

# A REVIEW OF THE GENUS *CANDIDULA* IN PORTUGAL WITH NOTES ON OTHER POPULATIONS IN WESTERN EUROPE (GASTROPODA, PULMONATA: HYGROMIIDAE)

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**Abstract** Portuguese populations of *Candidula* are reviewed using studies of shells and genital anatomy, based on extensive new collections. 12 species of the genus are recognised, 3 of which are newly described. *C. intersecta* has often been reported from Portugal, but there are only two confirmed records of established populations, from near Lisbon where it may have been introduced. Other Portuguese material hitherto placed as that species is mostly referable to the cryptic species *C. olisippensis* or *C. belemensis*, both of which differ from *C. intersecta* in having a much longer penial flagellum. *C. olisippensis* occurs widely in W. and C. Portugal northwards from near Lisbon; it is also newly reported here from NW. Spain, SW. England (Lizard peninsula in Cornwall) and the Azores. *C. belemensis* from WC. Portugal is very close to *C. olisippensis* in morphology, although usually larger. They are treated as separate species because they coexist extensively on Serra de Sicó and locally on Monte de Vez. The type locality of *C. belemensis* is restricted here. *C. ponsulensis* sp. nov. from EC. Portugal, is another cryptic species very close to *C. intersecta* in both shell characters and genital anatomy. The widespread *C. gigaxii* is very local in Portugal, with confirmed recent records only from eastern Alentejo, although subfossil shells have been found in the Algarve. The other species recognised are mainly localised endemics of rocky limestone habitats in Portugal, including two species with sharply keeled shells (*C. coudensis* in S. Beira Litoral; *C. setubalensis* in the Serra da Arrábida and near Cabo Espichel) and four with rounded shells (*C. arrabidensis* sp. nov. in the Serra da Arrábida and near Cabo Espichel; *C. codia* and *C. scabiosula* in the C. Algarve; *C. strucki* in the W. Algarve and locally on sand dunes in W. Baixo Alentejo). In addition, *C. carrapateirensis* sp. nov. is endemic on calcareous coastal sand dunes in the W. Algarve and W. Baixo Alentejo.

**Key words** *Candidula*, Hygromiidae, taxonomy, new species, genital anatomy, Cornwall, France, Portugal, Spain, habitats, distribution

## INTRODUCTION

The land-snail genus *Candidula* Kobelt 1871 has about 24 currently recognised species ranging from the eastern Canary Islands to the Balkans and northwards to Scotland and southernmost Sweden. In western and southern Europe the genus is widespread in open habitats such as rocky limestone areas, sand dunes and semi-natural grasslands. It is distinguishable from other "helicellids" by a combination of characters, among which the presence of a single large dart sac arising from the vagina is especially important (Hausdorf, 1988, 1991; Alonso, Ibañez & Henríquez, 1996; Schileyko, 2005: 1982). The "helicellids" (*Candidula*, *Helicella* A. Férussac 1821, and allied genera) are regarded as a polyphyletic assemblage and placed in the Hygromiidae subfamily Hygromiinae in current European lists, although regarded as a monophyletic group and maintained as the subfamily Helicellinae by Hausdorf & Sauer (2009: 374).

Several western European species of *Candidula* show great variability in shell characters, both

within and between populations, leading nineteenth century authors such as J.-R. Bourguignat (Bibliography: 1891) and A. Locard (1894, 1899) and others of the "Nouvelle École" (cf. Dance, 1970, 1986) to "split" them into many nominal species of dubious validity. During the twentieth century most of these superfluous taxa were reduced to synonyms, e.g. by Kennard & Woodward (1926) in Great Britain, Germain (1930) in France and Nobre (1941) in Portugal. However, occurrence within the genus of apparently valid species that coexist but show only subtle differences in shell characters and little or none in genital anatomy had also been recognised long ago, notably with *C. intersecta* (Poiret 1801) (as *Helicella caperata* (Montagu)) and *C. gigaxii* (L. Pfeiffer 1847) (as *Helicella heripensis* (Mabille)) by Stelfox (1912) and Boycott & Jackson (1914).

Gittenberger (1993a) reviewed the *Candidula* species known in Portugal and proposed that several forgotten names placed in synonymy by Nobre (1941) may represent conchologically rather similar but valid species. His seminal study was based mainly on old shell specimens, with scanty anatomical material that did not

represent some of the species. Nevertheless, his perceptive recognition of “cryptic” Portuguese species such as *C. olisippensis* and *C. belemensis* can now be confirmed.

The present study is based on large new collections from many localities (see Appendix). Most of this material was collected by us from 2009–2014 after we moved to live in central Portugal. Discovery of an undescribed species with a sharply keeled shell (*C. coudensis* G.A. Holyoak & D.T. Holyoak 2010) encouraged us to amass and study population samples of other, less distinctive looking *Candidula*, including spirit material. Other large collections made in Portugal by Álvaro de Oliveira and Rui da Costa Mendes were also made available to us, and J. Sebastián Torres Alba provided comparative specimens from S. Spain. This material has allowed study of the genital anatomy of all of the more distinctive looking populations and analysis of variability in shell and anatomical characters of most of them. Unfortunately though, few anatomical characters vary between the species, the length of the penial flagellum being the main taxonomically useful feature. Nevertheless, data on flagellum length added to shell characters and distributional data allow some of Gittenberger’s (1993a) conclusions to be confirmed or extended, as well as implying several additional local species require new names. These results are described in this paper.

Pfenninger, Epstein & Magnin (2003) presented mitochondrial DNA sequence data demonstrating that *C. olisippensis* (Servain 1880) from Portugal represents a different clade to the conchologically rather similar *C. intersecta* and the somewhat less similar *C. gigaxii*, but the Portuguese taxa have not received any further molecular study. It is to be hoped that in future a more refined modern study will integrate our data based on traditional techniques with much fuller molecular data.

## METHODS

Fieldwork targeting *Candidula* was carried out during 2009–2014 on visits to Cornwall, Brittany, N. Spain (Prov. Logrono to Galicia), W. Spain (mainly in Prov. Cáceres and Prov. Zamora) and widely in mainland Portugal. Localities and altitudes were recorded using hand-held GPS, from 2009 onwards a Garmin Etrex High Sensitivity GPS, accurate to within <10 m; map references are

based on the U.T.M. grid. Sites were given consecutive serial numbers (e.g. 2009.P21). Habitat notes (including bedrock type and vegetation) and associated Mollusca were also recorded at all sites.

Shells, external features of the body and the genital anatomy were studied using Meiji RZ series stereo-microscopes. Shell growth appears to be indeterminate, since it may continue after a white rib develops inside the peristome. Measurements were therefore made from samples of the larger shells collected from each locality which possessed a firm rather than membranous mouth edge and often a white rib inside the mouth. This approach does not allow calculation of population means and standard deviations, since the proportion of subadults (with distal genitalia not fully mature) among those selected for measuring will be unknown and probably vary between localities. Measurements of shell breadth and height and counts of whorls followed the methods illustrated by Kerney & Cameron (1979: 13); umbilicus width was taken as the maximum width across the umbilicus inside the body-whorl. Measurements of whole shells were made with an eyepiece graticule. Those of shell hairs were made using Infinity Analyze© software on images taken with an Infinity 1 camera on a Meiji RZ series stereo-microscope, these measurements being reproducible to  $\pm 2 \mu\text{m}$ .

Mature living specimens for anatomical study were deliberately sought during field work. Regular monthly observations by Baker (1968) showed that populations of *C. intersecta* in SW. England laid eggs in November–December in some years and early summer in others, the timing apparently varying according to rainfall and moisture balance. Although our observations on *Candidula* in Portugal were less regular and systematic, it was also clear that the seasonal timing of reproduction varied widely from year to year and to some extent between localities, with immature snails usually making up a majority of any population we sampled. When only subadult snails were found, a few of the largest were usually kept alive at home (for up to several months) until their shells matured. However, samples of individuals with shells that appeared fully mature sometimes had immature genitalia, so that repeated collections or rearing became necessary to obtain reproductively mature specimens for description.

Specimens for dissection were drowned in water for 12–20 hours, then kept in 80% industrial methylated spirit, the body being partly or wholly pulled from the shell after one or two days. The genitalia were examined while *in situ* in the dissected body or they were removed for description and drawing. Drawings of the distal genital anatomy were prepared using a Meiji drawing tube or by freehand drawing with a standardised arrangement of organs, usually assisted by measurements and use of the drawing tube. In descriptions of the genital anatomy, proximal and distal refer to the position in relation to the ovotestis.

The specimens studied are listed in the Appendix, where abbreviations e.g. of collectors and collections are defined. The legend to Fig. 4 gives additional abbreviations for parts of the distal genitalia. Other abbreviations used in the text are as follows: B: breadth of shell; H: height of shell; n: number (sample size); MHNG: Muséum d'Histoire Naturelle, Ville de Genève, Switzerland; MNHN: Muséum National d'Histoire Naturelle, Paris, France; MZUC: Museu de História Natural da Faculdade de Ciências da Universidade de Coimbra, Portugal; NMW.Z: National Museum of Wales, Cardiff, U.K.; RMNH: Netherlands Centre for Biodiversity Naturalis, Leiden, The Netherlands; U: maximum width of umbilicus of shell; U.T.M.: Universal Transverse Mercator map grid.

#### TAXONOMY, DESCRIPTIONS AND DISTRIBUTION

Family Hygromiidae Tryon 1866 (p. 55,  
Helicidae subfam.)

Subfamily Hygromiinae Tryon 1866

Tribe Helicellini Ihering 1909 (p. 429, pro subfam.)

Genus *Candidula* Kobelt 1871 (p. 22, as  
*Xerophila* sect.)

(Type species: *Glischrus candidula* Studer 1820,  
by absolute tautonymy)

Syn. *Xerovaga* Monterosato 1892 (p. 22). Type species: *Helix caperata* Montagu 1803, by subsequent designation of Kobelt (1892).

*Xerotringa* Monterosato 1892 (p. 22). Type species: *Helix tringa* Fagot 1884, by subsequent designation of Kobelt (1892).

*Xeroplexa* Monterosato 1892 (p. 23). Type species: *Helix setubalensis* L. Pfeiffer 1850, by subsequent designation of Kobelt (1892) (syn. *vide* Gittenberger, 1985: 59).

*Xeroalbina* Monterosato 1892 (p. 23). Type species: *Glischrus (Helix) candidula* Studer 1820, by subsequent designation of Kobelt (1892).

*Xerocodia* Monterosato 1892 (p. 23). Type species: *Helix codia* Bourguignat 1859, by subsequent designation of Kobelt (1892).

*Xerogyra* Monterosato 1892 (p. 24). Type species: *Helix spadae* Calcara 1845, by subsequent designation of Kobelt (1892).

*Etymology* Kennard & Woodward (1926: 218) stated that *Candidula* is "Lat. dimin. of *candidus*, white". Although this interpretation of the meaning of the name is presumably correct, it appears that the species epithet from *Glischrus candidula* Studer 1820 was adopted tautonymously as a sectional name by Kobelt (1871: 22), then raised to genus rank by later authors. The generic name *Candidula* has been treated by subsequent authors as a feminine noun.

*Generic characters* This section mainly describes features that appear to be common to all of the Portuguese species studied and which are therefore not described separately under the species headings. Some Spanish species of *Helicella* are virtually indistinguishable from *Candidula* on shell characters alone, but immediately separable when the genital anatomy is examined by the paired dart sacs of the former genus.

*Shell characters* Shell dextral, with 4.7–6.5 whorls when mature, variably convex above with low to high spire giving shell shape ranging from nearly discoid to conical or globular but commonly ± flattened below. Two species have shells with a sharp peripheral keel, the others have the body whorl of adult shells with a rounded periphery although juvenile shells have a slight to rather strong keel above the periphery. Whorls of spire thus vary from slightly convex with very shallow sutures to strongly convex with ± deep sutures. The umbilicus is open, exposing much of the spire, rather narrow and nearly symmetrical to moderately wide and eccentric because of more rapid expansion of the body whorl. The aperture is medium-sized for Hygromiidae, round or broadly ovate except where interrupted by

the penultimate whorl, with the body whorl expanding rather evenly and usually descending at least slightly near the mouth. The mouth edge is thin,  $\pm$  strongly reflected below to overlap the umbilicus, not reflected outwards and upwards. The inside of the mouth typically has a white rib set back from the palatal and columellar edges of the peristome, which develops when growth of subadults is interrupted and at maturity. The shell is usually of moderate thickness and well calcified, weakly translucent to opaque when mature, although in calcium-poor localities it is sometimes thinner and more fragile.

Shell colour is usually variable within and between populations, apparently involving complex polymorphisms. The ground colour commonly varies from white to light brown (often tinged yellowish or reddish), most often with several much darker blackish or brown spiral bands that form variable patterns, sometimes interrupted or blotched, sometimes fused (occasionally covering almost whole shell, to give blackish or dark brown coloration). The periostracum is glossy on fresh shells.

Two superimposed types of shell sculpture are usually present on all but the apical whorls. These types are named and described in detail here, so that notes in the descriptions of individual species are restricted mainly to features that vary interspecifically. The sculpture was examined on the body whorl, using clean fresh shells. (1) Transverse ribs, consisting of rather irregularly spaced ridges or ribs, varying in amplitude, arising parallel to the peristome edge, apparently recording alternating intervals of shell growth and inactivity ("growth lines"). (2) Spiral lines, are the finest sculpture seen, consisting of incised parallel grooves and present in all the species covered here, most easily visible on the underside of the body whorl just outside the aperture, where other sculpture is weak or lacking. In addition, (3) inconspicuous papillose microsculpture is often present in the umbilicus, and (4) Shell hairs are mainly lacking in the species covered in this paper, but present even in mature individuals of some Spanish *Candidula* species such as *C. arganica* (Servain 1880) (Ortiz de Zárate y López, 1950: 27–28). Among Portuguese species, they were detected only on juvenile shells of *C. codia* (Bourguignat 1859) (*q.v.*), where they are very short and were hitherto overlooked. On young shells the protoconch (apical semi-circle plus

whorl 0–0.5) is mainly smooth; transverse ribs start weakly from around whorl 0.5 onwards.

*External features of body* In the species dealt with here, the external structure and coloration of the body (Fig. 1) are similar to those of many other Hygromiidae. In pale-bodied individuals the forepart of the body is pale grey, grey, dark-grey, or grey-brown above, sometimes with a yellowish or rufous tinge, the eyes showing as black spots near the tip of the ommatophores and the retractor muscles of both pairs of tentacles  $\pm$  obvious as darker bands visible by translucence. The lower sides of the body, foot-fringe and sole of foot are normally paler than the dorsum, light greyish or brownish or almost white. The mantle is whitish, often with blackish markings of variable extent, the mantle-collar often wholly blackish. In dark-bodied individuals the foreparts of the body may be entirely blackish or dark-grey, or the tubercles may be tinged or edged with yellowish or rufous. The lower sides of the body, foot-fringe and sole of foot are normally lighter than the dorsum. The mantle may be all-black. Body coloration often varies within species, both individually and between populations, so it provides few if any useful identification characters. Different populations of *C. olisippensis* (Servain 1880) have the exposed parts of the body pale to blackish (Figs 1C, D) and similar variability sometimes occurs within a single population in *C. gigaxii* in Portugal. It may be significant, however, that the two species with keeled shells differ markedly in body colour: very pale in *C. setubalensis* (L. Pfeiffer 1850) (Fig. 1A), blackish in *C. coudensis* (Fig. 1F).

*Genital anatomy* Besides providing an overview for all W. European species of the genus, and defining the terminology used, this section mainly describes the many features which appear to be common to all species studied and which are therefore not described separately under the species headings. The species accounts thus concentrate on the few features that differ among the species, which have been studied only in the distal genitalia, especially the relative length of the penial flagellum.

The general structure of the genitalia is of semidiaulic monotrematic type. The gonad (ovotestis) is large and branched, giving rise to a long winding hermaphroditic duct functioning as a seminal



**Figure 1** Living *Candidula* species from Portugal: **A** *C. setubalensis*, Estremadura, Serra da Arrábida, site 2010.P29, photographed 2010.06.04 (collected 2010.04.12 and grown on in captivity); **B** *C. ponsulensis*, Beira Baixa, W. bank of Rio Ponsul W. of Ladoeiro, site 2010.P35, photographed 2010.06.05 (collected 2010.04.20 and grown on in captivity); **C** *C. olisippensis*, Beira Baixa, W. edge of Sertã, site 2010.P31, photographed 2010.06.05 (collected 2010.04.15–18 and grown on in captivity); **D** *C. olisippensis*, Beira Litoral, Praia da Tocha, site 2010.P83, 2010.11.18; **E** *C. codia*, Algarve, ca 2 km E. of Santa Barbara de Nexe, site 2011.P117, resting on underside of limestone boulder; **F** *C. coudensis*, Beira Litoral, Vale da Couda SE. of Almoster, site 2009.P19, photographed 2010.01.15 (collected 2009.12.12 and grown on in captivity).

vesicle, which ends in a small talon. The albumen gland is large and long; from its base arises the spermoviduct (second hermaphroditic duct), consisting of a female channel (with a seminal groove) and prostate gland fused to define a single lumen. The vas deferens is long and slender, following the sperm groove in the prostate gland of the spermoviduct, passing in a loop between the vagina and the penial complex, ending in the penial complex level with the point where flagellum enters epiphallus.

A penial flagellum of variable length is present (0.2–2.0×length of epiphallus). A well developed muscular epiphallus longer than the penis (mainly 1.3–2.0×penis length) connects the proximal end of the penis with the flagellum/vas deferens junction; the lumen of the epiphallus has three longitudinal ridges. The penial retractor muscle inserts near the distal end of the epiphallus, the other end being attached to the diaphragm. The penis in fully mature snails generally has the proximal part wider than the distal part. The proximal penis is ovoid (less often subcylindrical or subspherical), comprising a rather thin-walled sac or sheath, containing a muscular verge extruded from the body during mating. The subcylindrical verge tapers distally to a blunt point and possesses a slit-like pore at its distal end; its outer wall appears to be formed by invagination of the penis sheath, the inner wall by a thickened continuation of the inner epiphallus wall. The distal part of the penis is a narrower cylinder of variable length, joining the genital atrium distally. At maturity the junction of the proximal end of the penis and distal end of the epiphallus is defined by widening; internally this junction lies just proximal to the proximal end of the verge (i.e. the point where the sheath of the proximal penis separates internally from the verge).

The genital atrium is a short to very short cylinder, dividing proximally into the distal end of the penis and the distal end of the vagina. The vagina is shorter to somewhat longer than the penis, cylindrical distally, wider and subcylindrical to ovoid and often flattened proximally, with more or less muscular walls. The vagina passes proximally into the free oviduct, the transition being defined as the point where the distal end of the bursa copulatrix duct inserts. A single large oval muscular dart sac (“stylophore”; containing a slightly curved calcareous dart, which

is cylindrical in cross section with two very narrow wings on opposite sides) is attached to the outer side of the vagina for most of its length, only the proximal  $\frac{1}{4}$ – $\frac{1}{2}$  being free and tapering to a blunt point. The distal end of the dart sac enters the vagina in a conical papilla. A small concealed accessory sac (lacking a dart) is present between the dart sac and the vagina. Mucus glands (“digitiform glands”) arise around upper end of vagina just distal to separation of free oviduct. The mucus glands arise in 2–5 groups, forking at or near base into 1–3 (occasionally 5) branches, to give overall total of 5–11 branches. The branches, widen above narrowed base, remain ± narrowly cylindrical for most of their length, but often somewhat thickened near tip, subequal, normally ± convoluted, folded or contorted *in situ*.

The free oviduct is a very short to moderately short tube, generally shorter than the vagina. The bursa copulatrix (gametolytic gland) is a thin-walled sac, subspherical, ovate or subcylindrical with a bluntly pointed proximal apex, closely attached to the middle part of the spermoviduct. The bursa copulatrix duct is of only short to medium length for Hygromiidae, typically cylindrical and of moderate width throughout most of its length, widening ± progressively into the bursa at the proximal end, sometimes narrow at the distal end, but often as wide as free oviduct or wider. Remains of a spermatophore extracted from bursa and its duct are described for *C. arrabidensis* sp. nov. The right ommatophore passes free of the distal genitalia, not between penis and vagina as in some other genera of Hygromiidae.

*Arrangement of species accounts* We recognise 12 Portuguese species in the genus on the basis of genital anatomy and shell characters. The information available is insufficient to arrange the species in a natural or phylogenetic classification. Hence, to simplify presentation of information and discussion, we deal with the Portuguese taxa in an alphabetical sequence.

The species accounts avoid giving lengthy descriptions because only a few characters appear to be useful in distinguishing the species. The emphasis is therefore on diagnostic characters, mainly presented as comparisons with *C. intersecta* which is the commonest and most familiar species in NW. Europe as well as being the taxon with the oldest valid name among those

dealt with here. Nevertheless, besides this comparative diagnosis, somewhat fuller accounts are given for the three newly described species. The diagnostic characters of all Portuguese species are also summarised in a bipartite Key that follows the species descriptions. A summary of information on habitats of each species is presented and discussed following the Key.

*Candidula arrabidensis* G.A. Holyoak & D.T.

Holyoak sp. nov.

Figs 2A, 4A, B, 6A, 8

*Types* Holotype (Fig. 2A): Serra da Arrábida, 29S 05020/42602, N.- and S.-facing rocky limestone slopes with patches of scrub, 388 m alt., 2011.02.12, GAH & DTH, 2011.P129, NHMUK 20140013/1 (1 sh, breadth 10.2 mm) & 20140013/2 (bod). Paratypes in CGAH (listed in Appendix): 115 sh, 14 bod, 31 spm, from Serra da Arrábida; 45 sh and 3 bod from two localities near Cabo Espichel.

*Type-locality* Serra da Arrábida (Estremadura, Portugal).

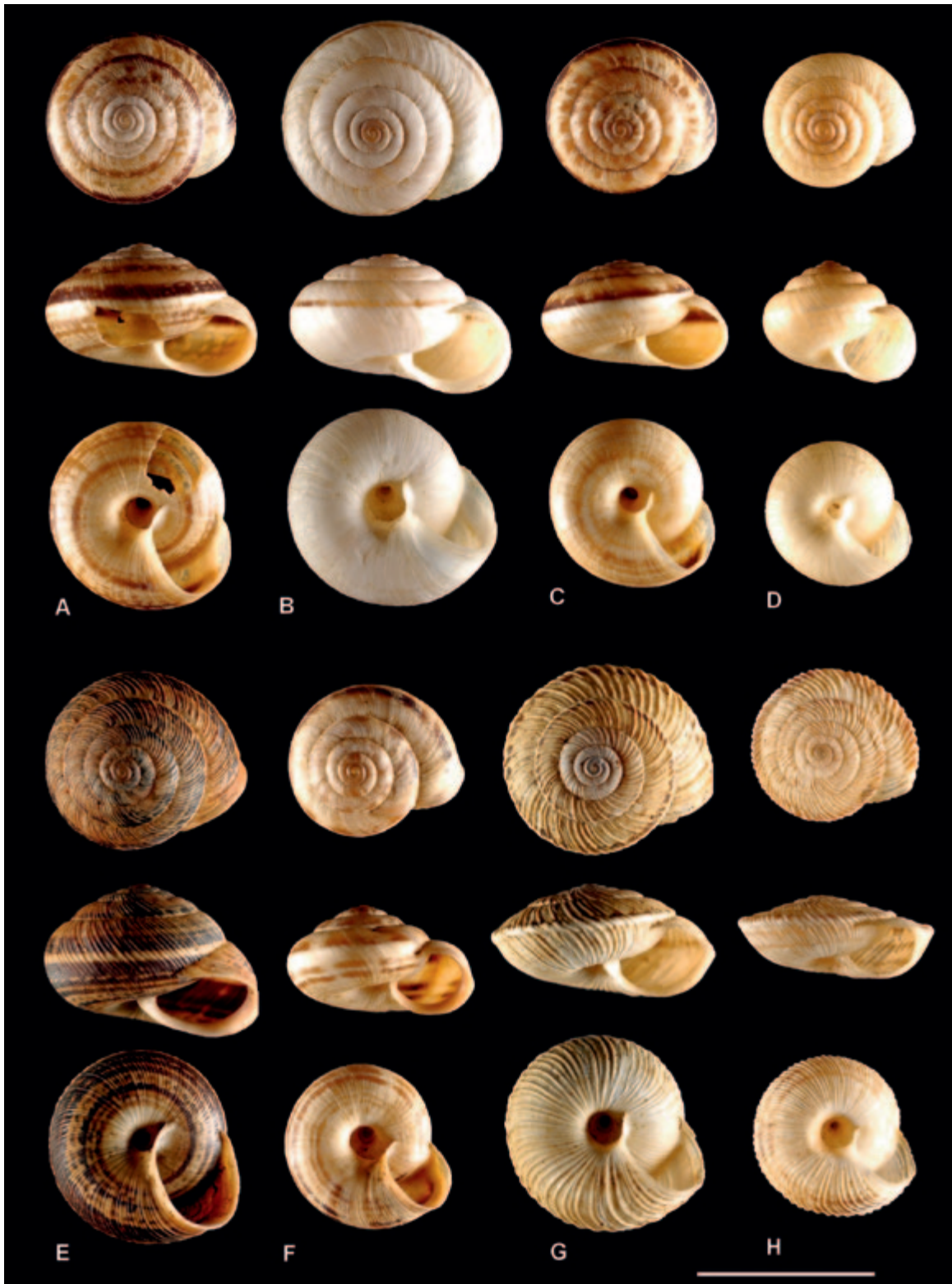
*Diagnosis* Very similar to *C. belemensis* s. str. in shell characters, but differing in the much shorter penial flagellum (0.2–0.4×length of epiphallus, cf. > 1.0 ×, normally > 1.3×in *C. belemensis*). *C. scabiosula* typically has smaller adult shells than both of these with ribbing even weaker or absent on dorsal surface of body whorl and penial flagellum 0.7–1.3×length of epiphallus.

