

***Albinaria* species in Crete (Alopiinae, Clausiliidae), with special regard to their closing apparatus**

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I. Species list

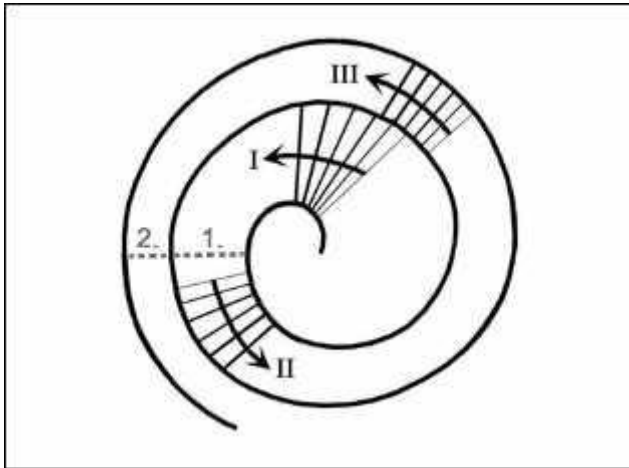
All clausiliid species in Crete (40) belong to the genus *Albinaria* Vest 1868. They are listed as follows (in alphabetical order):

- A. amalthea* (Westerlund 1878)
- A. ariadne* Schilthuizen & Gittenberger 1991
- A. arthuriana* (O. Boettger 1878)
- A. byzantina* (Charpentier 1852)
- A. candida* (L. Pfeiffer 1850)
- A. christae* Wiese 1989
- A. corrugata* (Bruguière 1792)
- A. cretensis* (Rossmässler 1836)
- A. eburnea* (L. Pfeiffer 1854)
- A. fulvula* Flach 1988
- A. hippolyti* (O. Boettger 1878)
- A. idaea* (L. Pfeiffer 1850)
- A. jaeckeli* Wiese 1989
- A. janicollis* Schultes & Wiese 1991
- A. janisadana* Loosjes 1955
- A. leonisorum* (O. Boettger 1901)
- A. li* Welter-Schultes 1999
- A. loosjesi* H. Nordsieck 1977
- A. maltzani* (O. Boettger 1883)
- A. manselli* (O. Boettger 1883)
- A. moreletiana* (O. Boettger 1878)
- A. parallelifera* (O. Boettger 1878)
- A. pondika* Welter-Schultes 2010
- A. praeclara* (L. Pfeiffer 1853)
- A. rebeli* A. J. Wagner 1924
- A. retusa* (Olivier 1801)
- A. rodakinensis* Wiese 1991
- A. sphakiota* (Maltzan 1887)
- A. spratti* (L. Pfeiffer 1846)
- A. sturanyi* A. J. Wagner 1924
- A. sublamellosa* (O. Boettger 1883)
- A. tenuicostata* (L. Pfeiffer 1864)
- A. terebra* (L. Pfeiffer 1853)
- A. teres* (Olivier 1801)
- A. torticollis* (Olivier 1801)
- A. troglodytes* (A. Schmidt 1868)
- A. ulrikae* Schilthuizen & Gittenberger 1990
- A. violacea* Schilthuizen & Gittenberger 1990
- A. virginea* (L. Pfeiffer 1846)
- A. wiesei* Gittenberger 1988
- A. xanthostoma* (O. Boettger 1883)

After having worked through the revisions of Welter-Schultes (2000, 2010), in which several species have been united with other ones, I see no reason to change the rank of the species (Nordsieck 2016). Because the shell

diagnoses of Welter-Schultes (2010) are mostly no diagnoses, in which the species are distinguished from related ones, but descriptions of characters and variabilities, I was forced to elaborate these diagnoses myself. This was no easy task, because a great amount of material had to be examined.

