

# Systematics of Ariantinae (Gastropoda, Pulmonata, Helicidae), a new approach to an old problem

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## Abstract

A new starting-point in Ariantinae systematics is presented by combining data on traditional shell morphology and genital anatomy, with phylogeny reconstructions based on DNA sequence data. For nearly all genera and subgenera one or more shells are depicted and drawings of the proximal part of the genital organs are shown to illustrate the morphological diversification within the subfamily. For as much as our material allowed it, partial sequences are presented for *Histone H3 (H3)*, *Cytochrome c oxidase subunit I (COI)*, *Cytochrome B (CytB)* and *16S ribosomal RNA (16S)*. Some of the allegedly speciose genera like *Chilostoma* and *Campylaea* (Zilch, 1960) do not represent monophyletic groups of species, whereas most of the remaining nominal taxa (e.g. *Causa*, *Dinarica*, *Josephinella*, *Faustina*, *Liburnica*, *Kosicia* and *Thiessea*) warrant a separate taxonomic status indeed. Sequence data from individual markers were informative at the species-level, but not for higher-level phylogenetics. Insight in genus-level relationships was obtained after concatenation of the individual datasets. The Ariantinae are estimated to have originated during the late Cretaceous (Campanian), not later than ca. 80 million years ago. The enigmatic and morphologically aberrant, monotypic genus *Cylindrus* is shown as the sister-group of *Arianta*, a genus including *A. arbustorum*, which is also unusual in shell-shape and habitat. *Ariantopsis* and *Wladislawia* are classified as subgenera of neither *Campylaea* nor *Chilostoma*, but *Cattania*. *Sabljaria* is considered a subgenus of *Dinarica*. The nominal genus *Superba* is shown to be paraphyletic; additional data should demonstrate whether *Superba* has to be synonymised with *Liburnica*. The Ariantinae are here divided in 21 genera (2 new) and 13 subgenera (3 new).

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## Introduction

The classification of the Ariantinae Mörch, 1864 (Gastropoda, Helicidae), a subfamily of terrestrial air-breathing snails, with a primary radiation in southern Europe, has been under debate for more than a century. Apart from a few exceptions such as *Cylindrus obtusus*, *Helicigona lapicida* and *Isognomostoma isognomostomos*, most species within this subfamily are conchologically close to a basic bauplan (see Appendix), with shells that are more or less depressed globular, with an open umbilicus and no apertural teeth. All species are characterized by a pair of accessory glands in the genital system, inserting between the dart sac (= bursa telae) and the bursa copulatrix. In the literature, these glands are often referred to as mucous glands, a term that should be preferentially used for glands in the snail's foot-sole, however. The accessory glands can either be undivided or more or less completely split and are always longer than the dart sac.

The conchological uniformity did not hamper the description of new species, and higher taxa, what made the delimitation of genera and subgenera increasingly subjective. In the literature, more than once, taxon status was changed from a generic to a subgeneric level, or the other way round, without proper argumentation. This led to the confusing situation of today, where

there is neither consensus on the identification and ranking of the taxa that should be accepted within the Ariantinae, nor about their mutual phylogenetic relationships.

Thus, the main issue regarding the systematics of this subfamily is not the delimitation of species, but the distinction between genera and subgenera. This is illustrated by the number of species-group taxa that have been described after Mörch (1864) erected the subfamily, and even more so by the number of genera used by different authors to classify the same species. *Ariantopsis pelia*, for example, has also been classified in *Arianta*, *Chilostoma*, *Faustina*, and *Helicigona*. In the taxonomic literature a variety of subdivisions of the Ariantinae has been proposed (*e.g.* Sturany and Wagner, 1914; Hesse, 1931; Knipper, 1939; Zilch, 1960; Subai, 1984, 1996; Bank *et al.*, 2001; Subai, 2002; Subai and Fehér, 2006; Schileyko, 2006, 2013), among which the enumeration by Zilch (Table 1) has been most frequently cited. The classification resulting from this study will be compared in some detail with only

the latter. This article is an extended version of a publication by Groenenberg *et al.* (2012), which was published only as a part of a doctoral thesis. In a recent article Cadahia *et al.* (2013) published similar data on the phylogeny of the Ariantinae, dealing with fewer taxa, however, and without discussing the implications for classification and nomenclature. Schileyko (2006, 2013) suggested classifications of the Ariantinae on the basis of morphological data. Initially (Schileyko, 2006) *Marmorana* Hartmann, 1844, with some generally accepted close relatives, and *Theba* Risso, 1826, were considered to belong to the Ariantinae. Later on, however (Schileyko, 2013), these genera were classified in other subfamilies, viz. Murellinae Hesse, 1918 and Thebinae Wenz, 1923. Interestingly, on the basis of a preliminary DNA analysis, using *COI* sequences in GenBank, *Marmorana*, *Murella*, and *Tyrrheniberus* showed up as Ariantinae indeed, whereas *Theba* has to be excluded as a genus of that subfamily. Thus, the status of the so-called Murellinae has to be studied in more detail.

Table 1. Selection of former classifications of the Ariantinae by different authors.

Sturany and Wagner (1914)		Zilch (1960)		Bank <i>et al.</i> (2001) 'Clecom'	
Genus	Subgenus	Genus	Subgenus	Genus	Subgenus
<i>Campylaea</i>	<i>Cattania</i> <i>Campylaea</i> <i>Dinarica</i> <i>Liburnica</i>	<i>Arianta</i> <i>Campylaea</i>	<i>Ariantopsis</i> <i>Campylaea</i> <i>Delphinatia</i> <i>Dinarica</i> <i>Faustina</i> (= <i>Cattania</i> ) <i>Liburnica</i> <i>Wladislawia</i>	<i>Arianta</i> <i>Causa</i> <i>Chilostoma</i>	<i>Ariantopsis</i> <i>Campylaea</i> <i>Campylaeopsis</i> <i>Cattania</i> <i>Chilostoma</i> <i>Cingulifera</i> <i>Corneola</i> <i>Delphinatia</i> <i>Dinarica</i> <i>Josephinella</i> <i>Kosicia</i> <i>Liburnica</i> <i>Thiessea</i> <i>Wladislawia</i>
<i>Cylindrus</i> <i>Helicigona</i>	<i>Arianta</i> <i>Campylaeopsis</i> <i>Cingulifera</i> <i>Drobacia</i> <i>Helicigona</i> <i>Thiessea</i>	<i>Chilostoma</i>	<i>Campylaeopsis</i> <i>Chilostoma</i> <i>Cingulifera</i> <i>Drobacia</i> <i>Josephinella</i> <i>Kosicia</i> <i>Thiessea</i>		
<i>Isognomostoma</i> <i>Vidovicica</i>		<i>Cylindrus</i> <i>Helicigona</i> <i>Isognomostoma</i> <i>Vidovicica</i>		<i>Cylindrus</i> <i>Drobacia</i> <i>Faustina</i> <i>Helicigona</i> <i>Isognomostoma</i> <i>Vidovicica</i>	
5 genera	10 subgenera	7 genera	14 subgenera	9 genera	14 subgenera

Material and methods

Taxon sampling

This study is based on 172 specimens (including 5 out-group specimens) from 85 (sub)species of Ariantinae from across Europe, representing about half of the known species and all the currently accepted genera (see Appendix). Specimens were collected in the period 1957-2012 and most material was fixed and conserved in 70% ethanol or isopropanol. Some (old) specimens were stored in “spiritus” (methylated spirits), whereas the more recently collected specimens were preserved in 97% ethanol.

Genital anatomy

For nearly all the (sub)genera the genital tract is illustrated (see Appendix). These figures are arranged according to the type of accessory glands, *i.e.* undivided versus one or both glands split. Only *Josephinella vikosensis*, with undivided accessory glands, was illustrated next to two congeneric species with split glands. For all the (sub)genera our personal observation regarding the accessory glands is presented. We refrained from an analysis of all the data that can be found in the literature (often without information on the actual number of individuals that was investigated). For the ease of comparison we only differentiate between undivided vs. split accessory glands, *i.e.* specimens in which only one of the glands was divid-

ed, as well as those with trifurcate glands, were considered split.

DNA extraction, PCR and sequencing

Total genomic DNA was extracted from small foot tissue samples using a DNeasy Tissue Kit (Qiagen) following the manufacturer’s instructions. As a follow-up of an earlier investigation (Gittenberger *et al.*, 2004), this study started with the amplification of *COI*, but due to the poor quality of some of the DNA extracts, mini-barcode primers (Hajibabaei *et al.*, 2006; Meusnier *et al.*, 2008) were occasionally used to amplify a smaller fragment of *COI* (124 bp fragment excluding primersites). These mini-barcode sequences grouped with those of conspecifics, or otherwise with congeners, for which the 655 bp *COI* fragment was obtained. Although most of the recognized (sub)genera formed well supported clades (based on Bayesian phylogeny inference), the relationships between the (sub)genera were poorly supported. Therefore nuclear marker *H3* and mitochondrial markers *CytB* and *16S* were added. PCR primers and references are given in Table 2. PCRs were carried out in 25 µl volumes using 1.25 units of Taq DNA polymerase (Qiagen), 0.4 mM of each primer and 0.2 mM dNTPs. For *COI* the final MgCl<sub>2</sub> concentration occasionally had to be increased to 2.5 mM (1x PCR buffer contains 1.5 mM; Qiagen). For *16S*, Q-solution (Qiagen; final concentration 1 x) was added to most of the reactions. PCR thermoprofile: initial denaturation 3 min. @ 94°C, followed by

Table 2. Primer information. \* Amplicon length excluding primer sequence. \*\* Annealing temperature. \*\*\* Minibarcodes Reverse primer has been modified to be more specific for Ariantinae.

Primer name	Sequence (5' to 3')	Marker	Length*	Source	AT**
H3-F H3-R	ATGGCTCGTACCAAGCAGACVGC ATATCCTTRGGCATRATRGTGAC	H3	328	Colgan, 2000	57
L1490 H2198	GGTCAACAAATCATAAAGATATTGG TAAACTTCAGGGTGACCAAAAAATCA	COI	655	Folmer, 1994	45-50
MB-F MB-R***	TCCACTAATCACAARGATATTGGTAC GAAAATTATKACAAARGCATGAGC	COI mini-barcode	124	Meusnier, 2008	50
151-F 270-R	TGTGGRGCNACYGTWATYACTAA AANAGGAARTAYCAYTCNGGYTG	CytB	361	Merritt, 1998	50
Pal-F Pal-R	CGGCCGCTGTTTATCAAAAACAT GGAGCTCCGGTTTGAAGTCAGATC	16S	404-412	Palumbi, 1991	50

Table 3. Information content per dataset. Inf. char. = The number of parsimony informative characters. Perc. inf. = The percentage of informative characters, calculated as  $100 \times (\text{Inform. char.} / \text{Total char.})$ .

Dataset	Specimens	Total char.	Constant char.	Inf. char.	Perc. inf.
H3	161	328	266	46	14.0
COI	149	655	339	300	45.8
CB	91	361	128	222	61.5
16S	82	335	163	149	44.5
H3-COI-CB	89	1344	748	558	41.5
H3-COI-CB-16S	103	1679	912	711	42.3

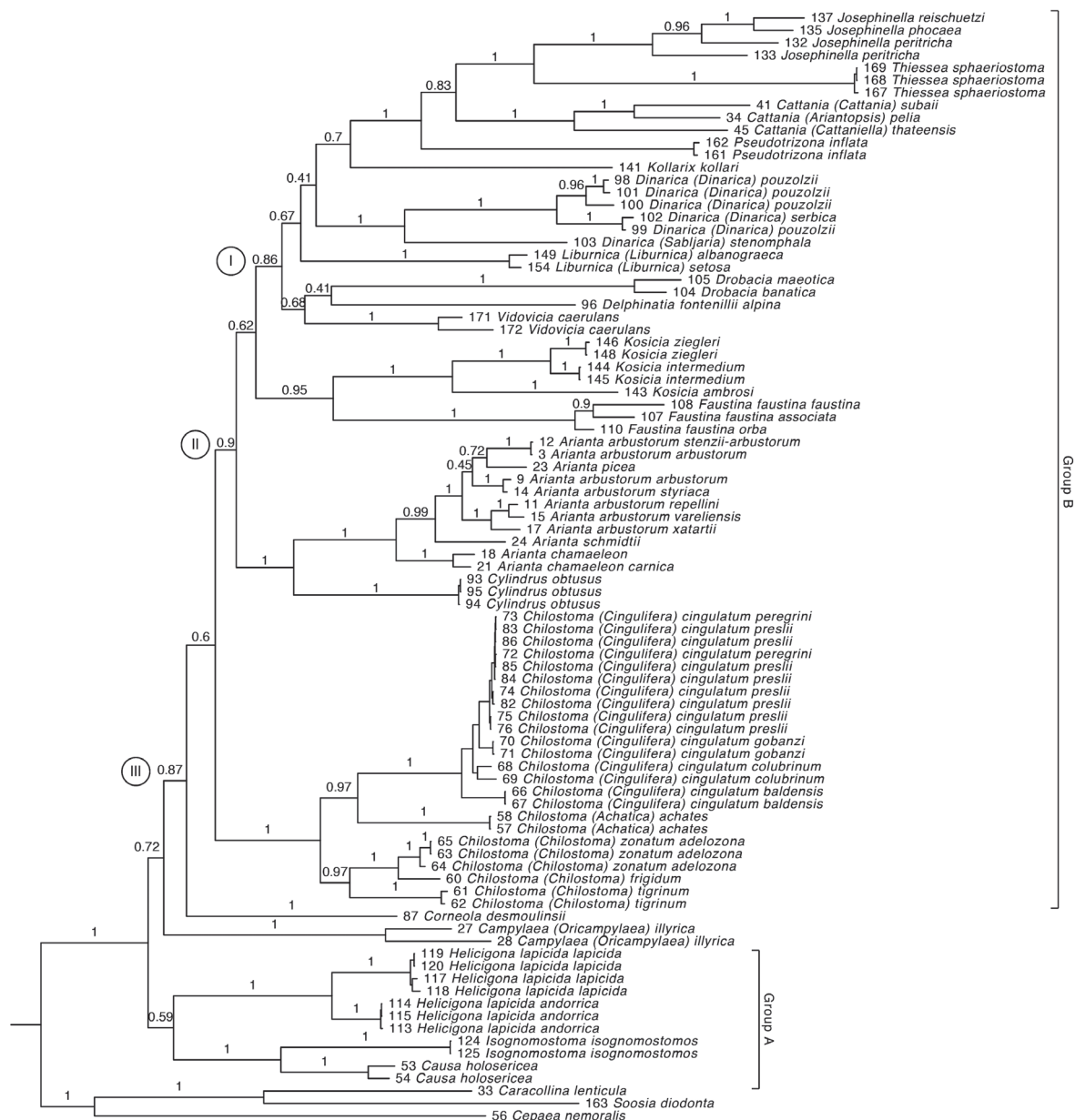


Fig. 1. MrBayes phylogeny based on the 'stringent' H3-COI-CytB dataset. Branch values show posterior probabilities.