*Shell* 188 examined, from 12 localities (7 of the localities had identification confirmed by dissection). Shape convex to low-convex above, flattened below; height 6.0–8.1 mm, breadth 10.6–12.5 mm, B/H 1.54–1.81, with 5.5–6.2 whorls. Whorls rounded, with shallow to very shallow sutures. Umbilicus moderately wide (1.9–2.3 mm, representing 16.2–20.2% of shell breadth), symmetrical, deep, exposing upper whorls, usually slightly overlapped by reflected peristome. Mouth broadly oval, except where interrupted by penultimate whorl; last part of body whorl expanding, descending near mouth. Mouth edge thin, reflected only near umbilicus. Inside of mouth usually with low white rib set back from edge of palatal and columellar areas. Shell moderately thick, slightly translucent; surface glossy above and often strongly glossy

below. Ground-colour pale brown throughout, or whitish beneath; upperside nearly always with brown to blackish-brown markings that are very variable in extent, but form sharply defined bands on only a minority of shells, consisting instead of interrupted bands or rows of irregular blotches, often with whitish rib crests; underside also with very variable dark markings, often in several thin interrupted bands; underside sometimes mainly dark brown. Transverse ribs on upperside of shell ± regular on higher whorls of spire, becoming weak or partly absent on body whorl; on underside generally weaker. Spiral lines inconspicuous, but present near mouth on underside of body whorl.

*Genital anatomy* Seven dissected (+ four immatures) from three localities in Serra da Arrábida (Figs 4A, B, 6A); two dissected (+ one immature) from two localities near Cabo Espichel.

Single snails in samples P129 and P130 each had a spermatophore in the bursa copulatrix and its duct. In P129 the individual involved had the wall of the duct stretched, appearing distended, sharply bent (“kinked”) at 1.5 mm from the distal end, with remainder of the duct 4.5 mm long. The spermatophore was removed from the P130 snail. It was 8.5 mm in overall length, with three distinct segments: (A) the narrow end from the distal part of the duct was white, cylindrical, 1.7 mm in length, tapering to a slender point; (B) beyond this, another white section was 1.3 mm long, becoming wider along its length; (C) the remaining 5.5 mm was much wider, subcylindrical, amber to light brown, apparently partly decayed or digested, with 1 or 2 low smooth external ridges, a small broken-off fragment of (another?) ridge having a few small teeth directed backwards from the pointed end of the spermatheca. It would appear that part (A) is formed in the penial flagellum, and the junction of parts (A) and (B) may have caused the sharp bend in the bursa duct of the snail from sample P129. These specimens are useful in confirming that sperm transfer is likely to occur in spermatophores, as normal in Hygromiidae. Also, that the shape of the spermatophore corresponds at least roughly to the form of the interior of penial flagellum plus epiphallus, and that after mating the spermatophore lodges in the partner’s bursa copulatrix duct with the narrow part formed in the flagellum lying very close to the distal end



**Figure 2** Shells of *Candidula* species from Portugal: **A** *C. arrabidensis* sp. nov., Estremadura, Serra da Arrábida, holotype, NHMUK 20140013/1; **B** *C. belemensis*, Estremadura, Serra de Montejunto, CGAH 2010.P33, from restricted type-locality; **C** *C. scabiosula*, Algarve, E. end of Rocha da Pena, CGAH 2011.P112; **D** *C. carrapateirensis* sp. nov., Algarve, 0.5 km W. of Carrapateira, holotype, NHMUK 20140014/1; **E** *C. codia*, Algarve, 2 km E. of Santa Barbara de Nexe, CGAH 2011.P117; **F** *C. gigaxii*, Baixo Alentejo, 1 km W. of Serpa, CGAH 2013.P339; **G** *C. coudensis*, Beira Litoral, Vale da Couda SE. of Almoester, paratype, CGAH 2009.P19; **H** *C. setubalensis*, Estremadura, Serra da Arrábida, CGAH 2007.P9/15. Scale line 10 mm.



of this duct adjoining the entrance to the free oviduct.

*Geographical range* Endemic to Portugal, where mainly restricted to rocky limestone habitats in Estremadura (Setúbal District) extending from Serra da Arrábida westwards to near Cabo Espichel (Fig. 8).

*Etymology* The species epithet *arrabidensis* is an adjective derived from the type locality Serra da Arrábida.

***Candidula belemensis* (Servain 1880)**  
Figs 2B, 4C–E, 6C, 8

*Helix Belemensis* Servain 1880 (p. 86). Type locality: “Alluvions du Tage, au-dessous de la tour de Belem, près de Lisbonne” [Estremadura]. Here restricted to summit area of Serra de Montejunto, Estremadura, for reasons discussed below. Gittenberger (1993a: 291 figs 33–35) figures “? topotype” at MHNG labelled “Lisbonne”; E. Neubert (*in litt.*) has located a possible syntype MHNG 14350 with original label “Belem, alluvion du Tage, près de Lisbonne”.

*Helix intersecta*, Poiret: Servain (1880: 91), pars?

*Helix belemensis*, Servain: Locard (1899: 95), pars, excluding records from S. of Lisbon.

*Helix absidata* Locard 1899 (p. 112). Type locality: “Environs de Lisbonne [Estremadura], Coimbra, Sernache [Beira Litoral] ([leg.] Castro)”. Lectotype from Lisbonne at MNHN designated by Gittenberger (1993a: 284, 288 figs 7–9). Locard (*loc. cit.*) also named varieties *major*, *minor*, *inflata*, *alta*, *depressa*, *fusca* and *monozona*, each of them being validated by a brief description, but most if not all being junior homonyms of earlier names in *Helix*.

*Candidula belemensis* (Servain 1880): Gittenberger (1993a: 284, 288 figs 1–3 & 7–9, 291 figs 33–35), pars, excluding records from S. of Lisbon.

*Candidula belemensis* (Servain 1880): Puente (1994: 344), pars, excluding records from S. of Lisbon.

*Candidula belemensis* (Servain 1880): Matos (2004: 72), pars, excluding records from S. of Lisbon.

*Candidula intersecta* (Poiret 1801): Matos (2004: 73), pars?

*Diagnosis* See notes under *C. arrabidensis* and *C. scabiosula* and the Key below for differences from those species.

*Shell* 409 examined from 10 localities where identification was confirmed by dissection (Figs 2B).

*Genital anatomy* 25 dissected (+ 5 immatures) from ten localities in Portugal (Figs 4C–E, 6C).

*Taxonomic history* Gittenberger (1993a: 284) noted that it is “very uncertain still” whether this species should be separated from *C. intersecta*. This has been resolved by our studies, which show that northern populations assigned to *C. belemensis* differ anatomically from *C. intersecta* in having a much longer penial flagellum. We restrict the type locality of *C. belemensis* here in order to ensure that the species only includes populations with a long penial flagellum. These occur only north of Lisbon; conchologically similar populations with a short flagellum in Serra da Arrábida are named here as *C. arrabidensis* and those in the Algarve are referred to *C. scabiosula*. Figs of the genital anatomy given by Gittenberger (1993a: 292 fig. 36) are based on specimens from Boliqueime in the Algarve that represent a population we refer to *C. scabiosula* (*q.v.*).

Altaba (1997: 3) figured a single shell from Valença do Minho in N. Portugal as this species and claimed that it represented a considerable extension of the species’ known range. However, the shell does not show characters that exclude identification as an extreme form of *C. olisippensis* or a more typical *C. intersecta*.

*Geographical range* Endemic to Portugal, with confirmed records from Beira Litoral and Estremadura (Fig. 8; Appendix). Distribution maps in Gittenberger (1993a: 293) and Puente (1994: 345) show a wider range in S. Portugal because they are based on broader delimitation of the species than that adopted here.

***Candidula carrapateirensis* G.A. Holyoak & D.T. Holyoak sp. nov.**  
Figs 2D, 5C, 6E, 9

*Types* Holotype (Fig. 2D): ca 0.5 km W. of Carrapateira, 29S 050845/411537, sand dunes with patchy vegetation of mainly low bushes, stony locally, 43 m alt., 2011.02.07, GAH & DTH 2011.P123, NHMUK 20140014/1 (1 sh, breadth 8.1 mm) & 20140014/2 (bod). Paratypes in CGAH (listed in Appendix): 327 sh, 3 bod and 13 spm from type locality; 104 sh from above Praia de

Monte Clérigo (W. of Aljezur) in Algarve; 69 sh from coast W. of Almogrove in Baixo Alentejo.

*Type-locality* Sand dunes ca 0.5 km W. of Carrapateira (W. Algarve, Portugal).

*Diagnosis* *C. carrapateirensis* resembles *C. strucki* from Almadena and Sagres (W. Algarve) in genital anatomy (although the penial flagellum may sometimes be shorter) but the shells differ considerably in having whorls of the spire rounded rather than flattened above, shell not flattened below, an almost round shell mouth (not oval) and the peristome always lacking a thickened white internal rib (whereas adults of *C. strucki* develop a strong rib). It may eventually be treated as a subspecies of *C. strucki*, but the conchological differences are striking and consistently present.

*Shell* 501 examined. Strongly convex to pyramidal above, rounded below; height 5.7–6.4 mm, breadth 7.5–8.7 mm, B/H 1.22–1.43, with 4.7–5.2 whorls. Whorls rounded, flattened above near the moderately deep sutures. Umbilicus narrow to very narrow (0.54–0.87 mm, representing 6.9–10.2% of shell breadth), deep,  $\pm$  symmetrical, partly overlapped by reflected peristome. Mouth almost round, except where interrupted by penultimate whorl, the last part of body whorl expanding markedly, descending slightly near mouth. Mouth edge thin, reflected only near umbilicus. Interior of mouth unthickened. Shell often rather thin and somewhat translucent, slightly glossy above, more strongly glossy below. Ground colour usually pale brown above, whitish below; upperside commonly with one strong band of brown to blackish-brown towards periphery and one or more diffuse interrupted bands above it, the crests of ribs whitish, but very variable; underside commonly with several thin translucent bands. Transverse ribs on upperside of later whorls typically strong but irregular and often discontinuous, much weaker on underside. Spiral lines obvious on underside of most shells.

*Genital anatomy* Three dissected (+ one immature) from the type locality (Figs 5C, 6E). General arrangement of distal genitalia typical for Portuguese species of the genus; penis proportionately short; penial flagellum 0.5–0.6 $\times$ length of epiphallus.

*Geographical range* Endemic in SW. Portugal where known only from coastal sands in W. Algarve (W. of Carrapateira, W. of Aljezur) and W. Baixo Alentejo (W. of Almogrove) (Figs 9, 12E; Appendix). Judging from the abundance of dead shells there appear to be large populations at all three known localities. Only a few living individuals were found (W. of Carrapateira) where fresh shells were locally abundant, but a few fresh shells were found at both of the other sites.

*Etymology* The species epithet *carrapateirensis* is an adjective derived from the type locality near Carrapateira.

*Candidula codia* (Bourguignat 1859)

Figs 1E, 2E, 4F, G, 6H, 10

*Helix intersepta*, Poiret: Morelet (1845: 64), pars? (“une variété plus forte”), non Poiret 1801.

*Helix codia* Bourguignat 1859 (Rev. et Mag. de Zool., (2) 11, p. 523, pl. 20 figs 10–13; also, reprinted separately in Aménités malacologiques, 2, p. 137, pl. 17 figs 10–13). Type locality: “en Portugal, les environs de Faro et de Loulé (Algarve)” by original designation. Lectotype from Faro at MHNG designated by Gittenberger (1993a: 284, 290 figs 23, 24).

*Helix codopsis* “Bourguignat 1877” Servain 1880 (p. 100). Type locality: “Boliquireime” [Algarve]. Syn. *vide* Gittenberger (1993a: 284, 290 figs 25, 26). E. Neubert (*in litt.*) supplied the following information: Servain is evidently author of the description; he copied the manuscript name from Bourguignat, adding “Bourguignat 1877” on Bourguignat’s original label. Hence, Servain must have consulted these specimens, so that Gittenberger (*loc. cit.*) was wrong in considering them as merely topotypes (although in the collection he left the note “lectotypes”); two lots of syntypes are registered as MHNG 14441/1 and MHNG 14442/3.

*Helix codia* Bourguignat: Hidalgo (1875: 193).

*Helix codia*, Bourguignat: Morelet (1877: 246) (regarded incorrectly as a syn. of *Helix caperata* Montagu).

*Helix codia*, Bourguignat: Servain (1880: 100).

*Helix codia*, Bourguignat “1879” [*sic*, error for 1859]: Locard (1899: 108). Locard (*loc. cit.*) also named “des var. *major* et *minor* ... des var. *alta*, ... *globulosa*” (all *nomina nuda*) and “var. *marmorata* ... [var.] *zonata* ... [var.] *bizonata*” with brief descriptions (although the three names are probably

junior homonyms). Locard (*op. cit.*, p. 108) also named var. *depressa* as a *nomen nudum*, but a brief description on his p. 110 serves to validate that name, although it is also a junior homonym of several earlier names in *Helix*.

*Helix codopsis* "Bourguignat, in" Servain 1880: Locard (1899: 108).

*Helix intersecta*, Poiret: Nobre (1941: 103), pars, non Poiret 1801.

*Candidula codia* (Bourguignat): Altimira (1969: 105).

*Candidula codia* (Bourguignat 1859): Gittenberger (1993a: 284).

*Candidula codia* (Bourguignat 1859): Puente (1994: 352).

*Candidula codia* (Bourguignat 1859): Matos (2004: 73, 108).

*Candidula codia* (Bourguignat, 1859): Simões (2006: 3–4, with figs).

**Diagnosis** The combination of a rather high domed spire with shallow sutures giving a depressed-globular shell shape and regular coarse ribs (Figs 1E, 2E) is distinctive among Portuguese *Candidula*. It is also the only one of our species with minute hairs on juvenile shells. The penial flagellum is very long, providing a clear distinction from *C. gigaxii* and *C. scabiosula* which are the only other *Candidula* known from the C. Algarve.

**Shell** 329 examined from 6 sites (with identification checked by dissection from 2 of the sites contributing 202 shells). Adult shells have B 9.5–12.2 mm, H 5.5–8.2 mm, H×100/B 57.8–70.9%, U 1.0–1.6 mm, U×100/B 9.3–12.8%.

Minute hairs were noticed in the field on the apical whorls of small juvenile shells, using a ×10 hand-lens. These were first noticed at site 2011.P117 which is a locality with no *Helicella cistorum* (Morelet 1845), a species in which hairs are known to be present. The hairs on *C. codia* occur on whorls 0.3–1.7 and are caducous, being lost rapidly as the shell grows larger. The hairs are pale, thin, ca 28–35 µm long (along chord measured from insertion to tip), tapering towards the tip, ascending from the base but ± strongly decurved back towards the shell surface, and orientated with the tip directed mainly towards the shell aperture. Shell figures are given by Bourguignat (1859: pl. 17 figs 10–13), Gittenberger (1993a: 290 figs 23–26), Kittel (2002: 6), Simões (2006: 3, 4)

and in our Figs 2E.

**Genital anatomy** Three mature individuals (and two immatures) dissected from two Portuguese populations (Figs 4F, G, 6H). These showed generally similar anatomy to that figured by Altimira (1969: 106).

**Geographical range** Endemic in Portugal where known only in the C. Algarve (Fig. 10). Distribution maps are given by Gittenberger (1993a: 293), Puente (1994: 353), and in more detail by Kittel (2002: 7), who recorded it since 1997 in 9 ten-km squares (from 29SNB17 to 29SPB00).

***Candidula coudensis*** G.A. Holyoak & D.T.

Holyoak 2010

Figs 1F, 2G, 6F, 10

*Candidula coudensis* G.A. Holyoak & D.T. Holyoak 2010 (p. 68).

**Type locality** Vale da Couda, by N348 road SE. of Almoester (district of Leiria, Portugal).

**Types** Holotype NHMUK 20100177. Paratypes: 7 sh and 4 bod in NHMUK; 145 shells, 7 bod and 2 spm in CGAH; as listed in Appendix.

**Diagnosis** Differs from other Portuguese *Candidula* except the allopatric *C. setubalensis* in having a sharply keeled shell. *C. coudensis* is distinct from *C. setubalensis* in having a longer penial flagellum (ca 1.5×length of epiphallus, cf. 0.5–0.7×epiphallus). There do not appear to be any consistent differences in their shell characters. The coloration of external parts of the body may differ consistently in these species, it being very pale in *C. setubalensis* (Fig. 1A), blackish in *C. coudensis* with the sole of the foot darker than the flanks (Fig. 1F).

**Shell** 166 examined, all from within 10 km of the type-locality. For detailed description and figures see Holyoak & Holyoak (2010: 68–69). However, larger samples obtained subsequently have revealed that the shell can be larger (up to a maximum of 11.5 mm in breadth, Fig. 2G) and that other differences from shells of *C. setubalensis* (less convex whorls of spire, more elliptical shell aperture, proportionately larger umbilicus) are inconstant.



**Figure 3** Shells of *Candidula* species, from Portugal (A–D, F–H) and Great Britain (E): **A** *C. ponsulensis* sp. nov., Beira Baixa, W. bank of Rio Pônsul W. of Ladoeiro, holotype, NHMUK 20140015/1; **B** *C. intersecta*, Estremadura, N. of Abrunheira, CGAH 2013.P347; **C** *C. strucki*, Algarve, 2 km NW. of Sagres, CGAH 2011.P125; **D** *C. olisippensis*, Beira Litoral, Praia da Tocha, CGAH 2010.P83; **E** *C. olisippensis*, Cornwall, Kynance Cliff, CGAH 2011; **F** *C. olisippensis*, Beira Litoral, 2 km NE. of Favaçal, CGAH 2011.P191; **G** *C. olisippensis*, Beira Litoral, Serra de Sicó (summit area), CGAH 2011.P98; **H** *C. olisippensis*, Estremadura, Nazaré, CGAH 2010.P91. Scale line 10 mm.

*Genital anatomy* Four mature individuals dissected from the type locality (Fig. 6F; Holyoak & Holyoak, 2010: 70). Generally very similar to *C. olisippensis* in anatomy of distal genitalia with the penial flagellum long as in that species, about 1.5×length of epiphallus.

*Taxonomic history* Discovered in January 2008 and described by Holyoak & Holyoak (2010).

*Geographical range* Endemic in Portugal, where known only from Vale da Couda in Beira Litoral (Leiria District) and surrounding regions on limestone substrata (Figs 10, 12B). Recent surveys arranged by Gonçalo Calado of Universidade do Algarve demonstrated its occurrence in ca 32 one-kilometre grid squares (in Ferreira, 2013).

*Candidula gigaxii* (L. Pfeiffer 1847)  
Figs 2F, 6L, 9

*Helix caperata* var.  $\beta$ , syn. *Helix gigaxii* "Charpentier MS." L. Pfeiffer 1847 (p. 167). Type locality: given by L. Pfeiffer as France, near Arles; and near "Highbycombe Bueks Britanniae". [*sic*, presumably High Wycombe, Bucks.]. In a widely overlooked note, Haas (1923) reported on study of Pfeiffer's original specimens on loan from the Stettin Natural History Museum. He found "... the original examples from Highbycombe, (the ones figured in Martini-Chemnitz) have nothing to do with the true Mediterranean *H. gigaxii*, but undoubtedly belong to *Helicella caperata* Mont." However, the French shells from Arles and Vaucluse were correctly identified. Dance (1986: 210) noted that L. Pfeiffer's collection at Stettin [now Szczecin, Poland] became part of the Collection of H. Dohrn which was "totally destroyed in 1939–45 war". A correctly identified *H. gigaxii* from High Wycombe that was undoubtedly seen by L. Pfeiffer might still exist in another collection, but unless this can be confirmed the type locality should not include Britain.

*Helix (Zenobia) fasciolata*,  $\delta$ : Moquin-Tandon (1855: 239).

*Helix Gigaxii* Charpentier: Hidalgo (1875: 196).

*Helix andalusica* Kobelt 1882 (p. 70, pl. 9).

*Helix limatula* Locard 1899 (p. 103). Type locality: "Lisbonne" [Estremadura]. Lectotype at MNHN designated by Gittenberger (1993a: 285, 288 figs 4–6); syn. *fide* Gittenberger (*loc. cit.*).

*Helicella heripensis* (Mabille): Stelfox (1912: 39).

*Helicella "heripensis"*: Boycott & Jackson (1914: 164).

*Helicella heripensis* (Mabille 1877): Ellis (1926: 199).  
*Helicella (Candidula) andalusica [sic]* (Kobelt): Ortiz de Zárate y López (1950: 24, 25 fig. 1).

*Candidula gigaxii* (Pfeiffer 1848): Gittenberger (1993a: 285).

*Candidula gigaxii* (Pfeiffer 1848): Puente (1994: 354).

*Candidula gigaxii* (L. Pfeiffer 1850): Matos (2004: 75).

See Kennard & Woodward (1926: 221–223), Germain (1930: 275–276) and Gittenberger (1993a: 285, 1993b: 310) for fuller synonymy.

*Diagnosis* The principal differences from congeners are in the shell characters, since the genital anatomy with short penial flagellum may lack any distinctive features. As noted in more detail below and in the Key, the most obvious shell differences are usually in the close regular ribs and shape of the umbilicus, but some populations in S. Spain differ only in the fine, close, regular ribbing.

Boycott & Jackson (1914) reported that English *C. gigaxii* mainly had darker external coloration of the body than *C. intersecta*, although the extremes overlapped. Nevertheless, the mantle edge in *C. gigaxii* differed in having a continuous band of bright brick-red pigment mixed with the black, the red being absent or limited to one or two spots in *C. intersecta*. This character is not useful for identifying Iberian specimens; indeed, *C. gigaxii* from a large population at Serpa, Baixo Alentejo, Portugal (sample 2013.P339) had body coloration varying from predominantly dark grey throughout to light grey above with whitish flanks, with no reddish pigmentation.

*Shell* 265 examined from 23 sites (England 4, Portugal 7, Spain 12); 203 of the shells were from 6 sites (Portugal 2, Spain 4) where identification was checked by dissection. Compared to *C. intersecta*, this species is normally distinct when samples of good mature shells can be studied in (1) the markedly more eccentric umbilicus, which expands greatly at the body whorl; (2) the closer, finer and more even ribbing; (3) the lower spire (Stelfox, 1913; Kerney & Cameron, 1979: 177). Figs of the shell are given e.g. by Ortiz de Zárate y López (1950: pl. 2 figs 29–30), Gittenberger, Backhuys & Ripken (1970: 140), Gittenberger (1993a: 288 figs 4–6; 1993b: 310), Kerney & Cameron (1979: pl. 15), Cossignani & Cossignani

(1995: 111) and in our Fig. 2F. Portuguese shells show similar characters to those from England.

