

A revision of the polytypic *Albinaria hippolyti* (Boettger, 1878) from Crete (Gastropoda Pulmonata: Clausiliidae)

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Key words: Gastropoda, Pulmonata, Clausiliidae, *Albinaria hippolyti*, taxonomy, hybrid zones, variability, zoogeography.

On the basis of both detailed distributional field studies and morphological analyses, a revision of the polytypic species *Albinaria hippolyti* from Central and Eastern Crete is presented. True subspecies are distinguished from mere geographic varieties by the presence of narrow hybrid zones. Using this criterion, four adjoining subspecies are recognised: *A. h. hippolyti* (Boettger, 1878), *A. h. aphrodite* (Boettger, 1883), *A. h. holtzi* (Sturany, 1904) and *A. h. harmonia* subsp. nov. Additionally, two geographically isolated and conchologically distinctive forms are also treated as subspecies: *A. h. arthuriana* (Boettger, 1878) and *A. h. asterousea* subsp. nov. The geographical distribution and variability of each subspecies is described in detail. *A. h. hieronymi* Schilthuizen & Gittenberger, 1990, *A. h. francisci* Schilthuizen & Gittenberger, 1990 and *A. h. neuteboomi* Schilthuizen & Gittenberger, 1990 are considered synonyms of *A. h. hippolyti*, *A. h. aphrodite* and *A. h. holtzi*, respectively.

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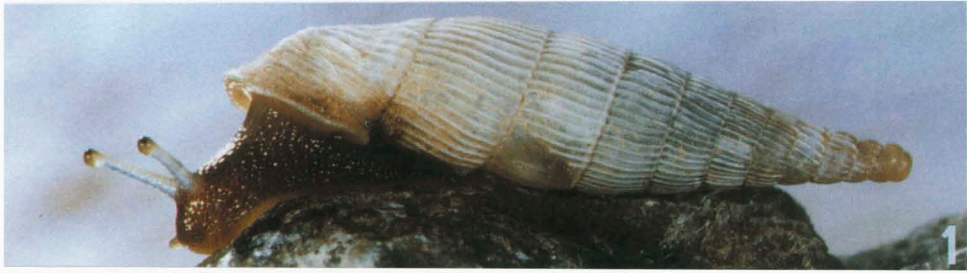
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Introduction

Currently, the strongly radiated genus *Albinaria* Vest, 1867, is being intensely studied by various malacologists. A first step towards a better understanding of the processes underlying the diversification in *Albinaria* is to establish a well-founded taxonomy of the species under study. In this paper, the intraspecific taxonomy of *A. hippolyti* is revised and detailed distributional data are presented (fig. 6).

A. hippolyti is a widely distributed species from Central and Eastern Crete. It belongs to the so-called "Gruppe der *candida*" (Nordsieck, 1977) and is characterised by a slender shell with radial ribs, the absence of a thick, white surface-layer and the presence of cervical ribs that are no more prominent than the radial ribs. The species shows a disjunct distribution of which large parts coincide with the position of parts of the island that were not submerged during the Pliocene (Dermitzakis, cited in Vardinoyannis & Mylonas, 1988). Other Cretan *Albinaria* species are largely distributed on parts of the island that only emerged after the Pliocene. Therefore, *A. hippolyti* might be considered a relatively old element in the *Albinaria* fauna of Crete.

Recently, three conchologically distinct forms of *A. hippolyti* were described as new subspecies by Schilthuizen & Gittenberger (1990). A great amount of new material, mainly collected by the first two authors of the present paper, revealed even more geographic variation, seemingly making the description of additional taxa necessary. At the same time, however, it was discovered that certain forms show a con-



tinuous intergradation, with many shell characters changing independently, while others are spatially separated by narrow contact zones, in which traits change in concert (Schilthuizen, 1992).

Such hybrid zones are generally held to separate genetically differentiated popu-

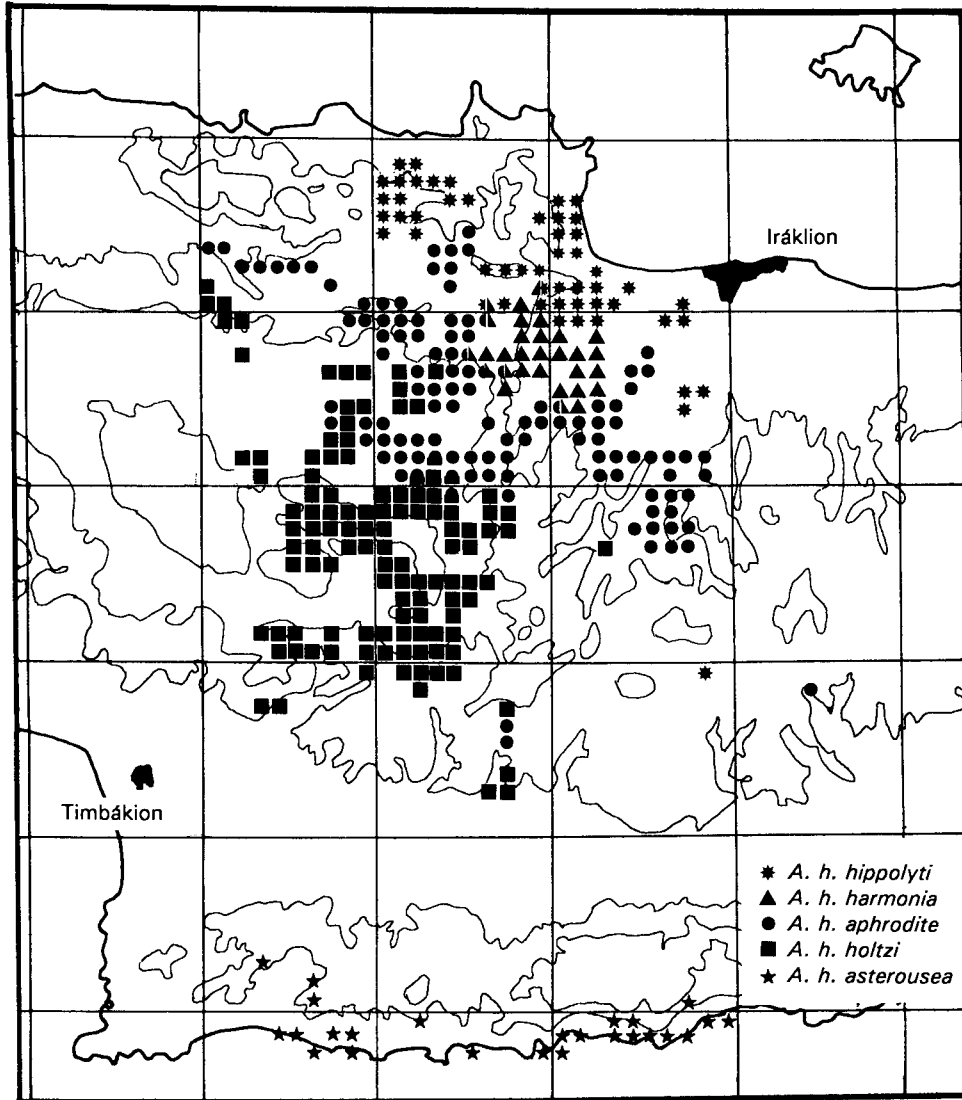


Fig. 6. Distribution of the Central Cretan populations of *Albinaria hippolyti*. The UTM 10x10 km grid and contours at 1000, 2000 and 5000 feet (305, 610 and 1524 m altitude, respectively) have been indicated. The collection localities are shown as 1x1 km UTM squares. Sampling localities of other *Albinaria* species from this area have been omitted.

Figs. 1-5, live specimens of *Albinaria hippolyti* subspecies; fig. 1, *A. h. aphrodite* from UTM LU3488; fig. 2, *A. h. asterousea* from UTM LU0568; fig. 3, *A. h. harmonia* from UTM LV1706; fig. 4, *A. h. holtzi* from UTM LV0906; fig. 5, *A. h. hippolyti* from UTM LV2015.

lations (Barton & Hewitt, 1985). Therefore, they provide the taxonomist with a means to distinguish between subspecies (in the sense of evolutionary entities; see Futuyma, 1986) and mere geographic varieties.

In this revision of *A. hippolyti*, the presence of relatively narrow hybrid zones between conchologically distinct forms is taken as a criterion for considering them subspecies - a detailed morphological and genetical analysis of these hybrid zones will be published elsewhere (Schilthuizen & Lombaerts, in prep.). In assigning sub-specific status to geographically isolated, and conchologically characterised, forms, however, a more subjective approach is taken.

In the subspecies accounts below, extensive conchological descriptions are avoided, as most distinctive traits are located in the apertural area of the shell. The nomenclature of the apertural folds is mainly based on Nordsieck (1978). The terms frontal upper palatal fold and distal upper palatal fold ("vordere obere Gaumenfalte" and "hintere obere Gaumenfalte", respectively: Nordsieck, 1978) are here abbreviated as FUP and DUP, respectively.

The approximately 1500 samples on which this study is based, have been deposited in the collections of Haus der Natur - Cismar (HNC) and the Nationaal Natuurhistorisch Museum in Leiden (RMNH). In view of this great amount of material, it is considered inappropriate to present full lists of exact localities, dates, etcetera. Instead, for each subspecies, only the exact data of the holotype are presented. For the additional material, only UTM (1 × 1 km) codes are given, with the corresponding HNC and RMNH inventory numbers. Type-specimens of taxa described by Boettger and Sturany were provided by the Senckenberg Museum in Frankfurt (SMF).

The exact area of distribution of the E-Cretan subspecies *A. h. arthuriana* is not yet known, nor is its full range of variability. For the sake of completeness, however, the subspecies is treated here, albeit with some caution.

