Therefore, it is questionable, whether the thickened peristome is actually an autapomorphy of the Helicoidea or whether the sharp peristome is an autapomorphy of the Limacoidea *sensu lato* (and of the Sagdidae). The diverticulum of the bursa copulatrix might be an additional autapomorphy of the Helicoidea. It is absent in the Sagdidae and all Limacoidea *sensu lato*. It is present in all Sphincterochilidae and Helicidae and several Xanthonychidae (*sensu lato*). However, it is absent in the Cepoliidae, Camaeniidae, Polygyridae, Arionoidea, Bradybaenidae and Hygromiidae.

Nordsieck (1987) and Schileyko (1978, 1991) have analysed the phylogeny of the Helicoidea. However, they have not shown a data matrix



**Figure 5.** Cladogram of the *Limacoidea sensu lato* (CI = 0.60; RI = 0.74). The numbering of the autapomorphies which are taken from the list of apomorphies calculated with the DELTRAN optimization of PAUP (see methods) refers to the character matrix (Table 3) and to the character analysis.

and they have not carried out a strictly cladistic analysis. Neither of these authors has made a thorough outgroup comparison. Moreover, they have neglected some groups which belong to the monophylum Helicoidea. The phylograms of Schileyko (1978, 1991) are not substantiated by any stated synapomorphies. Nordsieck (1987) has presented a cladogram of the Helicoidea with stated synapomorphies.

However, because of the lack of a data matrix one cannot readily ascertain how consistent this cladogram is with the data and how many convergences are involved. The only autapomorphy of the Helicoidea determined by Nordsieck (1987), the insertion of the stimulator on the atrium, is not an autapomorphy, but a symplesiomorphy shared with the *Limacoidea sensu lato*.

## Sphincterochilidae Zilch, 1960 (1909)

*Autapomorphies.* 13(1); accessory vesicula seminalis; shell whitish.

*Remarks.* In the Sphincterochilidae the stimulator section  $A_4$  inserts laterally at the section  $A_2$  and the peristome is thickened. Therefore, they are doubtlessly true Helicoidea. Their oxygnath jaw (usually with a distinct median projection) is only a symplesiomorphy shared with the Limacoidea *sensu lato* and the Cepoliidae and is therefore not an argument against the classification of the Sphincterochilidae with the Helicoidea (in contrast to Schileyko, 1991).

## Cepoliidae + odontognath Helicoidea

*Autapomorphies.* 7(1); 9(0).

*Remarks.* In the ancestral state of the Cepoliidae and the odontognath Helicoidea the stimulator is provided with a calcereous dart. Furthermore, in all Helicoidea except the Sphincterochilidae the stimulator section  $A_4$  is shortened in comparison with the section  $A_4$  in the Orthurethra, the Sagdidae, the Staffordiidae and in the ancestral state of the Dyakiidae. However, there are also Sphincterochilidae with a shortened stimulator section  $A_4$ .

Because of the lack of a thorough outgroup comparison, the ideas of Nordsieck (1987: fig. 1) about the plesiomorphous character states of the dart apparatus in the ancestral state of the Helicoidea except the Sphincterochilidae are wrong in several respects. In the ancestral state of the Cepoliidae + odontognath Helicoidea the dart apparatus does not insert on the vagina but on the atrium, as in the Sphincterochilidae and in the Limacoidea *sensu lato*. The stimulator section  $A_1$  is not short but long ('neophore', see below) as in the Sphincterochilidae. As in most other Stylommatophora, the stimulator sections  $A_4 + A_5$  are not duplicated and insert laterally on the section  $A_2$  and not basally on the section  $A_1$ .

## Cepoliidae Ihering, 1909

*Autapomorphies.* Entire stimulator enclosed within membranous envelope; bipartite accessory gland at the base of the membranous envelope; diverticulum absent (?).

*Remarks.* The Cepoliidae are the only 'xanthonychid' group with an oxygnath jaw and are probably the sister-group of the odontognath Helicoidea. Therefore, the Xanthonychidae in

the sense of Nordsieck (1987), which are not substantiated by any autapomorphies, are paraphyletic.

Nothing supports the assumption that the stimulator gland of the Cepoliidae is 'the product of fusion of the muscular swellings of ducts of the Helminthoglyptinae' as Schileyko (1991) suggested.

## odontognath Helicoidea

*Autapomorphies.* 35(2).

*Remarks.* The Helicoidea, except the Sphincterochilidae and the Cepoliidae, are characterized by an odontognath jaw with a few exceptions. Besides the families dealt with by Nordsieck (1987) and Schileyko (1978, 1991), at least the Arionoidea, Camaenidae and Polygyridae belong to this group. In some Camaenidae (which might be polyphyletic; see Scott, 1996) and Polygyridae there are simple penial appendages which were homologized with the stimulator by Nordsieck (1985, 1986, 1987). But these appendages have neither a separate gland nor a papilla. They are probably *de novo* developments.

