A REVIEW OF THE GENUS *PONENTINA* HESSE 1921 WITH DESCRIPTIONS OF SEVEN NEW SPECIES FROM PORTUGAL AND SPAIN (GASTROPODA, PULMONATA: HYGROMIIDAE)

DAVID T. HOLYOAK & GERALDINE A. HOLYOAK

Quinta da Cachopa, Barcoila, 6100–014 Cabeçudo, Portugal

Abstract *The genus* Ponentina *is reviewed. Characters of the distal genital anatomy in addition to shells were studied, allowing recognition of one species in Great Britain* (P. subvirescens), *two species in France* (P. revelata *and* P. subvirescens) *and four known species from the Iberian peninsula* (P. platylasia, P. ponentina, P. revelata, P. rosai). *In addition,* "Trichia" martigena *from Andalucia should probably be returned to the genus* Ponentina, *although generic distinctions between* Ponentina *and* Trochulus *are shown to be slight and intergrading. Seven new and apparently endemic species are named and described from Portugal or neighbouring provinces of western Spain. All the known species are redescribed and a key to all European species is presented, using characters from shells and genital anatomy. Nominal taxa from Morocco, Algeria and Tunisia are reviewed, although only shell specimens could be studied and the generic allocation of most of them remains tentative.* P. martigena *is newly recorded for NW. Africa in N. Morocco. The type localities of* P. revelata *and* P. ponentina *are restricted here. Habitats of each of the species are described: all are associated mainly with open sites, often rocky places; eight species are largely restricted to base-poor habitats and tend to have small ranges, often in the mountains; one* (P. platylasia) *is a strict calciphile; five occur in both basic and base-poor sites, most of the latter having wide geographical ranges. Reduction of the female genitalia is characteristic of most of the species which are restricted to base-poor habitats, but present in only one of those that occur in more basic places.*

Key words Ponentina, Trochulus, *Hygromiidae, taxonomy, new species, genital anatomy, shell hairs, France, Portugal, Spain, habitats, distribution*

INTRODUCTION

The genus *Ponentina* Hesse 1921 has often been regarded as having a single European species, *P. subvirescens* (Bellamy), as in Nobre (1941), Kerney & Cameron (1979) and Puente (1994). Older treatments recognised up to five species in France (e.g. Locard, 1894), from which Germain (1930), Falkner, Ripken & Falkner (2002) and Gargominy *et al*. (2011) recognised only two. The total recognised for Portugal rose to ten species during the nineteenth century (Servain, 1880; Castro, 1887; Locard, 1899), which Nobre (1913, 1941) reduced to one in the belief that the others were due only to excessive "splitting" of a single conchologically variable species by followers of the Nouvelle École.

Several workers have pointed out that there are wide differences between descriptions and figures of the genital anatomy of *Ponentina* that have been "lumped" together as *P. subvirescens*, notably Arrébola Burgos (1995). It therefore seems clear from the modern literature that the genus has several species, although uncertain how many, or which names should be used for some of them. It is also apparent that different names have been used in the various provinces of Spain for anatomically similar taxa. Thus Manga (1980: 45) figured "*P. ponentina*" from León very similar to the "*P. subvirescens*" later figured by Puente (1994: 663) from Burgos and Logrono. On the other hand, Arrébola & García (1999) figured "*P. subvirescens*" from Sevilla that differed from all of the material illustrated from northern Spain. More recently, Schileyko (2005: 1930) described and figured (nearly) topotypical *P. subvirescens* from S. Wales with anatomy very different to any of the Spanish material. Germain (1930) recognised two French species with different shell characters, that Falkner *et al.* (2002) treated as *P. subvirescens* and *P. revelata* (Michaud). Albuquerque de Matos (2004) continued to recognise only a single Portuguese species (as *P. revelata*) in a recent checklist, whereas Simões (2006) drew attention to the large conchological differences among Portuguese "*P. subvirescens*".

Our initial attempts to resolve these contradictions proved unsuccessful because of the lack of good mature anatomical specimens of most taxa and uncertainty about the extent of intraspecific variability in shells. Early in the present study it was realised that several Portuguese

---

Contact author : holyoak9187@gmail.com

species of *Ponentina* show clearly marked differences in the anatomy of their distal genitalia. Sustained efforts were therefore made to obtain mature specimens for anatomical study from as many localities as possible during 2009–2012, so as to characterise numerous populations of *Ponentina* from different regions and habitats. Shell characters were critically reviewed in the material studied anatomically, in order to seek reliable ways of identifying shells, which were eventually found for most of the species and indeed for all those known to occur in regions with or near any congeneric species. The newly circumscribed shell characters and better information on geographical ranges allow reinterpretation of original descriptions and type material of some taxa, clarifying application of names. Other taxa with distinctive characters evidently lack names, since no nominal species have been described from within their ranges, so these are named and described here.

We redescribe shells, external colouration of the body and the anatomy of the distal genitalia for all species of the genus. This is necessary because the standard literature has become muddled through copying from one source to another, sometimes starting with very early descriptions and often ignoring the varying taxonomic concepts used by different authors. For example, Michaud (1831: 28) described *Helix revelata* from France as having "*cinq tours convexes*", and coincidentally Bellamy (1839: 420) noted "in the extreme, five whorls" in naming and describing his *Helix subvirescens* from Cornwall. Taylor's (1916: 38) *Monograph* for the British Isles reduced the count to 4–4½ whorls for *Hygromia revelata*, which Ellis in his *British Snails* (1926: 212) repeated for *Trichia subvirescens*. The same 4–4½ whorls for *Ponentina subvirescens* reappeared in the text of Janus (1965: 125), despite a good figure showing only 3.5 whorls. Kerney & Cameron (1979: 197) also repeated 4–4½ whorls for the species, although their illustration (pl. 17, fig. 7a) shows about 3.7 whorls; 4–4½ whorls is further repeated in the Dutch and French language guides derived from Kerney & Cameron (*op. cit.*). However, our study of several hundred shells from Britain and France reveals a range in mature *P. subvirescens* of only 3.3–3.6 whorls, whereas *P. revelata* from France has 3.4–4.1 whorls.

METHODS

Field collections were made by direct searching, concentrating on the bases of herbaceous plants and the underside of loose rocks, often including large boulders. A deliberate effort was made to persist in searching thoroughly in dry open sites with acidic rocks, which commonly produced very few or no other land snails. However, *Ponentina* spp. were also found at times in species-rich limestone habitats, gardens, on tree trunks in parks and even in closed cover of mature *Betula* woodland, so an effort was made to collect a sample of specimens whenever the genus was encountered. Fieldwork targeting *Ponentina* was carried out in 2009–2012 on visits to Cornwall, Brittany, northern Spain (Prov. Logrono to Galicia), western Spain (mainly in Provinces Cáceres and Zamora) and throughout 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; grid references are based on the U.T.M. grid. Sites were given consecutive serial numbers (e.g. P38). Habitat notes (including bedrock type and vegetation) and associated Mollusca were also recorded at all sites. Additional shell specimens collected during 1983 and 1984 in Portugal, Spain, Morocco and Algeria were studied on loan from NMW.Z.

Shells, external features of the body and the genital anatomy were studied using a Meiji RZ series stereo-microscope. Drawings of shells were made with a Meiji drawing tube. Measurements of shell breadth and height [excluding hairs], and counts of whorls followed the method illustrated by Kerney & Cameron (1979: 13). Shells were mainly recognisable as having reached adult (full) size by the combination of a widened and often down-turned mouth and presence of a firm rather than membranous mouth edge. Measurements of whole shells were made with an eyepiece graticule; these data are summarised in Table 1. Measurements of shell hairs (and other microsculpture) were made using Infinity Analyze© software on images taken with an Infinity 1 camera on a Meiji RZ series stereo-microscope. The latter measurements were reproducible to ± < 2 μm. The measurements were made on the hairs from around the periphery of the last half of the body whorl, on unworn adult or nearly adult shells, taking great care to avoid measuring broken or dirty hairs. Length

Table 1 Measurements of adult shells of *Ponentina* species. See Methods for details of how measurements were made; [ ] = exceptional measurements; n* gives overall total number of shells studied (adults and immatures) in parentheses, where <25 adult shells were measured the number measured is given outside the parentheses; measurements are rounded to the nearest 0.1 mm, relative width of umbilicus to nearest 1%.

species	sample(s)	height (mm)	breadth (mm)	whorls (count)	umbilicus (U) (mm)	(U × 100)/ breadth	n*
P. curtivaginata	P172	4.4–4.6	8.2–8.4	3.2–3.4	0.7–1.0	8–12%	5 (15)
P. excentrica	all	4.2–4.9	7.6–10.1	3.6–3.9	1.0–1.9	13–19%	12 (32)
P. foiaensis	P120	5.4–6.1	7.6–8.5	3.6–3.7	0.6–0.7	7–8%	5 (44)
P. grandiducta	all	3.5–4.9	6.4–8.3	3.2–3.4	0.5–0.7	7–10%	(303)
P. martigena	all	4.6–6.0	7.6–9.8	3.7–4.2	0.7–1.0	9–12%	23 (38)
P. monoglandulosa	all	3.6–4.7	6.4–8.7	3.1–3.3	0.6–0.9	9–10%	(207)
P. octoglandulosa	E184	4.4, 5.1	6.2, 7.1	3.3, 3.3	0.4, 0.6	7%, 9%	2 (9)
P. papillosa	all	4.3–5.6	5.8–8.1	3.2–3.4	0.4–0.9	7–12%	(218)
P. platylasia	all	4.4–5.3	7.6–10.5	3.4–3.9	1.2–1.6	13–17%	(640)
		[3.5]	[5.4]		[1.0]	[11%]	
P. ponentina	all	5.2–7.6	8.3–11.3	3.7–4.2	0.8–1.0	9–12%	(1020)
P. revelata	all	4.5–6.1	7.1–10.1	3.4–4.1	0.8–1.2	9–13%	(1348)
					[0.7–1.4]	[8–16%]	
	F198	5.6–6.1	8.6–10.1			11–13%	(91)
	P93 & P190	4.5–4.9	7.3–8.1			10–11%	(197)
	P96	5.2–5.6	7.8–8.7			9%	(41)
P. rosai	all	1.9–2.7	3.5–4.6	3.2–3.4	0.6–0.9	15–20%	(88)
P. subvirescens	4 (see text)	4.2–5.2	6.9–8.5	3.3–3.6	0.6–0.7	7–9%	(96)
P. sordulenta	all	4.1–5.7	7.6–8.6	3.7–4.1	1.1–1.6	13–19%	13 (85)
	N. of Sétif, 1984.251.10				1.1–1.3	13–16%	3 (6)
	ENE. of Bouira, 1984.325.5				1.3–1.6	18–19%	3 (4)

of curved hairs was measured as the chord from the hair tip to the bottom of the papilla-like hair base; hair width was measured at the widest point low on the shaft (above the base or "foot plate"). Data on shell hairs are presented in Table 2. For some species counts of rows of hairs were made at a point just behind the peristome of fresh adult shells (see genus description for more details). These counts were only practicable with shells in perfect condition and difficult to achieve accurately with them, since careful rotation of the shell is required while looking obliquely over the peristome edge to see the hairs aligned in rows.

Mature living specimens for anatomical study were deliberately sought during field work. When only subadult snails were found, a few of the largest were usually kept alive at home (for up to six months) until their shells matured. However, samples of individuals with shells that appeared fully mature sometimes had immature genitalia, so repeated collections, rearing, or both, became necessary to obtain reproductively mature specimens for description. Specimens for dissection were drowned in water for at least 12 hours, then kept in 80% industrial methylated spirit, the body being partly or wholly pulled from the shell after one or two days. Because mature specimens of some species were scarce (unique in one of them), the genitalia were examined while *in situ* in the dissected body rather than being removed for description and drawing. Because of the compact arrangement of the genitalia and study of them being carried out *in situ*, drawings of the distal genital anatomy were prepared mainly by freehand drawing with a standardised arrangement of organs, assisted by measurements and occasional use of a Meiji drawing tube. In descriptions of the genital anatomy, proximal and distal refer to the position in relation to the ovotestis. As discussed under the genus heading below, "dart sacs" and "accessory

Table 2 Measurements of hairs (μm) on body-whorl of shells of *Ponentina* species. See Methods for details of how measurements were made; hair length includes the swollen hair-base or "foot-plate"; *for these species the measurements refer only to the papilla- or tubercle-like hair-base, plus the short hair sometimes present at its apex in *P. foiaensis*; †largest measured widths may include some dirt adhering to hairs.

species	**sample**	**hair length**				**hair width**			
		range	**mean**	**s.d.**	**n**	**range**	**mean**	**s.d.**	**n**
P. curtivaginata	P172	279–431	382.8	46.9	14	19–30	24.0	3.1	14
P. excentrica	E240	70–133	97.2	19.7	18	22–33	26.6	2.9	18
**P. foiaensis*	P120	43–77	55.9	9.4	25				
P. grandiducta	P36	171–308	216.9	35.0	16	17–28	20.8	3.0	16
	P85	93–217	155.5	36.4	19	21–30	26.8	3.6	19
P. martigena	2007/55	117–218	160.1	25.2	25	19–29	23.3	2.7	26
P. monoglandulosa	P84	186–391	312.3	43.6	28	18–41	26.8	5.0	28
	P87	218–375	314.9	33.5	34	26–62†	31.2	3.5	14
	P101	272–481	377.3	60.5	23	25–48	34.2	6.0	23
P. octoglandulosa	E184	85–180	142.1	23.7	32	15–29	21.3	3.7	32
**P. papillosa*	P55	21–45	32.9	7.1	23				
P. platylasia	P39	640–879	806	77	24	17–30	24.7	3.3	24
P. ponentina	P56	141–236	194.2	29	19	18–27	21.6	2.3	19
P. revelata	P96	335–726	571	89.1	30	14–30	22.7	4.4	30
P. rosai	P94	381–636	489	72	20	6–14	10.2	2.0	20
P. subvirescens	6.4.2011, Kynance	107–184	148.4	16.8	23	11–16	13.7	1.6	23
P. sordulenta	1984.338.13 SE. of Alger	311–635				16–19			
	1984.325.5, ENE. of Bouira	341–356				20–31			

sacs" were mainly recognised by their relative locations and shape; these organs were dissected in search of darts for only a few specimens, to avoid damage to scarce material.