Subspecies accounts

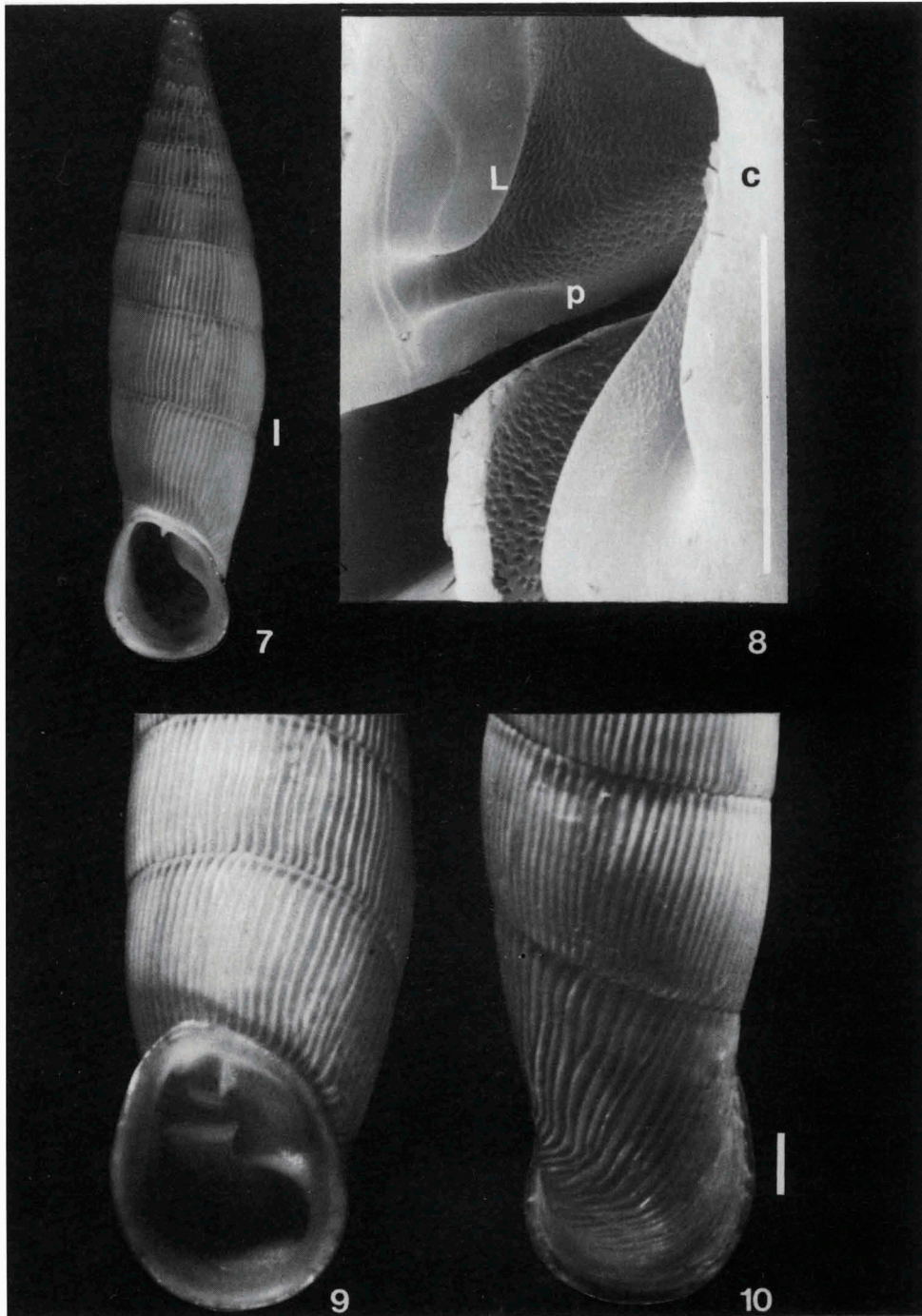
Albinaria hippolyti hippolyti (Boettger, 1878) (figs. 7-14, 51)

Clausilia hippolyti Boettger, 1878: 73-74, pl. 146 fig. 2a-e.

Albinaria hippolyti hippolyti; Nordsieck, 1977: 300.

Albinaria hippolyti hieronymi Schilthuizen & Gittenberger, 1990: 133-135, figs. 2, 3. *Syn. nov.*

Material.— Lectotype (SMF 66698): "Hippolyti Bttg Or. Expl. / Mt. Ega = Mte. Strombola b. Candia. Blanc u. Maltz.". Additional samples: LU2889 (HNC 26799; RMNH K1145, K1613, K1350); LV1014 (RMNH K1523); LV1015 (RMNH K1500, K1501); LV1016 (HNC 25827); LV1017 (HNC 25828; RMNH K0061); LV1115 (RMNH K1499); LV1116 (HNC 25829); LV1117 (HNC 25830; RMNH K0060); LV1118 (HNC 25831); LV1214 (RMNH K1497); LV1215 (RMNH K1498); LV1217 (HNC 25832); LV1218 (HNC 25833; RMNH K0059, K1630); LV1317 (HNC 25834); LV1416 (RMNH K0032); LV1417 (HNC 11129, 29324; RMNH K1644); LV1516 (RMNH K1492); LV1609 (RMNH K1450); LV1610 (RMNH K1451, K1452); LV1612 (RMNH K0039, K1438, K1439); LV1710 (RMNH K1453); LV1712 (HNC 10167, 26068, 29223, 29295; RMNH K0040, K1435, K1436, K1437, K1641); LV1812 (HNC 11020, 22794; RMNH K1434); LV 1909 (RMNH K1421); LV1910 (RMNH K1046, K1425, K1426); LV1911 (RMNH K1427, K1428, K1429); LV1912 (HNC 11123, 22597; RMNH K1047, K1430, K1431); LV1915 (K1528); LV2009 (HNC 26123; RMNH K0004); LV2010 (HNC 22714; RMNH K1045, K1424, K1470); LV2011 (RMNH K1474, K1639, K1640); LV2013 (HNC 26176; RMNH K0002); LV2014 (HNC 26177); LV2015 (HNC



Figs. 7-10. *Albinaria hippolyti hippolyti*, typical form. 7, habitus, ventral aspect; 8, apical part of principalis (p) and lunula (L), c, columella (UTM LV2210); 9, aperture, rostro-ventral aspect; 10, cervix, dorsal aspect; scale lines represent 1 mm.

26178); LV2016 (HNC 29227; RMNH K0049, K1248, K1635); LV2109 (HNC 10259, 22713; RMNH K0003); LV2110 (RMNH K1471, K1472, K1473); LV2111 (RMNH K1628, K1638); LV2113 (HNC 26182); LV2114 (HNC 26185); LV2115 (RMNH K1003); LV2116 (RMNH K0045); LV2209 (HNC 11023, 26140); LV2210 (HNC 26186; RMNH K1006); LV2211 (HNC 26187; RMNH K1626, K1627); LV2212 (HNC 26188); LV2310 (HNC 26189); LV2411 (HNC 10437); LV2609 (HNC 26158); LV2704 (HNC 26165); LV2705 (HNC 26166); LV2709 (HNC 26167); LV2710 (HNC 26191); LV2805 (HNC 26174); no locality: RMNH K0397, K0405; no exact locality: RMNH K0402, K0403, K0404, K1649.

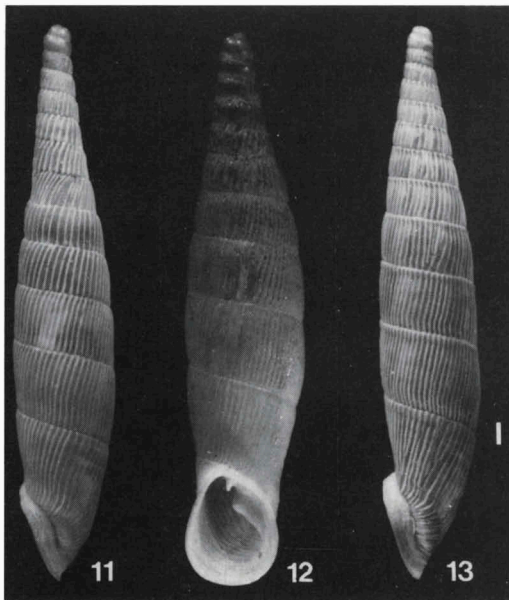
Diagnosis.— Radial ribs: Fine and narrow, 4-9 per mm on the penultimate whorl.

Cervical sculpture: Basal keel prominent, dorsal keel and basal furrow obsolete or absent.

Apertural armature: Lip little or not reflected; parietalis variable both in length and height; subcolumellaris usually inconspicuous: invisible in a perpendicular view of the aperture (in some populations more prominent, see below); suturalis present; parallallalis usually present; lunula dorsolaterally situated; basalis usually present, sometimes rudimentary; subclaustralis absent; principalis supersedes the DUP, its apical expansion is inconspicuous, some populations excepted (see below); spiralis does not extend deep into the shell; FUP absent.

Shell height: 14.1-20.1 mm (n=58).

Distribution and variability.— The exact type locality cannot be established, but the lectotype (fig. 51) is reminiscent of the form found on Mount Kerí, approximately 10 km west of Iráklion, and some three km east of Mount Stroúmboulas, the locality mentioned on the label. The UTM-square in which specimens were collected that most resemble the lectotype is LV2010. The typical form (figs. 7-10) occurs in the hills



Figs. 11-13. *Albinaria hippolyti hippolyti*, atypical forms. 11, habitus, lateral aspect (UTM LV2016); 12, habitus, ventral aspect (UTM LV1014); 13, habitus, lateral aspect (UTM LV2111); scale line represents 1 mm.



Fig. 14. *Albinaria hippolyti hippolyti*. Apertural lamellae: c, columellaris; s, subcolumellaris (UTM LV2111); scale line represents 0.1 mm.

immediately west and south-west of Iráklion, and also in an isolated population, some 20 km south, near the village of Damánia.