The long stimulator section  $A_1$  of the Cepoliidae and the *Helminthoglypta* group was called the atrial sac by Pilsbry (1939) and Baker (1943) and the neophore by Webb (1952) and Nordsieck (1987). Nordsieck (1987) claimed that this structure is an evagination of the vagina, which is an apomorphy. An outgroup comparison shows, however, that there is also a long stimulator section  $A_1$  in most Orthurethra (Fig. 1A), Sagdidae (Fig. 2A), Sphincterochilidae (Fig. 2B) and some Limacoidea *sensu lato* (e.g., in the ancestral state of the Dyakiidae; Fig. 2F). Therefore, in the Helicoidea the long stimulator section  $A_1$  is not an apomorphy but a plesiomorphy. Moreover, in the above-mentioned outgroups the long stimulator section  $A_1$  inserts either on the penis or on the atrium. Therefore, this structure cannot be an evagination of the vagina.

In an analysis of the phylogeny of some western North American Helicoidea which he united as Helminthoglyptidae (= Helminthoglyptinae *sensu* Nordsieck, 1987), Roth (1996) used *Monadenia* as outgroup and concluded that the presence of an atrial sac is an apomorphy. He scored this character twice (his characters 1 and 5). This led to the conclusion that the *Helminthoglypta* group is a positionally apomorphic group in the Helminthoglyptidae. The fact that the atrial sac is a symplesiomorphy within the Helicoidea makes a re-analysis of

Roth's data necessary. The different interpretation of the atrial sac will result at least in a different rooting of the cladogram. The Helminthoglyptidae *sensu* Roth might turn out not to be a monophyletic group, but a part of the stem group of most of the odontognath Helicoidea.

The aulacopod Arionoidea belong to the odontognath Helicoidea *sensu lato*, because they are also odontognath, because there is a short dart sac at the vagina in *Philomycus* (and possibly in *Binneya*) and, above all, because they share synapomorphies with a holopod group generally affiliated to the Helicoidea: the surrounding of the heart by the kidney is a unique synapomorphy of the Arionoidea and the Metostracidae (the reduction of the shell is an additional synapomorphy of both groups).

#### Limacoidea *sensu lato*

*Autapomorphies.* 19(1); 36(1); 37(2).

*Remarks.* The elongate radular marginals without entocones are the classical diagnostic feature of the Limacoidea *sensu lato* (Pilsbry, 1896; Baker, 1941). They are probably an adaptation to an omnivorous diet. The same is true for the reduction of the ectocones of the radular marginals. However, because of the variability of the latter character, it is doubtful whether this reduction is actually an autapomorphy of the Limacoidea *sensu lato* (see character analysis). The transition from a pure herbivorous to an omnivorous diet is probably the most important key event in the evolution of the Limacoidea *sensu lato*.

#### Staffordioidea Thiele, 1931

##### Staffordiidae Thiele, 1931

*Autapomorphies.* 9(0); 32(0); stimulator section A<sub>1</sub> shortened.

*Remarks.* This group comprises only one very insufficiently known genus.

#### Dyakioidea + Gastrodontoidea + Parmacelloidea + Zonitoidea + Helicarionoidea + Limacoidea *sensu stricto*

*Autapomorphies.* 27(0).

*Remarks.* The monophyly of this group is substantiated only by the transformation of the holopod into the aulacopod foot and is therefore tenuous.

#### Dyakioidea + Gastrodontoidea

*Autapomorphies.* 13(1); 23(0); 29(0).

*Remarks.* The potential autapomorphies of this group, namely the absence of the penial papilla and the development of an external capsular gland and a caudal pit, are also known from other groups of the Limacoidea *sensu lato*. Therefore the monophyly of this group is tenuous.

#### Dyakioidea Gude & Woodward, 1921

##### Dyakiidae Gude & Woodward, 1921

*Autapomorphies.* 9(0); two major gland lobes of the stimulator; insertion of the bursa copulatrix on the base of the stimulator; shell wider than 25 mm (Hausdorf, 1996).

*Remarks.* Van Mol (1973) has already realized that the Dyakiidae are not related to the Ariophantidae, in which they were included by Baker (1941). However, this finding has been ignored by the later authors (e.g. Solem, 1978; Schileiko, 1979; Boss, 1982; Nordsieck, 1986; Tillier, 1989). Although Tillier (1989) noticed the similarity of the stimulators of the Dyakiidae and the Bradybaenidae, which is only a symplesiomorphy, and even guessed that these two families possibly form a monophyletic group, he did not separate the Dyakiinae from the Helicarionoidea *sensu lato*. The phylogeny of the Dyakiidae has been discussed by Hausdorf (1996).