40 cycles of – denaturation 15 sec. @ 94°C, annealing 30 sec. @ AT (Table 2), extension 40 sec. @ 72°C – and a final extension of 5 min. @ 72°C. PCR products were cleaned with a Montage purification kit (Millipore) at Macrogen Inc. Europe (Amsterdam), where they were sequenced in both directions on an ABI37730XL using the same primers as used for the PCR. Forward and reverse sequences were assembled with Sequencher 4.10.1 (Gene Codes Corporation) and protein coding genes (*H3*, *COI* and *CytB*) were manually aligned in MacClade 4.08 (Maddison and Maddison, 2005). The alignment for *16S* was made with MAFFT (Katoh and Standley, 2013) as implemented in the software package Geneious Pro 7.0.6 using the default settings with the G-INS-i algorithm. Non-conserved blocks of sequence data were removed from the alignment with Gblocks (Castresana, 2002) conducted on the Gblocks Server ([http://molevol.cmima.csic.es/castresana/Gblocks\\_server.html](http://molevol.cmima.csic.es/castresana/Gblocks_server.html)), using only the ‘more stringent selection’ option (which restricts the introduction of contiguous nonconserved positions).

#### Phylogenetic analyses

For each dataset (each marker) a nucleotide substitution model was selected with MrModeltest 2.2 (Nylander, 2004). For the mitochondrial datasets the model was GTR+I+G, for *H3* it was HKY+I+G. Bayesian analyses were done in MrBayes 3.2.1. (Ronquist and Huelsenbeck, 2003) hosted on the CIPRES Science Gateway (Miller, 2010). For each marker the analysis consisted of two simultaneous, four chain, MCMC runs (10 M generations). Trees were sampled every 1000 generations, the first 2500 trees were discarded as burnin (relburnin = yes, burninfrac = 0.25). Examination of the .p output files in Tracer v.1.5 (Rambaut and Drummond, 2007) showed stationarity was reached with proper effective sample sizes for all parameters (ESS > 200). Sumtrees (Sukumaran and Holder, 2010) was used to calculate 25% majority rule consensus trees. Subsequently the datasets for the individual markers were combined into two concatenated datasets (from hereon referred to as): the ‘stringent’ and ‘relaxed’ datasets. The stringent dataset (89 taxa) consisted of only protein coding genes (*i.e.* *H3*, *COI* and *CytB*) and had no missing data. The relaxed dataset (103 taxa) consisted of all markers (*H3*, *COI*, *CytB* and *16S*); taxa for which only one marker was missing were also included. A partitioned analysis was set up

in MrBayes (same version) for both datasets; for each partition the GTR+I+G model was selected using the above described procedure.

#### Fossil occurrences and age of taxa

In a recent check-list of fossil land snails of western and central Europe, Nordsieck (2014) reviews fossil taxa based on stratigraphic ranges. The oldest and only indisputably identified Ariantinae fossil in that list is of a *Helicigona* species from the late Burdigalian, Early Miocene (17.5–16 MYA; references in Nordsieck, 2014). This fossil was used as a single calibration point imposing a normal distribution prior (mean 16.75 MY, stdev 0.375) allowing for soft minimum and maximum age boundaries. Initial BEAST analyses were performed with and without setting the monophyly of the Ariantinae *sensu auct.* as a constraint. Species of the genera *Cepaea*, *Caracollina* and *Soosia* were used as outgroup taxa that are traditionally classified in closely related taxa within the same superfamily Helicoidea. If the monophyly of the Ariantinae *sensu auct.* was not set as a constraint, many internodes appeared between these outgroup taxa and the root of the tree. Re-rooted with the outgroup taxa, the topology was virtually identical to the ML (not shown) and MrBayes phylogenies. In our BEAST analyses, clades I, II and III (PP ≥ 0.86) were therefore used as a constraint. Three runs consisting of 100 M generations were performed (for both the stringent and relaxed datasets) using a relaxed clock model (lognormal uncorrelated) and with the Yule process (Yule, 1924; Gernhard, 2008) set as tree prior (BEAUTi; Drummond *et al.*, 2012). After initial inspection with Tracer v.1.5 (Rambaut and Drummond, 2007), for each dataset the log and tree files were combined with Logcombiner v.1.7.5 (Rambaut and Drummond, 2007) disregarding 10 M generations (10%) as burnin. ESS values were all above 200. Subsequently TreeAnnotator v.1.7.5 (Rambaut and Drummond, 2007) was used (burnin set to zero) to generate the maximum clade credibility tree for both the combined tree files. Given the use of a single calibration point and the overall low posterior probabilities, the obtained ages should be considered indicative only. Confidence intervals (node bars) were so large (especially for the deeper nodes) that they obscured the tree and hence were omitted for clarity. Node ages were rounded to the first decimal to still visualize the differences in results between ‘stringent’ and ‘relaxed’ dataset, not to imply accuracy.



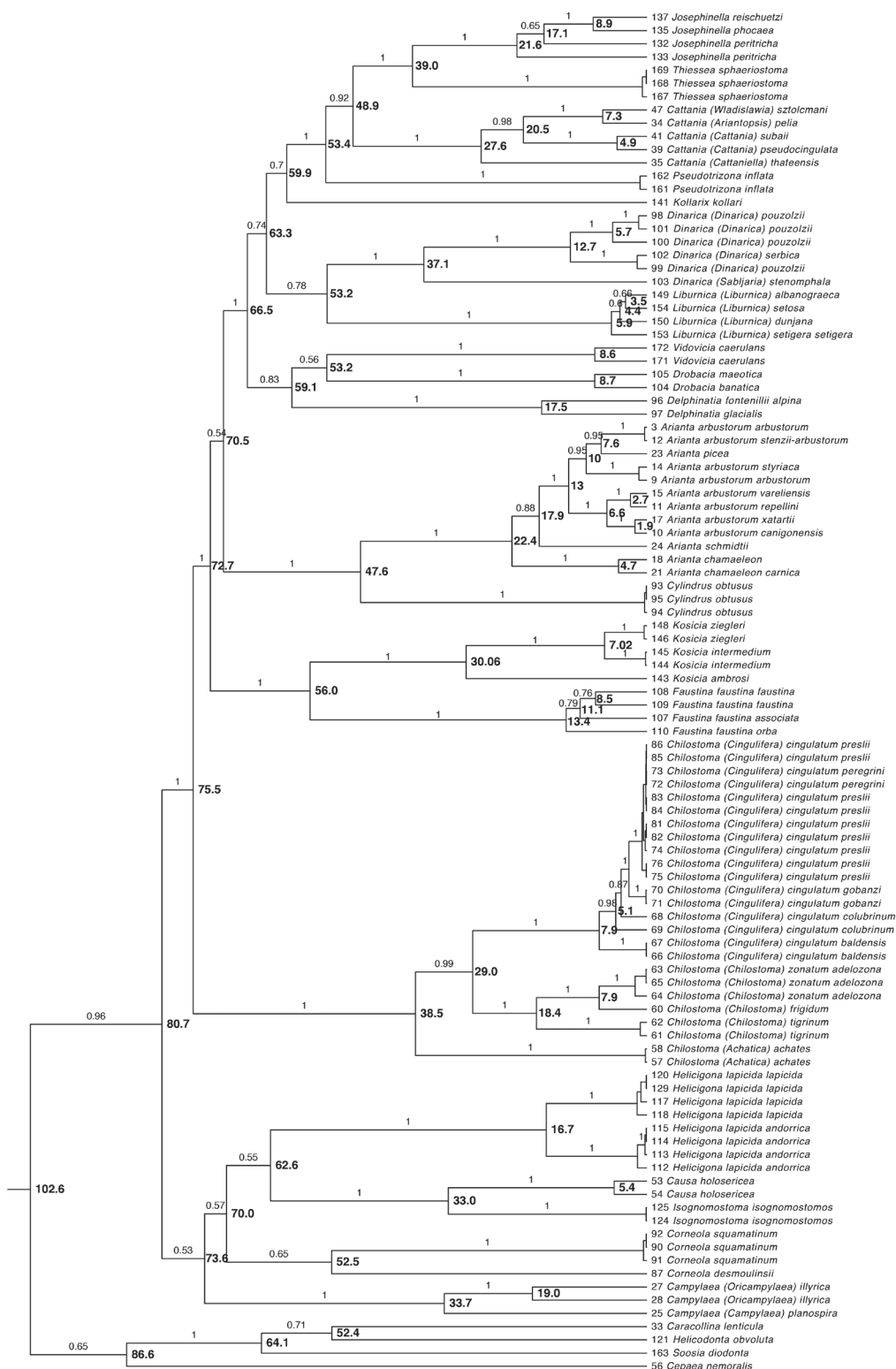


Fig. 2. BEAST phylogeny based on the 'relaxed' *H3-COI-CytB-16S* dataset. Branch values show posterior probabilities. Node values indicate divergence estimates in MYA.

### Genetic distances

Uncorrected pairwise ( $p$ ) distances were calculated with Paup 4.0b10 for Unix (Swofford, 2002) for each protein coding gene. Sequence divergence percentages were calculated as the uncorrected  $p$ -distance times 100.

### Systematics

Genera and subgenera are taxonomic ranks. To make the ranking less subjective, a cladistic approach is required. Throughout this study, clades that are sister-groups of one another do not differ in their taxonomic ranking. This leaves the option open to give the same ranking also to clades that do not have a sister-group relationship. As a consequence, a genus may have more than two subgenera. Since there are many more splitting points in evolutionary history than taxonomic ranks, this cannot be avoided. Genera are always based on monophyletic species groups. In some cases, at the subgeneric level, paraphyletic taxa are accepted. Genetic distances were not used as decisive in deciding upon the status of genus versus subgenus.

When morphologically cryptic taxa are unequivocally brought to light by the molecular analyses, these taxa are not neglected but formally characterized and named, as advocated by Cook *et al.* (2010), Gittenberger and Gittenberger (2011) and Jörger and Schrödl (2013). Abbreviations: PP = posterior probability, MYA = million years ago.

### Results

In total 483 sequences were obtained: 161, 149, 91 and 82 for the markers *H3*, *COI*, *CytB* and *16S*, respectively. A summary of the character statistics (as calculated with Paup 4.0b10 for Unix; Swofford, 2002) for each dataset is given in Table 3. Table 4 (Appendix) gives a summary of uncorrected  $p$ -distances.

Both the phylogeny reconstructions for the individual markers (Figs S1–S4; online supplementary information), as well as those for the concatenated datasets (Figs 1, 2, S5, S6) distinguish most of the (sub)genera that were traditionally characterized by subtle conchological differences and geographic origin (*e.g.* *Arianta*, *Cattania*, *Corneola*, *Chilostoma*, *Cingulifera*, *Dinarica*, *Faustina*, *Helicigona*, *Josephinella*, *Kosicia* and *Liburnica*). Although sister-group relationships between some taxa were shown explicitly (*e.g.* *Jose-*

*phinella* - *Thiessea*, *Ariantopsis* - *Wladislawia*), deeper nodes were hardly supported, particularly in the phylogenies based on the individual markers (Figs S1–S4). The *H3* dataset differs most from the other datasets by its relatively low percentage of parsimony informative characters (Table 3). The phylogeny based on this marker is not discriminative below the genus level, but can be useful for the assignment of species (or subgenera) to genera (*e.g.* *Ariantopsis pelia*, *Campylaeopsis moellendorffii*, *Superba spec.*, *Wladislawia sztolcmani*). The Histone gene cluster is multicopy (slight intercopy variation might exist and *H3* pseudogenes have been reported; Rooney *et al.*, 2002) and has been used in higher-level phylogenetics (Armbruster *et al.*, 2005; Colgan *et al.*, 2007 and references therein). For some species of mostly *Chilostoma*, double peaks were observed at a few positions within the *H3* sequence. This genus which is shown as monophyletic in nearly all phylogeny reconstructions (Figs 1, 2, S2, S3, S5 and S6), turns out paraphyletic in the phylogeny for *H3* (Fig. S1). It might be argued that the more extensive sampling of *Chilostoma* (*Cingulifera*) increased the chance of observing this apparent intercopy variation, but it was not observed in other genera for which multiple species were sequenced (*e.g.* *Arianta*, *Cattania*, *Josephinella* and *Liburnica*) either. In agreement with Colgan *et al.* (2000) we therefore conclude that intercopy variation in *H3* will not significantly interfere with the phylogeny reconstructions.

Initially no amplicons were obtained with the *COI* mini-barcode primers of Meusnier *et al.* (2008); to get these working for Ariantinae, the reverse primer was modified (Table 2). Hajibabaei *et al.* (2006) showed (in silico) that *COI* mini-barcodes (109 bp; compared to the full length barcode of 654 bp) are 3% less effective in the correct identification of closely related species and pointed out that mini-barcodes might be less useful for the classification of specimens in larger species assemblages. Based on those taxa for which both a complete and a mini-barcode sequence were obtained (*C. (Cattania) faueri*, *Corneola desmoulinsii*, *Helicigona lapicida andorrca* and *Vidovicica caerulans*), we conclude that the mini-barcodes (despite their short length) are placed correctly in the *COI* phylogeny (Fig. S2).

The phylogeny reconstructions for the concatenated datasets (Figs 1, 2, S5–S6) show a basal split within the Ariantinae, differentiating the ancestor of the genera *Causa*, *Isognomostoma* and *Helicigona*, referred to here as group A, from that of all other genera (except *Campylaea* and *Corneola*), collectively referred to as

group B. It remains unclear whether *Campylaea* and *Corneola* belong to A (Fig. 2) or B (Figs 1, S5), or should be considered a group on their own (Fig. S6).

All of the obtained sequences were deposited in GenBank; a complete list of taxa, sampling information and accession numbers is given in Table S7.

## Discussion

Left aside some exceptions, Ariantinae shells are rather monomorphic (Fig. 3, Appendix). Because of the limited number of conchological characters, many authors studied the genital tract for morphological characters that could discriminate species and especially higher taxa. However, the genital morphology within this subfamily is also very homogeneous, what is uncommon among pulmonates. The form of the accessory glands, which are either undivided or more or less completely split (Fig. 4, Appendix), has been used by some authors as a (partial) basis for the systematics of the Ariantinae (Sturany and Wagner, 1914; Schileyko, 2006), although according to other authors both types of accessory glands can occur within the same genus, or even species (Hesse, 1931; Knipper, 1939; Schileyko, 2013). A classification of the species of Ariantinae in only two genera, as for example *Helicigona* and *Campylaea* (sensu Sturany and Wagner, 1914; Table 1), or *Chilostoma* and *Campylaea* (sensu Zilch, 1960; Table 1) is an oversimplification according to all modern authors, but what classification should be accepted alternatively remains a matter of dispute. Recently it has been suggested that the structure of the penial papilla might be a useful character to clarify the phylogenetic relationships between the (sub)genera within the subfamily (Schileyko, 2013), but that view still has to be confirmed.

