



Succinea (Calcisuccinea) sp., an American land-snail newly established in Portugal and Spain (Gastropoda: Succineidae)

Succinea (Calcisuccinea) sp., un caracol terrestre americano nuevo para Portugal y España (Gastropoda: Succineidae)

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Recibido el 1-IV-2013. Aceptado el 21-VI-2013

ABSTRACT

During 2010-2013 populations of an unfamiliar species of Succineidae were found to be established in southern Spain (near Málaga), north-eastern Spain (provinces of Barcelona and Tarragona) and west-central Portugal (Leiria and Porto de Mós). The shells, mantle coloration and genital anatomy are described. It is demonstrated that they do not resemble any European species of the family. However, characters of the distal genital anatomy match those of *Succinea* subgenus *Calcisuccinea* Pilsbry, 1948, which is native in North and Central America. Nevertheless, there are clear differences from the taxa known anatomically which are currently placed in this subgenus, so it is suggested that the Iberian specimens may be referable to one of the American taxa of Succineidae for which the anatomy is currently unknown and the species level taxonomy unresolved. The anthropogenically disturbed habitats at the Portuguese and some Spanish sites were drier than those occupied by any of the native Succineidae of western Europe. It remains to be seen whether this taxon will become a pest in Europe, where it is probably now too widespread to be eradicated.

RESUMEN

Durante 2010-2013, se descubrió que distintas poblaciones de una especie desconocida de Succineidae se habían establecido en hábitats alterados del sur y noreste de España (provincias de Málaga, Barcelona y Tarragona respectivamente) y el centro-oeste de Portugal (Leiria y Porto de Mós). Las conchas, coloración del manto y anatomía genital son descritas y se ha llegado a la conclusión de que estas no se corresponden con ninguna de las especies europeas de la familia. Los caracteres, principalmente de la anatomía distal genital, se acercan mucho a *Succinea* subgénero *Calcisuccinea* Pilsbry, 1948, que es nativa de América del Norte. No obstante, hay diferencias claras con los táxones que actualmente están encuadrados dentro de este subgénero. Se sugiere así, que los especímenes ibéricos podrían tratarse de uno de los numerosos táxones americanos de Succineidae cuya anatomía es desconocida en la actualidad y su taxonomía a nivel de especie está aún por resolverse. Los hábitats antropogénicamente alterados de las localidades ibéricas eran mucho más secas que las que ocupa cualquier Succineidae nativo de Europa occidental. Queda por ver si este taxon llegará a ser una plaga en Europa, donde es probable que en este momento esté ya demasiado extendida para ser erradicada.

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INTRODUCTION

During 2010-2013 populations of an unfamiliar species of Succineidae were found to be established in gardens and other disturbed habitats in southern Spain (near Málaga), in north-eastern Spain (provinces of Barcelona and Tarragona) and in west-central Portugal (Leiria and Porto de Mós). Compared to the European species of the family it has a relatively broad oval shell and dark markings on the mantle, producing an overall impression suggesting *Radix* (Lymnaeidae).

Identification of European Succineidae from shells alone is notoriously difficult and unreliable, because shells show few characters and these are often not diagnostic even of the genus (e.g. KERNEY & CAMERON, 1979: 59-61). Instead, taxonomy and accurate identification rely mainly on characters of the distal genitalia (QUICK, 1933; HECKER, 1965; PATTERSON, 1971; GITTENBERGER, BACKHUYS & RIPKEN, 1984; SCHILEYKO, 2007), so these formed the main basis for (sub-) generic identification in the present study. This paper therefore provides a key to European species of Succineidae based on the genital anatomy, showing that the unfamiliar Iberian taxon differs clearly from any native European species. Details are given of its genital anatomy, shells, mantle coloration, Iberian localities and habitats.

The distal genital anatomy of the Iberian specimens resembles that of *Succinea* subgenus *Calcisuccinea* Pilsbry, 1948, which is native in North America. Accurate identification to species level is apparently impossible because of the lack of information on genital anatomy of many American Succineidae, leading to poor taxonomic understanding. Unfortunately their shells often show insufficient characters for accurate species identification (e.g. PATTERSON, 1971; PÉREZ & LÓPEZ, 2003: 420-421).

MATERIAL AND METHODS

Numerous shells were studied from eight localities listed in the next section,

six in Spain and two in Portugal. Living snails from both Portuguese sites were drowned in water overnight, then preserved in 80% Industrial Methylated Spirit. Dissections were carried out using a Meiji RZ Series stereo-microscope, drawings were made using a Meiji drawing tube and shell measurements were made with an eye-piece graticule. Proximal and distal refer to the position in relation to the ovotestis. "External" characters of the penial complex refer to those seen in dissected snails without opening the penial sheath.

Abbreviations: AH: height of shell aperture; B: shell breadth; CGAH: Collection of G.A. and D.T. Holyoak; CJSTA: Collection of J.S. Torres Alba; CRMCM: Collection of R.M. da Costa Mendes, CSQS: Collection of Sergio Quiñonero Salgado; DTH: D.T. Holyoak, GAH: G.A. Holyoak, H: shell height, IM: Inês Mendes, JSTA: J.S. Torres Alba, MM: Maricris Mendes, MNCN: Museum Nacional de Ciencias Naturales, Madrid, RMCM: R.M. da Costa Mendes, RRJ: Ramon Ruiz Jarillo, SQS: Sergio Quiñonero Salgado. The map references for localities are given as latitude and longitude (obtained from Flash Earth) or based on the U.T.M. grid. The Portuguese material described is in CGAH, CRMCM and MNCN, the Spanish material mainly in CJSTA and CSQS.