#### Gastrodontoidea Tryon, 1866

*Autapomorphies.* 3(1); 8(1)?; 34(1)?.

*Remarks.* This group is characterized by the loss of the stimulator section A<sub>5</sub> and the reduction of the papilla of the stimulator and the minor venation of the lung. However, in the Gastrodontoidea the section A<sub>5</sub> and the papilla of the stimulator is developed and there are several Gastrodontoidea with a distinct minor venation of the lung. Moreover, these potential autapomorphies are also known from other groups of the Limacoidea *sensu lato*. Therefore the monophyly of this group is questionable.

#### Vitreidae Thiele, 1931

*Autapomorphies.* 8(1)?; 21(1); 34(1)?.

*Remarks.* The Vitreini *sensu* Riedel (1980) are not a monophyletic group, since they include dwarf forms of different clades. Some genera of this polyphyletic conglomerate have already been transferred to other taxa, *Pycnogyra* to

the Gastrodontidae and *Paravitrea* to the Godwiniinae (Daudebardiidae) (see below). The monophyly of the remaining taxa still remains doubtful.

Chronidae + Euconulidae +  
Trochomorphidae + Gastrodontidae +  
Daudebardiidae

*Autapomorphies.* 2(0); 4(0)?; 11(0)?.

*Remarks.* This group is mainly characterized by a reversal of the features of the stimulator to a state which is more similar to that of the Sagdidae and Orthurethra than to that of the ancestral state of the Limacoidea *sensu lato*: the stimulator inserts on the penis and its section A<sub>5</sub>, if present, is bursa-like.

The relationships of the three main groups of the Gastrodontoidea, namely the Chronidae, the Euconulidae + Trochomorphidae and the Gastrodontidae + Daudebardiidae have not yet been resolved.

Chronidae Thiele, 1931

*Autapomorphies.* 19(0); 34(0)?.

*Remarks.* *Orpiella*, *Dendrotrochus* and *Ryssota* are not related to *Sesara* or the Helicarionidae, in which they were included by Baker (1941). In the Helicarionidae the stimulator inserts on the atrium, whereas at least some species of *Orpiella* (Baker, 1941), *Dendrotrochus* (Rensch, 1930) and *Antinous* (Burne, 1910) have a penial appendix similar to that of the Euconulidae and therefore probably homologous to the stimulator.

*Ryssota* shows some convergences with the Trochomorphidae: the central teeth of the radula are elongated with a short mesocone and weak ectocones and the flagellum is absent. But the spermatophore of *Ryssota* is thick-walled and there is a distinct minor venation in the lung.

*Chronos* and *Kaliella* are insufficiently known genera with club-shaped flagella (Blanford & Godwin-Austen, 1908; Robson, 1914) and probably belong here. Thiele (1931) proposed family-group names for both taxa without adequate diagnoses. As the first reviser I determine that Chroninae Thiele, 1931 has relative precedence over Kaliellinae Thiele, 1931 (Art. 24 ICZN).

Besides the mentioned groups, some Japanese genera with a penial appendix and a club-shaped flagellum (e.g., *Japanochlamys*, *Nipponochlamys*, *Otesiopsis*, *Takemasaia*, *Trochochlamys*, *Yamatochlamys*; see Azuma, 1982) probably belong to the Chronidae. Unfortu-

nately, nothing is known about their spermatophores and lung venation.

Euconulidae + Trochomorphidae

*Autapomorphies.* 18(1).

*Remarks.* Baker (1941) was the first to realize that the Euconulidae and the Trochomorphidae share the thin-walled spermatophore, but he took this to be a convergence.

Euconulidae Baker, 1928

*Autapomorphies.* 11(0)?; 14(1); 28(0); bursa copulatrix obsolete (usually shorter than oviduct).

*Remarks.* The Euconulidae were divided into the Euconulinae Baker, 1928 and the Microcystinae Thiele, 1931 by Baker (1941). The Microcystinae are characterized by the shift of the bursa copulatrix from the vagina to the penis and the partial detachment of the prostate. Furthermore, they are characterized by their ovoviviparous reproduction, which is reflected in the transformation of the female part of the spermooviduct to a voluminous 'uterus', and by the shortening of the prostate. The last-mentioned character states might, however, not be autapomorphies of the Microcystinae, but synapomorphies of the Microcystinae and the similarly ovoviviparous *Guppya*. Additional characteristics of the Microcystinae are the loss of the capsular gland and the reduction of the penial papilla. These character states might also be synapomorphies of the Microcystinae and subgroups of the Euconulinae, in which they occur too. The oviparous Euconulinae, of which no autapomorphies are known, are probably paraphyletic.

