

# Phylogeny and biogeography of the Vitrinidae (Gastropoda: Stylommatophora)

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The phylogeny of the Vitrinidae is reconstructed in a cladistic analysis based on characters of the genitalia, the copulation behaviour and the radula. The genera with an atrial stimulator turned out to be the earliest branches of the Vitrinidae, whereas the genera with a glandula amatoria form a monophyletic, taxonomically apomorphic group. The differences between the proposed phylogeny and previous hypotheses are discussed. The ancestral areas of the Vitrinidae and its sister group, the limacoid slugs Boettgerillidae–Limacidae–Agriolimacidae, are estimated using weighted ancestral area analysis. The Vitrinidae and the limacoid slugs might have originated by a vicariance event between Central Europe and the Near East. © 2002 The Linnean Society of London. *Zoological Journal of the Linnean Society*, 2002, 134, 347–358.

ADDITIONAL KEY WORDS: – cladistic analysis – ancestral area

## INTRODUCTION

The Vitrinidae Fitzinger, 1833 are mainly Palaearctic semislugs belonging to the Limacoidea (Gastropoda: Stylommatophora). They show unusual biogeographical and ecological patterns. There is one centre of diversity in alpine habitats in the European mountains. A second centre of diversity can be found on the Macaronesian Islands. Despite the warmer climate, a high diversity of vitrinids exists at lower altitudes on the Macaronesian Islands. In a first step towards a better understanding of these patterns it is necessary to examine how the various vitrinid groups are related and where they originated. Therefore, a phylogenetic analysis of the Vitrinidae and an analysis of their ancestral area of distribution are presented here.

The shell of the vitrinids is strongly reduced and is therefore not very useful for the systematics of the group. However, there is an accessory organ of the genital system, the so-called stimulator, which is very diverse within the Vitrinidae. It can be developed as an atrial appendage or it can be fused with the vagina

(and is then called the glandula amatoria). This diversity stimulated the early development of phylogenetic hypotheses.

Simroth (1886, 1889) considered the different stimulator types of the Vitrinidae to be homologous with stimulators of other Limacoidea *s. l.*, with the dart apparatus of the Helicoidea and even with glands of some opisthobranchs and platyhelminths. Based on this hypothesis, Simroth (1889) concluded that it is not the Vitrinidae with the simplest genitalia, namely *Vitrina*, but rather the Vitrinidae with an atrial stimulator, namely *Semilimax* and *Vitrinobrachium*, that are the most primitive Vitrinidae. According to Simroth (1889), the groups without a stimulator evolved from the groups with an atrial stimulator by the loss of the stimulator, whereas the groups with a glandula amatoria originated by a fusion of the atrial stimulator with the vagina.

Wiegmann (1886) rejected Simroth's hypothesis that the stimulator of the Vitrinidae is homologous with the dart sac of the Helicoidea. Instead, he assumed that the stimulator of the Vitrinidae evolved from the capsular (or perivaginal) gland of other Limacoidea. Based on this hypothesis, Wiegmann (1886) supposed that the Vitrinidae with a glandula amatoria, like

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*Phenacolimax*, are the most primitive Vitrinidae from which the other groups evolved.

H. Eckardt (1914) thought that the Vitrinidae without a stimulator are not derived from forms with a stimulator, concluding that the Vitrinidae are diphyletic.

Finally, Schileyko (1986) presented a narrative hypothesis of the phylogeny of the Vitrinidae which largely agrees with the ideas of Wiegmann (1886). He assumed that the glandula amatoria evolved from unspecialized glandular tissue around the vagina, like the capsular gland of many Limacoidea. According to Schileyko (1986), *Vitrina* is directly derived from the hypothetical stem-form, whereas the groups with an atrial stimulator are derived from groups with a glandula amatoria.

The different hypotheses about the phylogeny of the Vitrinidae depend especially on the homology of the stimulator. In an analysis of the phylogeny of the Limacoidea s. l., Hausdorf (1998a) has shown that the stimulator of the Vitrinidae and of other Limacoidea s. l. is indeed homologous with the dart apparatus of the Helicoidea. The capsular gland is not homologous with the stimulator, because there are many Limacoidea s. l. which possess a stimulator as well as a capsular gland.

The phylogenetic relationships of the Vitrinidae within the Limacoidea s. l. were discussed by Hausdorf (1998a).

The aim of the present investigation is to compile the available data about phylogenetically informative characters of the Vitrinidae and to reconstruct the phylogeny of the Vitrinidae in a cladistic analysis. Furthermore, the ancestral areas of the Vitrinidae and their sister group are analysed based on the cladograms.

## MATERIAL AND METHODS

The phylogenetic analysis of the Vitrinidae is based on my own investigations and an evaluation of the relevant literature (Appendix). The informative characters are compiled in Table 1. In this character matrix all character states found in a taxon are listed.

The groups that are usually ranked as genera (e.g. by Schileyko, 1986) are used as operational taxonomic units.

*Gallandia* Bourguignat, 1880 is a junior synonym of *Oligolimax* P. Fischer (in Paulucci), 1878 (Manganelli *et al.*, 1995; F. Giusti, pers. comm.). In contrast to the opinion of Schileyko (1986), *Oligolimax* is separated from *Phenacolimax* and *Trochovitrina* is considered as a synonym of *Oligolimax* (Hausdorf, 1995).

Alonso *et al.* (2000) united the Macaronesian groups *Insulivitrina*, *Canarivitrina*, *Guerrina*, *Madeirovitrina* and *Plutonia* in one genus, which has to bear the name *Plutonia* Stabile, 1864, which has priority

over the other names. Simroth (1891) had already recognized that the Azorean slug *Plutonia atlantica* (Morelet) is a highly specialized descendent of the Macaronesian vitrinids. This hypothesis is corroborated by the discovery that in an Azorean *Insulivitrina* species *P. finitima* (Morelet, 1860) the penial retractor is vestigial, or more usually absent, as in *Plutonia atlantica* (Mordan & Martins, 2001). *Insulivitrina* is a paraphyletic group from which the other, more specialized Macaronesian groups are derived.