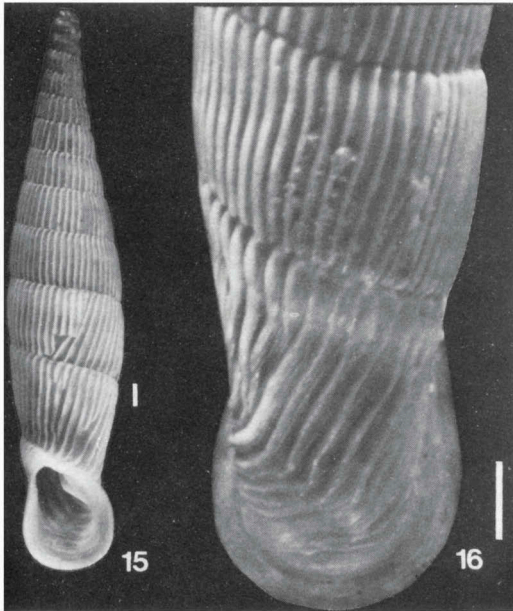
In the western parts of the subspecies' range atypical forms are found. The populations from the area of Máráthos (the type locality of *A. h. hieronymi*), are characterised by a more slender habitus, more widely spaced radial ribs, the absence of a reflected apertural lip (fig. 13), a conspicuous apical expansion of the principalis and a strongly developed subcolumellaris (fig. 14). The populations from the area of Ródia, some of which even live on rocks at the sea-side, are quite similar, but usually the shells are more slender (fig. 11), and provided with a less prominent subcolumellaris, which is invisible in a perpendicular view of the aperture. The populations from the extreme north-west finally, have small, but obese, usually translucently brownish and densely ribbed shells (fig. 12). The subcolumellaris is extremely weakly developed in these populations.

A. h. hippolyti is in certain places found sympatrically with *A. violacea violacea* Schilthuiszen & Gittenberger 1990, with *A. ulrikae* Schilthuiszen & Gittenberger, 1990, and with *A. spratti* (Pfeiffer, 1846). One hybrid with the latter species is known from UTM LV1712: K1641 (RMNH).

***Albinaria hippolyti harmonia* subsp. nov.**
(figs. 15, 16, 52)

Material.— Holotype (RMNH 56672): "Greece, Crete, prov. Iraklion, 1.5 km along the road from Tylisos dir. Gónies, on E-exposed rocks; 275 m alt.; 11.iv.1988; UTM LV1806; K0006; M. Schilthuiszen c.d.". Paratypes: LV1507 (RMNH K1414/56673; K1415/56674); LV1606 (RMNH K1419/56675); LV1607 (RMNH K1417/56676); LV1610 (RMNH K1449/56677); LV1705 (HNC 25817); LV1706 (HNC 10345, 25818;

RMNH K0008/56678, K0009/56679, K0010/56680, K0011/56681, K1302/56682, K1418/56683); LV1806 (HNC 22729; RMNH K0006/56684); LV1807 (HNC 10311; RMNH K0413/56685); LV1808 (RMNH K1465/56686, K1466/56687, K1467/56688, K1468/56689, K1469/56690); LV1809 (RMNH K1544/56691); LV1906 (HNC 25823; RMNH K1132/56692); LV1907 (HNC 25824); LV1908 (HNC 25825; RMNH K0005/56693, K1422/56694); LV1909 (HNC 25826); LV1911 (RMNH K1454/56695); LV2004 (HNC 26120); LV2005 (HNC 26121; RMNH K0042/56696); LV2007 (HNC 22605); LV2008 (HNC 26122); LV2104 (HNC 26126); LV2105 (HNC 26127; RMNH K0041/56697); LV2106 (HNC 26129); LV2107 (HNC 26130; RMNH K0043/57798); LV2205 (HNC 26136); LV2206 (HNC 26137); LV2207 (HNC 26138); LV2208 (HNC 26139).



Figs. 15, 16. *Albinaria hippolyti harmonia*, holotype (NNM 56672, UTM LV1806). 15, habitus, ventral aspect; 16, cervix, dorsal aspect; scale lines represent 1 mm.

Diagnosis.— Radial ribs: Prominent, sharp, widely spaced: 3-5, occasionally 6 per mm on the penultimate whorl.

Cervical sculpture: Basal and dorsal keel equally prominent. Basal furrow well developed.

Apertural armature: Lip strongly reflected; parietalis variable both in length and height; subcolumellaris weakly developed: invisible in a perpendicular view of the aperture; suturalis present; parallellalis usually present; lunula dorsally or dorsolaterally situated; basalis usually absent; subclaustralis absent; principalis supersedes the DUP, it carries an apical expansion; spiralis does not extend deep into the shell; FUP absent.

Shell height: 13.2-21.5 mm (n=145).

Derivatio nominis.—This new subspecies, in habitus reminiscent of *A. h. aphrodite*, is named after the deity Harmonia, in Greek mythology Aphrodite's daughter.

Distribution and variability.—*A. h. harmonia* is found in a restricted range, some six kilometers across, in the approximate centre of which lies the town of Tílisos. The subspecies exhibits hardly any geographical variation.

Apparently, it does not occur sympatrically with any other *Albinaria*.

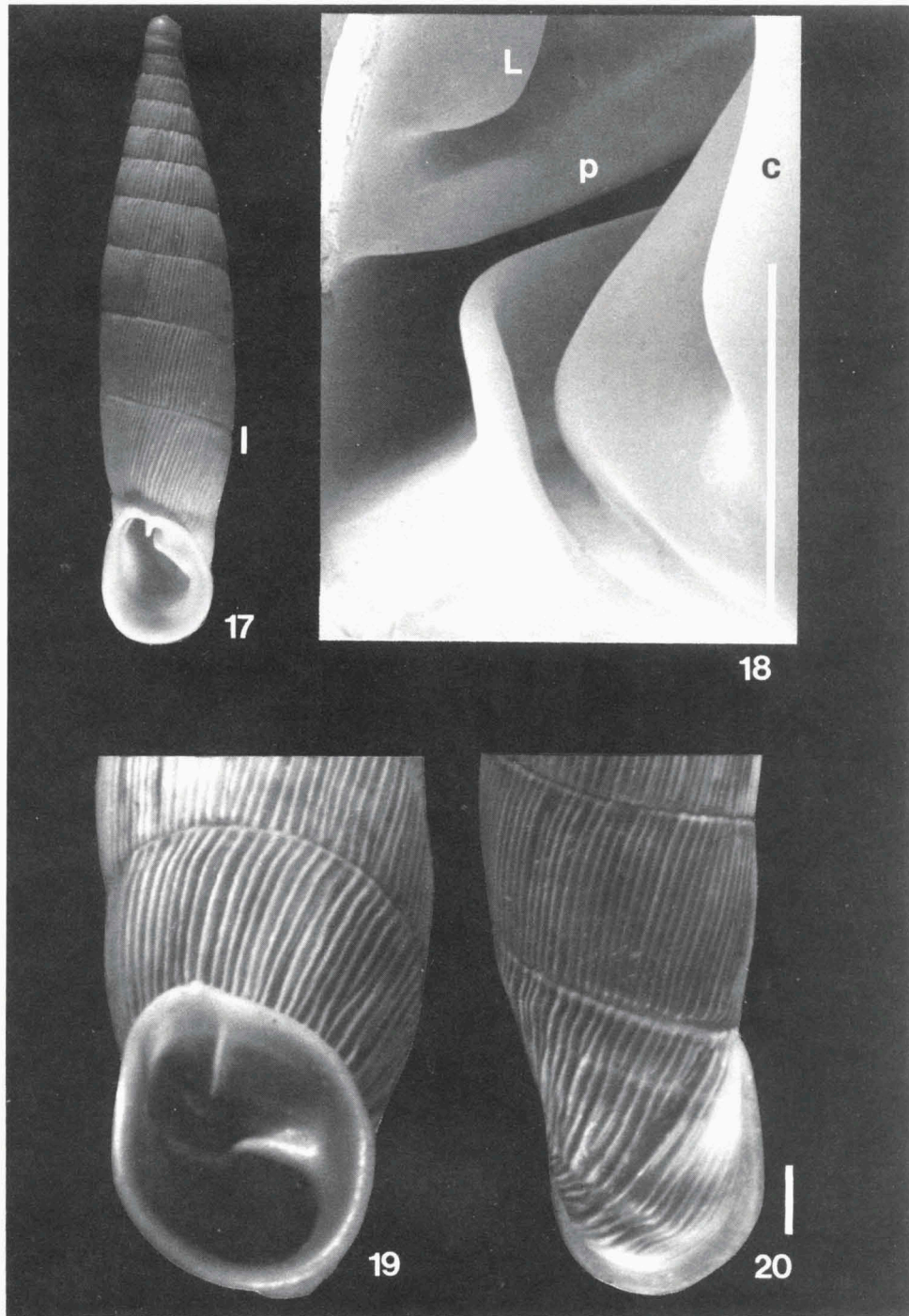
***Albinaria hippolyti holtzi* (Sturany, 1904)**
(figs. 17-21, 27, 53)

Clausilia (Albinaria) holtzi Sturany, 1904: 110-112, figs.

Albinaria hippolyti holtzi; Nordsieck, 1977: 300.