Trochomorphidae Möllendorff, 1890

*Autapomorphies.* 1(1); 11(1)?.

Gastrodontidae + Daudebardiidae

*Autapomorphies.* 9(0); 10(0); 26(1)?.

*Remarks.* The monophyly of this group is mainly supported by the possession of a dart and retractor muscle at stimulator section A<sub>2</sub>.

Gastrodontidae Tryon, 1866

*Autapomorphies.* 3(0); 6(1); 7(1); 8(0)?; 14(1); 26(1)?; duct connecting the penis with the female genitalia (the bursa copulatrix or the oviduct); bursa copulatrix inserts at the atrium.

*Remarks.* The duct connecting the penis with the female genitalia is an unique autapomorphy, which substantiates the monophyly of the Gastrodontiidae and the classification of the aberrant holopod *Poecilozonites* with this family.

Because the stimulator sections A<sub>4</sub> and A<sub>5</sub> are absent in the Daubebardiidae, it is questionable whether the lateral insertion of the stimulator section A<sub>4</sub> on section A<sub>2</sub> and the shortening of section A<sub>4</sub> are actually autapomorphies of the Gastrodontiidae or whether they are synapomorphies of the Gastrodontiidae and the Daubebardiidae.

*Pycnogyra berendti* (L. Pfeiffer, 1861), the only species of *Pycnogyra*, does not belong to the Vitreinae as stated by Baker (1928, 1941) and Riedel (1980), but to *Striatura* (*Pseudohyalina*) (Gastrodontiidae). In *Striatura berendti* the right ommatophoral retractor passes to the left of the genitalia just as in the Gastrodontiidae. The phylogenetic relationships of *S. berendti* were not recognized until now, because they are obscured by the reduction of the stimulator, the penis and the duct connecting the penis with the bursa copulatrix. However, the reduction of the stimulator is an autapomorphy of *Pseudohyalina* (or *Pseudohyalina* + *Striaturops*). *S. berendti* constitutes together with *Striatura* (*Pseudohyalina*) *meridionalis* (Pilsbry & Ferriss, 1906) and *Striatura* (*Pseudohyalina*) *pugetensis* (Dall, 1895) a monophyletic group which is characterized by the reduction of the penis and the duct connecting the penis with the bursa copulatrix. Therefore, *Pycnogyra* Strebel & Pfeiffer, 1880 is not 'an approach to the Gastrodontiidae' as Baker (1928, 1930) thought, but a junior synonym of *Pseudohyalina* Morse, 1864. In contrast to Baker's (1930) opinion, the structure of the atrium of *S. berendti* cannot serve as a model for the origin of the duct connecting the penis with the bursa copulatrix, but is the result of the fusion of this duct with the distal penis and the atrium to form a large cavity.

#### Daubebardiidae Kobelt, 1906

*Autapomorphies.* 1(1)?; 24(1); 25(1); 28(0)?.

*Remarks.* *Nastia* was affiliated to the Gastrodontiidae by Riedel (1989), because it has a similar stimulator (Fig. 2J). However, it differs from the Gastrodontiidae in the capsular gland which partly surrounds the vagina, the course of the right ommatophoral retractor, the distinct sole furrows, the shortened central teeth and the lack of the accessory lap of the left

mantle lobe. It shares these character states with the Oxychilinae. The similar stimulator could be a plesiomorphy, whereas at least the shift of the capsular gland, the shortened central teeth and the lack of the accessory lap of the left mantle lobe are apomorphies. Therefore, *Nastia* belongs to the Oxychilinae.

The Zonitidae *sensu auct.* have very different stimulator types. Whereas there is a penial stimulator similar to the stimulators of the Gastrodontiidae in *Nastia* (Oxychilinae), there are vaginal stimulators similar to those of the Helicarionoidea and the Vitrinidae in some Zonitinae *sensu stricto* (e.g. *Troglaeopis*). Therefore the monophyly of the Zonitidae *sensu auct.* is doubtful.

The monophyly of the Zonitinae *sensu* Riedel, 1980 is also doubtful, because no autapomorphies of this group have been found and it divides into two rather distinct groups of genera. There is always a penial tunica in the group of genera with larger shells from the Balkan peninsula and Asia minor, whereas it is absent in all other Zonitinae *sensu* Riedel, 1980. In *Zonites* fibres of the penial nerve run through the cerebral ganglion, whereas there are no such fibres running through the cerebral ganglion in *Aegopinella*, *Godwinia*, *Nesovitrea* and *Retinella*. Therefore the genera without penial tunica have been separated from the Zonitinae *sensu stricto* as Godwiniinae.