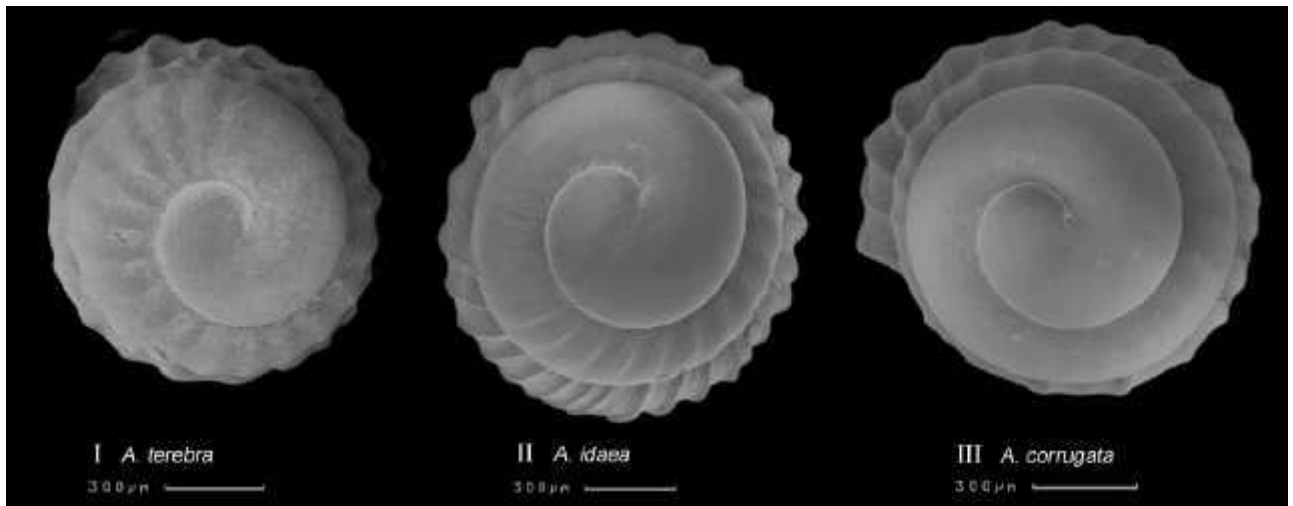
The given list corresponds with former ones (Nordsieck 1999, 2004), with the exception of some species which differ from their relatives in the protoconch sculpture (*A. manselli*, *A. parallelifera*, *A. rodakinensis*). In my former papers this character has been underestimated. An examination of all Cretan species revealed three groups which differ in the position of the beginning of the protoconch sculpture (text-figs. 1-2: groups I-III; see chapter IV).



Text-fig. 1. Protoconch of *Albinaria* species (from above, schematized).

1. = ending of first whorl, 2. = of second whorl.

I - III = groups with different positions of the beginning of protoconch sculpture: I = in the course of the first whorl; II = at about the beginning of the second whorl; III = in the course of the second whorl or near to its end.



Text-fig. 2. SEM-photos of the protoconch of *Albinaria* species (from above); prep. S. Hof, phot. S. & A. Hof.

Group I: *A. terebra*, Kefali peninsula near Kali Limenes;

Group II: *A. idaea*, Idi mountains between Kamares and Lochria;

Group III: *A. corrugata*, Knossos near Iraklion.

II. Grouping of species

According to shell morphology, the species have been assembled within five groups (Nordsieck 1999):

1. *candida* group: *A. amalthea*, *A. arthuriana*, *A. candida*, *A. fulvula*, *A. hippolyti*, *A. leonisorum*, *A. loosjesi*, *A. pondika*, *A. ulrikae*, *A. violacea*, *A. wiesei*, *A. xanthostoma*;
2. *torticollis* group: *A. christae*, *A. jaeckeli*, *A. torticollis*;
3. *cretensis* group: *A. byzantina*, *A. cretensis*, *A. eburnea*, *A. sphakiota*, *A. sublamellosa*, *A. tenuicostata*, *A. troglodytes*, *A. virginea*;
4. *teres* group: *A. ariadne*, *A. corrugata*, *A. idaea*, *A. janicollis*, *A. janisadana*, *A. li*, *A. maltzani*, *A. manselli*, *A. moreletiana*, *A. parallelifera*, *A. praeclara*, *A. retusa*, *A. rodakinensis*, *A. spratti*, *A. terebra*, *A. teres*;
5. *caerulea* group: *A. rebeli*, *A. sturanyi*.

The proposed groups are based only on shell morphology. The grouping does not claim to present monophyletic groups, as assumed by some authors, because it is clear that there is a certain amount of convergences in shell morphology. Therefore, a ranking of these groups as subgenera, as recently proposed again in the CLECOM list, is rejected.