According to Hausdorf (1998a), the limacoid slugs Boettgerillidae–Limacidae–Agriolimacidae are the sister group of the Vitrinidae (Fig. 1). In this group the stimulator is secondarily missing. Therefore, this group is not suitable as an outgroup. The sister group of the Limacoidea s. s. (the Vitrinidae and the limacoid slugs) are Zonitidae–Helicarionoidea. There are groups with well-developed stimulators in the Zonitidae as well as in the Helicarionoidea. Therefore, *Troglagopsis* (Zonitidae) (Riedel & Radja, 1983) and *Cryptozona* (Ariophantidae, Helicarionoidea) (Blanford & Godwin-Austen, 1908; Dasen, 1933) are used as outgroups.

For the cladistic analysis of the character matrix the program PAUP 3.1.1. (Swofford, 1993) has been used.

The distribution data were compiled from the following papers: Alonso *et al.* (1987), Alonso *et al.* (2000), Altonaga *et al.* (1994), Alzona (1971), Baker (1941), Forcart (1978), Groh (1983), Groh & Hemmen (1986), Grossu (1983), Hausdorf (1995), Ibáñez *et al.* (1987), Jaekel *et al.* (1958), Kerney *et al.* (1983), Manganelli *et al.* (1995), Morales *et al.* (1988), Mordan & Martins (2001), Neubert (1998), Pilsbry (1946), Rähle (1980), Schileyko (1986), Valido *et al.* (1990), Valido *et al.* (1993), Wiktor & Backeljau (1995).

## CHARACTERS

The characters of the genitalia are shown in Figure 2. The numbering refers to Table 1 and the cladogram (Fig. 3).

**1** The so-called stimulator, which is apparently an adaptation to reciprocal copulation, is one of the most important characters for the systematics of the Stylommatophora (Hausdorf 1998a). The glandula amatoria is considered to be homologous to the stimulator. A stimulator is present in most vitrinids except *Vitrina*, *Calidivitrina* and some species of *Plutonia*, namely *P. media* (Lowe, 1854) (see Appendix) and *P. brevispira* (Morelet, 1860) (Mordan & Martins, 2001).

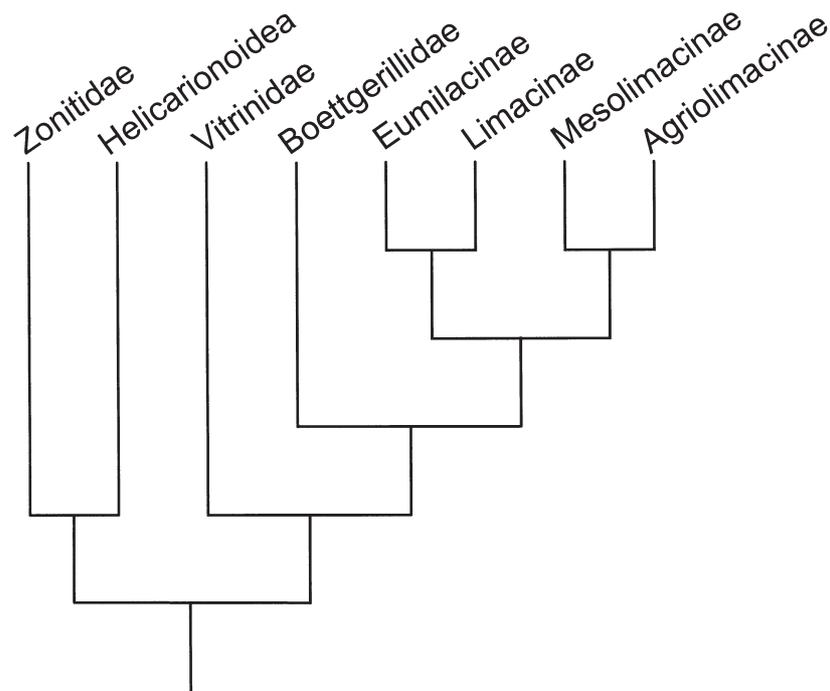
**2** In the outgroups, *Semilimax* and *Vitrinobrachium*, the stimulator inserts at the atrium. The stimulator of *Semilimacella cephalonica* (Rähle) is basally fused with the vagina (Rähle, 1980). In *Semilimacella carniolica* (O. Boettger) the stimulator apparently

**Table 1.** Character matrix used for the phylogenetic analysis. **1** Stimulator: 0 = present; 1 = missing. **2** Stimulator: 0 = inserts laterally at the atrium or the vagina; 1 = completely fused with the vagina (glandula amatoria); ? = not applicable because stimulator is missing (see character 1). **3** External gland of the stimulator: 0 = present; 1 = missing; ? = not applicable because stimulator is missing (see character 1). **4** External gland of the stimulator: 0 = distinctly longer than wide; 1 = about as long as or shorter than wide; ? = not applicable because stimulator or its gland is missing (see characters 1 and 3). **5** External gland of the stimulator: 0 = uniform sheath around the proximal stimulator section; 1 = divided into lobes; ? = not applicable because stimulator or its gland is missing (see characters 1 and 3). **6** Copulation behaviour: 0 = the stimulator does not fix the copulation partner; 1 = the stimulator is used to fix the partner; ? = unknown or not applicable because stimulator is missing (see character 1). **7** Copulation behaviour: 0 = the penis is inserted into the vagina or the bursa copulatrix of the partner; 1 = the penis is not inserted into the vagina or the bursa copulatrix of the partner. **8** Penial tunica: 0 = present; 1 = missing. **9** Penial tunica: 0 = covers especially the distal section of the penis; 1 = shifted towards the proximal section of the penis; ? = not applicable because penial tunica is missing (see character 8). **10** Main pilaster in penis: 0 = without a short, lamellated section or distal section divided; 1 = with a short, lamellated section distal of the glandular section and an undivided distal section; ? = not applicable because penial pilaster is missing. **11** Penial gland: 0 = missing; 1 = present. **12** Right ommatophoral retractor muscle: 0 = does not pass between the penis and the female genitalia; the right ommatophoral retractor muscle can be moved to the left without affecting the penis; 1 = passes between the penis and the female genitalia; the right ommatophoral retractor muscle cannot be moved to the left without affecting the penis. **13** Right ommatophoral retractor muscle: 0 = runs left of or below the penis retractor muscle; the right ommatophoral retractor muscle can be moved to the left without affecting the penis retractor muscle; 1 = runs right of or above the penis retractor muscle; the right ommatophoral retractor muscle cannot be moved to the left without affecting the penis retractor muscle. **14** Insertion site of the penial retractor muscle: 0 = at the diaphragma; 1 = at the columellar muscle. **15** Insertion of the vas deferens at the penis: 0 = terminally; 1 = subterminally or laterally; ? = not applicable because vas deferens does not insert at the penis. **16** Insertion site of the bursa copulatrix: 0 = vagina or atrium; 1 = penis. **17** Radular marginals: 0 = without ectocone or with one ectocone; 1 = with several ectocones