Shells from some populations in S. Spain (Prov. Málaga) differ markedly in shape, the extreme forms being globular with high rounded spire, very shallow sutures and small symmetrical umbilicus (notably material from Almorchón, Ardales, 30SUF3986 and 30SUF3988, on sandstone hills at 450–500 m alt.); they were placed as the present species mainly on the basis of the fine, regular shell ribbing, coloration and typical genital anatomy. Populations with intermediate shells also occur in Prov. Málaga (e.g. Baños de la Hedionda, Casares, 30STF9730, on calcareous slopes) and typical shells for the species are widespread in Andalucía.

*Genital anatomy* Four mature individuals dissected from Portugal, four from S. Spain. The distal genital anatomy is closely similar to that of *C. intersecta*, both species having a short penial flagellum, it being 0.2–0.25×length of epiphallus in most *C. gigaxii*. Boycott & Jackson (1914) compared the anatomy of English specimens of these species, noting the main difference between them as the dark pigment present only in *C. gigaxii* on the duct of the bursa copulatrix (“duct of the spermatheca”) and neck of the dart sac. This heavy internal pigmentation may share a common cause with the overall tendency for darker body pigmentation that these authors observed in *C. gigaxii*. The pigmentation is not useful for species identification in Iberia since similar dark marks are absent in Andalucian and Alentejo specimens of *C. gigaxii* we have dissected. Furthermore, the dart sac in some *C. intersecta* from Estremadura, Portugal (sample 2013.P347) has diffuse fine dark markings whereas other individuals there lack them. The genital anatomy is figured by Boycott & Jackson (1914: 168, as *H. heripensis* (Mabille)), Ortiz de Zárate y López (1950: 25, as *H. andalucica*), Gittenberger, Backhuys & Ripken (1970: 141), Alonso (1975: 22), Aparicio (1982: 624), Puente (1994: 360–361) and in our Fig. 6L.

*Taxonomic history* The conchological distinctions between *C. gigaxii* and *C. intersecta* were recognised long ago, e.g. by Albers (1850) who gave species rank to both. Nevertheless, many authoritative works such as Moquin-Tandon (1855: 239) continued to treat them as merely varieties of the same species. English shells were

clearly discriminated as separate species by Stelfox (1912), despite a lack of clear-cut differences in their genital anatomy (Boycott & Jackson, 1914).

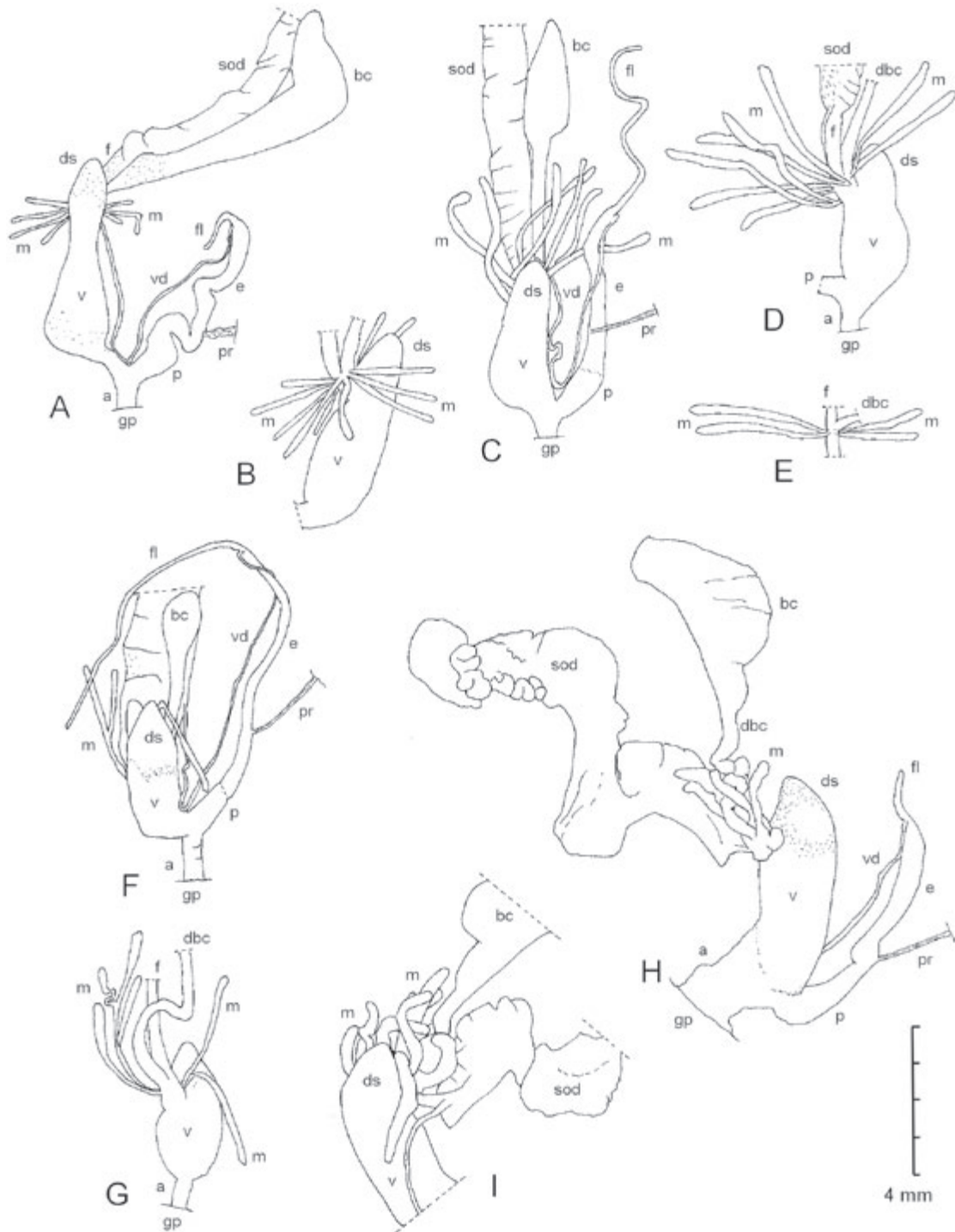
Gargominy *et al.* (2011: 362) and Kadolsky (2012: 84, Appendix 3) summarised information from Ruud Bank implying that the year of publication was 1847, not 1848 or 1850 as given in other recent literature. Kadolsky (2012: 78) gave further discussion of the original publication of the name by L. Pfeiffer (1847: 167), as a synonym, but later treated by the same author as a valid species name in 1850. Some additional details of the nomenclatural history are given on the Animalbase website [2013].

Records from S. Spain as *H. andalucica* Kobelt 1882 and other nominal taxa are treated as this species by Gittenberger (1993a: 285) and Puente (1994: 355).

*Geographical range* W. Europe from C. Ireland (very rare 1918–1945, probably now extinct), N. England, Belgium, W. Netherlands and N. Germany (rare, accidental introduction, at a few isolated sites in Brunswick and Thuringia) southwards through W. and C. France to Portugal and Spain. It was probably introduced to Britain as a “weed” species, perhaps in the Romano-British period, since it is not known there from older fossils (Kerney, 1999: 180).

The species is widespread in N., C., SW. and S. Spain and present very locally in Portugal (maps in Altonaga *et al.*, 1994: 269 and Puente, 1994: 359). Records from SW. Spain include Prov. Cáceres and Prov. Badajoz (Muñoz & Parejo, 1994: 192) and Prov. Huelva (Gasull, 1985: 133).

In Portugal the only confirmed modern records are from eastern parts of Alto Alentejo and Baixo Alentejo, where it is likely to be more widespread since there has been little fieldwork carried out. We have also found a few old, possibly subfossil, shells in the C. Algarve (Fig. 9). It has apparently also been found in Estremadura (“Lisbon”, recorded on basis of *Helix limatula* Locard, see above). Matos (2004: 108) cited a personal communication from E. Gittenberger stating that this “Centroeuropean” [*sic*] species does not live in Portugal, despite his (1993a: 285) treating *H. limatula* as a synonym (see above). She erroneously implied “that it is rarely found in Spain” and suggested that citations for *C. gigaxii* in Portugal “very probably refer to *C. intersecta*”. However,



**Figure 4** Anatomy of distal genitalia in *Candidula* species from Portugal: **A, B** *C. arrabidensis* sp. nov., Estremadura, Serra da Arrábida (site 2010.P27), two views of same specimen; **C–E** *C. belemensis*, Estremadura, ca 1 km S. of Livramento (site 2010.P12b), C and D are two views of same specimen, E is from another specimen with only four branches in mucus glands; **F, G** *C. codia*, Algarve, 3 km N. of Moncarapacho (site 2010.P21), two views of same specimen; **H, I** *C. ponsulensis* sp. nov., Baixo Alentejo, NW. of Pardais (N. of Alandroal; site 2013.P341), two views of same paratype specimen. Figs H and I were drawn with drawing tube; other figures are semi-schematic with mucus glands “straightened” and some organs displaced for clarity of presentation. Abbreviations: **a** genital atrium, **bc** bursa copulatrix, **dbc** duct of bursa copulatrix, **ds** dart sac, **e** epiphallus, **f** free oviduct, **fl** flagellum, **gp** genital pore, **m** mucus gland(s), **p** penis, **pr** penis retractor muscle, **sod** spermoviduct, **v** vagina, **vd** vas deferens. Blackish pigmentation is shown by stippling; position of some concealed organs shown by dotted outlines. All specimens in CGAH.

this is certainly untrue of our own records from the Algarve and Alentejo.

*Candidula intersecta* (Poiret 1801)

Figs 3B, 5A, B, 6B, 9

*Helix intersecta* Poiret 1801 (p. 81). Type locality: given only as *In collibus apricis*, but presumably in Dept. Aisne or near Paris in N. France.

*Helix caperata* Montagu 1803 (p. 430, pl. 11, fig. 11). Type locality: Wiltshire, S. Devon (especially about Stanborough and Woolcomb; also Plymouth Dock), Cornwall, Kent.

*Helix (Zenobia) fasciolata*: Moquin-Tandon (1855: 239), but excluding var.  $\delta$  (which represents *C. gigaxii*).

?*Helix expedenda* Locard 1899 (p. 113). Type locality: "Environs de Lisbonne ([leg.] Castro). Locard wrote "Nous rapprocherons l'*Helix expedenda* de l'*Helix absidata*". Gittenberger (1993a: 285, 290 fig. 27) designated a lectotype at MNHN (with name given incorrectly as *H. expedenda*) and treated the taxon as a syn. of *C. intersecta* (Poiret 1801).

?*Helix imula* Locard 1899 (p. 113). Type locality: "Lisbonne" [Extremadura]. Locard (*op. cit.*, p. 114) compared it to *Helix absidata*, but noted "taille plus petite" [8 mm in diameter], "son ombilic notablement plus petit". Gittenberger (1993a: 285, 290 figs 29, 30) designated a lectotype at MNHN and treated the taxon as a syn. of *C. intersecta* (Poiret 1801).

*Candidula intersecta* (Poiret 1801): Puente (1994: 361), pars.

See Kennard & Woodward (1926: 219–221), Germain (1930: 274) and Gittenberger (1993b: 311) for fuller synonymy.

*Diagnosis* See Key below for separation from species occurring in Portugal, and also the account of *C. gigaxii* above.

*Shell* 489 examined from 15 localities where identification was confirmed by dissection (England 2, France 7, Ireland 3, Portugal 3). For figures of correctly identified shells see Gittenberger, Backhuys & Ripken (1970: 140), Kerney & Cameron (1979: pl. 15) and our Fig. 3B.

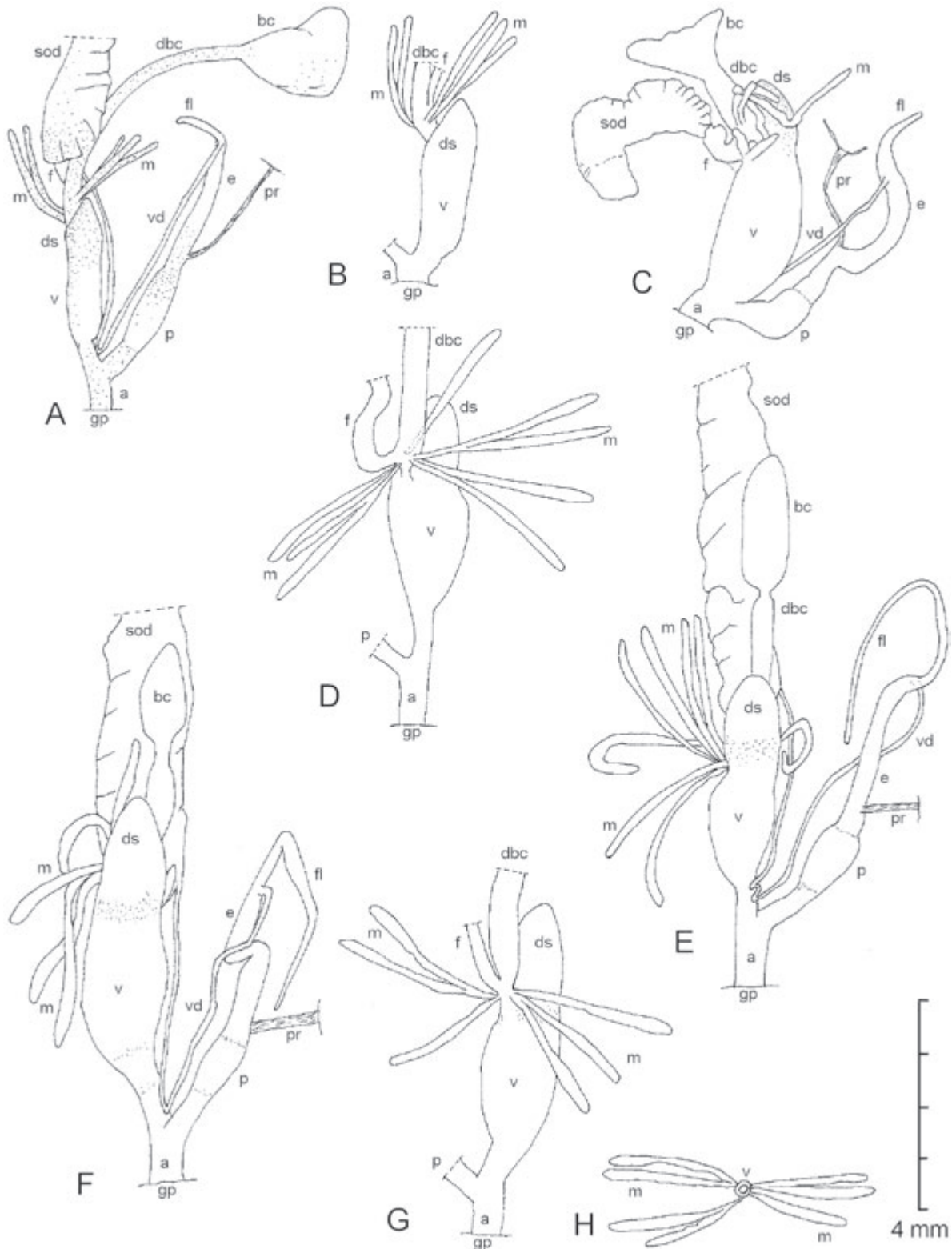
*Genital anatomy* 37 dissected (+ 2 immatures) from 15 populations (from Ireland, England, France and Portugal). The distal genital anatomy is generally very similar to that of the other species considered in this paper, the main character of note being the short penial flagellum, (0.1

0.2–0.4×length of epiphallus. Figs of the genital anatomy are given by Boycott & Jackson (1914: 168, as *H. caperata*), Ortiz de Zárate y López (1943: 70), Gittenberger, Backhuys & Ripken (1970: 141) and in our Figs 5A, B, 6B.

*Taxonomic history* This is the commonest species of the genus in NW. Europe and very variable in shell form and colour. *C. intersecta* was named from N. France (and from England as the synonymous *H. caperata*) before most other species of the genus were recognised, so early conchologists tended to identify shells resembling it from more distant localities as this species. The notes under *C. gigaxii* describe the history of separation of *C. intersecta* from that rather similar species. The literature thus attributed an unduly wide range to *C. intersecta*, especially in the Iberian Peninsula where similar "cryptic" species occur. Morelet (1845: 63) recorded it widely in mainland Portugal, and Nobre (1913, 1941) treated it as the only *Candidula* occurring in the country. More recently, Gittenberger (1993a) retained it as a Portuguese species and this was followed by Matos (2004). However, the present study shows that it is rare and local in mainland Portugal, where it may be introduced. The *Candidula* in the Azores was placed as *C. intersecta* by Backhuys (1975: 201) and by Bank, Groh & Ripken (2002: 126), but the only Azorean specimens we have dissected are *C. olisippensis*. Furthermore, it is unsafe to assume that all material from further north in Europe will be safely placed as *C. intersecta*, since we have found *C. olisippensis* in Cornwall (see below). Similar doubts must apply to records of introduced *C. intersecta* populations on other continents, at least until their shells and genital anatomy are carefully reassessed.

*Geographical range* W. Europe from N. Ireland, N. Scotland, Denmark, N. Germany and southernmost Sweden southwards through W. and NC. France to N. Spain. Also present locally near Lisbon in Portugal, where it may have been introduced. Introduced populations established in New Zealand are almost certainly of this species, since Barker (1999: 179) illustrated genital anatomy with a short penial flagellum. Other introduced populations attributed to this species but which need anatomical confirmation are reported from the U.S.A. (Purdue University website [2013]), Australia (Quick, 1952, 1953) and





**Figure 5** Anatomy of distal genitalia in *Candidula* species: **A, B** *C. intersecta*, England, Lincolnshire, NE. of Ropsley (collected 2010.03.21), two views of same individual; **C** *C. carrapateirensis* sp. nov., Portugal, Algarve, 0.5 km W. of Carrapateira (site 2011.P123), paratype; **D, E** *C. olisipennis*, Portugal, Beira Litoral, near Barragem do Cabril (site 2010.P24), two views of same individual; **F–H** *C. olisippensis*, Portugal, Beira Litoral, SE. of Almoster (site 2009. P19), F and G are two views of same individual, H is from a second individual. Fig. C was drawn with drawing tube; other figures are semi-schematic with mucus glands “straightened” and some organs displaced for clarity of presentation. Abbreviations and other conventions as in Fig. 4. All specimens in CGAH.

Colombia (Robinson, 1999, recording its interception on shipments from Colombia entering the U.S.A.); records from Chile have also been listed (idtools website [2013]).

The species appears to be a recent colonist of the British Isles, where there are no certain pre-mediaeval fossil records; indeed, it behaves as a “weed” in Britain colonizing suitable man-made habitats on well-drained calcareous soils (Kerney, 1999: 179).

Accepted Spanish records confirmed anatomically are only from N. Spain in Provinces Álava, León and Vizcaya (Ortiz de Zárate y López, 1943; Manga, 1979, 1983: 159–164; Manga & Cordero del Campillo, 1979: 64 fig. 2; Puente, 1994: 367); accepted records from shells are also largely restricted to the Cantabrians region (Prieto & Martín, 1988; Altonaga *et al.*, 1994). Reports from elsewhere in W. Spain were probably errors for other species (see account of *C. ponsulensis* below) as were those from Andalucía.

This species has been widely assumed to occur in Portugal (e.g. in Estremadura and Algarve) since the time of Morelet (1845), e.g. by Nobre (1941), Gittenberger (1993a: 285) and on maps in Puente (1994: 365) and Altonaga *et al.* (1994: 269). However, it appears from our own studies that conchologically similar taxa present here have a long penial flagellum or differ conchologically (with three exceptions, described below). The same is likely to apply to records from W. Spain (see account of *C. ponsulensis* below).

The only well established population we have found in Portugal (Fig. 9) was near Abrunheira, in Estremadura, in an area of disturbed limestone grassland with heaps of dumped masonry debris not far from extensive built up areas that are almost continuous with the western edge of the Lisbon conurbation. In addition, Rui Mendes collected a sample in February 2014 at Trafaria, Almada, Estremadura, on the S. bank of the R. Tejo opposite Lisbon, where it was living on low plants by a roadside. Elsewhere in Portugal, we have found a total of five specimens of typical *C. intersecta* in 2010 and 2011 in the garden of our house at Barcoila near Sertã, Beira Baixa, 29SNE70. Here, it was most likely to have been introduced with plants we brought in 2009 from Tuckingmill, Cornwall, U.K., where it was long established in the garden. Searches have provided no evidence that these accidental imports have spread further around Barcoila, but the

likelihood exists of the species arriving elsewhere in Portugal with horticultural material or e.g. attached to vehicles.

Records from the Azores appear dubious now that *C. olisippensis* has been recorded there (see above and the account of that species). Wollaston (1878) listed *C. intersecta* from Madeira, where there do not appear to be any subsequent records. The Madeiran shell in NMW.Z figured by Seddon (2008: 152) has a rather small umbilicus and might represent *C. olisippensis* rather than *C. intersecta*.

*Candidula olisippensis* (Servain 1880)  
Figs 1C, D, 3D–H, 5D–H, 6D, I, 7, 11

?*Helix candidula*. Fer.: Morelet (1845: 63), non *H. candidula* Studer 1820 (non A. Férussac) = *H. unifasciata* Poiret 1801. Morelet (1877: 245) revised this to a record of a small variety of “*H. caperata* Montagu”. Nobre (1941: 105–106) also suggested a small form of “*Helix intersecta*” might have been misidentified as this species. See also Matos (2004: 107).

*Helix intersecta*. Poiret: Morelet (1845: 63), pars? non Poiret 1801.

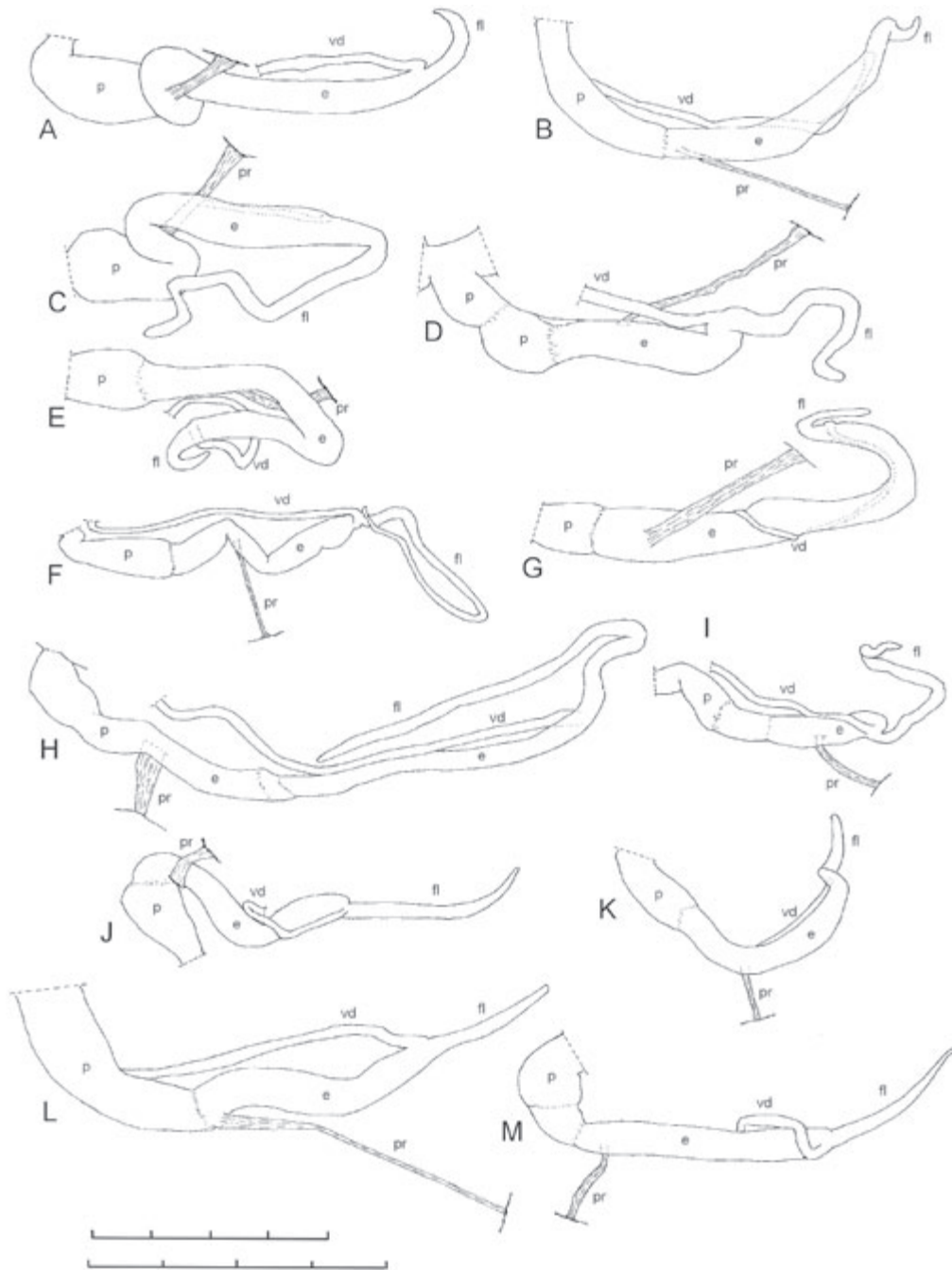
*Helix candidula* Studer: Hidalgo (1875: 191), pars?  
*Helix caperata* Montagu: Hidalgo (1875: 191), pars? non Montagu 1803.