Until now, the genital morphology of only few species from Crete has been examined (genital apparatus see Schilthuizen & Lombaerts 1994: 73, fig. 6, appendix = penial caecum). A. J. Wagner (1924) gave descriptions of the genitalia of eight species

(*A. arthuriana*, *A. corrugata*, *A. aphrodite* = *A. hippolyti*, *A. rebeli*, *A. cretensis* = *A. sphakiota*, *A. sturanyi*, *A. sublamellosa*, *A. virginea*). My own work is restricted to four species

(*A. byzantina*, *A. corrugata*, *A. tenuicostata*, *A. teres*). In the course of their work on hybrid zones in *A. hippolyti*, Schilthuizen & Lombaerts (1994) examined the genitalia of some subspecies of that species. By all workers it could be demonstrated that the length relations of the copulatory organs (especially of bursa copulatrix and male copulatory organs) are of importance for characterizing species taxa. A grouping of species by genital morphology, however, was not possible.

The results of different allozyme and DNA analyses are not consistent with shell morphology; compared to another, they are also contradictory. They result in the following different groups:

Allozyme analysis (Schilthuizen & Gittenberger 1996):

1. *A. hippolyti*, *A. arthuriana*, *A. cretensis* (= *A. virginea*), *A. christae*, *A. spratti*;
2. *A. idaea*, *A. terebra*, *A. sublamellosa*, *A. corrugata*, *A. moreletiana*.

mtDNA analysis (Douris et al. 1998):

1. *A. eburnea*, *A. cretensis* (= *A. virginea*), *A. violacea*, *A. spratti*, *A. ulrikae*, *A. hippolyti*, *A. corrugata*;
2. *A. praeclara*, *A. maltzani*, *A. moreletiana*, *A. retusa* (bridging 2. and 3.);
3. *A. torticollis*, *A. jaeckeli*, *A. teres*.

A. xanthostoma and *A. terebra* have an isolated position.

Combined nDNA and mtDNA analyses (Van Moorsel et al. 2001):

1. *A. ulrikae*, *A. spratti*, *A. praeclara*, *A. torticollis*, *A. cretensis* (= *A. virginea*);
2. *A. teres*, *A. corrugata*.

Depending on the gene used for analysis (: 94) the grouping is different.

nDNA analysis (Schilthuizen et al. 2004):

1. *A. hippolyti*, which is in the focus of the paper,
2. *A. candida*, *A. cretensis*;
3. *A. ulrikae*, *A. torticollis*;
4. *A. corrugata*, *A. teres*, *A. wiesei*, *A. arthuriana*;
5. *A. spratti*.

