

The subspecies concept in South European Clausiliidae, with special regard to the genus *Albinaria* Vest

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I. General remarks

The system of the South European Clausiliidae which has been worked out in the last decades (e. g., of the genus *Albinaria*, Nordsieck 1977, 1999) was based on the same species and subspecies concepts as those used by Kemperman (1992) for the revision of the Ionian *Albinaria* species. In the species concept also interspecies hybridization, which had been observed in South European clausiliids since the 1960s (Nordsieck 2007: 96), has been considered. The concepts are described by Kemperman & Gittenberger in Kemperman (: 223) as follows: „To be regarded ... as representing a species or subspecies, a population or group of populations should be characterized by ... unique, independent character states, or a unique combination of character states. The status of the taxa is then judged upon after data obtained by observations in contact zones. If two taxa are connected by a transitional zone in which populations with morphologically intermediate specimens bridge the gap between them, subspecific status is given to those taxa, assuming that they hybridize freely. If there is a contact zone with typical specimens of both taxa and few intermediate forms as well, the taxa are considered separate species, with the interpretation that under natural conditions only occasionally some hybridization occurs.“

The enormous task of recognition of species and subspecies has been much facilitated by the search for taxonomic important characters. The fact that characters are of different taxonomic value has made possible successful taxonomic work since the epoch-making revision of clausiliid groups by A. Schmidt (1856). He named those characters essential characters and wrote (: 5):

„ ... Merkmalen ... , von denen einzelne vor andern ... zu stehen scheinen, indem sie deutlich, beständig, zuverlässig ihren Charakter ausdrücken. Das sind die wesentlichen Merkmale, die nur durch das sorgfältigste Studium erkannt werden können ... Kriterien, welche an einer Art sehr wesentlich sind, erscheinen bei ... anderen als ganz bedeutungslos.“

These characters were used by me and others until today, as the following statement of Kemperman & Gittenberger in Kemperman (1992: 225-226) shows:

„The diagnostic value of certain conchological character states may vary considerably between conspecific subspecies in the various species, as was emphasized already by Schmidt ...“

Former attacks against the subspecies concept, e. g., those of Wilson & Brown (1953), were based on the statement that for subspecies definition any given characters were used, such which tend to vary independently across the range of the species, occur here and there within the range, characterize only populations, or are arbitrarily defined what concerns the lower levels of subspecies. These objections are, in general, not justified, if one uses characters of higher taxonomic value.

Since a long time it is known that not only for the recognition of species but also for that of subspecies the distributional relations are of importance, for subspecies especially the characters of individuals in contact zones. The problems concerning those zones are described by Kemperman & Gittenberger in Kemperman (1992: 224-225) as follows:

„Observations in contact zones are decisive for the status given to the various taxa ... Even when a contact zone between taxa exists in nature, the decision concerning the status given to those taxa may be a subjective one ... The amount of hybridization, judged upon after the frequency of intermediate forms, may ... vary considerably along a ... contact zone, ... “

This means that hybrids in contact zones must be carefully analyzed.

In this connection, a change to a more rigid delimitation of subspecies was demanded by Barton & Hewitt (1985). Parapatrically distributed subunits of species should only be regarded as subspecies if they differ by multiple characters and are separated by narrow hybrid zones.

On the other hand, at the same time, Haffer (1986) recognized two sorts of parapatric subspecies, those which exhibit broad intergradation zones, and those which are separated by narrow hybrid zones. The first were named by him subspecies, the second megasubspecies. If the latter are regarded as species which hybridize

occasionally, the term semispecies is used.

Schilthuizen (1994) studied those contact zones in *Albinaria hippolyti* (O. Boettger), a species of the genus which is rich in shell characters (closing apparatus in part with palatal plicae) and exhibits several subspecies which differ clearly in shell morphology. He found that they were more or less narrow hybrid zones with morphological anomalies and specific allozymes (hybrizymes). The results are interpreted by Schilthuizen & Lombaerts in Schilthuizen (1994: 90) as follows:

„This pattern, in which most change occurs in a narrow hybrid zone ... reflects a barrier to gene exchange ... The two populations may therefore be regarded as effectively isolated and could ... be seen as good species. However, in assigning subspecific status to the two forms, we have favoured the more strict view recommended by Barton & Hewitt ...”