OBSERVATIONS AND DISCUSSION

Key to European species of Succineidae Beck, 1837

The following key to all the European taxa of the family also includes the *Succinea* (*Calcisuccinea*) sp. from Iberian localities which is discussed in more detail in later sections of this paper. Fig. 1 shows the characters of the penial complex and vagina used in the key. Note that the narrow proximal part of the penis complex is described as an "epiphallus" in *Succinea* and *Succinella* e.g. by GITTENBERGER, BACKHUYS & RIPKEN (1984) and in this paper, but as part of the penis by SCHILEYKO (2007).

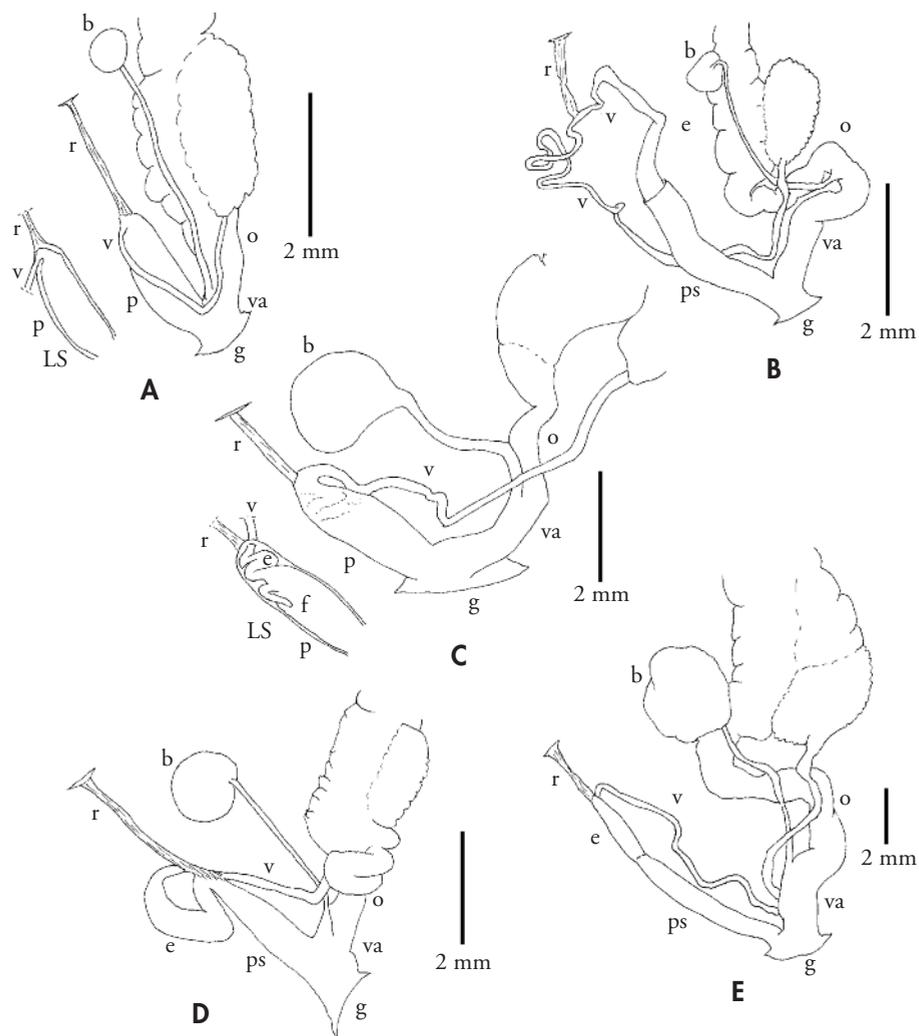


Figure 1. Penial complex and distal female genitalia in native European Succineidae and *Succinea* (*Calcisuccinea*) sp. A: *Quickella arenaria*, B: *Succinella oblonga*, C: *Oxyloma elegans*, D: *Succinea* (*Calcisuccinea*) sp. from Iberia, E: *Succinea* (*Succinea*) *putris*. A-C and E are redrawn with minor changes from SCHILEYKO (2007) after checking of all the species from the authors' dissections, which were also used to provide approximate scale bars; D is based on our Figure 4A. Abbreviations, b: bursa copulatrix; e: "epiphallus"; f: "flagellum"; g: opening of genital orifice; LS: longitudinal section of penis; o: free oviduct; p: penis; ps: penis sheath; r: penis retractor muscle; v: vas deferens; va: vagina.

Figura 1. Complejo penial y genitalia femenina distal en Succineidae nativos de Europa y *Succinea* (*Calcisuccinea*) sp. A: *Quickella arenaria*, B: *Succinella oblonga*, C: *Oxyloma elegans*, D: *Succinea* (*Calcisuccinea*) sp. de la Península Ibérica, E: *Succinea* (*Succinea*) *putris*. A-C y E están redibujadas con pequeños cambios de SCHILEYKO (2007), después de comprobar todas las especies en las disecciones de los autores, las cuales se usaron también para añadir las escalas; D está basada en nuestra Figura 4A. Abreviaturas, b: bolsa copulatrix, e: "epifalo"; f: "flagelo"; g: abertura del orificio genital; LS: sección longitudinal del pene; o: oviducto libre, p: pene; ps: vaina del pene; r: músculo retractor del pene; v: vaso deferente; va: vagina.