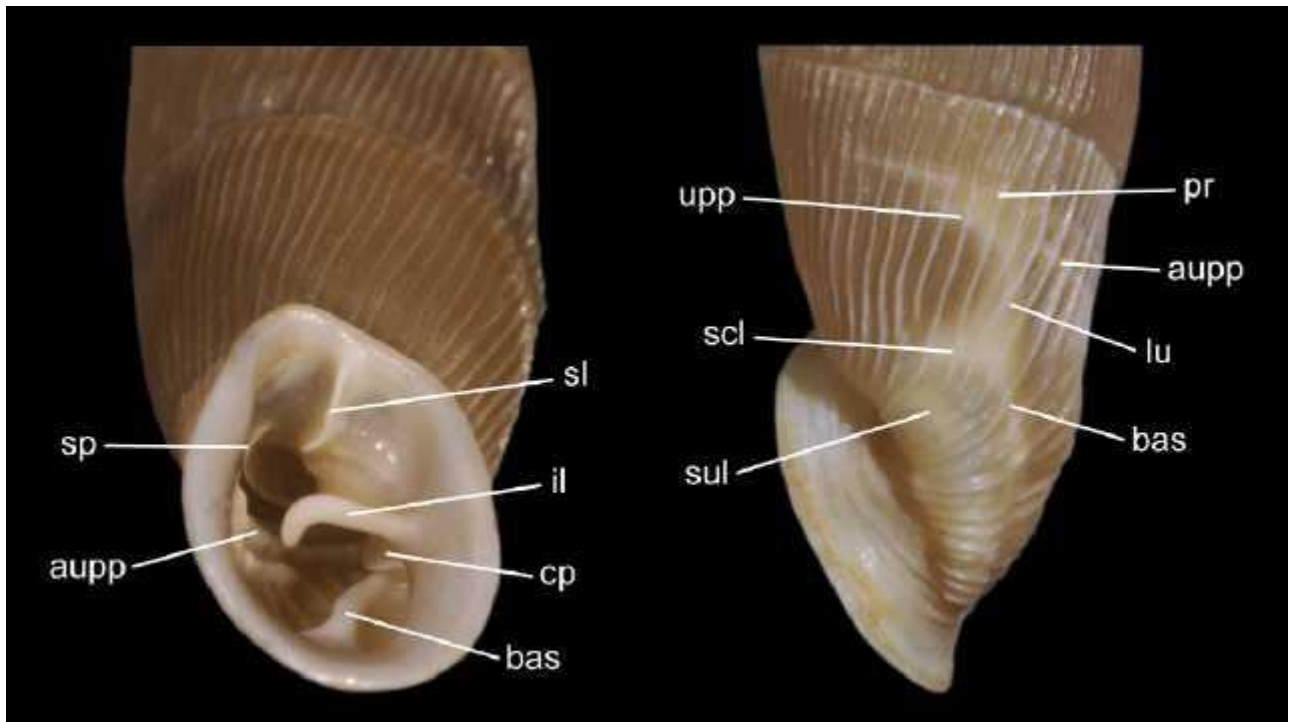
It is evident that the results of allozyme and DNA analyses mirrors the distribution of the species better than their morphological (shell) similarity. The conclusion, however, that shell morphology does not reflect the relationships of the species is premature. Horizontal gene transfer, e. g. by introgression caused by hybridization which is

frequent in *Albinaria* (examples in Crete are given by Welter-Schultes 1992: species from Dia island; Schilthuizen et al. 1993: hybrid form *A. arthuriana* x *A. maltzani*; Welter-Schultes 1998: intermediate forms of several species pairs; this article figs. 5-10), may influence the molecular analyses. Therefore, the hitherto presented analyses are not yet suited to serve as a basis for a classification of the Cretan *Albinaria* species.

III. Characters of closing apparatus

In the course of my diagnostic work I learned once more that like in other *Albinaria* groups (Nordsieck 1999) species with more plesiomorphic characters of the closing apparatus = CA and species with more apomorphic ones can be recognized.

The plesiomorphic CA of *Albinaria* is regarded as such, because it is improbable that its complex palatal system has evolved several times de novo from the reduced one which is the most common one. Like in other Aloiinae it is characterized as follows (Nordsieck 1997; text-fig. 3): Palatal plicae complete, i. e. all palatal plicae present, especially anterior upper palatal plica (aupp), anterior lower palatal plica = basalis (bas) and lowest palatal plica = sulcalis (sul), and clausilium plate (cp) normally developed (fitted in the frame of lunellar and subcolumellar lamella). The sulcalis (sul) may not be confounded with the posterior lower palatal plica = subclaustralis (scl), which is also present in several *Albinaria* species with plesiomorphic CA.



Text-fig. 3. Closing apparatus of *Albinaria ulrikae*.

Body whorl, view into the aperture and view on lunellar; phot. S. Hof.

Abbreviations: aupp = anterior upper palatal plica, bas = basalis, cp = clausilium plate, il = inferior lamella, lu = lunella, pr = principal plica, scl = subclaustralis, sl = superior lamella, sp = spiral lamella, sul = sulcalis, upp = (posterior) upper palatal plica.