Obviously, given the actual situation, a new approach is necessary, as was realized most recently by Groenenberg *et al.* (2012) and Cadahia *et al.* (2013), who tried to escape from the confusion by the use of molecular phylogenetics. Despite its shortcomings in the completeness of the molecular data, this article expands the reliability of the molecular phylogeny reconstructions, enabling a still better founded discussion regarding the subdivisions of the Ariantinae.

Our analyses do not support an evolutionary significance of the transformation series based by Schileyko (2013) on the structure of the penial papilla in several Ariantinae genera. *Dinarica* and *Cattania* are not closely related to *Helicigona*, for example, so that the depicted morphocline *Cattania* - *Helicigona* - *Dinarica*

(Schileyko, 2013) cannot be interpreted in an evolutionary context.

Aiming at a general classification of the Ariantinae, the shape of the accessory glands is equally uninformative. The transition from undivided to split gland(s), or the other way round, must have occurred more than once.

When the phylogeny reconstructions obtained with this study are compared to generic classifications based on conchology and geography, nearly all the named (sub)genera are recovered as distinct clades. A few additional (sub)generic groups were discovered and described, viz. *Campylaea* (*Oricampylaea*), *Chilostoma* (*Achatica*), *Cattania* (*Cattaniella*), *Pseudotrizona*, *Kollarix* (Table 5, Appendix). The phylogenetic relationships above the genus-level, as indicated by the lower posterior probabilities, remain less certain in many cases. For a limited number of genera, sister-group relationships were disclosed, i.e. *Arianta*-*Cylindrus*, *Causa*-*Isognomostoma*, *Josephinella*-*Thiessea* and *Kosicia*-*Faustina* (PP  $\geq 0.95$ ; Figs 1, 2, S5, S6). In particular the close relationship between *Cylindrus* and *Arianta* is intriguing. Clearly both genera are part of a lineage that was less restricted in the development of conchological novelties. The classification of *Cylindrus* as a member of the Ariantinae is now confirmed genetically.

We agree with Cadahia *et al.* (2013) that indications of evolutionary age are uncertain, to say the least. The fossil record is very incomplete indeed, and a molecular clock model is also not easily applicable. The unattractive alternative would have been to omit such speculations altogether.

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## Online Supplementary Information

- S1.* MrBayes phylogeny based on the *H3* dataset
- S2.* MrBayes phylogeny based on the *COI* dataset
- S3.* MrBayes phylogeny based on the *CytB* dataset
- S4.* MrBayes phylogeny based on the *16S* dataset
- S5.* BEAST phylogeny for the stringent *H3-COI-CytB* dataset
- S6.* MrBayes phylogeny based on the relaxed *H3-COI-CytB-16S* dataset
- S7.* Taxa and sampling information



## Appendix

### Systematics

Most nominal genus-group taxa, viz. *Cattania*, *Corneola*, *Delphinatia*, *Dinarica*, *Faustina*, *Josephinella*, *Kosicia*, *Liburnica* and *Thiessea*, are shown as distinct clades in our molecular analyses. These taxa are closely related to neither *Campylaea* nor *Chilostoma* and should no longer be regarded as subgenera of one of these genera. We consider the Ariantinae a subfamily with 21 genera (Table 5), five of which are subdivided into two (*Campylaea*, *Dinarica*, *Liburnica*), three (*Chilostoma*) or four (*Cattania*) subgenera. To some extent, the genetic distances may be used as a measure for the amount of (dis)similarity between taxa. For the status of taxa in the taxonomic hierarchy we use cladistic arguments, i.e. using identical ranking for clades that are sister-groups. Based on the phylogeny reconstructions we recognize the following genera and subgenera, listed in alphabetical order.

Subgenus nov. ***Achatica*** (monotypic), genus

#### ***Chilostoma***

Type species: *Helix achates* Rossmässler, 1835

**Abbreviations.** PS = P. Subai; RMNH = Naturalis Biodiversity Center, Leiden; SMF = Forschungsinstitut Senckenberg, Frankfurt am Main

**Diagnosis.** The diagnosis of this monotypic subgenus is by definition identical with that of its type species, i.e. *Chilostoma (Achatica) achates* (Rossmässler, 1835). *Achatica* subgen. nov. is also differentiated by a unique combination of nucleotides in the 655 bp *COI* sequence obtained with general barcoding primers (Folmer, 1994) at the following relative positions: 79 C, 88 C, 181 C, 197 A, 211 C, 272 G, 319 C, 352 A, 538 G, 595 C.

**Description.** Shell strongly depressed, nearly discoid, rather dark, yellowish brown, with a brown spiral band; umbilicus wide (Kerney and Cameron, 1979: 201, pl. 21 fig. 2; Boschi, 2011: 570–571; Welter-Schultes, 2012: 580). See “*Chilostoma (Chilostoma) achates*” in Schileyko (2006: fig. 2264B, C; 2013: 143, fig. 13) for details regarding the genital morphology. The accessory glands are undivided.

**Molecular data.** Two individuals have been used for the molecular analyses, viz. (a) a specimen collected in the northern limestone Alps (Berchtesgaden, Bayern, Germany), and (b) a specimen from the south-

ern limestone Alps (Greifenburg, Kärnten, Austria). The sequence divergences between these specimens, based on all four markers, is less than 0.2% (Table 4). When compared to sequence divergences of 3.3–6.5% between subspecies of *Chilostoma (Cingulifera)*, there is at least no genetic support for a classification of these two populations of *C. (Chilostoma) achates* as different subspecies (as suggested by Falkner, 1998).

**Age.** The unresolved sister-group relationships between the subgenera of *Chilostoma* (see *Chilostoma [Chilostoma]*) do not allow for an unequivocal estimate for the emergence of *Chilostoma (Achatica)*. If it dates back to the most basal node within the genus (Fig. 2), it is estimated at ca. 38.5 MYA (Fig. 2). When *C. (Achatica)* and *C. (Cingulifera)* are sister-groups (Fig. S5) the most recent common ancestor is estimated at ca. 24.7 MYA (Fig. S5).

**Distribution.** Austria, E Switzerland, S Germany (Bayern, Berchtesgadener Alps), N Italy.

**Remarks.** It is surprising that only a single, polytypic species is classified in *Achatica*, because *Chilostoma (C.) adelozona* (Strobel, 1857) and *Chilostoma (C.) zonatum* (Studer, 1820) have brown shells that look similar to *C. (A.) achates* at first sight. See *Chilostoma (Chilostoma)*.

**Derivatio nominis.** The name *Achatica* is supposed to recall the name of the type species.

Genus ***Arianta*** Turton, 1831

Type species: *Helix arbustorum* Linné, 1758

**Molecular data.** Four *Arianta* species could be studied, viz. *A. aethyops* (Bielz, 1851), *A. arbustorum* s. lat. (with five subspecies, two of which are considered separate species by some authors [Welter-Schultes, 2012]), *A. chamaeleon* (Pfeiffer, 1868), and *A. schmidtii* (Rossmässler, 1836). The monophyly of this broadly accepted genus is supported in all molecular phylogeny reconstructions (PP = 1.0; Figs 1, 2, S1–S6). The position of *A. arbustorum stenzii* (see Gittenberger et al. 2004) or *A. arbustorum stenzii-arbustorum* in phylogeny reconstructions presented in this study does not give any support for the introduction of *Altarianta* Schileyko, 2013, as a subgenus of *Arianta*. This is in accordance with the fact that *A. a. stenzii* and *A. a. arbustorum*, hybridize where they are in contact. *Arianta chamaeleon*, which is shown as the sister-group of the other *Arianta* species, is less closely related. The



conchologically unexpected sister-group relationship ( $PP = 1.0$ ; Figs 1-2, S1, S3-S6) between *Arianta* and *Cylindrus* (Fig. 3.3) was shown by Groenenberg et al. (2012) and has recently been confirmed by Cadahia et al. (2013).

**Age.** The most recent common ancestor for *Arianta* is estimated at ca. 23.1-22.4 MYA (Figs. S5, 2).

**Distribution.** *Arianta arbustorum* (Fig. 3.1) has the

largest distribution range of all the species within the subfamily Ariantinae. It occurs in north and central Europe, from Iceland, Norway, Sweden, N.-Ireland, Great Britain, and central France eastwards to the Baltic countries, Poland, Ukraine and Romania (Carpathians). The southern border ranges from the N.-Italian Alps through Slovenia, Croatia and Serbia into Bulgaria (up to Stara Planina); except for some localities

Fig 3. Compilation of shells representing

most of the currently recognized genera of

Ariantinae. 1. *Arianta arbustorum* (Lin-

naeus, 1758) B 24.1 mm [RMNH G2131]

Austria, Steiermark, near Gstatteboden;

E. Gittenberger leg., 10-IX-1964. 2. *Ari-*

*anta chamaeleon wiedermayeri* (Kobelt,

1903) B 18.3 mm [RMNH G2608] Aus-

tria, East Tirol, S of Kartitsch; E. Gitten-

berger leg., VIII-1974. 3. *Cylindrus ob-*

*tusus* (Draparnaud, 1805) B 13.7 mm

[RMNH 73877] Austria, Oberösterreich,

Bledigupf; W.H. Neuteboom leg., 22-VII-

1966. 4. *Isognomostoma isognomostomos*

(Schröter, 1784) B 9.7 mm [RMNH 74226]

Austria, Kärnten, Plöckenpass; W.H. Neu-

teboom leg., 14-IX-1952. 5. *Causa holos-*

*ericea* (Studer, 1820) B 10.5 mm [RMNH

74311] Austria, Salzburg, Amerthal; W.H.

Neuteboom leg., 16-VII-1968. 6. *Chilosto-*

*ma (Achatia) achates* (Rossmässler,

1835) B 21.9 mm [RMNH G2410] Austria,

Steiermark, E of Brandtriedl; A. and E.

Gittenberger leg., 19-V-1972. 7. *Chilo-*

*stoma (Chilostoma) zonatum rhaeticum*

(Strobel, 1857) B 25.2 [RMNH G54412]

Switzerland, Graubünden, E of Martins-

bruck; E. Gittenberger leg., IX-1963. 8.

*Chilostoma (Chilostoma) tigrinum* (De

Cristofori and Jan, 1832) B 24.7 mm

[RMNH 73434] Italy, Como, Pasturo;

W.H. Neuteboom leg., 3-VIII-1954. 9.