The specimens studied are listed in Appendix 1, where abbreviations of collectors and collections are defined. The legend to Fig. 6 gives additional abbreviations for parts of the distal genitalia. Other abbreviations used in the text are as follows: B breadth of shell; FCUP Museu de Zoologia, Faculdade de Ciências, Universidade de Porto, Portugal; H height of shell; N number (sample size); MNHN Muséum National d'Histoire Naturelle, Paris, France; pe1, pe2, pe3: distal, middle and proximal parts of penis; RMNH Netherlands Centre for Biodiversity Naturalis, Leiden, The Netherlands; U maximum width of umbilicus of shell; va1, va2, va3: distal, middle and proximal parts of vagina. Most specimens studied are in CGAH, with holotypes of the new taxa named here in NHMUK; other material studied is in CÁDO, CRCM, NHMUK, NMW.Z.

Taxonomy, descriptions and distribution

Family Hygromiidae Tryon 1866

Subfamily Trochulinae Lindholm 1927

(syn. Ponentininae Schileyko 1991)

Genus *Ponentina* P. Hesse 1921

(syn. *Henkia* E. Gittenberger 2012: 71–73; see discussion under *P. rosai* below)

Allocation to subfamily Schileyko (1991: 228; 2005: 1930) and Falkner *et al*. (2002: 50) placed *Ponentina* as the sole genus within the subfamily Ponentininae [Ponentiniinae in Schileyko, 1991: 228]. However, as discussed under *Ponentina martigena* below, the present study has revealed greater diversity in anatomy of the distal genitalia within *Ponentina* than was hitherto known, and Proćków (2009) has demonstrated greater interspecific differentiation among *Trochulus* Chemnitz 1786, so that the two genera cannot easily be distinguished. Hence, separation of *Ponentina* and *Trochulus* in separate subfamilies is unwarranted.

Generic nomenclature Nineteenth-century authors mainly placed the species now included in *Ponentina* within their all embracing genus *Helix*, whereas later authors often allocated them to the segregate genera *Fruticicola*, *Hygromia* or *Trichia*. Hesse (1921) introduced the genus-group name *Ponentina*, as a "Sektion" of genus *Fruticicola* Held 1837 (*op. cit*.: 60), then as *Fruticicola* subgenus *Ponentina* (pp. 65, 76). Uncertainty regarding the type species of *Ponentina* might arise from Hesse's account. On p. 59 he stated as the very brief diagnosis of Section *Ponentina* that "*Nach Ashford's Untersuchungen gehört die englische Form zweifellos in die nähere Verwandtschaft der hispida-Gruppe, denn sie hat vier rudimentäre Pfeilsäcke, und gleichfalls verkümmerte Glandulae mucosae*." That is, the English form has four rudimentary dart sacs and stunted vaginal mucus glands. This is puzzling since as described below, the English *P. subvirescens* has only two small dart sacs and no accompanying accessory sacs which might be mistaken for additional dart sacs, whereas *P. revelata* which is known from France but not in England has an accessory sac proximal to each dart sac, giving an impression that there are two pairs of dart sacs, as does the Iberian *P. ponentina*. In the same text introducing the name *Ponentina*, Hesse (*op. cit*.: 60) referred to the paper on the group by Kennard & Woodward (1919), which listed *Helix ponentina* Morelet among other species, as did Hesse himself (on his p. 75). Since the Section name *Ponentina* is undoubtedly a tautonym derived from *Helix ponentina*, this might suggest *H. ponentina* was intended as the type species. However, Hesse (*op. cit*.: 76) later clearly listed *subvirescens* Bellamy as the type, which is here assumed to be correct "by original designation", especially since Hesse (p. 65) gave *subvirescens* as the only species of his subgenus for which the anatomy was known and, as noted above, the "*englische Form*" is mentioned at the outset. The gender of the generic name has generally been regarded as feminine to judge from endings of species epiphets placed within it. The AnimalBase website (2012) also regards it as feminine. Hence, since *Helix* is also feminine, epiphets of names introduced in that genus remain unchanged when transferred to *Ponentina*.

Generic characters This section mainly describes features that appear to be common to all species studied and which are therefore not described separately under the species headings. For discussion of distinctions from *Trochulus* see account of *P. martigena* below.

Shell characters Shell dextral, convex to flat above, with few whorls (3.1–4.2 when mature) that expand rapidly. The mouth is relatively large, round or broadly ovate except where interrupted by the penultimate whorl, with the last part of the body whorl widened and usually descending near the mouth. The mouth edge is thin, ± strongly reflected below, not or less strongly reflected outwards and upwards. The inside of the mouth sometimes has a white rib or other thickening. The umbilicus is open, often narrow, usually partly overlapped by the reflected edge of the peristome. The shell is usually thin or very thin, partly translucent even when mature (e.g. Fig. 1A, B, F). In taxa living on base-poor rocks it is sometimes almost completely uncalcified and remains flexible when mature, but in other taxa occurring on base rich substrata a strong white shell persists after loss of the periostracum. Shell colour varies from light brown to light greenish-brown in different species, with a pale (translucent) peripheral band in some species. Shells of live snails are commonly coated with a layer of soil (e.g. Fig. 1C–F).

Four superimposed types of shell sculpture are usually present on the periostracum of 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) *Spiral lines*, are the finest sculpture and present in most species, visible only locally with the high power of a stereo-microscope (×50 or more) when bright light is reflected by the lines, which are typically 9–10 μm apart. (2) *Spiral ridges*, mainly 20–60 μm apart (varying interspecifically), visible as dark lines at ×20-×50 magnifications (e.g. Fig. 5C, D, J), the adjacent ridges closely parallel, wavy, converging on bases of hairs. At magnifications above ×50 in oblique view each ridge appears as a low narrow lamella, *ca* 5 μm high. The ribs are inconspicuous among other types of sculpture in *P. papillosa*, where other sculptural elements are strong. (3) Transverse *ribs*, rather irregularly spaced ridges or ribs, varying in amplitude, arising parallel to the peristome edge, apparently

Figure 1 Living snails of the genus *Ponentina* from localities in Portugal: A *P. grandiducta* sp. nov., Beira Baixa, CGAH P36, paratype from type locality; B *P. papillosa* sp. nov., Trás-os-Montes e Alto Douro, CGAH P167, paratype; C *P. platylasia*, Beira Litoral, CGAH P40, adult aestivating above ground on trunk of *Olea europaea* L.; D *P. platylasia*, Estremadura, CGAH P59, aestivating on underside of limestone boulder; E *P. curtivaginata* sp. nov., Trás-os-Montes e Alto Douro, CGAH P172, paratype from type locality; F *P. ponentina*, Estremadura, CGAH P30. A, B and F show blackish markings on the mantle that are visible through the translucent shell. Characteristic layers of soil adhering to the shell surface are absent in A and B, thin in C and D and on spire of F, thick in E. The typical loss of most shell hairs in adults is shown in A and F, whereas the larger hairs in C, D and E mainly persist; B always lacks hairs.

recording alternating intervals of shell growth and inactivity ("growth lines"). In *P. papillosa* the ribs on the early whorls consist of transversely elongate papillae or lamellae. (4) Shell *hairs* are discussed in detail in the next section. They vary in size and to a lesser extent in form between different species of *Ponentina* and hence provide characters useful for species identification (Fig. 5, Table 2). On young shells the protoconch (apical semi-circle plus whorl 0–0.5) is mainly smooth, although spiral lines, spiral ridges, ribs and hairs start variously at whorls 0–1.3.

Structure and formation of shell hairs in *Trochulus* have recently been studied in detail by Allgaier (2011). This genus is very closely related to *Ponentina* (see discussion under *P. martigena* below) with closely similar shell hairs. Allgaier's results indicate a complex mechanism of formation with each hair being secreted in one of a row of glands in the periostracal groove of the mantle edge, independently of the periostracum. The hair is then attached to the edge of the periostracum (with "viscous periostracal cement material"), drawn out of the tissue, and finally swivelled to the upper side of the periostracum. Upon further growth of the periostracum, the hairs are finally fixed upright on the shell. The presence of "hair pits" in the calcified shell (exposed after loss of periostracum) results from thickened bases of hairs having projected below the general level of the underside of the periostracum as shell calcification occurred. As in *Ponentina* (e.g. Fig. 5O), each hair consists of a wider base ("foot plate"), a long shaft that is approximately cylindrical but tapering upwards, and a more rapidly tapering tip. Shell formation is not continuous, but occurs during alternating intervals of several days of activity and inactivity. New hairs are created at the edge of the shell (out of sight in the periostracal groove) only during the phases of shell formation. New hairs which are initially flexible only become visible after the snail has retracted into its shell, when the periostracal groove has been detached from the edge of the shell. The alignment of hairs in rows on the shell (e.g. Fig. 5A, H) results from production of successive hairs by the same gland. The spacing between successive hairs corresponds to the amount of new periostracum grown during each period of active shell growth.

Our observations on *Ponentina* show that shell growth results in rows of hairs oblique rather than perpendicular to the peristome edge. Thus, each new row arises on the outside of the lower palatal area of the shell mouth, ascends to the periphery of the whorl, before eventually disappearing into the upper suture defining the top of the visible part of the body whorl. Counts of rows of hairs (see also Methods above) close behind the peristome started with the short row of very small hairs on top of the body whorl and ended with the last hair close to the peristome near the base of the shell. Rows of mainly very short hairs nearer the umbilicus with hairs not reaching close to the peristome were not counted.

Genital anatomy Besides providing an overview for all species of the genus, and defining the terminology used, this section mainly describes features that 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 features that differ among the species, which have been studied only in the distal genitalia. 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 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. A penial flagellum of variable length is present. 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 well developed muscular epiphallus connects the proximal end of the penis with the flagellum/vas deferens junction; its distal end is defined approximately by the often collar-like insertion of the penial retractor muscle, the other end of the latter being attached to the body wall. The penis generally consists of three parts, the ovoid or subspherical centre part (pe2) which is widest, comprising a rather thin-walled sac or sheath, containing a muscular verge extruded from the body during mating. The verge tapers distally to a blunt point and possesses a sometimes deep longitudinal groove which the epiphallic pore enters at the bottom of its proximal end. The distal part of the penis (pe1) is a narrower cylinder of variable length, joining the genital atrium distally. The proximal part of the penis (pe3) narrows markedly from pe2 to the point where it passes into the epiphallus approximately where the penial retractor muscle inserts. The genital atrium is a very short cylinder, dividing proximally into pe1 and the distal end of the vagina. The vagina is short or long, cylindrical, ovoid, or subtriangular, often flattened, 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 spermatheca duct inserts. In taxa showing "unreduced" distal female genitalia, a pair of rounded muscular dart sacs ("stylophores"; each containing a short slightly curved calcareous dart) inserts symmetrically on almost opposite sides of the vagina near its proximal end. An accessory sac (sometimes apparently muscular, but lacking a dart) inserts inside the axil on the proximal side of each dart sac, with the slender base of a mucus gland ("digitiform gland") arising laterally or subterminally on it and a thin internal duct passing distally to enter the vagina at a point distal from the base of the accessory sac and close to or in the pore exiting from the subtending dart sac. Each mucus gland divides into two branches above the slender common basal duct, with typically each branch rapidly becoming much thicker and often convoluted. Dart sacs and accessory sacs may be reduced from a pair of structures present on both sides of proximal vagina to a single structure present on both sides (the dart sac or the accessory sac), or further reduced to a single structure (sometimes of uncertain homology as dart sac or accessory sac) on only one side of the proximal vagina. In different species, mucus glands may arise from the accessory sac (the "unreduced" condition) or directly from the proximal vagina near or in the axil of the dart sac or accessory sac. Mucus gland branches may also be duplicated giving eight branches in total (two glands each with two branches on each side), or reduced from the usual four branches to one, two or three branches, the lowest numbers consisting of glands present on only one side of the vagina. The free oviduct is a very short to moderately short tube. The spermatheca ("reservoir" or "bursa copulatrix") is a subspherical, ovate or sub-triangular thin-walled sac that is closely attached to the middle part of the spermoviduct. The spermatheca duct is typically slender throughout most of its length, widening progressively into the spermatheca at the proximal end. The distal spermatheca duct is much narrower than the adjoining vagina in most species, but markedly thicker and stronger (>60% width of vagina) in some species; one side of the distal spermatheca duct often has a short line of small muscle attachments extending proximally along its length from the junction with the proximal end of the vagina. The right ommatophore passes through the penial-vaginal angle.

We recognise 13 species in the genus on the basis of genital anatomy and shell characters, which will rise to at least 14 if N. African taxa with undescribed anatomy such as *P. sordulenta* can be confirmed as belonging in *Ponentina*. 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 European taxa in the following order: (1) six species for which names are already available and the genital anatomy is known, commencing with those having unreduced distal female genitalia (*P. revelata*, *P. platylasia, P. martigena*), then moving on to those with reduced distal female genitalia (*P. ponentina*, *P. subvirescens*, *P. rosai*); (2) seven new species named here, again treated in approximate order from less reduced to more reduced structure of distal female genitalia; (3) a multi-access key to European species of *Ponentina*. This is followed by: (4) nominal species of *Ponentina* from Morocco, for which the genital anatomy is unknown; (5) nominal species of *Ponentina* from Algeria and Tunisia, for which the genital anatomy is unknown. Appendix 2 deals with nominal taxa from Europe which are or have been assigned to *Ponentina* but which are of uncertain identity.

