# On altitude dependent characters in *Albinaria idaea* (L. Pfeiffer, 1849), with a revision of the species (Gastropoda Pulmonata: Clausiliidae)

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Several forms of *Albinaria idaea* (L. Pfeiffer, 1849) have been described as (sub)species from various sites on Mt. Ida (Central Crete). In recent years, however, much additional material has been collected, which made clear that no sharp boundaries exist between these forms. Moreover, several characters proved to be altitude dependent to a certain extent. It may be concluded that on Mt. Ida only a single evolutionary entity can be distinguished, viz. *A. i. idaea*. On the isolated Mt. Kedros, south-west of Mt. Ida, an undescribed allopatric form was found, which because of its smaller size and differences in altitude dependent characters was given subspecific rank as *A. i. amabilis* ssp. nov. On the Paximadia Isles, south of Central Crete, a percostate and a finely ribbed subspecies occur allopatrically. The finely ribbed one seems consubspecific with *A. i. idaea*; the percostate one was recently described as the separate subspecies *A. i. pichcapunlla* Schultes & Wiese, 1991.

## Introduction

In Europe, no land snail genus has radiated as strongly as *Albinaria* Vest, 1867. A wealth of species and subspecies is found from the Ionian islands to southern Asia Minor. For an understanding of the taxonomy and speciation scenarios of the species of Crete, where the genus is extremely speciose, detailed distributional data are highly relevant. Until recently, little was known about the snails that occur south-west of Mt. Ida (2546 m), in the vicinity of the Mts. Kedros (1777 m), Siderotas (1136 m) and Vouvala (947 m). During an expedition to this area, a new, allopatric form of *A. idaea* was found on Mt. Kedros.

While comparing the form from Mt. Kedros with the alleged subspecies of *A. idaea* from Mt. Ida, the existing classification seemed unsatisfactory. According to Nordsieck (1977), the species is distributed over the latter mountain with four subspecies. However, many samples that have been collected on Mt. Ida in recent years cannot be classified with one of these subspecies, but seem to be intermediate in characters. This implies that either additional subspecies should be described or the diagnoses of currently recognized ones revised. This paper deals with these questions.

## Materials and methods

In this analysis, the samples of *A. idaea* present in the Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie, = RMNH), Leiden were used. The RMNH inventory K-numbers and the corresponding UTM (1 × 1 km) codes are listed below; alc. refers to material in alcohol 70%. Additional material from other collections is referred to with the following abbreviations: BM = British Museum (Natural History); HCN = Haus der Natur, Cismar; Ma = W. J. M. Maassen, Duivendrecht; NHMW = Naturhistorisches Museum, Wien; No = H. Nordsieck, Villingen-Schwenningen; PKI = Panepistimio Kritis, Iraklion; SMF = Senckenberg Museum, Frankfurt am Main; Su = P. Subai, Aachen.

Whenever possible, ten specimens per sample were analysed. The holo- or lectotypes of all the nominal taxa within *Albinaria idaea* were also studied.

The following characters were used: 1, number of whorls; 2, height of the shell; 3, width of the shell; 4, outside height of the aperture; 5, outside width of the aperture; 6, height of the parietalis, measured in front; 7, the shortest distance between the umbilical chink and the apertural margin, seen from the side, as a measure of protrusion of the aperture; 8, number of spiral ribs on the dorsal side of the penultimate whorl, measured across 2 mm; 9, number of cervical ribs along the suture, measured across 2 mm; 10, number of cervical ribs along the midline of the cervix, measured across 2 mm; 11, number of smooth apical whorls; 12, prominence of growth lines.

For each character, mean values were calculated per sample. The geographical distribution of the characters was studied by plotting these averages on a geographical map of the area. The relation between characters and altitude was analysed by scatterplots and Spearman rank correlation coefficients.

## Results

In *Albinaria idaea*, three geographically isolated groups of populations can be distinguished (see fig. 1). One covers most of Mt. Ida, another is confined to a relatively small area on Mt. Kedros, and the third is found on the Paximadia Isles. On Mt. Ida, the species is quite variable. The populations on Mt. Kedros show little variation. On the Paximadia Isles, two distinct forms can be distinguished.

On Mt. Ida the species occurs on the east, south, west and north-west slopes from approximately 300 to 1600 m above sea level. So far no specimens have been found on the highest parts of the mountain. The variability on Mt. Ida is great, but gradual for most measured characters. When compared with altitude (see table 1, figs. 2-12), the following characters show significant ($p < 0.05$) and positive correlations: width of the shell, height and width of the aperture, height of the parietalis, spiral and cervical rib density. The spiral and cervical rib densities are the characters that are most clearly correlated with the altitude at which the snails in question occurred.

On Mt. Kedros *Albinaria idaea* lives from 1200 m above sea level up to the summit (1777 m). Here no altitude dependent characters have been detected (see table 1). The samples have generally lower character values than Ida samples of similar altitudes (figs. 2-12).

On the Paximadia Isles two allopatrically distributed forms of *Albinaria idaea* can be distinguished. One of these is percostate and is only found on limestone cliffs of the eastern part of the eastern islet. The other is finely ribbed and resembles the Mt. Ida forms; it lives all over both islets, on schist. The two forms are interconnected by a narrow hybrid zone (Schultes & Wiese, 1992). We have measured typical specimens of both forms from a single sample (NMW 80255), containing intermediate shells as well (figs. 29, 30).

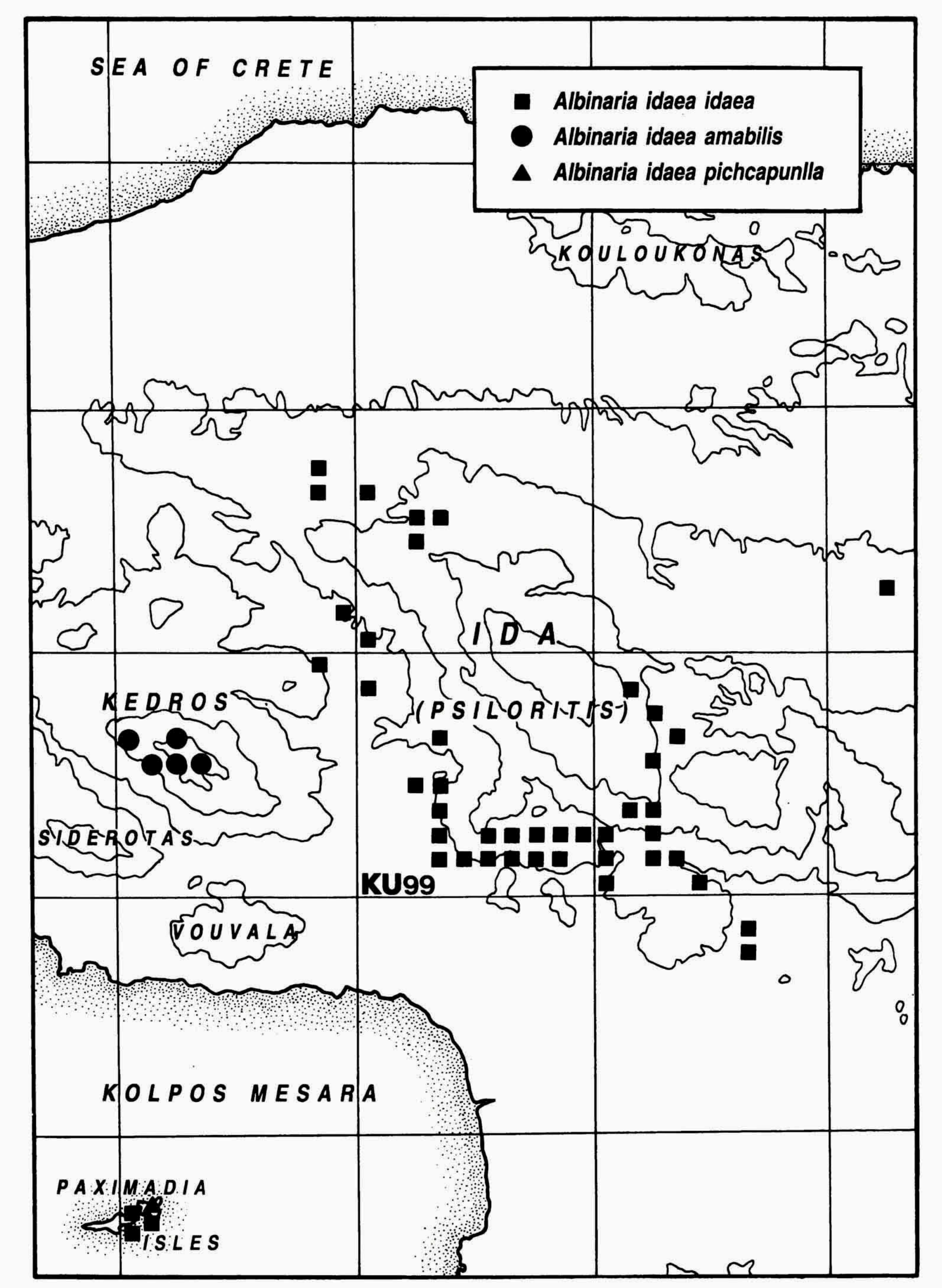



Fig. 1. Map of central Crete, showing the location of the studied samples of *Albinaria idaea*. The 10 x 10 km UTM grid and the 500, 1000, 1500 and 2000 m contour lines have been indicated. Records of other *Albinaria* species within this area have been omitted.

Table 1. Spearman rank correlation coefficients and corresponding p- values of shell characters with altitude in samples from Mt. Ida and Mt. Kedros. Significant correlations (p < 0.05) are marked with *.

| | Mt. Ida 25 samples | | Mt. Kedros 9 samples | |
|---|---|---|---|---|
| number of whorls | - 0.2698 | (p = 0.1862) | 0.5588 | (p = 0.1140) |
| height of shell | 0.2341 | (p = 0.2514) | 0.4352 | (p = 0.2184) |
| width of shell | 0.6592 * | (p = 0.0012) | - 0.1841 | (p = 0.6026) |
| height of aperture | 0.5237 * | (p = 0.0103) | 0.0672 | (p = 0.8492) |
| width of aperture | 0.6147 * | (p = 0.0026) | - 0.0840 | (p = 0.8121) |
| height of parietalis | 0.6484 * | (p = 0.0015) | 0.1172 | (p = 0.7404) |
| distance umbilicus - apertural margin | 0.2895 | (p = 0.1561) | 0.5607 | (p = 0.1128) |
| ribs/mm on penultimate whorl | 0.7556 * | (p = 0.0002) | - 0.0084 | (p = 0.9811) |
| ribs/mm near suture of cervix | 0.8805 * | (p = 0.0000) | - 0.3613 | (p = 0.3068) |
| ribs/mm near periphery of cervix | 0.8369 * | (p = 0.0000) | - 0.5021 | (p = 0.1556) |
| number of unribbed initial whorls | 0.2309 | (p = 0.2579) | 0.1172 | (p = 0.7404) |

The following list summarizes quantitative data concerning 35 samples (34 in RMNH, with K numbers; 1 in NNM) with altitudes of the localities in question. Abbreviations used: NW = number of whorls; HS = height of the shell (mm); WS = width of the shell (mm); HA = height of the aperture (mm); WA = width of the aperture (mm); HP = height of the parietalis (mm); UA = distance from umbilicus to apertural margin (mm); RP = rib density of the penultimate whorl (per mm); RCS = rib density of the cervix along the suture (per mm); RCP = rib density of the cervix near the periphery (per mm); UIW = number of unribbed initial whorls; GL = prominence of growth lines. For each character (except for GL) we give: mean ± standard deviation, minimum-maximum (number). The prominence of growth lines is indicated, giving numbers of specimens with or without this microsculpture; this distinction cannot always be made objectively, however.