*Chilostoma (Cingulifera) cingulatum cin-*

*gulatum* (Studer, 1820) B 20.5 mm

[RMNH H1938] Switzerland, Tessin,

Melide along Lago di Lugano; J.T. Henrard

leg., 28.VIII.1938. 10. *Chilostoma (Cing-*

*ulifera) cingulatum gobanzi* (Frauenfeld,

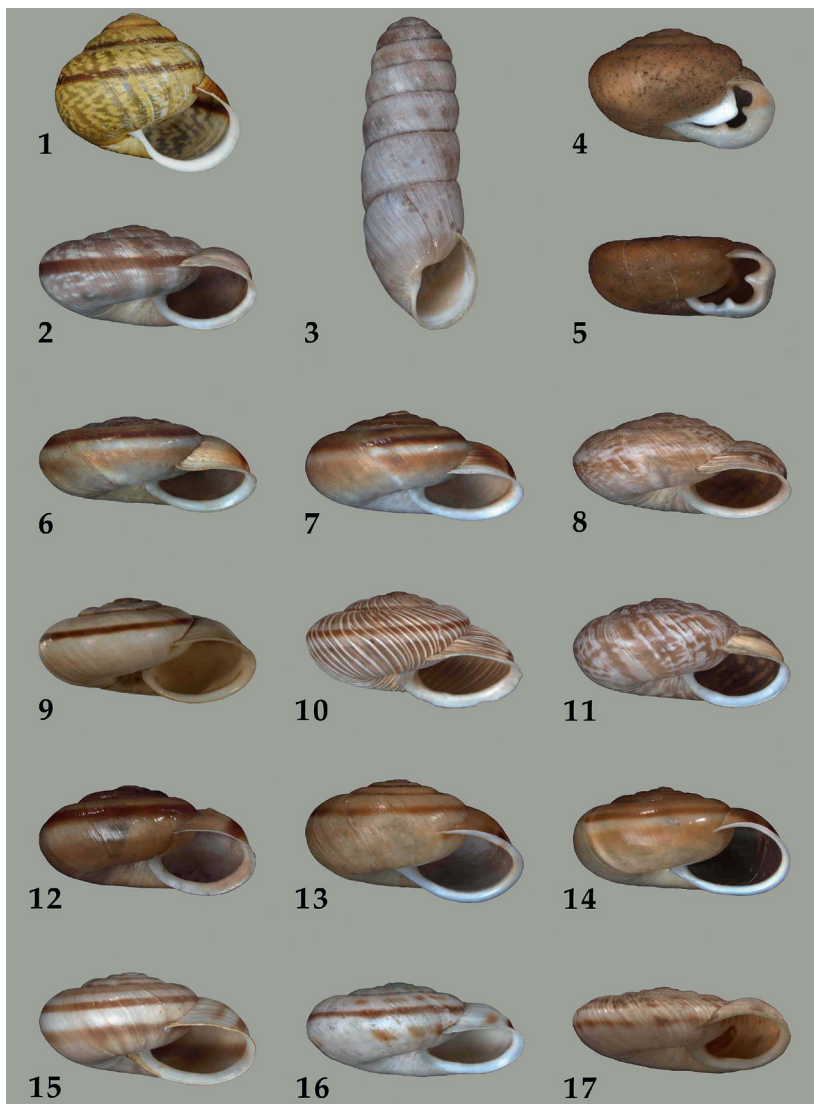
1867) B 22.8 mm [RMNH 73408] Italy,

Brescia, Val Toscolano; W.H. Neuteboom

leg., 05-VIII-1954. 11. *Delphinatia fon-*

*tenillii alpina* (Michaud, 1831) B 19.6 mm

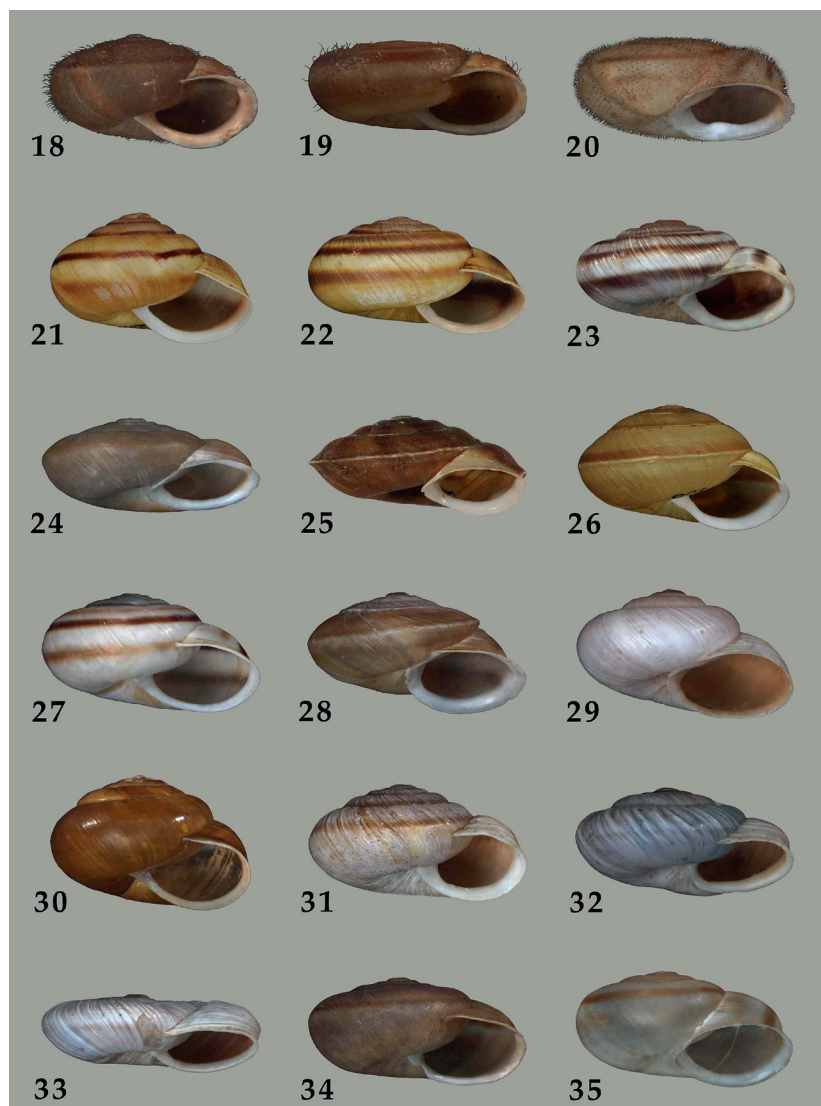
[RMNH G3646] France, Isère, SSE of Laurent-du-Pont; E. Gittenberger leg., 12-IX-1975. 12. *Faustina faustina* (Rossmässler, 1835) B 19.6 mm [RMNH 53576] Hungary, Bükk, Szalajkavölgy; Agócsy leg., 21-V-1921. 13. *Campylaea (Campylaea) planospira planospira* (Lamarck, 1822) B 25.9 mm [RMNH 73625] Italy, Torino, Santvaris di Montebruno; W.H. Neuteboom leg., 8-VII-1977. 14. *Campylaea (Oricampylaea) illyrica* (Stabile, 1864) B 25.4 mm [RMNH 11124] Italy, Friuli, SSE of Tarvisio; E. Gittenberger leg., VI-1992. 15. *Kosicia ambrosi* (Strobel, 1852) B 12.5 mm [RMNH 24940] Italy, Vicenza, Valstagna; W.H. Neuteboom leg., 22-VII-1968. 16. *Kosicia intermedia* (Pfeiffer, 1828) B 15.3 mm [RMNH 54440] Austria, Kärnten, Deutschpeter; E. Gittenberger leg., IX-1964. 17. *Kosicia ziegleri* (Rossmässler, 1836) B 17.7 mm [RMNH G2350] Slovenia, Kamniške Alps, Igla Studenec; A. and E. Gittenberger leg., 26-VIII-1971.



in the Spanish Pyrenees south of the watershed (*A. arbustorum xatarti* Farines, 1834) it does not occur in the Iberian peninsula.

**Remarks.** Four or five *Arianta* species have been described, some of which are polytypic. *Campylaea apfelbecki* Sturany, 1901, which was considered a subspecies of *A. chamaeleon* by Knipper (1939), could not be investigated; it might be either a fifth *Arianta* spe-

cies or belong to *Cattania* (*Cattaniella*). The exceptionally widespread *Arianta arbustorum arbustorum* is aberrant also in terms of shell morphology and in its ecological requirements, occurring independently of limestone from the lowland to high in the mountains. The other *Arianta* species are restricted to (high) alpine habitats. While nearly all Ariantinae have a depressed shell and an open umbilicus, *A. a. arbustorum*



18. *Campylaeopsis moellendorffii* (Kobelt, 1871) B 18.4 mm [RMNH AJW898] Bosnia-Herzegovina, Vrelo Bosne, near Ilidza; A.J. de Winter leg., 17-IX-1980. 19. *Kollarix kollari* (Pfeiffer, 1856) B 24.3 mm [RMNH YU.429] Serbia, along Ovcar Banja; W.J.M. Maassen leg., V-1984. 20. *Liburnica* (*Liburnica*) *setosa setosa* (Férussac, 1832) B 23.6 mm [RMNH 94272] Croatia, Lovrec, S of Imotski; W.J.M. Maassen leg., IV-1989. 21. *Dinarica* (*Sabljaria*) *stenomphala* (Menke, 1830) B 30.7 mm [col. PS.21228] Croatia, Velebit Mts, near Krasno Polje; P. Subai leg., 29-VII-2002. 22. *Dinarica* (*Dinarica*) *pouzolzii* (Deshayes, 1830) B 40.1 mm [RMNH 53508 / 413] Croatia, Dalmatia, E of Biokovo Mts; J.J. ter Pelkwijk leg., 12-VIII-1939. 23. *Liburnica* (*Superba*) *skipetarica skipetarica* (Subai, 1995) B 19.6 mm [col. PS.20215] Albania, Periferi Berat, Tommorit; P. Subai leg., VIII-2004. 24. *Corneola desmoulinsii* (Farines, 1834) B 17.2 mm [RMNH 93925] Andorra, Canillo, northern wall; W.J.M. Maassen leg., VII-1990. 25. *Helicigona lapicida lapicida* (Linnaeus, 1758) B 17.6 mm [SMF3254 26/1] Germany, Hessen, Schlüchtern; M. Pfenninger leg. 26. *Drobacia banatica* (Rossmässler, 1838) B 29.5 mm [RMNH 54500 / 485] Romania, Siebenbürgen; H. de Wever leg. 27. *Cattania* (*Cattania*) *trizona* (Rossmässler, 1834) B 24.4 mm [RMNH 99615] Romania, Banat Mts, Mt Domogled; Kroupa leg., 21-VI-1985. 28. *Cattania* (*Cattania*) *subaii* (Fauer, 1991) B 22.9 mm [RMNH GU.9921 / EK5558] Greece, Makedonia, W of Kozani; E. Gittenberger and D. Uit de Weerd leg., 23-V-1999. 29. *Vidovicia caeruleans* (Pfeiffer, 1828) B 15.4 mm [RMNH 93836] Croatia, Velebit near Starigrad; W.J.M. Maassen

leg., IX-1982. 30. *Cattania* (*Ariantopsis*) *pelia* (Hesse, 1912) B 17.9 mm [col. PS.23572] Bulgaria, Vitosha, Bistrisko branishte; I. Dedoy leg., 8-VII-2004. 31. *Cattania* (*Wladislawia*) *polinskii* (Wagner, 1928) B 16.4 mm [RMNH G3749] Bulgaria, Pirin Mts, Mt Vihren; A. Riedel leg., 24-VI-1977. 32. *Cattania* (*Wladislawia*) *sztolcmani* (Wagner, 1928) B 10.6 mm [RMNH G3749] Bulgaria, Pirin Mts, Mt Vihren; A. Riedel leg., 24-VI-1977. 33. *Josephinella vikosensis* (Subai, 1990) B 18.8 mm [RMNH EG.9703 / DK8112] Greece, Ipiros, Vikos valley; E. Gittenberger leg., 23-VII-1997. 34. *Josephinella hemonica* (Thiesse, 1884) B 19.1 mm Greece, Makedhonia, SE of Grevena; E. Gittenberger leg., 18-VII-1986. 35. *Thiessea sphaeriotoma* (Bourguignat, 1857) B 21.0 mm [RMNH 75078] Greece, Sterea Ellas, SE of Mariolates; E. Gittenberger and D. Uit de Weerd leg., 19-V-2000.

has a globular shell with a closed umbilicus (Gittenberger et al., 2004). Other *Arianta* species, such as *A. chamaeleon* (Fig. 3.2) and *A. schmidtii* retained the plesiomorphic, depressed shell phenotype. Some subspecies of *A. arbustorum* that are characterized by depressed shells (Gittenberger et al., 2004; Haase and Misof, 2009) might have evolved that character state by reversal. See also *Arianta* in Schileyko (2013) for details regarding the genital morphology. The accessory glands are undivided (Fig. 4.1). Specimens of *A. arbustorum stenzii* from several localities should be dissected to investigate the status of *Altarianta* Schileyko, 2013, in more detail.

Subgenus ***Ariantopsis*** Wagner, 1928 (monotypic), genus *Cattania*

Type species: *Helicigona (Arianta) pelia* Hesse, 1912

**Molecular data.** Both MrBayes and BEAST phylogeny reconstructions for the relaxed dataset highly support a sister-group relation (PP = 1.0) between *Ariantopsis* and *Wladislawia* (Figs 2, S6), which are here considered subgenera of *Cattania* Brusina, 1904.

**Age.** The most recent common ancestor of *Cattania (Ariantopsis)* and *C. (Wladislawia)* is estimated at ca. 7.3 MYA (Fig. 2).

**Distribution.** *Ariantopsis* is endemic to SW and W Bulgaria. The eastern boundary of its distribution is situated near Plovdiv, the northern boundary is near Lakatnik in the Iskar-valley, and its western distribution is formed by Mt Vitoshka and the Rila Mts.

**Remarks.** The taxonomic position of *Cattania (Ariantopsis) pelia* (Fig. 3.30) has long been uncertain. Conchologically it somewhat resembles *Arianta aethyops*. It has been assigned to various genera, viz. *Arianta* by Kroupa (1994) and Dedov (1998), *Helicigona* by Hesse (1912), *Chilostoma* by Bank et al. (2001) and *Faustina* by Damjanov and Likharev (1975). See also *Campylaea (Ariantopsis)* and *Ariantopsis* in Schileyko (2006, 2013) for details regarding the shell and genital morphology. The accessory glands can be undivided, but are mostly split up to half of their length (Fig. 4.29).

Subgenus ***Campylaea*** Beck, 1837 (monotypic?), genus ***Campylaea***

Type species: *Campylaea planospira* Lamarck, 1822

**Molecular data.** *Campylaea (C.) planospira* (Fig. 3.13) is the sister-group of a clade with three species,

referred to below as *Campylaea (Oricampylaea)* (PP > 0.92; Figs S1, S2). Together, the subgenera *Campylaea* and *Oricampylaea*, form a monophyletic group (PP = 1.0; Figs 2, S1, S2, S4, S6), viz. the genus *Campylaea*. The genetic distances between *C. (Campylaea)* and *C. (Oricampylaea)* are comparatively large (COI sequence divergence up to 22.1%; Table 4). It is unclear to which genus *Campylaea* is most closely related. Except for the phylogeny reconstruction according to COI, which suggest a sister-group relationship between *Campylaea* and *Kollarix* (PP = 0.86; Fig. S2), none of the other datasets provides information regarding possible sister-group relationships of *Campylaea*. In the phylogenies based on the concatenated datasets *Campylaea* branches off early in either group A (Figs 1, S6) or group B (Fig. 2).

**Age.** The most recent common ancestor of *Campylaea* is estimated at ca. 34.0 MYA (Fig. 2).

**Distribution.** *Campylaea (C.) planospira* is represented in S Austria, N Balkans, mainland Italy, and the island of Sicily.

**Remarks.** See also *Campylaea (Campylaea)* and *Chilostoma (Campylaea)* in Schileyko (2006, 2013) for details regarding the shell and genital morphology. The accessory glands can be undivided (Fig. 4.14), but Sturany and Wagner (1914) and Knipper (1939) showed split accessory glands in *C. (Campylaea) planospira*. Penial papilla small, conical, with fine transverse ridges and an obtuse apex with a short, transverse, slit-like pore. Secondary ureter entirely open. For the moment being, only a single, polytypic species is accepted in *Campylaea* s. str. Some of the so-called subspecies could be considered separate species, however.

Genus ***Campylaeopsis*** Sturany and Wagner, 1914 (monotypic)

Type species: *Helicigona moellendorffii* Kobelt, 1871.

**Molecular data.** Only an *H3* sequence was obtained for this taxon. In the respective phylogeny *Campylaeopsis* is placed in a clade with *Delphinatia*, *Drobacia*, *Pseudotrizona*, and *Vidovicica* (PP = 0.8; Fig. S1). *Campylaeopsis moellendorffii* shares a substantial part of its distribution area with *Pseudotrizona inflata*.

**Age.** Not enough sequence information was obtained to include *Campylaeopsis* in the time calibrated analyses (Figs. 2, S5).

**Distribution.** The mountains of Bosnia-Herzegovina and Montenegro.



**Remarks.** *Campylaeopsis moellendorffii* (Fig. 3.18) has a characteristic shell with regularly arranged, widely spaced hairs. It has been assigned to *Helicigona* by Knipper (1939) and to *Chilostoma* by Bank (2001).

See also *Helicigona* (*Campylaeopsis*) and *Chilostoma* (*Campylaeopsis*) in Schileyko (2006, 2013) for details regarding the shell and genital morphology. The accessory glands are undivided (Fig. 4.10).

Subgenus ***Cattania*** Brusina, 1904, genus ***Cattania***

Type species: *Helix trizona* Rossmässler, 1835

**Molecular data.** Five of the ca. 9 *Cattania* (C.) species are included in this study. The genus *Cattania* is shown to be monophyletic (PP = 1.0; all phylogenies except S1). It includes the subgenera: *Cattania* (*Ariantopsis*), *C. (Cattania)*, *Cattania* (*Cattaniella*) and *C. (Wladislawia)*. *Cattania* is the sister-group of the clade *Josephinella-Thiessea* (PP ≥ 0.8; Figs 1, 2, S1-S3 and S6). *Cattania* (*Cattania*) constitutes a monophyletic group within *Cattania* (PP = 1.0; Fig. S2) and is in this study

represented by *C. (C.) faueri*, *C. (C.) kattingeri*, *C. (C.) pseudocingulata*, *C. (C.) subaii* and the type species *C. (C.) trizona*. It is the sister-group of the clade *C. (Ariantopsis)*-*C. (Wladislawia)* (PP ≥ 0.95; Figs S2, S6). The COI sequence divergences between *C. (Cattania)* and *C. (Ariantopsis)*, and between the former and *C. (Wladislawia)* are 13.4% and 14.7%, respectively. The data of Cadhaia *et al.* 2013 show that *C. (Cattania) haberhaueri* belongs to this subgenus as well. Future research will have to make clear whether *C. balcanica* and *C. rumelica* should also be classified here. All phylogeny reconstructions indicate that the species referred to as *Cattania inflata* (Kobelt, 1876) by Subai (1995) represents a separate lineage (Figs 1, 2, S1-S6) that is clearly distinct from *Cattania*. We consider this lineage a separate genus, referred to below as *Pseudotrizona* gen. nov.