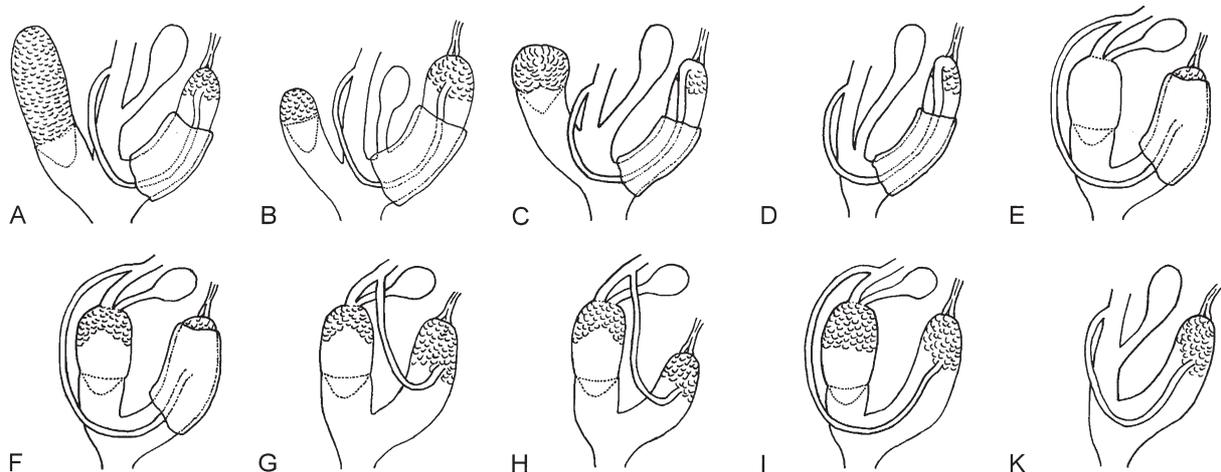
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Troglægopis</i>	0	0	0	0	0	?	?	0	0	?	0	0	0	0	?	0	0
<i>Cryptozona</i>	0	0	0	0	0	0	0	0	0	?	0	1	1	0	?	0	0
<i>Semilimax</i>	0	0	0	0	0	1	0	0	0	0	1	0/1	1	0	1	0	0
<i>Vitrinobrachium</i>	0	0	0	1	0	1	1	0	0	0	1	0	1	1	1	1	0
<i>Semilimacella</i>	0	0	0	1	1	?	?	0	0	0	1	0	0	0	0	0	1
<i>Vitrina</i>	1	0	?	?	?	?	0	0	0	0	1	0	0	0	0	0	1
<i>Eucobresia</i>	0	1	1	?	?	0	0	0	1	0	1	1	1	0	1	0	0
<i>Phenacolimax</i>	0	1	0	1	1	0	1	0	1	0	1	1	1	0	1	0	0
<i>Plutonia</i>	0/1	1	0/1	1	0/1	?	1	1	?	0/1	1	0	1	0	1	0	0/1
<i>Oligolimax</i>	0	1	0/1	1	1	?	?	1	?	0	1	0	0	0	1	0	0/1
<i>Arabivitrina</i>	0	1	0	1	0	?	?	1	?	1	1	1	1	0	1	0	0
<i>Calidivitrina</i>	1	?	?	?	?	?	?	1	?	1	1	0/1	1	0	1	0	0

inserts at the vagina (Mildner, 1982) and in *Semilimacella bonelli* (Targioni Tozzetti) it inserts at the atrium (Forcart, 1960; re-examined). *Semilimacella carniolica* and *Semilimacella bonelli* are probably sister species. Both species are characterized by duplicated stimulator papillae. In *Semilimacella cephalonica* the gland of the stimulator is bilobed, but there is only a single stimulator papilla. It is assumed that the stimulator of *Semilimacella cephalonica* represents the plesiomorphic state in *Semilimacella*. The situation in *Semilimacella carniolica* can easily be derived from that state by a further fusion of the distal sections of vagina and stimulator. If this is true, the atrial insertion of the stimulator of *Semilimacella bonelli* must be due to a shortening of the fused section and is therefore a secondarily derived state. On the

basis of this interpretation, the stimulator of *Semilimacella* might represent an intermediate state between the atrial stimulator and the glandula amatoria, where the stimulator is completely fused with the vagina. In *Vitrina* there is a vestige of a stimulator at the atrium of juvenile specimens (Umiński, 1968). However, it cannot be excluded that this is a rudiment of a stimulator which was basally fused with the vagina, because the vagina is missing in *Vitrina*. In *Eucobresia*, *Phenacolimax*, *Plutonia*, *Oligolimax* and *Arabivitrina* the stimulator is completely fused with the vagina and forms the glandula amatoria. **3** *Eucobresia* and some *Plutonia* and *Oligolimax* species have no external stimulator gland. **4** The external gland of the stimulator is distinctly longer than it is wide in the outgroups and in *Semili-*



**Figure 1.** Outgroup relationships of the Vitrinidae (Hausdorf 1998a).



**Figure 2.** Schemes of the distal genitalia (based on the species and references listed in Appendix): A, *Semilimax*; B, *Vitrinobrachium*; C, *Semilimacella*; D, *Vitrina*; E, *Eucobresia*; F, *Phenacolimax*; G, *Plutonia*; H, *Oligolimax*; I, *Arabivitrina*; K, *Calidivitrina*.