K1040 (550 m): NW = 12.8 ± 0.9, 11-14 (10); HS = 19.8 ± 1.4, 17.8-21.6 (10); WS = 4.1 ± 0.1, 4.0-4.3 (10); HA = 4.1 ± 0.3, 3.6-4.6 (10); WA = 3.3 ± 0.2, 3.0-3.8 (10); HP = 0.30 ± 0.06, 0.19-0.38 (10); UA = 1.1 ± 0.1, 0.9-1.3 (10); RP = 4.6 ± 0.8, 3.7-5.8 (10); RCS = 3.0 ± 0.5, 2.6-3.7 (10); RCP = 2.6 ± 0.4, 2.1-3.1 (10); UIW = 1.6 ± 0.3, 1.3-2 (10); GL = absent (10).

K1042 (550 m): NW = 12.6 ± 0.5, 12-13 (10); HS = 20.4 ± 1.0, 18.8-22.6 (10); WS = 4.2 ± 0.2, 3.9-4.5 (10); HA = 4.2 ± 0.3, 3.8-4.5 (10); WA = 3.3 ± 0.3, 2.7-3.6 (10); HP = 0.26 ± 0.08, 0.06-0.32 (10); UA = 1.1 ± 0.1, 0.9-1.2 (10); RP = 3.7 ± 0.4, 3.1-4.7 (10); RCS = 2.4 ± 0.3, 2.1-3.1 (10); RCP = 2.0 ± 0.2, 1.6-2.1 (10); UIW = 1.3 ± 0.2, 1-1.5 (10); GL = absent (10).

K1043 (650 m): NW = 12.7 ± 0.6, 12-14 (10); HS = 19.4 ± 0.9, 18.0-21.3 (10); WS = 4.0 ± 0.2, 3.6-4.4 (10); HA = 4.0 ± 0.3, 3.6-4.6 (10); WA = 3.2 ± 0.1, 3.0-3.4 (10); HP = 0.21 ± 0.04, 0.14-0.28 (10); UA = 1.1 ± 0.1, 0.96-1.4 (10); RP = 4.3 ± 0.3, 3.8-5.0 (10); RCS = 2.8 ± 0.2, 2.5-2.9 (10); RCP = 2.2 ± 0.2, 1.7-2.5 (10); UIW = 2.1 ± 0.4, 1.5-3 (10); GL = present (9), absent (1).

K1044 (400 m): NW = 12.2 ± 0.2, 12-12.5 (3); HS = 18.9 ± 0.1, 18.8-19.0 (2); WS = 3.9 ± 0.1, 3.8-4.2 (7); HA = 3.5 ± 0.2, 3.2-3.7 (3); WA = 2.9 ± 0.1, 2.8-2.9 (2); HP = 0.09 ± 0.02, 0.06-0.12 (4); UA = 1.2 ± 0.1, 1.1-1.3 (3); RP = 3.9 ± 0.4, 3.1-4.2 (7); RCS = 2.0 ± 0.3, 1.5-2.5 (7); RCP = 1.5 ± 0.3, 1.0-1.9 (7); UIW = 1.3 ± 0.2, 1-1.5 (5); GL = present (8).

K1078 (520 m): NW = 12.9 ± 0.2, 12.5-13 (5); HS = 18.2 ± 0.6, 17.2-18.8 (5); WS = 3.9 ± 0.2, 3.5-4.4 (10); HA = 3.7 ± 0.2, 3.4-3.9 (5); WA = 3.0 ± 0.1, 2.9-3.1 (5); HP = 0.12 ± 0.04, 0.07-0.16 (6); UA = 1.0 ± 0.07, 0.88-1.1 (7); RP = 4.3 ± 0.3, 3.8-5.0 (9); RCS = 2.5 ± 0.3, 2.1-2.9 (9); RCP = 1.9 ± 0.2, 1.5-2.1 (9); UIW = 1.4

± 0.2, 1-1.5 (7); GL = present (8).
K1079 (430 m): NW = 12.5 ± 0.4, 12-13 (5); HS = 17.7 ± 0.8, 16.4-18.4 (5); WS = 3.7 ± 0.1, 3.5-3.9 (9); HA = 3.6 ± 0.2, 3.4-4.0 (5); WA = 2.9 ± 0.1, 2.7-3.0 (4); HP = 0.09 ± 0.01, 0.08-0.10 (7); UA = 1.2 ± 0.2, 1.1-0.4 (6); RP = 3.4 ± 0.4, 2.9-4.2 (9); RCS = 1.7 ± 0.1, 1.5-1.7 (6); RCP = 1.2 ± 0.2, 1.0-1.3 (6); UIW = 1.4 ± 0.3, 1-2 (8); GL = present (9).
K1080 (350 m): NW = 12.3 ± 0.3, 12-12.5 (2); HS = 17.8 ± 0.05, 17.7-17.8 (2); WS = 3.6 ± 0.2, 3.5-3.9 (4); HA = 3.4 ± 0.05, 3.3-3.4 (2); WA = 2.5 ± 0.3, 2.2-2.7 (2); HP = 0.09 ± 0.02, 0.08-0.12 (3); UA = 1.1 ± 0.1, 1.0-1.2 (3); RP = 3.9 ± 0.7, 3.3-5.0 (4); RCS = 1.8 ± 0.2, 1.5-2.1 (3); RCP = 1.5 ± 0.2, 1.3-1.7 (3); UIW = 1 ± 0, 1-1 (3); GL = present (4).
K1081 (1550 m): NW = 11.1 ± 0.7, 10-12 (10); HS = 18.3 ± 1.2, 16.3-20.2 (10); WS = 4.2 ± 0.1, 3.9-4.3 (10); HA = 4.0 ± 0.5, 3.3-5.2 (10); WA = 3.3 ± 0.3, 2.6-3.6 (10); HP = 0.30 ± 0.09, 0.13-0.45 (10); UA = 1.0 ± 0.1, 0.9-1.3 (10); RP = 6.2 ± 0.9, 5.2-8.4 (10); RCS = 4.6 ± 1.0, 3.7-6.3 (10); RCP = 3.2 ± 0.6, 2.6-4.7 (10); UIW = 2.3 ± 0.5, 1.5-3.0 (10); GL = present (2), absent (8).
K1084 (1270 m): NW = 12.5 ± 0.5, 12-13 (8); HS = 21.2 ± 1.7, 18.1-23.6 (7); WS = 4.6 ± 0.3, 4.1-5.3 (10); HA = 4.3 ± 0.4, 3.8-5.1 (9); WA = 3.5 ± 0.3, 3.1-4.0 (9); HP = 0.31 ± 0.05, 0.25-0.38 (9); UA = 1.2 ± 0.1, 1.1-1.3 (10); RP = 6.2 ± 1.0, 4.7-8.4 (10); RCS = 4.2 ± 0.4, 3.7-5.2 (10); RCP = 2.9 ± 0.4, 2.1-3.7 (10); UIW = 1.8 ± 0.2, 1.5-2.3 (8); GL = present (3), absent (7).
K1192 (480 m): NW = 12.5 ± 0, 12.5-12.5 (3); HS = 18.1 ± 0.4, 17.7-18.4 (2); WS = 4.1 ± 0.2, 3.7-4.4 (6); HA = 3.8 ± 0.1, 3.6-3.9 (3); WA = 2.9 ± 0.2, 2.6-3.0 (3); HP = 0.15 ± 0.01, 0.14-0.16 (3); UA = 1.1 ± 0.1, 1.0-1.3 (5); RP = 4.4 ± 0.6, 3.8-5.8 (7); RCS = 2.4 ± 0.3, 2.1-2.9 (6); RCP = 2.3 ± 0.3, 1.9-2.9 (6); UIW = 2.1 ± 0.4, 1.5-2.5 (4); GL = present (5).
K1193 (400 m): NW = 12.6 ± 0.6, 12-13.5 (6); HS = 20.1 ± 0.7, 18.9-20.4 (5); WS = 4.1 ± 0.2, 3.8-4.4 (10); HA = 3.8 ± 0.3, 3.4-4.5 (8); WA = 2.9 ± 0.1, 2.7-3.0 (8); HP = 0.15 ± 0.05, 0.08-0.22 (8); UA = 1.0 ± 0.1, 0.8-1.1 (8); RP = 3.8 ± 0.3, 3.3-4.2 (10); RCS = 2.2 ± 0.2, 2.1-2.5 (10); RCP = 1.7 ± 0.2, 1.3-2.1 (10); UIW = 1.6 ± 0.5, 1-2.5 (7); GL = present (10).
K1196 (750 m): NW = 11.1 ± 0.6, 10-12 (8); HS = 17.8 ± 0.6, 16.8-18.7 (7); WS = 4.2 ± 0.2, 4.0-4.4 (9); HA = 3.9 ± 0.1, 3.8-4.1 (9); WA = 3.2 ± 0.1, 2.9-3.4 (9); HP = 0.29 ± 0.03, 0.25-0.32 (9); UA = 1.2 ± 0.2, 1.0-1.6 (9); RP = 5.2 ± 0.6, 4.2-5.2 (10); RCS = 2.8 ± 0.5, 2.1-3.7 (10); RCP = 2.3 ± 0.2, 2.1-2.6 (10); UIW = 1.3 ± 0.1, 1-1.5 (8); GL = present (9).
K1201 (860 m): NW = 12 ± 0, 12-12 (3); HS = 17.8 ± 0.4, 17.3-18.1 (3); WS = 3.9 ± 0.2, 3.6-4.1 (4); HA = 3.8 ± 0.3, 3.6-4.3 (4); WA = 2.8 ± 0.1, 2.7-2.9 (4); HP = 0.22 ± 0.03, 0.19-0.25 (4); UA = 1.1 ± 0.1, 1.0-1.2 (4); RP = 6.2 ± 0.6, 5.2-6.8 (4); RCS = 4.1 ± 0.2, 3.7-4.2 (4); RCP = 3.4 ± 0.6, 2.6-4.2 (4); UIW = 1.1 ± 0.1, 1-1.3 (3); GL = present (3), absent (1).
K1203 (1000 m): NW = 12.9 ± 0.5, 12-14 (10); HS = 19.4 ± 1.1, 18.0-21.0 (10); WS = 4.4 ± 0.2, 4.0-4.7 (10); HA = 4.0 ± 0.2, 3.8-4.3 (10); WA = 3.2 ± 0.1, 3.2-3.4 (10); HP = 0.18 ± 0.07, 0.06-0.32 (10); UA = 1.3 ± 0.1, 1.1-1.5 (10); RP = 6.2 ± 0.6, 5.2-7.3 (10); RCS = 3.9 ± 0.6, 3.1-4.7 (10); RCP = 2.4 ± 0.4, 2.1-3.1 (10); UIW = 1.4 ± 0.2, 1-1.8 (10); GL = present (7), absent (1).
K1218 (1050 m): NW = 12.7 ± 0.5, 12-13 (7); HS = 20.1 ± 0.6, 18.8-21.0 (7); WS = 4.2 ± 0.2, 3.7-4.4 (10); HA = 39 ± 0.3, 3.5-4.5 (7); WA = 3.1 ± 0.2, 2.8-3.4 (8); HP = 0.19 ± 0.1, 0.13-0.32 (9); UA = 1.1 ± 0.2, 0.5-1.3 (9); RP = 5.7 ± 0.7, 4.7-6.8 (10); RCS = 3.5 ± 0.8, 2.6-5.2 (10); RCP = 3.0 ± 0.7, 2.1-4.2 (10); UIW = 1.4 ± 0.2, 1.3-1.8 (7); GL = present (8), absent (1).
K1219 (1150 m): NW = 12.5 ± 0.5, 12-13 (2); HS = 17.4 (1); WS = 4.5 ± 0.4, 3.8-5.0 (4); HA = 3.9 ± 0.3, 3.6-4.3 (3); WA = 3.2 ± 0.2, 2.9-3.4 (3); HP = 0.21 ± 0.03, 0.19-0.25 (3); UA = 1.3 ± 0.1, 1.1-1.4 (3); RP = 6.3 ± 0.4, 5.8-6.8 (4); RCS = 4.0 ± 0.3, 3.7-4.2 (4); RCP = 2.7 ± 0.2, 2.6-3.1 (4); UIW = 1.5 ± 0, 1.5-1.5 (2); GL = present (4).
K1220 (1130 m): NW = 12.4 ± 0.5, 12-13 (7); HS = 19.5 ± 0.9, 18.5-20.7 (7); WS = 4.5 ± 0.2, 4.2-4.7 (10); HA = 4.1 ± 0.1, 3.9-4.4 (9); WA = 3.1 ± 0.3, 2.6-3.7 (9); HP = 0.20 ± 0.06, 0.13-0.32 (9); UA = 1.2 ± 0.1, 1.1-1.4 (9); RP = 5.8 ± 0.9, 4.7-7.9 (10); RCS = 3.5 ± 0.5, 2.6-4.7 (10); RCP = 2.6 ± 0.4, 2.1-3.1 (10); UIW = 1.6 ± 0.3, 1-2 (7); GL = present (9), absent (1).
K1332 (750 m): NW = 12.3 ± 0.6, 11-13 (9); HS = 18.0 ± 0.6, 17.1-18.9 (6); WS = 3.9 ± 0.2, 3.6-4.3 (10); HA = 3.5 ± 0.1, 3.4-3.8 (6); WA = 2.9 ± 0.1, 2.7-3.0 (6); HP = 0.18 ± 0.04, 0.12-0.24 (8); UA = 1.0 ± 0.1, 0.88-1.2 (8); RP = 5.1 ± 0.4, 4.2-5.8 (10); RCS = 2.6 ± 0.4, 1.9-3.3 (10); RCP = 2.1 ± 0.3, 1.7-2.5 (10); UIW = 2.6 ± 0.3, 2-3 (6); GL = present (5), absent (2).