Ponentina revelata (Michaud 1831)
Figs 2A, B, 5M, 6A–J, 10, 14E

Helix (sub-gen. *Helicella*) *revelata* Férussac 1821, *Tableau famille des Limaçons*, Jan. ed., p. 48 (June ed., p. 44, no. 273), *nomen nudum*. Type locality: "La France, les environs de Paris et d'Angers".
Helix revelata Fér.: Tryon (1887) *Manual of Conchology* (2)3: 180, pl. 41, figs 80–82.
Helix revelata Michaud 1831, *Complément de l'Histoire des Mollusques terrestres et fluviatiles de*

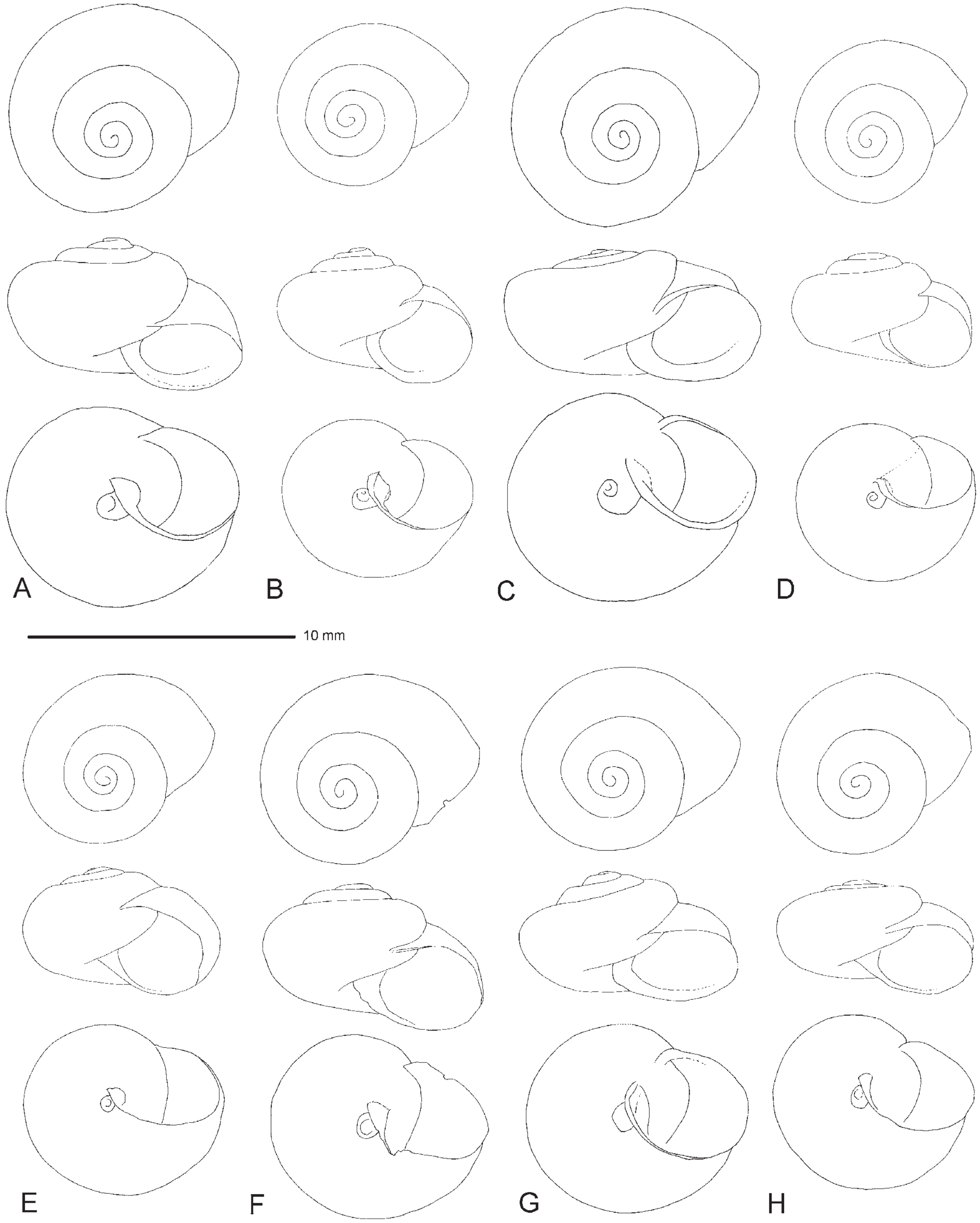

Figure 2 Shells of *Ponentina* species: A *P. revelata*, France, Dept. Maine-et-Loire, E. of Angevine, CGAH F198 (from restricted type locality); B *P. revelata*, Portugal, Estremadura, N. of Praia da Vieira, CGAH P93; C *P. platylasia*, Portugal, Beira Litoral, by Ruínas de Conimbriga, near-topotype, CGAH P39; D *P. subvirescens*, Great Britain, W. Cornwall, Kynance Cliff, 6 Apr. 2011, CGAH; E *P. octoglandulosa* sp. nov., Spain, Prov. Pontevedra, holotype, NHMUK 20120215; F *P. grandiducta* sp. nov., Portugal, Beira Baixa, holotype, NHMUK 20120217; G *P. curtivaginata* sp. nov., Portugal, Trás-os-Montes e Alto Douro, holotype, NHMUK 20120218; H *P. monoglandulosa* sp. nov., Portugal, Beira Baixa, holotype, NHMUK 20120221.

France de J.P.R. Draparnaud, pp. 27–28, no. 44, pl. 15, figs. 6–8. Type locality: "les environs de Paris et d'Angers" [also, erroneously,"les vallons des Alpes"], here restricted to Angevine, near Angers, Dept. Maine-et-Loire.

Helix villula Castro 1887, *Jornal de Sciencias mathematicas, physicas, e naturaes, Lisboa* 11(44): 235–236 (part; non *H. villula* Locard 1882).

Fruticicola (*Ponentina*) *subvirescens* Bellamy: Germain (1930) *Faune de France* 21: 245 (non Bellamy 1839).

Ponentina ponentina (Morelet 1845): Manga (1980) *Comunicaciones del primer Congreso Nacional Malacologia, Madrid*: 41–45, figs 1, 2 (non Morelet 1845).

Ponentina ponentina (Morelet 1845): Raven (1984) *Basteria* **48:** 19, fig. 2 (non Morelet 1845).

Ponentina subvirescens (Bellamy 1839): Puente (1994) *Estudio taxonómico y biogeográfico de la Superfamilia Helicoidea de la Península Ibérica e Islas Baleares*, unpublished Doctoral Thesis, Universidad del País Vasco: 656–663, pl. 123, figs 1–5 (non Bellamy 1839).

Description of shell 1348 examined, from 28 localities (of which 1109 from sites confirmed by dissection in France (4), Spain (3) and Portugal (11)). Convex to depressed convex above, somewhat flattened below; height 4.5–6.1 mm, breadth 7.1–10.1 mm, with 3.4–4.1 whorls. Whorls rounded, the body whorl somewhat flattened above; sutures moderately deep. Umbilicus narrow to medium width (0.7–1.35 mm, representing 8–16% of shell breadth, but usually 9–13%, although varying between populations as discussed below), symmetrical to slightly asymmetrical (but rendered asymmetrical by diverging body whorl in some shells that have an atypically wide umbilicus), partly overlapped by reflected peristome, deep, with upper whorls visible. Mouth nearly round except where interrupted by the penultimate whorl, the last part of the body whorl descending at least slightly and widening markedly, especially below. Mouth edge thin, strongly reflected below, not or slightly reflected outwards and not reflected upwards. Interior of mouth unthickened, or in adult shells of some populations with a low white rib set back from the peristome, the white thickening continuing further back into the shell along the palatal/parietal and columellar/parietal junctions but lacking from the parietal area). Shell thin, rather weakly calcified and translucent except where thickened behind mouth, light brown to brown or pale brown. Many populations with majority of shells having thin complete or incomplete covering of soil particles. Exposed periostracum with waxy lustre, or glossy, especially below near mouth. Spiral lines start at least by whorl 0.5, mainly inconspicuous amongst other sculpture. Spiral ridges seen from whorl 1.6 onwards, prominent on top of body whorl of unsoiled fresh shells. Transverse ribs start around whorl 0.3; on later whorls irregular, mainly low, often partly discontinuous around periphery of whorl. Shell hairs start around whorl 1.2 as low papillae, becoming short hairs by whorl 1.4; on body whorl moderately long, rather sparse, length 335–726 μm (mean 571 μm), medium width, 14–30 μm (mean 22.7 μm); in detail, mainly hooked in apical one-fifth of length, gently curved or swept back.

Populations studied anatomically differ markedly in mean size and relative width of the umbilicus (Table 1), the Angevine (F198) shells being large (breadth 8.6–10.1 mm) with a relatively large umbilicus (11–13% of shell breadth) (Fig. 2A). Some populations from coastal sand dunes in Portugal (e.g. P93 & P190) are distinctly smaller-shelled (breadth 7.3–8.1 mm) with a relatively small umbilicus (10–11% of shell breadth) (Fig. 2B). Another Portuguese population (P96) is slightly larger (breadth 7.8–8.7 mm) but with a relatively narrow umbilicus (9% of shell breadth). Nevertheless, other populations are clearly intermediate in mean shell size and relative size of the umbilicus varies independently of overall size.

External features of body Top of head and body pale grey to grey or dark grey; lower sides of body, tail and sole of foot whitish (occasionally light grey to grey). Mantle whitish to cream (occasionally pale brown) with individually variable blackish to grey spots, or blotches and short lines, that may enlarge to become bold irregular lines and bars or a bold reticulate pattern; the anterior fringe with unmarked narrow band of whitish (or occasionally pale grey, or with pale grey line along anterior edge). Upper whorls whitish or light to dark brown (sometimes partly whitish) with variable blackish blotches and bars. The dark markings show through the translucent shells of those individuals lacking a covering of soil. (Based on 412 bodies from 18 sites where

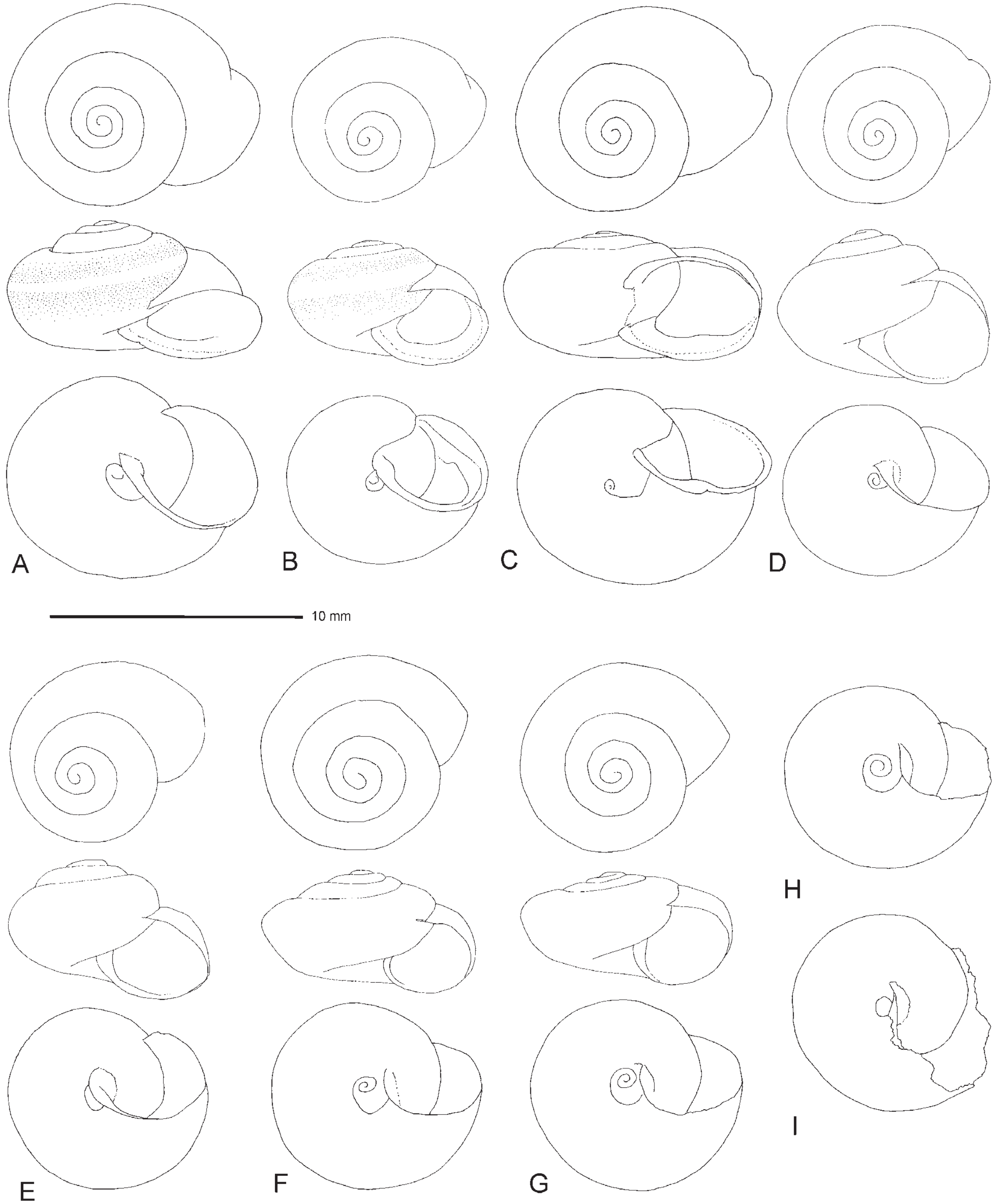

Figure 3 Shells of *Ponentina* species: A *P. martigena*, Spain, Prov. Cádiz, Alto al Cabrito, CGAH 2007/55; B *P. ponentina*, Portugal, Estremadura, Sintra, from restricted type locality, CGAH; C *P. excentrica* sp. nov., Spain, Prov. Badajoz, holotype, NHMUK 20120216; D *P. foiaensis* sp. nov., Portugal, Algarve, holotype, NHMUK 20120220; E *P. papillosa* sp. nov., Portugal, Alto Alentejo, holotype, NHMUK 20120219; F *P. sordulenta*, Algeria, N. of Biskra, NMW.Z. 1993.051.00089; G *P. sordulenta*, Algeria, N. of Sétif, NMW.Z. 1993.051.00096; H *P. sordulenta*, Algeria, ENE. of Bouira, NMW.Z. 1993.051.00094 (with large umbilicus); I *P. sordulenta*, Algeria, WNW. of Batna, NMW.Z. 1993.051.00093 (with small umbilicus).

identification checked by dissection, as noted for shells above).