- 1 - Penial complex not divided into distinct parts externally 2
 - Exterior of penial complex with wide distal part clearly demarcated from narrower proximal part 3
- 2 - Penis entirely covered by sheath, inside which convoluted epiphallus present at proximal end and blind appendix (“flagellum”) on junction between penis and epiphallus (Fig. 1C) *Oxyloma* (3 spp.)
 - Penis lacking sheath, epiphallus or “flagellum” (Fig. 1A) *Quickella arenaria*
- 3 - Proximal part of penis (“epiphallus”) forming an almost closed loop, due to attachment of retractor muscle to proximal end of epiphallus, distal end of vas deferens and proximal end of penis sheath; vagina so short that it is indistinct, or absent (Fig. 1D) *Succinea* (*Calcisuccinea*) sp. from Iberia
 - Proximal part of penis not forming an almost closed loop; vagina distinct 4
- 4 - Penis retractor muscle attached to distal part of vas deferens; vagina relatively long (Fig. 1B) *Succinella oblonga*
 - Penis retractor muscle attached to proximal end of penis (“epiphallus”) or proximal end of penis sheath; vagina short (Fig. 1E) *Succinea* (*Succinea*) *putris*

Native Succineidae of the Iberian Peninsula and NW. Africa

All of the western European species of Succineidae have been reported from the Iberian Peninsula, although occurrence of some of them has not been confirmed anatomically. Only *Oxyloma elegans* (Risso, 1826) is widespread and common, with numerous records confirmed by dissection. *Quickella arenaria* (Potiez & Michaud, 1835) has recently been confirmed anatomically from a few montane sites in Prov. Asturias (HOLYOAK & HOLYOAK, 2009) and Prov. Castellón (MARTÍNEZ-ORTÍ & PÉREZ FERRER, 2012). Records of the other species appear to have been based only on shells: *Succinea putris* (Linnaeus, 1758) is reported from NE. Spain (HAAS, 1991: 355; BECH, 1990: 81) and Andorra (MARTÍNEZ-ORTÍ, BORREDÀ & NICOLAU, 2010); *Succinella oblonga* (Draparnaud, 1801) has a few reports from NE. Spain (HAAS, 1991: 356; BECH, 1990: 82) and an old and unconfirmed report from N.

Portugal (NOBRE, 1941); *Oxyloma sarsii* (Esmark, 1886) has reports from NE. Spain (as *S. elegans* in HAAS, 1991: 353; BECH, 1990: 82) along with an isolated modern record from Prov. Madrid at a garden centre where it was presumed to be an accidental introduction (SOLER, MORENO, ARAUJO & RAMOS, 2006: 230). The only records from NW Africa that have been confirmed anatomically are of *Oxyloma elegans* and *Quickella arenaria* (SEDDON & HOLYOAK, 1993).

There can be little doubt that the taxon we discuss in the following section is a recent arrival in the Iberian Peninsula, or at least one that has only become noticeably common and widespread in recent years. Its relatively wide shells immediately attract attention as different to those of any of the native Succineidae of western Europe. The prevalence of records in anthropogenically disturbed habitats may also point to an introduced rather than native species.

Succinea Draparnaud, 1801

Subgenus *Calcisuccinea* Pilsbry, 1948 (Pilsbry, 1948: 826, *pro sect.*; type species *Succinea campestris* Say, 1817 by original designation)

Localities and other data on specimens.
Portugal, Prov. Beira Litoral [Leiria dis-

trict]: Leiria, on exterior of north wall of Escola Secundária de Domingos

Table I. Measurements (mm) of shells of *Succinea* (subgenus *Calcisuccinea*) sp. from Spain and Portugal.

 Tabla I. Medidas (mm) de conchas de *Succinea* (subgénero *Calcisuccinea*) sp. de España y Portugal.

Locality	Sample no.		H	B	AH	B/H
Prov. Málaga: Mijas	10636	largest shell	13.3	8.7	9.0	0.65
Prov. Málaga: Benalmádena	11494	largest shell	9.9	6.6	6.3	0.67
Prov. Tarragona: El Vendrell	SQS leg.	largest shell	10.0	6.6	6.3	0.66
Estremadura: Porto de Mós	P207	largest shell	9.6	6.2	7.0	0.65
Beira Litoral: Leiria	P208	largest shell	13.6	8.3	9.8	0.61
	P208	next largest	11.0	7.4	8.0	0.67

Sequeira, Rua dos Mártires do Tarrafal, near the foot of the slope below the western side of the Castelo de Leiria (ca 39°44'48.2"N., 8°48'46.6"W.; 29SND19), leg. IM and RMCM, 24 Sept. 2011, 7 shells (collected alive) CRMCM; by Escola Secundária de Domingos Sequeira on Rua Mártires do Tarrafal, Leiria (29SND161/996), 94 m alt., and nearby on exterior of wall surrounding this school, leg. DTH, GAH, IM, MM and RMCM, 9 Oct. 2011, many shells and material in alcohol in CGAH (site P208), 1 shell CRMCM; 14 Apr. 2012, 61 specimens in alcohol, leg. RMCM, to be lodged at MNCN. Prov. Estremadura [Leiria district]: Porto de Mós, Parque Verde (ca 39°35'54.8"N., 8°49'14.0"W.; 29SND18), on wall surfaced with marble beside an artificial pool, leg. MM and RMCM, 24 Sept. 2011, 4 shells (collected alive) CRMCM; Parque Verde, at Porto de Mós (29SND15400/83182), 139 m alt., leg. GAH, DTH and RMCM, 9 Oct. 2011, shells and material in alcohol CGAH (site P207), 4 shells (collected alive) CRMCM.