*Helix olisippensis* Servain 1880 (p. 93). Type locality: “Environs de Lisbonne, dans les endroits ombragés et un peu humides” [Estremadura]. “Topotype” in MHNG figured by Gittenberger (1993a: 288, figs 10–12); E. Neubert (*in litt.*) suggests this and other “topotypes” (MHNG 14426/1, MHNG 14427/2) should be considered possible syntypes.

*Helix defectiva* Locard 1899 (p. 85). Type locality: “Environs de Lisbonne [Estremadura], Sernache, Coimbra ([leg.] Castro)” [Beira Litoral]. Lectotype at MNHN from Coimbra designated by Gittenberger (1993a: 286), syn. *fide* Gittenberger (*loc. cit.*).

?*Helix micida* Locard 1899 (p. 86). Type locality: “Faro ([leg.] Castro)” [Algarve]; possibly an error of locality since *C. olisippensis* does not occur in the Algarve. Lectotype at MNHN designated by Gittenberger (1993a: 286, 289 figs 17, 18), syn. *fide* Gittenberger (*loc. cit.*).

*Helix portionalis* Locard 1899 (p. 88). Type locality: not stated in original description, but Lectotype at MNHN designated by Gittenberger (1993a:



**Figure 6** Penis and associated organs in *Candidula* species, all drawn to scale with drawing tube: **A** *C. arrabidensis* sp. nov., Portugal, Estremadura, Serra da Arrábida (site 2011.P130), paratype; **B** *C. intersecta*, Portugal, Estremadura, N. of Abrunheira (SE. of Sintra) (site 2013.P347); **C** *C. belemensis*, Portugal, Estremadura, Serra de Montejunto (site 2010.P33), from restricted type-locality; **D** *C. olisippensis*, Great Britain, Cornwall, Kynance (collected 2011.04.06); **E** *C. carrapateirensis* sp. nov., Portugal, Algarve, 0.5 km W. of Carrapateira (site 2011.P123), paratype; **F** *C. coudensis*, Portugal, Beira Litoral, SE. of Almoster (site 2008.65), paratype figured by Holyoak & Holyoak (2010: 70); **G** *C. ponsulensis* sp. nov., Portugal, Baixo Alentejo, NW. of Pardais (N. of Alandroal, site 2013.P341), paratype; **H** *C. codia*, Portugal, Algarve, N. of Moncarapacho (site 2009.P23); **I** *C. olisippensis*, Spain, Prov. Pontevedra, just NW. of San Vicente do Grove (site 2011.E182); **J** *C. scabiosula*, Portugal, Algarve, Rocha da Pena, Loulé (leg. Á. de Oliveira, 2007.09.19); **K** *C. setubalensis*, Portugal, Estremadura, Serra da Arrábida (site 2011.P131); **L** *C. gigaxii*, Portugal, Baixo Alentejo, ca 1 km W. of Serpa (site 2013.P339); **M** *C. strucki*, Portugal, Algarve, ca 2 km NW. of Sagres (site 2011.P125). Both scale bars represent 4 mm; upper bar is for Fig. H, lower bar for all other drawings. Abbreviations and other conventions as in Fig. 4. All specimens are different individuals to those used in Figs 4 and 5 and all are in CGAH.

286, 289 fig. 21) from "Lisbonne" [Estremadura], syn. *fide* Gittenberger (*loc. cit.*).

?*Helix arganica*, Servain: Locard (1899: 96).

?*Helix unifasciata*, Poiret: Locard (1899: 96) non *H. unifasciata* Poiret 1801.

*Helix putilla* Locard 1899 (p. 97). Type locality: "Environs de Lisbonne ([leg.] Castro)" [Estremadura]. Lectotype at MNHN designated by Gittenberger (1993a: 286, 289 fig. 20), syn. *fide* Gittenberger (*loc. cit.*).

*Helix ofellata* Locard 1899 (p. 98). Type locality: "Sernache, environs de Lisbonne ([leg.] Castro)". Gittenberger (1993a: 286, 293) cited only "Sernache", which was interpreted and mapped by him as "Sernache", Beira Baixa [i.e. Cernache do Bonjardim], but probably in error for Cernache in Beira Litoral (ca 7 km SSW. of Coimbra) where Castro collected other specimens he passed on to Locard. Lectotype at MNHN from "Sernache" designated by Gittenberger (1993a: 286, 289 figs 13–15 [incorrectly given as figs 1–3 in text on p. 286]), syn. *fide* Gittenberger (*loc. cit.*).

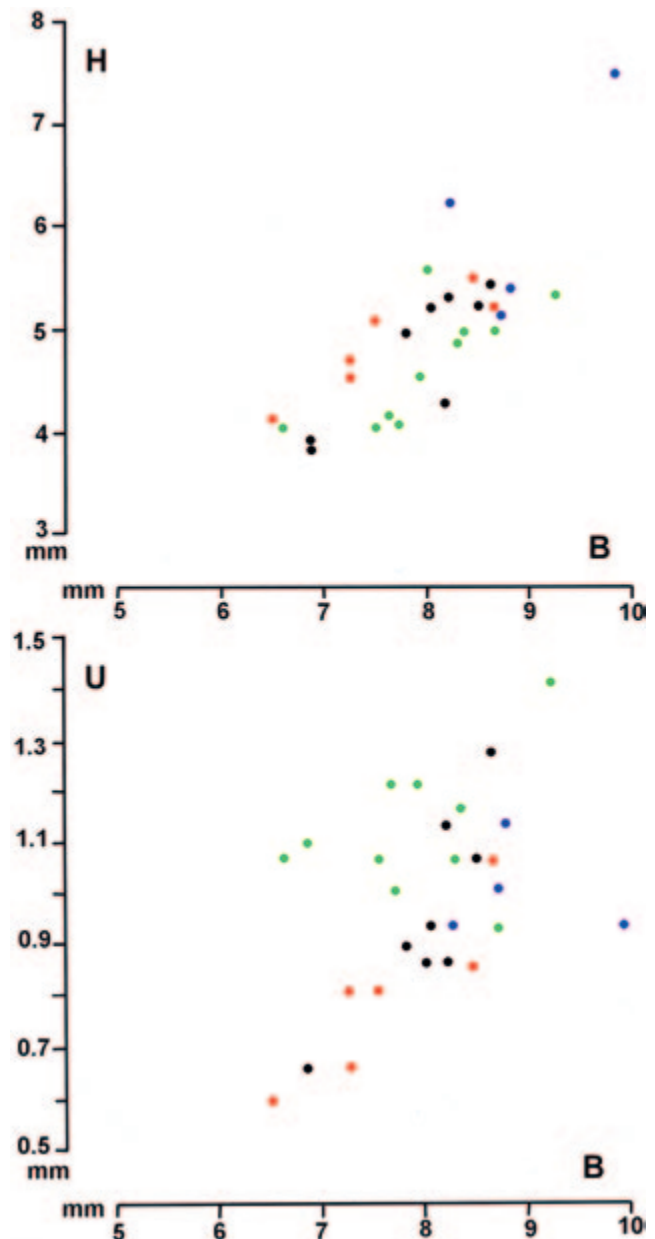
?*Helix protumida* Locard 1899 (p. 99), pars, from Lisbonne. Type locality: "Faro, environs de Lisbonne ([leg.] Castro)". Gittenberger (1993a: 286, 289 fig. 22) cited only "Faro" [Algarve] and designated a Lectotype at MNHN; syn. *fide* Gittenberger (*loc. cit.*).

?*Helix Lusoi*, Servain, 1880: Locard (1899: 100) non *H. lusoi* Servain 1880 (p. 84). Servain's type material came from "Alluvions de l'Arta, à Pampelune" [Spain] (syntypes MHNG 14422/1, MHNG 14423/1, MHNG 14424/3 *fide* E. Neubert *in litt.*) so it is unlikely to be of the same species as Locard's report of a shell resembling his *Helix ofellata* from "Environs de Lisbonne ([leg.] Castro)".

*Helix intersecta*, Poiret: Locard (1899: 104), pars?, non Poiret 1801. Locard (*op. cit.*, p. 105) named the following varieties from Portugal: "les var. *grisea*, *luteola*, *fusca*, *marmorata*, *flammulata*, *zonata*, etc."; all are *nomina nuda* since none of them has its own description.

*Helix olisippensis* Servain 1880: Locard (1899: 105).

?*Helix herbarum*, Servain 1880: Locard (1899: 106), ? non Servain 1880 (p. 92). Servain's type came from "alluvions du Guadalquivir, à Seville" [Spain] (syntype MHNG 14412/1, *fide* E. Neubert *in litt.*) so it is likely that Locard's material from "Environs de Lisbonne et de Coimbra ([leg.] Castro)" was not of the same species. Locard (*loc.*



**Figure 7** Graphs of variation in shell form of populations of *Candidula olisippensis* from different types of habitat in Portugal; B shell breadth, H shell height, U maximum width of umbilicus. Each point represents mean data for a local population; red points: coastal sand dunes; green points: rocky limestone habitats; blue points: habitats with calcium-poor rocks exposed; black points: other habitats (ruderal and grassland); specimens are in CGAH and listed in the Appendix.

*cit.*) also named "les formes *minor* ... formes *major* ... des var. *grisea*, *luteola*, *marmorata* et *zonata*", all of which are *nomina nuda*.

?*Helix pictonum*, "Bourguignat in" Locard 1882: Locard (1899: 106), ? non "Bourguignat in" Locard 1882. The type locality of *H. pictonum* was in

W. France so it is unlikely that Locard's Portuguese material which resembled *Helix herbarum* was the same species. Locard (*loc. cit.*) named "var. *grisea*, *luteola*, *marmorata*, *unizonata*, *multizonata*, etc.", all of them *nomina nuda*.

?*Helix specialis*, "Bourguignat, in" Servain 1880: Locard (1899: 106), ? non Servain 1880 (p. 95). The taxon was originally described as "abondante en Algérie" and also from Spain "environs de Grenade, de Cordoue et de Badajoz"; Locard's material from "Estoy [Algarve] ([leg.] Castro" was compared by him to *Helix pictonum* and attached to the "groupe de l'*Helix intersecta*" but it is unlikely that the same species was involved, or *H. intersecta* Poiret 1801.

?*Helix hispalina*, Servain 1880: Locard (1899: 197), ? non *H. hispalina* Servain 1880 (p. 90)=*C. gigaxii* *vide* Gittenberger (1993a: 285). Locard's material from "Porto, [and] environs de Lisbonne ([leg.] Castro)" was compared to *H. specialis* and described as part of a group of forms intermediate between the "groupe de *Helix unifasciata* et ceux du groupe de l'*Helix intersecta*"; nevertheless, it is unlikely that it was conspecific with Castro's type material or either of the other two species he mentioned.

?*Helix evula* "Bourguignat" Locard 1899 (p. 100), pars, from Lisbonne. Type locality: "Environs de Lisbonne (collect. Bourguignat); Estoy [Algarve] [=Estói] ([leg.] Castro)". Syntype MHNG 14443/1 (E. Neubert *in litt.*). This name was not discussed by Gittenberger (1993a), although Locard compared it with *H. intersecta* and *H. codopsis*; its identity remains uncertain.

*Helix intersecta*, Poiret: Nobre (1913: 197), pars, non Poiret 1801.

*Helix intersecta*, Poiret: Nobre (1941: 103), pars, non Poiret 1801.

*Candidula intersecta* (Poiret, 1801): Backhuys (1975: 201), non Poiret 1801.

*Candidula olisippensis* (Servain 1880): Gittenberger (1993a: 285), pars, excluding *Helix strucki* (*q.v.*).

*Candidula olisippensis* (Servain 1880): Puente (1994: 372), pars, excluding *Helix strucki* (*q.v.*).

*Candidula intersecta* (Poiret 1801): Matos (2004: 73), pars, non Poiret 1801.

*Candidula olisippensis* (Servain 1880): Matos (2004: 74), pars, excluding *Helix strucki* (*q.v.*).

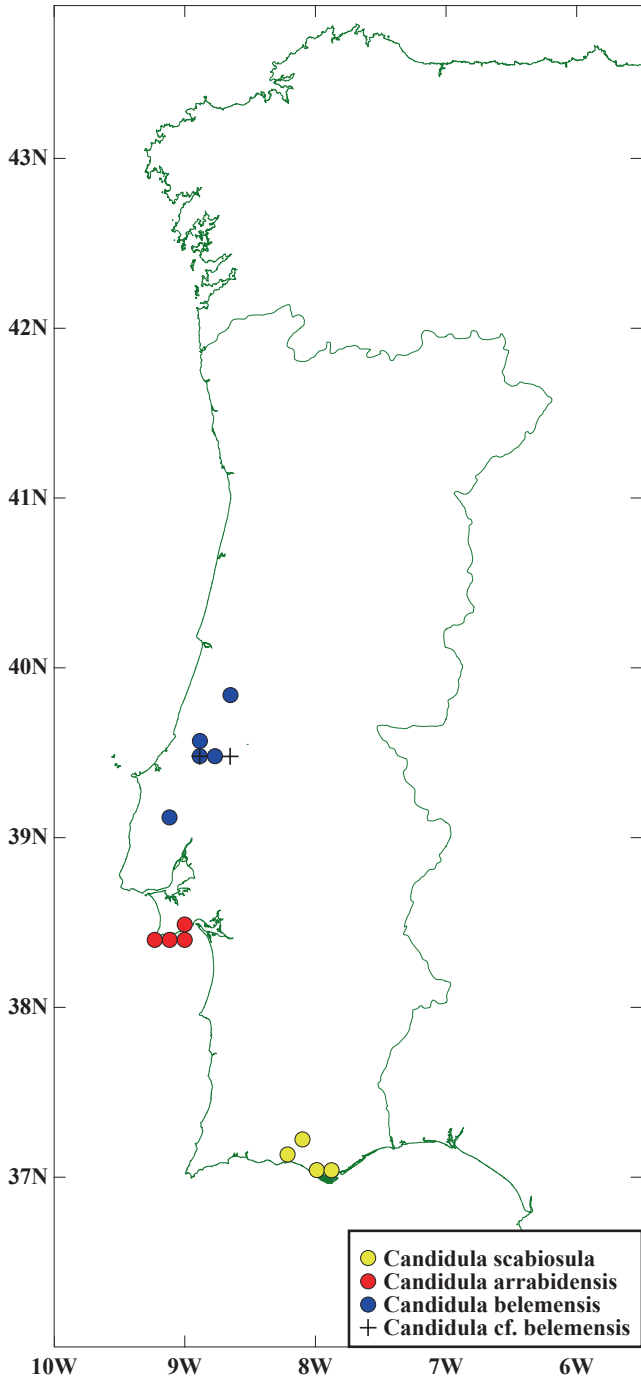
*Diagnosis* Separation from *C. intersecta*, *C. ponsulensis*, *C. strucki*, *C. scabiosa* and *C. arrabidensis*

is only reliable when based on the longer penial flagellum of *C. olisippensis*, although shell characters are usually indicative. Among those species, only *C. intersecta* shows limited range overlap (S. Estremadura, W. Beira Baixa, and in Cornwall); the others are allopatric.

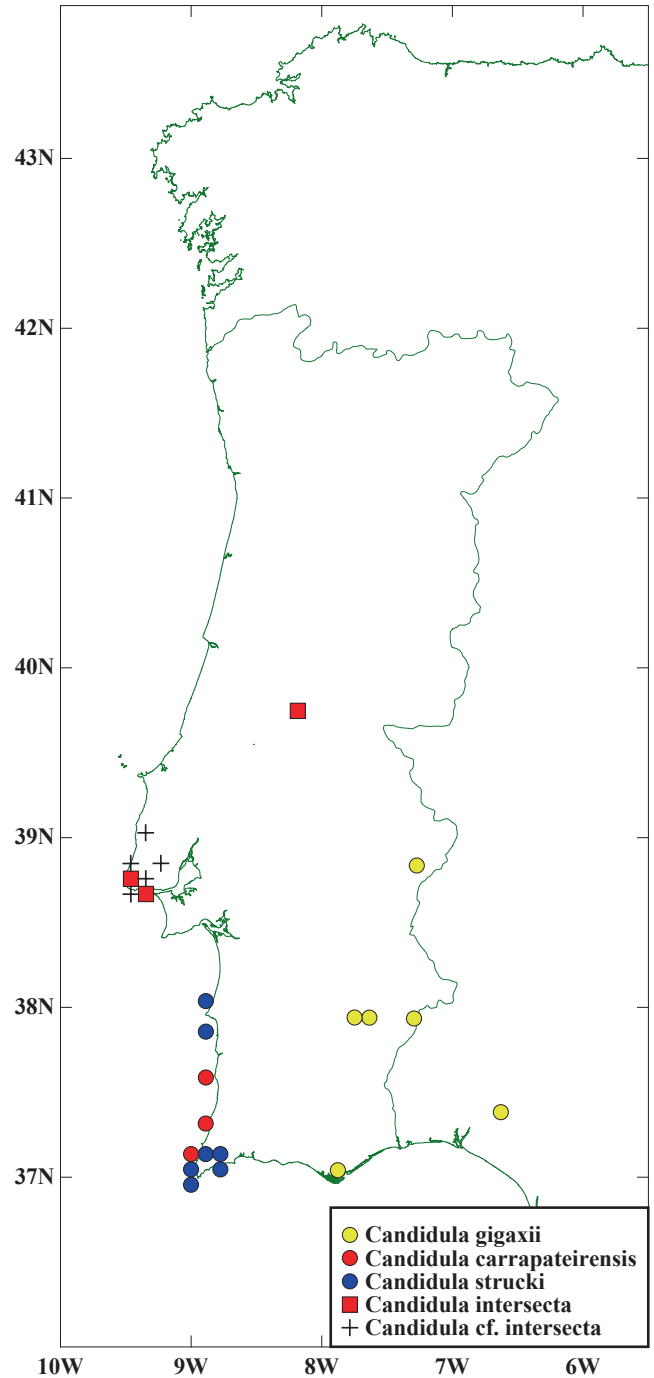
Separation of small-shelled *C. belemensis* from *C. olisippensis* is more troublesome since they are widely sympatric, both have a long penial flagellum and shells of *C. olisippensis* are very variable. However, the latter species usually has a smaller shell with a disproportionately smaller umbilicus, the whorl profile on the spire tends to be rounder, producing deeper sutures, and the ribbing on the upperside of the body whorl is usually more clearly defined. These two species coexist in Beira Litoral, extensively near the summit of Serra de Sicó (Fig. 12A) and at least locally on Monte de Vez (ca 2 km SE. of S. Sebastião), confirming that distinct species are involved.

*Shell* 1555 examined from 44 sites where identification was confirmed by dissection (mainland Portugal 41 sites, Azores 1, NW. Spain 1, SW. England 1). As discussed below, shells of this species differ widely between populations (Figs 3, 7) as well as being polymorphic in coloration and banding within many populations, so species identification often needs confirmation using anatomy (long penial flagellum). However, most populations have a smaller umbilicus than usual in *C. intersecta* or *C. belemensis*, the U/B×100 being 9.2–16.1% (mean 12.44, s.d. 2.17%) in 28 populations. Adult shell size is usually smaller than in *C. belemensis*, the maximum breadth being 6.5–9.0 mm in most populations of *C. olisippensis*, rarely 9.9 mm. *C. belemensis* often has the whorls of the spire flatter, so the suture appears less deep, e.g. where populations of both coexist high on the Serra de Sicó. Nevertheless, many individual shells and even good samples from some populations cannot be reliably distinguished from those of *C. intersecta*, and small-shelled individuals and populations of *C. belemensis* are probably inseparable. *C. ponsulensis* and *C. strucki* are also very close to *C. olisippensis* in shell characters, so separable only by the genital anatomy. Figs of shells are given by Gittenberger (1993a: 288 figs 10–12, 289 figs 13–22) and in our Figs 3D–H.

Portuguese populations often differ widely in shell characters, including overall size, height/



**Figure 8** Distribution of *Candidula scabiosa*, *C. arrabidensis* sp. nov., *C. belemensis* (confirmed by dissection) and *C. cf. belemensis* (shells) based on specimens studied by the authors, mapped by ten-kilometre squares of the U.T.M. grid.

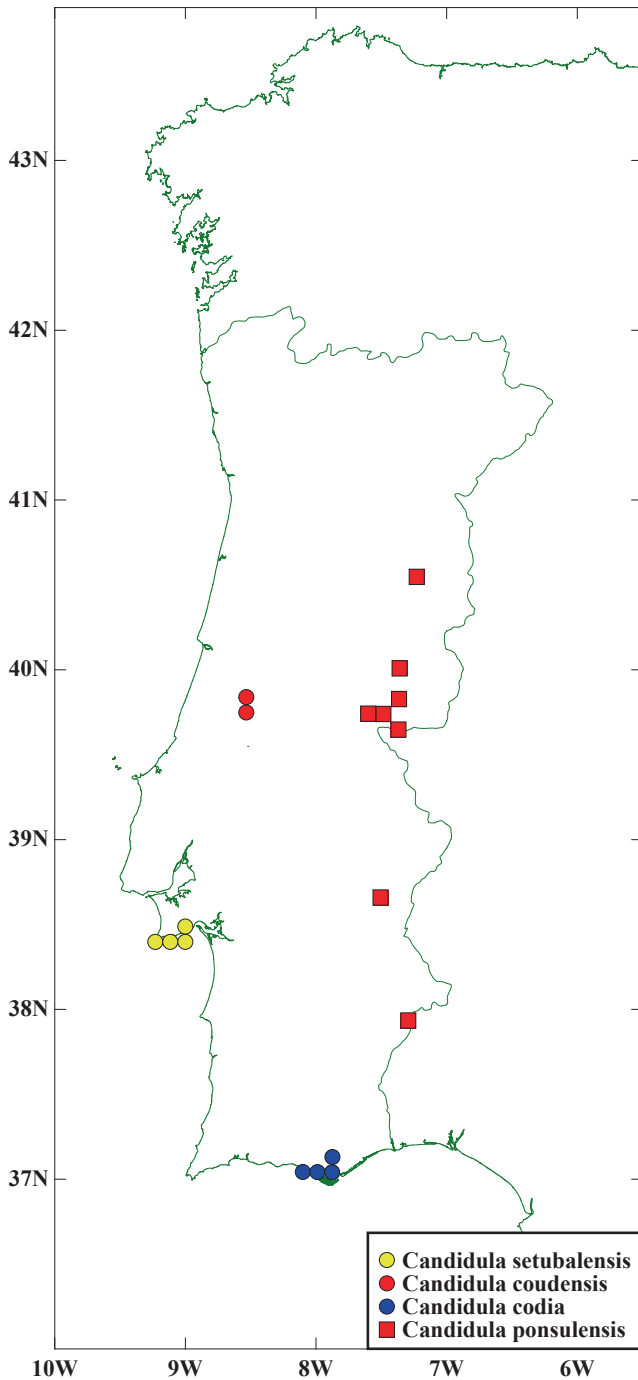


**Figure 9** Distribution in western Iberia of *Candidula gigaxii*, *C. carrapateirensis* sp. nov., *C. strucki* and *C. intersecta* (confirmed by dissection) and *C. cf. intersecta* (shells) based on specimens studied by the authors, mapped by ten-kilometre squares of the U.T.M. grid.

breadth ratio and size of the umbilicus. There are correlations of shell type with habitat type, that initially led us to suspect that more than one species might be involved, or at least several sub-species. We therefore measured representative samples of the larger shells (largest 20% of whole

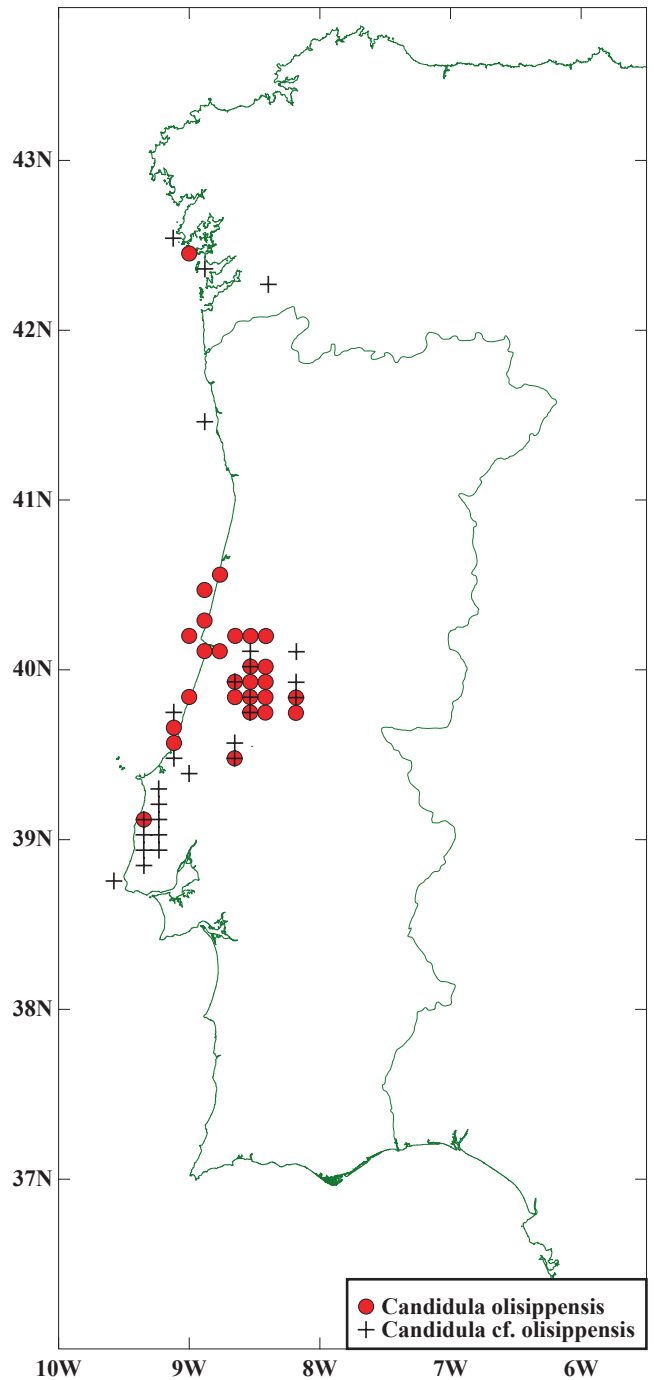
sample) from 28 populations, providing the data shown in Fig. 7 as graphs of mean H versus B and U versus B for each population.