Genital anatomy 12 mature specimens dissected from France (four sites: F198, F203, F205, F206), eight mature specimens dissected from N. Spain (three sites: E182, E210, E213), 16 mature specimens dissected from Portugal (ten sites: P83, P91, P93, P96, P97, P190, P222, R. do Abade, NF2660, NF3654) and 23 immatures dissected from Portugal (ten sites, including P247). Flagellum medium to large (33–75% length of epiphallus), medium thickness to stout distally (thinner than to as wide as epiphallus), shortly cylindrical, tapering proximally to curved blunt point. Vas deferens narrow, with short conical thickened area adjoining flagellum/epiphallus junction, sometimes sharply curved just before start of thickening, passing distally alongside penis, under right ommatophore retractor and deep into pe1/vaginal angle, then returning proximally alongside vagina and free oviduct. Epiphallus short to medium in length (33–67% penis length), stout, cylindrical, muscular, shiny, often abruptly curved near proximal end. Penis with three parts: pe1 distal, cylindrical, sometimes narrowed at junction with atrium, varying from very short to medium length (10–80% length of pe2), thin-walled; pe2 large, ovoid-elliptical, thin-walled, with large verge partly visible by transparency; the verge strong, muscular, bluntly lingulate with rounded apex near opening into pe1, transverse groove in proximal third, weak longitudinal groove along distal two-thirds of length; pe3 short (up to 50% length of pe2), often with oblique line of demarcation from pe2, firm, sub-conical, tapering from pe2 to epiphallus. Penis retractor muscle with wide collar-like insertion around pe3/epiphallus junction, the muscle short, wide, attached to body wall (proximal end sometimes trapped behind vas deferens). Genital atrium short, cylindrical, dividing proximally into pe1 and distal vagina. Vagina very variable in length, divided into two or sometimes three parts: va1 distal, short (occasionally absent) to long, subcylindrical but widening proximally, often sharply bent near distal end; va2 middle or proximal vagina, funnel-shaped to subtriangular, widest in middle or close to proximal end, slightly flattened; va3 proximal, sometimes lacking, sometimes half as long as va2 when whole vagina short, narrower than va1. Dart sacs two, one each side of vagina near proximal end, slightly approximate rather than opposite, each of them muscular, hemispherical to slightly ovoid with blunt rounded tip; small dart sometimes present within. Accessory sacs two, one each side, arising inside proximal axil of each dart sac at proximal end of vagina (just distal to point of separation of free oviduct and spermatheca duct), each cylindrical or narrower basally, with rounded end, narrower than dart sac but up to twice as long, thus extending further proximally. Two mucus glands, one each side, arising at or close to tip of accessory sac, basal duct very slender with a short initial section often deflexed sharply or reflexed alongside sac before passing laterally or proximally and dividing into two branches; branches moderately long, subequal, rather narrow to wide, often widest towards rounded tips and sometimes slightly bulbous near tip, often contorted or twisted *in situ*, sometimes yellow. Free oviduct short to medium length (25–75% length of vagina), its distal end offset to side of proximal end of vagina or continuing from it almost in line. Spermatheca duct of medium length, with moderately wide distal part, which sometimes ends proximally with a sharp bend, narrow to moderately narrow in at least some of longer middle section, widening again at proximal end. Outside of distal part of spermatheca duct often with weak muscle band or sheet along mid-line that sometimes continues onto proximal part of va3 (sometimes lacking). Spermatheca ovoid, ovoid-triangular or rounded-triangular, tapering into duct, flattened, thin-walled, lying closely appressed to middle part of spermoviduct.

The same anatomy was figured from N. Spain by Manga (1980: 45) from Prov. León, by Puente (1994: 663) from Prov. Burgos and (*fide* C. Prieto) Prov. Logrono.

Species recognition Shells of *P. revelata* show only rather subtle differences from those of four other species. Compared to *P. subvirescens*, *P. octoglandulosa*, *P. grandiducta* and *P. monoglandulosa* the shell hairs are longer (Fig. 5M, cf. Fig. 5E, F, I, J; Table 2) and the number of whorls in adult shells is slightly greater (Table 1). Shells of the localised *P. curtivaginata* (NE. Portugal) (Fig. 5K) are very similar overall to those of *P. revelata*, although the count of whorls in adult shells is lower at 3.2–3.4, compared to 3.4–4.1). The remaining

European species are more obviously distinct in shell characters.

The anatomy of the distal genitalia, with unreduced female tract and each mucus gland arising apically from a large accessory sac, is closely similar only to that of *P. platylasia*, although the latter is usually larger overall. Our recognition of *P. platylasia* as a species distinct from *P. revelata* is therefore based largely on shell characters, as discussed below.

Variability of genitalia was quite conspicuous between some populations (see Fig. 6A–J), leading to initial suspicions that more than one species might be involved, but these doubts were set aside later when intermediates were found elsewhere, as well as divergent individuals at the same localities. Among French samples, F198 (near Angevine, Dept. Maine-et-Loire) had very short pe1, va1 of medium length, va2 subtriangular and va3 well developed (one snail) to short (two snails) (Fig. 6B). In contrast, F205 (la Roche-Bernard, Dept. Morbihan, three dissected) had pe1 of short to moderate length, va1 almost lacking to short, va2 ovoid-rectangular to globose and va3 virtually lacking to short (Fig. 6A). A Spanish sample (E210, SW. of Villadiego, Prov. Burgos) resembled F205 in the long pe1 but was closer to F198 in the longer va1 and subtriangular va2, thus bridging the gap between them. Another Spanish sample (E213, S. of Salas de la Ribera, Prov. León) included individual snails intermediate in characters between F198 and F205, with pe1 long, va1 long, va2 subtriangular (widest at dart sacs).

P91 (Nazaré, Portugal) had the proximal vagina asymmetrical, apparently lop-sided or twisted, with longer dart sac (shortly cylindrical in shape) on shorter inner side of curve than on outer side (Fig. 6H). A second mature individual from this site was similar but with asymmetry of proximal vagina less developed and little difference in size of the dart sacs (Fig. 6G). One of four snails from a Spanish sample (E210, SW. of Villadiego, Prov. Burgos) also had va2 abruptly bent sideways just distal to insertion of the dart sacs.

Taxonomic history Potiez & Michaud (1838: 105) made it clear that *Helix revelata* Férussac (1821), a *nomen nudum*, was validated by Michaud (1831). Bourguignat (1864: 163) agreed with this and reproduced Michaud's description, noting that it was "parfaitement caractérisée" but "Figs mauvaises". Many nineteenth century authors thus adopted the name *revelata* for the species widespread in France. It was also reported from localities as far apart as England, Portugal, Morocco and Algeria (Gray in Turton, 1840: 152; Bourguignat, 1864: 163; Castro, 1887: 234; Pallary, 1904: 10, 44). However, Michaud also added the locality "les vallons des Alpes" which is outside the range of all *Ponentina* spp., leading Kennard & Woodward (1919: 136) to suggest that Michaud had confused *Trichia* and *Ponentina* species under this name, and consequently to reject it as unidentifiable, a conclusion accepted by most subsequent authors.

Falkner *et al*. (2002: 147) reiterated that Michaud (1831) made Férussac's (1821) *nomen nudum* of *H. revelata* available by supplying a description. Falkner *et al*. examined original material in Férussac's collection (two syntypes, MNHN) which was explicitly cited by Michaud (1831: 28: "les environs de Paris et d'Angers. De Férussac"), and therefore syntypes of *Helix revelata* Michaud, demonstrating they were *Ponentina*. Falkner *et al*. argued that two shell types occur in W. France, comprising *P. subvirescens* (with short and strongly curved shell hairs and a greenish shell) and *P. revelata* (with long and tousled ["embroussaillés"] hairs and a corneous tint to the shell colour). They regarded *P. subvirescens s. str*. as narrowly localised in France in the coastal regions of Finistère and Morbihan (Morlaix, Brest, Lorient, Vannes, La Roche-Bernard). At the last two localities listed it was collected along with the more widespread *P. revelata*, which ranges throughout coastal regions of W. France from Normandy southwards, and penetrates inland in the Loire basin. Our collections of *Ponentina* made near Angers in 2011 confirm the occurrence of two species differing in length of the shell hairs and in genital anatomy, as described above for *P. revelata* and discussed further below under *P. subvirescens*.

Geographical range From W. France (Brittany) southwards to NW. Spain and W. Portugal southwards to Estremadura (Fig. 10).

P. platylasia (Castro 1887)

Figs 1C, D, 2C, 5N, O, 7A–G, 13, 14C

Helix villula Castro 1887, *Jornal de Sciencias mathematicas, physicas, e naturaes, Lisboa* 11(44): 235–236 (part; not *H. villula* Locard 1882).

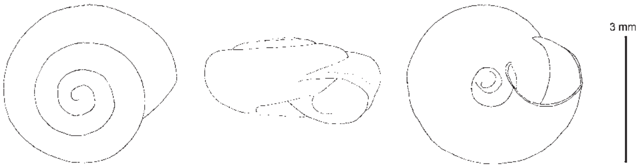

Figure 4 Shell of *Ponentina rosai*, Portugal, Beira Baixa, Rio Pônsul, CGAH P94.

Helix platylasia ["Bourguignat, in mss., 1886"] Castro 1887, *Jornal de Sciencias mathematicas, physicas, e naturaes, Lisboa* 11(44): 236. Type locality: "Sernache dos Alhos" [i.e. Cernache, *ca* 7 km SW. of Coimbra, Beira Litoral, Portugal: see below]. Type perhaps no. 278 at FCUP (cf. Simões, 2006: fig. 1).

Description of shell 640 examined, from 33 localities (of which 105 were from localities where identification was confirmed by dissection). Depressed convex to flat above, flattened below (frequently discoid except for body whorl descending towards mouth; occasionally with protoconch slightly below upper whorls). Height [exceptionally 3.5] 4.4–5.3 mm, breadth [exceptionally 5.4] 7.6–10.5 mm, with 3.4–3.9 whorls [whorls difficult to count because protoconch partly overlapped by first whorl]. Whorls rounded, the body whorl flattened above and below; sutures deep. Umbilicus relatively wide ([exceptionally 1.0] 1.2–1.6 mm, representing [11.2%] 13.4–16.5% of shell breadth), symmetrical to slightly asymmetrical, partly overlapped by reflected peristome, deep with upper whorls visible. Mouth nearly round except where interrupted by penultimate whorl, the last part of the body whorl descending and widening markedly, especially below. Mouth edge thin, strongly reflected below, especially over umbilicus, less reflected outwards, slightly or not reflected upwards. Inside mouth of mature shells usually with thickened whitish rim inside peristome, becoming gradually thinner inwards, thickening absent from parietal area, but well developed inwards along columellar/parietal junction and palatal/parietal junction.

Shell thin and remaining somewhat translucent when mature, except for area inside mouth with strong calcification, light brown to pale or slightly yellowish brown. A few populations have a proportion of shells with a pale band on periphery of body whorl. Some shells clean or almost clean, most with incomplete thin layer of dirt adhering (e.g. Fig. 1C), but in some populations most shells with nearly complete thin cover of soil (e.g. Fig. 1D). Periostracum glossy where exposed. Spiral lines start at whorl 0.5, on body whorl *ca* 10 μm apart, fine, evenly spaced, parallel. Spiral ridges start at whorl 1.3, on body whorl subparallel, wavy and rather irregular, (35) 40–54 (62) μm apart. Transverse ribs start at whorl 0.1, on body whorl low, rounded, rather irregularly spaced, variable in amplitude. Shell hairs start at whorl 0.2 (at least as basal papillae); on body whorl long, length 640–879 μm (mean 806 μm), relatively slender, width 17–30 μm (mean 24.7 μm); in detail, hairs with wide basal area, tapering abruptly, then gradually tapering to long fine acumen (Fig. 5N); in (15) 19–20 rows, apparently being in numerous rows because of widely expanded body whorl giving a wide shell mouth. Populations differ appreciably in mean shell size and relatively height of the spire. The southernmost population at Serra de Montejunto (P32) has longer shell hairs, up to 1235 μm in some individuals (Fig. 5O).

External features of body Top of head and body grey to dark grey; lower sides of body, tail and sole of foot whitish to grey. Mantle pale cream or whitish (or partly pale brown), occasionally unmarked, more often with individually variable grey to blackish spots, or some of them enlarged as blotches or elongated as longitudinal streaks, or increased to form bold blotched or reticulate pattern (the markings tending to be boldest on dorsal side); the anterior fringe bordered with grey to blackish line, behind which is narrow unmarked pale band. Upper whorls pale to light brown (or partly whitish), unmarked, dark-spotted, or with ± bold blackish blotches or barring (sometimes predominantly blackish with few pale bars). The dark markings show through the translucent shells, except where there is a heavy covering of soil. (Based on 55 bodies and nine whole specimens in alcohol from ten sites where identification confirmed by dissection, including several studied and photographed alive).