**Age.** The most recent common ancestor of *Cattania* is estimated at ca. 27.6-26.9 MYA (Figs 2, S5).

**Distribution.** Central Balkans, SW Romania, E and S Serbia, SW Bulgaria and N Greece (Thraci).

**Remarks.** See *Campylaea* (*Cattania*) and *Chilostoma* (*Cattania*) in Schileyko (2006, 2013) for details

Table 4. Uncorrected p-distances (in percentages) for a selection of taxa.

From	To	H3	COI	CB
25 <i>Campylaea</i> ( <i>Campylaea</i> ) <i>planospira</i>	26 <i>Campylaea</i> ( <i>Oricampylaea</i> ) <i>illyrica</i>	2,4	22,1	-
25 <i>Campylaea</i> ( <i>Campylaea</i> ) <i>planospira</i>	30 <i>Campylaea</i> ( <i>Oricampylaea</i> ) <i>lefeburianna</i>	2,4	20,5	-
41 <i>Cattania</i> ( <i>Cattania</i> ) <i>subaii</i>	34 <i>Cattania</i> ( <i>Ariantopsis</i> ) <i>pelia</i>	0	13,4	18
41 <i>Cattania</i> ( <i>Cattania</i> ) <i>subaii</i>	46 <i>Cattania</i> ( <i>Wladislawia</i> ) <i>sztolcmani</i>	0,3	14,7	-
41 <i>Cattania</i> ( <i>Cattania</i> ) <i>subaii</i>	45 <i>Cattania</i> ( <i>Cattaniella</i> ) <i>thateensis</i>	0,3	15,4	-
54 <i>Causa holosericea</i>	125 <i>Isognomostoma isognomostomos</i>	1,2	20,2	23
63 <i>Chilostoma</i> ( <i>Chilostoma</i> ) <i>zonatum adelozona</i>	83 <i>Chilostoma</i> ( <i>Cingulifera</i> ) <i>cingulatum preslii</i>	0	14,5	18,6
63 <i>Chilostoma</i> ( <i>Chilostoma</i> ) <i>zonatum adelozona</i>	57 <i>Chilostoma</i> ( <i>Achatica</i> ) <i>achates</i>	0	14,7	18,6
83 <i>Chilostoma</i> ( <i>Cingulifera</i> ) <i>cingulatum preslii</i>	57 <i>Chilostoma</i> ( <i>Achatica</i> ) <i>achates</i>	0	14,8	18
57 <i>Chilostoma</i> ( <i>Achatica</i> ) <i>achates</i>	58 <i>Chilostoma</i> ( <i>Achatica</i> ) <i>achates</i>	0	0,2	0,3
72 <i>Chilostoma</i> ( <i>Cingulifera</i> ) <i>cingulatum peregrini</i>	74 <i>Chilostoma</i> ( <i>Cingulifera</i> ) <i>cingulatum preslii</i>	0,3	0,6	0,6
72 <i>Chilostoma</i> ( <i>Cingulifera</i> ) <i>cingulatum peregrini</i>	86 <i>Chilostoma</i> ( <i>Cingulifera</i> ) <i>cingulatum preslii</i>	0,3	0	0
90 <i>Corneola squamatinum</i>	88 <i>Corneola desmoulinsii</i>	0,6	16,9	-
94 <i>Cylindrus obtusus</i>	18 <i>Arianta chamaeleon</i>	0,9	18,8	24,9
94 <i>Cylindrus obtusus</i>	9 <i>Arianta arbustorum arbustorum</i>	0,9	20	23,8
100 <i>Dinarica</i> ( <i>Dinarica</i> ) <i>pouzolzii</i>	102 <i>Dinarica</i> ( <i>Dinarica</i> ) <i>serbica</i>	0,9	11	13,6
100 <i>Dinarica</i> ( <i>Dinarica</i> ) <i>pouzolzii</i>	103 <i>Dinarica</i> ( <i>Sablaria</i> ) <i>stenomphala</i>	1,8	16	24,7
110 <i>Faustina faustina orba</i>	111 <i>Faustina kiralikoeica</i>	0	17,4	-
107 <i>Faustina faustina associata</i>	108 <i>Faustina faustina faustina</i>	0	10,7	13
113 <i>Helicigona lapicida andorraca</i>	115 <i>Helicigona lapicida andorraca</i>	0	0,3	0,3
119 <i>Helicigona lapicida lapicida</i>	117 <i>Helicigona lapicida lapicida</i>	0,6	1,8	0,6
113 <i>Helicigona lapicida andorraca</i>	117 <i>Helicigona lapicida lapicida</i>	0,6	11,8	14,1
154 <i>Liburnica</i> ( <i>Liburnica</i> ) <i>setosa</i>	149 <i>Liburnica</i> ( <i>Liburnica</i> ) <i>albanograeca</i>	0	3,4	-
150 <i>Liburnica</i> ( <i>Liburnica</i> ) <i>dunjana</i>	153 <i>Liburnica</i> ( <i>Liburnica</i> ) <i>setigera setigera</i>	0	6,3	-
158 <i>Liburnica</i> ( <i>Superba</i> ) <i>skipetarica</i>	156 <i>Liburnica</i> ( <i>Superba</i> ) <i>kulmankana</i>	0	2,1	-
153 <i>Liburnica</i> ( <i>Liburnica</i> ) <i>setigera setigera</i>	157 <i>Liburnica</i> ( <i>Superba</i> ) <i>skipetarica</i>	0	6,9	-

regarding the shell and genital morphology. In *C. (Cattania)* the accessory glands are usually split (Fig. 4.27); occasionally one of the glands is undivided.

Subgenus nov. *Cattaniella*, genus *Cattania*

Type species: *Helix cingulata olympica* Roth, 1855

**Diagnosis.** The two *Cattaniella* species share a unique combination of nucleotides in the 655 bp *COI* sequence obtained with general barcoding primers (Folmer, 1994) at the following relative positions: 87 A, 95 T, 235 A, 331 G, 365 G, 406 T, 499 G, 542 A, 543 G, 583 A.

**Description.** Shell depressed globular to low conical, nearly discoid, whitish, corneous or brown, with one to three brown spiral bands. The accessory glands in *C. (Cattaniella) thateensis* are split (Subai, 2012).

**Molecular data.** *Cattania (Cattaniella)* is represented by *C. (Cattaniella) olympica* and *C. (Cattaniella) thateensis* (Subai, 2012). It is the sister-group of the combined three other subgenera (Figs 2, S2, S3, S6) of *Cattania*. Clearly *C. (Cattaniella) olympica* should no longer be considered a subspecies of *C. (Cattania) trizona* (see Knipper, 1939). Likewise, *C. (Cattaniella) thateensis* cannot be classified in *Wladislavia* (see Subai, 2012). Future research will have to show whether *Campylaea apfelbecki* Sturany, 1901 and *Campylaea zebiana* Sturany, 1907 belong to *Cattania (Cattaniella)* as well (Subai, 2012).

**Distribution.** Higher montane areas of E Albania (Thäte mountains); Olympos and Ossa mountain areas of Thessaly, Greece.

**Remarks.** For the moment being, only the two species that could be investigated for this study are classified in *Cattaniella*.

**Derivatio nominis.** *Cattaniella* refers to *Cattania*.

Genus *Causa* Schileyko, 1971 (monotypic)

Type species: *Glischrus (Helix) holosericea* Studer, 1820

**Molecular data.** The sister-group relationship, as well as a substantial genetic distance between *Causa* and *Isognomostoma* are established (PP = 1.0; Figs 1, 2, S2-S6; Table 4). Only the *H3* data failed to show a direct sister-group relation, but still placed both genera in the same clade (PP = 0.42, Fig. S1).

**Age.** The most recent common ancestor of *Causa* and *Isognomostoma* is estimated at ca. 33.0-30.1 MYA (Figs 2, S5).

**Distribution.** Alps, Sudetes and W Carpathians (Tatra Mts), isolated in S Germany (Franconian Jura).

**Remarks.** Conchologically, *Causa holosericea* (Fig. 3.5) and *Isognomostoma isognomostomos* (Fig. 3.4) are both aberrant among the Ariantinae by the dentate aperture. These species were considered congeneric until Schileyko (1971), primarily based on differences in genital anatomy, introduced *Causa* as a new genus. See also *Causa* in Schileyko (2006, 2013) for details regarding the shell and genital morphology. The accessory glands in both *Causa* and *Isognomostoma* are undivided (Fig. 4.7-4.8).

Subgenus *Chilostoma* Fitzinger, 1833, genus *Chilostoma*

Type species: *Glischrus (Helix) foetens* Studer, 1820

**Molecular data.** Four or five species can be classified in *Chilostoma* s. str., three of which are included in this study. Within the genus *Chilostoma* (PP = 1.0; Figs 1, 2, S2, S3, S5, S6), three well supported clades can be discerned: I) *Chilostoma (Chilostoma)*, II) *Chilostoma (Cingulifera)* Held, 1838 and III) *Chilostoma (Achatia)* subgen. nov. The *COI* sequence divergences between each of the three subgenera are about 15%. *Chilostoma* is the sister-group of all other Ariantinae taxa in group B (PP ≥ 0.6, Figs 1, 2, S6). Only Figs S3 and S5 specifically indicate *Corneola* as its sister-group (PP = 0.94). The latter relationship is not observed if both of the studied *Corneola* species are included (Figs 2, S1, S2, S6). The phylogenetic relationships between the subgenera of *Chilostoma* are not resolved. Figs 2, S4 and S6 support (PP ≥ 0.95) a sister-group relationship between *C. (Chilostoma)* and *C. (Cingulifera)*, whereas Figs 1, S3 and S5 indicate *Chilostoma (Achatia)* as the sister-group of *C. (Cingulifera)* (PP ≥ 0.95).

**Age.** The most recent common ancestor of the genus *Chilostoma* is estimated at ca. 38.5-31.3 MYA, whereas that of *C. (Chilostoma)* is estimated at ca. 20.3-18.4 MYA (Figs 3 and S5).

**Distribution.** The Alps (SE France, S Switzerland, N Italy).

**Remarks.** Unexpectedly, from a conchological perspective, *C. (Chilostoma) zonatum* (Fig. 3.7) turns out to be more closely related to *C. (Chilostoma) frigidum* and *C. (Chilostoma) tigrinum* (Fig. 3.8), than to *C. (Achatia) achates* (Fig. 3.6), which shares the chestnut brown colour of the shell. That colour might be the plesiomorphic character state in *Chilostoma*. Nowa-



days, *Helix foetens* is either synonymised with *C. (Chilostoma) zonatum*, as by Turner *et al.* (1998) or it is considered a subspecies of that species (Bank *et al.*, 2001). In the past many subgenera have been assigned to *Chilostoma* (Zilch, 1960; Bank *et al.*, 2001). It is unclear which, if any, character states of the genital tract are diagnostic for the subgenera of *Chilostoma*. The accessory glands are undivided (Fig. 4.3, 4.4).

Subgenus ***Cingulifera*** Held, 1838 (monotypic), genus ***Chilostoma***

Type species: *Glischrus (Helix) cingulata* Studer, 1820. The type species can be subdivided into several subspecies, five of which are included in this study

*Molecular data.* See *Chilostoma (Chilostoma)*.

*Age.* The most recent common ancestor of *C. (Cingulifera)* is estimated at ca. 7.9–7.0 MYA (Figs 2, S5). The split between *C. (Cingulifera)* and either *C. (Chilostoma)* or *C. (Achatica)* subgen. nov. (see *Chilostoma*) is estimated at ca. 29 and 24.7 MYA, respectively.

*Distribution.* NE Italy, SW Austria, SE Switzerland, locally in the French Alps, Central Italy and S Germany (partly introduced). *Chilostoma (Chilostoma)* and *C. (Cingulifera)* have a parapatric distribution. Generally the former subgenus is distributed in the western Alps, whereas the latter one has its main range in the eastern Alps. Additionally, our preliminary results indicate a strong separation between the *Chilostoma* species east versus west of the Camonica valley (Valcamonica, Italy).

*Remarks.* *Chilostoma (Cingulifera)* is a generally accepted subgenus of *Chilostoma* (Zilch, 1960; Bank *et al.*, 2001). Taxonomically it was supposed to encompass only a single species, i.e. *Chilostoma (Cingulifera) cingulatum* (Studer, 1820) (Fig. 3.9, 3.10) with a large number of alleged subspecies (Pfeiffer, 1951), some of which are here classified differently, however, viz. *Chilostoma (C.) frigidum* and *Chilostoma (C.) tigrinum* (De Cristofori and Jan, 1832; Fig. 3.8).

*Chilostoma (Cingulifera) cingulatum peregrini* Falkner, 1998 was introduced as a replacement name for *Chilostoma (Cingulifera) cingulatum cingulina* (Strobel, 1844), not *Helix cingulina* Deshayes, 1839 (in Férussac and Deshayes). Contrary to the prevailing view, Falkner suggested that the northern alpine populations of *Chilostoma (Cingulifera) cingulatum* might belong to two instead of only a single subspecies, viz. *Chilostoma (Cingulifera) c. peregrini* from near Inns-

bruck (Austria) and *Chilostoma (Cingulifera) c. preslii* from near Berchtesgaden (Falkner, 1998; Kierdorf-Traut, 2012). *COI* and *CytB* sequences for specimens from both northern alpine localities (Table S7, 72–73 versus 83–86) are virtually identical and differ about 0.5 % (Table 4) from sequences of southern alpine, undisputed *Chilostoma (Cingulifera) c. preslii* (78–82, Table S7). These data indicate that *Chilostoma (Cingulifera) c. peregrini* is a junior synonym of *Chilostoma (Cingulifera) c. preslii*, which has a disjunct range, occurring in both the northern and the southern limestone Alps. See *Helicigona (Cingulifera)* and *Chilostoma (Cingulifera)* in Schileyko (2006, 2013) for details regarding the shell and genital morphology. *Chilostoma (Cingulifera)* has undivided accessory glands (Fig. 4.4).

Genus ***Corneola*** Held, 1838

Type species: *Helix cornea* Draparnaud, 1801

*Molecular data.* *Corneola squamatinum* (Rossmässler, 1835) and *C. desmoulinsii* (Farines, 1834) together are monophyletic (PP = 0.86 and 0.77; Figs 2, S6). The *COI* sequence divergence between these species is 16.9% (Table 4). The phylogeny reconstructions are indistinct regarding the position of this genus. In the concatenated analyses it is shown between *Campylaea* and *Chilostoma* (Fig 1), as the sister-group of either of these (Figs S6 and S5) or as the sister-group of *Causa*, *Isognomostoma* and *Helicigona* (Fig. 2). *Corneola* is here regarded as a genus.