Albinaria hippolyti neuteboomi Schilthuizen & Gittenberger, 1990: 136, fig. 6, 7. *Syn. nov.*

Material.— Lectotype (here designated; SMF 66314/1): "Alb. (Striata) holtzi (Sturany) Paratypus Kreta: Assitae b. Candia Sturany 1904 Sammlung O. Boettger". Additional samples: LU0387 (HNC 25356); LU0391 (HNC 25397; RMNH K1040); LU0487 (HNC 25362); LU0490 (HNC 25403); LU0491 (HNC 25404; RMNH K1039); LU0590 (HNC 25408); LU0591 (HNC 22732); LU0595 (HNC 25410); LU0596 (HNC 25412); LU0597 (HNC 25413); LU0598 (HNC 25414, 25415; RMNH K0418, K1222); LU0690 (HNC 25416; RMNH K1037); LU0695 (HNC 25417); LU0696 (HNC 25418); LU0697 (HNC 25419; RMNH K1223, K1510, K1547); LU0698 (HNC 25420); LU0699 (HNC 25421); LU0790 (RMNH K0469); LU0791 (HNC 22624, 22731); LU0795 (HNC 25423); LU0797 (HNC 25424; RMNH K1227); LU0798 (HNC 25425; RMNH K1224, K1225, K1460); LU0799 (HNC 25426); LU0896 (HNC 25428; RMNH K1229); LU0897 (HNC 25429; RMNH K1228); LU0898 (HNC 25430; RMNH K1226); LU0989 (HNC 22730); LU0990 (HNC 25432; RMNH K1036); LU0991 (HNC 25433); LU0996 (HNC 25434); LU0997 (HNC 25435); LU0998 (HNC 25436); LU1090 (HNC 25667); LU1091 (HNC 25668); LU1094 (HNC 25699); LU1095 (HNC 25670); LU1096 (HNC 25672); LU1097 (HNC 25673); LU1098 (HNC 25675); LU1099 (HNC 25676); LU1189 (HNC 25618); LU1190 (HNC 25677); LU1191 (HNC 25678); LU1192 (HNC 25679); LU1193 (HNC 25680); LU1194 (HNC 25683); LU1195 (HNC 25684); LU1198 (HNC 25685; RMNH K1140); LU1199 (HNC 25688); LU1288 (HNC 25627); LU1289 (HNC 25628); LU1290 (HNC 25689); LU1291 (HNC 25691); LU1292 (HNC 25693); LU1293 (HNC 25694); LU1294 (HNC 25695); LU1298 (HNC 25696); LU1299 (HNC 25698, 38410; RMNH K1139); LU1389 (HNC 25631); LU1390 (HNC 25700); LU1391 (HNC 25699); LU1394 (RMNH K1608, K1609); LU1398 (HNC 25702); LU1399 (HNC 25705; RMNH K1138); LU1489 (HNC 22727, 25633); LU1490 (HNC 25706; RMNH K0468, K1033); LU1491 (HNC 25707); LU1492 (HNC 25708); LU1493 (HNC 25710); LU1494 (RMNH K1605, K1606, K1607); LU1496 (HNC 25711); LU1497 (HNC 25713); LU1498 (HNC 25714); LU1499 (HNC 22725, 25175; RMNH K1141); LU1593 (HNC 25717, 25718); LU1594 (HNC 25721; RMNH K1603, K1604); LU1596 (HNC 25722); LU1597 (HNC 25723); LU1682 (HNC 29108); LU1694 (HNC 25727); LU1697 (HNC 25731); LU1698 (RMNH K0027); LU1699 (HNC 25733); LU1782 (HNC 25649); LU1783 (HNC 25650; RMNH K1106); LU1787 (HNC 29813); LU1797 (RMNH K0025); LU1798 (RMNH K0028); LU2296 (HNC 25964); LV0010 (HNC 25516); LV0011 (HNC 25517); LV0109 (HNC 22604); LV0110 (RMNH K1240, K1534); LV0201 (HNC 25453); LV0207 (RMNH K1016); LV0209 (HNC 29233); LV0300 (HNC 25459); LV0301 (HNC 25460); LV0600 (HNC 25468); LV0601 (HNC 25469); LV0701 (HNC 25474; RMNH K1083); LV0702 (HNC 25475); LV0706 (RMNH K1548); LV0801 (HNC 25480); LV0802 (HNC 25482); LV0803 (HNC 25484); LV0804 (HNC 25486; RMNH K0020); LV0806 (HNC 22719); LV0904 (HNC 25491); LV0906 (HNC 22594, 25493, 29210); LV1104 (HNC 25770); LV1105 (HNC 25772; RMNH K1126); LV1106 (HNC 25773; RMNH K1125); LV1200 (HNC 25777, 25778, 25780; RMNH K1136); LV1204 (HNC 25783); LV1300 (HNC 25789); LV1301 (RMNH K0058); LV1306 (HNC 25794); LV1700 (RMNH K0051).



Figs. 17-20 *Albinaria hippolyti holtzi*, typical form. 17, habitus, ventral aspect (UTM LU1798); 18, apical part of principalis (p) and lunula (L), c, columella (UTM LU1490); 19, aperture, rostro-ventral aspect (UTM LU0990); 20, cervix, dorsal aspect (UTM LU0990); scale lines represent 1 mm.

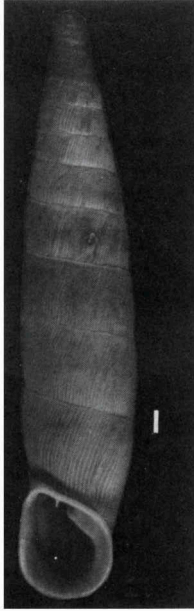


Fig. 21. *Albinaria hippolyti holtzi*, atypical form (UTM LU0598). Habitus, ventral aspect; scale line represents 1 mm.

Diagnosis.— Radial ribs: Variable both in density and prominence, partly dependent on the altitude of the locality; 5-10 per mm on the penultimate whorl.

Cervical sculpture: Basal and dorsal keel equally prominent, close together, separated by a narrow but distinct basal furrow.

Apertural armature: Lip reflected; parietalis long and high; subcolumellaris weakly developed: hardly visible or invisible in a perpendicular view of the aperture; suturalis usually absent; parallelaris usually absent; lunula laterally situated; basalis present, in a few populations absent (see below); subclaustralis absent; apical development of the principalis variable (it supersedes the DUP in some populations, in others it does not), its apical expansion always present; spiralis extends deep into the shell; FUP usually absent.

Shell height: 15.6-23.0 mm (n=115).

Distribution and variability.— The lectotype (fig. 53) stems from the area of Asítes, possibly from the UTM square LU1697. The typical form (figs. 17-20) is distributed all along the eastern and western slopes of the Ida-plateau. Isolated populations are found further away, to the north-east of the town of Ágii Déka and near the village of Veneráto. Shells from populations occurring on the Ida-plateau itself (roughly between 800 and 1800 m altitude) are characterised by their large size, slenderly fusiform habitus, relatively large aperture and obsolete radial ribs (fig. 21; this form used to be known as *A. h. neuteboomi*). The distribution of this form extends north to the town of Anógia. Further to the north, separated from the main range, in a restricted area near the village of Livádia, some scattered populations occur, which are in most aspects identical to the typical form, although they show a more weakly developed subcolumellaris (invisible in a perpendicular view of the aperture) and no trace of a basalis.

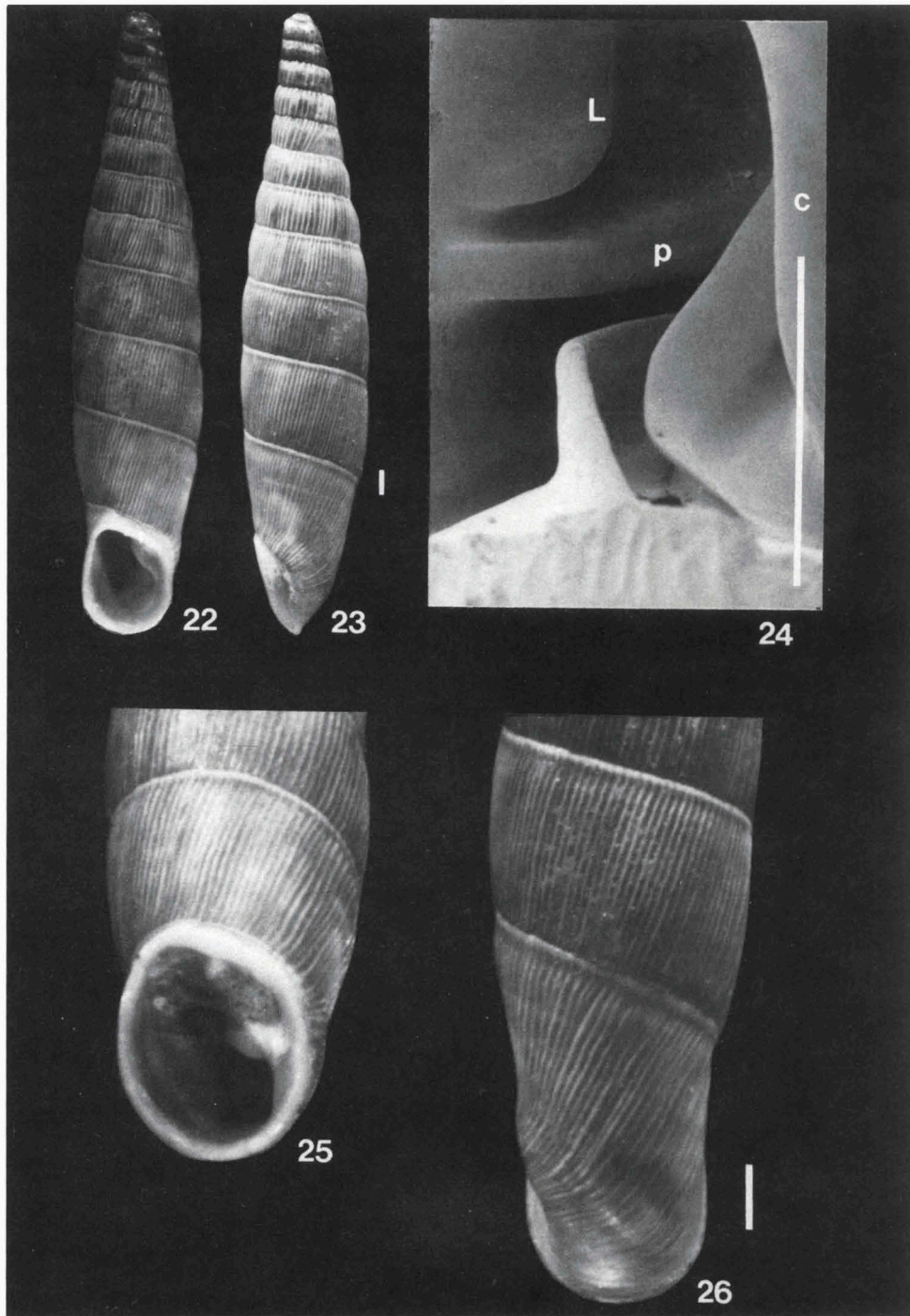
In certain places, *A. h. holtzi* is found sympatrically with *A. spratti* and with *A. idaea* (Pfeiffer, 1849). It forms occasional hybrids with both these species.