The data confirm the impression that sand dune populations (n=6 populations) tend to have high shells with a small umbilicus (e.g.



**Figure 10** Distribution of *Candidula setubalensis*, *C. coudensis*, *C. codia* and *C. ponsulensis* sp. nov. based on specimens studied by the authors, mapped by ten-kilometre squares of the U.T.M. grid.

Fig. 3D), but their characters overlap those from inland in rocky limestone habitats (n=10) (e.g. Fig. 3G) and grassland/ruderal habitats (n=8). Populations living on acidic (calcium-poor) substrata inland tend to have large shells with a small umbilicus (e.g. Fig. 3F), but again there are exceptions. None of these habitats has a shell



**Figure 11** Distribution in western Iberia of *Candidula olisippensis* (confirmed by dissection) and *C. cf. olisippensis* (shells) based on specimens studied by the authors, mapped by ten-kilometre squares of the U.T.M. grid.

type that is clearly distinct from those in different types of habitat, and no other characters appear to differ among them. Shell ribbing also varies continuously between different populations from rather weak (e.g. Fig. 3F) to strong (Fig. 3H). Hence there seems little purpose in recognising

subspecies which would be hard to diagnose because of intra-population variability and also because some population means depart from the general trend. The possible adaptive significance of differences of shell shape in the different habitats is considered in the Discussion later in this paper.

*Genital anatomy* 99 dissected (+ 14 immatures) from 44 populations (42 in Portugal, one each in NW. Spain and Cornwall, U.K.) (Figs 5D–H, 6D, I). The only really distinctive character appears to be the long penial flagellum, which on mature snails is usually 1.0–1.8×the length of the epiphallus (minimum recorded 0.8 ×, maximum 2.0 ×). Mature snails never had the flagellum as short as in *C. intersepta*; immatures with genitalia about half-sized or larger can be identified using flagellum length.

Castillejo (1986: 14–15) figured genital anatomy of five individuals of "*Candidula intersepta*" from Galicia that all have the penial flagellum longer than in that species (0.9–1.5×length of epiphallus), much more similar to that of *C. olisippensis*. Altaba (1997: 2) suggested *C. belemensis* might be involved, because he wrongly attributed a short epiphallus to *C. olisippensis*. Thus, Altaba (1997: 3) figured genitalia of two (very) immature specimens attributed to this species from N. Portugal (near Braga), with a relatively short penial flagellum. However, study of fully mature specimens from this locality is needed to check the size eventually reached by the flagellum; if it remains shorter than the epiphallus a species other than *C. olisippensis* is presumably involved.

*Taxonomic history* Gittenberger (1993a: 286) hinted that this might represent a complex of species, but gave few details to support his suggestion. We have partly confirmed this by showing that *C. strucki* (see below) from the W. Algarve differs in having a shorter penial flagellum.

Intraspecific variation in shell form within *C. olisippensis* s. str. remains striking now that the "single recently collected large sample" available to Gittenberger (1993a: 286) has been greatly increased, with anatomical data from 42 of the populations. Nevertheless, as discussed above, presence of intermediate shell types suggests there is little value in recognising subspecies.

Pfenninger *et al.* (2003: 617) presented analyses of mitochondrial (16S rDNA +CO1) DNA

showing that *C. olisippensis* (from Torreira [Beira Litoral], Portugal) is clearly distinct from *C. intersepta* (from Belgium) and *C. gigaxii* (from France).

*Helix Letourneuxiana*, Bourguignat 1864 was listed by Locard (1899: 107) from "Environs de Lisbonne ([leg.] Castro)" and said to approach *H. herbarum*. However, it is highly unlikely that it was conspecific with Bourguignat's (1864: 195) type material of *H. letourneuxiana* from Algeria, which E. Neubert (*in litt.*) has identified as a *Xerotracha* not a *Candidula*.

Matos (2014: 204–205) claimed to have added *Candidula unifasciata* (Poiret 1801) to the Portuguese list on the basis of shell specimens in the Coimbra Museum (MZUC). However, the photographs show these were almost certainly misidentified, along with several of the other photos of *Candidula* species in her book: figura 166 of a shell from near Coimbra (MZUC. CP.502) probably shows small-shelled *C. olisippensis* much like material we have dissected from that region; figura 167 of a shell from Barreiro (MZUC. CP.507) named as *C. unifasciata rugosiuscula* (Michaud 1831) shows either *Microxeromagna lowei* (Potiez & Michaud 1835) or *Xerotracha conspurcata* (Draparnaud 1801).

*Geographical range* The range in Portugal includes records confirmed anatomically from Minho, Beira Alta, Beira Baixa, Beira Litoral, Estremadura and Ribatejo (Fig. 11; Appendix); it doubtless also occurs in Douro Litoral where shells are reported. However, reports based only on shells from the Algarve are probably referable to *C. strucki* (*q.v.*) and possibly other species. Distribution maps in Gittenberger (1993a: 293) and Puente (1994: 373) showed a wider range because they were based on a broader delimitation of the species than that adopted here.

The present study has obtained new records from NW. Spain (SW. Galicia: Fig. 11). Castillejo's (1986: 14–15) figures of the anatomy of "*C. intersepta*" from elsewhere in Galicia probably also show this species, as discussed above. It was more surprising to record it from SW. England (Kynance, Lizard pen., Cornwall: see Appendix, Fig. 12D), new to the British Isles, in native vegetation on top of a sea cliff, away from habitation. The only adult material we have dissected from the Azores (Santa Maria) was also of *C. olisippensis*, not *C. intersepta* as previously reported from Santa Maria and São Miguel (Backhuys,



1975: 201; Bank *et al.*, 2002: 126), presumably implying introduction of the genus to this archipelago from Portugal rather than further north in Europe. Locard (1894: 182–183) reported the species from France among numerous other segregate species that appear to have been listed only on the basis of shell characters; anatomical confirmation of its possible occurrence in France is therefore needed.

*Candidula ponsulensis* D.T. Holyoak & G.A.

Holyoak sp. nov.

Figs 1B, 3A, 4H, I, 6G, 10

*Types* Holotype (Fig. 3A): by N240 on W. bank of Rio Pônsul, W. of Ladoeiro, 29S 064235/441332, S.-facing rocky (sandstone) banks/cutting with patchy scrub and grasses, 183 m alt., 2010.12.23, GAH & DTH 2010.P88, NHMUK 20140015/1 (1 sh, breadth 9.8 mm) & 20140015/2 (bod). Paratypes: 128 shells, 49 bod, from several localities, in CGAH (listed in Appendix).

*Type-locality* By N240 on W. bank of Rio Pônsul, W. of Ladoeiro (Beira Baixa, Portugal).

*Synonyms* *Helix intersecta*, Poiret: Nobre (1941: 103), pars, non Poiret 1801.

*Candidula intersecta* (Poiret 1801): Puente (1994: 361) pars? (see below).

*Diagnosis* Resembles the allopatric *C. intersecta*, very closely in genital anatomy, with penial flagellum 0.2–0.35×length of epiphallus. The general appearance of the shell is also similar (Fig. 3A cf. 3B), but *C. ponsulensis* differs subtly in several shell characters: transverse ribs weaker, usually low or lacking on ventral surface of shell; upper whorls of spire less rounded, so suture shallower in upper part of shell; umbilicus averaging narrower, usually not becoming slightly excentric on mature shells through expansion of body whorl; papillose micro-sculpture in umbilicus more extensive, typically reaching its periphery. The range of shell coloration also appears to be different in *C. ponsulensis*, with none of the shells seen having sharply defined continuous dark bands on the upperside, whereas these are frequent in most populations of *C. intersecta*.

*Shell* 134 examined from 8 localities (of which 126 were from 6 localities where identification was confirmed by dissection). Strongly convex

to convex above, flattened below; height 5.8–7.0 mm, breadth 9.1–10.3 mm, B/H 1.47–1.65, with 5.2–5.8 whorls. Whorls rounded, sometimes with slight peripheral keel (the keel prominent in subadults); sutures shallow on most of spire, often deeper above last half of body whorl. Umbilicus rather narrow (1.1–1.4 mm, representing 11.0–12.6% [occasionally 13.7%] of shell breadth), symmetrical, deep, partly overlapped by reflected peristome, exposing upper whorls in oblique view. Mouth broadly oval, except where interrupted by penultimate whorl; last half of body whorl expanding and often descending markedly below penultimate whorl, sometimes also with downturn just behind edge of mouth. Mouth edge thin, reflected only near umbilicus. Inside of mouth on some mature shells with low white rib developed, the rib set back from palatal and columellar edges. Shell rather thin, often translucent; weakly glossy above, more strongly glossy beneath. Ground colour on upperside pale to light brown, often with orange or pinkish tinge, paler on underside; the upperside usually with interrupted band of red-brown to dark brown blotches near periphery, remainder variably blotched or suffused brown and light buff, the rib crests often pale; underside almost unmarked to weakly marked with thin brown bands (often interrupted), thin translucent bands, or buff spots. Transverse ribs mainly rather weak, especially on underside of shell where they are sometimes absent or weakly indicated. Spiral lines strong on underside of shell.

Populations apparently differ slightly in mean shell size and coloration. Samples from N. of Bizarrinho in Beira Baixa (P303, P305) mainly have ground colour of shell paler, the lightest being whitish above and below, with few dark markings.

*Genital anatomy* 11 dissected (+ one immature) from six Portuguese populations (Figs 4H, I, 6G).

*Geographical range* Our records confirmed by anatomical and detailed conchological study are only from E. Portugal, from localities in dry regions on acidic rocks in S. Beira Alta, Beira Baixa and E. Baixo Alentejo (Figs 10, 12F). Genital anatomy of “*C. intersecta*” with a short penial flagellum was figured from similarly dry parts of the interior of W. Spain from the Provinces

of Cáceres, Salamanca, Segovia, Valladolid and Zamora by Puente (1994: 364–373). Some of these specimens were from localities close to the Portuguese records of the closely similar *C. ponsulensis*, so it is most likely this cryptic taxon rather than *C. intersecta* that was involved. Single reports of “*C. intersecta*” from Prov. Cáceres and S. Prov. Badajoz in Muñoz & Parejo (1994: 192–193) also seem likely to be referable to *C. ponsulensis*.

*Etymology* The species epithet *ponsulensis* is an adjective derived from the type locality near the Rio Pônsul.

***Candidula scabiosa*** (Locard 1899)  
Figs 2C, 6J, 8

*Helix scabiosa* Locard 1899 (p. 87). Type locality “Estoy [Algarve] ([leg.] Castro)” [= Estói]. Lectotype at MNHN designated by Gittenberger (1993a: 285, 290 fig. 28).

?*Helix Barcinensis*, Bourguignat 1864: Locard (1899: 11) non Bourguignat 1864 (2: 355, *nomen nudum*), non Bourguignat 1868 (pp. 303–304, pl. 42 figs 12–16). The type was from Barcelona and it is now regarded as a synonym of *Helicella madritensis* (Rambur 1868), following Martínez-Ortí & Gittenberger (2004); that species was recently recorded for the first time in Portugal in Alto Alentejo (Holyoak, Holyoak & Mendes, 2014: 50), but it is unlikely that Locard’s material from “Faro [Algarve] ([leg.] Castro)” was the same taxon.

?*Helix callisona* Locard 1899 (p. 93). Type locality: “Estoy” [Estói, Algarve]. Lectotype at MNHN designated by Gittenberger (1993a: 286, 289 fig. 19).

?*Helix protumida* Locard 1899 (p. 99), pars, from Algarve. Type locality: “Faro, environs de Lisbonne ([leg.] Castro)”. Gittenberger (1993a: 286, 289 fig. 22) cited only “Faro” [Algarve] and designated a Lectotype at MNHN.

?*Helix evula* “Bourguignat” Locard 1899 (p. 100), pars, from Estoy. Type locality: “Environs de Lisbonne (collect. Bourguignat); Estoy [Algarve] [= Estói] ([leg.] Castro)”. Type perhaps in MHNG. This name was not discussed by Gittenberger (1993a), although Locard compared it with *H. intersecta* and *H. codopsis*; its identity remains uncertain.

?*Helix Iberica*, Rambur 1869: Locard (1899: 111) non Rambur 1869. *Helicella iberica* (Rambur

1869) is an endemic species from N. Spain, so it is unlikely that Locard’s material from “Faro [Algarve] ([leg.] Castro)” is the same species; however, the shell characters are rather similar to those of *C. scabiosa*. Locard (*loc. cit.*) also named *H. iberica* “var. major et minor ... var. globulosa, depressa, conica et subcarinata”, none of them being linked individually to the few words of description so therefore apparently *nomina nuda*. *Helix intersecta*, Poiret: Nobre (1913: 197), pars non Poiret 1801.

*Candidula belemensis* (Servain 1880): Gittenberger (1993a: 284), pars non *Helix belemensis* Servain 1880 as restricted here (excluding records from N. of Lisbon: see notes above under *C. belemensis*).

*Candidula belemensis* (Servain 1880): Puente (1994: 344), pars non *Helix belemensis* Servain 1880 restricted here (excluding records from N. of Lisbon: see notes above under *C. belemensis*).

*Candidula intersecta* (Poiret 1801): Matos (2004: 73), pars.

*Diagnosis* See notes above under *C. arrabidensis* for differences from that species and *C. belemensis*; also the following two sections and the Key below.

*Shell* 78 examined from 6 sites (including 39 from 1 site where identification was confirmed by dissection). Shells very similar to those of *C. arrabidensis* and *C. belemensis*, with a relatively large umbilicus, but shell breadth smaller at maturity and ribs on dorsal surface of body whorl less developed (absent or very weak) (Figs 2C). It was figured as *C. belemensis* by Gittenberger (1993a: 290 fig. 28).

*Genital anatomy* Seven dissected (+ five immatures) from localities in the Algarve, Portugal (Fig. 6J). It differs from *C. belemensis* in the much shorter penial flagellum. The genital anatomy was figured by Gittenberger (1993a: 292 fig. 36) as “*C. belemensis*”, from near Boliqueime.

*Taxonomic history* Although this species was named by Locard (1899), it was treated as a synonym of *C. belemensis* by Gittenberger (1993a).

*Geographical range* Endemic in Portugal, where restricted to limestone districts of C. Algarve (Fig. 8).

*Candidula setubalensis* (L. Pfeiffer 1850)

Figs 1A, 2H, 6K, 10

*Helix serrula* Fer.: Morelet (1845: 61, pl. 7, fig. 2), non *H. serrula* Benson 1836. Type locality: les collines rocheuses qui s'élèvent au nord de Setúbal sur le bord de la mer [= Serra da Arrábida].

*Helix setubalensis* L. Pfeiffer 1850 (p. 88). Type locality: in Lusitania; *prope* Setubal [= Setúbal, Estremadura], "ex colln. Morelet". Type specimens not located.

*Helix serrula*. Morlt.: Silva (1871: 192).

*Helix Setubalensis* Pfeiffer: Hidalgo (1875: 207), pars.

*Helix Setubalensis*, Pfeiffer: Hidalgo (1878: 229).

*Helix setubalensis* Pfeiffer: Kobelt (1884: 54, pl. 19, fig., 156).

*Helix setubalensis*, Pfeiffer: Nobre (1913: 192).

*Helix setubalensis*, Pfeiffer: Nobre (1941: 98).

*Trochoidea (Xeroplexa) setubalensis*: Zilch (1960: 670), as type species of the new subgenus *Xeroplexa*.

*Candidula setubalensis* (Pfeiffer 1850): Gittenberger (1985: 61).

*Candidula setubalensis* (Pfeiffer 1850): Gittenberger (1993a: 286).

*Candidula setubalensis* (Pfeiffer 1850): Puente (1994: 378).

*Candidula setubalensis* (L. Pfeiffer 1850): Matos (2004: 75).

**Diagnosis** The only other Portuguese *Candidula* with a keeled shell is the allopatric *C. coudensis*, which differs in having a much longer penial flagellum.

**Shell** 193 examined from five sites in Serra da Arrábida and one SE. of Azóia (near Cabo Espichel). The differences in shell characters between *C. coudensis* and *C. setubalensis* suggested by Holyoak & Holyoak (2010) have been found to be inconstant based on larger samples. Shells of *C. setubalensis* are figured by Hidalgo (1884: pl. 32, figs 360–362), Kobelt (1884: pl. 19, fig. 156), Matos (2005: 5), Kittel (2000: 16) and in our Fig. 2H.

**Genital anatomy** Three dissected (+ one immature) from one locality (Fig. 6K). The genital anatomy was first described and figured by Gittenberger (1985: 60–61). In its distal genital anatomy it is generally similar to the other Portuguese *Candidula*; it has a short penial flagellum (0.5–0.7×length of the epiphallus).

**Taxonomic history** First named as *Helix serrula* by Morelet (1845) but the name he used was preoccupied; Pfeiffer (1850) provided the valid replacement name *H. setubalensis*. During the mid-nineteenth century *H. setubalensis* was reported in error from Alicante (by Rossmässler, Hidalgo), Mallorca (by Dohrn, Barceló) and Menorca (Barceló); Hidalgo (1878: 229) pointed out that only the report from Setúbal is correct. Zilch (1960: 670) placed it in a subgenus of *Trochoidea* on the basis of the keeled shell, but Gittenberger (1985) provided details of the genital anatomy which confirmed that it belongs in *Candidula*.

**Geographical range** Endemic in Estremadura, Portugal, where hitherto regarded as restricted to Serra da Arrábida (W. of Setúbal), but also found by us in 2014 on limestone rocks above the coast SE. of Azóia, near Cabo Espichel (Fig. 10; Appendix). The schematic distribution map published by Kittel (2000: 17) implied the range extends north of Setúbal in the Serra de S. Luis and for a short distance south-east of the city, but although this is quite probable the basis for it is unclear from the accompanying text.

The IUCN Red List currently treats *C. setubalensis* as Endangered (Martínez-Ortí, 2011), stating "This is a Portuguese endemic restricted to the Serra da Arrabida. It has a restricted extent of occurrence (EOO=100 km<sup>2</sup>) and area of occupancy (AOO=10 km<sup>2</sup>), and one location. The main threats to this species are fires, road construction and tourism, which cause a decline in the quality and extent of its habitat. Significant parts of the area have been destroyed by a fire in 2004, and it is to assume that the population of this species has been heavily affected. Therefore it is assessed as Endangered (EN) B1ab(iii)+2ab(iii). More research on the population size, the distribution and the effects of human disturbances and the recent fire event is needed." Our records from 2010–2014 (Appendix) were based on brief visits not detailed surveys. They nevertheless revealed living populations at two localities in the Serra da Arrábida (one of them on a road-cutting) and a third on coastal slopes ca 17 km further to the south-west (outside the Parque Nacional da Arrábida). Hence its threat status should probably be revised to "Vulnerable", pending detailed surveys.

*Candidula strucki* (Maltzan 1886)  
Figs 3C, 6M, 9

*Helix Strucki* Maltzan 1886 (p. 26). Type locality: Almadena et St. Vincent, Algarve (Portugal); restricted to "Cabo de São Vicente, Algarve" by Gittenberger (1993a: 285) although he apparently only saw material from "along the road between Cabo de São Vicente and Sagres" (*ibid.*, p. 286) or "Cabo de São Vicente – Sagres (RMNH)" (*ibid.*, p. 291, p. 293 Map C); we have failed to find any *Candidula* on the exposed Cabo de São Vicente headland, although they are common nearer Sagres.

*Helix codia* var. *strucki* Maltz.: Westerlund (1889: 258).

*Helix Strucki*, Maltzin [*sic*], 1883: Locard (1899: 109).

*Helix intersecta* var. *struchii* [*sic*] Maltzan: Nobre (1941: 106).

*Candidula olisippensis* (Servain 1880): Gittenberger (1993a: 285), pars non *Helix olisippensis* Servain 1880 (see above under *C. olisippensis* and the notes below).

*Candidula olisippensis* (Servain 1880): Matos (2004: 74–75), pars non *Helix olisippensis* Servain 1880 (see above under *C. olisippensis* and note under "Taxonomic history" below).

**Diagnosis** Close to the allopatric *C. olisippensis* in shell characters, but differing in having a shorter penial flagellum. The allopatric *C. intersecta* has similar anatomy, although its penial flagellum is typically shorter (0.2–0.35×length of epiphallus,

cf. 0.2–0.7×in *C. strucki*); it also differs in several shell characters including the (usually) wider umbilicus. *C. carrapateirensis* (*q.v.*) from sand dunes in the W. Algarve and W. Baixo Alentejo differs markedly in shell characters.

**Shell** 396 examined from 8 localities (of which 366 were from 5 localities where identification was confirmed by dissection). Much like some populations of *C. olisippensis* in shell characters, being rather small and typically with a very narrow or narrow umbilicus (Fig. 3C), but several populations have the umbilicus larger. Shells of this species were figured as *C. olisippensis* by Gittenberger (1993a: 291 figs 31, 32) and Simões (2007: 3, 4).

**Genital anatomy** Six dissected (+ five immatures) from three localities in the Algarve (Fig. 6M); two dissected (+ eight immatures) from two localities in Baixo Alentejo.

**Taxonomic history** Although named by Maltzan (1886), no differences from *C. olisippensis* were indicated and Gittenberger (1993a: 285) therefore treated them as synonyms. However, the present study has revealed that the W. Algarve populations named as *strucki* and similar snails from the coast of W. Baixo Alentejo differ consistently in having a much shorter penial flagellum.

**Geographical range** Endemic in SW. Portugal where known only in W. Algarve (over limestone and on sandy coastal slopes) and on coastal sands of W. Baixo Alentejo northwards to Costa de San André (Fig. 9; Appendix).