*Age.* The most recent common ancestor of *Corneola* is estimated at ca. 52.5 MYA (Fig. 2).

*Distribution.* *Corneola acrotricha* (Fischer, 1877) and *C. desmoulinsii* are mainly found in the Pyrenees. *Corneola squamatinum* extends also further into southern and central France, along the Atlantic coast up to Brittany, whereas *C. crombezi* (Bourguignat, 1880) inhabits the Alpes-Maritimes (Falkner *et al.*, 2002).

*Remarks.* In the most recent literature (Bank *et al.*, 2001; Falkner *et al.*, 2002) *Corneola* is regarded as a subgenus of *Chilostoma*, with four species. Two of these, viz. *Corneola desmoulinsii* (Fig. 1.24) and *C. squamatinum*, are included in this study. See *Corneola* in Schileyko (2013) for details regarding the shell and genital morphology. The accessory glands are undivided (Fig. 4.5)

Genus *Cylindrus* Fitzinger, 1833 (monotypic)

Type species: *Pupa obtusa* Draparnaud, 1805

**Molecular data.** The phylogeny reconstructions for the combined datasets show strong support for a sister-group relation between *Cylindrus* and *Arianta* (PP = 1.0, Figs 1, 2, S5, S6). Only the phylogeny based on *COI* fails to indicate that these taxa are sister-groups, thus sharing a unique common ancestor. The sequence divergence between *Cylindrus* and *Arianta* is ca. 19% for *COI* and up to 25% for *CytB* (table 4).

**Age.** The common ancestor of *Arianta* and *Cylindrus* is estimated to have diverged at ca. 47.6–46.4 MYA (Figs 2, S5).

**Distribution.** Endemic to the Austrian Alps (between 1600 and 2500 m), known from Oberösterreich, Niederösterreich, Salzburg, Steiermark and Kärnten.

**Remarks.** Among the (sub)genera of Ariantinae that can be distinguished by shell-morphology, *Cylindrus* is the most distinctive because the shell is cylindrical and much higher than broad (Fig. 3.3). Its sister-group, the genus *Arianta*, is characterized by much larger shells that vary in shape between flattened and globular. This close relationship, which is surprising in view of the morphological data, was reported by Groenenberg et al. (2012) and later on confirmed by Cadahia et al. (2013). Despite the long geological history of *Cylindrus* that is indicated by the molecular data and is also suggested by its aberrant shell morphology, no clear fossil representatives of this genus, or forms that are transitional in shell-shape, are known from before the Würm (Zilch, 1960; Frank, 2006). See *Cylindruini* in Schileyko (2006, 2013) for details regarding the structure of the genital tract. *Cylindrus* has undivided accessory glands (Fig. 4.2).

Genus *Delphinatia* Hesse, 1931

Type species: *Helix alpina* Michaud, 1831

**Molecular data.** *Delphinatia fontenillii alpina* (Michaud, 1831), and *D. glacialis* (Férussac, 1832) together are monophyletic (PP ≥ 0.93, Figs 2, S1, S2, S6) and form a clade with *Drobacia* and *Vidovicia* in the phylogeny reconstructions for the combined datasets (0.5 ≤ PP ≤ 0.86, Figs 1, 2, S5, S6). However, in the trees based on individual markers, this clade is only observed with *H3* (PP = 0.8, Fig. S1). There is no consensus regarding the sister-group relations of these three taxa. Only of *D. f. alpina* sufficient sequence data were obtained to include it in the phylogeny re-

constructions of the stringent dataset (Figs 1, S5).

**Age.** The most recent common ancestor of the combined group *Delphinatia-Drobacia-Vidovicia* is estimated at ca. 59.1–53.3 MYA (Figs 2, S5); that of *Delphinatia* is estimated at ca. 17.5 MYA (Fig 2).

**Distribution.** French Alps (departments of Hautes-Alpes, Haute-Savoie, Isère and Savoie) to the adjacent Italian Alps (Alpi Cozie and Graie) (Gavetti et al., 2008).

**Remarks.** *Delphinatia* is considered a subgenus of *Chilostoma* by Bank et al. (2001), but has been classified as a subgenus of *Campylaea* as well (Zilch, 1960). Only two species are generally recognized in *Delphinatia*, viz. *D. fontenillii* (Michaud, 1829), and *D. glacialis*, which are both included in this study. Falkner et al. (2002) distinguished *D. f. fontenillii* and *D. f. alpina* (Fig. 3.11) next to the monotypic *D. glacialis*. See *Campylaea (Delphinatia)* and *Chilostoma (Delphinatia)* in Schileyko (2006, 2013) for details regarding the shell and genital morphology. The accessory glands (Fig. 4.12) are undivided, or one of them is split for up to 25–50% of its length.

Subgenus *Dinarica* Kobelt, 1902, genus *Dinarica*

Type species: *Helix pouzolzii* Deshayes, 1830

**Molecular data.** Two subgenera of *Dinarica* can be recognized, viz. *Dinarica (Dinarica)* and *D. (Sabljaria)*. In this study, the former taxon is represented by *D. (Dinarica) pouzolzii* (Fig. 3.22) and *D. (D.) serbica* Kobelt, 1872. *Dinarica (Dinarica)*, as well as the genus itself, are shown to be monophyletic (PP = 1, Figs 1, 2, S5, S6). The *COI* sequence divergence between *D. (Dinarica) serbica* and *D. (Dinarica) pouzolzii* is about 10% (Table 4).

The phylogenies based on the concatenated datasets slightly differ regarding to the position of *Dinarica*. Figures 2, S5 and S6 suggest a sister-group relationship between *Dinarica* and *Liburnica* (0.44 ≤ PP ≤ 0.78). In these figures *Dinarica - Liburnica* has a sister-group relation with the clade *Kollarix - Pseudotrizona - Cattania - Thiessea - Josephinella*. Basically Fig 1 shows the same topology, but here *Liburnica* is the sister-group of the latter genera including *Dinarica*.

**Age.** The most recent common ancestor of *Dinarica* is estimated at ca. 37.1–36.2 MYA (Figs 2, S5).

**Distribution.** Along the NE coast of the Adriatic sea, in SE Croatia, Bosnia-Herzegovina, S Serbia, Montenegro, Kosovo, Albania, the western border of

Macedonia and NW Greece. *Dinarnica* (*D.*) *pouzolzii* and *D.* (*D.*) *serbica* have partially overlapping ranges. Where the former dominates the coastal region of Montenegro, the latter occurs more inland.

**Remarks.** See *Campylaea* (*Dinarica*) and *Chilosoma* (*Dinarica*) in Schileyko (2006, 2013) for details regarding the shell and genital morphology. *Dinarica* (*Dinarica*) has split accessory glands (Fig. 4.23).

#### Genus ***Drobacia*** Brusina, 1904

Type species: *Helix banatica* Rossmässler, 1838

**Molecular data.** Both *Drobacia* species, viz. *D. banatica* (Fig. 3.26) and *D. cf maeotica* Wenz, 1926 (in Krejci and Wenz, 1926), are included in this study. The taxon is shown to be monophyletic (PP = 1.0 Figs 1, 2, S5, S6). The position of *Drobacia* within the subfamily Ariantinae is still unclear. The phylogeny reconstructions indicate that *Drobacia* forms a clade with *Delphinatia* and *Vidovicia* (see *Delphinatia*). Only the phylogeny for *COI* supports a sister-group relationship with *Liburnica* (PP = 0.86; Fig. S2).

**Age.** For an age estimation of the most recent common ancestor of *Drobacia*, *Delphinatia* and *Vidovicia*, see *Delphinatia*. *Drobacia banatica* and *D. cf maeotica* are estimated to have diverged ca. 8.7–7.8 MYA (Figs 2, S5).

**Distribution.** W and SW Romania and locally in E Hungary. In the Pleistocene *Drobacia* reached as far as the Harz Mts in Thüringen, Germany (Jaeckel, 1962).

**Remarks.** See *Helicigona* (*Drobacia*) and *Drobacia* in Schileyko (2006, 2013) for details regarding the shell and genital morphology. *Drobacia* has undivided accessory glands (Fig. 4.9).

#### Genus ***Faustina*** Kobelt, 1904

Type species: *Helix faustina* Rossmässler, 1835

**Molecular data.** *Faustina* is shown monophyletic in all our phylogeny reconstructions (PP ≥ 0.99), but *CytB* and *I6S* sequences were only obtained for subspecies of *F. faustina*. Consequently the monophyly of the genus could only be assessed with the data for *H3* and *COI*. Sequence divergences within *Faustina* are generally large; between *F. faustina orba* (von Kimakowicz, 1890) and *F. kiralikoeica* (von Kimakowicz, 1890) the sequence divergence for *COI* is 17.4%. Even between the alleged subspecies *F. f. faustina* (Ross-

mässler, 1835) and *F. f. associata* (Rossmässler, 1835) divergences reach up to 10.7% (Table 4). A sister-group relationship between *Faustina* and *Kosicia* is shown with the phylogeny reconstructions for the concatenated datasets (PP ≥ 0.95; Figs 1, 2, S5, S6). The phylogeny for *H3* indicates *Faustina* as the sister-group of all other Ariantinae, but this is not supported by any of the other phylogeny reconstructions.

**Age.** The most recent common ancestor of the investigated *Faustina* specimens is estimated at ca. 13.4–11.3 MYA. The split between *Faustina* and *Kosicia* is estimated at 56–51.7 MYA (Figs 2, S5).

**Distribution.** The Carpathian Mts, E Czech, Slovakia, S Poland, W Ukraine and Romania; also in NE Hungary. *Faustina faustina* (Fig. 3.12) has the widest distribution, *F. rossmaessleri* (Pfeifer, 1848) and *F. cingulella* (Rossmässler, 1837) are mainly found in Slovakia, *F. barcensis* (von Kimakowicz, 1890) and *F. kiralikoeica* are found in Romania.

**Remarks.** There are at least 5 *Faustina* species, 3 of which are included in this study, viz. the nominate subspecies of *F. faustina*, two additional subspecies [*F. faustina associata* and *F. faustina orba*], and *F. kiralikoeica*. See *Campylaea* (*Faustina*) and *Faustina* in Schileyko (2006, 2013) for details regarding the shell and genital morphology. In *Faustina* both types of accessory glands occur. *Faustina cingulella* and *F. rossmaessleri* have undivided glands, whereas they are split up to half their length in *F. faustina* (Fig. 4.19), *F. barcensis* and *F. kiralikoeica*.

#### Genus ***Helicigona*** Férussac, 1821

Type species: *Helix lapicida* Linnaeus, 1758

**Molecular data.** In the past this generic name has been used for many taxa of the Ariantinae (Hesse, 1931; Knipper, 1939; Zilch, 1960; Subai, 1984). None of our phylogeny reconstructions support these views. The phylogeny reconstructions of the concatenated datasets indicate that *Causa* and *Isognomostoma* together, are most likely the sister-group of *Helicigona* (group A; Figs 1, 2, S5, S6). The monophyly of the two alleged subspecies of *H. lapicida* is beyond dispute (PP = 1.0; Figs 1, 2, S1–S6). *COI* and *CytB* sequence divergences within each subspecies are less than 2.5% (n = 4), but between both subspecies they reach up to 12% and 14%, respectively.

**Age.** The only fossil that can be indisputably assigned to any of the currently recognized Ariantinae is a representative of *Helicigona* (see Nordsieck, 2014

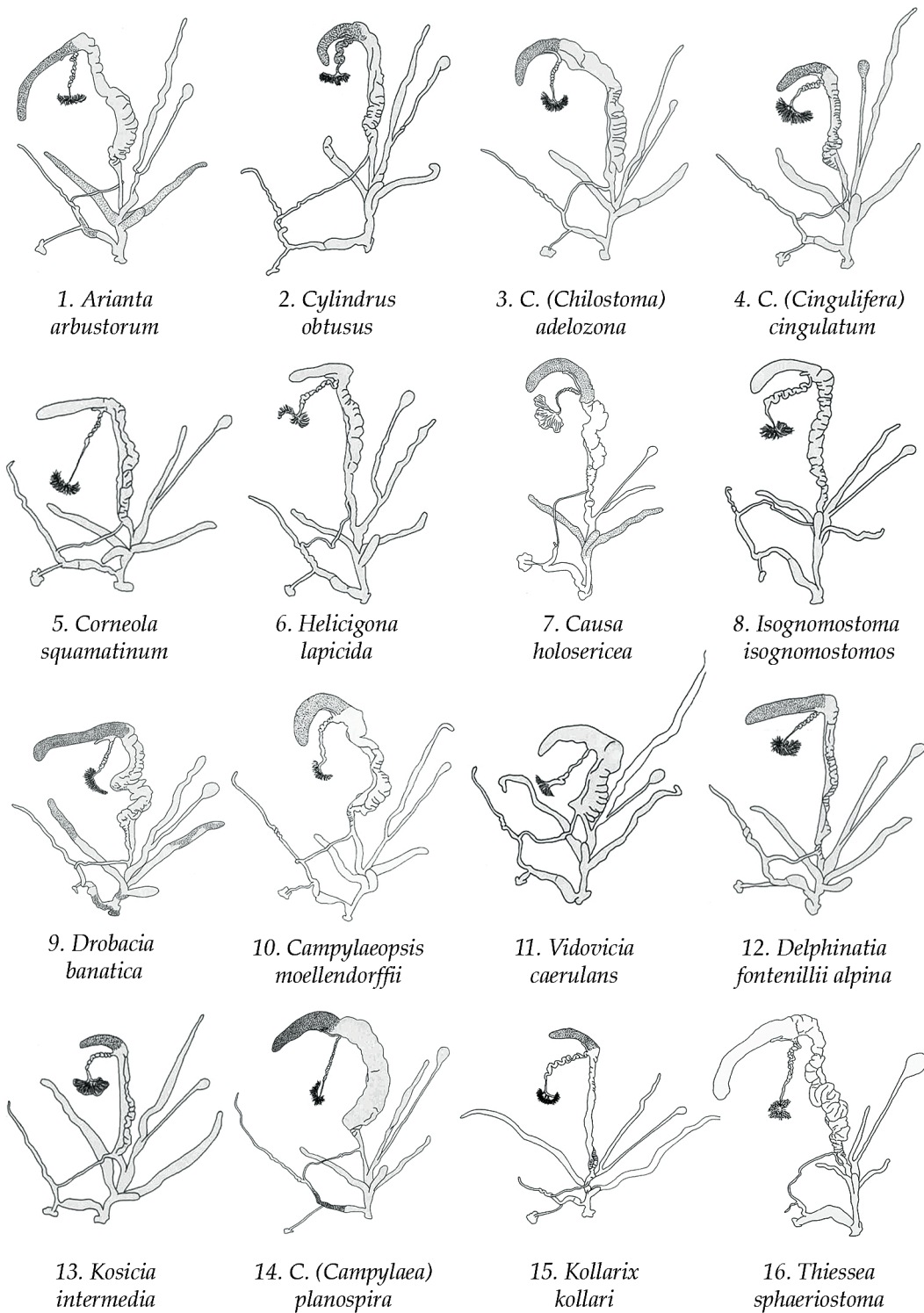
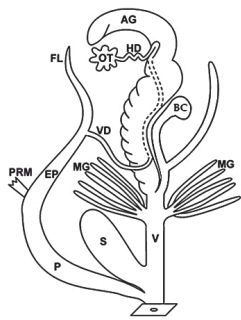