Genital anatomy Twelve mature specimens dissected (from ten sites: P8, P12b, P14, P32, P39, P40, P256, ND0576, ND1479, NE3218) and nine immature (from seven sites). Flagellum moderately long (>50% length of epiphallus), stout,

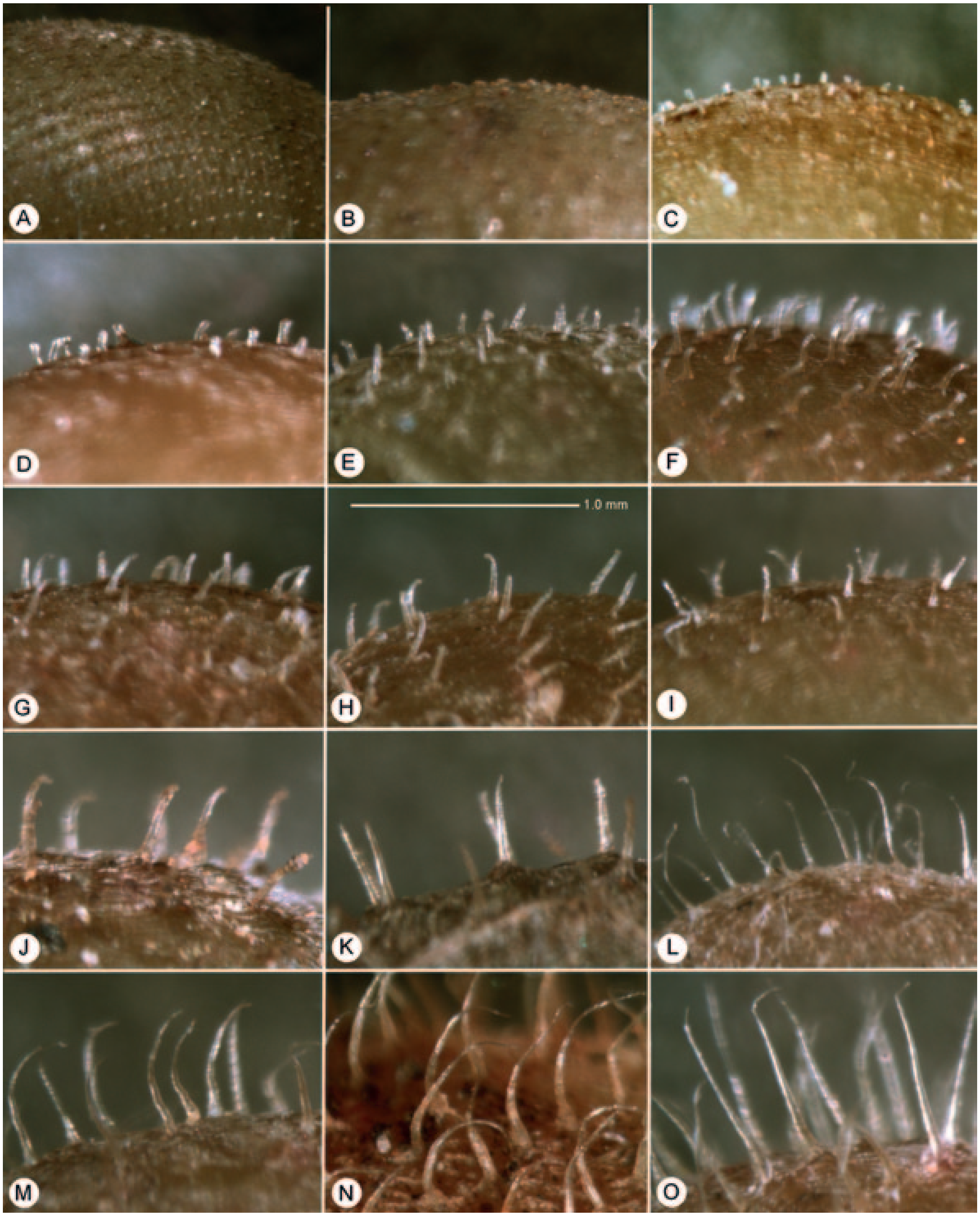

Figure 5 Shell hairs on body whorl of *Ponentina* species: A *P. papillosa* sp. nov., Portugal, Trás-os-Montes e Alto Douro, P167; B *P. papillosa* sp. nov., Portugal, Trás-os-Montes e Alto Douro, P167; C *P. foiaensis* sp. nov., Portugal, Algarve, P120; D *P. excentrica* sp. nov., Spain, Prov. Badajoz, E240; E *P. octoglandulosa* sp. nov., Spain, Prov. Pontevedra, E184; F *P. subvirescens*, Great Britain, W. Cornwall, Kynance Cliff, 6 Apr. 2011; G *P. martigena*, Spain, Prov. Cádiz, Alto al Cabrito, 2007/55; H *P. ponentina*, Portugal, Estremadura, Sintra, from restricted type locality; I *P. grandiducta* sp. nov., Portugal, Beira Baixa, P209; J *P. monoglandulosa* sp. nov., Portugal, Beira Baixa, P87; K *P. curtivaginata* sp. nov., Portugal, Trás-os-Montes e Alto Douro, P172; L *P. rosai*, Portugal, Beira Baixa, Rio Pônsul, P94; M *P. revelata*, France, Dept. Maine-et-Loire, E. of Angevine, F198 (from restricted type locality); N *P. platylasia*, Portugal, Beira Litoral, by Ruínas de Conimbriga, near-topotype, P39; O *P. platylasia*, Portugal, Estremadura, Serra de Montejunto, P237; all specimens are in CGAH.

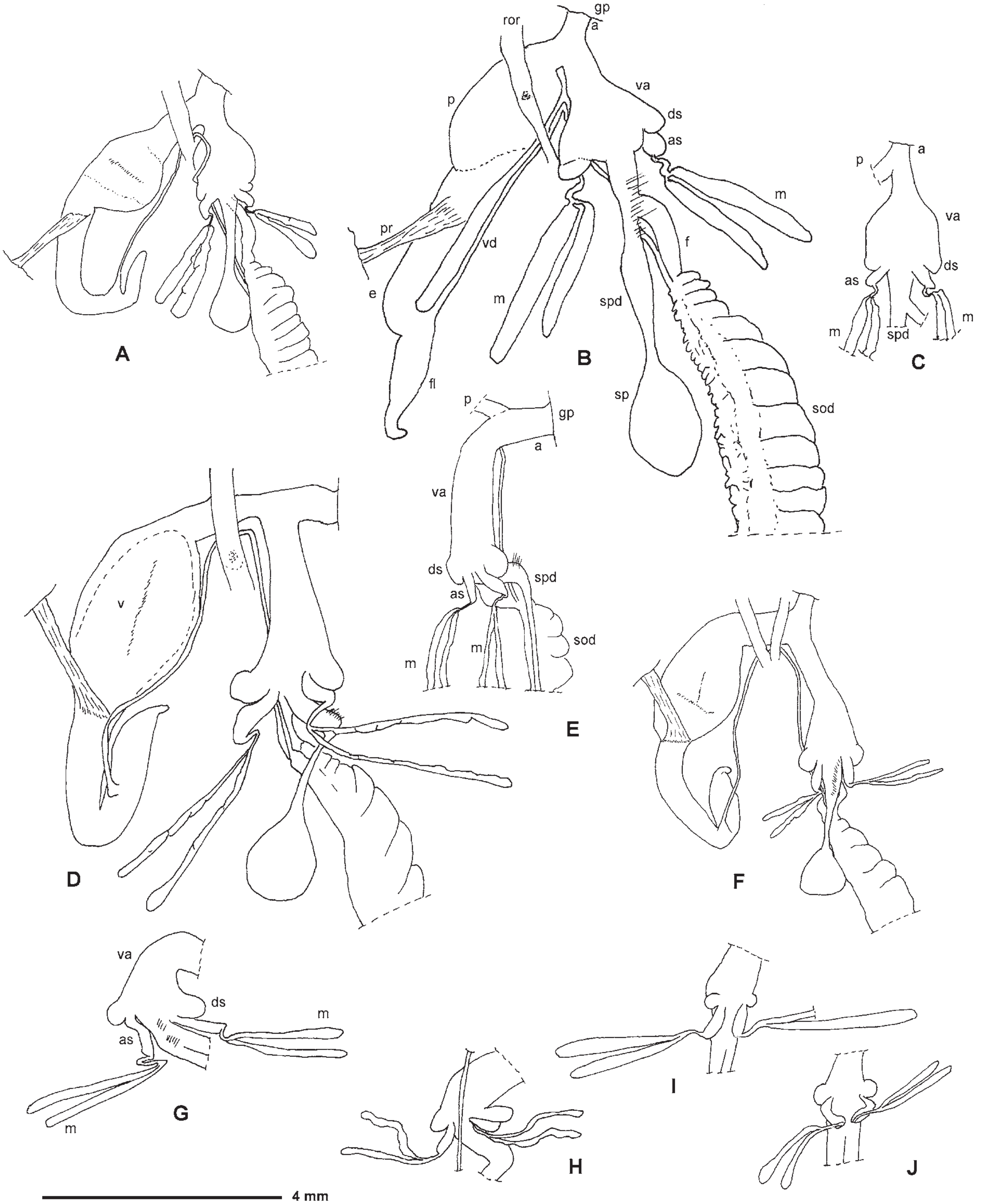

Figure 6 Distal genital anatomy of *Ponentina revelata*: A France, Dept. Morbihan, CGAH F205; B France, Dept. Maine-et-Loire, CGAH F198, from restricted type locality; C France, Dept. Morbihan, CGAH F203, detail of distal female tract; D Portugal, Beira Litoral, CGAH P83; E CGAH P83, side view of distal female tract in same specimen; F Portugal, Douro Litoral, Gondomar, leg. ÁDO, CGAH; G–J, detail of proximal part of vagina in four snails; G, H Portugal, Estremadura, CGAH P91; I, J Portugal, Estremadura, CGAH P93. Abbreviations: a genital atrium, as accessory sac, ds dart sac, e epiphallus, f free oviduct, fl flagellum, g genital pore, m mucus gland(s), mu small muscle, p penis, pr penial retractor muscle, ror right ommatophore retractor, sd spermatheca duct, sod spermoviduct, sp spermatheca, v verge, va vagina, vd vas deferens.

whitish, muscular, tapering from near base or from around middle to shortly acute or blunt tip that is twisted to one side. Vas deferens narrow, with small area of thickening close to flagellum/epiphallus junction, passing distally alongside penis and under right ommatophore retractor into pe1/vaginal angle, then returning proximally alongside vagina and free oviduct. Epiphallus shorter than penis, stout, muscular, sometimes bent in middle. Penis in three parts: pe1 distal, cylindrical, length medium to rather long (up to nearly equal to length of pe2), medium width; pe2 broadly ovoid to subspherical, with loose, rather thin, whitish outer wall, containing large muscular verge; verge ending in bluntly rounded apex close to opening into pe1, with hollow in proximal third deep (reaching half-way through verge) and bounded by thick muscular wall and containing narrow slit-like epiphallar pore, distal half on same side with slight and shallow median groove; pe3 short or very short, firm walled, tapering from pe2 to epiphallus. Penial retractor muscle with broad insertion approximately at pe3/epiphallus junction, muscle very short to short and wide, whitish, attached to body wall. Genital atrium a very short cylinder just inside genital pore, dividing proximally into pe1 and distal vagina. Vagina moderately long (67–100% penis length), in two parts of approximately equal length: distal part cylindrical with thick muscular wall, internally with few irregular longitudinal ridges; proximal part wider, broadly cylindrical or enlarging slightly towards proximal end, with thin muscular wall, internally with duct from each dart sac and accessory sac entering as slit-like pore in a low rounded papilla. Dart sacs two, one on each side of vagina near its proximal end, slightly approximate rather than opposite, each whitish, hemispherical, up to 0.6 mm high, dart not found in two dissected. Accessory sacs two, one each side, arising inside proximal part of dart sac from proximal end of vagina, each shortly cylindrical to elliptical (sometimes markedly narrowed towards insertion), narrower than dart sac but about twice as long, with internal duct that apparently unites basally with duct from dart sac before entering vagina. Mucus glands two, one each side, arising from apex (proximal end) of each accessory sac, divided into two branches almost from slender base, branches widening proximally, often slightly bulbous towards apices, blunt-tipped, dull light yellow, often twisted or contorted or recurved distally when *in situ*, reaching about as far proximally as flagellum when dissected. Free oviduct shorter and much narrower than vagina, arising in line with proximal end of vagina or slightly offset to side, with sharp bend. Spermatheca duct moderately long and of medium width in middle, tapering from wider distal end (arising in line with much wider proximal vagina) and enlarging again towards proximal end. Outside of proximal end of vagina and adjoining distal end of spermatheca duct with small thin muscles attached along mid-line. Spermatheca ovoid, tapering into duct, placed on middle part of spermoviduct.

Species recognition The shell is distinctive, being large with a low or flat spire and proportionately large umbilicus (Table 1) and long to very long shell hairs (Table 2). Except for larger overall size, the genital anatomy is closely similar to that of *P. revelata*, with an unreduced distal female tract and each mucus gland arising apically from a large accessory sac. Our treatment of *P. platylasia* as a species distinct from *P. revelata* is thus based largely on shell characters, the present species usually having longer shell hairs (640–879 μm, even up to 1235 μm in some populations, cf. 335–726 μm; Fig. 5M, cf. Fig. 5N, O, Table 2) and usually a lower spire (shell depressed convex to flat above, cf. convex to depressed convex in *P. revelata*) (cf. Figs 2C and 2A–B). *P. revelata* from Portugal also have a narrower umbilicus (9.0–12.7% of shell breadth, compared to 13.4–16.5% in *P. platylasia*), although in France and Spain the relative width of the umbilicus is more variable in *P. revelata* (8.1–16.3%). Their geographical ranges approach closely in central-western Portugal, but apparently without overlap since *P. platylasia* occurs in areas with Mesozoic limestone bedrock, typically in rocky sites, whereas *P. revelata* in its southernmost Portuguese localities was found mainly on coastal sand dunes (P83, P93, P97), once on sandy sea-cliff slopes (P91), once in a disused limestone quarry (P96), once in a grassy park with mature trees beside a lake (P247) (cf. Figs 10 and 13).