K1502 (1000 m): NW = 13 ± 0, 13-13 (10); HS = 21.0 ± 1.2, 19.8-24.1 (10); WS = 4.3 ± 0.3, 3.7-4.7 (10); HA = 4.2 ± 0.2, 3.9-4.4 (10); WA = 3.2 ± 0.1, 3.1-3.5 (10); HP = 0.19 ± 0.03, 0.13-0.25 (10); UA = 1.3 ± 0.1, 1.2-1.6 (10); RP = 5.2 ± 0.2, 4.7-5.8 (10); RCS = 2.8 ± 0.4, 2.1-3.7 (10); RCP = 2.2 ± 0.4, 1.6-2.6 (10); UIW = 1.3 ± 0.2, 1-1.5 (10); GL = present (10).
K1545 (1400 m): NW = 11.9 ± 0.6, 11-13 (7); HS = 18.3 ± 1.4, 16.6-20.5 (7); WS = 4.1 ± 0.2, 3.8-4.4 (10); HA = 3.8 ± 0.3, 3.3-4.4 (10); WA = 3.1 ± 0.3, 2.7-3.7 (10); HP = 0.28 ± 0.04, 0.25-0.38 (10); UA = 1.1 ± 0.1, 0.8-1.3 (10); RP = 6.1 ± 1.3, 4.7-8.9 (10); RCS = 3.8 ± 0.5, 3.1-4.7 (10); RCP = 3.0 ± 0.6, 2.1-4.2 (10); UIW = 2.0 ± 0.3, 1.5-2.5 (7); GL = present (7), absent (3).
K1546 (1400 m): NW = 11.8 ± 0.6, 11-13 (10); HS = 19.9 ± 1.4, 18.0-21.6 (10); WS = 4.4 ± 0.2, 4.0-4.6 (10); HA = 4.1 ± 0.3, 3.6-4.6 (10); WA = 3.5 ± 0.2, 3.2-3.8 (10); HP = 0.31 ± 0.07, 0.19-0.44 (10); UA = 1.2 ± 0.1, 1.1-1.4 (10); RP = 4.8 ± 0.5, 4.2-5.8 (10); RCS = 3.2 ± 0.3, 2.6-3.7 (10); RCP = 2.9 ± 0.5, 2.6-4.2 (10); UIW = 1.7 ± 0.4, 1-2.3 (10); GL = present (8), absent (1).
K2545 (1210 m): NW = 10.7 ± 0.5, 10-11 (10); HS = 15.8 ± 0.7, 14.9-16.8 (10); WS = 3.6 ± 0.1, 3.5-3.7 (10); HA = 3.5 ± 0.1, 3.3-3.7 (10); WA = 2.9 ± 0.1, 2.6-2.9 (10); HP = 0.13 ± 0.06, 0.032-0.25 (10); UA = 0.97 ± 0.07, 0.89-1.1 (10); RP = 5.6 ± 0.9, 4.2-7.3 (10); RCS = 4.1 ± 0.8, 2.6-4.7 (10); RCP = 3.2 ± 0.7, 2.1-4.2 (10); UIW = 2.0 ± 0.2, 1.3-2.3 (10); GL = present (9).
K2546 (1300 m): NW = 10.8 ± 0.6, 10-11.5 (3); HS = 16.1 ± 1.3, 14.3-16.6 (3); WS = 3.4 ± 0.1, 3.2-3.5 (6); HA = 3.4 ± 0.05, 3.3-3.4 (6); WA = 2.7 ± 0.2, 2.5-2.9 (7); HP = 0.12 ± 0.06, 0.04-0.24 (7); UA = 0.87 ± 0.08, 0.80-0.96 (7); RP = 4.3 ± 0.4, 3.8-5.0 (7); RCS = 2.5 ± 0.4, 1.7-2.9 (7); RCP = 2.2 ± 0.4, 1.3-2.1 (7); UIW = 2.3 ± 0.2, 2-2.5 (6); GL = present (7).
K2547 (1400 m): NW = 12.0 ± 0.6, 11-13 (10); HS = 16.6 ± 1.0, 15.0-18.2 (10); WS = 3.4 ± 0.1, 3.3-3.6 (10); HA = 3.2 ± 0.1, 3.1-3.4 (10); WA = 2.7 ± 0.1, 2.6-2.8 (10); HP = 0.16 ± 0.03, 0.11-0.23 (10); UA = 0.97 ± 0.07, 0.88-1.1 (10); RP = 5.2 ± 0.6, 4.2-6.3 (10); RCS = 3.3 ± 0.7, 2.3-4.6 (9); RCP = 2.3 ± 0.5, 1.7-3.3 (10); UIW = 2.5 ± 0.4, 1.5-3 (10); GL = present (9).
K2548 (1400 m): NW = 10.4 ± 0.5, 10-11 (5); HS = 16.2 ± 0.9, 14.9-17.5 (5); WS = 3.8 ± 0.1, 3.7-4.0 (7); HA = 3.6 ± 0.2, 3.4-3.9 (5); WA = 3.1 ± 0.1, 3.0-3.3 (5); HP = 0.18 ± 0.06, 0.12-0.26 (5); UA = 0.95 ± 0.06, 0.88-1.0 (5); RP = 6.4 ± 0.9, 5.8-7.9 (7); RCS = 3.3 ± 0.2, 2.9-3.7 (6); RCP = 2.2 ± 0.2, 1.9-2.5 (6); UIW = 2.2 ± 0.2, 2-2.5 (6); GL = present (3), absent (2).
K2549 (1480 m): NW = 11.1 ± 0.3, 11-12 (10); HS = 15.6 ± 0.6, 14.7-16.5 (10); WS = 3.5 ± 0.1, 3.4-3.8 (10); HA = 3.4 ± 0.1, 3.3-3.5 (10); WA = 2.9 ± 0.1, 2.6-3.0 (10); HP = 0.16 ± 0.06, 0.09-0.26 (10); UA = 0.90 ± 0.09, 0.80-1.04 (10); RP = 6.2 ± 0.8, 5.0-7.1 (10); RCS = 3.5 ± 0.8, 2.5-5.4 (10); RCP = 2.3 ± 0.3, 1.7-2.9 (10); UIW = 2.3 ± 0.2, 2-2.5 (10); GL = present (3), absent (7).
K2551 (1700 m): NW = 11.8 ± 0.5, 11-12.5 (10); HS = 16.9 ± 1.1, 15.3-18.7 (10); WS = 3.5 ± 0.1, 3.4-3.6 (10); HA = 3.4 ± 0.2, 3.1-3.8 (9); WA = 2.8 ± 0.1, 2.6-3.0 (9); HP = 0.15 ± 0.06, 0.07-0.24 (10); UA = 0.96 ± 0.13, 0.88-1.20 (9); RP = 5.1 ± 0.9, 3.8-6.7 (10); RCS = 2.9 ± 0.7, 2.1-4.2 (10); RCP = 1.8 ± 0.4, 1.3-2.3 (10); UIW = 2.1 ± 0.4, 1.5-2.5 (10); GL = present (3), absent (4).
K2552 (1777 m): NW = 11.8 ± 0.4, 11-12 (6); HS = 16.2 ± 1.0, 14.8-17.3 (4); WS = 3.4 ± 0.1, 3.1-3.6 (10); HA = 3.5 ± 0.1, 3.3-3.6 (7); WA = 2.8 ± 0.2, 2.6-3.0 (6); HP = 0.14 ± 0.05, 0.04-0.24 (9); UA = 1.1 ± 0.1, 0.88-1.4 (10); RP = 6.0 ± 0.7, 5.0-7.5 (10); RCS = 3.3 ± 0.3, 2.9-3.8 (9); RCP = 2.2 ± 0.3, 1.7-2.5 (10); UIW = 2.3 ± 0.4, 1.5-3 (8); GL = present (3), absent (2).
K2553 (1600 m): NW = 11.3 ± 0.4, 11-12 (8); HS = 16.4 ± 1.0, 15.3-18.1 (8); WS = 3.5 ± 0.2, 3.0-3.6 (10); HA = 3.5 ± 0.2, 3.2-3.8 (10); WA = 2.9 ± 0.2, 2.6-3.2 (10); HP = 0.14 ± 0.03, 0.08-0.20 (10); UA = 1.0 ± 0.1, 0.8-1.2 (10); RP = 5.0 ± 0.6, 4.2-6.2 (10); RCS = 2.7 ± 0.4, 2.1-3.3 (10); RCP = 2.0 ± 0.3, 1.5-2.5 (10); UIW = 2.4 ± 0.3, 2-3 (8); GL = present (6), absent (2).
K2554 (1500 m): NW = 12.0 ± 0.7, 10.5-13 (10); HS = 17.6 ± 1.4, 15.0-19.4 (10); WS = 3.6 ± 0.2, 3.3-3.9 (10); HA = 3.5 ± 0.2, 3.2-3.8 (10); WA = 2.9 ± 0.2, 2.6-3.2 (10); HP = 0.13 ± 0.04, 0.09-0.19 (10); UA = 1.1 ± 0.1, 0.9-1.2 (10); RP = 5.5 ± 1.0, 4.2-7.9 (10); RCS = 3.2 ± 0.5, 2.3-3.8 (10); RCP = 2.1 ± 0.2, 1.7-2.5 (10); UIW = 2.4 ± 0.2, 2-2.5 (10); GL = present(3), absent(4).
K2583 (500 m): NW = 12.0 ± 0, 12-12 (8); HS = 20.2 ± 0.9, 18.6-21.6 (8); WS = 4.3 ± 0.3, 3.9-4.9 (10); HA = 4.3 ± 0.4, 3.9-4.8 (10); WA = 3.1 ± 0.2, 2.9-3.4 (10); HP = 0.30 ± 0.06, 0.19-0.38 (10); UA = 1.0 ± 0.1, 0.8-1.1 (10); RP = 4.2 ± 0.5, 3.7-5.2 (10); RCS = 2.4 ± 0.3, 2.1-2.6 (10); RCP = 1.8 ± 0.2, 1.6-2.1 (10); UIW = 1.6 ± 0.4, 1.3-2.5 (6); GL = absent (10).
K2584 (500 m): NW = 13.0 ± 0.7, 12-14 (4); HS = 19.4 ± 0.4, 19.1-20.0 (4); WS = 4.2 ± 0.2, 3.9-4.4 (4); HA