Albinaria hippolyti asterousea subsp. nov.

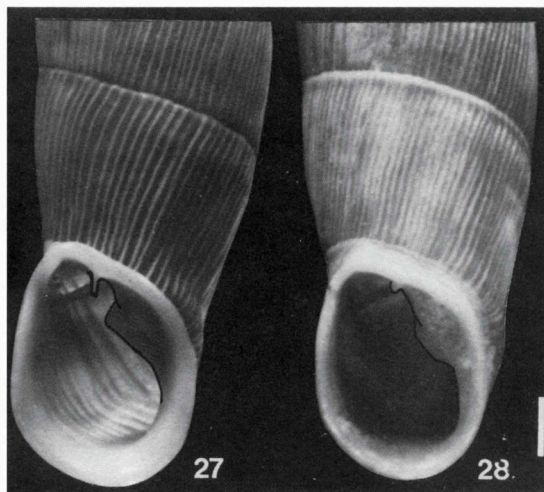
(figs. 22-26, 28, 54)

Material.— Holotype (HNC 26010): "GR, Kreta, Nómos Iráklίου, Ep. Monofatsiou, 1,5 km SW Paránimfi = 1,5 km NW Tris Eklisiés, Südhänge, ca. 600 m NN, UTM LU2770, 27.2.1992, lg.W.WELTER-SCHULTES". Paratypes: LU0372 (HNC 26245; RMNH K1115/56700, K1551/56701); LU0468 (HNC 25275); LU0567 (HNC 29123); LU0568 (HNC 25279); LU0667 (HNC 25281); LU0670 (HNC 25325); LU0671 (HNC 25328); LU0768 (HNC 25285); LU0867 (HNC 25287); LU0868 (HNC 25289); LU0967 (HNC 29124); LU1269 (RMNH K1166/56702); LU2067 (HNC 29113); LU2068 (HNC 29111); LU2168 (HNC 29115); LU2368 (HNC 29112); LU2369 (HNC 29119); LU2468 (HNC 29116); LU2469 (HNC 29110); LU2568 (HNC 29114); LU2668 (HNC 29117); LU2768 (HNC 29121); LU2770 (HNC 29109; RMNH K1654/56703); LU2869 (HNC 29125); LU2969 (HNC 29122).

Diagnosis.— Radial ribs: Not very prominent; 7.5-12 per mm on the penultimate whorl.



Figs. 22-26 *Albinaria hippolyti asterousea*, paratype (RMNH 56701, UTM LU0372). 22, habitus, ventral aspect; 23, habitus, lateral aspect; 24, apical part of principalis (p) and lunula (L), c, columella; 25, aperture, rostro-ventral aspect; 26, cervix, dorsal aspect; scale lines represent 1 mm.



Figs. 27. *Albinaria hippolyti holtzi*. Aperture, ventral aspect (UTM LU0990); 28, *Albinaria hippolyti asterousea*. Aperture, ventral aspect (UTM LU0372); scale line represents 1 mm. Apertural armature accentuated by black line.

Cervical sculpture: Basal keel distinct, dorsal keel obsolete. Both keels are separated by a rudimentary basal furrow.

Apertural armature: Lip narrow, not reflected; parietalis variable both in length and height; columellaris low and twisted around the columella in a very narrow bend: in a perpendicular view of the aperture, the columellaris disappears behind the columella at a much lower position than in any of the other subspecies; subcolumellaris weakly developed: usually invisible in a perpendicular view of the aperture; suturalis absent; parallellaris absent; lunula laterally or even ventrolaterally situated; basalis absent; subclaustralis absent; principalis supersedes the DUP only slightly,

its apical expansion is obsolete; spiralis extends deep into the shell; FUP absent.

Shell height: 13.5-18.8 mm (n=141).

Derivatio nominis.— This new subspecies is named after the Asteroúsia Mountains, the mountain range along the south coast of central Crete to which it is confined.

Distribution and variability.— *A. h. asterousea* is found in the south of the Asteroúsia-range between Trís Eklisiés and Kalí Liménes and is thus isolated from the main range of the species. In the western and central part of its area of distribution, small and isolated populations are found. In the eastern parts, especially south around Mount Kófinas and apparently due to the geologic formations, it inhabits larger areas. The subspecies exhibits little geographical variation (shells from eastern populations tend to be larger).

In some places in the western part of its range, it is found sympatrically with *A. terebra* (Pfeiffer, 1853). In other parts in the western and in large areas in the eastern part of its range, it is found sympatrically with *A. corrugata doerfleri* Wagner, 1924. At two localities, the three species were found together (LU0372 and LU1567). In the eastern part of its range (at some rocks in a gorge north of Trís Eklisiés) it may occur sympatrically with *A. teres extensa* (L. Pfeiffer, 1864), although these areas were not examined, due to the dangerous access. Hybrids with any of these species were never encountered.

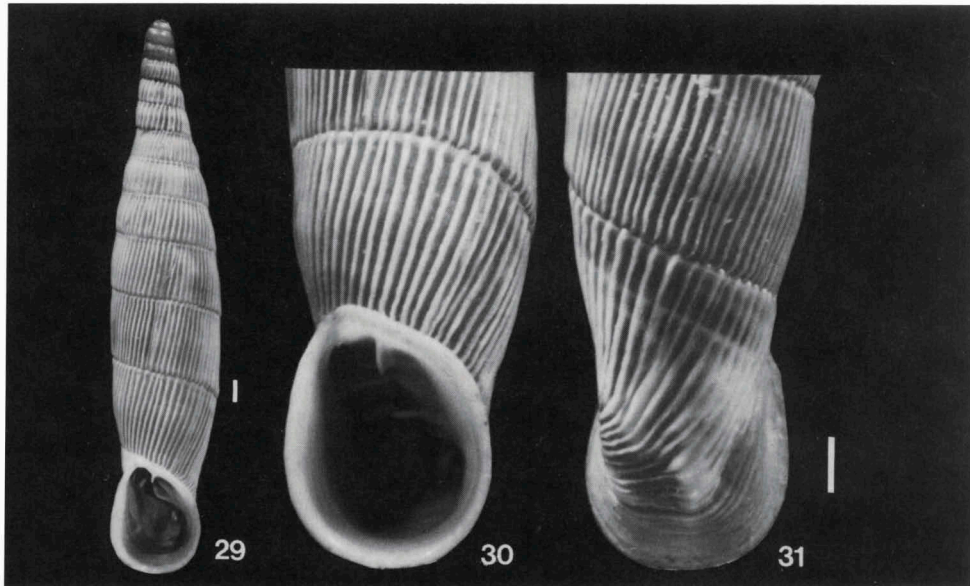
***Albinaria hippolyti aphrodite* (Boettger, 1883)**
(figs. 29-42, 55)

Clausilia aphrodite Boettger, 1883: 329, pl. 33 fig. 3a-c.

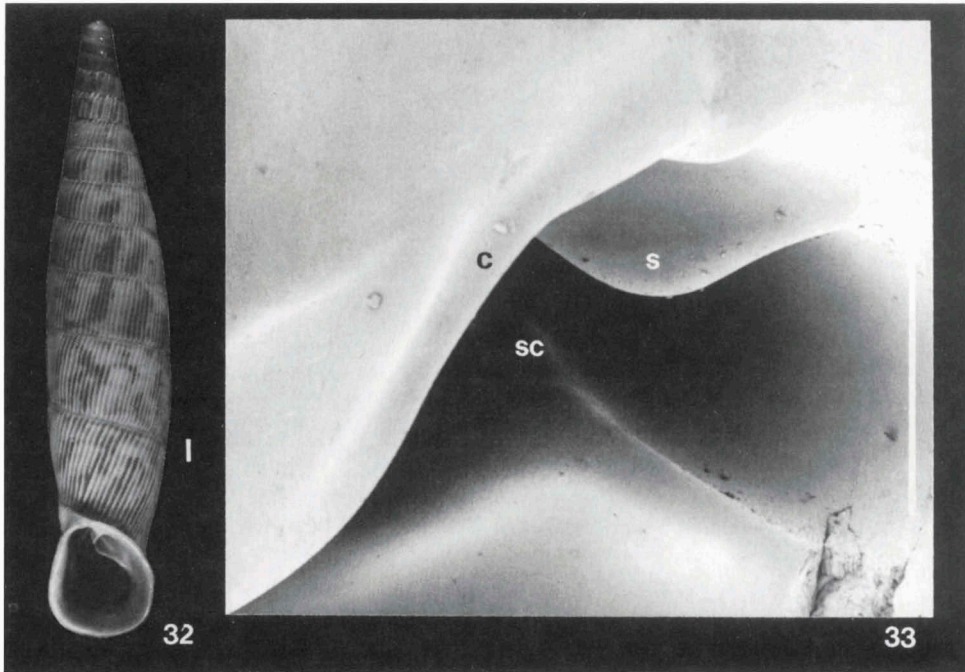
Albinaria hippolyti aphrodite; Nordsieck, 1977: 300.