Based on these results, Schilthuizen et al. (1993: 140) required for subspecies a more rigid concept as follows:

„ ... that certain forms show a continuous intergradation, with many shell characters changing independently, while others are spatially separated by narrow contact zones, in which traits change in concert. In this revision ... the presence of relatively narrow hybrid zones between conchologically distinct forms is taken as a criterion for considering them subspecies ... In assigning subspecific status to geographically isolated, and conchologically characterised, forms ... a more subjective approach is taken.”

Engelhard & Slik (1994) and Welter-Schultes (2000) applied this concept also to an *Albinaria* species, *A. idaea* (L. Pfeiffer), which is less rich in shell characters (closing apparatus without palatal plicae) and is continuously distributed within its main range. Therein forms with different shell morphology, until now treated as subspecies, are connected by broad intergradation zones. In order to base their examinations mainly on measurable characters, they used the available characters without considering their different taxonomic value. As result the subunit of *A. idaea* from the main range was only recognized as one extremely variable subspecies (Engelhard & Slik) or even only as one geographic form (Welter-Schultes). However, it is so diverse that it can be diagnosed no more.

Welter-Schultes (2000) extended this concept to all Cretan *Albinaria* species which are less rich in shell characters and are continuously distributed within their main ranges exhibiting a high diversity there. Some of these species hybridize in contact zones with other species which are often clearly different in shell morphology (e. g., *A. teres* (Olivier) with *A. sturanyi* A. J. Wagner, see chapter III). These hybrid zones were interpreted by Welter-Schultes like those of *A. hippolyti* by Schilthuizen so that these different species were lumped together with the highly diverse main species as subspecies in one „polytypic” species.

Finally, Welter-Schultes (2010) abandoned even his term geographic forms and presented these highly diverse species as „monotypic species”. His comment to this procedure (: 148) is as follows:

„... individual specimens [of the „monotypic species”] found at some distance from each other may differ substantially, they may differ more than subspecies differ among each other in polytypic species ... The decisive criterion for polytypic and monotypic species is presence or absence of hybrid zones, and not the degree of morphological difference between distant populations.”

The results of his character examination within those „monotypic species”, based on a mixture of measurable characters without considering if informative or not, were given in spatial distribution maps which finally were combined to so-called combined characters plots. If spatial distribution maps of characters of different taxonomic value are combined, it is not astonishing that the result cannot be used for recognizing subspecies which should be characterized by informative characters. Besides, Welter-Schultes selected only a part of the available characters and omitted sometimes informative ones (e. g., in *A. teres*, see chapter III).

I have serious doubts if this is the appropriate way to describe and name the diversity of South European clausiliids. The arguments are the following:

- 1.** To accept subspecies only if they are separated by narrow hybrid zones or are allopatric, though they are morphologically not more distinct than others with broad transition zones, creates an imbalance of judging upon intraspecific units. Forms with comparable morphogenetic differences have then not the same taxonomic rank.
- 2.** Species can include parapatric subunits with all kinds of contact zones and allopatric subunits. Such a case may be *Leucostigma candidescens*, in which different geographic forms border upon other ones by broad transition zones in one region and occur in another region in immediate neighbourhood with sudden character changes (Nordsieck 2011).

3. In most species intraspecific units and their spatial relations are insufficiently known. Subspecies bordered by well-examined narrow hybrid zones are rare, and the number of subspecies will therefore be considerably reduced. This leads to a serious loss of information of the diversity within the species. The possibility to demonstrate this diversity for conservation purposes is reduced.