*max*, whereas it is about as long as or shorter than it is wide in the other vitrinids.

**5** The external gland of the stimulator forms a uniform sheath around the proximal stimulator section in the outgroups and in *Semilimax*, *Vitrinobrachium*, *Arabivitrina*, and some *Plutonia* species. In the other vitrinids, it is divided into lobes.

**6** In *Semilimax* and *Vitrinobrachium* the stimulator is used to fix the copulation partner (Künkel, 1933),

whereas the stimulator contacts the partner only temporarily during copulation in the other Stylomatophora for which the mating behaviour is known. **7** The penis is inserted into the vagina or the bursa copulatrix of the copulation partner in most Stylomatophora; however, it transfers the sperm on external parts of the everted genitalia in *Vitrinobrachium*, *Phenacolimax*, *Plutonia* and, probably, all other genera with a well-developed glandula amatoria.

**8** A penial tunica is present in the outgroups and in most genera of the Vitrinidae. It is missing in *Plutonia*, *Oligolimax*, *Arabivitrina* and *Calidivitrina*.

**9** The penial tunica usually covers most of the distal part of the penis, except in *Eucobresia* and *Phenacolimax*.

**10** There is at least one distinct pilaster in the penis of the vitrinids which is partly formed by the penial gland. In *Arabivitrina* and *Calidivitrina* the pilaster is partitioned into a proximal glandular section, a short median section with a distinctly lamellated structure (Neubert, 1998: figs 97 and 106), and an undifferentiated distal section. The penial pilaster of the two Azorean *Plutonia* species *P. pelagica* (Morelet, 1860) and *P. laxata* (Morelet, 1860) is also partitioned into a proximal glandular section and a median section with a distinctly lamellated structure (Mordan & Martins, 2001). However, in contrast to the pilaster of *Arabivitrina* and *Calidivitrina*, the distal section is divided into two branches. Nevertheless, it should be checked more thoroughly whether the lamellated median section of *Arabivitrina* and *Calidivitrina* might be homologous to that of the two Azorean *Plutonia* species.

**11** A more or less well-developed penial gland is present in all vitrinids, but is missing in the outgroups. The secretions of this gland are probably involved in sperm transfer and thus undertake some of the functions of the spermatophore, which is missing in the Vitrinidae.

**12** The right ommatophoral retractor muscle passes between the penis and the female genitalia in *Cryptozona*, *Eucobresia*, *Phenacolimax*, *Arabivitrina* and some *Semilimax* and *Calidivitrina* species.

**13** The right ommatophoral retractor muscle runs left of or below the penis retractor muscle in *Troglaeopis*, *Semilimacella*, *Vitrina* and *Oligolimax*, but it runs right of or above the penis retractor muscle in all other vitrinids.

**14** The penial retractor inserts at the diaphragma in the outgroups and in most groups of the Vitrinidae. It inserts at the columellar muscle only in *Vitrinobranchium*.

**15** The vas deferens enters the penis terminally in *Semilimacella*, *Vitrina*, and *Plutonia finitima* (Morelet, 1860), whereas it inserts at the penis subterminally or laterally in all other groups of the Vitrinidae.

**16** The bursa copulatrix inserts at the vagina or at the atrium in the outgroups and in all groups of the Vitrinidae except in *Vitrinobranchium* in which it inserts at the penis.

**17** The radular marginals are unicuspid or have at most one ectoconus in the outgroups and in most Vitrinidae. They are multicuspid in *Vitrina*, *Semilimacella* and in a few species of *Plutonia* and *Oligolimax*.

## PHYLOGENY

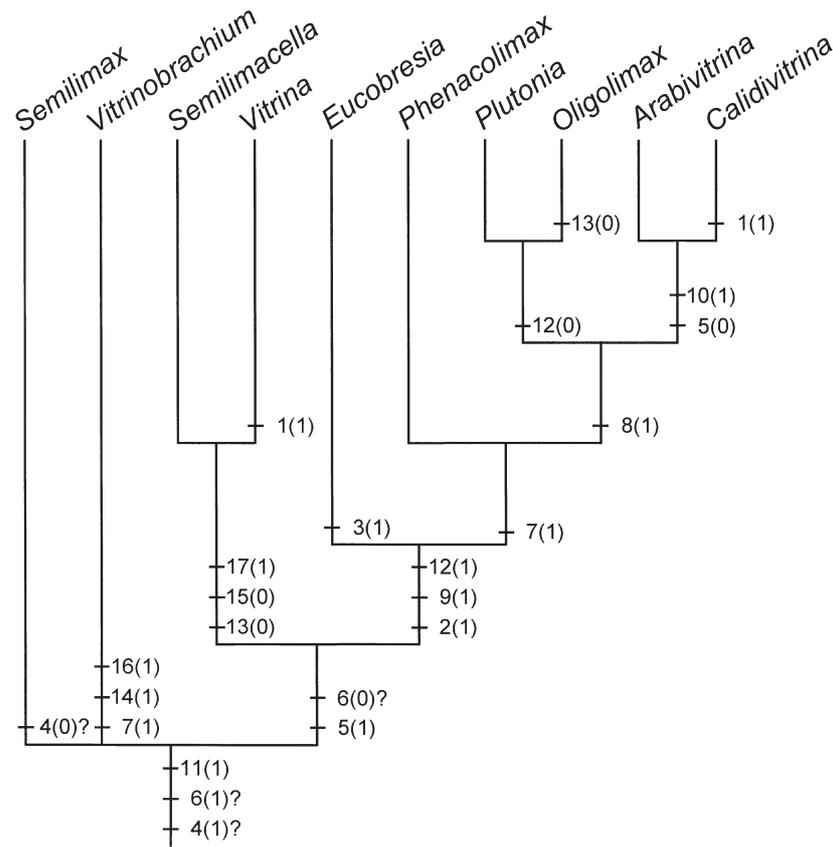
Two equally and maximally parsimonious trees (length 25 steps, consistency index excluding uninformative characters = 0.636) have been found in a branch-and-bound search with the program PAUP and the character matrix (Table 1). The two trees differ only in the relationships of *Semilimax* and *Vitrinobranchium*. A consensus tree of the two trees is shown in Figure 3.