If one compares the *Albinaria* species from Crete, species with all states from most plesiomorphic CA to most apomorphic one are present. Especially the recognition of species with plesiomorphic CA may be of interest for the reconstruction of *Albinaria* phylogeny on Crete. 11 from 40 species, i. e. about a fourth of the species, exhibit a more plesiomorphic CA. These are the following (in alphabetical order, with range information):

- A. amalthea*, N. W. Crete: aupp and bas present;
- A. ariadne*, N. W. central Crete: bas present;
- A. arthuriana*, N. E. central Crete: aupp, bas and sul present;
- A. candida*, N. W. Crete: aupp and bas present, aupp in part reduced;

A. fulvula, S. E. central Crete (fig. 3): bas present;
A. hippolyti (*aphrodite* O. Boettger), N. W. central Crete: aupp and bas present;
A. hippolyti (*hippolyti*, *holtzi* Sturany), N. W. central Crete: bas present;
A. pondika, Pondikonisi island (N. W. Crete): aupp and bas present;
A. ulrikae (fig. 1), *A. violacea*, N. W. central Crete: aupp (in part two), bas and sul present;
A. wiesei, N. W. E. Crete (fig. 2): aupp and bas present;
A. loosjesi H. Nordsieck, N. W. Crete: aupp present, bas reduced;
A. xanthostoma, N. W. Crete: bas present.

According to the degree of reduction, the Cretan species are ordered as follows:

1. *A. arthuriana*, *A. ulrikae* (fig. 1), *A. violacea*: sul still present;
2. *A. amalthea*, *A. h. aphrodite*, *A. pondika*, *A. wiesei* (fig. 2): only aupp and bas present; also *A. candida*, but aupp in part reduced, and *A. loosjesi*, but bas reduced;
3. *A. fulvula* (fig. 3), *A. h. hippolyti*, *A. h. holtzi*, *A. xanthostoma*: only bas present;
4. *A. leonisorum*, *A. rodakinensis*, *A. sublamellosa*, *A. troglodytes*: bas partly or rudimentary present;
5. remaining species (e. g., *A. idaea* fig. 4): named palatal plicae absent.

A further important character of the CA is the position of the lunellar. In most species taxa the lunellar is dorsally to dorsolaterally situated. In some taxa, however, it is in deeper position, lateral or deeper. These are the following: *A. amalthea* (*a.*), *A. hippolyti* (*asterousea* Schilthuizen, Welter-Schultes & Wiese), *A. leonisorum*, *A. sphakiota*, *A. troglodytes* (*vexans* O. Boettger), *A. violacea* (*dextrogyra* Schilthuizen & Gittenberger). An extreme case is *A. jaeckeli*, in which the lunellar is in ventral position. Like in other clausiliids, the change to a deeper position of the lunellar is regarded as a better protection against evaporation. It is interesting that – except for *A. jaeckeli* – all taxa with deeply situated lunellar belong to the groups with plesiomorphic CA (1 - 4). In the taxa with apomorphic CA (group 5) the lunellar is nearly invariable. Protection against desiccation is achieved by the secretion of an epiphragma in aestivation. According to my experience species with much plesiomorphic CA do not secrete such epiphragmas.

It is striking that the species with the most plesiomorphic CA (group 1) have also the plesiomorphic character white surface layer of the shell missing (fig. 1). In several species with plesiomorphic CA the inferior lamella is high; like in other Aloiinae this is also regarded as a plesiomorphic character (figs. 1-2).

If one compares the ranges of the Cretan *Albinaria* species it results that all species with plesiomorphic CA (except *A. fulvula*) are distributed in the northern part of Crete or on northwestern accessory islands. The reason may be that these parts of Crete have not so extreme climatic conditions than the other parts of the island (southern part, mountains, other accessory islands).

IV. Character protoconch sculpture

The position of the beginning of the protoconch sculpture has revealed to be an important character for the definition of species taxa in Crete (see chapter I and text-figs. 1-2). The three named groups contain the following taxa:

I (ribbing begins in the course of the first whorl): *A. idaea* (part), *A. janicollis*, *A. manselli*, *A. praeclara*, *A. rodakinensis*, *A. terebra*;