4. It is inappropriate to use uninformative characters for defining taxa only because they are measurable. One should take warning from the work of Käufel who defined species of the genus *Clausilia* mainly by their shell size and shape, with the result that he could not distinguish the actual species (Nordsieck 1990: 137). It is certainly not easy to recognize the characters of higher value; this needs careful examination of the whole group to which the respective species belongs. Informative characters are weakened, if they are used together with uninformative ones, as can be seen in Welter-Schultes' (2010) combined characters plots.

Therefore, I think it better, following the proposals of Haffer (1986), to distinguish two categories of intraspecific subunits: subspecies, connected by contact zones with broad intergradation (as a rule, of primary origin), and megasubspecies or semispecies, connected by narrow hybrid zones (as a rule, of secondary origin). For a revision, characters of higher taxonomic value should be found out, and the named intraspecific units should be defined by such characters.

One should consider that also subspecies which are only slightly different in shell characters can differ genetically more than expected (example *Albinaria lycica* H. Nordsieck, Pall-Gergely et al. 2012).

In the following, for example of two species, *Albinaria caerulea* and *A. teres*, both with uniform closing apparatus, the problems of species subdivision shall be demonstrated. The examined shell material comes from the collection of the Forschungsinstitut Senckenberg, Frankfurt am Main (abbreviation: SMF), and my own collection (abbreviation: N), altogether including more than 500 samples of both species.

II. *Albinaria caerulea*

A. caerulea (Deshayes 1835) has been classified with the *caerulea* subgroup of one of the eastern *Albinaria* groups (Nordsieck 1999: 5).

Distributional range: Cyclades from Andros in the north to Thira in the south and from Folegandros in the west to Levitha in the east, southern Sporades: Chios, Samos, Kos, adjacent Anatolian coastal region; introduced in Turkish Thracia (with Istanbul) and Attica.

A. caerulea is similar to the neighbouring species *A. brevicollis* (L. Pfeiffer 1850) and *A. turrita* (L. Pfeiffer 1850), which were classified with the same subgroup. DNA analysis by Douris et al. (2007), however, revealed that *A. turrita* is not closely related to the other two species, but may belong to another *Albinaria* group. *A. caerulea* and *A. brevicollis* have a sister-group relationship and a vicariant distribution. The results of Douris et al. (2007) are somewhat problematic, because it is not quite clear which taxa have been examined. No particulars of the examined material are given (except for information about the shell sculpture of some specimens from Folegandros), subspecies are ignored, only the localities are named. The system proposed by me (Nordsieck 1977, 1999) is used without control, though it is disparaged as „typological“ (: 1227). This is of special importance in taxa which in shell morphology are intermediate between *A. caerulea* and *A. brevicollis*, as, e. g., in *A. anaphiensis* (O. Boettger 1878) and *A. maculata kosensis* K. L. Pfeiffer 1955. Both have been affiliated by me (1977: 294) to *A. brevicollis*, but the results of DNA analysis are not consistent with that classification. Those of *A. b. anaphiensis* are ambiguous, while *A. b. kosensis* appears in a clade of *A. caerulea* (Douris et al.: fig. 3). The recent examination of further material of both taxa had the following result: Now as before, *A. b. anaphiensis* is classified with *A. brevicollis*. On the other hand, *A. b. kosensis* is re-transferred to *A. caerulea*.

The subunits of *A. caerulea* (Nordsieck 2002: 291; 2007: 45) differ mainly by the strength of white surface layer, the sculpture and the development of the dorsal keel.

The main subunit, distributed nearly all over the species range, *A. c. caerulea* (figs. 1-2), is characterized by weakly sculptured lower whorls and \pm distinct dorsal keel.

From several islands and the Anatolian coastal region more strongly sculptured forms, either with well-developed or with reduced dorsal keel, were described: *A. c. amorgia* (O. Boettger 1878) (fig. 3) from Amorgos, *A. c. maculata* (Rossmässler 1836) (fig. 4) from the Anatolian coastal region, *A. c. milleri* (L. Pfeiffer

1850) (fig. 5) from Paros, *A. c. kreglingeri* (L. Pfeiffer 1866) and *A. c. altecostata* (L. Pfeiffer 1866) (fig. 6) from islands near Naxos, *A. c. pholegandrica* H. Nordsieck 2002 (fig. 7) and *A. c. scaletta* H. Nordsieck 2002 (fig. 8) from Folegandros.