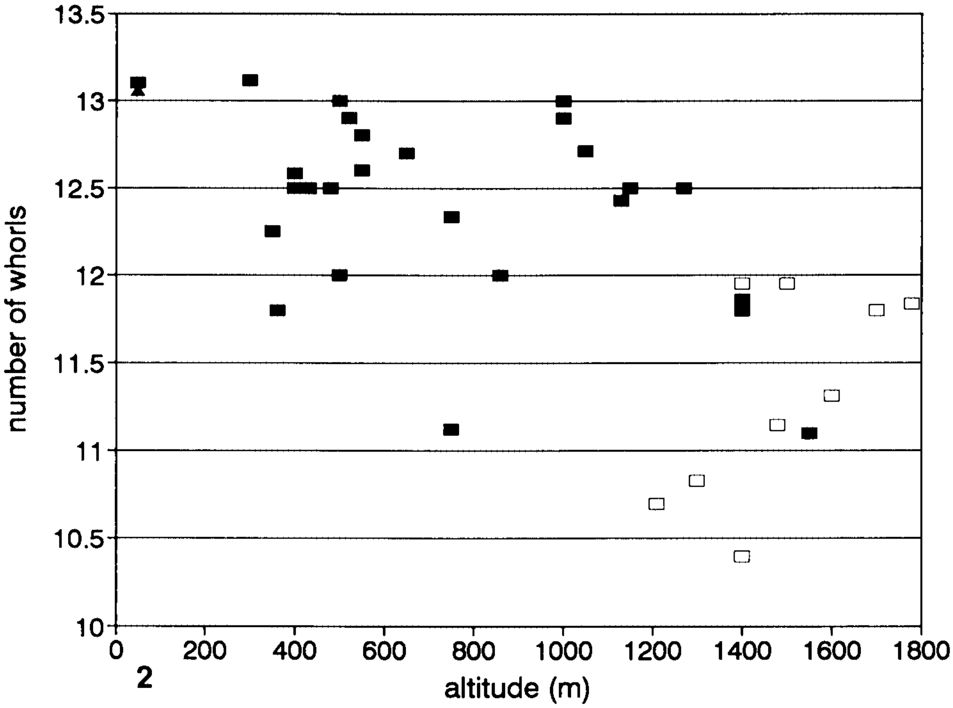
= 4.0 ± 0.2, 3.8-4.3 (4); WA = 3.2 ± 0.2, 2.9-3.4 (4); HP = 0.37 ± 0.03, 0.32-0.38 (4); UA = 1.2 ± 0.1, 1.1-1.2 (4); RP = 4.7 ± 0.5, 4.2-5.2 (4); RCS = 2.6 ± 0.4, 2.1-3.1 (4); RCP = 2.4 ± 0.3, 2.1-2.6 (4); UIW = 1.5 ± 0.2, 1.3-1.8 (4); GL = absent (4).

K2597 (300 m): NW = 13.1 ± 0.6, 12-14 (9); HS = 19.2 ± 0.8, 17.6-20.1 (9); WS = 4.0 ± 0.3, 3.5-4.4 (10); HA = 3.7 ± 0.2, 3.4-4.0 (10); WA = 2.9 ± 0.1, 2.7-3.1 (9); HP = 0.06 ± 0.04, 0.02-0.16 (10); UA = 1.2 ± 0.1, 1.0-1.3 (10); RP = 4.5 ± 0.3, 4.2-5.0 (10); RCS = 2.4 ± 0.3, 2.1-2.9 (10); RCP = 1.7 ± 0.1, 1.5-1.9 (10); UIW = 1.8 ± 0.4, 1.5-2.5 (9); GL = present (6), absent (4).

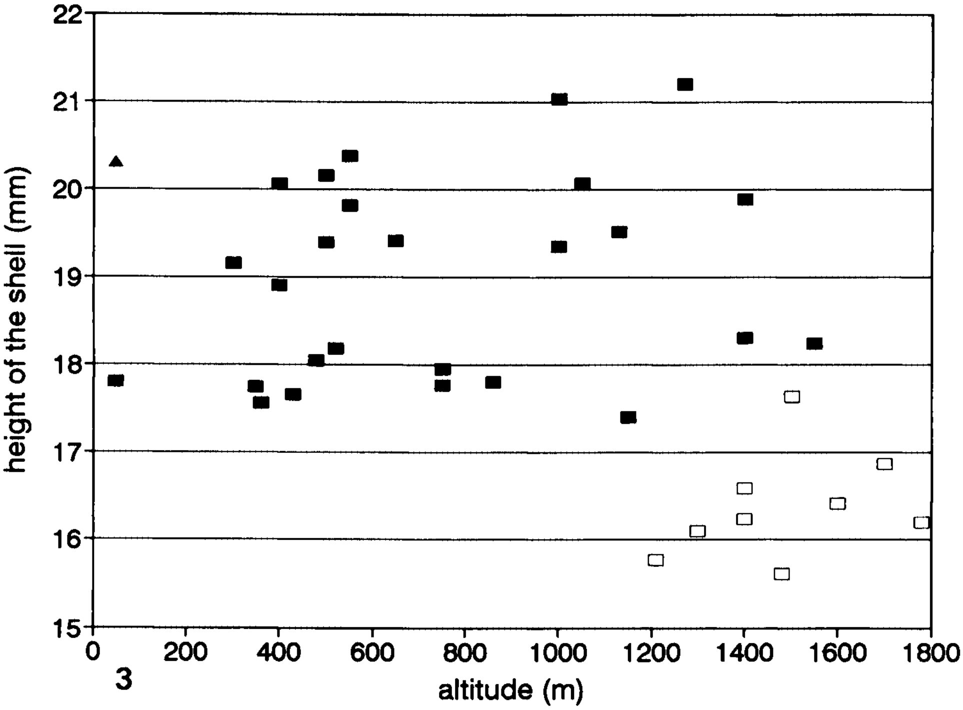
K2601 (360 m): NW = 11.8 ± 0.5, 11-12.5 (10); HS = 17.6 ± 0.8, 16.2-19.2 (10); WS = 3.8 ± 0.1, 3.7-4.0 (10); HA = 3.6 ± 0.1, 3.4-3.8 (9); WA = 2.8 ± 0.1, 2.7-3.0 (9); HP = 0.13 ± 0.02, 0.08-0.16 (9); UA = 0.96 ± 0.08, 0.80-1.1 (9); RP = 5.2 ± 0.5, 4.6-6.2 (10); RCS = 2.4 ± 0.2, 2.1-2.9 (10); RCP = 2.1 ± 0.2, 1.7-2.5 (10); UIW = 1.6 ± 0.5, 1-2.5 (10); GL = present (3), absent (4).

NMW 80255, finely ribbed form: NW = 13.1 ± 1.0, 12-15 (7); HS = 17.8 ± 2.1, 16.0-22.3 (7); WS = 3.5 ± 0.5, 3.1-4.8 (10); HA = 3.5 ± 0.3, 3.1-4.2 (9); WA = 2.7 ± 0.3, 2.3-3.2 (8); HP = 0.20 ± 0.06, 0.13-0.31 (10); UA = 1.0 ± 0.1, 0.9-1.2 (10); RP = 3.7 ± 0.4, 3.2-4.3 (10); RCS = 1.9 ± 0.4, 1.6-2.7 (10); RCP = 2.0 ± 0.6, 1.6-3.2 (10); UIW = 1.4 ± 0.2, 1.3-1.8 (7); GL = present (4), absent (5).