When the subfamilies of the Zonitidae *sensu auct.* were analysed separately, it turned out that the Zonitidae *sensu auct.* are actually polyphyletic. The Oxychilinae constitute together with the Godwiniinae and the Daubebardiinae the sister-group of the Gastrodontiidae, whereas the Zonitinae *sensu stricto* appear to be the sister-group of the Helicarionoidea. Consequently, the Oxychilinae, Godwiniinae and Daubebardiinae are separated from the Zonitidae *sensu stricto* as Daubebardiidae.

The Daubebardiidae are characterized mainly by the capsular gland which surrounds the vagina at least partly and the posteriorly shifted genital orifice. Both potential autapomorphies can also be found in some Zonitidae. Therefore, the classification of the Godwiniinae and the Daubebardiinae, in which there are no taxa with a stimulator, with the Oxychilinae needs further corroboration.

The relationships of the three subfamilies of the Daubebardiidae have yet not been determined.

Godwiniinae Cooke, 1921. Potential autapomorphies: 11(1); 14(1). Genera: *Aegopinella*, *Godwinia*, *Glyphalinia*, *Mesomphix*, *Nesovitrea*,



*Paravitrea*, *Retinella* and *Vitrinizonites*. In all genera except *Glyphalinia* the capsular gland is absent. So far, most genera of the Godwiniinae were included in the Zonitinae (Riedel, 1980). *Paravitrea* has been included in the Vitreinae by Baker (1931) and Riedel (1980), but has been transferred to the Zonitinae by Baker (1941). This genus shows the autapomorphies of the Daudebardiidae (shifted genital orifice) and of the Godwiniinae (penial tunica absent) and hence belongs to this subfamily. The indistinct sole furrows of *Paravitrea* can be interpreted as a secondary reduction due to the diminished body size.

Oxychilinae Hesse in Geyer, 1927. Potential autapomorphies: 26(0)?; central teeth of the radula shortened; left mantle lobe without accessory lap. The reduction of the central teeth and the accessory lap of the left mantle lobe might actually be synapomorphies with the strongly modified Daudebardiinae.

Daudebardiinae Kobelt, 1906. Potential autapomorphies: 21(1); 30(1); 35(3); radula without central and lateral teeth; carnivorous. The Daudebardiinae are the most specialized subfamily of the Daudebardiidae and they were sometimes ranked as a separate family for phenetic reasons alone.

Parmacelloidea + Zonitoidea +  
Helicarionoidea + Limacoidea *sensu stricto*

*Autapomorphies*. 28(0).

*Remarks*. The only potential autapomorphy of this group, the distinct sole furrows, are also known from other groups of the Limacoidea *sensu lato*. Therefore the monophyly of this group needs further corroboration.

Parmacelloidea Gray, 1860

*Autapomorphies*. 30(2); 33(0)

*Remarks*. The monophyly of the Parmacelloidea which is substantiated mainly by the horseshoe-shaped groove on the mantle of these slugs was already recognized by Hesse (1926). It is difficult to understand why later authors have neglected these findings. The relationships between the Trigonochlamydidae, the Parmacellidae and the Milacidae remain unsettled.

Trigonochlamydidae Hesse, 1882

*Autapomorphies*. 1(1); 11(0); 13(1); 21(1); 35(3); all radular teeth aculeate, unicuspid; carnivorous.

*Remarks*. There is probably a sister-group relationship between *Parmacellilla* in which the embryonic shell is not covered by the mantle, just as in the Parmacellidae, and the other groups in which the shell is completely covered by the mantle. Therefore, the subdivision of the Trigonochlamydidae into Parmacellillinae Hesse, 1926 and Trigonochlamydidinae Hesse, 1882 is accepted. On the other hand the separation of *Selenochlamys* as a monotypic subfamily by Likharev & Wiktor (1980) is a mere typological act, which is not justified by this analysis.

Parmacellidae Gray, 1860

*Autapomorphies*. 6(3); 8(1); proximal part of the prostate differentiated; glandula acini-formis; spermatophore spirally coiled, with a flagelliform tail terminating in an anchor-like disc; mantle covering one half or more of the body.

Milacidae Ellis, 1926

*Autapomorphies*. 14(1); 25(1); 26(1); spermatophore with appendages; large renal lobe; shell completely covered by the mantle.

*Remarks*. There is a sister-group relationship between *Micromilax* and all other Milacidae in which the stimulator section A<sub>1</sub> is reduced and the stimulator section A<sub>4</sub> is shortened and multiplied (secondarily reduced to one in *Milax verrucosus*?). Wiktor (1987) considered the structure of the stimulator of *Micromilax* to be the 'result of a high specialization'. However, an outgroup comparison shows that the stimulator of *Micromilax* represents the plesiomorphous character state.