Spain, Prov. Barcelona: Cubelles (31TCF86), in greenhouse, leg. SQS & RRJ, Aug. 2012, shells only, CSQS. Prov. Málaga: Benalmádena (30SUF6249), leg. Juan Antonio Salamanca, 65 shells in CJSTA (no. 11494); Cala de Mijas, Mijas (30SUF5041), leg. José Antonio Aranda, 5 shells in CJSTA (no. 10636); El Chaparral, Mijas (30SUF5242), living specimen observed and photographed by Katrina Roberts, 12 Mar. 2011. Prov. Tarragona:

El Vendrell (31TCF76), detritus in very humid site, 30 m alt., leg. SQS, Aug. 2011, material in alcohol, CGAH & CSQS; Altafulla, around River Gaià (31TCF65), 8 m alt., leg. SQS & RRJ, 11 Feb. 2013, shells only, CSQS.

Description and identification to subgenus. Representative shells are illustrated in Fig. 2. They resemble shells of European Succineidae in having few whorls (up to 3.5) and being thin, more or less translucent, with weak and rather irregular sculpture consisting mainly of growth lines. Fresh shells vary in colour from light yellowish or buff to pinkish tinged, but not as bright as the amber colour often present in European *Oxyloma* spp. The aperture is relatively large and the spire short, as in European *Succinea putris* (Linnaeus) and *Oxyloma*, but the overall shell shape is broader in proportion to its height (B/H 0.61-0.67 in the largest shells) in comparison to normal individuals of the European species. Measurements of the largest shells in each of our samples are given in Table I.

The snails at the two Portuguese localities and El Vendrell (Prov. Tarragona) mainly showed striking patterns of dark or dark and light coloration on external surfaces of the mantle. Many of the shells are translucent, so that the dark pattern on the body inside results in an appearance recalling that of *Radix* spp. (Lymnaeidae). This differs markedly from the appearance of all native Succineidae of western Europe, which

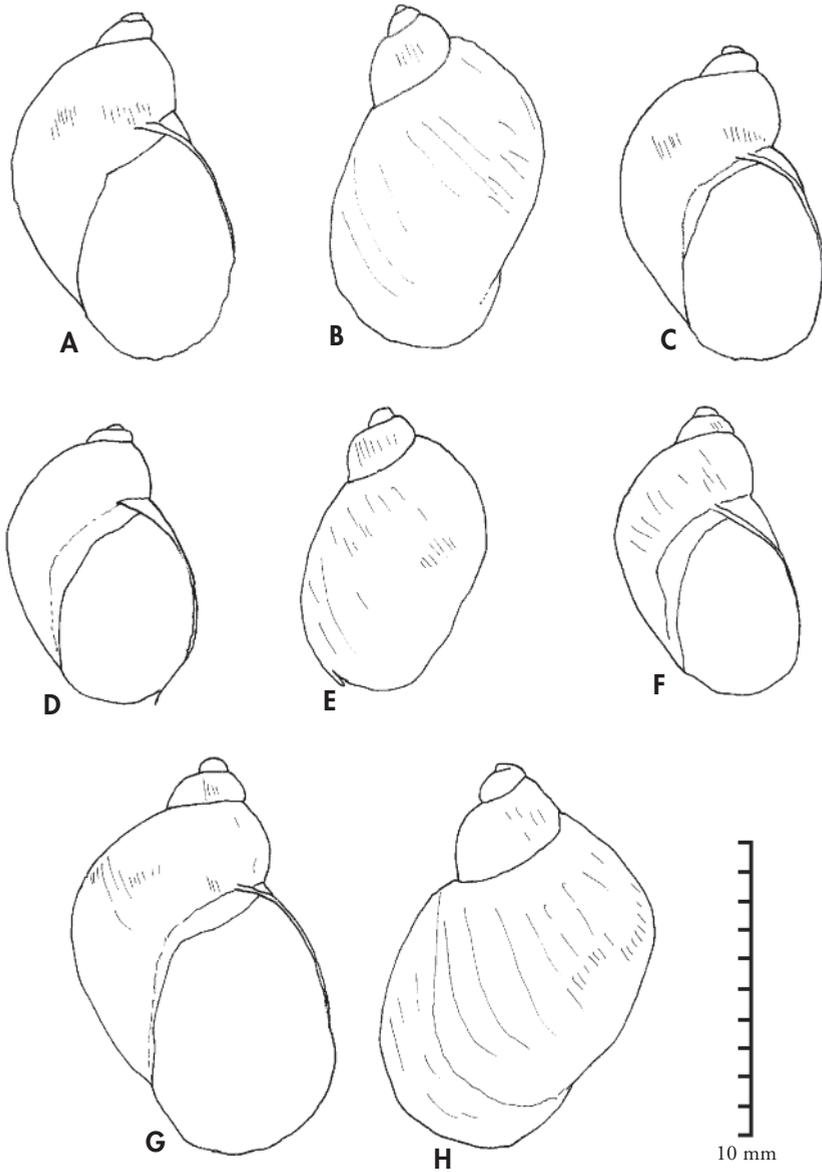


Figure 2. Shells of *Succinea* (*Calcsuccinea*) sp. A-C: Portugal, Prov. Beira Litoral, Leiria (CGAH site P208), A and B show apertural and abapertural views of same shell; D, E: Portugal, Prov. Estremadura: Porto de Mós (CGAH site P207), apertural and abapertural views of same shell; F: Spain, Prov. Málaga: Benalmádena (CJSTA no. 11494); G, H: Spain, Prov. Málaga: Cala de Mijas, Mijas (CJSTA no. 10636), apertural and abapertural views of same shell.