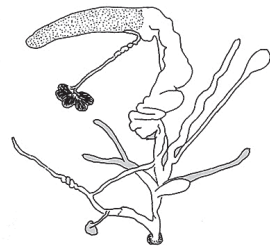
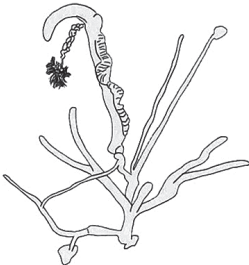
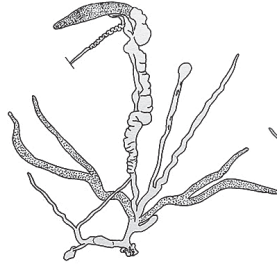
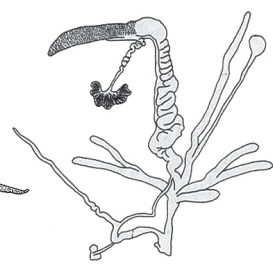
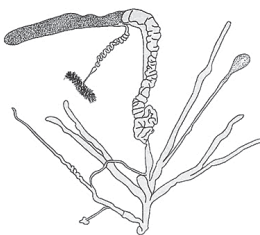
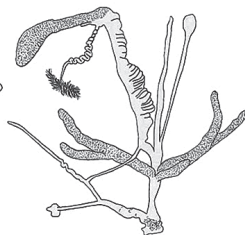
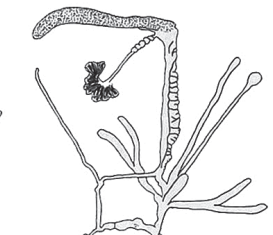
Fig. 4. Genital anatomy for most of the currently recognized genera of Ariantinae. The simplified diagram of the genital morphology was reproduced and adapted from Koene and Schulenburg (2005; Creative Commons Attribution License 2.0).





Genital morphology

AG = albumen gland  
 BC = bursa copulatrix  
 BTD = diverticulum  
 EP = epiphallus  
 FL = flagellum  
 HD = hermaphroditic duct  
 MG = accessory glands  
 OT = ovotestis  
 P = penis  
 PRM = penis retractor muscle  
 S = dart sac (bursa telae)  
 V = vagina  
 VD = vas deferens

17. *L. (Superba) skipetarica*18. *Josephinella reischuetzi*19. *Faustina faustina*20. *L. (Liburnica) setosa*21. *L. (Superba) kulmakana*22. *Josephinella hemonica*23. *D. (Dinarica) pouzolzii*24. *D. (Sabljaria) stenomphala*25. *C. (Oricampylaea) ljubetenensis*26. *Josephinella vikosensis*27. *C. (Cattania) trizona*28. *Pseudotrizona inflata*29. *C. (Ariantopsis) pelia*30. *C. (Wladislawia) polinskii*



and references therein) from the Late Burdigalian (~17.5–16.0 MYA). This date was the only calibration point used in our BEAST analyses. The split between *Helicigona* and the lineage *Causa-Isognomostoma* is estimated at ca. 62.6–61.2 MYA (Figs 2, S5).

**Distribution.** The nominate subspecies is widely distributed in W and N Europe, from S Scandinavia and central England to the south up to S France, to the east up to Czech and W Poland. *Helicigona lapicida andorrica* (Bourguignat, 1876) is restricted to the eastern Pyrenees.

**Remarks.** *Helicigona* is considered a monotypic genus with only two clearly differentiated subspecies, viz. *Helicigona l. lapicida* (Fig. 3.25) and *H. l. andorrica*, which are both included in this study. See *Helicigona* (*Helicigona*) and *Chilostoma* (*Helicigona*) in Schileyko (2006, 2013) for details regarding the shell and genital morphology. The accessory glands are undivided (Fig. 4.6).

**Genus *Isognomostoma*** Fitzinger, 1833 (monotypic)  
Type species: *Helix personata* Lamarck, 1792 [= *Isognomostoma isognomostomos* (Schröter, 1784)]

**Molecular data.** *Isognomostoma isognomostomos* (Fig. 3.4) and *Causa holosericea* (Fig. 3.5) have long been regarded as congeneric. All phylogeny reconstructions, except the one based on *H3* (Fig. S4), explicitly show *Causa* and *Isognomostoma* together as a monophyletic group (PP ≥ 0.99; Figs 1, 2, S2–S6). See also the paragraph on *Causa*.

**Distribution.** Mountains of central Europe, S of the line Eifel, Sauerland and the Harz Mts. From E France eastwards in Switzerland, Austria, N Italy, Slovenia, Croatia, Czech, Slovenia, S Poland (Carpathians), NE Hungary and Rumania.

**Remarks.** See *Isognomostoma* in Schileyko (2006, 2013) for details regarding the shell and genital morphology. The accessory glands are undivided (Fig. 4.8).

**Genus *Josephinella*** Haas, 1936  
Type species: *Helix hemonica* Thiesse, 1884 (Fig. 3.34)

**Molecular data.** Based on 11 included species (2 undescribed; Table S7), *Josephinella* is considered a monophyletic group (PP = 1.0; Figs 1, 2, S2–S6). The phylogeny reconstructions for the combined datasets show *Thiessea* as the sister-group of *Josephinella* (PP

= 1.0; Figs 1, 2, S5, S6). *Josephinella reischuetzi* (Subai, 1990) and *J. vikosensis* (Subai, 1990) together, which were once classified in *Superba* by Subai and Fehér (2006) are shown to belong to *Josephinella* (PP ≥ 0.87; Figs S1, S2).

**Age.** The most recent common ancestor of *Josephinella* (based on four taxa) is estimated at ca. 22–21.6 MYA (Figs S5, 2).

**Distribution.** Southern half of Albania, the SW border area of Macedonia (FYROM), the Ionian islands, mainland Greece and the Peloponnese.

**Remarks.** With at least 18 named species, and more than 10 still to be described (Subai, in prep.), *Josephinella* is the most speciose genus of the Ariantinae. For this study 11 species were included.

See *Helicigona* (*Josephinella*) and *Chilostoma* (*Josephinella*) in Schileyko (2006, 2013) for details regarding the shell and genital morphology. The accessory glands are generally split from halfway up to 2/3 of their length (Fig. 4.22); specimens with one or both glands undivided (*J. vikosensis* and *J. reischuetzi*; Fig. 4.26 and Fig. 4.18) or trifurcate accessory glands are rare (n=60: 4 undivided, 56 split, of which 3 specimens had only one divided gland).

**Genus nov. *Kollarix***  
Type species: *Helix kollari* Pfeiffer, 1856 (monotypic)

**Diagnosis.** The diagnosis of this monotypic subgenus is by definition identical with that of its type species, i.e. *Kollarix kollari* (Pfeiffer, 1856). *Kollarix* gen. nov. is also differentiated by a unique combination of nucleotides in the 655 bp *COI* sequence obtained with general barcoding primers (Folmer, 1994) at the following relative positions: 16 C, 67 A, 68 A, 84 G, 94 T, 357 G, 475 A, 493 G, 556 G, 625 C.

**Description.** Shell strongly depressed, nearly discoid, with 4¾–5¼ whorls; umbilicus wide, measuring 1/5–1/6 of the total shell width; corneous brown, with a brown spiral band in a whitish zone (see Welter-Schultes, 2012: 595, *Helicigona kollari*); surface finely granulated, with growth lines and hairs. Height 8.5–12.0 mm; width 18.5–27.0 mm. The accessory glands are always undivided (Fig. 4.15). Stimulator broad, flattened, filling the genital atrium and reaching far into the vagina; an extension ends at the insertion of the penis. Penial papilla small, conical, with fine transverse ridges and an obtuse apex with a short, transverse, slit-like pore. Secondary ureter closed for 0.5–1.0 mm and open for the remaining 2–3 cm.

**Molecular data.** Genetically, *Kollarix kollari* cannot be assigned to *Liburnica* (Subai, 2002), nor any other of the described genera. *Kollarix* is shown to be a separate lineage within the Ariantinae, which is more closely related to *Pseudotrizona* gen. nov., than to *Liburnica* Kobelt, 1904 (Figs 1, 2, S5, S6).

**Age.** The most recent common ancestor of *Kollarix* and the clade (*Pseudotrizona* - *Cattania* - *Josephinella* - *Thiessea*) is estimated at ca. 55.9–55.8 MYA (Figs 2, S5).

**Distribution.** Endemic to Serbia, S of the Donau up to Aleksinac, between Šabac and Bor districts.

**Remarks.** *Helix kollari* Pfeiffer, 1856 (Fig. 3.19) has been classified in *Campylaea* (by Tomić, 1959), in *Helicigona* (by Knipper, 1939; Maassen, 1985) and most recently in *Liburnica* (by Subai, 2002; Bank, 2012). In his treatise on *Liburnica*, Subai (2002) hypothesized that *Kollarix kollari* might be the oldest representative of *Liburnica*. Since *Kollarix kollari* cannot be assigned to any of the described genera, neither genetically nor morphologically, it is here given generic status. The name *Kollarix* has been used by Groenenberg *et al.* (2012) and Schileyko (2013: 146), but in both cases with the explicit note that this was not for purposes of zoological nomenclature.

**Derivatio nominis.** *Kollarix* refers to *kollari*.

#### Genus *Kosicia* Brusina, 1904

Type species: *Helix intermedia* Pfeiffer, 1828

**Molecular data.** *Kosicia* is usually regarded as a subgenus of *Chilostoma* (Zilch, 1960; Bank *et al.*, 2001), but should be given generic status based on our phylogeny reconstructions. Its three species, viz. *Kosicia ambrosi* (Strobel, 1852) (Fig. 3.15), *K. intermedia* (Fig. 3.16) and *K. ziegleri* (Rossmässler, 1836) (Fig. 3.17) form a monophyletic group (PP  $\geq$  0.94; Figs 1, 2, S1–S6). *Kosicia ambrosi*, which is much smaller than the other two species, is the sister-group of *K. intermedia* and *K. ziegleri* together (Figs 1, 2, S2, S3, S5, S6). The phylogeny reconstructions for the concatenated datasets show *Faustina* as the sister-group of *Kosicia* (PP = 1.0; Figs 1, 2, S5 and S6).

**Age.** The most recent common ancestor of *Kosicia* is estimated at ca. 30.1–28.0 MYA (Figs 2, S5); that of *K. intermedia* and *K. ziegleri* is estimated at ca. 7 MYA (Figs 2, S5).

**Distribution.** *Kosicia intermedia* is most widely distributed; it occurs in NE Italy, S Austria (Kärnten), NE Italy, Slovenia and NW Croatia. *Kosicia ambrosi*

has the smallest range; it is endemic to E Trentino and the Prealps of Veneto (Italy). *Kosicia ziegleri* occurs in S Kärnten (Austria) and in the border area between Italy and Slovenia.

**Remarks.** All three known *Kosicia* species were included in this study. See *Helicigona* (*Kosicia*) and *Kosicia* in Schileyko (2006, 2013) for details regarding the shell and genital morphology. The accessory glands are always undivided (Fig. 4.13).

#### Subgenus *Liburnica* Kobelt, 1904, genus *Liburnica*

Type species: *Helix setosa* Férussac, 1832 (Fig. 3.20)

**Molecular data.** *Liburnica* has been regarded a subgenus of *Campylaea* (Zilch, 1960) and *Chilostoma* by Bank *et al.* (2001), but none of our phylogeny reconstructions indicate a close relationship between any of these taxa. *Liburnica* represents a distinct, monophyletic lineage (PP = 1.0; Figs 1, 2 and S1–S6), which includes *Superba* (Subai and Fehér, 2006) according to *H3* and *COI* sequences (Figs S1, S2; see *Superba*). The position of *Liburnica* is only partly resolved; our data hint at a sister-group relation with *Dinarica* ( $0.44 \leq$  PP  $\leq$  0.78; Figs 2, S5, S6; see *Dinarica*). Only the phylogeny based on *COI* explicitly supports another sister-group relation; see *Drobacia*. Six species of *Liburnica* (*Liburnica*) could be investigated. The subgenus is shown as a monophyletic group in the phylogeny based on *COI* (PP = 0.75; Fig. S2). *COI* sequence divergences within *L. (Liburnica)* range from 6.3% to 3.4%. Between *L. (Liburnica)* and *L. (Superba)* the *COI* sequence divergence is  $\leq$  6.9% (Table 4).

**Age.** The most recent common ancestor of *Liburnica* and *Dinarica* is estimated at ca. 53.2–51.4 MYA; that of *Liburnica (Liburnica)* is estimated at ca. 5.9–3.1 MYA (Figs 2, S5).

**Distribution.** Mts. along the NE coast of the Adriatic Sea in Croatia, Bosnia-Herzegovina, Montenegro, Kosovo, Albania, W Macedonia, southwards to Epirus in NW Greece.

**Remarks.** With over 15 described species, *Liburnica* is among the most speciose genera of Ariantinae. Conchologically *Liburnica* is quite variable (Fig. 3.20, 3.23). The 6 species used in this study (10 including *Superba*), suggest that these forms radiated rapidly ( $< \sim 6$  MYA; see Age). See Subai (2002) and Schileyko (2013) for details regarding the shell and genital morphology. The upper 1/3 to 2/3 of the accessory glands in *L. (Liburnica)* are generally split (Fig. 4.20); occasionally one (Fig. 4.17) or both glands are undivided.

Subgenus nov. *Oricampylaea*, genus *Campylaea*

Type species: *Faustina (Campylaea) illyrica* Stabile, 1864

**Diagnosis.** *Oricampylaea* subgen. nov. is differentiated by a unique combination of nucleotides in the 655 bp *COI* sequence obtained with general barcoding primers (Folmer, 1994) at the following relative positions: 88 T, 187 T, 220 T, 301 T, 385 A, 409 C, 556 T, 575 T, 578 C, 650 C.

**Molecular data.** This clade (PP = 1.0; Fig. S2) consists of at least the species *Campylaea (Oricampylaea) illyrica* and *C. (Oricampylaea) lefeburiana* (Férussac, 1821). After our *H3* sequence, *Helicigona (Arianta) ljubetenensis* Wagner, 1914 (in Sturany and Wagner, 1914), which was regarded as a subspecies of *Cattania (C.) trizona* by Knipper (1939) and Bank (2012), has to be added as a third species.