Zonitoidea + Helicarionoidea + Limacoidea  
*sensu stricto*

*Autapomorphies*. 6(2).

*Remarks*. This group is supported only by the fusion of the stimulator sections A<sub>5</sub> and A<sub>2</sub>. Nevertheless, the group seems to be well supported, because this character state is consistently present in all members of the group that have a stimulator, and because this transformation happened only once outside this group (in the Dyakiidae).

Zonitoidea + Helicarionoidea

*Autapomorphies*. 5(0); 11(0); 23(0); 29(0).

*Remarks*. This group is mainly supported by

the presence of retractor muscles at stimulator section A<sub>5</sub>. Because the homology of these muscles within the Zonitoidea and the Helicarionoidea is questionable, the monophyly of this group needs further corroboration.

Zonitoidea Mörch, 1864  
Zonitidae Mörch, 1864

*Autapomorphies.* 24(1).

*Remarks.* This group is only supported by the shift of the capsular gland to the vagina. The same character state is present in the Daudebardiidae. For further remarks look there.

After the separation of the Godwiniinae, the other Daudebardiidae and Vitreidae the Zonitidae include the following genera: *Aegopsis*, *Allaegopsis*, *Balcanodiscus*, *Doraegopsis*, *Meledella*, *Paraegopsis*, *Troglaeopsis* and *Zonites*.

Helicarionoidea Bourguignat, 1883

*Autapomorphies.* 16(0); 19(0); 20(0); 32(0).

*Remarks.* The Helicarionoidea are mainly characterized by the presence of an epiphallal caecum and a flagellum. However, these appendages are absent in some subgroups. Moreover, the retractor muscles at stimulator section A<sub>5</sub> insert at the columellar muscle. It cannot be determined whether or not this is an autapomorphy of the Helicarionoidea, because such muscles are absent in all taxa except the Helicarionoidea and the Zonitoidea.

Because of the exclusion of the Staffordiidae, Dyakiidae, Chronidae, Euconulidae and Trochomorphidae the delimitation of the Helicarionoidea is essentially different from all previous classifications.

Helicarionidae Bourguignat, 1883

*Autapomorphies.* None known.

*Remarks.* In the classifications of Baker (1941) and Solem (1966) the delimitation of the Helicarionidae and Ariophantidae is vague. In the present analysis the attachment of the penial tunica to the epiphallus is regarded as a synapomorphy of the Ariophantidae and Urocyclidae. Therefore, the delimitation of the Helicarionidae and the Ariophantidae is based on the state of the penial tunica. As a consequence of this new definition and the exclusion of the Chronidae and Dyakiidae, the systematic position of several groups has to be reconsidered. For example, the Durgellinae and

Girasiinae, which were included in the Ariophantidae by Baker (1941) and Solem (1966), *Xesta*, which was included in the Ariophantidae by Baker (1941) and Solem (1966), and the genera *Sesara*, *Sarika* and *Teraia*, which were ranked with the Macrochlamydiae by Solem (1966), have to be transferred to the Helicarionidae.

No autapomorphies of the Helicarionidae are known. This family is probably paraphyletic. Baker (1941) has subdivided the Helicarionidae in the Helicarioninae and the Sesarinae Thiele, 1931 according to the presence or absence of an epiphallal caecum. However, the epiphallal caecum has been reduced several times in the Helicarionidae. Moreover, Baker (1941) included several Chronidae in the Sesarinae. Therefore, the Sesarinae *sensu* Baker are polyphyletic.

At present the only subgroup of the Helicarionidae for which the monophyly can be substantiated is the Durgellinae Godwin-Austen, 1888 (inclusive Girasiinae Collinge, 1902). This subfamily is characterized by the reduced flagellum, large shell lobes (apparently secondarily reduced in *Sitala*) and perhaps a prominent papilla at the base of the penis. This papilla has been found in *Durgella*, *Cryptaustenia* and *Megaustenia* by Solem (1966), who called it penial stimulator; it is certainly not homologous with the true stimulator, which is also present in the mentioned genera. Unfortunately, the other genera of the Durgellinae and most genera of the other Helicarionidae have not been examined thoroughly enough to allow conclusions about the systematic distribution of this papilla. It is apparently lacking at least in *Epiglypta* (inner structures of the penis described by Baker, 1941), *Helicarion* (Kershaw, 1979), *Sarika* (Solem, 1966), *Sesara* (Solem, 1966), *Teraia* (Solem, 1966), *Westracystis* (Solem, 1981) and *Xesta* (Wiegmann, 1898).