A. c. kosensis K. L. Pfeiffer from Kos and the neighbouring Anatolian coastal region is added as a subspecies.

A. freytagi (O. Boettger 1889) from Samos and neighbouring islands, formerly listed as subspecies of *A. caerulea*, is regarded as an independent species (Nordsieck 1999: 6, 14, note 23).

The exact distribution and the spatial relations of these provisional subspecies are insufficiently known; those relations seem to be more complicated than assumed until now.

A. c. caerulea and *A. c. amorgia* have been collected on Amorgos without intermediates (O. Boettger 1878: 92). There are forms transitional between *A. c. caerulea* and *A. c. milleri*, e. g. on Paros and Naxos (Fuchs & Käufel 1936: 579, own investigations), but in some islands (e. g. Keros, Anidros, Fuchs & Käufel: 579) both subspecies are said to occur without intermediates.

The spatial relations of the subspecies from Folegandros are better known, because a rich material could be examined (Nordsieck 2002: 292-293):

On that island, four different forms of *A. caerulea* have been found: *A. c. caerulea* (lower whorls either smooth or with weak ribs, with intermediates), and *A. c. pholegandrica* and *A. c. scaletta*, both distinctly ribbed, without transitions to the *A. c. caerulea* forms.

In AgiosEleftherios *A. c. caerulea* (mostly with weak ribs) and many *A. c. pholegandrica* have been collected, but no transitional individuals (: 292).

In Paleokastro *A. c. pholegandrica* and (more frequently) *A. c. scaletta* occur, nearly without intermediates (: 293).

From the collection results reduced gene exchange of the subspecies could be inferred. On the other hand, Douris et al. (2007: 1229) stated that the examined mtDNA fragments of some smooth and ribbed *Albinaria* individuals from Folegandros are very similar or identical.



Figs. 1-8. *Albinaria caerulea*.

Frontal x5, body whorl dorsal x7; phot. S. Hof. Actual shell height = H (mm).

1. *A. c. caerulea*, GR, Cyclades, Amorgos, ex SMF 58313, H 15.6.

2. *A. c. caerulea*, GR, Cyclades, Folegandros: Karavostasis, ex SMF 323139, H 13.9.

3. *A. c. amorgia*, GR, Cyclades, Amorgos, paratype, ex SMF 93349, H 15.35.
4. *A. c. maculata*, TR, S. W. Anatolia, Ephesus, ex SMF 230825, H 16.7.
5. *A. c. milleri*, GR, Cyclades, Paros, syntype, SMF 66982, H 18.8.
6. *A. c. altecostata*, GR, Cyclades, Strongili near Naxos, ex SMF 93338, H 15.6.
7. *A. c. pholegandrica*, GR, Cyclades, Folegandros: Paleokastro, ex SMF 323131, H 14.9.
8. *A. c. scaletta*, GR, Cyclades, Folegandros: Paleokastro, paratype, ex SMF 323133, H 14.5.

III. *Albinaria teres* (Olivier)

A. teres (Olivier 1801) has been classified with the *teres* subgroup of the southern *Albinaria* group (Nordsieck 1999: 5).

Distributional range: Eastern Crete from southeastern Dikti mountains, eastern border of Mesara plain and easternmost Asterousia mountains to the eastern end of the island, with adjacent islands; introduced on Dia island and Chalki island, Dodecanese.

A. teres is similar to the neighbouring species of the *teres* subgroup: *A. janisadana* Loosjes 1955, *A. li* Welter-Schultes 1999, *A. corrugata* (Bruguère 1792) and *A. praeclara* (L. Pfeiffer 1853). *A. sturanyi* A. J. Wagner 1924, classified with the *caerulea* subgroup of one of the eastern *Albinaria* groups (Nordsieck 1999: 5), has been found in the midst of the range of *A. teres*. *A. teres* occurs syntopically with *A. praeclara* in many and with *A. corrugata* in several localities; the other named species occur allopatrically.