Figura 2. Conchas de Succinea (Calcsuccinea) sp. A-C: Portugal, Prov. Beira Litoral, Leiria (CGAH localidad P208), A y B muestran vistas frontal y dorsal de la misma concha; D, E: Portugal, Prov. Estremadura: Porto de Mós (CGAH localidad P207), vistas frontal y dorsal de la misma concha; F: España, Prov. Málaga: Benalmádena (CJSTA nº 11494); G, H: España, Prov. Málaga: Cala de Mijas, Mijas (CJSTA nº 10636), vistas frontal y dorsal de la misma concha.

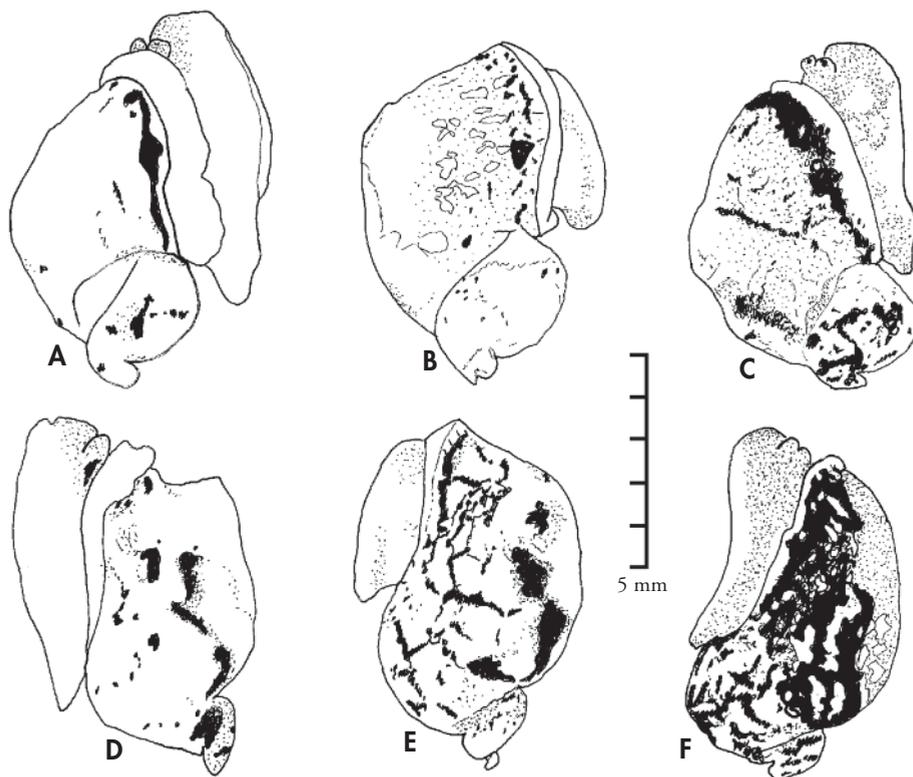


Figure 3. Drawings of colour patterns on bodies of *Succinea* (*Calcisuccinea*) sp. preserved in spirit from Portugal, Prov. Beira Litoral, Leiria (CGAH site P208). A/D, B/E and C/F show right and left sides of the body of three snails with light, medium and heavy pigmentation respectively.

Figura 3. Dibujos de los patrones de color en el animal de Succinea (Calcisuccinea) sp. conservados en alcohol de Portugal, Prov. Beira Litoral, Leiria (CGAH localidad P208). A/D, B/E y C/F muestran los lados derecho e izquierdo respectivamente de tres caracoles con pigmentación clara, media y fuerte.

have plain mantle coloration, varying from cream to grey or dark grey (due to tiny dots of black pigmentation), without any conspicuous darker or paler markings. As shown in Fig. 3, the dark patterns on our *Succinea* (*Calcisuccinea*) varied widely between individuals at the same site. The least pigmented snails had almost no markings on their whitish, pale cream or pale grey mantles; others had a few blackish lines and scattered blackish and grey spots and blotches (Figs. 3 A/D). More heavily marked individuals had whitish blotches and spots and black blotches, lines and spots, the black marks often forming a

reticulate pattern (Figs. 3 B/E). Dark individuals had large areas of black and grey on the mantle, the black often forming bold irregular lines and contrasting sharply with adjacent whitish markings (Figs. 3 C/F). It seems likely that the markings on the mantle tend to conceal resting snails on natural substrata, but they are ineffective for this on smooth marble and white-painted masonry of walls. Parts of the body that extend outside the shell lack striking markings, the foot being consistently pale, whereas dorsal areas of the exposed body vary from pale to dark grey, often darkest on the top of the head and tail.