**KEY TO CANDIDULA SPECIES OCCURRING ON THE MAINLAND OF PORTUGAL**

- |  |                        |
|--|------------------------|
| 1. Adult shell with periphery of body whorl sharply keeled   | 2.                     |
| —Adult shell with periphery of body whorl ± rounded  | 3.                     |
| 2. Penial flagellum shorter than epiphallus; Serra da Arrábida and near Cabo Espichel (S. Estremadura)   | <i>C. setubalensis</i> |
| —Penial flagellum longer than epiphallus; Vale da Couda and nearby (Beira Litoral)   | <i>C. coudensis</i>    |
| 3. Shell with close regular ribbing on body whorl (Fig. 2F); umbilicus rather wide and excentric because of rapid expansion of body whorl; spire low; penial flagellum much shorter than epiphallus                                    | <i>C. gigaxii</i>      |
| —Shell with ribbing on body whorl more widely spaced or ± obsolete; umbilicus often narrower, less excentric; spire low or high; penial flagellum shorter or longer than epiphallus  | 4.                     |
| 4. Shell depressed globular with domed spire; sutures of upper part of spire very shallow; sculpture of strong to very strong regular ribs; penial flagellum longer than epiphallus; juvenile shell with minute hairs; C. Algarve only | <i>C. codia</i>        |
| —This combination of characters lacking; juvenile shell lacking hairs  | 5.                     |

5. Penial flagellum (0.8) 1.0–1.8 (2.0)×length of epiphallus at maturity (population mean >1.2); in Portugal known only from R. Tejo estuary northwards 6.  
 —Penial flagellum (0.1) 0.2–1.2 (1.3)×length of epiphallus at maturity (population mean <1.2); in Portugal known mainly from south of R. Tejo estuary and eastern Beira Baixa 7.
6. Adult shells usually smaller (breadth < 10 mm); umbilicus typically narrow, sometimes medium width; whorls of upper spire rounded, so suture relatively deep; ribs on body whorl usually strong (occasionally very strong); on limestone and acidic hills, sand dunes, roadsides, disturbed ground, etc. *C. olisippensis*  
 —Adult shells usually larger (breadth > 10 mm); umbilicus typically medium width to wide; whorls of upper spire flattened, so suture relatively shallow; ribs on body whorl usually weaker, sometimes almost obsolete; typically on rocky limestone hills *C. belemensis s. str.*
7. Shells medium sized to large (breadth often > 10 mm) with wide umbilicus (≥ 16% of shell breadth); ribs on dorsal surface of body whorl often weak to obsolete; upper whorls flattened with shallow suture; occurring on rocky limestone hills 8.  
 —Shells small to medium sized (breadth < 10.5 mm), usually with narrow umbilicus (≤ 16% of shell breadth); ribs on dorsal side of body whorl well developed; upper whorls flattened to rounded with suture shallow or deeper; occurring on limestone, over acidic rocks, on sand dunes, etc. 9.
8. Penial flagellum 0.2–0.4×length of epiphallus; shells often large; ribs on dorsal surface of body whorl weak or obsolete in places; Serra da Arrábida and near Cabo Espichel (Estremadura) *C. arrabidensis*  
 —Penial flagellum 0.7–1.3×length of epiphallus; medium-sized shells; ribs absent or very weak on dorsal surface of body whorl; C. Algarve *C. scabiosa*
9. Flagellum 0.25–0.7×length of epiphallus; heavy blackish pigmentation around base of dart sac; umbilicus very narrow to narrow; whorls of spire flattened with shallow suture or rounded with deep suture; taxa restricted to W. Algarve and coast of W. Baixo Alentejo 10.  
 —Flagellum (0.1)0.2–0.35 (0.4)×length of epiphallus; often little or no blackish pigmentation around base of dart sac; umbilicus narrow to medium width; whorls of spire flattened with shallow suture; taxa not known from Algarve or coast of Baixo Alentejo 11.
10. Whorls of spire flattened above; shell flattened below; mouth oval; peristome with thickened white internal rib in adult shells *C. strucki*  
 —Whorls of spire rounded above; shell not flattened below; mouth almost round; peristome always lacking a thickened white internal rib *C. carrapateirensis*
11. Transverse ribs weaker, on ventral surface of shell usually weak or lacking; upper whorls of spire less rounded, so suture shallower in upper part of shell; umbilicus averaging narrower (usually 11–12% of shell breadth, maximum 13.7%), usually not becoming slightly excentric on mature shells through expansion of body whorl; papillose micro-sculpture in umbilicus more extensive, typically reaching its periphery; sharply defined continuous bands of dark colour absent from upperside of shell *C. ponsulensis*  
 —Transverse ribs stronger, on ventral surface of shell usually present and often well developed, although weaker than on dorsal surface; upper whorls of spire more rounded, so suture deeper in upper part of shell; umbilicus averaging wider, becoming slightly excentric on mature shells through expansion of body whorl; papillose micro-sculpture in umbilicus less developed, usually not reaching its periphery; upperside of shell often with sharply defined continuous bands of dark colour *C. intersecta*  
 (very local in Portugal)

### HABITATS AND ECOLOGY

The W. European *Candidula* species are generally associated with grasslands and other open habitats, avoiding closed woodland cover and mainly preferring dry or at least freely-draining habitats and calcareous substrata. Several authors have pointed out differences between the species in habitat preferences, e.g., in England *C. gigaxii* often occurs in somewhat taller vegetation of herbs and grasses than *C. intersecta*, which can live in very open, heavily grazed grasslands (Stelfox, 1912; Ellis, 1926: 200; Kerney & Cameron, 1979: 177; pers. obs.). Pfenninger, Nowak & Magnin (2007) provided quantitative data on niche differences between *C. gigaxii* and both *C. unifasciata* and *C. rugosiuscula*, showing that only *C. gigaxii* has occupied a wider range of habitats as it expanded its range northwards.

The 12 *Candidula* species known in Portugal also show some interspecific differences in habitats. Five of them are mainly restricted to open and rocky limestone habitats such as in grasslands, on limestone pavement, or around crags (*C. belemensis*, *C. codia*, *C. coudensis*, *C. scabiosula*, *C. setubalensis*) (e.g. Figs 12A, B). *C. arrabidensis* is also nearly restricted to limestone karst habitats, but with one record of a few shells on sandy coastal slopes above sea-cliffs (W. of Meco, P357). *C. strucki* also occurs over exposed limestone, but with single records also from open disturbed grassland with few rocks (of limestone), a slaty road cutting and stable sand dunes and two records from rocky (shale) coastal sites with blown sand. *C. carrapateirensis* is known from only three localities, on dunes of calcareous sand (e.g. Fig. 12E), where it lives in places with more mobile sand than is tolerated by congeners. The few Portuguese records of *C. gigaxii* and one of a large population of *C. intersecta* are from open disturbed sites with grassland and at least locally calcareous substrata (due to masonry), but with few or no natural limestone rock outcrops. *C. ponsulensis* differs from all the other species in occurring only on calcium-poor substrata, with no records from limestone regions or sand dunes; its sites are mainly on slaty and sandstone road cuttings (e.g. Fig. 12F), all of them in regions with hot summers and low rainfall. The last of the species, *C. olisippensis*, is clearly the most tolerant, occurring in a wide range of habitats, on sand dunes (Fig. 12C), limestone karst (Figs 12A, B),

grasslands, slaty and other roadsides and gravel car parks. It extends from sandy coasts and their hinterlands on Tertiary sands, through regions with hills of Mesozoic limestones to higher hills of calcium-poor Palaeozoic rock.

There are surprisingly few records of different Portuguese *Candidula* species coexisting. The exceptions include both of the very localised species with keeled shells, which live with round-shelled congeners: thus, *C. coudensis* normally lives alongside *C. olisippensis*, *C. setubalensis* alongside *C. arrabidensis*, without obvious niche differences, the round-shelled and keeled taxa occurring intermixed. Otherwise, we have found only two instances of the extensive coexistence of living *C. belemensis* with *C. olisippensis* (see below for further details from one of the localities), and one of a few *C. gigaxii* near a few *C. ponsulensis*. There are several records of a few old shells of a second species at or near living populations, involving old *C. gigaxii* and old *C. scabiosula* shells near each other or living *C. codia*, but these do not confirm that the species coexisted.

Since some of the *Candidula* species are locally common in Portugal the scarcity of records of them coexisting is noteworthy and suggests competitive interactions may be responsible. However, species of other helicellid genera very often coexist with *Candidula* in Portugal, especially *Cernuella virgata* (Da Costa 1778), *Helicella cistorum*, *Microxeromagna lowei*, *Xerotricha apicina* (Lamarck 1822) and *X. conspurcata*, less often *Xerosecta promissa* (Westerlund 1893) and rarely others.

Our field notes record several instances where different Portuguese *Candidula* species appear to occupy differing daytime resting sites, although much fuller studies are necessary to establish whether the differences are local, seasonal, related to weather, or consistent species-specific preferences.

For example, living animals of *C. codia* found during January and February 2011 were encountered only beneath limestone rocks, mostly small to large boulders, occasionally smaller flakes of rock. They typically rested during the day stuck onto the underside of rocks (Fig. 1E), with a few on the shaded soil surfaces. They were mostly scarce and hard to find, but locally frequent at site P117. *C. scabiosula* was also found during January-February 2011 at Rocha da Pena only beneath limestone rocks, usually stuck onto the



**Figure 12** Habitats of *Candidula* species, in Portugal (A–C, E, F) and Great Britain (D): **A** Beira Litoral, Serra de Sicó summit area, site 2011.P132, limestone karst near hill top, 2011.02.24, in area with *C. belemensis* and *C. olisippensis* coexisting; **B** Beira Litoral, edge of Vale da Couda ESE. of Almoester, limestone slope with crags, 2009.12.08, area with *C. coudensis* (close to its type locality) and *C. olisippensis* coexisting; **C** Beira Litoral, just N. of Praia da Tocha (site 2010.P49), dunes of calcareous sand with patches of low bushes, 2010.06.06, with *C. olisippensis*; **D** West Cornwall, Kynance Cliff, short herb-rich grassland on exposed top of serpentinite sea-cliff, 2011.04.06, with *C. olisippensis* from here newly recorded for Great Britain; **E** Algarve, ca 0.5 km W. of Carrapateira (site 2011.P123), dunes of calcareous sand with mainly low bushes, 2011.02.07, type locality of *C. carrapateirensis*; **F** Beira Baixa, by N240 on W. bank of Rio Pônsul W. of Ladoeiro (site 2010.P94), calcium-poor slopes with exposed slaty and sandstone rock, 2010.12.27, type locality of *C. ponsulensis*.

underside of boulders. Similarly, *C. ponsulensis* was found mainly on the underside of rocks, but of slaty or fine-grained sandstone lithologies, much like the *Helicella cistorum* that was often present at the same localities.

These observations contrast with those made over several years in WC. Portugal, where *C. belemensis* and *C. olisippensis* were often found resting during the day on grasses or herbs, as well as occurring beneath rocks. Fewer observations made it clear that the keeled *C. coudensis* and *C. setubalensis* showed similarly varied preferences, with both species frequently collected from resting places above ground on herbs and grasses in addition to sites beneath limestone rocks. Along the sand dunes of the coasts of WC. Portugal the trochoid-shelled forms of *C. olisippensis* were found alive mainly under edges of low *Cistus* bushes (e.g. Fig. 12C) on sparse leaf-litter and damp sand. There is normally very little grass and no boulders within the habitats of those populations.

On the summit area of Serra de Sicó (Fig. 12A) populations of *C. belemensis* and *C. olisippensis* were found living together over a sloping area of rocky limestone karst and flatter ground with patchy bushes measuring at least 300×300 metres. On 24<sup>th</sup> February 2011 the *C. belemensis* were much the more common of the two species, resting 0.3–1.2 m above the ground on bushes (*Erica*, *Cistus*, etc.), where they were conspicuous with one or occasionally two snails on each small bush. This species was not seen alive on the underside of stones. The accompanying *C. olisippensis*, in contrast, were often on the underside of stones, sometimes three or four snails together, less often they rested above the ground on grasses, herbs, or bushes. However, at other limestone karst sites with only one of the species, such as the Serra de Montejunto or Serro Ventoso (with *C. belemensis*) and Vale da Couda (with *C. olisippensis*) both species were sometimes found resting during the day on bushes, herbs, grasses or under stones, without evident inter-specific differences.

#### NOTES ON EVOLUTION WITHIN THE GENUS *CANDIDULA*

The 12 species recognised here for the genus *Candidula* in Portugal are notable for the small differences that distinguish most of the species.

However, evolution has evidently produced sharply keeled shells in two separate lineages, resulting in *C. setubalensis* and *C. coudensis* (Figs 2G, H). There is no reason to consider these are more closely related to each other than to neighbouring forms with rounded (unkeeled) shells. Indeed, in the Serra da Arrábida *C. setubalensis* lives alongside the round-shelled *C. arrabidensis* (Fig. 2A) and both have a short penial flagellum. In Vale da Couda *C. coudensis* lives alongside *C. olisippensis* (cf. Fig. 3G) and both have a long penial flagellum. It is possible therefore that each keeled form arose from the local round-shelled form.

Development of sharply keeled shells in local populations of Helicidae and Hygromiidae of numerous genera has been commented on by many authors, notably De Bartolomé (1982), Alonso *et al.* (1985) and Goodfriend (1986). More recently, detailed morphological and molecular studies investigating the phenomenon have been reported by Teshima *et al.* (2003) for *Ainohelix editha* (A. Adams 1868) (Bradybaenidae), by Stankovski (2011) for *Rhagada* (Camaenidae) and by Fiorentino *et al.* (2012) for *Murella muralis* (O.F. Müller 1774) (Helicidae). Each of those studies found that keeled shells had evolved independently on more than one occasion from round-shelled progenitors, as suggested for the keeled *Candidula* in Portugal. However, molecular data imply the keeled *Ainohelix*, *Murella* and *Rhagada* remain as intraspecific forms allowing genetic introgression from their round-shelled relatives, whereas both of the keeled *Candidula* in Portugal appear to be distinct species that show no (morphological) evidence of introgression from coexisting round-shelled taxa. Like these *Candidula*, *Theba* (Helicidae) has keeled forms that are known to represent distinct species (e.g. *T. subdentata* (A. Férussac 1821)), but it also has others that intergrade with round-shelled forms and are treated as subspecies (*T. pisana arietina* (Rossmässler 1846)) (Gittenberger & Ripken, 1987).

The adaptive significance of the keeled forms has not been securely established, but much circumstantial evidence suggests the flatter shells in at least some of the genera enable deeper retreat into rock crevices or beneath stones. This explanation seems likely to also be true for the two keeled *Candidula* in Portugal, which are both closely associated with limestone rocks,



including steep crags. Fiorentino *et al.* (2012: 14) argued that the divergent selective forces which generated globular and keeled-flat shells of *Murella* in Sicily ceased to act during the Holocene, apparently as the open landscapes of the late Pleistocene became forested. With the Portuguese *Candidula* one may speculate that the keeled forms may have evolved in isolation in a similar manner, during drier, cooler periods in the Pleistocene, in the absence of the round-shelled congeners that now coexist with them.

Variation in shell form among the round-shelled (unkeeled) Portuguese taxa of *Candidula* is less striking, apparently consisting of repetition of certain themes (Figs 2, 3). Thus, some species have discoid shells with a convex spire (e.g. Figs 2A–C, F, 3A–C), others are  $\pm$  globular (e.g. Figs 2D, E), or nearly pyramidal (“trochoid”, e.g. Figs 3D, E, H). Inter-population variability of *C. olisippensis* is described and analysed above in the account of that species. As shown in Fig. 7, there was a strong tendency for its populations occurring on sand dunes to have high “trochoid” shells with a small umbilicus (e.g. Fig. 3D), compared to those in other habitats (rocky limestone slopes, grasslands, ruderal habitats), which support populations with more discoid shells having a  $\pm$  convex spire (e.g. Fig. 3G). Similar selective pressures may have resulted in the globular shell with small umbilicus (Fig. 2D) of *C. carrapateirensis*, a species which is only known from calcareous coastal sand dunes.

The adaptive significance of the “trochoid” and globular shell forms is uncertain but might relate to the substrata on which the snails feed. Cain & Cowie (1978) investigated activity of land-snails at night on surfaces of different inclinations. They found a tendency for high-spired snails (other than burrowers) to prefer vertical surfaces when crawling, whereas those with disc-like shells preferred horizontal surfaces. Species with  $\pm$  globular shells showed little preference, although they possibly preferred live herbaceous vegetation which was not favoured by either high-spired or disc-shaped shells. It was concluded that shell form may be adapted to minimise the problems of shell balance on different substrates. Similar observations by Cameron (1978) showed that most species with flattened shell shapes preferred bared soil, whereas those with the tallest shells preferred hard vertical surfaces.

Nevertheless, the relevance of these studies of the significance of differences in shell form between snails from different orders and families to interpretation of smaller differences within-species or among a group of congeneric species is apparently not confirmed in the literature. Instead, the review by Goodfriend (1986: 213–214) reported a positive correlation between shell height and rainfall within species of the genera *Levantina* and *Buliminus* in Israel and *Cepaea* in Belgium, but a negative correlation in *Discus* in Germany and various tropical species. The possible explanations for these different trends remained conjectural.

Among the few studies of the significance of geographical variation of shell form within a species, that by S. Ginnot Lahav on *Xerocrassa simulata* (Ehrenberg 1831) (Hygromiidae) in the Negev Desert and adjoining parts of Israel deals with a helicellid species closely related to *Candidula*; the original thesis in Hebrew [1986] remains unpublished, but Heller (2009: 28–29) provides a lengthy abstract. *X. simulata* has the highest population densities, the largest shells and  $\pm$  globose shells (conical, lacking an umbilicus) in the centre of its range, but smaller shells that become flat and discoid (with a large umbilicus) in more arid regions. The thesis suggested that the snail can more easily pull a flat discoid shell beneath boulders during periods of inactivity.

Quantitative observations on substrate preferences of Portuguese *Candidula* when they are most active (at night?) would be interesting. As noted above, sand-dune populations of *C. olisippensis* rest mainly amongst leaf-litter under low bushes during the day-time, but some are found resting above ground on twigs or leaves. The populations of this species on rocky limestone sites often rest under plants on the soil or beneath stones, but some of them may also be found above ground on bushes, herbs or grasses.

Interspecific variation in the distal genitalia of all 12 Portuguese species of *Candidula* is slight, with the length of the penial flagellum being the principal character showing clear-cut differences (Fig. 6), although length of the epiphallus and duct of the bursa copulatrix are also rather variable (Figs 4–6). Koene & Schulenberg (2005) found a positive scaling between the lengths of male spermatophore-producing organs (epiphallus and flagellum) and the female spermatophore-receiving organs (bursa copulatrix and its duct) in

a range of helicoid snails, implying sexual coevolution in the mechanism associated with control of fertility. Sauer & Hausdorf (2009) found similar scaling in the helicellid genus *Xerocrassa* on Crete, forming part of their evidence that length of the flagellum may form a species-isolating mechanism that resulted from selection against hybrids. There is some evidence of similar positive scaling in Portuguese *Candidula*, e.g. with the species-pair *C. arrabidensis* and *C. belemensis* (Fig. 4A cf. 4C), but certainly not in other species, e.g. *C. intersecta* compared to *C. olisipensis* and *C. carrapateirensis* (Fig. 5A, cf. 5C, E, F). Furthermore, in Portuguese *Candidula* all four of the pairs of species that coexist do not differ much in length of the flagellum (long in *C. olisipensis* and *C. belemensis*, *C. coudensis* and *C. olisipensis*; short in *C. arrabidensis* and *C. setubalensis*, *C. gigaxii* and *C. ponsulensis*). This implies that other differences now serve as species-isolating mechanisms between these pairs of species, but it does not refute the possibility that sexual selection against hybrids in the more distant past was originally responsible for the divergence of flagellum length.

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#### APPENDIX. MATERIAL STUDIED

Data are listed in sequence for each species as country, province, locality name, U.T.M. grid reference (or latitude and longitude, or U.K. grid reference from original data), habitat description, altitude, date (yyyy. mm.dd), collector's initial(s) and collector's field number, Determined by (with date), collection where housed, registration number if any, number of shells, bodies in spirit or specimens, additional comments (if any). Except where type specimens or anatomical material is involved, only one collection from the same locality with similar data is listed (\*\* indicates that additional material which was studied is not listed). To save space, identical information on species, country and province is not repeated; a semi-colon is used only to separate each sample. Abbreviations: AdO=Á. de Oliveira, bod=bodies in spirit, bod†=dissected bodies providing information at least on length of penial flagellum, CGAH=Collection of G.A. and D.T. Holyoak (Sertã, Portugal), CRM=Collection of R. da Costa Mendes (Maфра, Portugal), Det.=determined, DTH=D.T. Holyoak, GAH=G.A. Holyoak, incl.=including, JSTA=J.S. Torres Alba, NHMUK=The Natural History Museum, London, U.K., RCM=R. da Costa Mendes, sh=number of shells, spm=number of whole specimens in alcohol. For *C. belemensis* and *C. olisippensis* localities with records checked by dissection (based on length of penial flagellum) are listed separately from more tentative identifications based only on shells.

*Candidula arrabidensis*, Portugal, Estremadura, Serra da Arrábida, 29S 04999/42576, S.-facing limestone crags and rocky slopes, 250 m, 2007.05.16 & 18, GAH 2007.09 & 15, CGAH, 41 sh, 1 bod, paratypes; Serra da Arrábida, 29S 05021/42601, N.- to NW.-facing limestone crags and rocky slopes, 380 m, 2007.05.17, GAH 2007.10, CGAH, 21 sh, 1 bod†, paratypes; Serra da Arrábida, 29S 04996/42573, limestone slopes and road cutting with patchy herbs, ca 266 m, 2010.02.27, GAH & DTH 2010.P26, CGAH, 14 sh, 2 bod†, paratypes; Serra da Arrábida, 29S 04990/42568, open disturbed ground near roads with patchy low herbs, grasses and bushes, ca 260 m, 2010.02.27, GAH & DTH 2010.P27, CGAH, 15 sh, 3 bod†, 2 spm, paratypes; Serra da Arrábida, 29S 05011/42587, under open grasses and herbs on ledges and at base of limestone

road-cutting, ca 122 m, 2010.02.27, GAH & DTH 2010.P28, CGAH, 2 sh, paratypes; Serra da Arrábida, 29S 05032/42604, high on rocky S.-facing limestone slope with patchy low scrub, 351 m, 2011.02.12, GAH & DTH 2011.P128, CGAH, 1 sh, 1 bod†, 5 spm, paratypes; Serra da Arrábida, 29S 05020/42602, N.- and S.-facing rocky limestone slopes with patches of scrub, 388 m, 2011.02.12, GAH & DTH 2011.P129, CGAH, 13 sh, 3 bod†, 21 spm, paratypes; Serra da Arrábida, 29S 05020/42602, N.- and S.-facing rocky limestone slopes with patches of scrub, 388 m, 2011.02.12, GAH & DTH, 2011.P129, NHMUK reg. no. 20140013/1 (1 sh) & 20140013/2 (1 bod†), holotype; Serra da Arrábida, 29S 05000/42577, rocky limestone slope and road-cutting facing S. and E., with patchy scrub, 263 m, 2011.02.12, GAH & DTH 2011.P130, CGAH, 6 sh, 3 bod†, 3 spm, paratypes; Serra da Arrábida, 29S 050117/425874, herbs and grasses at base of S.-facing limestone road-cutting, 131 m, 2011.02.12, GAH & DTH 2011.P131, CGAH, 2 sh, paratypes; Arrábida (Convento), Setúbal, 29S NC05, 2011.07.05, RCM, Det. DTH 2012.12.22, CRM, 17 sh; Portinho da Arrábida, Setúbal, 29S NC05, 2010.12.11, RCM, Det. DTH 2012.12.22, CRM, 2 sh; just NE. of Cabo Espichel, 29S 0481/4252, open areas with grassland among scrub on limestone headland, ca 150 m, 2014.03.18, GAH P356, CGAH, 7 sh, 2 bod†, paratypes; near Campimeco, W. of Meco, 29S 0483/4257, open sandy slopes above coast with low scrub locally, ca 48 m, 2014.03.19, GAH P357, CGAH, 8 sh; SE. of Azóia, 29S 04854/42540, limestone crags and slopes, ca 168 m, 2014.03.19, GAH & DTH P358, CGAH, 38 sh, 1 bod†, paratypes.