A. manselli (O. Boettger 1883), which is treated by Welter-Schultes (2000: 64; 2010: 181) as an independent species, had formerly been classified with *A. teres*. The differences (shell smaller; apex ribbed) were not regarded as sufficient for species separation (Nordsieck 1999: 14, note 20).

According to the observations of Welter-Schultes (2000: 58, 63), *A. sturanyi* hybridizes with *A. teres*. Therefore, he (: 58) treated it as a subspecies of *A. teres*, but later on (2010: 181), on grounds of different morphology, he separated it as an independent species again.

Apparently, it is difficult to specify the shell differences of *A. teres* and the neighbouring species. Information about these differences given in the so-called diagnoses of Welter-Schultes (2010) is scanty.

A. janisadana (: 205) is separated only because of the extreme development of the cervix.

A. li (: 203-204) is said to be somewhat smaller than *A. teres*, largest shell diameter often located closer to the aperture. Other differences mentioned in Welter-Schultes (1999: 70) are not repeated later on.

No diagnosis is given for *A. corrugata* (: 189), but elsewhere (: 176) the difference cervix more strongly corrugated is given.

For *A. praeclara* as a whole (: 183) no differences (except shell colour) are given. The eastern subspecies sensu Welter-Schultes, *A. p. praeclara* (: 183), differs by the ribbed apex (which, however, is also a character of *A. manselli*).

A. sturanyi (: 181) is said to differ from *A. teres* by the characteristic cervix and more rounded aperture.

As can be seen, most of these characters are not or not easily measurable. It is interesting that *A. sturanyi* and *A. manselli* (which is also separated as a species) are not recognizable in the spatial distribution maps of characters given by Welter-Schultes for *A. teres* and these species. It is clear that subspecies of *A. teres* which are not defined by the examined characters are not recognizable there as well.

In the past decades I recognized subunits of *A. teres* in the material available to me which differ mainly by the same characters as those of *A. caerulea* (see chapter II): strength of white surface layer, sculpture and development of the cervix. These subunits are provisionally regarded as subspecies (Nordsieck 2007: 47), exhibiting more or less broad intergradation zones within the continuous range of the species. They are listed as follows (*A. manselli* not considered): *A. t. teres* (fig. 9) from AkraSideros, introduced on Dia island; *A. t. extensa* (L. Pfeiffer 1864) (fig. 10), distributed from Ierapetra to Sitia, AkraSideros and Paleokastro; *A. t. toplouensis* Schultes & Wiese 1991 (fig. 11), percostate form of the foregoing, occurring near Moni Toplou; *A. t. nordsiecki* Zilch 1977 (fig. 12), distributed in the central and southeastern part of the species range from southeastern Dikti mountains to west of Sitia and east of Ierapetra, with region of Goudouras and

Koufonisi island; *A. t. distans* sensu Boettger 1889 (fig. 13), distributed from western boundary of the species range to southeastern Dikti mountains; *A. t. distans* (L. Pfeiffer 1864) (fig. 14), percostate form of the foregoing, occurring near Tsoutsouros; *A. t. vermiculata* (O. Boettger 1883) (figs. 15-16), distributed in the easternmost part of the species range from south of Sitia and Palekastro to the regions of Ziros and Xerokambos.

Gittenberger (1991: 266, fig. 1A) gave a distribution map of *A. teres* and its subspecies which largely corresponds to my results.

The forms from the Dionisades islands differ from *A. teres* only by a cervix, which in comparison with *A. t. vermiculata* exhibits more pronounced characters (figs. 17-19); they are separated as an independent species, *A. janisadana* (Nordsieck 1999: 5, 13, note 19).