Albinaria hippolyti francisci Schilthuizen & Gittenberger, 1990: 135, 136, fig. 4, 5. Syn. nov.

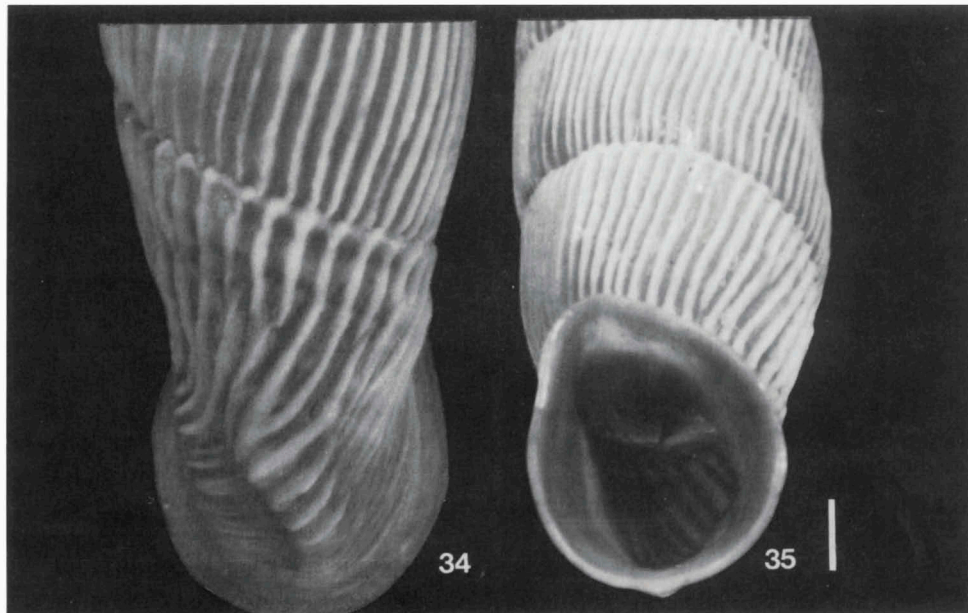
Material.— Holotype (SMF 66293): "Kreta: Alb. (Striata) aphrodite (Boettger), Typus: Boettger 1883 T.33 F.3, Pass o. Tylisso b. Megalocastron, Spratt. S. Sammlung O. Boettger". Additional samples: LU1499 (RMNH K0056); LU1785 (HNC 25652); LU1786 (HNC 25653; RMNH K1655, K1349); LU1799 (RMNH K0029, K1616); LU2497 (HNC 25979); LU2596 (HNC 25989); LU2598 (HNC 25990; RMNH K1624); LU2599 (HNC 25991); LU2696 (HNC 25998); LU2697 (HNC 25999); LU2698 (RMNH K1621, K1622, K1625); LU2699 (HNC 26003; RMNH K1617, K1620); LU2796 (HNC 26009, 38403); LU2797 (HNC 26011; RMNH K1347); LU2799 (RMNH K1615); LU3488 (HNC 26244, 26245; RMNH K1348); LV0013 (HNC 25520); LV0113 (HNC 11126, 25526; RMNH K1054); LV0212 (HNC 25530); LV0312 (HNC 25535); LV0412 (HNC 25544; RMNH K1053); LV0512 (HNC 25551); LV0612 (RMNH K1539); LV0703 (HNC 29259); LV0704 (HNC 29216); LV0711 (RMNH K1543); LV0809 (RMNH K0071); LV0902 (HNC 25487; RMNH K1486); LV0903 (HNC 25489); LV0909 (HNC 10434; RMNH K1514); LV0910 (RMNH K1245); LV1001 (HNC 25762); LV1002 (HNC 25763; RMNH K1484); LV1003 (HNC 25764); LV1007 (HNC 25765); LV1008 (HNC 25766, 29190; RMNH K1012); LV1009 (RMNH K1011); LV1010 (RMNH K1244); LV1100 (HNC 25767); LV1101 (HNC 25768); LV1102 (HNC 25769); LV1108 (HNC 25774); LV1109 (HNC 29229); LV1110 (HNC 29175; RMNH K1515); LV1200 (HNC 25775, 25776); LV1201 (HNC 25781; RMNH K1135); LV1202 (HNC 25782); LV1205 (HNC 25784; RMNH K1127, K1128, K1459, K1549); LV1206 (HNC 25785; RMNH K0016, K1301); LV1208 (RMNH K0015); LV1209 (HNC 10171; RMNH K1010); LV1301 (HNC 25790; RMNH K1487); LV1302 (HNC 25791; RMNH K1503); LV1304 (HNC 25792; RMNH K1130, K1463, K1464); LV1305 (HNC 25793); LV1307 (HNC 22718); LV1312 (RMNH K1519); LV1313 (HNC 10597); LV1400 (HNC 25795, 25798; HNC 38411; RMNH K1134); LV1401 (HNC 25799; RMNH K0057); LV1404 (RMNH K1131); LV1405 (HNC 25800; RMNH K1409, K1410, K1411, K1461, K1462); LV1406 (HNC 25801; RMNH K1408); LV1407 (HNC 10513, 22606; RMNH K1404, K1405, K1406); LV1408 (HNC 25803, 29251; RMNH K1008, K1009); LV1409 (HNC 25805; RMNH K1420, K1516); LV1411 (RMNH K1517); LV1412 (HNC 10408); LV1413 (RMNH K1048); LV1500 (HNC 25806); LV1501 (HNC 25807); LV1505 (HNC 25808); LV1506 (HNC 10292, 29293; RMNH K0013); LV1507 (HNC 25809; RMNH K1412, K1413, K1416); LV1508 (HNC 25810; RMNH K1456, K1457); LV1509 (RMNH K1445, K1446); LV1513 (HNC 10246); LV1514 (RMNH K0037); LV1600 (HNC 25812); LV1601 (HNC 25813); LV1603 (RMNH K1505, K1506, K1507, K1508, K1509); LV1606 (HNC 10333; RMNH K1007); LV1609 (RMNH K1444, K1447, K1448, K1455); LV1700 (HNC 22728, 25814);



Figs. 29-31. *Albinaria hippolyti aphrodite*, typical form (UTM LV1413). 29, habitus, ventral aspect; 30, aperture, rostro-ventral aspect; 31, cervix, dorsal aspect; scale lines represent 1 mm.

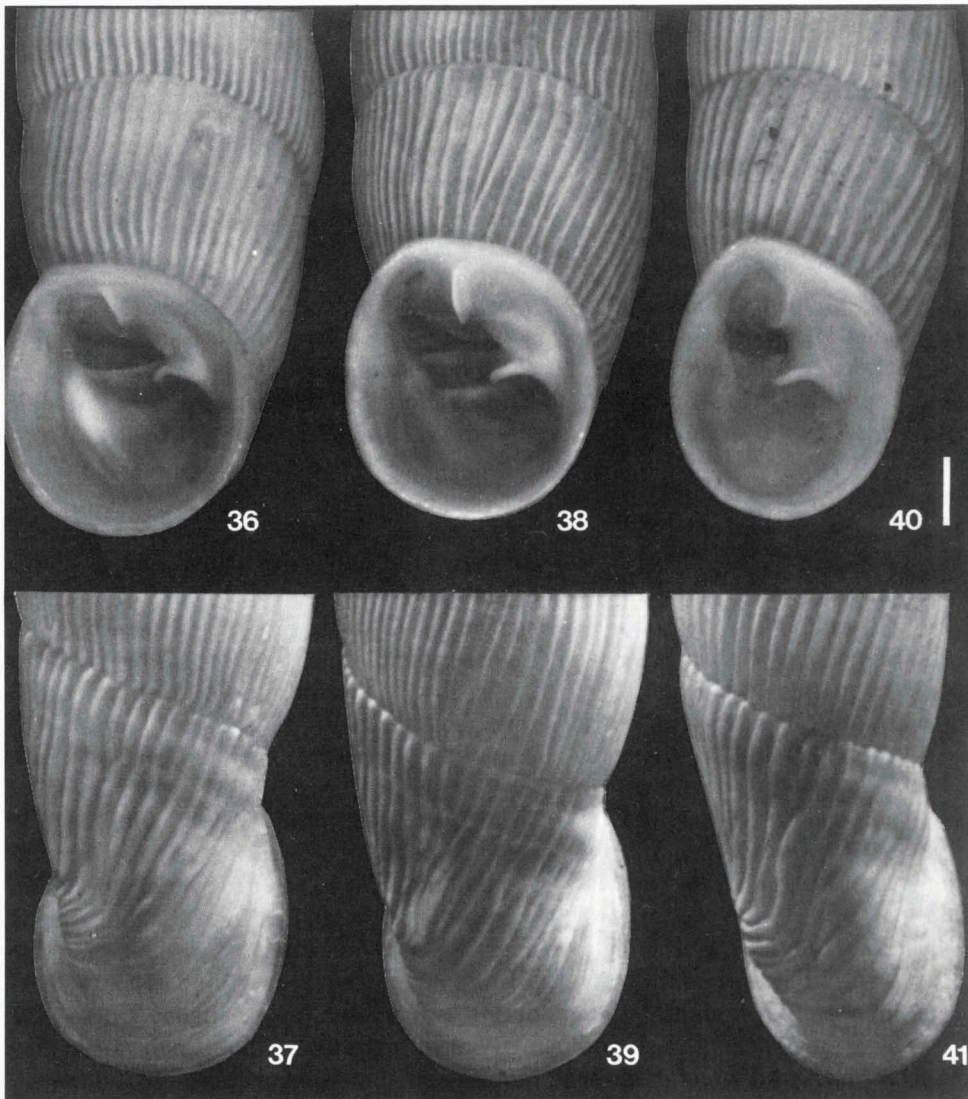


Figs. 32, 33. *Albinaria hippolyti aphrodite*, atypical form. 32, habitus, ventral aspect (UTM LV1206); 33, apertural lamellae: c, columellaris, s, subcolumellaris, sc, subclaustralis (UTM LV1205); scale lines represent 1 mm.