The unresolved trichotomy is due to two conflicting characters, the function of the stimulator vs. the length of the stimulator gland. Among the Stylommatophora for which the mating behaviour has been studied, *Semilimax* and *Vitrinobranchium* are the only ones which use the stimulator to fix the copulation partner (Künkel, 1933). In the other Stylommatophora the stimulator contacts the mating partner only temporarily during copulation. Therefore the use of the stimulator to fix the mating partner might be a synapomorphy of *Semilimax* and *Vitrinobranchium*. Unfortunately, the mating behaviour of *Troglaeopis* (Zonitidae) (the stimulator of which resembles that of *Semilimax*) as well as the mating behaviour of several other vitrinids, e.g. *Semilimacella*, is unknown. Therefore, it cannot be excluded that the unusual function of the stimulator is an autapomorphy of the Vitrinidae or originated even earlier.

If this insufficiently known character is excluded from the cladistic analysis only a single most-parsimonious tree is found, in which *Semilimax* is the sister group of the remaining vitrinids, as in one of the two maximally parsimonious trees based on all characters. The clade including all vitrinids except *Semilimax* is supported by the shortening of the stimulator gland.

The result of the present cladistic analysis differs fundamentally from the hypothetical scheme proposed by Schileyko (1986). The differences are primarily due to the assumption of Schileyko (1986) that the glandula amatoria is the plesiomorphic character state of the stimulator. This assumption is based on the supposed homology of the stimulator of the Vitrinidae with the capsular gland of other Limacoidea s. l. However, Hausdorf (1998a) has shown that the capsular gland is not homologous with the stimulator. An outgroup comparison with the stimulator of the Zonitidae or the Helicarionoidea demonstrates that the atrial stimulator represents the plesiomorphic character state and that the glandula amatoria is apomorphic.

Moreover, Schileyko (1986) ignored the findings of Umiński (1968), who discovered a rudiment of an atrial stimulator in *Vitrina*. Therefore, Schileyko (1986) derived *Vitrina* directly from his hypothetical stem form, which has only a capsular gland but no



**Figure 3.** Consensus tree of the two equally and maximally parsimonious trees (25 steps, consistency index excluding uninformative characters = 0.636). The numbering of the apomorphies, which are taken from the list of apomorphies of PAUP (see methods), refers to the character matrix (Table 1) and the discussion of the characters.

stimulator. Actually, the stem species of the Vitrinidae did not have a capsular gland, because this organ is missing in all vitrinids as well as in their sister group, the Boettgerillidae–Limacidae–Agriolimacidae. Schileyko (1986) overlooked the fact that *Vitrina* only differs from *Semilimacella* in that the atrial stimulator is reduced.

Finally, Schileyko (1986) did not realize the homology of the vaginal papilla of *Eucobresia* with the papilla of the glandula amatoria. This homology is corroborated by the fact that there is a well-developed muscular section of the stimulator in *Eucobresia glacialis* (Forbes), which has to be included into *Eucobresia* (see Appendix). Moreover, the relationship of *Eucobresia* to *Phenacolimax* and the other groups with a glandula amatoria is corroborated by the development of the penial tunica, which surrounds only the proximal section of the penis in *Eucobresia* and *Phenacolimax*, whereas it also surrounds parts of the distal section in all groups with an atrial stimulator.

The subdivision of the Vitrinidae proposed by Schileyko (1986) cannot be maintained. The Vitrininae Fitzinger, 1833 *sensu* Schileyko include the groups in which the stimulator has been lost, namely *Vitrina* and *Calidivitrina*, and are polyphyletic. The Semilimacinae Schileyko, 1986 include the groups with an atrial stimulator, *Semilimacella*, *Semilimax* and *Vitrinobrachium*, as well as *Eucobresia* and are paraphyletic. Only the Phenacolimacinae Schileyko, 1986; which are characterized by the glandula amatoria are monophyletic. However, Plutoniinae Cockerell, 1893 is an older name for this group. Because of the low number of genera, a formal division of the Vitrinidae into subfamilies is not necessary.

## BIOGEOGRAPHY

The distribution of the genera of the Vitrinidae is summarized in Table 2 and Figure 4. The range of the Vitrinidae largely overlaps with the range of its sister group, the limacoid slugs Boettgerillidae–

Limacidae–Agriolimacidae. If one assumes that the ancestors of the two sister groups originated by allopatric speciation, their original ranges were smaller than those of the two sister groups are today. For the estimation of the ancestral area of the Vitrinidae and of the limacoid slugs a weighted ancestral area analysis (Hausdorf, 1998b) has been applied.

The PI values of the Vitrinidae (Table 2), which indicate the relative probability that an individual area was part of the ancestral area, are maximal for the Alps followed by West and Central Europe. The PI value of the Vitrinidae for the Near East (including the Caucasus region) is distinctly lower.

The PI values of the limacoid slugs Boettgerillidae–Limacidae–Agriolimacidae (Table 3) are maximal for the Near East, because the positionally plesiomorphic lineages, namely the Boettgerillidae, Eumilacinae and Mesolimacinae are restricted to that area. Therefore, this region is probably the ancestral area of the Boettgerillidae–Limacidae–Agriolimacidae. Consequently, the Vitrinidae and the Boettgerillidae–Limacidae–Agriolimacidae might have originated by a vicariance event between Central Europe and the Near East.