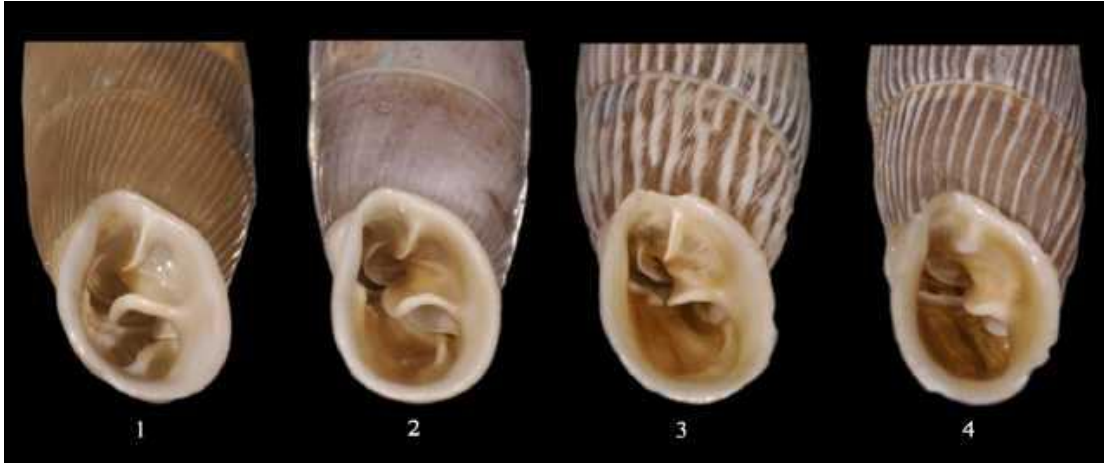
II (ribbing begins at about the beginning of the second whorl): *A. ariadne*, *A. idaea* (part), *A. maltzani*, *A. parallelifera*;

III (ribbing begins in the course of the second whorl or near to its end): remaining species.

As a rule, the belonging to a group is specific for a species (but a certain variability has to be considered). The arguments for species rank of some above mentioned taxa are the following: *A. manselli* is regarded as species, because it differs from the parapatrically occurring forms of *A. teres*, with which it had been classified, not only in the protoconch sculpture, but also in size and sculpture (Welter-Schultes 2010). *A. rodakinensis* is regarded as species, because it is separated from the parapatrically occurring form of *A. virginea*, with which it had been classified, not only by the protoconch sculpture, but also by the cervix formation and sculpture and the basalis, which is occasionally present. Consequently also *A. parallelifera*, which differs from *A. praeclara* in the protoconch sculpture, is separated as a species of its own.

A. idaea, in which subspecies of groups I and II could be stated, is an especially interesting case. The differences of this character within the species have not been noticed until now. Engelhard & Slik (1994) gave a number of unribbed apical whorls (1-2.6), which, however, is higher than that of the first smooth part of the protoconch. Nordsieck (1998) meant that ribbing always begins with the second whorl. Welter-Schultes (2000, 2010) studied only number and prominence of the ribs of the second whorl, not the position of their first appearance. In this respect, *A. i. rolli* and the two subspecies from the Paximadia Islands belong to group I, the remaining subspecies to group II. Because the difference between *A. i. rolli* and *A. i. venosa* (one of the remaining subspecies) is bridged by samples which are intermediate between both subspecies (Nordsieck 1998), a species separation of the former is not appropriate.





Figs. 1-4. *Albinaria* species in Crete.

Body whorl, frontal view, view on lunellar and view into the aperture; phot. S. Hof.