Figs. 34, 35. *Albinaria hippolyti aphrodite*, atypical form. 34, cervix, dorsal aspect (UTM LV1401); 35, aperture, rostro-ventral aspect (UTM LV1400); scale line represents 1 mm.

RMNH K0052); LV1701 (HNC 25185); LV1702 (HNC 25816; RMNH K1504); LV1706 (RMNH K0007, K0012, K1643); LV1802 (HNC 25819); LV1803 (HNC 25820); LV1903 (HNC 25821); LV1904 (HNC 25822); LV2003 (HNC 26118); LV2004 (RMNH K1133); LV2102 (HNC 26124); LV2103 (HNC 26125); LV2200 (HNC 26131); LV2201 (HNC 26132); LV2202 (HNC 26133; RMNH K0050); LV2203 (HNC 26134); LV2204 (HNC 26135); LV2300 (HNC 26142); LV2301 (HNC 26143); LV2303 (HNC 26144); LV2304 (HNC 26145); LV2401 (HNC 26146); LV2405 (HNC 26147); LV2406 (HNC 26149); LV2501 (HNC 26150); LV2506 (HNC 26151); LV2507 (HNC 26152); LV2600 (HNC 26155); LV2601 (HNC 26156); LV2701 (HNC 26162); LV2800 (HNC 26168); LV2801 (HNC 16171); no exact locality: RMNH K0410, K0411, K0412.



Figs. 36-41. *Albinaria hippolyti* aphrodite, atypical forms. 36, aperture, rostro-ventral aspect (UTM LU2797); 37, cervix, dorsal aspect (UTM LU2797); 38, aperture, rostro-ventral aspect (UTM LU3488); 39, cervix, dorsal aspect (UTM LU3488); 40, aperture, rostro-ventral aspect (UTM LU1786); 41, cervix, dorsal aspect (UTM LU1786); scale line represents 1 mm.

Diagnosis.— Radial ribs: Usually sharp and widely spaced, 3-6 per mm on the penultimate whorl. In certain populations, however, sometimes more densely arranged, with up to 9 per mm.

Cervical sculpture: Basal keel usually weakly developed, in some populations more prominent. Dorsal keel moderately to very strongly developed, crest-like in some populations; the northern populations however, carry very weak dorsal keels. A basal furrow is often present.

Apertural armature: Lip usually reflected; parietalis variable both in length and height: ranging from completely absent to strongly developed; subcolumellaris moderately to very prominent: usually visible in a perpendicular view of the aperture; suturalis present; parallellaris absent in some populations, present in others; lunula dorsally to dorsolaterally situated; basalis present, in some populations weakly developed; subclaustralis rarely present; principalis supersedes the DUP in varying degrees, its apical expansion often present; spiralis variable in length; FUP usually present.

Shell height: 14.6-24.0 mm (n=202).

Distribution and variability.— The label of the holotype (fig. 55) reads: "Pass over Tylisso". The present day pass west of Tylisso is situated exactly at the edge of the subspecies' range. However, in view of its habitus, the holotype probably stems from UTM-square LV1507, which may have been the position of a pass in Boettger's days.

The typical form (figs. 29-31) is found to the immediate west of the range of *A. h. harmonia*. To the south, roughly in the area of Goniés, where the subspecies' range touches the range of *A. h. holtzi*, the shells are more densely ribbed (fig. 32), with a dorsolaterally, rather than dorsally, situated lunula, a weakly developed dorsal keel and often a subclaustralis (fig. 33).

East and south of this area, the shells are of the form formerly known as *A. h. francisci* (fig. 34, 35): it has widely spaced radial ribs, an extremely well developed, crest-like dorsal keel, an often obsolete parietalis, no parallellaris and a poorly developed, often fully absent, FUP. Further towards the east, in the area of Profitis Ilias, the parietalis, the parallellaris and the FUP tend to gain prominence, with, in contrast, the dorsal keel becoming less conspicuous (figs. 36, 37). This tendency finds its extreme in the isolated population near the village of Amourgéles, in which most shells carry a well-developed FUP and parietalis (figs. 38, 39). The form found in isolated populations near the village of Ano Mouília shows yet another combination of traits (figs. 40, 41): the shell carries sharp and widely spaced radial ribs, a strong, crest-like dorsal keel, a relatively weakly developed parietalis and quite a prominent FUP; the parallellaris is absent.

In an area along the southern foot-hills of the Koulókonas range, some isolated populations occur of a form which is in many ways intermediate between *A. h. hippolyti* and *A. h. aphrodite*: like the former, it is densely ribbed, also on the cervix, where the two keels are little

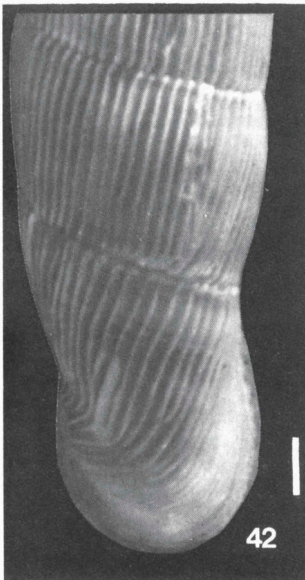


Fig. 42. *Albinaria hippolyti aphrodite*, atypical form (UTM LV0113). Cervix, dorsal aspect; scale line represents 1 mm.

prominent (fig. 42); with the latter, however, it shares the possession of a well-developed FUP. Its range does not appear to merge into that of *A. h. hippolyti* or some *A. h. aphrodite* form. Here, it is treated as belonging to *A. h. aphrodite*, mainly because of its possession of a FUP.

A. h. aphrodite is found sympatrically with *A. spratti* in some places, with *A. corrugata inflata* (Olivier, 1801), in others.

***Albinaria hippolyti arthuriana* (Boettger, 1878)**
(figs. 43-46)

Clausilia arthuriana Boettger, 1878: 72-73, pl. 146: figs. 1a-e
Albinaria hippolyti arthuriana Boettger; Nordsieck, 1977: 300.

Material.— Holotype (SMF 66285): "Insel Spinalunga in der Baia di Mirabello". Additional samples: LU8499 (RMNH K1645); LV7002 (HNC 22679); LV7003 (HNC 15436; RMNH K1650); LV7008 (HNC 11132, 15438); LV7105 (RMNH K1123, K1550); LV7107 (HNC 29871; RMNH K1648, K1652); LV7310 (RMNH K1646); LV8506 (HNC 15437; RMNH K1647); no exact locality: RMNH K1653.

Diagnosis.— Radial ribs: Usually densely ribbed, 10-12 ribs per mm on the penultimate whorl. In some western populations however, the ribs are more widely spaced, with sometimes as few as 7 per mm.

Cervical sculpture: Both keels and the basal furrow weakly developed; in some populations the dorsal keel is obsolete.

Apertural armature: Lip little to broadly reflected; parietalis variable both in length and height; subcolumellaris well developed, but often invisible in a perpendicular view of the aperture; suturalis present; parallellaris absent; lunula dorsally situated; basalis present; subclaustralis present; principalis barely supersedes the DUP, its apical expansion usually present, but weakly developed; spiralis extends deep into the shell; FUP present.

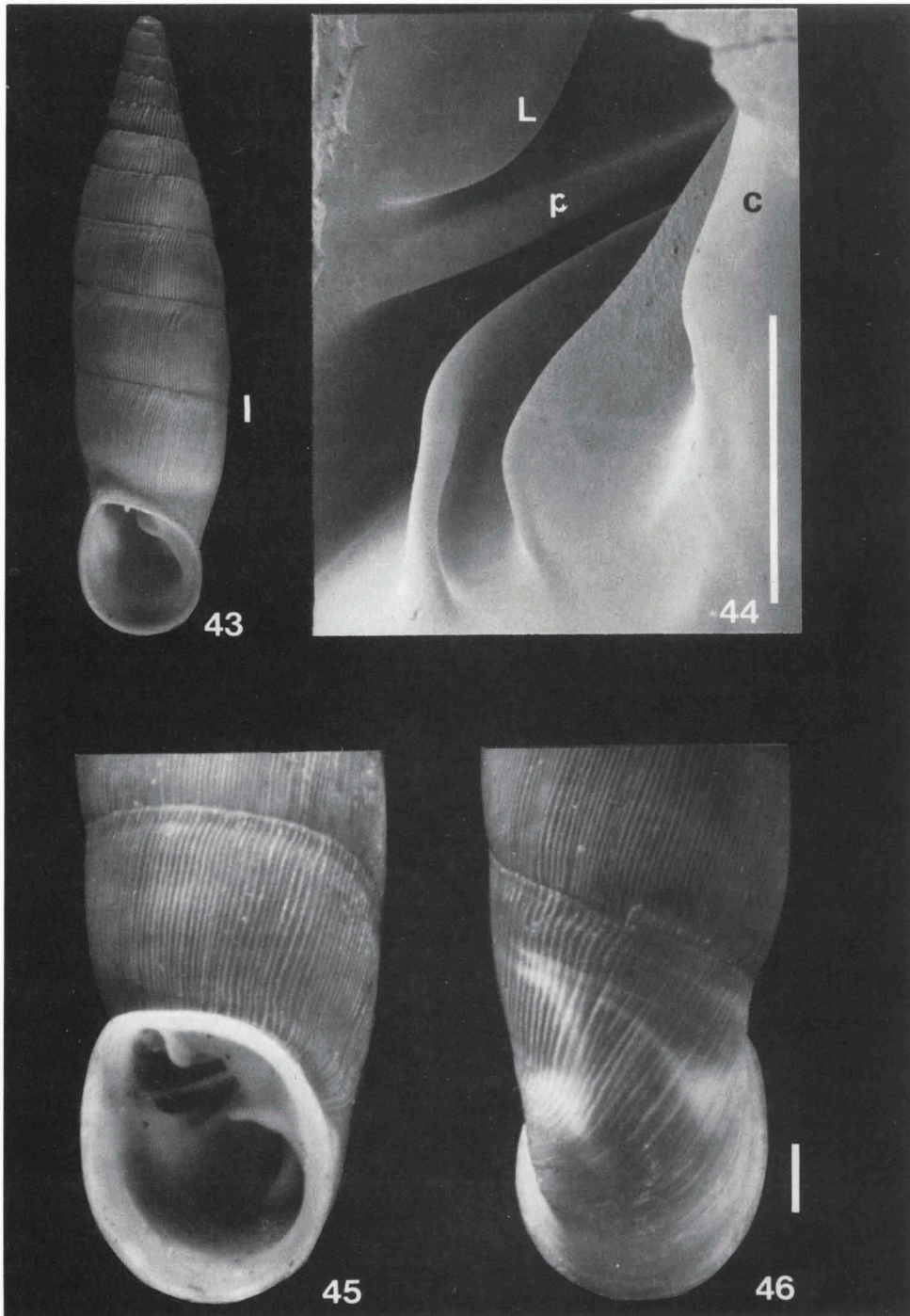
Shell height: 13.7-21.2 mm (n=69).