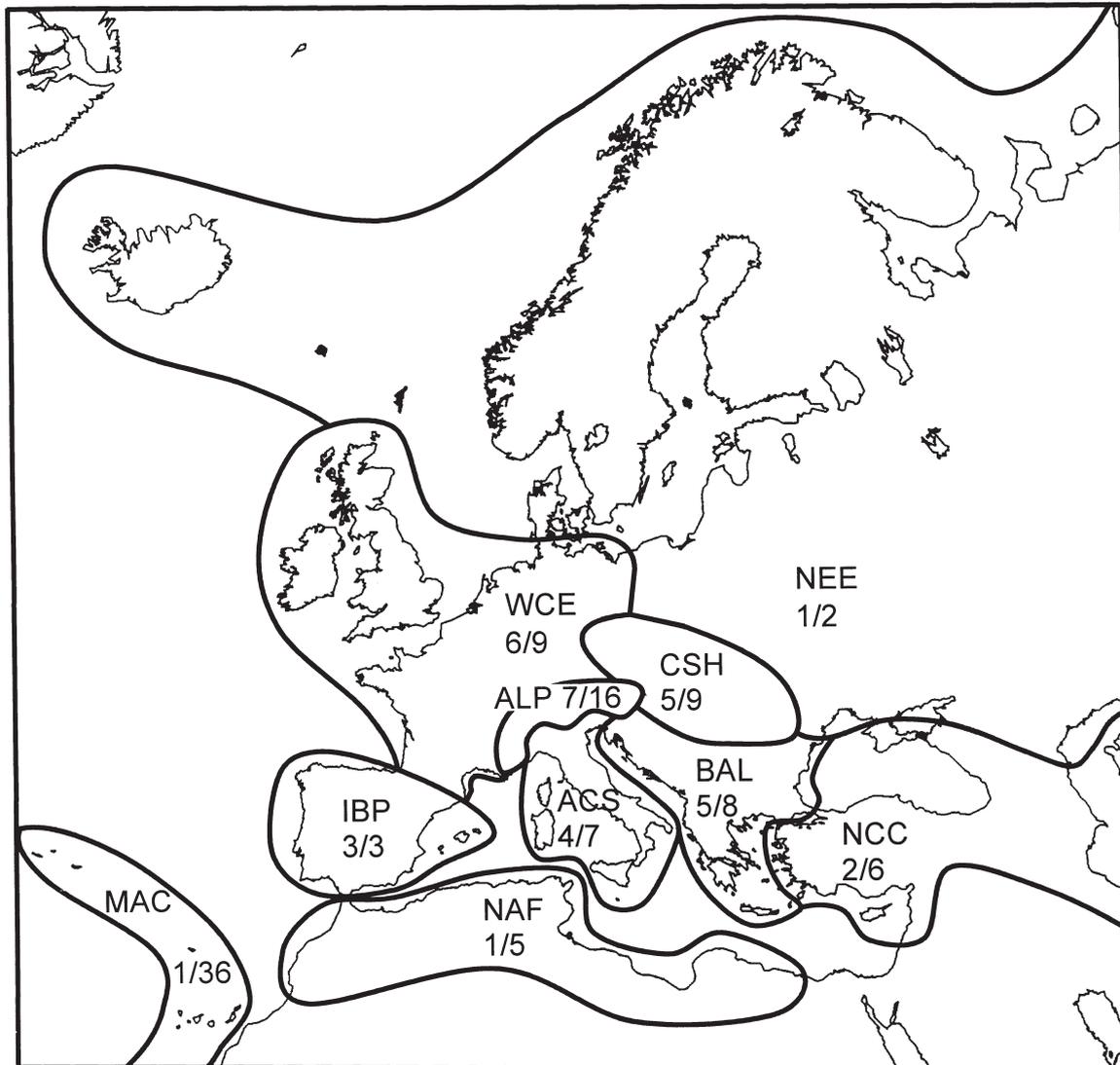
Some lineages of the Vitrinidae spread from the European mainland. *Vitrina* dispersed into Asia and

**Table 2.** Number of vitrinid species present in the following regions: WCE = West and Central Europe (west of 15°E, including Pyrenees); IBP = Iberian Peninsula; ALP = Alps; ACS = Appenine Peninsula, Corsica and Sardinia; CSH = Carpathes, Sudetes, Czech Republic, Slovakia and Hungarian Lowland; BAL = Balkan Peninsula; NEE = Northern and Eastern Europe; NAS = Northern Asia; NCC = Near East, Caucasus region and the Crimea; CAS = Central Asia; ARA = Arabia; MAC = Macaronesian Islands; NAF = North Africa; EAF = East Africa; NAM = North America including Greenland; HAW = Hawaii (see also Fig. 4). Estimation of the ancestral area of the Vitrinidae is based on Figure 3 using weighted ancestral area analysis (Hausdorf, 1998b). GSW = weighted gain step values; LSW = weighted loss step values; PI = GSW/LSW quotients

	WCE	IBP	ALP	ACS	CSH	BAL	NEE	NAS	NCC	CAS	ARA	MAC	NAF	EAF	NAM	HAW
<i>Semilimax</i>	3	1	3	0	4	2	0	0	0	0	0	0	0	0	0	0
<i>Vitrinobrachium</i>	1	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0
<i>Semilimacella</i>	0	0	1	1	1	3	0	0	0	0	0	0	0	0	0	0
<i>Vitrina</i>	1	1	1	1	1	1	2	2	1	2	0	0	0	0	2	1
<i>Eucobresia</i>	3	0	4	0	2	1	0	0	0	0	0	0	0	0	0	0
<i>Phenacolimax</i>	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Plutonia</i>	0	0	0	0	0	0	0	0	0	0	0	35	0	0	0	0
<i>Oligolimax</i>	1	1	1	3	1	1	0	0	3	1	0	0	1	0	0	0
<i>Arabivitrina</i>	0	0	0	0	0	0	0	0	0	0	2	0	0	5	0	0
<i>Calidivitrina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0
systematic position unknown	0	0	0	0	1	0	0	0	2	0	1	1	4	?	0	0
GSW	3.17	1.50	3.17	1.67	2.17	2.17	0.33	0.33	0.50	0.50	0.17	0.17	0.17	0.20	0.33	0.33
LSW	0.58	2.00	0.25	1.50	1.33	1.33	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
PI	5.43	0.75	12.17	1.11	1.67	1.67	0.11	0.11	0.17	0.17	0.06	0.06	0.06	0.07	0.11	0.11

**Table 3.** Distribution of the Boettgerillidae, Eumilacinae, Limacinae, Mesolimacinae and Agriolimacinae (0 = absent; 1 = present) and weighted ancestral area analysis of the Boettgerillidae–Limacidae–Agriolimacidae based on Figure 1. Abbreviations as in Table 2