The genital anatomy has been studied in six specimens from Portugal (all \pm mature) and two from El Vendrell in Prov. Tarragona (one immature, one nearly mature). It was similar in mature individuals from both the Leiria and Porto de Mós localities (Fig. 4) and the nearly mature specimen from Prov. Tarragona. Characters of genus *Succinea sensu lato* were present as follows: right ommatophore passing through angle between penis and oviduct; penis a simple tube, provided with a sheath and passing proximally into an epiphallus, lacking any appendix at proximal end; vas deferens slender. Characters of subgenus *Calcisuccinea* (as described by PILSBRY, 1948: 826 and SCHILEYKO, 2007: 2084) present were as follows: penis slender with ample sheath, from which the epiphallus emerges; the junction of the vas deferens with the epiphallus enveloped in the distal part of the penial retractor muscle, which is also attached to the proximal end of the penis sheath, so that the epiphallus is held in an almost closed loop; duct of bursa copulatrix slender almost throughout its length; free oviduct not coiled around proximal part of duct of bursa copulatrix; vagina very short or absent.

Subgenus *Novisuccinea* Pilsbry, 1948 is similar in having the epiphallus forming a loop free from the penis sheath with the distal end of the penial retractor muscle attached to the proximal end of the penis sheath. Furthermore, its type species *Succinea ovalis* Say, 1817 also has very similar shell shape and dark mantle pigmentation to our Iberian material (PILSBRY, 1948: 800-806). Nevertheless, *S. ovalis* and other taxa in subgenus *Novisuccinea* show clear anatomical differences from our Iberian specimens in having a long vagina and the duct of the bursa copulatrix very wide at its distal end and tapering gradually to the proximal end, with the coiled oviduct wrapped around the proximal part (PILSBRY, 1948; FRANZEN, 1959; HOAGLAND AND DAVIS, 1987).

Difficulties in species identification. PILSBRY (1948) referred only three taxa comprising two species without doubt

to his Section *Calcisuccinea*, which he regarded as "a subdivision of *Novisuccinea*": *S. campestris* Say, 1817 (type-species of the Section and now of the subgenus; ranging from North Carolina to Florida), *S. luteola* Gould, 1848 (ranging from Louisiana to Arizona and widespread in Mexico) and *S. luteola floridana* Pilsbry, 1905, possibly a distinct species (from Florida and Alabama). More detailed anatomical studies by FRANZEN (1971) later confirmed that *S. vaginacontorta* Lee, 1951 from Kansas is also a *Calcisuccinea*, bringing the total number of species confirmed for the subgenus to three, or four if *floridana* is distinct from *S. luteola*. SCHILEYKO (2007: 2085) gave the distribution as N. America with "8 spp.", but the basis for this total is unclear unless it includes taxa with differing anatomy (*S. concordialis* Gould, 1848; *S. avara* Say, 1824) or undescribed anatomy (*S. gabbi* Tryon, 1866; *S. californica* Fischer and Crosse, 1878; *S. oregonensis* Lea, 1841).

The three well understood North American species of *Succinea* (*Calcisuccinea*) appear to differ from the Iberian specimens in features of the genital anatomy and most also differ in shell characters (cf. PILSBRY, 1948; FRANZEN, 1971). *S. campestris* has a similarly wide, globose shell, but the penis is shorter and wider, the wall of the penis sheath much thicker, and the loop of the epiphallus is much smaller relative to the penis length (less than one-third: PILSBRY, 1948: 829; SCHILEYKO, 2007: 2085). *S. luteola* and *S. luteola floridana* have a somewhat longer penis and thinner-walled penis sheath, but this and the other North American species again differ in having the epiphallus loop shorter in proportion to penis length. With the possible exception of a few *S. l. floridana*, they also differ in having relatively much taller shells with more whorls in the spire. Furthermore, none of the *Calcisuccinea* species is reported as showing a distinctive dark colour pattern on the mantle except for *S. concordialis* which has markedly different penial anatomy, so that its subgeneric allocation is questionable (PILSBRY, 1948: 826, 829, 835).