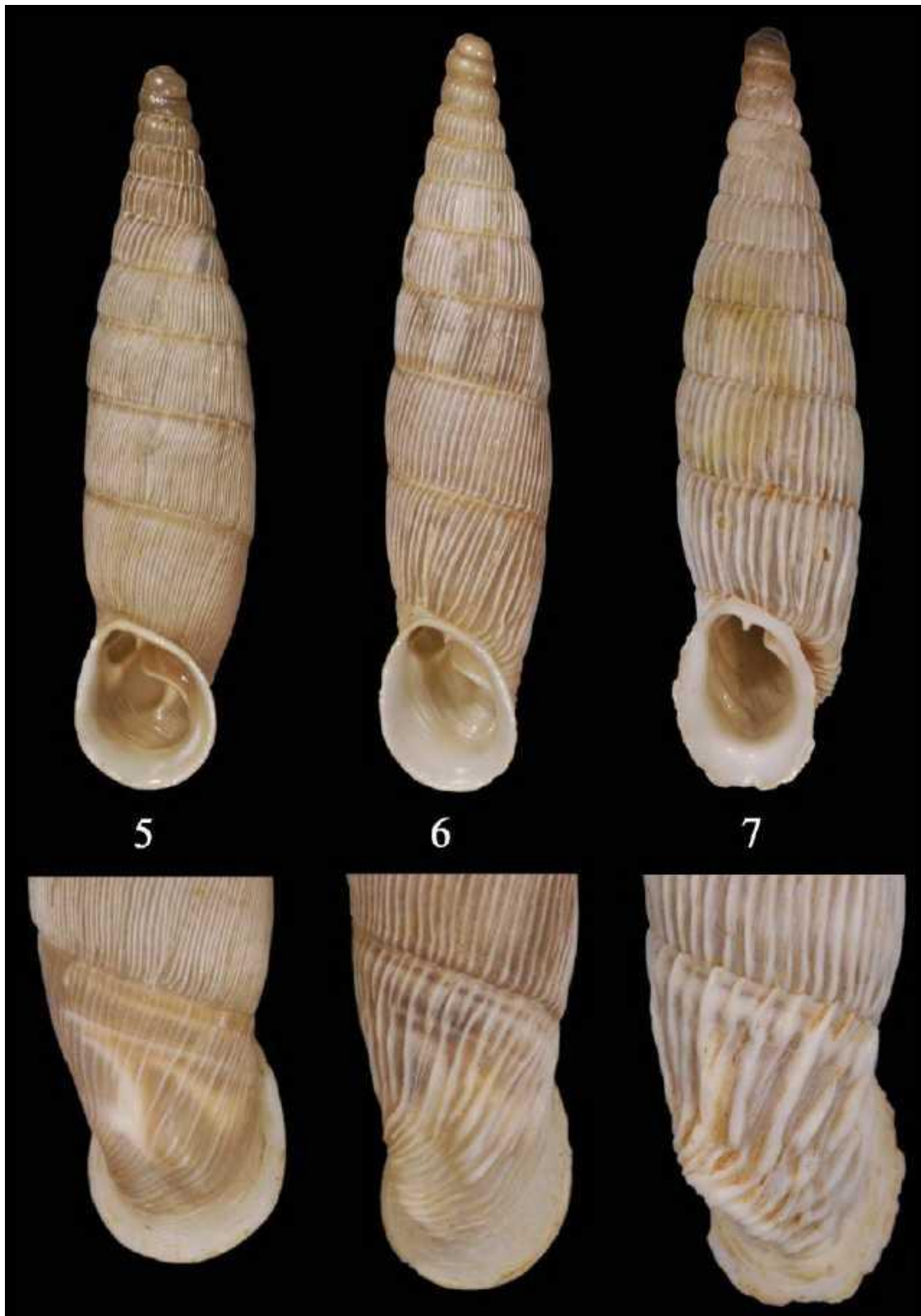
Abbreviations of collections: K = Kittel, N = Nordsieck, NNM = Nationaal Natuurhistorisch Museum Leiden.
Shell height = H (mm).

Fig. 1. *A. ulrikae*, Crete, Iraklion prov., near Rodia, ex N; H 22.1.

Fig. 2. *A. wiesei*, Crete, Lassithi prov., Selinari church near Neapoli, ex NNM 56084, paratype; H 16.85.

Fig. 3. *A. fulvula*, Crete, Lassithi prov., north of Anatoli, ex NNM 56092, paratype; H 17.1.

Fig. 4. *A. idaea*, Crete, Rethimno prov., Kedros mountains, ex NNM 56824, paratype *amabilis*; H 16.9.