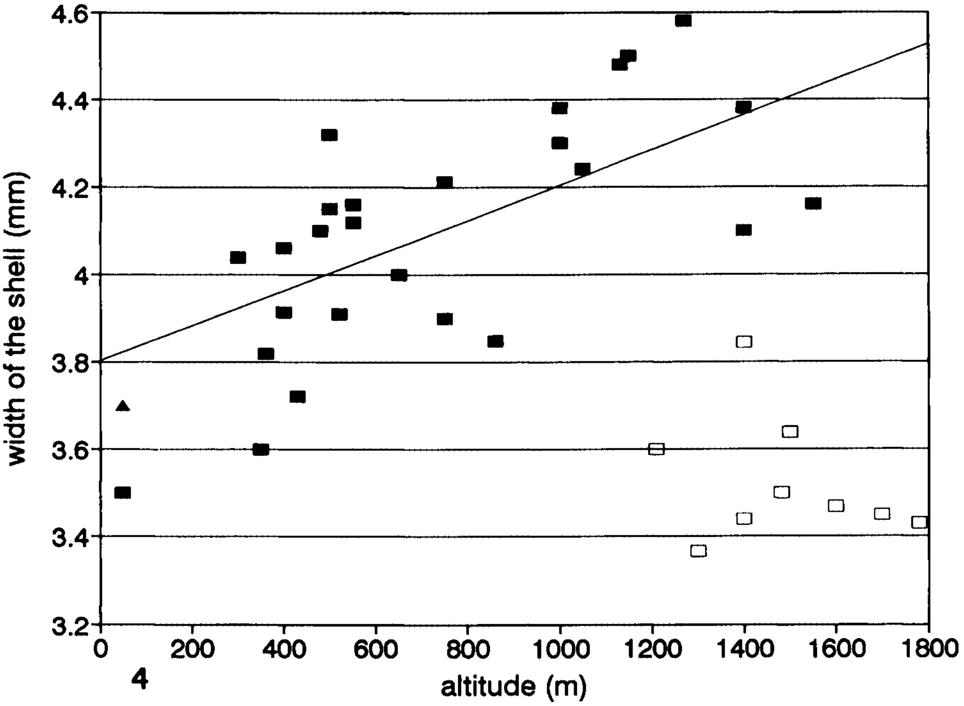
NMW 80255, percostate form: NW = 13.1 ± 0.6, 12.5-14 (5); HS = 20.3 ± 0.7, 19.6-21.4 (5); WS = 3.7 ± 0.2, 3.5-4.1 (10); HA = 3.9 ± 0.3, 3.5-4.3 (10); WA = 3.1 ± 0.2, 2.9-3.4 (9); HP = 0.22 ± 0.04, 0.16-0.25 (10); UA = 1.2 ± 0.1, 1.0-1.6 (10); RP = 1.1 ± 0.1, 1.0-1.4 (10); RCS = 0.7 ± 0.2, 0.4-1.0 (10); RCP = 0.7 ± 0.2, 0.4-1.3 (10); UIW = 2.1 ± 0.2, 2-2.5 (4); GL = present (9).



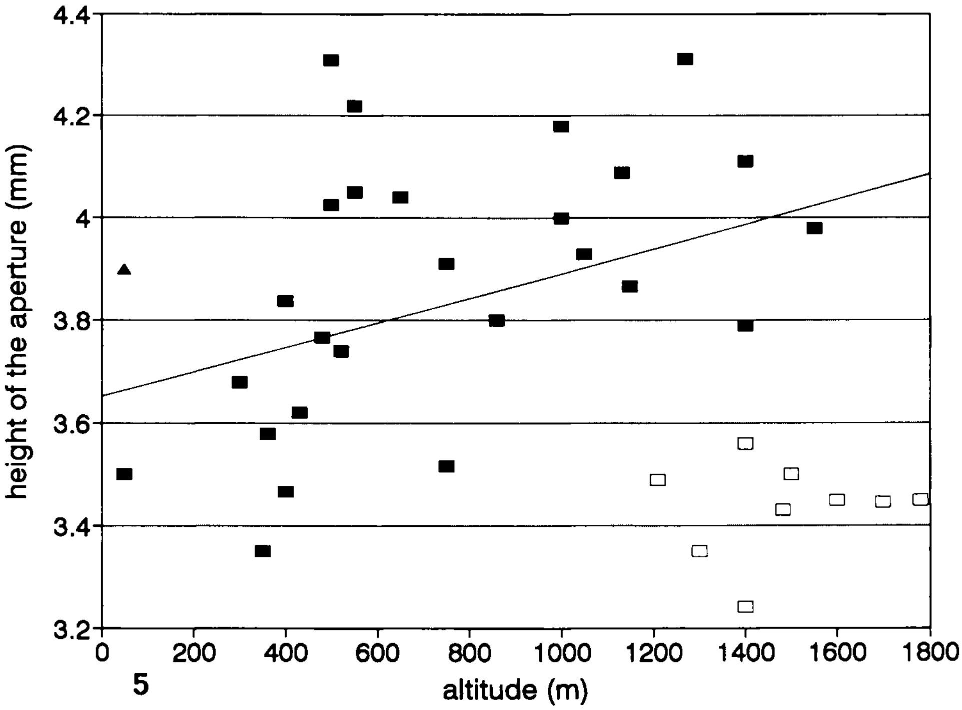

Figs. 2-12. Scatterplots showing the distribution of various shell characters in samples of *Albinaria idaea* in relation to the altitudes at which the samples were taken. Filled squares: *A. i. idaea* (Mt. Ida, Paximadia Isles); open squares: *A. i. amabilis* (Mt. Kedros); triangles: *A. i. pichcapunlla* (Paximadia East Isle). For *A. i. idaea* a regression line is shown in cases where significant correlations between character state and altitude were found (see table 1). Note that *A. i. amabilis* of Mt. Kedros does not fit well into the clinal variation of *A. i. idaea*.

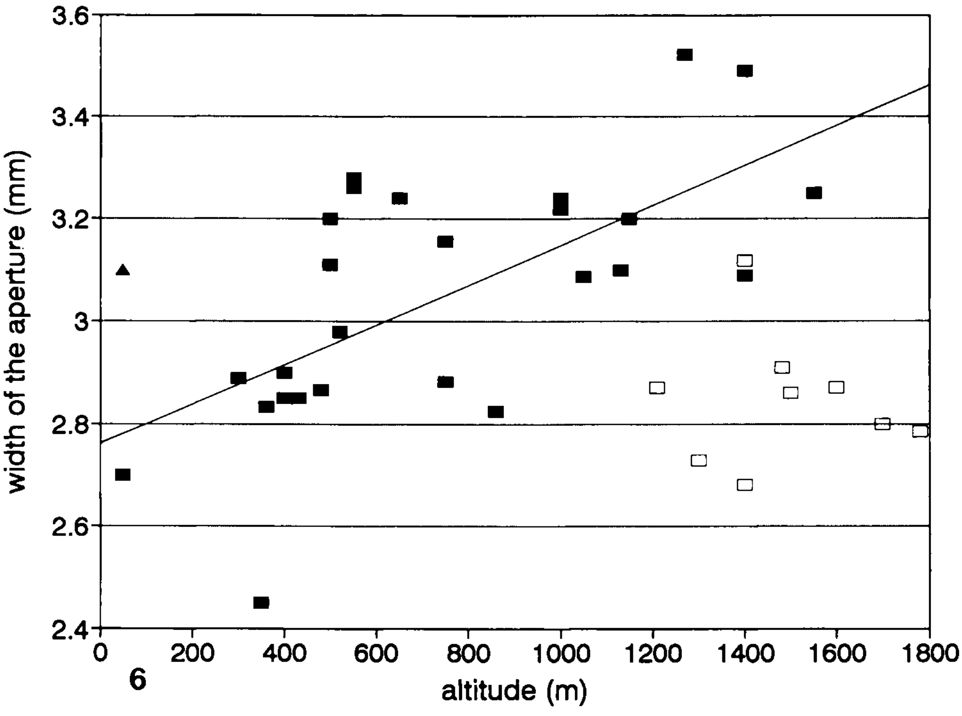

height of the shell (mm)
22
21
20
19
18
17
16
15
0
200
400
600
800
1000
1200
1400
1600
1800
altitude (m)

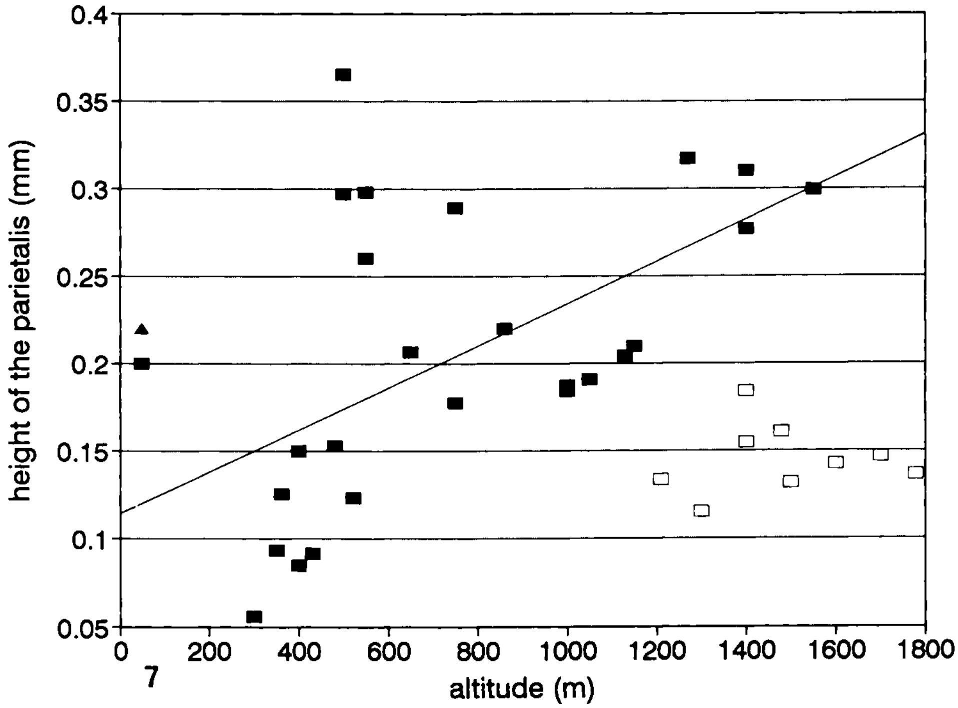
3


width of the shell (mm)
4.6
4.4
4.2
4
3.8
3.6
3.4
3.2
0
200
400
600
800
1000
1200
1400
1600
1800
altitude (m)

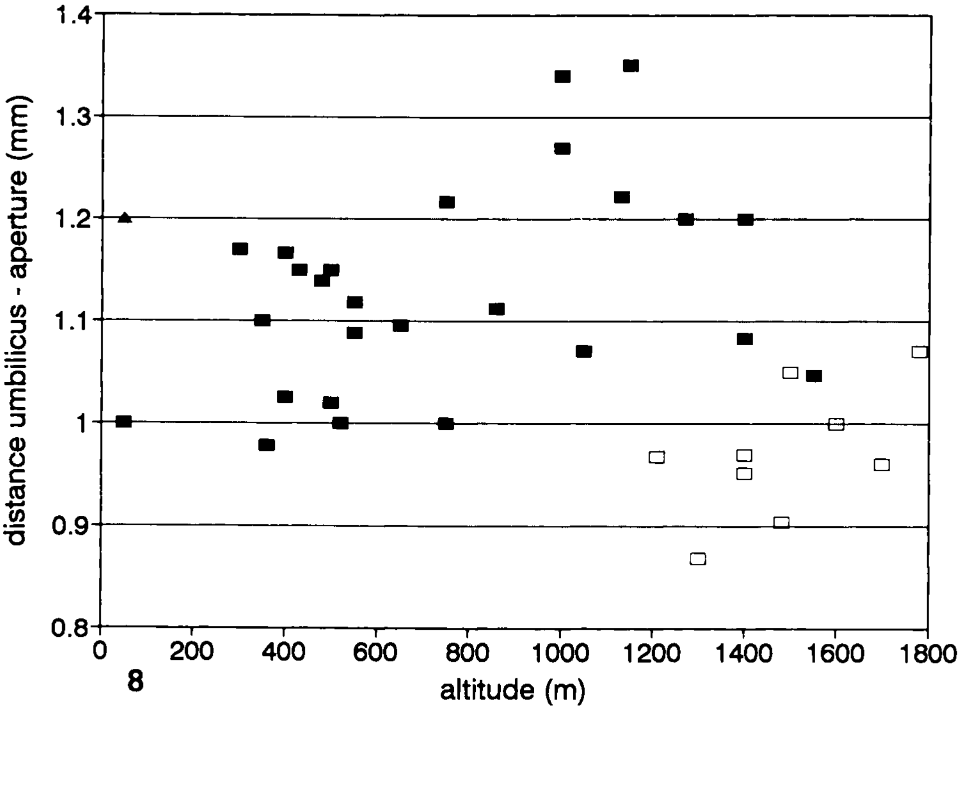
4


height of the aperture (mm)
4.4
4.2
4
3.8
3.6
3.4
3.2
0 200 400 600 800 1000 1200 1400 1600 1800
altitude (m)
5