Taxonomic history The description of *Helix villula* given by Castro (1887: 235–236) probably included the present species, at least for the records from near Coimbra, along with forms of

H. revelata. However, the original description of *H. villula* by Locard (1882: 74, 317) was based on specimens from France and the present species appears to be endemic in central Portugal. *H. platylasia* was also described by Castro (1887: 236) and attributed to "Bourguignat, in mss., 1886", but it appears the mss. were never published. Bourguignat informed Castro that the "type de cette espèce" was discovered in Algeria "à la Bouzagra à l'est d'Alger" and, also at "Roknia, Constantine, etc.", but this appears to be incorrect. It is unclear whether the two paragraphs of description given in French by Castro (*loc. cit.*) are his own words or copied from a letter or other unpublished note by Bourguignat, but in the absence of further evidence for Bourguignat's involvement, authorship of the species should be attributed to Castro, with only the name coming from Bourguignat. Since Castro (*loc. cit.*) noted that he had found the species in Portugal at "Sernache dos Alhos" [i.e. Cernache, *ca* 7 km S. of Coimbra, Beira Litoral] this is taken as the type locality. We have collected numerous specimens, some of which have been studied anatomically, from 5 km SW. of Cernache at Conimbriga (P39). We searched at Cernache and in its immediate vicinity, but did find any easily accessible habitat remaining there that was suitable for the species, owing to extensive development of houses and gardens.

Nobre (1913: 213–216) ignored this taxon completely, listing *Helix occidentalis* as his only *Ponentina* and giving only the early "synonyms" under that name, apparently reflecting his dislike for what he regarded as excessive splitting of species by Castro, Servain and Locard by choosing to avoid all detailed citation of their taxa. Later, he merely made passing reference to it as one of several "*formas*" (Nobre, 1941: 125). Consequently, this and other distinctive Portuguese species of *Ponentina* have mainly been ignored in the modern literature. Simões (2006) drew attention to the large conchological differences among Portuguese "*Ponentina subvirescens*" and figured shells of *P. platylasia* from Sernache and Serra de Montejunto.

Geographical range Endemic in western-central Portugal, ranging from just south of Coimbra to the Serra de Montejunto (Fig. 13), where apparently confined to regions with outcrops of Mesozoic limestone.

P. martigena (Férussac 1832)
Figs 3A, 5G, 10

Helix martigena Férussac 1821, *Tableaux systematiques des Animaux Mollusques, classés en familles naturelles, dans lesquels ou est etabli la concordance de tous les systèmes*, p. 38 (*nomen nudum*).
Helix martigena Férussac 1832, in Férussac & Deshayes, *Histoire naturelle . . . des Mollusques . . .*, 1, p. 69, pl. 69, fig. 4. Type locality: Les montagnes de Ronda, sur le champ de bataille d'Atahate [Spain].
Fruticicola (*Trichia*) *occidentalis* ssp. *boetica* Aguilar-Amat: Sacchi (1957) *Publicaciones del Instituto de Biología Aplicada Barcelona* 25: 21. From "regioni montuose tra Siviglia e Cádice (?)".
Trichia martigena (Férussac, 1832): Arrébola & García (1999) *Iberus* **17**(1): 23–29, figs 1, 2, 4–9.

Description of shell 38 examined, from three localities (including 23 adult shells, six of them live-collected; none confirmed by dissection). Convex to depressed-convex above, distinctly flattened below; height 4.6–6.0 mm, breadth 7.6–9.8 mm, with 3.7–4.2 whorls. Whorls rounded, distinctly flattened above, the body whorl with slight angle at periphery; sutures of medium depth (slightly shallower than usual in the genus). Umbilicus narrow (0.7–1.0 mm, representing 8.8–11.5% of shell breadth), asymmetrical because of enlarged body whorl, deep, exposing some of upper whorls, overlapped by reflected edge of peristome. Mouth very broadly oval except where interrupted by penultimate whorl, the last part of the body whorl descending and widening towards mouth. Mouth edge thin, strongly reflected below, especially over umbilicus, moderately reflected outwards, not or slightly reflected upwards; inside mouth of adults of some populations with thickened white rib, slightly set back from peristome edge, extending across entire palatal and columellar sides of mouth; sometimes also with white thickening extending back on interior of last part of body whorl. Shell thin and often rather weakly calcified except for thickening inside mouth (*q.v.*) of some populations, remaining translucent ± throughout in others; brown to light brown, with well defined narrow pale (translucent) band at or slightly above periphery. Soil covering slight or lacking on the few live-collected snails examined. Periostracum with waxy lustre. Spiral lines begin at whorl 0.2,

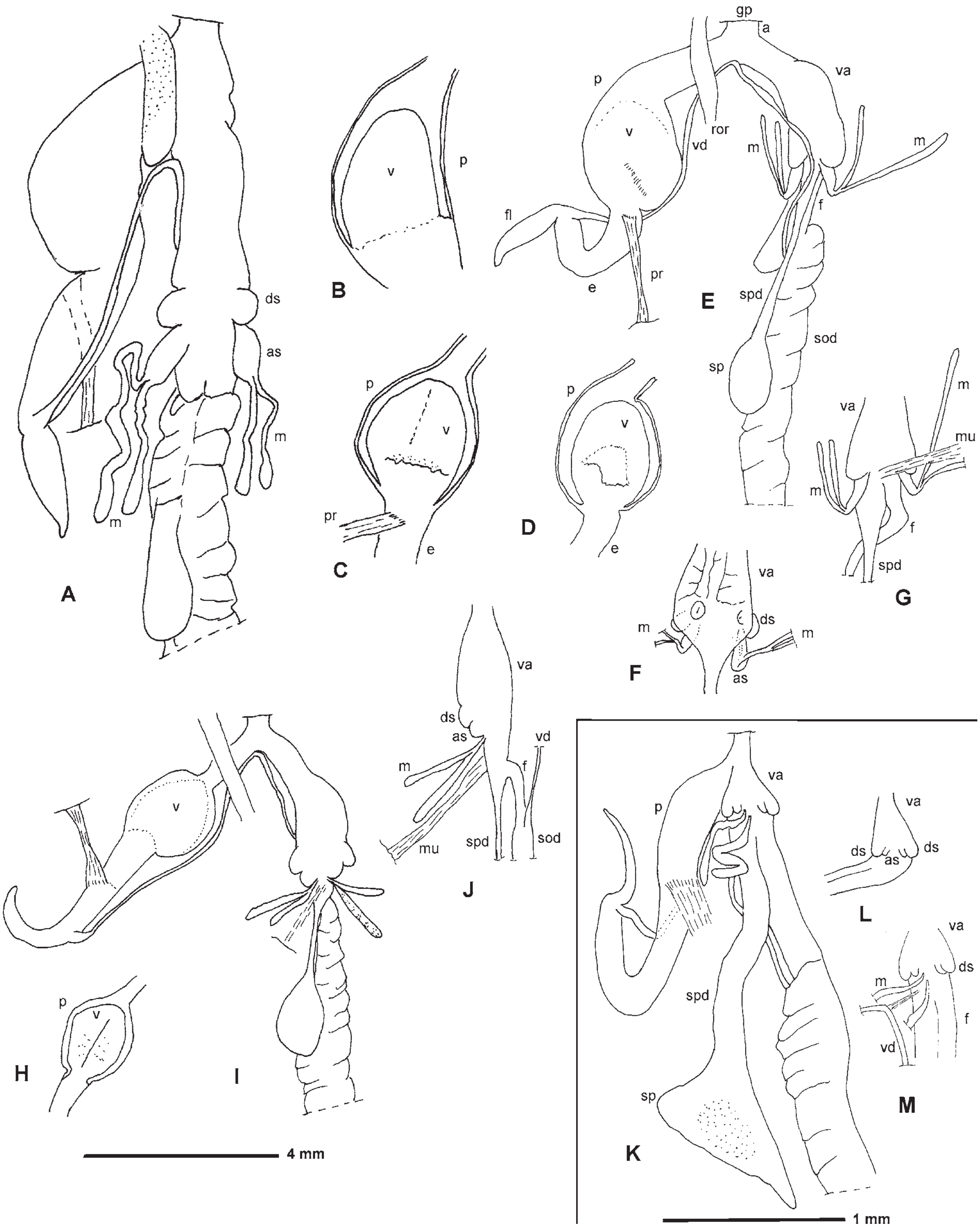

Figure 7 Distal genital anatomy of *Ponentina* species: A–G *P. platylasia*, A, B Portugal, Beira, Litoral, CGAH P8; B section through pe2 of same specimen; C Portugal, Estremadura, CGAH P12B, section through penis; D–G, Portugal, Beira Litoral, CGAH P39, in same specimen: D section through penis, F interior of vagina, G detail of proximal part of vagina; H–J *P. ponentina*, Portugal, Alto Alentejo, P56, in same specimen: H section through penis, J side view of distal female tract; K–M *P. rosai*, Portugal, Beira Baixa, CGAH P88, in same specimen: L vagina *in situ* to show curvature, M detail of proximal end of vagina and attachment of vas deferens. See legend to Fig. 6 for abbreviations.

becoming strong over whorls 0.7–2.0, but lost among other sculpture on later whorls, e.g. being faintly visible on parts of underside of body whorl near mouth. Spiral ridges start at *ca* whorl 1.8, becoming distinct on body whorl of fresh shells, where typically 17–27 μm apart, mainly ± parallel, but converging where 'attracted' to hair bases. Transverse ribs begin weakly on first whorl, becoming stronger on later whorls, somewhat irregular in height and spacing, but mainly low and mainly interrupted or discontinuous around periphery of whorl. Very small shell hairs start at whorl 1.8 on an immature shell, but two adult shells have only low conical hair bases persisting on early whorls (2.0 onwards), with small hairs first evident from whorl 2.4–3.0 onwards; on body whorl hairs short, length 117–218 μm (mean 160.1 μm), width 19–29 μm (mean 23.3 μm). In detail, hairs have broadly conical base, above which they taper over much of hair length, most being curved or hooked. The hairs are soon lost from old shells. Small samples of shells from two Spanish populations (Prov. Cádiz and Prov. Málaga) differ in mean shell size, relative height of the shell and in presence or absence of a white rib inside the mouth. A larger Moroccan sample is intermediate in size.

External features of body Top of head and body pale to light grey; lower sides of body, tail and sole of foot whitish. Mantle cream to pale brown, with individually variable spots, irregular, blotches or a few bold lines of blackish; the anterior fringe with unmarked band of whitish, sometimes with grey line along front edge. Upper whorls brown with blackish spots or blotches. The dark markings show through the translucent shells. (Based on five bodies and four specimens preserved in alcohol from one locality in Prov. Cádiz).

Genital anatomy Based on Arrébola Burgos (1995) and Arrébola & García (1999); only immature specimens dissected in present study. Flagellum short, wide at base, narrowing abruptly to slender cylindrical appendage that is recurved. Vas deferens narrow throughout, passing distally alongside penis to pe1/vaginal angle, then returning proximally alongside vagina and free oviduct. Epiphallus of similar length to penis, but narrower. Penis in three parts: pe1, distal, short, cylindrical; pe2 ovoid-cylindrical, wider than other parts, containing muscular verge with bluntly pointed tip ending near opening into pe1; pe3 broadly conical, tapering from pe2 proximally to epiphallus. Penis retractor muscle inserting approximately on pe3/epiphallus junction, short and wide, attached to body wall. Genital atrium short and narrow. Vagina moderately long, broadly cylindrical but widening proximally, the inner wall with *ca* five muscular longitudinal ridges interrupted around insertion of mucus glands. Two dart sacs arising symmetrically on opposite sides of vagina towards its proximal end, each sac shortly cylindrical, rounded apically. Two accessory sacs, one arising inside the proximal part of each dart sac and joined to it, of similar size to the dart sac or somewhat longer, with rounded apex. Four mucus glands, two each side, arising at proximal end of vagina a short distance proximal to apices of accessory sacs and separated from base of each sac by a short but distinct gap; each mucus gland usually divides close to the base into two moderately long branches, but a few are unbranched. Free oviduct short and moderately narrow. Spermatheca duct short (ending at about same level as flagellum), of medium width distally, tapering proximally. Spermatheca rounded.