The Durgellinae *sensu lato* can probably be subdivided into two monophyletic groups, the Durgellini and the Girasiini Collinge, 1902, although the limits of these groups are not as clear as suggested by earlier authors (e.g. Baker, 1941; Solem, 1966). The Girasiini have to be restricted to the genera *Girasa*, *Mariaella*, *Austenia* and probably some of the insufficiently known genera with strongly reduced shell. The Girasiini are characterized by the vitriniform shell (consisting of less than two whorls) and the peculiar form of the spermatophore. The spermatophore consists of a broad fusiform proximal part with a thin terminal process and a tube-like distal part. There are large, ramified

appendages at the distal base of the fusiform part and near the distal end of the tube-like part (Blanford & Godwin-Austen, 1908).

The Durgellini are characterized by the basally swollen duct of the bursa copulatrix. In the Durgellini there is a tendency towards shell reduction. But in the ancestral state of the Durgellini the shell had at least five whorls. *Megaustenia* and *Pseudaustenia*, which were included in the Girasiinae by Solem (1966), are probably the earliest branches of the Durgellini. All other genera of the Durgellini are characterized by a shortening of the epiphallus section proximal of the penial retractor. Among these other genera there is a large monophyletic group, which is characterized by a distinct lengthening of the tail (the cephalopodium posterior of the visceral hump). For example, the following genera belong to this group: *Bekkochlamys*, *Eurychlamys*, *Satiella*, *Cryptaustenia* and *Durgella*. The exact relationships of the genera of the Durgellinae are difficult to determine, because most potential synapomorphies are reductions (e.g. of shell, flagellum, caecum, stimulator) which obviously happened convergently several times.

The genus *Papuarion* was originally included in the Durgellinae by Van Mol (1973). According to Van Mol's (1973: fig. 5c) figure of the penial complex there is a rudiment of a penial appendix in the type species, *Papuarion novaguineae* (C. Boettger), which is, however, not mentioned in the text. If there actually is a penial appendix in this species, *Papuarion* has to be transferred to the Euconulidae. Perhaps it is closely related to *Sabalimax* Tillier & Bouchet, 1988, with which it shares the reduced shell and the bicuspid radular marginals.

#### Ariophantidae + Urocyclidae

*Autapomorphies*. 12(1).

#### Ariophantidae Godwin-Austen, 1888

*Autapomorphies*. 14(1).

*Remarks*. The Ariophantidae are only characterized by the absence of fibres of the penial nerve running through the cerebral ganglion. Because this character state evolved several times in the Limacoidea, additional autapomorphies are needed to corroborate the monophyly of the Ariophantidae.

There is probably a sister-group relationship between the Macrochlamydiae and the Ariophantinae + Ostracolethinae.

Macrochlamydiae Godwin-Austen, 1888. Autapomorphy: penis retractor inserts laterally on the epiphallic caecum. The coiled caecum could be an additional autapomorphy of this subfamily. However, the caecum is not coiled in some species. It is unclear whether it is secondarily uncoiled in these species or whether some of these species belong to the stem group of the Macrochlamydiae.

Ariophantinae + Ostracolethinae. Autapomorphies: flagellum and bursa copulatrix very short. At first sight the two characters seem to be correlated. One could suppose that in a short flagellum a short spermatophore is produced, which is taken up in the short bursa copulatrix. However, the spermatophore is at least partly formed in the epiphallus and there are Ariophantinae (Dasen, 1933) as well as Ostracolethinae (Collinge, 1902; Hoffmann, 1940) with long spermatophores, which are too large for their short bursas.

Ariophantinae Godwin-Austen, 1888. Autapomorphy: sole furrows indistinct.

Ostracolethinae Simroth, 1901. Autapomorphies: (semi-)slugs; shell vitriniform; stimulator with calcareous dart; penis retractor inserts directly at the epiphallus. *Ostracolethe* differs from the Parmarioninae *sensu auct.* in the absence of a stimulator and the rather distinct duct of the bursa copulatrix, but shares the autapomorphies of the Parmarioninae. The insertion of the penial retractor at the epiphallus distally to the caecum especially demonstrates that *Ostracolethe* is related to the Parmarioninae *sensu auct.* and not to the Durgellinae (Helicarionidae) as assumed by Thiele (1931) and Baker (1941). The geographical distribution of *Ostracolethe*, Tonkin, supports this conclusion, because it lies inside the range of the Parmarioninae but outside of the range of the Durgellinae. The loss of the stimulator is doubtlessly an autapomorphy of *Ostracolethe*. The distinct duct of the bursa copulatrix is apparently a reversal to the ancestral character state of the Ariophantidae, and therefore also an autapomorphy of *Ostracolethe*. The names *Ostracolethe* Simroth and *Myotesta* Collinge were both published on the 30.12.1901. Although Collinge (1902) and Simroth (1902, 1904) considered the identity of *Myotesta* and *Ostracolethe*, neither one has unambiguously synonymized the two names. As first reviser Hoffmann (1924) has determined the relative precedence of *Ostracolethe* Simroth, 1901 (Art. 24 ICZN). Unfortunately, Ostracolethidae Simroth, 1901 has priority over Parmarioninae Godwin-Austen in Blanford & Godwin-Austen, 1908.