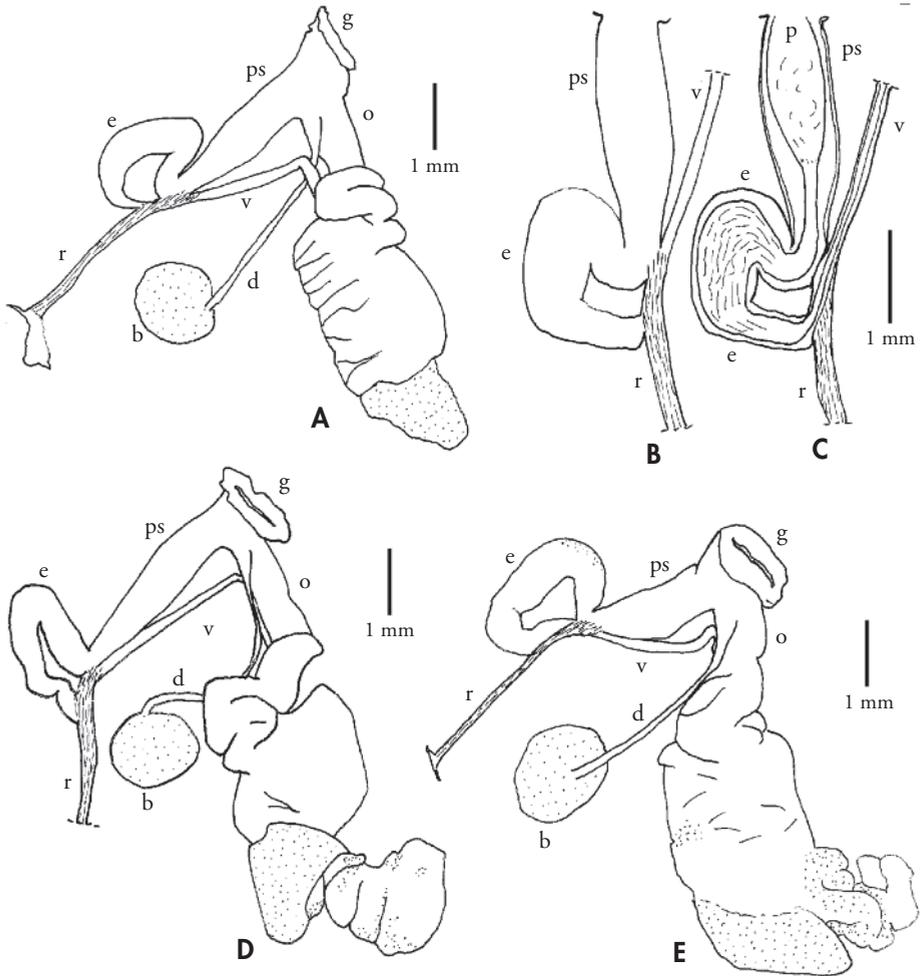


Figure 4. Genital anatomy of *Succinea* (*Calcsuccinea*) sp. from Portugal. A-C and D: two individuals from Prov. Beira Litoral, Leiria (CGAH site P208); E: from Prov. Estremadura: Porto de Mós (CGAH site P207); B and C show details of the penial complex in the same specimen as drawing A, at a larger scale, from the exterior in B, in cross-section in C; b: bursa copulatrix; d: duct of bursa copulatrix; e: epiphallus; g: opening of genital orifice; o: free oviduct; p: penis; ps: penis sheath; r: penis retractor muscle; v: vas deferens.

Figura 4. Anatomía genital de *Succinea* (*Calcsuccinea*) sp. de Portugal. A-C y D: dos individuos de Prov. Beira Litoral, Leiria (CGAH localidad P208); E: de Prov. Estremadura: Porto de Mós (CGAH localidad P207); B y C muestran detalles del complejo penial en el mismo espécimen. A, a mayor escala, desde el exterior en B, en sección cruzada en C; b: bolsa copulatrix; d: conducto de la bolsa copulatrix; e: epifalo; g: abertura del orificio genital; o: oviducto libre; p: pene; ps: vaina del pene; r: músculo retractor del pene; v: vaso deferente.

The genital anatomy thus apparently remains undescribed for several N. American *Succinea* (see above) that

might belong in subgenus *Calcsuccinea*. Indeed, the comments by PATTERSON (1971: 183) still remain true, that: "There

are a great many succineid species in North America and especially in the southern United States. Most of these species have not been critically examined with regard to reproductive anatomy (especially the forms from the western United States), and until this is done it is premature to classify the North American *Succinea* species into sections or subgenera."

The same applies to numerous other nominal taxa named as *Succinea* species from the West Indies (e.g. *S. dominicensis* L. Pfeiffer, 1851, from Haiti) and Central America (e.g. *Succinea recisa* Morelet, 1851 named from a type locality in eastern Guatemala, *S. costaricana* von Martens, 1898 named from Costa Rica). *S. recisa* was reported from as far south as Panama by VON MARTENS (1890-1901: 339), who described it as distinct from the other Central American Succineidae species in its very short spire. Nevertheless, PÉREZ & LÓPEZ (2003: 420-421) noted that *S. recisa* in western Nicaragua may approach *S. costaricana* in shell form although they are "perfectamente diferenciables desde el punto de vista anatómico", but they did not describe or figure the anatomy of either species.

The Iberian populations resemble *S. costaricana* in having a broadly ovate shell, of similar size at 8-13.5 mm high, with spire and aperture similar in shape to those of that species (VON MARTENS, 1890-1901: 338, pl. 19 figs 6; VILLALOBOS AND MONGE-NÁJERA, 2004; cf. our Table I), and also in having dark markings on the mantle (VILLALOBOS, MONGE-NÁJERA, BARRIENTOS AND FRANCO, 1995). The latter authors also reported this "tropical agricultural pest" species as living at high density (282,900 individuals/ha) away from water, on an ornamental plant farm in Costa Rica which grew mainly *Dracaena* spp. Although F.G. Thompson is thanked for corroborating their species identification, it nevertheless seems uncertain that *S. costaricana* is the correct name for the species involved. Other Central American *Succinea* with older names have shells of generally similar form, notably *S. undulata* Say, 1829, *S. guatemalensis*

Morelet, 1849, *S. virgata* von Martens, 1868 and *S. pueblensis* Fischer and Crosse, 1877. Secure identification of the Costa Rican snails would therefore need to exclude all these taxa with earlier names through detailed studies, including studies of the genital anatomy, which have not been reported in the literature.

The website of the GEORGIA INVASIVE SPECIES TASK FORCE ("2006") lists *Succinea dominicensis* and *Calcisuccinea dominicensis* (Pfeiffer), noting that "These Mollusks have recently been determined to be "actionable" snails. They have been known to arrive in the United States from Haiti and the Dominican Republic. Inspectors should watch for these snails when inspecting any agricultural items from these countries." [They] "can reproduce rapidly in a greenhouse or nursery, resulting in severe losses. They can also become established outdoors where temperatures and humidity are favorable. Their introduction is a significant threat to the US fruit and horticultural plant industries." Identification notes add that they "closely resemble another "actionable" snail, *Succinea costaricana* have a thicker shell than most other *Succinea* spp., they are usually light to pale brown in color, and tend to have a somewhat whitish cast to the shell. Their length is approximately 1 cm ... or smaller." It is unclear why this taxon is placed in *Calcisuccinea*, but unpublished anatomical studies perhaps lie behind it. The original description (PFEIFFER, 1851: 147) is of an oval, solid shell of 3½ whorls, 11.5 mm long, 7 mm wide, with aperture 7.5 mm long, from St. Domingo [Haiti] collected by Sallé. The description could apply to our Iberian shells, but also to various other species of Succineidae with broad shells. It is unclear that *S. dominicensis* is a valid species in the apparent absence of detailed published studies, particularly the lack of data on its genital anatomy. Admittedly most *Succinea* from the West Indies were described after 1851, but *S. sagra* d'Orbigny, 1842, is an older name, as are those of two of the Central American taxa listed above.