Species recognition Arrébola & García (1999) clarified the characters distinguishing *P. martigena* (which they placed in *Trichia* i.e. *Trochulus*, see below) from *P. ponentina* from Prov. Sevilla (which they misidentified as *P. subvirescens*: see above). Ruiz *et al*. (2006: 142–143, 154–155) also illustrated shells of the same taxa, using the same names for each of them. They listed (*op. cit*.: 155) various differences in the shells, but their comparison is partly misleading because both often have a pale peripheral band (albeit weaker and inconspicuous in *P. ponentina*), there is much overlap in length and curvature of shell hairs, and supposed differences in microsculpture are incorrectly described. In fact, shells of *P. martigena* and *P. ponentina* (Fig. 3A, cf. Fig. 3B; Table 1) are much more similar to each other than to those of any congeners, sharing a shallow suture, short shell hairs (often lost), narrow eccentric umbilicus, 3.7–4.2 whorls in adults and frequent presence of a white rib inside the mouth. They are most easily separated by the stronger pale peripheral band already noted for *P. martigena*, and by geographical range, with *P. ponentina* known only from north of the R. Guadalquivir,

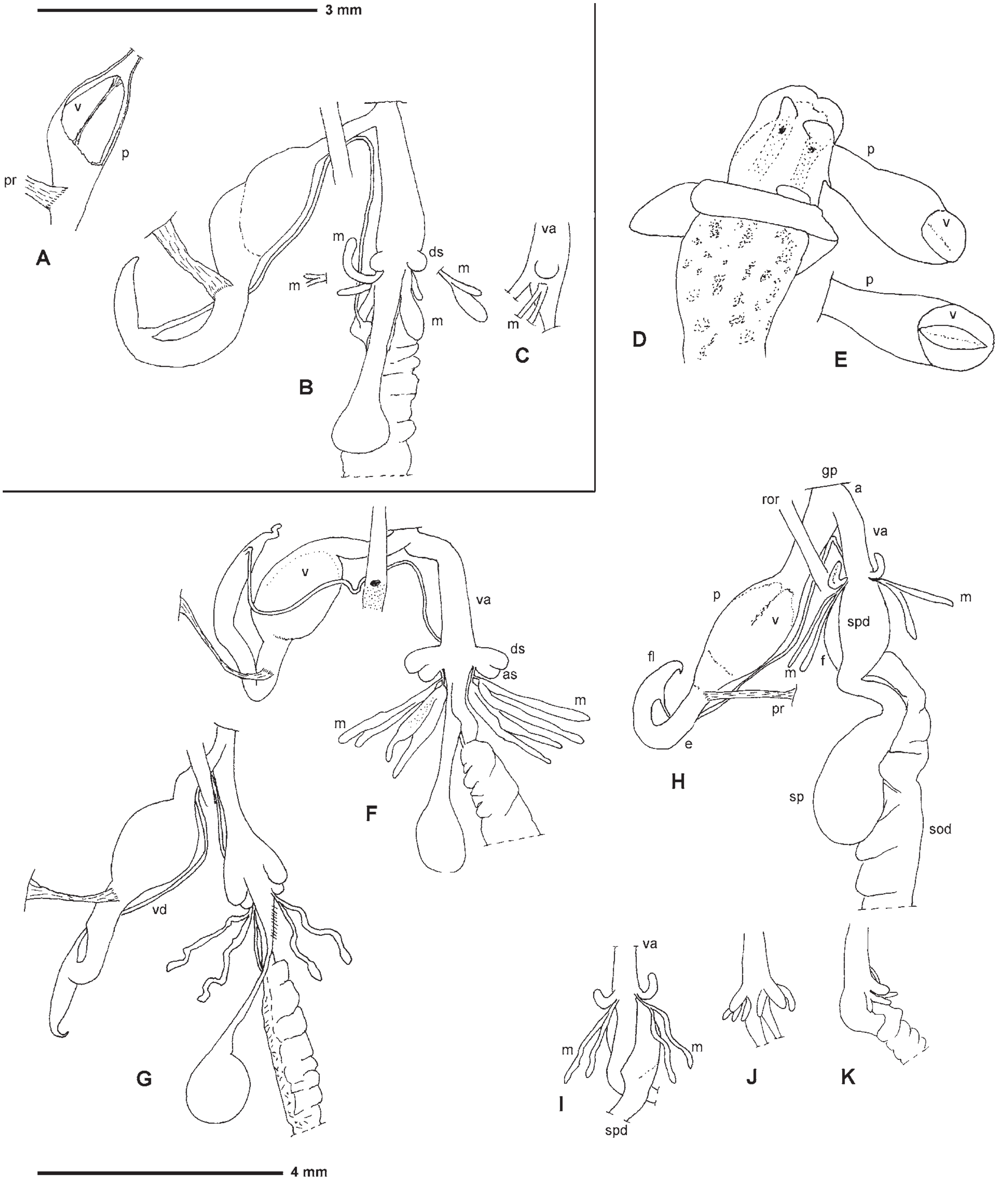

Figure 8 Distal genital anatomy of *Ponentina* species: A–E *P. subvirescens*: A–C England, Isles of Scilly, Bryher, CGAH, in same specimen: A penis opened to show verge, B distal genital anatomy with separate detail of each mucus gland, C side view of proximal part of vagina to show dart sac and origin of mucus gland; D, E France, Dept. Maine-et-Loire, CGAH F199, dorsal view of snail preserved in alcohol that died with penis extruded; E detail of extruded penis to show apex; F *P. octoglandulosa* sp. nov., Spain, Prov. Pontevedra, body of holotype, NHMUK; G *P. excentrica* sp. nov., Spain, Prov. Badajoz, body of holotype, NHMUK; H–K *P. grandiducta* sp. nov., H, I Portugal, Beira Baixa, body of holotype, NHMUK, in same specimen: I proximal part of vagina viewed from opposite side; J, K Portugal, Beira Baixa, CGAH P140, two views of same specimen with additional small unbranched mucus gland on each side of vagina. See legend to Fig. 6 for abbreviations.

P. martigena only from south of it in west-central Andalucia (cf. Figs 10 and 12). Diagnostic differences in their genital anatomy were clearly described by Arrébola & García (1999), as discussed in the next section.

Taxonomic history *P. martigena* was regarded as a senior synonym of *P. ponentina* by Ortiz de Zárate Rocandio & Ortiz de Zárate Lopez (1961), which is unsurprising as their shells are very similar. However, Arrébola & García (1999) demonstrated clear differences between the genital anatomy of *martigena* and *P. ponentina* from Prov. Sevilla [as '*P. subvirescens*']. These differences led them to reinterpret *martigena* as a species of *Trichia* Hartmann 1840 (a synonym of *Trochulus* Chemnitz 1786, with type species *Helix hispida* Linnaeus 1758), on the basis of the following characters: (a) presence of four not two mucus glands; (b) mucus glands arising a short distance from the accessory sacs, not directly from these sacs; (c) different morphology of verge; (d) relatively short penial flagellum, compared to epiphallus length; (e) presence of several longitudinal folds on interior of vagina, compared to single fold in their "*P. subvirescens*" [= *P. ponentina*, see above].

The present study has revealed greater diversity in the genital anatomy of *Ponentina* than was formerly known. The usual number of mucus glands is now known to vary from one (with single branch) to two (with total of eight branches in *P. octoglandulosa*), but an atypical individual of *P. grandiducta* (*q.v.*) had four mucus glands. In *P. rosai* the mucus glands arise from the vagina a short distance proximal to the dart/accessory sacs, not directly from them as in most *Ponentina*. The verge varies in form among species of *Ponentina* where it has been investigated and the flagellum varies considerably in length relative to that of the epiphallus. The inner wall of the distal part of the vagina has a few irregular longitudinal ridges (not one) in *P. platylasia* but the internal structure of the vagina has not been investigated for most species in the genus. Better comparative information on the genital anatomy of *Trochulus* spp. is also now available, in the monograph of that genus by Proćków (2009), which did not treat *martigena* as a species of *Trochulus*, although it was not explicitly excluded. The monograph demonstrated that in *Trochulus* the number of mucus gland branches ranges from four to ten, the position of insertion of the mucus glands varies from just above the dart sacs to higher on the proximal vagina, the internal walls of the vagina have four to six longitudinal folds depending on the species. Thus, distinctions between *Ponentina* and *Trochulus* in genital anatomy are not clearcut.

Shells of *martigena* are very similar indeed to those of *P. ponentina*, as discussed above, with fewer whorls than in any *Trichia*, and *P. ponentina* does not show characters of the genital anatomy suggesting affinity to *Trochulus* rather than other *Ponentina* spp. The genus *Trochulus* has 22 species, found mostly in central Europe, principally in the Alps, Carpathians and Balkan mountains, with only *T. hispidus* extending to the Iberian peninsula in northern Spain (Proćków, *op. cit.*). Hence, the range of *martigena* in S. Andalucia and N. Morocco is closer to that of some *Ponentina*, which shows greatest species diversity in Portugal, than it is to *Trochulus*. Treatment of *martigena* in *Trochulus* rather than *Ponentina* therefore appears to be unwarranted, although an extensive phylogenetic analysis using molecular characters is needed to provide a secure understanding of relationships among *Trochulus*, *Ponentina* and allied genera.

Geographical range The review of literature and specimens by Arrébola Burgos (1995) and Arrébola & García (1999) established that this species occurs in west-central Andalucía, mainly in the eastern half of Prov. Cádiz, but also the extreme west of Prov. Málaga and the south-east of Prov. Sevilla. Thus it was apparently endemic in S. Spain. Studies by J.S. Torres Alba (pers. comm.) have revealed a much wider range in Prov. Málaga. The present study adds N. Morocco to the known range on the basis of shells collected *ca* 6 km NE. of Taounate in Er Rif in 1984 (see Appendix 1; Fig. 10).

P. ponentina (Morelet 1845)
Figs 1F, 3B, 5H, 7H–J, 12

Helix ponentina Morelet 1845, *Description des Mollusques terrestres, et fluviatiles du Portugal*, pp. 65–66, pl. 6, fig. 4. Type locality: Portugal, here restricted to Atalaia, Colares, Sintra [Cintra] in Estremadura.
Helix occidentalis Récluz 1845, *Revue Zoologique, par La Société Cuvierienne*, 8, p. 311 (as new name

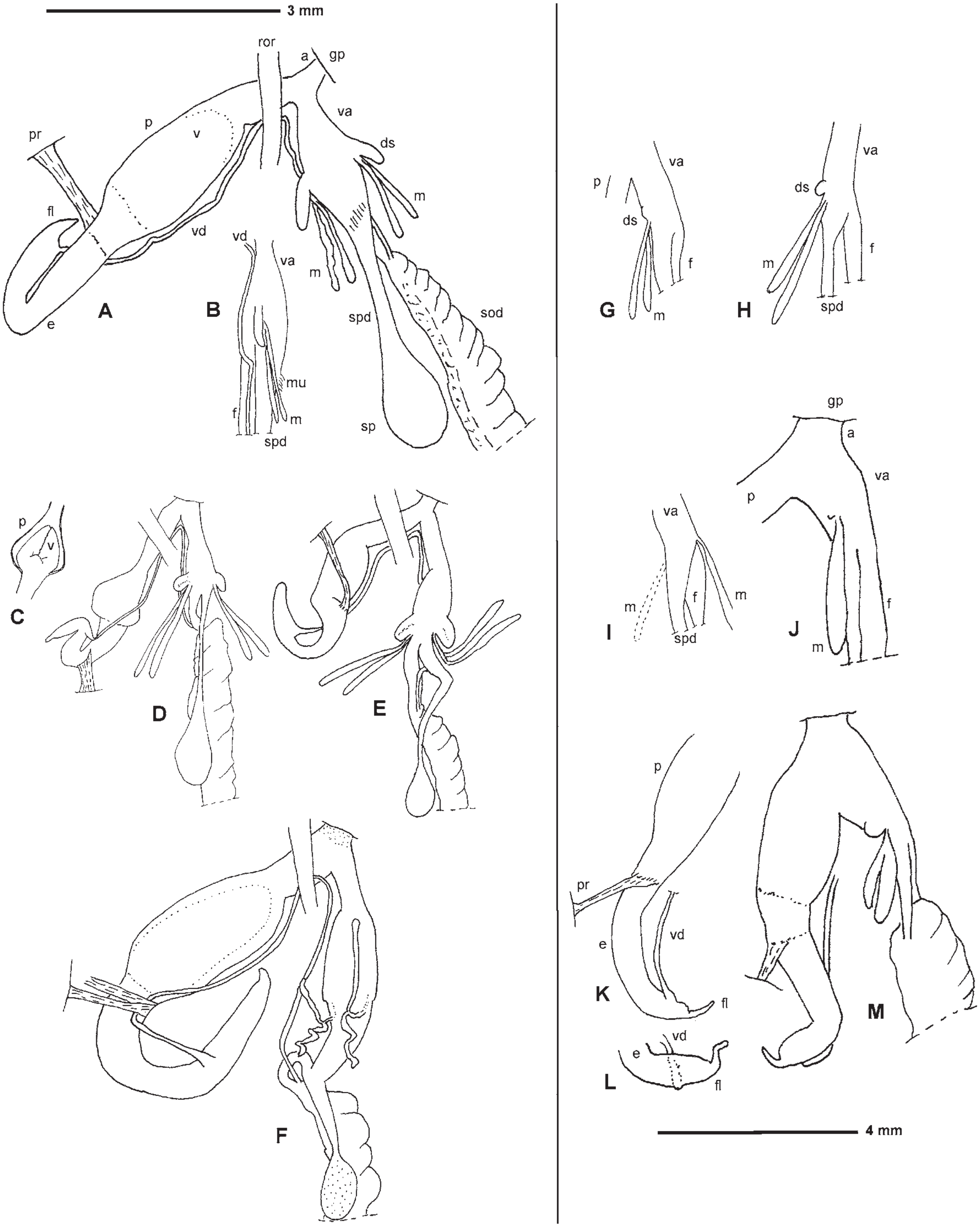

Figure 9 Distal genital anatomy of *Ponentina* species: A, B *P. curtivaginata* sp. nov., Portugal, Trás-os-Montes e Alto Douro, body of holotype, NHMUK, in same specimen: B side view of distal female tract; C–E *P. papillosa* sp. nov., C, D Portugal, Alto Alentejo, body of holotype, NHMUK, in same specimen: C shows section through penis; E Trás-os-Montes e Alto Douro, CGAH P168; F *P. foiaensis* sp. nov., Portugal, Algarve, body of holotype, NHMUK; G–M *P. monoglandulosa* sp. nov., G–I Portugal, Beira Baixa, CGAH P84, detail of proximal end of vagina in three snails to show variation (in I outline of mucus gland inserting in axil of a dart sac on opposite side of vagina shown by dotted line); J Portugal, Beira Baixa, CGAH P87, distal female tract of paratype; K Portugal, Beira Baixa, CGAH P84, penis, epiphallus and flagellum; L Portugal, Beira Baixa, CGAH P87, proximal end of epiphallus and flagellum in a paratype; M Portugal, Beira Baixa, body of holotype, NHMUK. See legend to Fig. 6 for abbreviations.

for *H. ponentina*, not Latin); *Helix revelata* Fér. var. *occidentalis* Récluz: Tryon, 1887, *Manual of Conchology* (2) 3, p. 180, pl. 41, figs 89–91.

Helix lisbonensis L. Pfeiffer 1846, *Symbolae ad Historiam Heliceorum*, 3, p. 68.

Helix labiosa Locard 1899, *Archives du Muséum d'Histoire Naturelle de Lyon*, pp. 88–89. Type-locality: Lisbonne. Syntype in MNHN (figured by Gittenberger, 1978: 14).

Ponentina subvirescens (Bellamy, 1839): Arrébola & García (1999) *Iberus* **17** (1): 21–29, figs 10–13 (non Bellamy 1839).