	WCE	IBP	ALP	ACS	CSH	BAL	NEE	NAS	NCC	CAS	ARA	MAC	NAF	EAF	NAM	HAW
Boettgerillidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Eumilacinae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Limacinae	1	1	1	1	1	1	1	0	1	1	0	0	1	0	0	0
Mesolimacinae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Agriolimacinae	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	0
GSW	0.67	0.67	0.67	0.67	0.67	0.67	0.67	0.33	2.00	0.67	0.00	0.00	0.67	0.33	0.33	0.00
LSW	1.67	1.67	1.67	1.67	1.67	1.67	1.67	2.00	0.00	1.67	2.00	2.00	1.67	2.00	2.00	2.00
PI	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.17	∞	0.40	0.00	0.00	0.40	0.17	0.17	0.00



**Figure 4.** Number of vitrinid genera (first number) and species (second number) present in the following regions (see also Table 2): ACS = Appenine Peninsula, Corsica and Sardinia; ALP = Alps; BAL = Balkan Peninsula; CSH = Carpathes, Sudetes, Czech Republic, Slovakia and Hungarian Lowland; IBP = Iberian Peninsula; MAC = Macaronesian Islands; NAF = North Africa; NCC = Near East, Caucasus region and the Crimea; NEE = Northern and Eastern Europe; WCE = West and Central Europe (west of 15°E, including Pyrenees).

North America (and one species even reached Hawaii), *Oligolimax* also dispersed into Asia and North Africa, *Plutonia* colonized the Macaronesian Islands (Azores, Madeira, Canary Islands and Cap Verde) and *Arabi-vitrina* and *Calidivitrina* colonized Arabia and East Africa.

Concerning species number, the most important radiation of the Vitrinidae occurred on the Macaronesian Islands. There are more species on the Macaronesian Islands than on the European mainland. The apomorphic position of *Plutonia* in the cladogram of the Vitrinidae (Fig. 3) and the uniform bauplan of

the genitalia of the Macaronesian species indicate that this radiation is younger than the radiation on the European mainland. On the other hand, the Macaronesian radiation resulted in some of the most extreme forms concerning the body bauplan, namely the only vitrinid slug, *Plutonia* (*Plutonia*) *atlantica* (Morelet 1860), and *Plutonia* (*Guerrina*), which can entirely withdraw into their ribbed and keeled shells. The ecology of the Macaronesian vitrinids differs from that of the European vitrinids. Whereas the highest diversity of European vitrinids can be found above 1000 m altitude, the highest diversity of vitrinids is

below 500 m altitude on the Canary Islands. These biogeographical and ecological patterns are very unusual. The reasons for these patterns have been discussed elsewhere (Hausdorf, 2001).

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## APPENDIX

List of genera and anatomically known species of the Vitrinidae with main references for anatomical data. The type species of the genera are underlined.