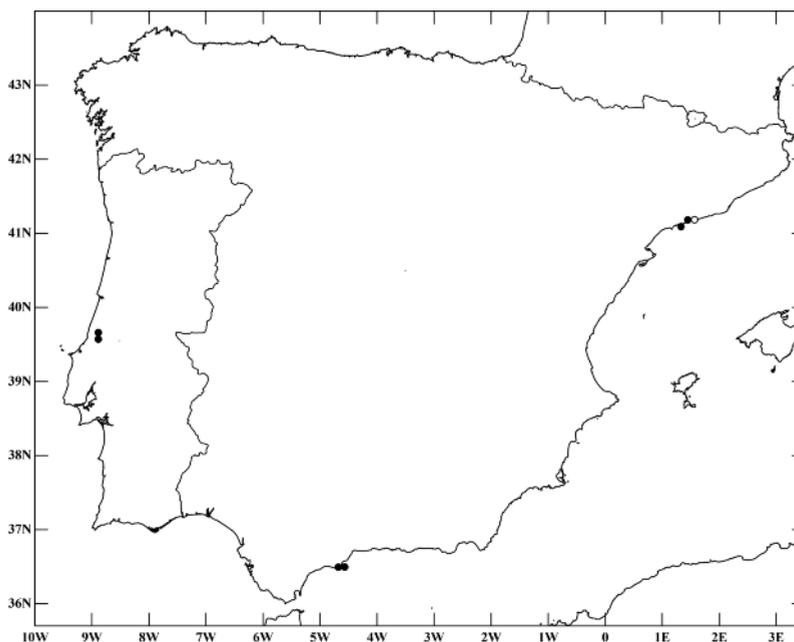


Figure 5. Localities at which *Succinea* (*Calcisuccinea*) sp. has been found in Spain and Portugal, plotted in ten-kilometre squares of the U.T.M. Grid. An open symbol represents a record from a greenhouse; closed symbols represent sites in the open air.

Figura 5. Localidades en las que Succinea (Calcisuccinea) sp. ha sido hallada en España y Portugal, situadas en cuadrados de diez kilómetros dentro de la cuadrícula U.T.M. Un símbolo vacío representa un registro de invernadero; los símbolos sólidos representan localidades al aire libre.

The specific identity of the Iberian material is thus an unsolved problem at present. It is likely to remain unclear until the taxonomy and especially the genital anatomy of Succineidae from Central America, the West Indies and the south-western U.S.A. is studied in more detail.

Habitats and behaviour. At the Leiria locality the snails were aestivating or resting singly on masonry (mostly painted white) of modern walls up to 2 m above ground level, along several hundred metres of the boundary around grounds of a school. The adjoining garden was sparsely planted with bushes and herbs and only a few trees were present. There was no standing water, ditch, or other aquatic habitat. At Porto de Mós it was found in a small area in an open, grassy, public park that

had been created within the past few years. Some snails were resting or aestivating on vertical marble surfaces of walls, up to 2.5 m above the ground; others were resting in wet grasses at the base of this wall. This part of the site lacked any persistent standing water, although a shallow hollow at the foot of the wall may flood after rain and an artificial pond is not far away. A ditch containing a small diverted stream was present about 30 metres away, but the only succineid found there was *Oxyloma elegans*.

In Prov. Málaga, empty shells were found in a dry ravine between gardens of a residential area. The other two populations there were found in gardens, among dry litter. The only living specimen found was active after rain. In Prov. Barcelona shells were found in a green-

house; in Prov. Tarragona it was found living in detritus at a humid locality and as dead shells near a river.

The habitats at both the Portuguese and Prov. Málaga sites were therefore much drier than those normally occupied by any of the native west European Succineidae. These habitats were also greatly disturbed by man, at least four of the five sites having only planted vegetation in heavily managed situations. As noted above, a species of Succineidae is regarded as an agricultural pest in Costa Rica and several species of the family are at least potential pests in Georgia, U.S.A. It remains to be seen whether the taxon that has become established in Portugal and Spain will prove troublesome. Our records of its occurrence here at eight localities up to >800 km apart (Fig. 5) must hint at many more populations as yet unfound having become established, so that it is almost certainly too late to eradicate it.

ACKNOWLEDGEMENTS

Thanks are due to José Antonio Aranda and Juan Antonio Salamanca for informing JSTA of the populations they discovered near Málaga and for passing on specimens and to Katrina Roberts for photographs and data. Ramon Ruiz Jarillo helped SQS to find specimens in

Prov. Barcelona and Prov. Tarragona. Inês and Maricris Mendes gave skilful help in finding specimens. Fig. 5 was prepared using the DMAP software written by Dr A.J. Morton. Two referees are also thanked for their helpful comments.

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