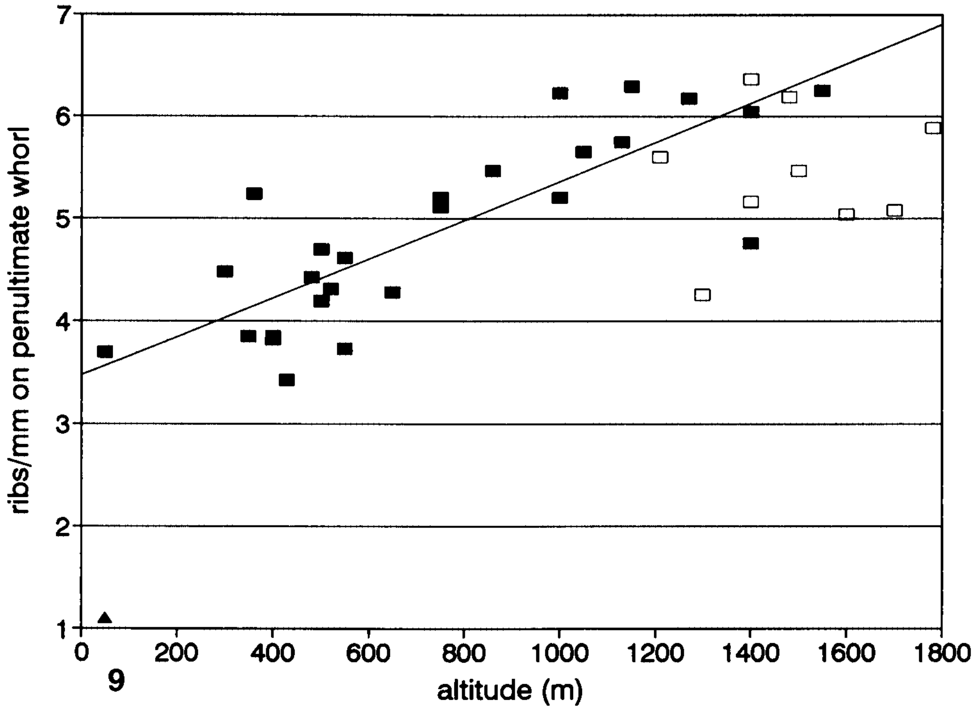

width of the aperture (mm)
3.6
3.4
3.2
3
2.8
2.6
2.4
0 200 400 600 800 1000 1200 1400 1600 1800
altitude (m)
6


height of the parietalis (mm)
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
200
400
600
800
1000
1200
1400
1600
1800
altitude (m)

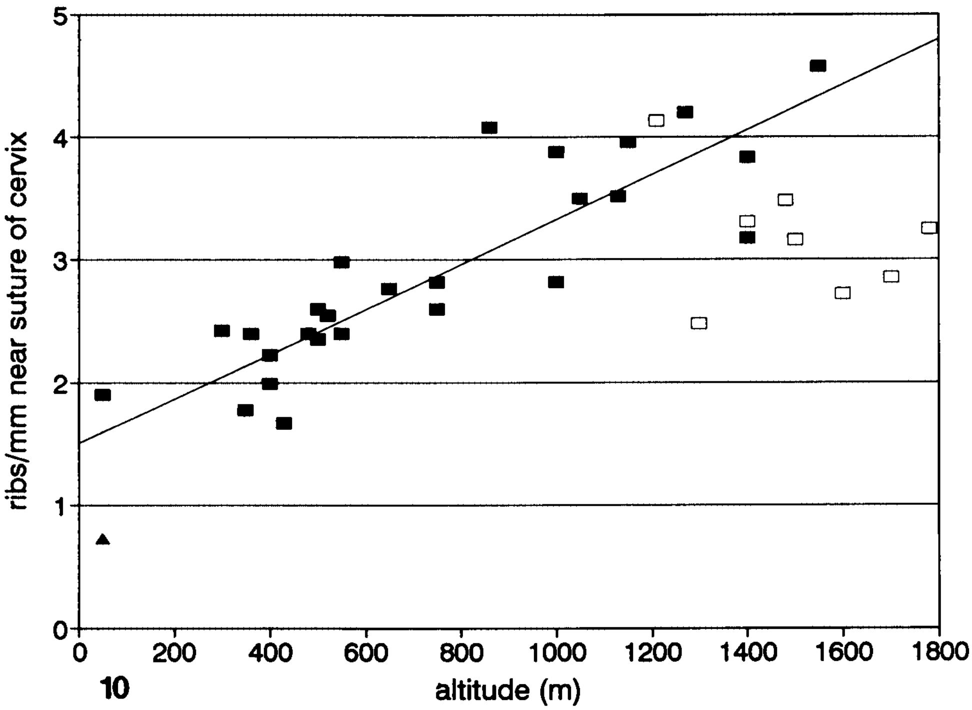
7


distance umbilicus - aperture (mm)
1.4
1.3
1.2
1.1
1
0.9
0.8
0
200
400
600
800
1000
1200
1400
1600
1800
altitude (m)

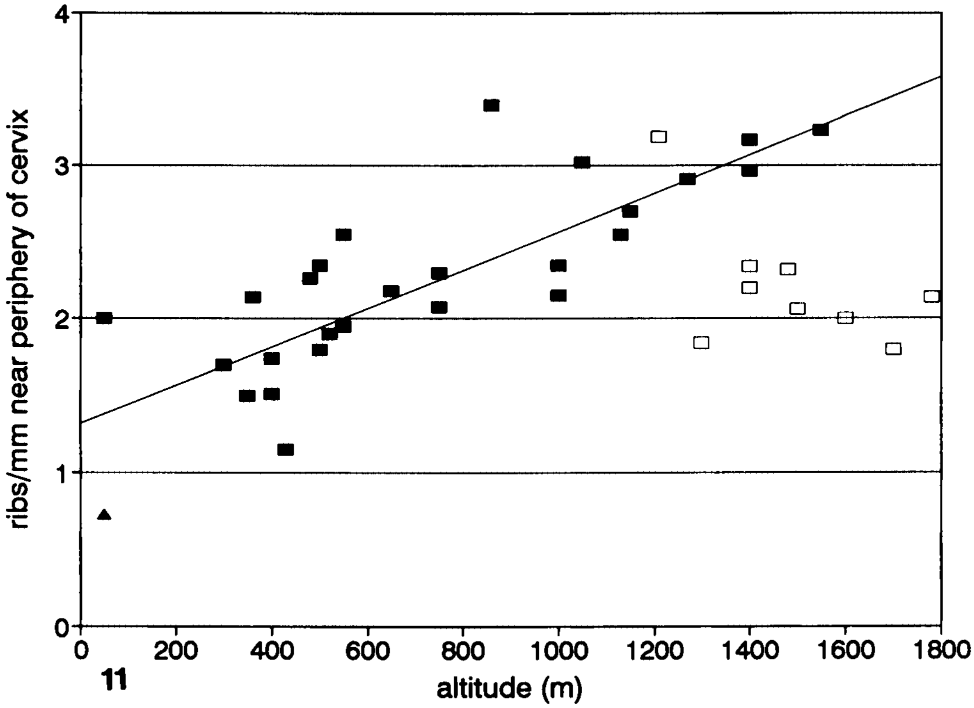
8


ribs/mm on penultimate whorl
7
6
5
4
3
2
1
0
200
400
600
800
1000
1200
1400
1600
1800
altitude (m)

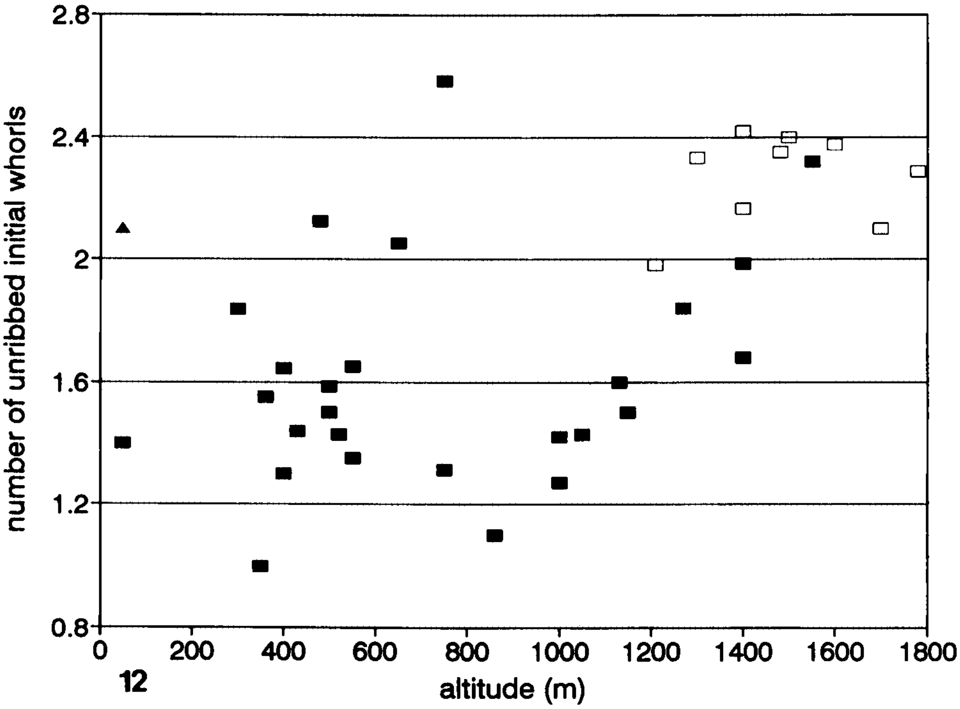
9


ribs/mm near suture of cervix
5
4
3
2
1
0
0
200
400
600
800
1000
1200
1400
1600
1800
altitude (m)

10


ribs/mm near periphery of cervix
4
3
2
1
0
0 200 400 600 800 1000 1200 1400 1600 1800
altitude (m)

11


number of unribbed initial whorls
2.8
2.4
2
1.6
1.2
0.8
0 200 400 600 800 1000 1200 1400 1600 1800
altitude (m)

12

## Discussion

The morphological variation of *Albinaria idaea* around Mt. Ida does not allow the delimitation of borderlines separating lower rank taxa. Thus only a single evolutionary entity can be distinguished here.