Distribution and variability.— The subspecies appears to occur in a relatively large area in Eastern Crete, roughly between the town of Mílatos and the Spinalónga peninsula. In the west, near Mílatos Cave, a broad area exists, in which extensive hybridisation occurs with *A. maltzani* (Boettger, 1883), resulting in shells with intermediate features.

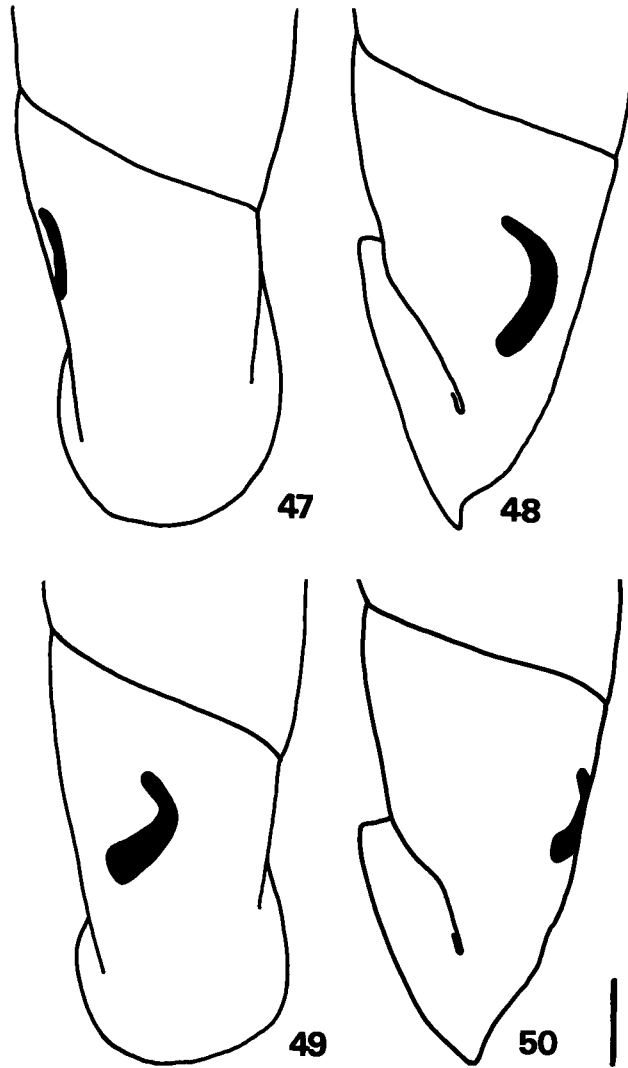
More work on *A. h. arthuriana* seems necessary. Therefore, a treatment of its distribution and variability would be premature.

A simplified key to the subspecies of *A. hippolyti*

1. Lunula laterally situated (figs. 47, 48) 2
- Lunula dorsally to dorsolaterally situated (figs. 49, 50) 3
2. Columellaris low and twisted around the columella in a very narrow bend (fig. 28) *A. hippolyti asterousea* nov. subspec.
- Columellaris high and twisted around the columella in a wide bend (fig. 27)
..... *A. hippolyti holtzi* (Sturany, 1904)

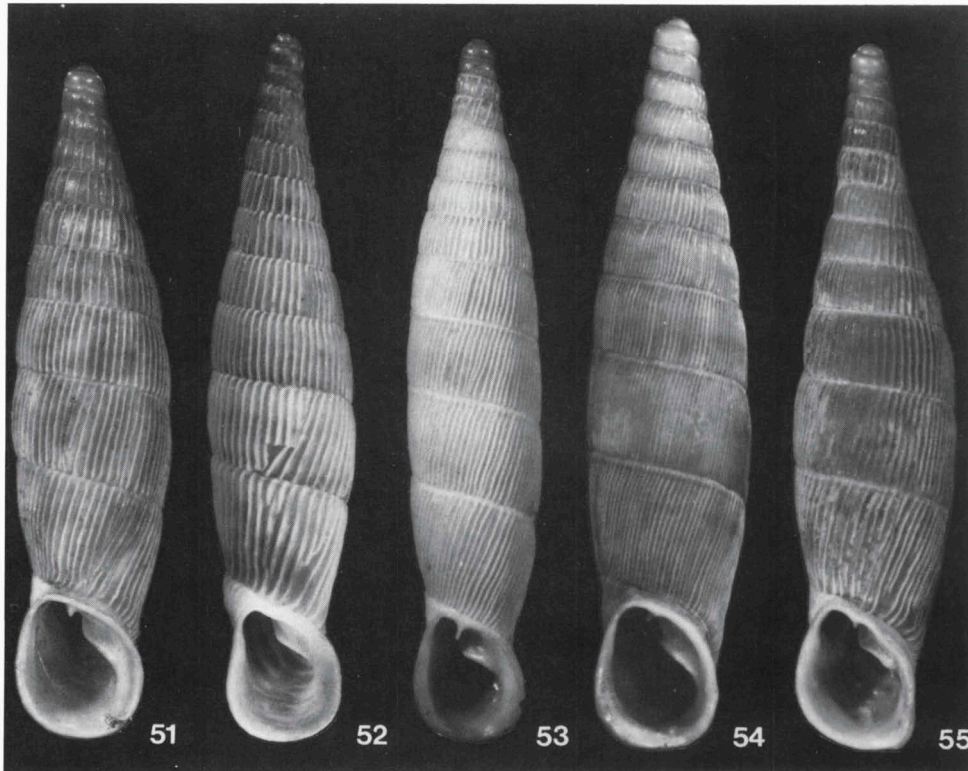


Figs. 43-46. *Albinaria hippolyti arthuriana*. 43, habitus, ventral aspect (UTM LU8499); 44, apical part of principalis (p) and lunula (L), c, columella (UTM LV7310); 45, aperture, rostro-ventral aspect (UTM LV7310); 46, cervix, dorsal aspect (UTM LV7310); scale lines represent 1 mm.



Figs. 47-50. Cervices with laterally and dorsally situated lunulae. 47, lateral lunula, dorsal aspect; 48, lateral lunula, lateral aspect; 49, dorsal lunula, dorsal aspect; 50, dorsal lunula, lateral aspect. Scale line represents 1 mm.

- 3. FUP strongly developed (cf. fig. 45) 4
- Any trace of a FUP absent (cf. fig. 9) 5
- 4. Radial ribs sharp and densely arranged, usually >10 per mm (fig. 43). Eastern Crete *A. hippolyti arthuriana* (Boettger, 1878)
- Radial ribs more widely separated, <10 per mm (fig. 29, 32). Central Crete *A. hippolyti aphrodite* (Boettger, 1883), p.p.
- 5. Dorsal keel less prominent than the basal keel or equally prominent: when viewed from the palatal side, the basal keel is usually visible behind the dorsal keel 6



Figs. 51-55. *Albinaria hippolyti*. Ventral aspects of type-specimens. 51, *Albinaria hippolyti hippolyti*, holotype (SMF 66698); 52, *A. hippolyti harmonia*, holotype (RMNH 56672); 53, *A. hippolyti holtzi*, lectotype (SMF 66314/1); 54, *A. hippolyti asterousea*, holotype (HNC 26010); *A. hippolyti aphrodite*, holotype (SMF 66293) (not to scale).

- Dorsal keel more prominent than the basal keel: when viewed from the palatal side, the basal keel is hidden behind the dorsal keel
..... *A. hippolyti aphrodite* (Boettger, 1883), p.p.
- 6. Dorsal and basal keel both quite prominent, separated by a distinct depression. Radial ribs usually sharp and widely spaced (fig. 16). Apertural lip deflected
..... *A. hippolyti harmonia* subsp. nov.
- Dorsal keel obsolete, hardly visible; a rudimentary dorsal furrow is sometimes present. Radial ribs usually inconspicuous, closely spaced (fig. 10). Apertural lip little or not deflected (figs. 11, 13) *A. hippolyti hippolyti* (Boettger, 1878)

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