Genera	Species
<i>Semilimacella</i> Soós, 1917	<i>carniolica</i> (O. Boettger) (?synonym <i>velebitica</i> Soós <sup>1</sup> ) (Mildner, 1982); <i>bonelli</i> (Targioni Tozzetti) (Forcart, 1960; re-examined); <i>cephalonica</i> (Rähle) (Rähle, 1980)
<i>Vitrina</i> Draparnaud, 1801	<i>angelicae</i> Beck (Forcart, 1955); <i>pellucida</i> (O. F. Müller) (Eckhardt, 1914; Schileyko, 1986; Umiński, 1968; re-examined); <i>rugulosa</i> Martens (Schileyko, 1986)
<i>Semilimax</i> Agassiz, 1845	(?) <i>apatelus</i> (Soós) (Soós, 1924); <i>carinthiacus</i> (Westerlund) (Forcart, 1956); <i>kotulae</i> (Westerlund) (Hesse, 1923; Schileyko, 1986; re-examined); <i>pyrenaicus</i> (A. Férussac) (Boycott, 1914); <i>semilimax</i> (J. Férussac) (Hesse, 1923; Künkel, 1933; Schileyko, 1986; re-examined)
<i>Vitrinobrachium</i> Künkel, 1929	<i>baccettii</i> Giusti & Mazzini (Giusti & Mazzini, 1971); <i>breve</i> (A. Férussac) (Hesse, 1923; Künkel, 1933; Schileyko, 1986; re-examined); <i>tridentinum</i> Forcart (Forcart, 1956)
<i>Eucobresia</i> Baker, 1929	<i>diaphana</i> (Draparnaud) (Gerhardt, 1936; Hesse, 1923; Schileyko, 1986; re-examined); <i>glacialis</i> (Forbes) (Forcart, 1944; re-examined <sup>2</sup> ); <i>nivalis</i> (Dumont & Mortillet) (Forcart, 1944; Schileyko, 1986); <i>pegorarii</i> (Pollonera) (Forcart, 1944)
<i>Phenacolimax</i> Stabile, 1859	<i>blanci</i> (Pollonera) (Boato <i>et al.</i> , 1982); <i>major</i> (A. Férussac) (Forcart, 1949; Hesse, 1923; Neubert, 1998; re-examined) <i>stabilei</i> (Lesson) (de Winter, 1990)
<i>Plutonia</i> Stabile, 1864	
<i>Canarivitrina</i> Valido & Alonso, 2000	<i>dianae</i> Valido & Alonso (Alonso <i>et al.</i> , 2000); <i>falcifera</i> Ibáñez & Groh (Alonso <i>et al.</i> , 2000); <i>mascaensis</i> (Morales) (Ibáñez <i>et al.</i> , 1987); <i>ripkeni</i> Alonso & Ibáñez (Alonso <i>et al.</i> , 2000); <i>taborientensis</i> Groh & Valido (Alonso <i>et al.</i> , 2000)
<i>Guerrina</i> Odhner, 1954	<i>christinae</i> (Groh) (Valido <i>et al.</i> , 1993); <i>cuticula</i> (Shuttleworth) (Ibáñez <i>et al.</i> , 1987; Odhner, 1954)
<i>Insulivitrina</i> Hesse, 1923	<i>angulosa</i> (Morelet) (Mordan & Martins, 2001); <i>blaueneri</i> (Shuttleworth) (Ibáñez <i>et al.</i> , 1987); <i>brevispira</i> (Morelet) (Mordan & Martins, 2001); <i>brumalis</i> (Morelet) (Mordan & Martins, 2001); <i>canariensis</i> (Mousson) (Alonso <i>et al.</i> , 1987); <i>eceroensis</i> (Alonso & Ibáñez) (Alonso <i>et al.</i> , 1987); <i>emersoni</i> (Morales) (Morales <i>et al.</i> , 1988); <i>fnitima</i> (Morelet) (Mordan & Martins, 2001); <i>gomerensis</i> (Alonso & Ibáñez) (Morales <i>et al.</i> , 1988; re-examined); <i>lamarckii</i> (A. Férussac) (Ibáñez <i>et al.</i> , 1987); <i>latebasis</i> (Mousson) (Alonso <i>et al.</i> , 1987); <i>laxata</i> (Morelet) (Mordan & Martins, 2001); <i>machadoi</i> (Ibáñez & Alonso) (Valido <i>et al.</i> , 1990); <i>nogalesi</i> (Alonso & Ibáñez) (Valido <i>et al.</i> , 1990); <i>oromii</i> (Ibáñez & Alonso) (Morales <i>et al.</i> , 1988); <i>parryi</i> (Gude) (Valido <i>et al.</i> , 1990); <i>pelagica</i> (Morelet) (Mordan & Martins, 2001); <i>reticulata</i> (Mousson) (Ibáñez <i>et al.</i> , 1987); <i>tamaranensis</i> (Valido) (Valido <i>et al.</i> , 1990); <i>tuberculata</i> (Ibáñez & Alonso) (Ibáñez <i>et al.</i> , 1987)
<i>Madeirovitrina</i> Groh & Hemmen, 1986	(?) <i>albopalliata</i> (Groh & Hemmen) (Groh & Hemmen, 1986); <i>behni</i> (Lowe) (Odhner, 1937); <i>marcida</i> (Gould) (Groh & Hemmen, 1986); (?) <i>media</i> (Lowe) (Groh & Hemmen, 1986 <sup>3</sup> ); <i>nitida</i> (Gould) (Groh & Hemmen, 1986); <i>ruivensis</i> (Gould) (Groh & Hemmen, 1986)
<i>Plutonia s. s.</i>	<i>atlantica</i> (Morelet) (Wiktor & Backeljau, 1995)
<i>Oligolimax</i> P. Fischer (in Paulucci), 1878	<i>annularis</i> (Studer) (Hausdorf, 1995; Schileyko, 1986; re-examined); <i>lederi</i> (O. Boettger) (Schileyko, 1986); <i>olympicus</i> (Hausdorf) (Hausdorf, 1995); <i>paulucciae</i> (P. Fischer) (Giusti, in prep.); <i>pollonerianus</i> (Fra Piero) (Giusti, in prep.); <i>sturanyi</i> (Forcart) (Forcart, 1959)
<i>Arabivitrina</i> Thiele, 1931	<i>abyssinica</i> (L. Pfeiffer) (Forcart, 1957); <i>arabica</i> (Thiele) (Hesse, 1923; Neubert, 1998; re-examined); <i>darnaudi</i> (L. Pfeiffer) (Forcart, 1957); <i>jamjamensis</i> (Kobelt) (Thiele, 1933); <i>neumanni</i> (Thiele) (Hubendick, 1954); <i>riepiana</i> (Jickeli) (Forcart, 1957); <i>jansseni</i> Neubert (Neubert, 1998)

## APPENDIX

Cont.

Genera	Species
<i>Calidivitrina</i> Pilsbry, 1919	<i>ericinella</i> (d'Ailly) (Hubendick, 1954; re-examined); <i>kiboschensis</i> (d'Ailly) (Hubendick, 1954); <i>lactea</i> (Connolly) (Hubendick, 1954); <i>nigrocincta</i> (Martens) (Hubendick, 1954; re-examined); <i>oleosa</i> (Martens) (Hubendick, 1954; Pilsbry, 1919); <i>tenuissima</i> (Thiele) (Hubendick, 1954); <i>variopunctata</i> (Connolly) (Hubendick, 1954); <i>virisplendens</i> (d'Ailly) (Hubendick, 1954)

<sup>1</sup>Forcart (1960) placed *Vitrina velebitica* Soós, 1917 in the synonymy of *Vitrina bonelli* Targioni Tozzetti, 1872. However, in *Vitrina velebitica* the two stimulator glands and their papillae are distinctly separated (Soós, 1924) just as in *Semilimacella carniolica* (O. Boettger, 1884) (Mildner, 1982), whereas they open into a common duct in *Semilimacella bonelli*. Therefore *Vitrina velebitica* might be a synonym of *Semilimacella carniolica*, but not of *Semilimacella bonelli*. This question has to be re-examined on the basis of topotypes.

<sup>2</sup>Forcart (1944) classified *Eucobresia glacialis* (Forbes, 1837) as *Insulivitrina* with which it shares the well-developed muscular section of the glandula amatoria. However, *Eucobresia glacialis* differs from the *Insulivitrina* species in the presence of a penial tunica and the course of the right ommatophoral retractor muscle, which passes between penis and vagina (contrary to the description of Forcart, 1944). It shares the lack of the external stimulator gland with *Eucobresia*. The well-developed muscular section of the glandula amatoria is only a symplesiomorphy, whereas the lack of the external stimulator gland is an autapomorphy of *Eucobresia*. Therefore, *Eucobresia glacialis* does not belong to *Insulivitrina*, but to *Eucobresia*. All other *Eucobresia* species differ from *Eucobresia glacialis* in the reduction of the muscular section of the glandula amatoria, but there is still a papilla in the vagina.

<sup>3</sup>Groh & Hemmen (1986) tentatively included *Plutonia media* (Lowe, 1854) in *Eucobresia*. However, *Plutonia media* differs from *Eucobresia* in the lack of a penial tunica and of a vaginal papilla. It probably evolved from *Plutonia* by the loss of the glandula amatoria.