The name *A. t. nordsiecki* is valid, because Zilch (1977: 336) proposed it as a new replacement name for *C. t.* var. *insularis* O. Boettger 1883 [non Heude] alone, not for the other two preoccupied names, which Zilch listed in the following text as synonyms of *A. t. nordsiecki* (in brackets, as he usually did in his publication series). The choice of a lectotype (Nordsieck 1996: 94) was therefore not necessary (art. 72.7 ICZN). The opinion of Welter-Schultes (2010: 176) that it was proposed as replacement name for all three preoccupied names and therefore a *nomennudum*, is wrong; to put it mildly, it is an example of his special nomenclatural „interventions“.

Welter-Schultes (2010) did not accept parapatric subspecies of Cretan *Albinaria* species, e. g., *A. teres*, which are not bordered by a narrow hybrid zone (see chapter I). He examined five characters of this species, with the result that there are no such zones within the continuous range of this species. However, several characters (development of cervix, characters of the closing apparatus), which, e. g., Boettger (1889: 43-47) used to define varieties of *A. teres*, were not considered, without foundation. Within the genus some of them are of higher taxonomic value (Nordsieck 1999: 2), in species with uniform closing apparatus especially the development of the cervix.

In most subunits of *A. teres* basal furrow and dorsal keel of the cervix are relatively weak (fig. 17).

In *A. t. vermiculata* (fig. 18) both are more distinct; within the aperture the basal furrow is marked by an indistinct elevation which Boettger (1889: 45) regarded as a lower palatal plica. Even if this character is variable within *A. t. vermiculata*, it should be examined. In the forms from the Dionisades islands, *A. janisadana* (fig. 19), basal furrow and dorsal keel are more distinct. Here, this character is used for the separation as an independent species.

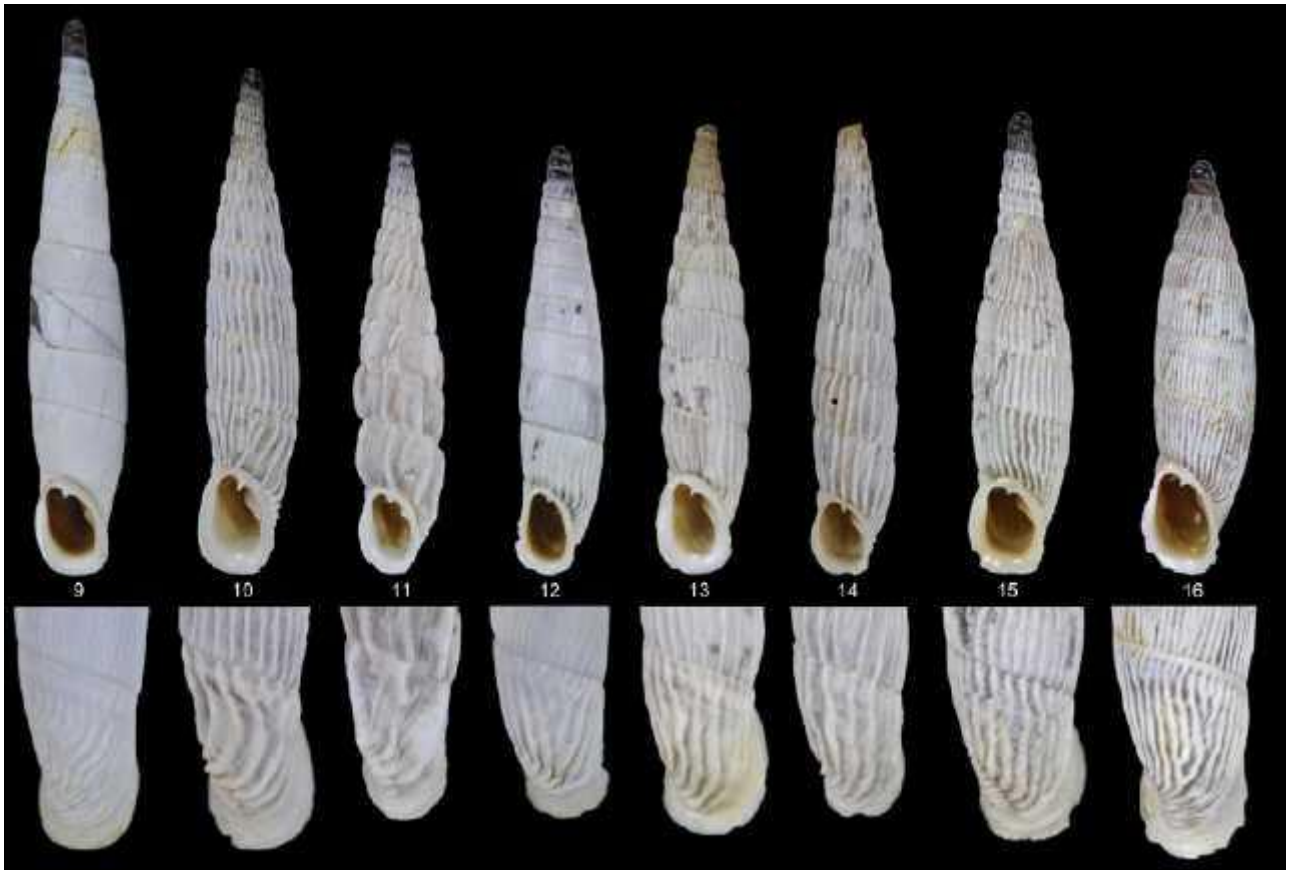
The contact zones of the subunits within the range of *A. teres* are apparently not only broad intergradation zones. There are indications of narrow hybrid zones between different subspecies:

Gittenberger (1991: 270) found no intermediates between the three subspecies in the southeasternmost part of the Lasithi province, though their ranges come close together there.

I studied samples of *A. t. extensa* and *A. t. vermiculata* occurring in close neighbourhood in their western and northern border regions.

In Welter-Schultes' (2010) spatial distribution maps of rib prominence (which is correlated with the strength of white surface layer) and (or) rib number on penultimate whorl (: figs. 19A, B) sudden transitions near Moni Toplou and Tsoutsouros and narrow hybrid zones at the western boundary of *A. t. vermiculata* near Chandras and the eastern boundary of the Orino form of *A. t. nordsiecki* are recognizable. Near Itanos he (: 177) discovered a syntopic occurrence of two distinct forms of *A. teres*, he did not write which, but instead gave the explanation that this occurrence might be due to human activities.

As a result of chapters II and III, it can be stated that, as it seems, in both *Albinaria* species subunits with all kinds of contact zones occur (see chapter I, argument 2.).



Figs. 9-16. *Albinaria teres*.

Frontal x5, body whorl dorsal x7; phot. S. Hof. Actual shell height = H (mm).

9. *A. t. teres*, GR, Crete, Diaisland, ex SMF 93655, H 24.3.

10. *A. t. extensa*, GR, Crete, Sitia, ex SMF 60123, H 22.2.

11. *A. t. toplouensis*, GR, Crete, 4.5 km NNE Moni Toplou near Palekastro, paratype, ex SMF 309251, H 19.0.

12. *A. t. nordsiecki*, GR, Crete, Platanos near Kavousi, ex SMF 337130, H 18.8.

13. *A. t. distans* sensu Boettger, GR, Crete, Viannos, ex SMF 69002, H 19.7.

14. *A. t. distans*, GR, Crete, Tsoutsouros, ex SMF 69001, H 19.8 (protoconch lost).

15. *A. t. vermiculata*, GR, Crete, Kato Zakros, ex SMF 60140, H 20.3.

16. *A. t. vermiculata*, GR, Crete, Mangasa (= Langada) near Sitia, ex SMF 66284, H 18.15.



Figs. 17-19. Cervix of *Albinaria* species.

Body whorl dorsal; phot. S. Hof. Actual shell height = H (mm).

17. *A. t. extensa*, GR, Crete, Sitia, ex SMF 60123, H 20.9.

18. *A. t. vermiculata*, GR, Crete, Kato Zakros, ex SMF 60140, H 21.1.

19. *A. j. janisadana*, GR, Crete, Gianisadaisland, paratype, ex N 8182, H 24.6.

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