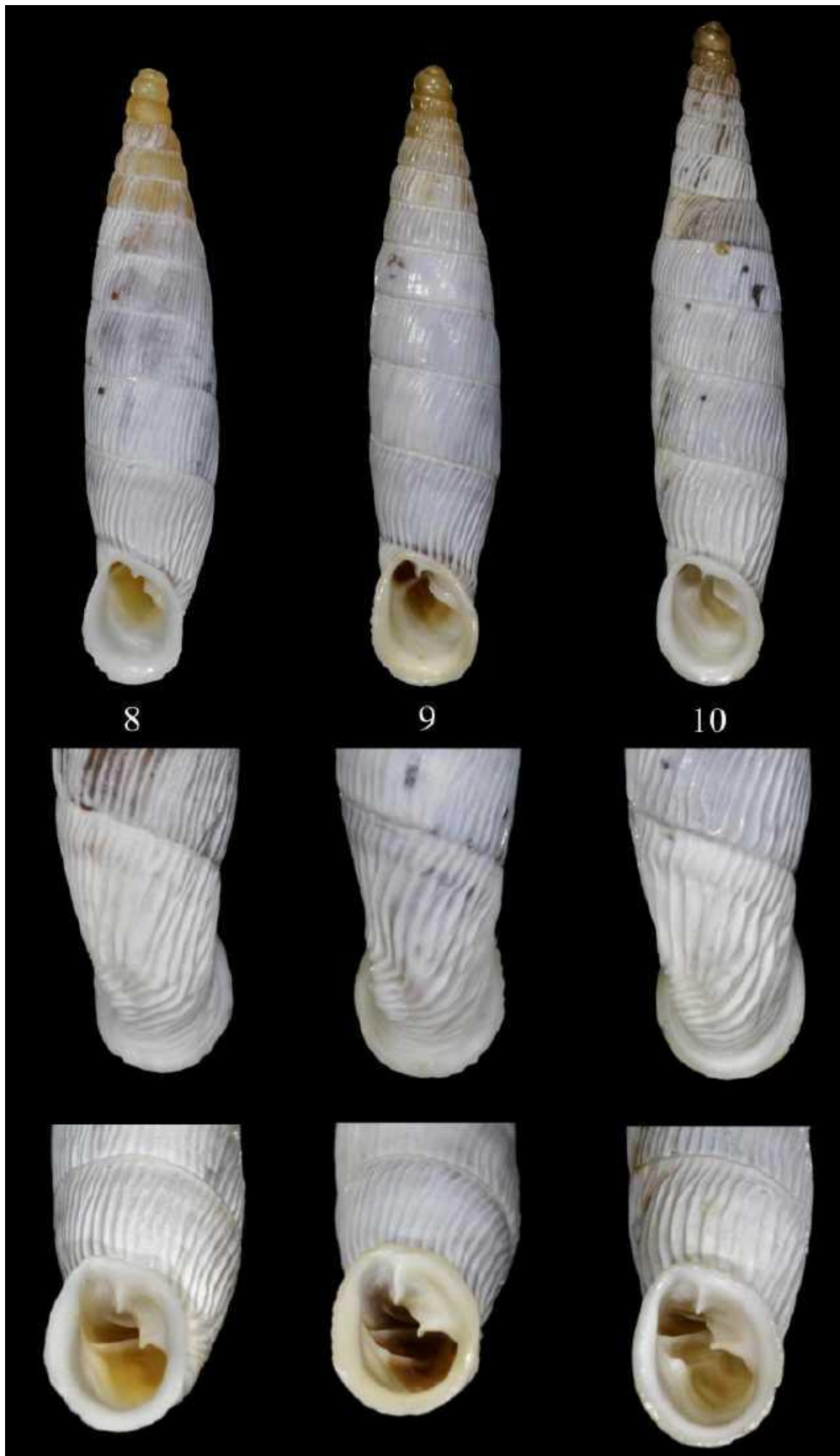


Figs. 5-10. Examples for *Albinaria* interspecific hybrid forms.
Body whorl, frontal view and view on lunellar; phot. S. Hof.
Shell height = H (mm).

Fig. 5. *A. arthuriana*, Crete, Lassithi prov., Milatos cave, ex N 10267b; H 16.9.

Fig. 6. *A. arthuriana* x *A. maltzani*, Crete, Lassithi prov., Milatos cave, ex N 10267a; H 17.7.

Fig. 7. *A. maltzani*, Crete, Lassithi prov., near Milatos cave, ex SMF322822; H 17.8.



Figs. 8-10 also oblique view into aperture.

Fig. 8. *A. tenuicostata*, Crete, Chania prov., Gramvousa peninsula, Balos beach, ex K, H 16.6.

Fig. 9. *A. tenuicostata* x *A. loosjesi*, Crete, Chania prov., Gramvousa peninsula, Balos beach, ex K, H 16.7.

Fig. 10. *A. loosjesi*, Crete, Chania prov., Gramvousa island (Venetian fortress), ex K, H 17.9.

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