*Candidula belemensis*, checked by dissection, Portugal, Beira Litoral, Serra de Sicó (summit area), 29S 05390/44191, rocky limestone slopes with patchy low scrub, 542 m, 2011.02.24, GAH & DTH 2011.P132, CGAH, 16 sh, 3 bod†, 55 spm; Serra de Sicó (summit area), 29S 053909/441909, rocky limestone slopes with patchy low scrub and grassland, 548 m, 2011.01.13, GAH 2011.P98, CGAH, 13 sh, 3 bod†, 6 spm; Monte de Vez (ca 2 km SE. of S. Sebastião), 29S 05508/44281, limestone slopes, ca 489 m, 2014.05.05, GAH & DTH.P385, CGAH, 5 sh, 2 bod†, 16 spm; Estremadura, above Grutas de Alvalados (W. of Mira de Aire), 29S 05220/43768, limestone rocks and scrub-covered slopes, ca 535 m, 2009.11.18, GAH 2009.P14, CGAH, 12 sh, 1 bod†; ca 1 km S. of Livramento by N236 (S. of Porto de Mós), 29S 05170/43809, on vegetation at base of limestone crags on wooded slope, ca 270 m, 2009.11.01, GAH 2009.P12a, CGAH, 1 sh, 1 bod†; ca 1 km S. of Livramento by N236 (S. of Porto de Mós), 29S 051708/438095, rough grassland amongst limestone rocks, ca 250 m, 2009.11.01, GAH & DTH 2009.P12b, CGAH, 34 sh, 27 bod†, 9 spm; ca 2 km NW. of Serro Ventoso, 29S 05129/43809, on underside of limestone boulders on rocky slope with

low crags and scrub, 2010.07.30, GAH & DTH 2010.P62, CGAH, 18 sh, 9 bod†, 9 spm; up to 1 km SW. of Serro Ventoso, 29S 05140/43784, rocky limestone slopes and road cutting, with short vegetation and scrub, ca 380 m, 2010.07.19, GAH & DTH 2010.P59, CGAH, 68 sh, 2 bod†, 6 spm; Fórnea (SE. of Alcaria), 29S 05170/43789, limestone crags, scree and slopes, patchy scrub, ca 275 m, 2010.05.02, GAH & DTH 2010.P43, CGAH, 24 sh, 2 bod†, 1 spm; Fórnea (SE. of Alcaria), 29S 05170/43790, rocky limestone slopes and valley with scrub, ca 275 m, 2012.02.18, GAH, DTH & RCM 2012.P226, CGAH, 23 sh; near summit of Serra de Montejunto, 29S 049487/433620, walls of ruins, limestone rocks and slopes, 651 m, 2012.03.24, GAH, DTH & RCM 2012.P237, CGAH, 57 sh, 24 bod†, from restricted type-locality; junto à Capela da Nossa Senhora das Neves, Montejunto, 29S MD93, vazio no solo & vivo sobre pedras calcárias, 2011.09.03, RCM, Det. DTH 2012.12.22, CRM, 63 sh; Serra de Montejunto, 29S 049299/433625, on limestone bank with patchy grassland and herbs, ca 445 m, 2010.04.19, DTH 2010.P33, CGAH, 77 sh, 7 bod†; Estremadura and Ribatejo, ca 4 km NNW. of Serra Santo António, 29S 05223/43759, grassland, limestone rock exposures and stone walls, ca 494 m, 2012.02.18, GAH, DTH & RCM 2012.P227, CGAH, 5 sh, 2 bod†.

*Candidula cf. belemensis*, not checked by dissection, Portugal, Beira Litoral, junto ao Castelo de Pombal, Pombal, 29S NE31, 2011.08.13, RCM, Det. DTH 2012.12.22, CRM, 18 sh; Estremadura, Serro Ventoso, Porto de Mós, 29S ND1479, 2008.02.12, ÁDo (7), CGAH, 4 sh; junto à Estrada de Serro Ventoso para Mendigo (à saída de Serro Ventoso), Porto de Mós, 29S ND17, debaixo de pedras, 2011.04.09, RCM, Det. DTH 2012.12.22, CRM, 3 sh; zona de estacionamento, Vale da Fórnea, Alcaria, Porto de Mós, 29S ND17 (N39°33'39.30", W8°48'05.84"), vazio no solo, ca 287 m, 2012.02.18, RCM, Det. DTH 2012.12.22, CRM, 12 sh; Ribatejo, NE. of Moitas Venda, 29S 05311/43717, limestone crags and rocky slopes with scrub, ca 195 m, 2010.05.02, GAH & DTH 2010.P41, CGAH, 12 sh.

*Candidula carrapateirensis*, Portugal, Algarve, ca 0.5 km W. of Carrapateira, 29S 050845/411537, sand dunes with patchy vegetation of mainly low bushes, stony locally, 43 m, 2011.02.07, GAH & DTH 2011.P123, NHMUK reg. no. 20140014/1 (1 sh) & 20140014/2 (1 bod†), holotype; ca 0.5 km W. of Carrapateira, 29S 050845/411537, sand dunes with patchy vegetation of mainly low bushes, stony locally, 43 m, 2011.02.07, GAH & DTH 2011.P123, CGAH, 327 sh, 3 bod†, 13 spm, paratypes; above Praia de Monte Clérigo (W. of Aljezur), 29S 0513/4133, among patchy low scrub on blown sand on coastal slopes of sandstone, ca 55 m, 2014.03.21, GAH & DTH P363, CGAH, 104 sh, paratypes; Baixo Alentejo, coast W. of Almogrove, 29S 0517/4167, sand dunes on coastal

slopes, 32 m, 2014.03.26, GAH & DTH P370, CGAH, 69 sh, paratypes.

*Candidula codia*, Portugal, Algarve, 3 km SE. of Loulé, 29S 058884/410560, rocky limestone slope with patchy cover of low bushes, 85 m, 2011.01.03, GAH & DTH 2011.P115, CGAH, 19 sh; by A22 Junction 15 and N398 at 3 km N. of Moncarapacho, 29S 06069/41075, beneath rubbish on track and in low scrub on limestone slope, 2009.12.25, GAH & DTH 2009.P21, CGAH, 48 sh, 1 bod†; by N398 at ca 2 km N. of Moncarapacho, 29S 06068/41078, limestone slope with low rocks and patches of scrub, ca 121 m, 2011.01.29, GAH & DTH 2011.P108, CGAH, 12 sh, 4 spm; ca 3 km NNW. of Moncarapacho (just S. of A22), 29S 060695/410771, rocky limestone hill-slopes with patchy bushes, 131 m, 2011.02.04, GAH & DTH 2011.P118, CGAH, 13 sh; N. of Moncarapacho, 29S 06087/41071, among herbs and low scrub on limestone slope, 2009.12.29, GAH & DTH 2009.P23, CGAH, 47 sh, 2 bod†; ca 2 km E. of Santa Barbara de Nexe, 29S 059428/410732, rocky limestone hill-slopes with patchy low scrub, 261 m, 2011.02.03, GAH & DTH 2011.P117, CGAH, 82 sh, 2 bod†, 60 spm; Cerro da Cabeça (NE. of Olhão), 29S 06081/41075, limestone crags on slope, ca 200 m, 2008.01.11, GAH 2008.59, CGAH, 17 sh, 1 bod, 1 spm; just NW. of Barroqueira (ca 7 km NW. of Moncarapacho), 29S 060291/411092, rocky limestone slopes and quarries with patchy bushes, 183 m, 2011.01.29, GAH & DTH 2011.P107, CGAH, 41 sh, 18 spm; São Miguel, NW. of Moncarapacho, 29S 06043/41067, under scrub and trees on limestone hill, ca 390 m, 2009.12.26, GAH 2009.P22, CGAH, 28 sh; Serra de São Miguel (ca 4 km NW. of Moncarapacho), 29S 06043/41067, rocky limestone slopes with patchy scrub and grassland, 340 m, 2011.02.04, GAH & DTH 2011.P119, CGAH, 22 sh, 26 spm.

*Candidula coudensis*, Portugal, Beira Litoral, by N348 road, Vale da Couda, SE. of Almoester, 29S 05498/44099, herb-rich grassland and low shrubs by road, ca 390 m, 2009.12.12, GAH 2009.P19, CGAH, 62 sh, 5 bod, 2 spm, paratypes; by N348 SE. of Almoester, 29S 05498/44099, in crevices and under stones, low limestone crags and slopes, ca 370 m, 2009.06.10, GAH 2009.P3, CGAH, 33 sh, 1 bod, paratypes; SE. of Almoester, 29S 05497/44096, scrub-covered limestone hillside with low walls and scree, ca 390 m, 2009.12.12, GAH 2009.P18, CGAH, 39 sh, paratypes; SE. of Almoester, 29S 05497/44096, scrub covered limestone hillside with low walls and scree, ca 390 m, 2009.12.12, GAH 2009.P18, NHMUK 20100177, 1 sh, 1 bod†, holotype; SE. of Almoester, 29S 05497/44096, scrub-covered limestone hillside with low walls and scree, ca 390 m, 2009.12.12, GAH 2009.P18, NHMUK 20100178 & 20100179, 7 sh, 4 bod, paratypes; by N348 SE. of Almoester, 29S 05498/44099, limestone crags and slopes, 2008.01.31, GAH 2008.65, CGAH, 11 sh,

1 bod†, paratypes; Vale da Couda (SE. of Almoester), 29S 05487/44103, limestone valley with low crags and patchy oak woodland, ca 263 m, 2010.05.29, GAH & DTH 2010.P45, CGAH, 2 sh; SW. of Chao de Couce, 29S 05502/44145, under stones on limestone slopes, ca 456 m, 2014.04.28, GAH 2014.P384, CGAH, 11 sh.

*Candidula gigaxii*, Great Britain, E. Gloucestershire (v.c. 33), Leckhampton, Cheltenham, 30U WC64 (UK grid: SO942011), garden, 2003.08.30, D.C. Long, CGAH, 2 sh; E. Sussex (v.c. 14), SE. of Ovingdean, 30U YB03 (UK grid: TQ359025), rough grass beside road, edge of arable, 2001.01.24, DTH, CGAH, 2 sh; SE. of Ovingdean, 30U YB03 (UK grid: TQ361029), rough grass on bank beside arable field, 2001.01.24, DTH, CGAH, 2 sh; Lincolnshire (v.c. 53), NE. of Ropsley, 30U XD66 (UK grid: TF0038/3628), patchy grasses and herbs on slope at edge of old limestone quarry, ca 80 m, 2010.03.21, DTH, CGAH, 16 sh, 1 bod; Portugal, Algarve, by A22 Junction 15 and N398 at 3 km N. of Moncarapacho, 29S 06069/41075, beneath low scrub on limestone slope, 2009.12.25, GAH & DTH 2009.P21, CGAH, 3 sh (old shells); by N398 at ca 2 km N. of Moncarapacho, 29S 06068/41078, limestone slope with low rocks and patches of scrub, ca 121 m, 2011.01.29, GAH & DTH 2011.P108, CGAH, 1 sh (old shell); ca 3 km NNW. of Moncarapacho (just S. of A22), 29S 060695/410771, rocky limestone hill-slopes with patchy bushes, 131 m, 2011.02.04, GAH & DTH 2011.P118, CGAH, 1 sh (old shell); Serra de São Miguel (ca 4 km NW. of Moncarapacho), 29S 06043/41067, rocky limestone slopes with patchy scrub and grassland, 340 m, 2011.02.04, GAH & DTH 2011.P119, CGAH, 8 sh (old shells); Alto Alentejo, Forte de Santa Luzia, Elvas, 29S 06597/43043, large old walls of fort and grassland on slopes, 320 m alt., 2013.10.30, GAH & DTH, CGAH, 1 sh, \*\*; Baixo Alentejo, Santa Maria, Serpa (entre o IP8 e a Rua da Boa Vista), 29S PC20 (N37°57'03", W7°36'16"), vivo sobre muros, ca 175 m, 2012.12.17, RCM, CGAH, 5 sh; Santa Maria, Serpa (entre o IP8 e a Rua da Boa Vista), 29S PC20 (N37°57'03", W7°36'16"), vivo sobre muros, ca 175 m, 2012.12.17, RCM, Det. DTH, CRM, 63 sh; ca 1 km W. of Serpa, 29S 06226/42012, roadside verges and walls, grassland, spring, 178 m alt., 2013.10.29, GAH & DTH 2013.P339, CGAH, ca 60 spm, 95 sh, 41 bod†; Santa Maria, Serpa (na N260/IP8, a 5.1 km da Ponte de Serpa), 29S PC10 (N37°58'41", W7°39'09"), debaixo de pedras, ca 84 m, 2012.12.17, RCM, Det. DTH, CRM, 3 sh; near Ermida das Pazes, ca 2 km SE. of Vila Verde de Ficalho, 29S 06515/42002, N.-facing roadside cutting of shaly rock, patchy grasses and herbs, 195 m alt., 2013.10.29, GAH & DTH 2013.P340, CGAH, 4 sh, 1 bod†; Spain, Prov. Cádiz, Alto el Cabrito by E5 NE. of Tarifa, 30S 02698/39928, sandstone crags and scrub-covered slopes, 2007.12.31, GAH 2007.55, CGAH, 19 sh, 19 bod†; near Embalse de Almodóvar (E. of

Facinas), 30S 02618/40046, rocky slope near reservoir, 2007.12.30, GAH 2007.53b, CGAH, 4 sh, 1 bod; Road to Punta Paloma, Tarifa, 30S TE5694, under stones in sandy slopes with mixed pines-*Eucalyptus*, sea-level, 1998.03., JSTA 5694, CGAH, 2 sh; Prov. Huelva, N. of La Palma del Condado, 29S 071452/414600, on herbs and grasses on roadside, 2008.01.09, GAH 2008.57, CGAH, 3 sh, 3 bod†; Prov. Málaga, Almorchón, Ardales, 30S UF3986, in sandstone hills with pines and *Rosmarinus* bushes, 500 m, 2011.01., JSTA, CGAH, 9 sh, 9 bod†; Baños de la Hedionda, Casares, 30S TF9730, in low bushes on calcareous slopes, 2010.06., JSTA, CGAH, 5 sh, 5 bod†; Baños de la Hedionda, Casares, 30S TF9730, in low bushes in calcareous slopes, 2010.10., JSTA 3201, CGAH, 2 sh; by A369 ca 15.3 km S. along the road from Ronda, 30S UF05 (36°39'N 5°14'W), limestone rocks with patchy scrub, ca 895 m, 2001.06.05, GAH 2001.23, Det. DTH 2009.07.20, not kept, (adult checked by dissection); La Araña beach, 30S UF8164, under stones and in low bushes in limestone hills, sea-level, 2010.06., JSTA 1940, CGAH, 2 sh; Artola, Marbella, 30S UF4240, under stones in sandy slopes with pines, 25 m, 1998.03., JSTA 4518, CGAH, 2 sh; Almorchón, Sierra de la Pizarra, Ardales, 30S UF3988, Areniscas with pines and *Cistus*, 450 m, 1994.04., JSTA 2862, CGAH, 2 sh; Los Riscos, Catajima, 30S UF0658, under stones in calcareous mountains, 1000 m, 2003.11., JSTA 8209, CGAH, 2 sh; La Fuensanta, Sierra de las Nieves, El Burgo, 30S UF2571, under stones and in low bushes in calcareous mountains, 800 m, 1989.03., JSTA 1522, CGAH, 2 sh.

*Candidula intersecta*, Great Britain, Cornwall (v.c. 1), Pentire Point East, 30U UA48 (UK grid: SW785612), short patchy grassland on open slope just above slaty sea-cliff, ca 8 m, 2010.03.30, DTH, CGAH, 22 sh, 5, bod†; Lincolnshire (v.c. 53), NE. of Ropsley, 30U XD66 (UK grid: TF0038/3628), patchy grasses and herbs on slope at edge of old limestone quarry, ca 80 m, 2010.03.21, DTH, CGAH, 91 sh, 8 bod†, 7, spm; Ireland, Co. Carlow (v.c. H13), Goresbridge, 29U PU33 (Irish grid: S6853), grassy river bank, 2005.09.05, GAH, CGAH, 6 sh, 4 bod†; Co. Kerry (v.c. H2), W. of Crow's Point, 29U MT37 (Irish grid: V699996), edge of saltmarsh, 2005.06.07, GAH, CGAH, 18 sh, 8 bod†; Co. Kildare (v.c. H19), Ballymore Eustace, 29U PU58 (Irish grid: N925098), wall, 2005.09.01, GAH, CGAH, 1 sh, 1 bod†; France, Dept. Loire Atlantique, near Pointe de Chémoulin (SW. of St Nazaire), 30T 055285/523159, sandy cliff slopes on coastal headland of hard metamorphic rock, with patchy low grasses and herbs, 18 m, 2011.09.25, GAH & DTH 2011.F206, CGAH, 8 sh, 3 bod†, 19 spm; Dept. Maine-et-Loire, by D723/N23 at km 61 (1 km E. of Champocé-sur-Loire), 30T 066188/525324, open, S.-facing, roadside bank with exposed calcareous sandstone rock, patchy herbs and grasses, 31 m, 2011.09.24, GAH & DTH 2011.F202,

CGAH, 15 sh, 2 bod†, 18 spm; by D952 on N. bank of R. Loire at les Rosiers-sur-Loire, 30T 07096/52476, mortared-stone masonry of river embankment, with patchy herbs and grasses, 31 m, 2011.09.23, GAH & DTH 2011.F201, CGAH, 25 sh, 3 bod†, 24 spm; ca 2 km N. of St Lambert du Lattay, 30T 068029/524300, quarried limestone rocks on S.-facing slope, with patchy grassland and scrub, 28 m, 2011.09.23, GAH & DTH 2011.F196, CGAH, 72 sh, 3 bod†, 7 spm; N. edge of D54 at ca 4 km E. of Angevine, 30T 067447/524549, S.-facing sandstone bank above roadside ditch, below vineyard, with patchy low herbs and grasses, 63 m, 2011.09.23, GAH & DTH 2011.F198, CGAH, 19 sh, 3 bod†, 31 spm; Dept. Morbihan, E. of D768 N. of Penthièvre, 30T 04898/52694, low sand dunes with short herb-rich grassland (rabbit-grazed), 8 m, 2011.09.25, GAH & DTH 2011.F204, CGAH, 98 sh, 3 bod†, 34 spm; la Roche-Bernard, 30T 055225/526300, crags and slopes of hard metamorphic rock, with patchy herbs and grasses, 16 m, 2011.09.25, GAH & DTH 2011.F205, CGAH, 20 sh, 3 bod†, 38 spm; Portugal, Beira Baixa, Barcoila, near Sertã, 29S 05741/44096, painted wall of house near flower garden, 410 m alt., 2010.06.16, GAH 2010.P51, CGAH, 1 sh, 1 bod†, \*\*; Estremadura, W. of N249–2 N. of Abrunheira (SE. of Sintra), 29S 04689/42922, grassland with low limestone rocks and masonry debris, scrub patches, 177 m alt., DTH 2013.P347, CGAH, 84 sh, 42 bod†, 2 spm; na EM377–1, Trafaria, Almada, 29S MC79976/80206, em ervas rasteiras e no solo, 28 m, 2014.02.15, RCM, CGAH, 3 sh, 3 bod†, 6 spm.

*Candidula cf. intersecta*, records based only on shells (that could include forms of *C. belemensis* or *C. olisippensis*), Portugal, Estremadura, Rua da Fonte, Barreira, São João das Lampas, Sintra, 29S MD60 (N38°53'21", W9°21'54"), vazio junto a fonte de água doce, 2012.09.01, RCM, Det. DTH 2012.12.22, CRM, 5 sh; Forte de São Vicente, Torres Vedras, 29SMD72, 2010.11.06, RCM, Det. DTH 2012.12.22, CRM, 3 sh; Forte de São Vicente, Torres Vedras, 29S MD72, vazios, 2010.10.09, RCM, Det. DTH 2012.12.22, CRM, 9 sh; Vale de Lobos, 29S 04762/42974, roadside verges, walls, grassland, 259 m, 2013.04.27, DTH, GAH, RCM 2013.P311, CGAH, 56 sh; junto ao cume do Cabeço de Montachique, Lousa, Loures, 29S MD80 (N38°53'53.9", W9°11'38.7"), vazio no solo, ca 409 m, 2012.06.07, RCM, Det. DTH 2012.12.22, CRM, 32 sh; Estrada da Fonte Velha, Charneca, Cascais, 29S MC68 (N38°43'57.75", W9°27'32.84"), vazio no solo, ca 60 m, 2012.10.05, RCM, Det. DTH 2012.12.22, CRM, 53 sh.

*Candidula olisippensis*, checked by dissection, Great Britain, Cornwall (v.c. 1), Kynance Cliff, 30U UA33 (UK grid: SW677135), SW.-facing slope and tops of serpentinite sea-cliff, with patchy short vegetation, 60 m, 2011.04.06, GAH & DTH, CGAH, 25 sh, 21 bod†, 1 spm; Portugal, Azores, Ilha de Santa Maria,