In the past, four subspecies were reported from Mt. Ida (Nordsieck, 1977), viz., *A. i. idaea* (L. Pfeiffer, 1849), *A. i. venosa* (Boettger, 1883), *A. i. zeus* Nordsieck, 1977 and *A. i. rolli* Nordsieck, 1977. *A. i. venosa* was separated from *A. i. idaea* because of its smaller dimensions, the less fusiform shape, a smaller, more protruding and less broadly labiate aperture, and less prominently developed lamellae (Boettger, 1883). *A. i. zeus* was distinguished because of its blunter apex, weaker and more densely spaced ribs, a violet-brown shell with a sutural line, and a somewhat better visible subcolumellaris (Nordsieck, 1977). *A. i. rolli* was supposed to differ from the most similar subspecies *A. i. venosa* by its coarser ribs, especially on the cervix, a more conspicuously protruding aperture, and a more prominently developed parietalis (Nordsieck, 1977). Almost all these characters proved to be altitude dependent and gradually varying (table 1; figs. 2-12). For this reason these nominal taxa are seen here as representing forms within a continuum, which should be referred to as *A. i. idaea*. Obviously, "*rolli*" and "*venosa*" are lowland forms with a slender shell with a small aperture, a low parietalis and coarse ribs, while "*zeus*" is a high altitude extreme with a broader shell with a large aperture, a high parietalis and fine ribs.

The populations on Mt. Kedros do not fit into the clines of altitude dependent characters that are found on Mt. Ida (table 1; figs. 2-12). In none of the characters studied, significant correlations with altitude were found. Because of these differences, the Mt. Kedros populations are treated as representing a separate subspecies.

On the Paximadia Isles two clearly distinct forms occur, separated by a narrow contact zone (Schultes & Wiese, 1991); so these forms can be treated as different subspecies. The finely ribbed form, occurring on schist, is very similar to the lowland forms of *A. i. idaea* from limestone on the south-west slopes of Mt. Ida. Therefore it is classified as *A. i. idaea*, despite the ecological difference. The other, percostate form, was named *Albinaria idaea pichcapunlla* Schultes & Wiese, 1991.

## Descriptions of *Albinaria idaea* and its subspecies

### *Albinaria idaea* (L. Pfeiffer, 1849)

*Albinaria idaea* is usually regarded as a member of the *teres* species group (Nordsieck, 1977), because of its coarse and branched cervical ribs, presence of growth lines and absence of plicae palatales below the principalis. It is subdivided into three subspecies, described below. Each of these is characterized by a small to medium-sized, more or less fusiform shell, with white ribs on a dark (brown to violet) background. Except for the percostate *A. i. pichcapunlla*, the ribs are very fine in comparison to the cervical ribs. The clausilial apparatus is simple. In apertural view, only the parietalis, principalis and columellaris are visible. The columellaris is placed far back in the aperture and is just partly visible. The lunella is situated dorsally or slightly deeper inside the shell.

## *Albinaria idaea idaea* (L. Pfeiffer, 1849)
(figs. 13-24)

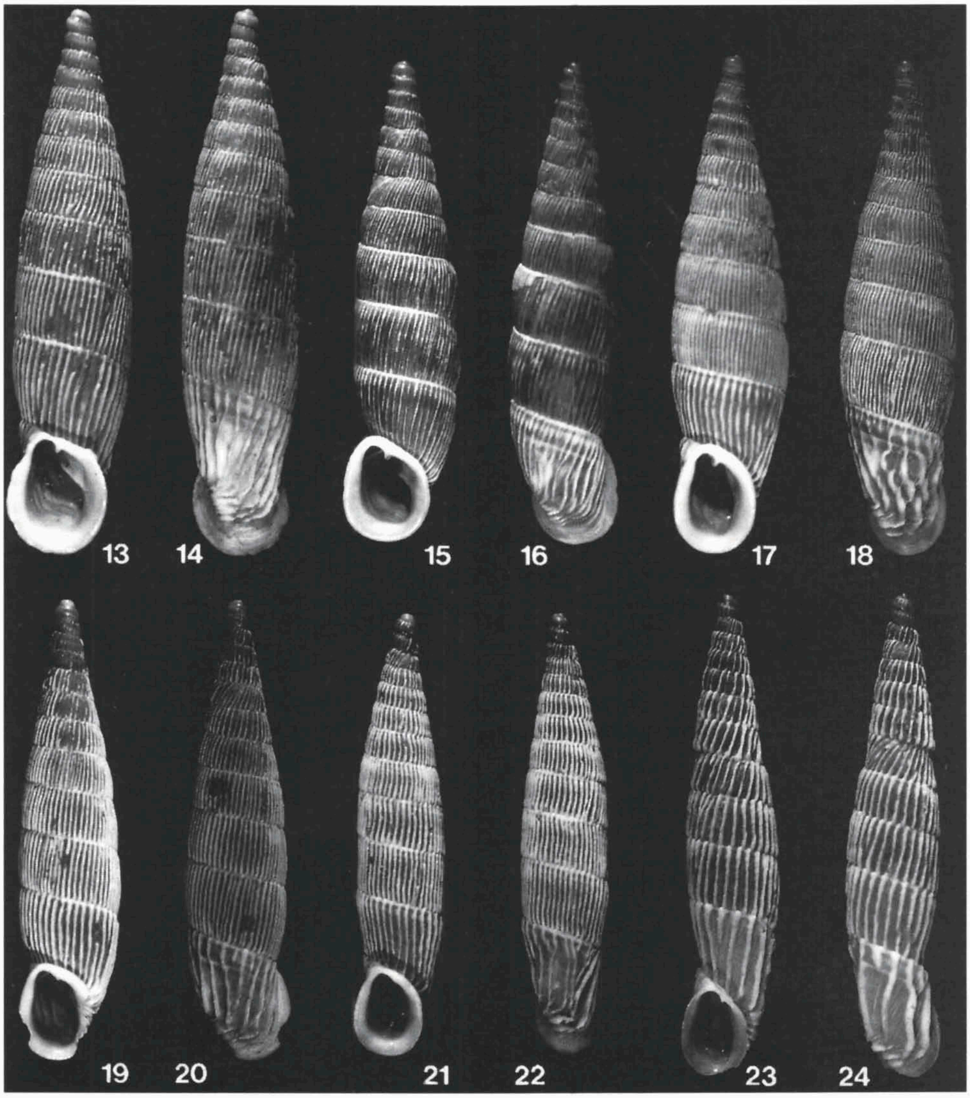
*Clausilia idaea* L. Pfeiffer, 1849: 140 (Greece, Crete, "Mt. Ida, 5500 ft."). Holotype: BM 197616.
*Clausilia (Albinaria) venosa* O. Boettger, 1883: 106-113 (Greece, "Kreta, Asomato am Ida, 4-5000'"). Lectotype, design. Nordsieck (1977: 78): SMF 68743. Paratypes: SMF 68744/2 (Greece, "Kreta, Asomato am Ida, 2500'"). **Syn. nov.**
*Albinaria idaea zeus* Nordsieck, 1977: 79 (Greece, "Kreta, Ideon Antron im Idi-Gebirge"). Holotype: SMF 80645 (Nordsieck, 1977: pl. 3 fig. 6); paratypes: SMF 247188/5. **Syn. nov.**
*Albinaria idaea rolli* Nordsieck, 1977: 79-80 (Greece, "Kreta, Apodoulou bei Platanos"). Holotype: SMF 247210 (Nordsieck, 1977: pl. 3 fig. 7). **Syn. nov.**

Material.— KU8075 (HNC 25495); KU8076 (HNC 25496); KU8176 (HNC 25498); KU8899 (K2601); KU9098 (K2597); KU9294 (K1080); KU9391 (HNC 25189); KU9392 (HNC 25190); KU9393 (HNC 15191); KU9394 (K1079); KU9396 (K1078); KU9491 (HNC 25206); KU9591 (K1044, HNC 25197); KU9592 (HNC 25198); KU9691 (HNC 25199); KU9692 (HNC 25200); KU9791 (HNC 25201); KU9792 (HNC 25202); KU9891 (HNC 25203); KU9892 (K1043, HNC 25204); KU9992 (HNC 25205); KV8806 (K1201); KV8807 (K1332); KV8901 (K1192); KV9000 (K1193); KV9006 (K1203); KV9204 (K1219); KV9205 (K1218); KV9305 (K1220); LU0090 (K2583); LU0091 (K2584, HNC 13010, HNC 25438); LU0092 (K1042, HNC 25439); LU0193 (HNC 29816); LU0198 (K1081); LU0291 (HNC 25391); LU0292 (K1196); LU0293 (HNC 38407); LU0295 (K1085); LU0297 (K1084); LU0391 (K1040, HNC 25396); LU0396 (K1546, K1545); LU0490 (HNC 25068); LU0687 (HNC 25371); LU0688 (HNC 25373); LV1202 (K1502).

Description (with both extreme and mean values).— Shell small to medium-sized (height 16.2-19.0-24.1 mm [n = 167], width 3.5-4.1-5.4 mm [n = 217]), with 10-12.4-14 (n = 176) slightly convex, brown to violet whorls, whitish ribs, and yellowish brown aperture. Initial 1-1.5-3 whorls unribbed (n = 181). Radial ribs of the spire (very) fine and (very) narrowly spaced, on the penultimate whorl 2.9-5.0-8.9 per mm (n = 218). Cervical ribs fine to coarse, irregular and often branched, near the suture 1.5-2.9-6.3 per mm (n = 213), near the periphery of the cervix 1.0-2.3-4.7 per mm (n = 213). Growth lines more or less prominent to absent. Aperture oval, height 2.7-3.8-5.2 mm (n = 186), width 2.2-3.1-4.0 mm (n = 185). Height of the parietalis 0.02-0.21- 0.45 mm (n = 195).

Distribution (fig. 1).— *A. i. idaea* is found on the slopes of Mt. Ida from 300 m up to 1600 m altitude. It seems to occur neither on the highest parts of the mountain, nor on the north-eastern slopes. It is also known from an isolated site 11 km north-east of the most north-eastern population on Mt. Ida (K1502) and from the two Paximadia Isles, 12 km south-west of Agia Galini, at less than 100 m altitude on schist. At a site on the south-west slope of Mt. Ida, it was found sympatrically with *A. cretensis* (Rossmässler, 1836); on the south-east slope it was collected together with *A. hippolyti holtzi* (Sturany, 1904), and on the north-west slope with *Albinaria spratti* (L. Pfeiffer, 1846). The exact locality of the holotype of *A. idaea* is not known, but it resembles shells collected near the cave Ideon Antron, situated at an altitude of 1550 m. This corresponds with the given altitude of "5500 ft" if Prussian feet are meant.