## Urocyclidae Simroth, 1889

*Autapomorphies.* 3(1).

*Remarks.* The Urocyclidae are usually divided into the Trochonanininae Connolly, 1912 (or Trochozonitinae Iredale, 1914) and the Urocyclinae Simroth, 1889 (Baker, 1941). The Trochonanininae are probably paraphyletic, whereas the Urocyclinae, which are characterized by the incorporation of the visceral mass into the foot and the reduction of the shell (which has less than two whorls), are probably monophyletic. *Trochozonites* Pfeffer, 1883 is probably the sister-group of the remaining Urocyclidae, which are characterized by the shift of the penis retractor from the epiphallic caecum to the epiphallus. Some additional points concerning the phylogeny of the Urocyclidae will be discussed elsewhere.

## Limacoidea Lamarck, 1801

*Autapomorphies.* 15(1); 17(1); 21(2).

*Remarks.* The Limacoidea *sensu stricto* comprise only semislugs and slugs. They are a lineage which is evolving in more humid biotops. Whether there is a functional connection between their ecology and their most important autapomorphies, namely the reduction of the spermatophore and the epiphallus, is not clear (see character analysis).

The relationships of the Vitrinidae and the limacid slugs were already understood by Hesse (1926). Therefore, it is difficult to understand why almost all later authors have connected the Vitrinidae with other groups, e.g. the Zonitoidea (Baker, 1941; Solem, 1978; Boss, 1982; Nordsieck, 1986), the Helicarionoidea (Schileyko, 1979) or the Haplotrematidae (Tillier, 1989).

## Vitrinidae Fitzinger, 1833

*Autapomorphies.* 11(0); 13(1); 14(1); 30(1); 32(0); penial gland.

*Remarks.* The vitriniform shell (30(1)) and the shell lobes (32(0)) are in reality synapomorphies of the Vitrinidae and the following slug families. Schileyko (1986) divided the Vitrinidae into three subfamilies, the Vitrininae Fitzinger, 1833, the Semilimacinae Schileyko, 1986 and the Phenacolimacinae Schileyko, 1986. This system cannot be accepted, because the Vitrininae are polyphyletic, the Semilimacinae are paraphyletic and only the Phenacolimacinae (= Plutoniinae Cockerell, 1893) are monophyletic (unpublished results). The

phylogeny of the Vitrinidae will be discussed in a separate paper (in prep.).

Boettgerillidae + Limacidae +  
Agriolimacidae

*Autapomorphies.* 1(1); 30(2).

*Remarks.* The monophyly and the relationships of the families of this group have already been demonstrated by Likharev & Wiktor (1980).

## Boettgerillidae Van Goethem, 1972

*Autapomorphies.* 34(1); corpus fusiformis (differentiation of the vas deferens); groove on the right side of the mantle.

## Limacidae + Agriolimacidae

*Autapomorphies.* 13(1); 22(1).

## Limacidae Lamarck, 1801

*Autapomorphies.* Left lobe of the digestive gland at the end of the tail; large body (longer than 45 mm).

*Remarks.* There is a sister-group relationship between the Eumilacinae Likharev & Wiktor, 1980 and the Limacinae Lamarck, 1801. The Eumilacinae are characterized by the antemedian pneumostome, whereas the Limacinae are characterized by a third intestinal loop. This autapomorphy of the Limacinae is also present in *Bielzia*. The separation of this particular genus from the Limacinae as a monotypic subfamily is not justified from a cladistic point of view. A more detailed analysis of the phylogeny of the Limacidae is in preparation.

## Agriolimacidae H. Wagner, 1935

*Autapomorphies.* Mantle covering more than one-third of the body; pneumostome surrounded by well-delimited round plate; central field of the sole with v-shaped grooves.

*Remarks.* There is a sister-group relationship between *Mesolimax* and the remaining Agriolimacidae. The differences between these groups are large enough to justify the separation of a subfamily Mesolimacinae *n. subfam.* The monotypic Mesolimacinae are characterized by the presence of a penial tunica, diagonal grooves on the side fields of the sole and the course of the intestine, which passes between the cephalic retractor muscle (Wiktor & Likharev, 1980). The Agriolimacinae are characterized by a

large lobe of the kidney and the position of the shell, which extends anteriorwards beyond the kidney area (Wiktor & Likharev, 1980).

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