Cruz Teixeira, 26S PF6693, 2007.05.01, *Ádo* (SM R 001–5), CGAH, 1 sh, 1 bod†; Beira Baixa, at Barragem do Cabril, 29S 05742/44186, under stones on grassy roadside banks, ca 305 m, 2009.08.10, GAH 2009.P10, CGAH, 110 sh, 2 bod†, 1 spm; Barcoila, near Sertã, 29S 05741/44096, garden near house, 410 m, 2012.05.07, GAH, 2012.P245, CGAH, 1 sh, adult checked by dissection; just N. of Barcoila, near Sertã, 29S 0574/4409, wall beside minor road near house and gardens, ca 410 m, 2014.01.11, GAH, 2014.P350, not kept, 3 spm (1 adult and 1 immature checked by dissection); Rio Zêzere valley W. of Pedrógão Pequeno, 29S 05737/44176, rocky granitic slopes of valley side with open *Pinus* and *Quercus* woodland, ca 250 m, 2011.04.27, GAH & DTH 2011.P140, CGAH, 9 sh, 9 bod†; W. edge of Sertã, 29S 05769/44065, from under cardboard on roadside verge with patchy herbs, ca 240 m, 2010.04.15, GAH 2010.P31, CGAH, 41 sh, 8 bod†; Cabeçudo, 29S 0573/4409, from wall at edge of cemetery in village, ca 350 m, 2012.10.07, GAH 2012.P262, 2 sh, 2 bod†; Beira Litoral, Ancos (S. of Redinha), 29S 05364/44254, limestone gravel in park area near river, unshaded, with patchy tall herbs, 68 m, 2012.08.17, GAH & DTH 2012.P259, CGAH, 48 sh, 17 bod†, 79 spm; by IC8 just NE. of Ansião, 29S 054915/441926, grassland over limestone, 210 m, 2011.04.29, GAH & DTH 2011.P141, CGAH, 37 sh, 13 bod†; by N348 SE. of Almoester, 29S 05498/44099, limestone crags and slopes, 2008.01.31, GAH 2008.65, CGAH, 6 sh; by N348 SE. of Almoester, 29S 05498/44099, herb-rich grassland and low shrubs by road, 345 m, 2009.12.12, GAH, 2009.P19, CGAH, 73 sh, 2 bod†, 9 spm; by Paúl do Taipal near Montemor-Velho, 29T 05271/44481, disused limestone quarry with patches of short vegetation, 45 m, 2011.01.09, GAH 2011.P96, CGAH, 36 sh, 37 bod†; by Ruínas de Conimbriga, 29T 054352/443878, open olive-grove with grassland and herbs beneath, ca 100 m, 2010.04.27, GAH & DTH 2010.P39, CGAH, 1 sh, 1 bod†, 3 spm; ca 1 km NW. of Gafanha do Areão (SW. of Aveiro), 29T 05188/44862, sand dunes, with much *Acacia* scrub, 8 m, 2010.10.27, GAH & DTH 2010.P76, CGAH, 5 sh, 2 bod†; ca 1 km SW. of Alfarelos, 29T 05283/44439, limestone crags and grassland, 13 m, 2010.11.03, GAH & DTH 2010.P79, CGAH, 98 sh, 39 bod†; ca 1 km SW. of Ateanha village (E. of Alvorge), 29S 05498/44262, S.-facing limestone hillside with grassland, patchy scrub and rocks, 310 m, 2010.05.29, GAH & DTH, 2010.P46, CGAH, 33 sh, 3 bod†, 7 spm; ca 1 km SW. of Barragem do Cabril, 29S 05736/44184, base of herbs and grasses near roadside, ca 335 m, 2010.02.14, GAH & DTH 2010.P24, CGAH, 172 sh, 8 bod†, 12 spm; ca 2 km NE. of Favacal, 29S 05576/44272, quartzite slope, grassland, bushes and concrete walls of chapel, 755 m, 2011.09.06, GAH & DTH 2011.P191, CGAH, 22 sh, 19 bod†; Capela de Nossa Senhora de Covões, 29S 05511/44073, rocky limestone hill with

low vegetation, 2008.09.01, GAH 2008.P8, CGAH, 11 sh, 1 spm; Capela de Nossa Senhora de Covões, 29S 05511/44070, low limestone boulders in managed 'park' area, ca 345 m, 2009.11.23, GAH 2009.P16, CGAH, 6 sh, 3 bod†, 3 spm; Casal de São Simão (NE. of Aguda), 29S 05562/44188, walls of chapel, grassland on quartzite slopes, 385 m, 2011.09.06, GAH & DTH 2011.P192, CGAH, 53 sh, 35 bod†; Castelo do Rabaçal, 29T 05489/44309, rocky limestone slopes, grassland and scrub, ca 315 m, 2010.04.27, GAH & DTH 2010.P40, CGAH, 39 sh, 2 bod†; just S. of S. Pedro (S. of Figueira da Foz), 29T 05117/44412, coastal sand dunes with patchy low scrub, ca 10 m, 2011.01.13, GAH 2011.P97, CGAH, 16 sh, 11 bod†; N. of Ameal, 29T 05393/44502, grassland and limestone boulders on bank, ca 12 m, 2010.11.03, GAH & DTH 2010.P80, CGAH, 27 sh, 14 bod†; N. of Covões (SE. of Candal), 29S 05507/44070, limestone slope with patchy scrub, ca 560 m, 2009.11.23, GAH 2009.P15, CGAH, 23 sh, 8 bod†, 7 spm; Penedo da Meditação, Coimbra, 29T NE5052, 2010.01.19, *Ádo* (3), CGAH, 6 sh, 2 bod†, 4 spm; Penela Castle, Penela, 29T NE5231, 2008.10.18, *Ádo* (4), CGAH, 3 sh, 3 bod†, 5 spm; Pombal Castle, Pombal, 29S NE3218, 2008.12.16, *Ádo* (5), CGAH, 6 sh, 4 bod†, 4 spm; Praia da Tocha, 29T 05134/44648, coastal sand dunes with patchy low scrub and herbs, ca 10 m, 2010.06.06, GAH & DTH 2010.P49, CGAH, 70 sh, 2 bod†; Praia da Tocha, 29T 05134/44647, sand dunes with patches of low bushes, 14 m, 2010.11.18, GAH & DTH 2010.P83, CGAH, 42 sh, 36 bod†; Ribeira de Coselhas, Coimbra, 29T NE4852, 2009.04.21, *Ádo* (2), CGAH, 8 sh, 3 bod†, 3 spm; S. of IC8 at ca 3 km W. of Avelar, 29S 05520/44192, limestone slopes with short grasses and herbs, scrub locally, 288 m, 2011.02.24, GAH & DTH 2011.P133, CGAH, 122 sh, 8 bod†; Serra de Sicó (summit area), 29S 05390/44191, rocky limestone slopes with patchy low scrub, 542 m, 2011.02.24, GAH & DTH 2011.P132, CGAH, 29 sh, 104 spm; Serra de Sicó (summit area), 29S 053909/441909, rocky limestone slopes with patchy low scrub and grassland, 548 m, 2011.01.13, GAH 2011.P98, CGAH, 35 sh, 20 bod†; Vista Alegre, Ílhavo, 29T NE2793, 2009.10.26, *Ádo* (1), CGAH, 2 sh, 2 bod†, 2 spm; just N. of Praia de Quiaios (W. of Quiaios), 29T 05093/44524, coastal dunes with low patchy vegetation, scrub locally, 21 m, 2012.12.30, GAH & DTH 2012.P268, CGAH, 5 sh, 3 bod†; ca 1 km N. of Serra da Boa Viagem village, 29T 05121/44495, limestone quarry, grassland, roadside, 216 m, 2013.03.02, GAH 2012.P289, CGAH, 11 sh, 1 bod†; near N348 (N347–1) ca 0.5 km NE. of Alvorge, 29S 05471/44257, limestone grassland, ca 236 m, 2013.05.13, GAH 2013.P317, CGAH, 5 sh, 3 bod†; near Capela Santo Antonio Degracias, ca 1 km NNW. of Degracias, 29T 0540/4430, limestone grassland and rocky slopes with low crags, ca 400 m, 2014.03.10, GAH & DTH P352, CGAH, 5 sh, 3 bod†; Jardim

Botânico, Coimbra, 29T 0549/4450, botanic garden with lawns, cultivated areas, etc., ca 84 m, 2014.03.15, GAH & DTH P354, with RCM, not kept, 2 sh; Monte de Vez (ca 2 km SE. of S. Sebastião), 29S 05508/44281, limestone slopes, ca 489 m, 2014.05.05, GAH & DTH P385, CGAH, 7 sh, 2 bod†, 8 spm; Estremadura, just E. of lighthouse at Nazaré, 29S 049282/438393, sandy and gravelly coastal slope with short patchy vegetation, 52 m, 2010.12.25, GAH & DTH 2010.P91, CGAH, 51 sh, 15 bod†; Nazaré Lighthouse, Nazaré, 29S MD9284, 2007.02.18, ÁDO (6), CGAH, 28 sh; just N. of Praia da Vieira, 29S 050275/441459, sand dunes with patchy low scrub, 7 m, 2010.12.25, GAH & DTH 2010.P93, CGAH, 21 sh, 2 bod†; just SW. of Vale de Paredes, 29S 049561/439426, narrow strip of dune vegetation on sand at base of cliff-slope, 12 m, 2010.12.25, GAH & DTH 2010.P92, CGAH, 29 sh, 13 bod†; S. Bartolomeu, 2 km SE. of Nazaré, 29S 04955/43825, granitic hill with crags, wooded slopes and old buildings, ca 155 m, 2011.06.04, GAH & DTH 2011.P162, CGAH, 8 sh, 1 bod†; Rua do Segrel, Pedra do Ouro, Pataias, Alcobaca, 29S MD96105/97480, em ervas rasteiras das dunas, 29 m, 2013.07.02, RCM, CGAH, 2 sh, 2 bod†, 2 spm; Rua Casal do Brejo, Ramalhal, Torres Vedras, 29S MD79960/32636, vivo em muros, ca 50 m, 2013.12.28, RCM, CGAH, 3 sh, 3 bod†, 16 spm; Ribatejo, Almonda River Spring, Torres Novas, 29S ND3372, 2007.12.08, ÁDO (8), CGAH, 2 sh, 1 bod†; Spain, Prov. Pontevedra, just NW. of San Vicente do Grove, 29T 050522/470284, open slopes above beach with blown sand over granite, patchy herbs and grasses, 15 m, 2011.08.27, GAH & DTH 2011.E182, CGAH, 145 sh, 18 bod†.

*Candidula cf. olisippensis*, not checked by dissection, Portugal, Azores, Ilha de Santa Maria, Almagreira, 26S PF6892, 2007.05.02, ÁDO (SM R 001 T7–3), CGAH, 3 sh; Beira Alta, Góis (margem direita do Rio Ceira), 29TNE74, 2011.06.24, RCM, Det. DTH 2012.12.22, CRM, 6 sh; Beira Baixa, by Senhora da Confiança, near Pedrógão Pequeno, 29S 05743/44182, grassland, slopes, rocks, 468 m, 2013.02.07, DTH 2012.P279, not kept, 3 sh; NW. edge of Pedrógão Pequeno village, 29S 05742/44174, rocky slope, 354 m, 2013.02.07, DTH 2012.P281, not kept, 2 sh; Beira Litoral, ca 0.5 km S. of IC8 at ca 1.5 km WNW. of Ansião, 29S 05466/44185, limestone slopes, with scrub, crags and grassland, ca 185–194 m, 2010.09.26, GAH & DTH 2010.P73c&d, CGAH, 21 sh; ca 1 km N. of Pedrogão Grande, 29S 057223/442063, rocky bank with patchy open scrub, 330 m, 2011.08.11, GAH & DTH 2011.P179, CGAH, 3 sh; SE. of Almoester, 29S 05497/44096, scrub covered limestone hillside with low walls and scree, ca 390 m, 2009.12.12, GAH 2009.P18, CGAH, 19 sh; Vale de Poios (ca 1.5 km SE. of Poios), 29S 05380/44257, N.-facing limestone crags and slopes near valley bottom, with much low scrubby woodland, ca 140 m, 2012.08.17, GAH & DTH 2012.P260, CGAH, 13 sh;

perto o Castelo, Nossa Senhora das Misericórdias, Ourém, 29S ND38 (N39°38'35" W8°35'24"), no solo, ca 248 m, 2012.10.25, RCM, Det. DTH 2012.12.22, CRM, 4 sh; junto à Estrada N348 à saída de Vale da Couda, em direção a Alvaiázere, Almoester, Alvaiázere, 29S NE41 (N39°50'22.9" W8°25'50.9"), vazio no solo, ca 275 m, 2012.04.14, RCM, Det. DTH 2012.12.22, CRM, 65 sh; Ruínas de Conimbriga, Condeixa-a-Velha, Condeixa-a-Nova, 29T NE43 (N40°05'55.6" W8°29'29.0"), vivo sobre muros, 2012.05.12, RCM, Det. DTH 2012.12.22, CRM, 3 sh; na Rotunda, Quinta das Lágrimas, Quinta da Várzea, Coimbra, 29TNE44, vivo em troncos de árvores, 2011.05.14, RCM, Det. DTH 2012.12.22, CRM, 1 sh; Estremadura, just E. of Cabo da Roca, 29S 045705/429290, dry slopes above sea-cliffs with patchy grasses and herbs on exposed soil, 129 m, 2012.07.17, DTH 2012.P251, CGAH, 1 sh; Pedras Negras, ca 3 km N. of São Pedro de Moel, 29S 049813/440313, dunes with patchy low grasses and herbs, 20 m, 2010.08.12, GAH & DTH 2010.P68, CGAH, 49 sh; Est. de Alcobertas para Casais Monizes, Rio Maior, 29SMD06, 2011.01.15, RCM, Det. DTH 2012.12.22, CRM, 14 sh; junto à Estrada de Alcobertas para Casais Monizes, Alcobertas, Rio Maior, 29SMD06, vivo e vazio debaixo de pedras, 2011.02.12, RCM, Det. DTH 2012.12.22, CRM, 21 sh & 19 sh; Abrunheira, Mafra, 29SMD70, 2010.11.27, RCM, Det. DTH 2012.12.22, CRM, 6 sh, \*\*; Entre Salgados e A-da-Perra, Mafra, 29SMD71, 2010.12.27, RCM, Det. DTH 2012.12.22, CRM, 17 sh; Salgados, Mafra, 29SMD71, 2010.11.20, etc., RCM, Det. DTH 2012.12.22, CRM, 8 sh, \*\*; Estrada de acesso ao Castro do Zambujal, Ribeira dos Pedregulhos, Torres Vedras, 29SMD72, vivos sobre ervas, 2010.11.13, RCM, Det. DTH 2012.12.22, CRM, 6 sh, \*\*; para Este da ponte sobre o Rio Alcabrichel, Maceira, Torres Vedras, 29SMD73 (N39°10'57.2" W9°19'27.4"), no solo debaixo da manta morta, 2011.11.28, RCM, Det. DTH 2012.12.22, CRM, 2 sh; Ruínas de Salvador (junto ao cemitério), Estrada Cabêda – Sobral de Monte Agraço, Sobral de Monte Agraço, 29SMD81, 2010.12.04, RCM, Det. DTH 2012.12.22, CRM, 2 sh; na Rua da Fonte Velha, Valdevez, Santo Quintino, Sobral de Monte Agraço, 29SMD81 (N38°59'17" W9°10'46"), vivo em ervas rasteiras e no solo, junto a Fonte, ca 248 m, 2012.10.23, RCM, Det. DTH 2012.12.22, CRM, 27 sh, \*\*; no CM 1084 Rua da Fonte, Ereira, Maxial, Torres Vedras, 29SMD82 (N39°06'51.5" W9°09'42.9"), no talude Sul da estrada, ca 278 m, 2012.10.26, RCM, Det. DTH 2012.12.22, CRM, 1 sh; EN 115–2 (Cadaval –Maxial – Ermegeira – T. Vedras) Km 11.6, 29SMD83, 2010.12.26, RCM, Det. DTH 2012.12.22, CRM, 1 sh; Quinta dos Loridos, Carvalhal, Bombarral, 29SMD84, 2010.11.20, RCM, Det. DTH 2012.12.22, CRM, 2 sh; Parque da Vila, Óbidos, 29SMD85, vivo no solo debaixo de pedras, 2011.10.25, RCM, Det. DTH 2012.12.22, CRM, 10 sh, \*\*; Óbidos, 29SMD85, 2011.12.23,

RCM, Det. DTH 2012.12.22, CRM, 3 sh; na Rua 4 de Julho (talude Norte), Ribeira do Marete, Vimeiro, Alcobaça, 29SMD97 (N39°28'47" W9°03'01"), vivo no solo, 2012.04.21, RCM, Det. DTH 2012.12.22, CRM, 7 sh, \*\*; junto à Estrada da Fonte, Chãos, Alcobertas, Rio Maior, 29SND06, no solo, 2011.10.27, RCM, Det. DTH 2012.12.22, CRM, 4 sh, \*\*; Turquel, Alcobaça, 29SND06 (N39°27'50" W8°58'36"), no solo junto a mura de pedra, 2012.04.21, RCM, Det. DTH 2012.12.22, CRM, 1 sh; junto à Estrada de Alcobertas para Casais Monizes (junto à torre de observação de incêndias), Alcobertas, Rio Maior, 29SND06, vazio sobre e debaixo de pedras, 2011.04.09, RCM, Det. DTH 2012.12.22, CRM, 11 sh, \*\*; Estrada da Serra da Vila (junto à Escola EB3 São Gonçalves), Torres Vedras, 29SMD72, vivo no solo entre manta morta, 2010.12.01, RCM, Det. DTH 2012.12.22, CRM, 4 sh; Mafra, 29S 047085/431166, gardens and walls, 207 m, 2013.04.27, GAH & RCM 2012.P308, not kept, 5 sh; Minho, Ofir, Fáo, Esposende, 29TNF19 (N41°31'06" W8°47'10"), 2012.07.02, RCM, Det. DTH 2012.12.22, CRM, 1 sh; Ribatejo, NE. of Moitas Venda, 29S 05311/43717, limestone crags and rocky slopes with scrub, ca 195 m, 2010.05.02, GAH & DTH 2010.P41, CGAH, 23 sh, 2 bod; Spain, Prov. La Coruña, E. edge of P. N. de Corrubedo, 29T 049808/471162, exposures of low granitic rocks with moss locally and very sparse grasses, at edge of pine wood, 48 m, 2011.08.27, GAH & DTH 2011.E183, CGAH, 1 sh; Prov. Ourense, by OU533 ca 0.5 km S. of Santa Cruz, 29T 065415/468485, low granitic rocks of road cutting with short patchy herbs and grasses, bushes locally, 621 m, 2011.10.17, GAH & DTH 2011.E214, CGAH, 9 sh; ca 1 km N. of Porto de Moncelos (N. of A Cañiza), 29T 05578/46801, granitic slopes with much bare rock, patchy grasses and herbs and burnt *Ulex*, 758 m, 2011.08.28, GAH & DTH 2011.E185, CGAH, 4 sh; ca 3 km NW. of Sanxenxo, 29T 051032/469590, slaty sea-cliffs with low scrub and patches of grasses and herbs, 15 m, 2011.08.26, GAH & DTH 2011.E181, CGAH, 1 sh.

*Candidula ponsulensis*, Portugal, Baixo Alentejo, Vila Verde de Ficalho, Serpa (junto à Ermida das Pazes), 29SPC50 (N37°56'11" W7°16'30"), vivo sobre muros, ca 175 m, 2012.12.17, RCM, Det. DTH 2013.10.22, CRM, 2 sh; near Ermida das Pazes, ca 2 km SE. of Vila Verde de Ficalho, 29S 06515/42002, small N.-facing roadside cutting of shaly rock, patchy grasses and herbs, 195 m alt., 2013.10.29, GAH & DTH 2013.P340, CGAH, 8 sh, 3 bod†, paratypes; NW. of Pardais, N. of Alandroal, 29S 06387/42889, olive groves and spoil from marble quarry, 382 m alt., 2013.10.30, GAH & DTH 2013.P341, 6 sh, 4 bod†, paratypes; Beira Alta, by N16 on W. edge of Gonçalbocas, 29T 065385/449325, granitic slopes with much bare rock, patchy herbs and grasses, bushes locally, 814 m, 2011.10.14, GAH & DTH 2011.P209, CGAH, 10 sh, 1 bod†; Beira Baixa, by N239 just

SW. of Proença-a-Velha, 29T 064964/443134, rocky (slate) bank beside road, facing S., sparse vegetation, 375 m, 2011.01.15, GAH & DTH 2011.P100, CGAH, 31 sh, 22 bod†, paratypes; by N240 on W. bank of Rio Pônsul (W. of Ladoeiro), 29S 064247/441342, under stones and pieces of concrete along road cutting with slaty rock and concrete gutter, patchy herbs and grasses, ca 180 m, 2010.04.20, GAH 2010.P35, CGAH, 33 sh, paratypes; by N240 on W. bank of Rio Pônsul, W. of Ladoeiro, 29S 064235/441332, S.-facing rocky (sandstone) banks/cutting with patchy scrub and grasses, 183 m, 2010.12.23, GAH & DTH 2010.P88, CGAH, 21 sh, 15 bod†, paratypes; by N240 on W. bank of Rio Pônsul, W. of Ladoeiro, 29S 064235/441332, S.-facing rocky (sandstone) banks/cutting with patchy scrub and grasses, 183 m, 2010.12.23, GAH & DTH, 2010.P88, NHMUK reg. no. 20140015/1 (1 sh) & 20140015/2 (1 bod†), holotype; by Rio Pônsul and N18–8 at Ponte do Pônsul (ca 8 km SE. of Castelo Branco), 29S 06329/44029, slaty and granitic road cuttings, rocky outcrops along river banks and flushed hillslope, 127 m, 2013.04.02, GAH 2013.P301, CGAH, 1 sh, paratype; S. of N3 at ca 1.5 km SE. of Benquerenças, 29S 06223/44029, slaty outcrops with low *Cistus* scrub and waste ground, 392 m, 2013.04.02, GAH 2013.P302, CGAH, 5 sh; E. of Malpica do Tejo, 29S 06412/43971, flushed grassland, 328 m, 2013.04.06, GAH 2013.P303, CGAH, 3 sh, paratypes; by M1267 ca 2 km NE. of Bizarrinho (SW. of Monforte da Beira), 29S 06412/43971, flushed grassland, 323 m, 2013.04.21, GAH 2013.P305, CGAH, 14 sh, 3 bod†, paratypes.

*Candidula scabiosula*, Portugal, Algarve, E. end of Rocha da Pena, 29S 05803/41234, rocky limestone slope and plateau with patches of bushes, 460 m, 2011.01.28, GAH & DTH 2011.P104, CGAH, 28 sh; E. end of Rocha da Pena, 29S 058033/412344, rocky limestone slope with patches of tall bushes, 462 m, 2011.01.31, GAH & DTH 2011.P112, CGAH, 2 sh, 2 bod; Rocha da Pena, Loulé, 29S NB8023, 2007.09.19, Ádo (9), CGAH, 9 sh, 6 bod†, 2 spm; by A22 Junction 15 and N398 at 3 km N. of Moncarapacho, 29S 06069/41075, beneath rubbish on track and in low scrub on limestone slope, 2009.12.25, GAH & DTH, 2009.P21, CGAH, 5 sh; N. of Moncarapacho, 29S 06087/41071, among herbs and low scrub on limestone slope, 2009.12.29, GAH & DTH 2009.P23, CGAH, 22 sh; São Miguel, NW. of Moncarapacho, 29S 06043/41067, amongst scrub and trees on limestone hill, ca 390 m, 2009.12.26, GAH 2009.P22, CGAH, 1 sh; ca 2 km E. of Santa Barbara de Nexe, 29S 059428/410732, rocky limestone hill-slopes with patchy low scrub, 261 m, 2011.02.03, GAH & DTH 2011.P117, CGAH, 3 sh; Cerro da Cabeça (NE. of Olhão), 29S 06081/41075, limestone crags on slope, ca 200 m, 2008.01.11, GAH 2008.59, CGAH, 2 sh; Algibre River valley NE. of Paderne, 29S 0574/4115,

limestone slopes and scree, ca 79 m, 2014.03.22, GAH P364, CGAH, 6 sh.

*Candidula setubalensis*, Portugal, Estremadura, Serra da Arrábida, 29S 04999/42576, S.-facing limestone crags and rocky slopes, 250 m, 2007.05.16 & 18, GAH 2007.09 & 15, CGAH, 22 sh; Serra da Arrábida, 29S 05032/42604, S.-facing limestone crags and rocky slope, 300–350 m, 2007.05.16, GAH 2007.11A, CGAH, 20 sh; Serra da Arrábida, 29S 04990/42568, open disturbed ground near roads with patchy low herbs, grasses and bushes, ca 260 m, 2010.02.27, GAH & DTH 2010.P27, CGAH, 35 sh, 6 bod\*\*; Serra da Arrábida, 29S 05011/42587, under open grasses and herbs on ledges and at base of limestone road-cutting, ca 122 m, 2010.02.27, GAH & DTH, 2010.P28, CGAH, 26 sh; Serra da Arrábida, 29S 05012/42587, base of patchy herbs and grasses at foot of limestone road cutting on hillside, ca 110 m, 2010.04.12, GAH 2010.P29, CGAH, 21 sh, 1 bod†, 1 spm; Serra da Arrábida, 29S 050117/425874, herbs and grasses at base of S.-facing limestone road-cutting, 131 m, 2011.02.12, GAH & DTH 2011.P131, CGAH, 10 sh, 3 bod†, 8 spm\*\*; SE. of Azóia, 29S 04854/42540, limestone crags and slopes, ca 168 m, 2014.03.19, GAH & DTH P358, CGAH, 29 sh, 18 spm.

*Candidula strucki*, Portugal, Algarve, by N268 at ca 2 km SW. of Vilarinha, 29S 051163/411189, roadside

cuttings of mainly bare slaty rock, patchy grasses and herbs, *Cistus* above, 135 m, 2011.02.07, GAH & DTH 2011.P124, CGAH, 1 sh; ca 0.5 km S. of Bensafrim, 29S 05237/41116, S.-facing limestone slope, with bare soil and low herbs, scattered bushes, 76 m, 2011.02.06, GAH & DTH 2011.P121, CGAH, 62 sh, 4 bod†, 52 spm; ca 2 km NW. of Sagres, 29S 05045/40971, flat ground with patchy bushes, grassland and scattered limestone rocks, 15 m, 2011.02.07, GAH & DTH, 2011. P125, CGAH, 75 sh, 3 bod†, 21 spm; NW. of Sagres, 29S 05042/40965, among patchy low scrub over limestone, 20 m, 2014.03.25, GAH P368, CGAH, 24 sh; just NW. of Almádena, 29S 052017/410618, nearly flat ground over limestone with short herbs and grasses, scattered rocks, patchy low scrub, 47 m, 2011.02.06, GAH & DTH 2011.P122, CGAH, 66 sh, 4 bod†, 68 spm; inland of Praia da Cordama, NW. of Vila do Bispo, 29S 0505/4106, rocky (shale) and sandy coastal slopes, ca 20 m, 2014.03.25, GAH P369, CGAH, 5 sh; Baixo Alentejo, N. of Porto Covo, 29S 05177/41953, among patchy low scrub on shaly slope with blown sand, ca 15 m, 2014.03.21, GAH & DTH P362, CGAH, 59 sh, 10 bod†, 5 spm; Costa de San André, 29S 05179/42189, stable sand dunes with patchy low scrub, 17 m, 2014.03.20, GAH & DTH P360, CGAH, 63 sh, 13 bod†, 36 spm.