Variability.— Several characters show considerable changes throughout the range of this subspecies. Some of these are correlated with altitude. At high altitudes, the shell is wider and more clearly violet, the aperture is higher and wider, the parietalis is higher and the ribs on the spire as well as the cervical ribs are more narrowly spaced and finer than at low altitudes. On the western parts of Mt. Ida, growth lines are usually more prominent and the parietalis is generally lower than in the east. On the Paximadia Isles hybrids with *Albinaria idaea pichcapunlla* are found which have very coarse ribs.




Figs. 13-24. *Albinaria idaea idaea* (L. Pfeiffer, 1849), Mt. Ida, Crete. 13, 14, holotype, "Mt. Ida", actual height 21.8 mm (BM 197616); 15, 16, highland form, paratype "*zeus*", Ideon Antron, 1550 m alt., actual height 19.3 mm (SMF 247188); 17, 18, highland form, 5.4 km N Platania, 1000 m alt., actual height 19.8 mm (RMNH K1203); 19, 20, lowland form, lectotype "*venosa*", "Kreta, Asomato am Ida, 4-5000'", actual height 18.3 mm (SMF 68743); 21, 22, lowland form, 0.1 km from Vizari to Petrohori, 300 m alt., actual height 17.7 mm (RMNH K2597); 23, 24, lowland form, holotype "*rolli*", "Apodoulou b. Platanos", actual height 19.3 mm (SMF 247210). Photos: A. 't Hooft, Rijksuniversiteit, Leiden.

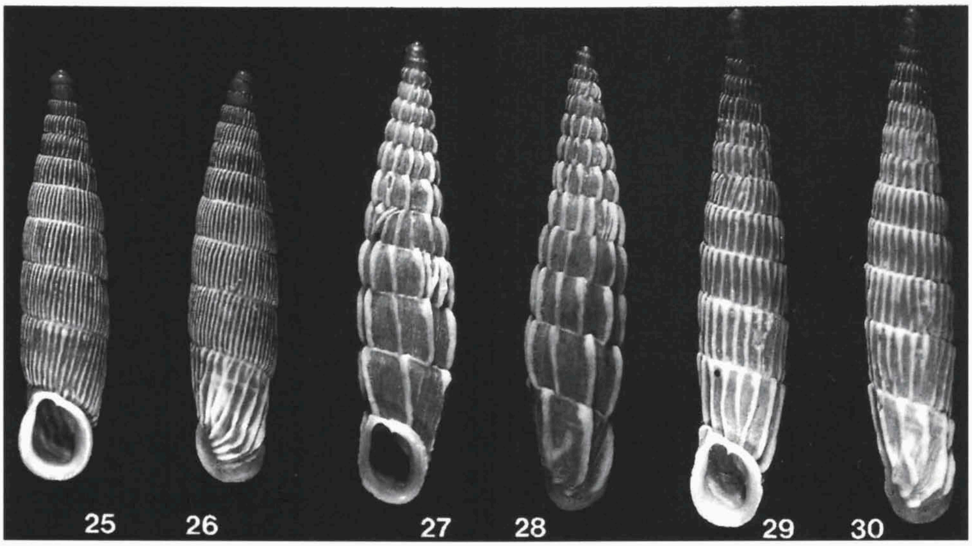
### *Albinaria idaea amabilis* subsp. nov.
(figs. 25, 26)

Material.— Holotype (RMNH 56832/K2545): Greece, Crete, Rethimnon, 3.2 km W of the Mt. Kedros summit, on W ridge (22 km SE of Rethimnon); NW exposed; 1210 m alt.; UTM KU8096; G. H. Engelhard & J. W. F. Slik leg., 26-IX-1991. Paratypes: KU8096 (K 2545: HCN 31694/2; No/2; RMNH 56833/19, alc. 9368/11; SMF 310365/2 - K2546: RMNH 56834/7, alc. 9369/8); KU8195 (K 2547: RMNH 56835/17, alc. 9370/9; Su/2 - K2548: RMNH 56836/7, alc. 9371/5 - K2549: HCN 31695/2; RMNH 56837/16, alc. 9372/10); KU8295 (K 2551: PKI/2; RMNH 56838/17, alc. 9373/10); KU8296 (K 2553: HCN 31696/2; RMNH 56840/18, alc. 9375/9 - K2554: Ma/2; NHMW 87184/2; RMNH 56841/22, alc. 9376/9); KU8395 (K 2552: RMNH 56839/15, alc. 9374/8).

Diagnosis.— Shell relatively small and slender, with a low parietalis, a very finely ribbed spire and a coarsely ribbed cervix.

Description.— Shell small and slender (height 14.3-16.4-19.4 mm [n = 70], width 3.0-3.5-4.0 mm [n = 83]), with 10-11.3-13 (n = 72) flattened whorls, whitish ribs, and yellowish brown aperture; apical and cervical whorls yellowish brown, lower ones violet. Initial 1.3-2.3- 3 whorls unribbed (n = 75). Radial ribs of the spire very fine and very narrowly spaced, on the penultimate whorl 3.8-5.5-7.9 per mm (n = 83). Cervical ribs coarse and irregular, often branched, near the suture 1.7-3.2-5.4 per mm (n = 81), near the periphery of the cervix 1.3-2.3- 4.2 per mm (n = 83). Growth lines more or less prominent to absent. Aperture oval, height 3.1-3.4-3.9 mm (n = 77), width 2.5-2.9-3.3 mm (n = 77). Height of parietalis 0.03-0.15-0.26 mm (n = 81).

Distribution.— *A. i. amabilis* is found on Mt. Kedros above an altitude of 1200 m. Here it lives sympatrically with an unribbed form of *A. cretensis* (Rossmässler, 1836),




Figs. 25-30. *Albinaria idaea* ssp. 25, 26, *Albinaria idaea amabilis* ssp. nov., holotype, 3.2 km W of summit of Mt. Kedros, 1210 m alt., actual actual height 16.5 mm (RMNH 56832 K2545); 27, 28, *A. i. pichcapunlla* Schultes & Wiese, 1991, holotype, E rocks of Paximadia East Isle, 50- 70 m alt., actual height 18.7 mm (HNC 25500); 29, 30, intermediate between *A. i. pichcapunlla* and *A. i. idaea*, eastern Paximadia Isle, actual height 20.7 mm (NMW 80255). Photos: A. 't Hooft, Rijksuniversiteit, Leiden.

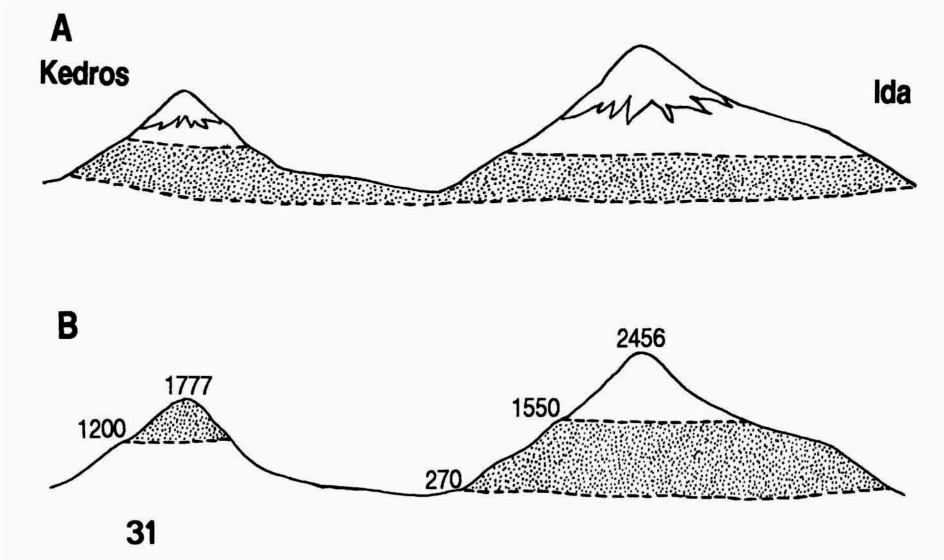



Fig. 31. Actual (B) and hypothetical (A) Pleistocene, last-glacial-maximum distribution of *Albinaria idaea* on Mt. Kedros and Mt. Ida. The species' range is shaded. See the text.

which is less numerous. It is isolated from *A. i. idaea* of Mt. Ida by a zone in which only *A. cretensis* occurs; this zone roughly coincides with the valley between these mountains. The distribution of *A. idaea* on Mt. Ida and Mt. Kedros is disjunct nowadays, but this was probably not the case during Pleistocene glacial periods, when average temperatures in Crete were 5-8°C below the present level (Gittenberger & Goodfriend, 1993: 113) and the specific climatic zones on the mountains most probably were situated correspondingly lower. The species may have had a continuous range throughout the lower regions of both mountains and the valley (fig. 31, A). Secondarily, when the climate became warmer, the species became restricted to higher altitudes and so diverged into two isolated subpopulations that evolved independently into *A. i. idaea* and *A. i. amabilis* (fig. 31, B). If this scenario is correct, the differentiation between the two subspecies dates from after the last glacial maximum, thus from less than 15,000 years ago.

Variability.— The subspecies is quite uniform throughout its range. It shows no obvious altitude-correlated characters.

Derivatio nominis.— Because of the lovely appearance of this little snail, it was given the subspecific name *amabilis*.

### *Albinaria idaea pichcapunlla* Schultes & Wiese, 1991
(figs. 27, 28)

Albinaria idaea pichcapunlla Schultes & Wiese, 1991: 68-69 (Greece, "Ostfelsen der Paximadia-Ostinsel, UTM KV8176 [KU8176!], Nomos Rethimnis, 50-70 m NN."). Holotype: KU8176 (HNC 25500). Paratypes: KU8176 (HNC 25499/42; SMF 309249/3; NMW 85938/2; PKI/2; RMNH 56854/6).

Material.— Additional sample: KU8176 (NMW 80255).

Description.— Shell medium-sized and slender (height 18.0-19.6- 21.4 mm [n = 9], width 3.4-3.6-4.1 mm [n = 20]), with 12.5-13.1-14 (n = 9) slightly convex, reddish or reddish-violet whorls, with white, percostate ribs, and a yellowish brown aperture. Initial 1.5-2.1-3 whorls unribbed (n = 7). Spiral ribs very coarse and widely spaced, on the penultimate whorl 1.0-1.3-1.8 per mm (n = 20). Cervical ribs very coarse and regular, sometimes branched, near the suture 0.4-0.9-1.3 per mm (n = 20), near the cervical periphery 0.4-0.8-1.3 per mm (n = 20). Growth lines present. Aperture oval, height 3.4-3.8-4.3 mm (n = 20), width 2.8-3.0-3.4 mm (n = 19). Height of parietalis 0.16-0.21-0.29 mm (n = 19).

Distribution.— This subspecies has been reported from only a zone with steep limestone cliffs, c. 0.5 km wide, at 50-70 m altitude on the eastside of the eastern Paximadia Isle. On some rocks here, specimens could be found that are supposed to belong to a narrow hybrid zone with *Albinaria idaea idaea*, which occurs on schist of the westside of the islet (Schultes & Wiese, 1991).

Note.— The NMW sample from the eastern islet contains many specimens of both subspecies and several shells that are intermediate in sculpture (figs. 29, 30). Obviously it concerns material collected in a deposit with empty shells of mixed origin.

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