**Age.** Based on the intraspecific divergence in *C. (Oricampylaea) illyrica*, the most recent common ancestor of *C. (Oricampylaea)* is estimated at, at least, ca. 19–17.9 MYA (Figs 2, S5).

**Distribution.** Southern Germany (introduced), southern Austria, from Slovenia southwards to W and N Croatia. *Campylaea (Oricampylaea) illyrica* also occurs along the SW Hungarian border, in N Serbia and in SW Romania. *Campylaea (Oricampylaea) ljubetenensis* is restricted to the Šar Mts (between Kosovo and NW Macedonia).

**Remarks.** The phylogeny reconstructions based on *H3* and *COI* show a clade within *Campylaea* that separates *C. (Oricampylaea) illyrica* and *C. (Oricampylaea) lefeburiana* from *C. (Campylaea) planospira*. Here we denoted this group *Oricampylaea* subgen. nov., because this clade persists even in case the untimely inclusion of *C. (Oricampylaea) ljubetenensis* would turn out to be incorrect. Observing *C. (Oricampylaea) ljubetenensis* in a clade (data for *H3* only) with *C. (Oricampylaea) illyrica* is surprising both morphologically as well as geographically; in shell shape *C. (Oricampylaea) ljubetenensis* resembles *C. (Cattania) trizona* more than *C. (Oricampylaea) illyrica*, whereas it occurs ca. 250 km south of the distribution area of the latter species. Future research has to show if the provisional assignment of *C. ljubetenensis* to *C. (Oricampylaea)* will uphold and whether *Campylaea hirta* (Menke, 1830), *C. macrostoma* (Rossmässler, 1836), *C. schlaerotricha* (Bourguignat, 1870), and *C. sadleriana* (Rossmässler, 1838) should be assigned to this new subgenus as well. The accessory glands for *C. (Oricampylaea) lefeburiana* and *C. (Oricampylaea)*

*ljubetenensis* (Fig. 4.25) are split, whereas those for *C. (Oricampylaea) illyrica* are undivided (Knipper, 1939). The name *Ljubotenina* has been used for *C. (Oricampylaea) ljubetenensis* by Groenenberg et al. (2012) and Schileyko (2013: 146), but in both cases with the explicit note that this was not for purposes of zoological nomenclature.

**Derivatio nominis.** The epithet *Oricampylaea* is used for a group of oriental *Campylaea* species, which cannot yet be diagnosed with morphological characters.

Genus nov. *Pseudotrizona*

Type species: *Helix inflata* Kobelt, 1876 (monotypic)

**Diagnosis.** The diagnosis of this monotypic subgenus is by definition identical with that of its type species, i.e. *Pseudotrizona inflata* (Kobelt, 1876). Shell light corneous with three brown spiral bands and a narrow umbilicus. *Pseudotrizona* gen. nov. is also differentiated by a unique combination of nucleotides in the 655 bp *COI* sequence obtained with general barcoding primers (Folmer, 1994) at the following relative positions: 22 A, 181 A, 265 G, 271 G, 304 A, 325 A, 413 C, 481 G, 616 A, 649 C.

**Description.** Shell depressed conical, whitish to light corneous, with three brown spiral bands (Welter-Schultes, 2012: 594, *Helicigona inflata*). Surface with growthlines only. With 4¾–5½ whorls; umbilicus narrow, measuring c. 1/10 of the total shell width. Height 10.5–18.0 mm; width 20.3–31.5 mm.

The accessory glands (Fig. 4.28) may be split for 1/3 to 1/2 of their length, but occasionally specimens with both an undivided and a split glandula occur as well. Stimulator more or less rounded triangular, prominently protruding obliquely in the central part of the genital atrium. Penial papilla slender conical, sometimes narrowed in the middle, with fine transverse ridges. Secondary ureter closed for 0.1–0.15 mm and open for the remaining 3.5–4.0 cm.

**Molecular data.** In the phylogeny reconstructions based on the concatenated datasets this species is always the sister-group of the clade *Cattania-Josephinella-Thiessea* (PP = 1.0; Figs 1, 2, S5, S6). None of the phylogenies show a species group exclusively consisting of *Pseudotrizona* and *Cattania*, thus *Pseudotrizona inflata* is not a species of *Cattania*.

**Age.** The lineage that gave rise to *Pseudotrizona* is estimated to have diverged from the common ancestor of *Cattania-Josephinella-Thiessea* at ca. 53.4–48.8 MYA (Figs 2, S5).

**Distribution.** N Albania, Montenegro, Kosovo, SW Serbia.

**Remarks.** *Pseudotrizona inflata* (Kobelt, 1876) has long been considered a subspecies of *Cattania trizona*, which was classified in *Campylaea* by Sturany and Wagner (1914), and in *Helicigona* by Knipper (1939) and Subai (1995).

**Derivatio nominis.** The epithet *Pseudotrizona* refers to the former incorrect classification of the type species as a subspecies of *Cattania* (*C.*) *trizona*.

Subgenus **Sabljaria** Brusina, 1904 (monotypic), genus **Dinarica**

Type species: *Helix stenomphala* Menke, 1830

**Molecular data.** All phylogenies based on the concatenated datasets depict *Dinarica* (*Sabljaria*) and *D. (Dinarica)* as a monophyletic group, see *Dinarica* (genus-level sister-group relations are also discussed). The subgenera *D. (Sabljaria)* and *D. (Dinarica)* are genetically clearly different. The *COI* and *CytB* sequence divergences between *D. (Sabljaria)* and *D. (Dinarica)* are 16.3% and 23.8%, respectively (Table 4).

**Age.** See *D. (Dinarica)* for the estimated age of the genus.

**Distribution.** Endemic to the Velebit Mts along the coast of Croatia.

**Remarks.** *Dinarica (Sabljaria)* differs from *D. (Dinarica)* both conchologically (Fig. 3.21, 3.22) and in genital anatomy (Fig. 4.23, 4.24). These subgenera are allopatrically distributed. See *Chilostoma (Sabljaria)* in Schileyko (2013) for details regarding the shell and genital morphology. *Dinarica (Sabljaria)* has split accessory glands (Fig. 4.24).

Subgenus **Superba** Subai and Fehér, 2006, genus **Liburnica**

Type species: *Helicigona skipetaricus [sic]* Subai, 1995

**Molecular data.** No *CytB* or *16S* sequences were obtained for *L. (Superba)* and *H3* does not discriminate between the alleged subgenera of *Liburnica* (Fig. S1). Therefore the taxonomic status of *L. (Superba)* could only be assessed with *COI*. The phylogeny based on that marker shows *L. (Liburnica)* as a monophyletic group ( $n = 4$ ) and *L. (Superba)* as paraphyletic ( $n = 4$ ). Which of these subgenera is monophyletic depends on

the selected outgroup. A phylogeny in which both are monophyletic, was not obtained. Partly based on these results, Subai (2012) synonymized *Superba* with *Liburnica*. The *COI* sequence divergences within *L. (Superba)* are less than 2.1% (Table 4).

**Age.** Due to missing data, *L. (Superba)* was not included in the BEAST analyses. Given the limited amount of sequence divergence within *Liburnica* (and the larger intraspecific divergence in *L. (Liburnica)*; Table 4), we expect *L. (Superba)* not to be older than *L. (Liburnica)*; see *L. (Liburnica)*.

**Distribution.** Albania, Tomor and Kulmakës Mts.

**Remarks.** *Liburnica (Superba)* contains three species, viz. *L. (S.) skipetarica* (Subai, 1995) (Fig. 3.23), *L. (S.) grisea* (Subai and Fehér, 2006) and *L. (S.) kulmankana* (Subai and Fehér, 2006), which are all included in this study (for remarks on *J. reischuetzi* and *J. vikosensis*; see sub *Josephinella*). See Subai and Fehér (2006) for details regarding the shell and genital morphology. The accessory glands are generally split (Fig. 4.21), one gland undivided is also observed (Fig. 4.17).

Genus **Thiessea** Kobelt, 1904

Type species: *Helix cyclolabris* Deshayes, 1839 (in Férussac and Deshayes, 1819-1851)

**Molecular data.** *Thiessea* is generally considered a subgenus of *Chilostoma* (Zilch, 1960; Bank *et al.*, 2001). This view cannot be accepted, since both taxa are not shown to be closely related in any of our phylogeny reconstructions. The data obtained for *Thiessea* are limited; for three out of the four included species, only *H3* sequences were obtained. The *H3* phylogeny indicates the four *Thiessea* species as a monophyletic group (PP = 0.49; Fig. S1). A sister-group relation is shown between *Thiessea* and *Josephinella* (PP = 1.0; Figs 1, 2, S1, S5, S6).

**Age.** The most recent common ancestor of *Thiessea* and *Josephinella* is estimated at ca. 39-36.6 MYA (Figs 2, S5).

**Distribution.** Mainland SE Greece, NE Peloponnese, Aegean Islands and SW Turkey.

**Remarks.** With at least 16 species (of which only 4 included in this study), *Thiessea* is one of the larger genera of Ariantinae. See *Helicigona (Thiessea)* in Subai (1996) and Schileyko (2006), and *Chilostoma (Thiessea)* in Schileyko (2013) for details regarding the shell and genital morphology. The accessory glands are undivided (Fig. 4.16; Subai, 1996).



Genus **Vidovicia** Brusina, 1904 (monotypic)

Type species: *Helix lacticina* Rossmässler, 1837 [= *Vidovicia caerulans* (Pfeiffer, 1828)]

**Molecular data.** *Vidovicia* is shown in a clade with *Delphinatia* and *Drobacia* in all phylogeny reconstructions based on the concatenated datasets (Figs 1, 2, S5, S6); see *Delphinatia*. The sister-group relationships of the genera within this clade remain elusive. The phylogeny reconstructions based on *COI* and *CytB* are uninformative regarding the position of *Vidovicia* (Figs S2, S3). That for *H3* shows the mentioned clade (PP = 0.8; Fig S1), while *16S* supports a sister-group relation between *Vidovicia* and *Corneola* (PP = 0.94; Fig. S4).

**Distribution.** The Dalmatian mountains along the Croatian coast, from the Velebit Mts to the Peljesac peninsula. Found only on limestone rocks, generally below 1400 m.

**Age.** Based on the two included specimens of this monotypic genus, the origin of *Vidovicia* is estimated at ca. 8.6 MYA (Figs 2, S5). For an age estimation of the clade *Delphinatia-Drobacia-Vidovicia*, see *Delphinatia*.

**Remarks.** *Vidovicia* (Fig. 3.29) has a typical depressed shell with a pointed apex and a fine to nearly rib-like radial sculpture. See *Vidovicia* in Schileyko (2006, 2013) for details regarding the shell and genital morphology. The accessory glands are undivided (Fig. 4.11).

Subgenus **Wladislawia** Wagner, 1928, genus **Cattania**

Type species: *Campylaea polinskii* Wagner, 1928

**Molecular data.** None of our results indicate a close relationship between *Cattania* (*Wladislawia*) and *Campylaea*, *Faustina* or *Chilostoma* (see remarks). Instead, our phylogeny reconstructions always show *Wladislawia* within the clade of *Cattania* ( $0.75 \leq \text{PP} \leq 1.0$ ; Figs 2, S1, S2, S5, S6). *Cattania* (*Ariantopsis*) and *C. (Wladislawia)* are sister-groups; see *Ariantopsis*.

**Age.** The most recent common ancestor of *C. (Wladislawia)* and *C. (Ariantopsis)* is estimated at ca. 7.3 MYA (Fig. 2); see *Ariantopsis*.

**Distribution.** Endemic to the Pirin Mts of SW Bulgaria, where it is found only at high altitudes.

**Remarks.** Only two *Cattania* (*Wladislawia*) species are known, viz. *C. (W.) polinskii* (Fig. 3.31) and *C. (W.) sztolcmani* Wagner, 1928 (Fig. 3.32). The latter species, thus not the type species, is included in this study. *Wladislawia* has been considered a subgenus of *Campylaea* by Zilch (1960), of *Faustina* by Damjanov and Likharev (1975) and more recently of *Chilostoma* by Bank et al. (2001). See *Campylaea* (*Wladislawia*) and *Chilostoma* (*Wladislawia*) in Schileyko (2006, 2013) for details regarding the shell and genital morphology. The accessory glands are split in *C. (W.) polinskii* (Fig. 4.30) and undivided in *C. (W.) sztolcmani*.



Table 5. Proposed classification of the subfamily Ariantinae. <sup>1</sup> our data indicate that *Campylaea ljubetenensis* is not a subspecies of *Cattania trizona*. <sup>2</sup> genus provisionally retained based on *H3* data. <sup>3</sup> subgenus represented by *Chilostoma (Achatica) achates*. <sup>4</sup> genus (Brusina, 1904) reintroduced, but given subgeneric ranking. <sup>5</sup> *Kollarix kollari* does not belong to *Liburnica* s.str. <sup>6</sup> genus (Subai and Fehér, 2006) given subgeneric ranking. <sup>7</sup> *Pseudotrizona inflata* does not belong to *Cattania* s.lat.

## Family Helicidae

subfamily **Ariantinae**

Genera	Subgenera	Included [Estimated] number of species
<i>Arianta</i>		4 [5] one with 5 subspecies
<i>Campylaea</i>	<i>Campylaea</i>	1 [1] single polytypic species?
	<i>Oricampylaea</i> subgen. nov.	3 [7] <sup>1</sup>
<i>Cattania</i>	<i>Ariantopsis</i>	1 [1] monotypic
	<i>Cattania</i>	5 [9]
	<i>Cattaniella</i> subgen. nov.	2 [?]
	<i>Wladislawia</i>	1[ 2] type species not included
<i>Campylaeopsis</i>		1 [1] monotypic <sup>2</sup>
<i>Causa</i>		1 [1] monotypic
<i>Chilostoma</i>	<i>Achatica</i> subgen. nov.	1 [1] single polytypic species? <sup>3</sup>
	<i>Chilostoma</i>	3 [4?]
	<i>Cingulifera</i>	1 [1] polytypic species
<i>Corneola</i>		2 [4]
<i>Cylindrus</i>		1 [1] monotypic
<i>Delphinatia</i>		2 [2]
<i>Dinarica</i>	<i>Dinarica</i>	2 [2]
	<i>Sabljarica</i>	1 [1] <sup>4</sup>
<i>Drobacia</i>		2 [2]
<i>Faustina</i>		3 [5]
<i>Helicigona</i>		1 [1] monotypic (two subspecies both included)
<i>Isognomostoma</i>		1 [1] monotypic
<i>Josephinella</i>		11 [20]
<i>Kollarix</i> gen. nov.		1 [1] monotypic <sup>5</sup>
<i>Kosicia</i>		3 [3]
<i>Liburnica</i>	<i>Liburnica</i>	6 [15]
	<i>Superba</i>	3 [3] <sup>6</sup>
<i>Pseudotrizona</i> gen. nov.		1 [1] monotypic <sup>7</sup>
<i>Thiessea</i>		4 [16]
<i>Vidovicica</i>		1 [1]