Description of shell 1020 examined, from 51 localities (of which 226 shells were from 12 localities at which identification was confirmed by dissection). Depressed convex above, somewhat flattened below; height 5.2–7.6 mm, breadth 8.3–11.3 mm, with 3.7–4.2 whorls. Whorls rounded but usually with slight angle at periphery, distinctly flattened above; sutures of medium depth (slightly shallower than usual in the genus). Umbilicus narrow (0.8–1.0 mm, representing 9–12% of shell breadth), asymmetrical because of enlarged body whorl, deep, with at least some upper whorls usually visible, overlapped at edge by reflected peristome. Mouth almost round to very broadly oval except where interrupted by penultimate whorl, the last part of the body whorl descending and widening, especially below. Mouth edge thin, reflected to widely reflected below, slightly to moderately reflected outwards and upwards; inside mouth often with prominent white thickened (calcified) band in adults, somewhat set back from but parallel to palatal lip and extending deeper into shell along parietal/columellar junction and parietal/palatal junction; the white thickening heavy in some populations, virtually lacking in others. Shell often thin, with variable and sometimes moderately heavy calcification, especially inside mouth (*q.v.*); the upper whorls often remaining partly translucent in adults. Colour light brown to light greenish-brown, often with narrow slightly paler (or more translucent) band around periphery of body whorl. Shell often clean, with glossy periostracum and little or no soil adhering (e.g. P56, Portagem), but some shells (e.g. among P128 from Serra da Arrábida) with thin soil covering. On periostracum, spiral lines start at whorl 0.6; on body whorl absent or weakly developed over most of shell, but regular parallel lines present on underside outside parietal area of mouth, and also on early whorls of spire. Spiral ridges, on body whorl rather inconspicuous, apparently irregular and low, (20) 24–42 (47) μm apart, almost invisible on some fresh shells of live-collected adults, much more prominent on immatures of some populations when shells weakly calcified (notably on P128 from Serra da Arrábida). Transverse ribs begin weakly at whorl 0.3, becoming strong from whorl 1.0; on body whorl as low, rounded ribs or ridges, somewhat irregularly spaced, prominent on many shells, usually strongest on upper parts of whorls near suture. Shell hairs present as basal papillae from whorl 1.6; on body whorl rather short, length 141–236 μm (mean 194 μm), medium thickness, width 18–27 μm (mean 21.6 μm); in detail, rather short, stiff, mainly with strong curve towards shell mouth in upper half, caducous or brittle, being lost from most of shell of most adults, but with shortly conical hair bases persisting as rows of papillae; body whorl with *ca* 12–13 rows of hair bases near shell mouth, but very difficult to count these accurately. Populations differ in mean shell size (although some large samples show wide intra-population variability) and in extent of calcification of the shell, especially development of a white thickening inside the mouth (see above).

External features of body Top of head and body pale to light grey, or very pale grey-brown; lower sides of body, tail and sole of foot whitish. Mantle cream (sometimes pale brown towards front edge), sometimes unmarked, usually with black or greyish spots and blotches of very variable extent (both within and between populations), in darker individuals the markings forming irregular lines, or mainly blackish reticulate patterns; the anterior fringe with narrow unmarked whitish band (occasionally partly grey) sometimes with grey line at anterior edge. Upper whorls pale to light brown (occasionally partly white), occasionally unmarked, more often with blackish spots and blotches that may be extensive, much as on mantle of same individuals. The dark body markings usually show through the shells by translucence, at least on the upper whorls. (Based on 78 bodies and 26 whole specimens in alcohol from 11 localities confirmed by dissection and several living individuals which were photographed, e.g. Fig. 1F).

Genital anatomy 26 mature individuals dissected (from 12 sites: P30, P56, P124, P128, P165, P173, P208, P254, MC59, NF2946, NF2947, Castelo de Alcobaça) and 15 immatures (from eight sites). Flagellum rather long (sometimes equal to epiphallus), stout (nearly as wide as epiphallus), curved, tapering to point near tip. Vas deferens mainly narrow, markedly thickened in short section near flagellum/epiphallus junction, passing distally alongside penis, beneath right ommatophore retractor to pe1/vaginal angle, then returning proximally alongside vagina and free oviduct. Epiphallus relatively short to medium length (varying from *ca* 33–100% penis length), stout, muscular. Penis divided into three parts: pe1 distal, moderately long (*ca* 33–50% total penis length), cylindrical, rather narrow, thin-walled; pe2 ovoid to subspherical, very thin walled, with large verge visible through wall, the verge thick, muscular, ovoid, with rounded point near opening to pe1 and narrow, deep, slit-like, longitudinal median groove that apparently does not reach apex or proximal end); pe3 medium length (<33% total penis length), cylindrical or subconical, tapering from pe2 to junction with epiphallus. Penis retractor muscle inserts widely approximately at pe3/epiphallus junction, the muscle short and wide, attached to body wall. Genital atrium a short and rather narrow cylinder, opening proximally into pe1 and distal end of vagina. Vagina long, in two parts: va1, distal, subcylindrical, gradually widening proximally; va2, proximal, broadly cylindrical or elliptical to triangular and widest proximally; whole vagina sometimes strongly curved. Dart sacs two, one each side, symmetrically placed 67–75% of distance along vagina towards its proximal end, slightly approximate rather than opposite, each of them forming a low hemispherical protuberance with muscular walls that is somewhat elongated longitudinally (presence of internal dart not confirmed). Accessory sacs two, one each side, located inside proximal edge of dart sac and partly attached to it on proximal vagina, slightly smaller than subtending dart sac, muscular walled, with the rounded apex extending further proximally. Mucus glands two, one each side, arising inside axil of accessory sac (or sometimes from inner edge of accessory sac about half way along its length); each gland with very short and slender common basal duct, dividing into two branches just above, the branches widening upwards, only moderately long and usually unequal, sometimes swollen and appearing irregularly segmented proximally (one individual from NF2946 with short third branch arising high on one branch of each gland). Free oviduct short, rather narrow, distal end placed laterally on proximal vagina/spermatheca duct junction. Spermatheca duct narrow, tapering rapidly at distal end; outer side of proximal end of vagina and adjoining distal end of spermatheca duct often with insertion of a line of weak muscles or sometimes a long, weak (retractor?) muscle. Spermatheca ovate, slightly asymmetrical, tapering to insertion with duct, lying on middle part of spermoviduct.

Species recognition Adult shells are distinctive in combining: a rather flat profile to the whorls of the spire which are separated by a rather shallow suture, often a narrow pale (or translucent) band around the periphery of the body whorl, short shell hairs that are quickly lost and leave a rather glossy surface to the periostracum, and, in shells from base-rich habitats, strong whitish thickening forming a rib inside the mouth that continues back into the body whorl. Less calcified shells can be thin and translucent, so they are much more similar at first sight to other *Ponentina* spp., as are juvenile shells, but they show the same characters except for the mouth rib and thickening, although the narrow pale peripheral band is often lacking or very inconspicuous. Hence, this species can usually be identified from shells alone, at least when a sample of several good fresh mature shells is available. *P. excentrica* has a flatter spire, shell mouth wider than high rather than rounded, shorter shell hairs (Table 2), and a small range in eastern Baixo Alentejo and Prov. Badajoz. Otherwise, only *P. martigena* is rather similar, but its range apparently does not overlap that of *P. ponentina* and it normally has a much clearer peripheral band on the shell and clear anatomical differences (see above). Characters of the distal genitalia are also distinctive of *P. ponentina*, the paired dart sac and small accessory sac giving an impression of a "double dart sac" peculiar to this species (which can be detected when genitalia are only half mature size), reinforced by the combination of several other characters that are distinctive when present together: four mucus gland branches, short free oviduct, slender distal spermatheca duct, long vagina,

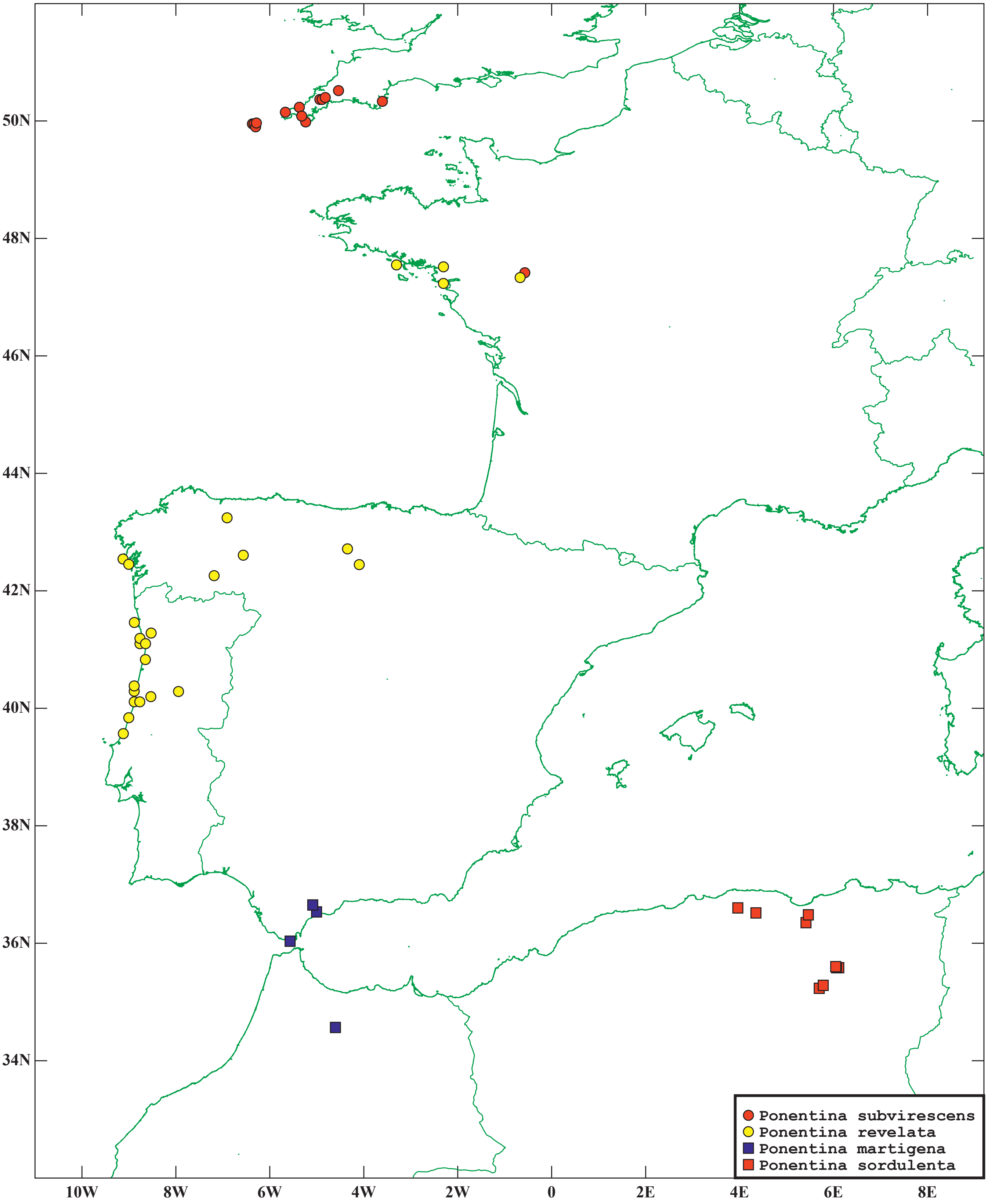

Figure 10 Distribution of *Ponentina subvirescens*, *P. revelata*, *P. martigena* and *P. sordulenta*, based on specimens studied by the authors.

long pe1, long flagellum, sometimes relatively short epiphallus.

Taxonomic history Now that this species can be clearly characterised anatomically and recognised by shell characters, reexamination of Morelet's (1845: 65–66) original description leaves no doubt that the name *P. ponentina* should be used. His descriptions noted that the shell is *ferrugineo obscurè bifasciatâ* and *orné de deux fascies rousses extrêmement obscures, et d'une zone terminale d'un jaune pâle qui résulte de la combinaison du ton qui lui est propre avec la substance vitreuse déposée à l'intérieur;* also, *ouverture arrondie ... bordée intérieurement d'un bourrelet épais d'un blanc de porcelaine, qui empâte quelquefois le péristome, diminue sensiblement la capacité de l'ouverture, et en tapisse l'intérieur à une certaine profondeur. Cette callosité, remarquable par sa couleur tranchée et par son épaisseur, ne commence à se déposer que quand l'animal est parfaitement adulte.* These details closely match those of the taxon we have found with genitalia and shell described above and are different from those of all other Portuguese *Ponentina*. Furthermore, Morelet (*loc. cit.*) described the distribution as: *d'une extrémité du Portugal à l'autre; néanmoins, ce n'est qu'à Cintra où je l'ai vue en grande abondance*. The present species is the only *Ponentina* that occurs from the far north of Portugal to the Algarve and the only one recorded reliably from Sintra (found by Rui da Costa Mendes, pers. comm.; three mature specimens dissected by us from Atalaia, Colares, Sintra; MC59; in CGAH). We therefore adopt Morelet's name and restrict the type locality to Sintra.

The name *Helix occidentalis* Récluz (1845: 311) was introduced in a review of the book by Morelet (1845) published later the same year, changing the name from *ponentina* to *occidentalis* because the former was regarded as an improperly formed name (not Latin: see below). Many other nineteenth-century authors refused to use the name *ponentina*, which was noted as "*Nomen pessime formatum, nec adoptandum*" by L. Pfeiffer, and "Nom anticlassique" contrasting with "celui plus méthodique d'*occidentalis*" by Bourguignat (1864: 164). Nevertheless, other authors did continue to use the name *ponentina*, albeit often in error for taxa that would now be given other names (e.g. Dupuy, 1848: 189; Gassies, 1849: 91; Desmars, 1873: 26). The name *occidentalis* thus represents an emendation of *ponentina* that was adopted by some but not all subsequent authors; the emendation would be regarded as unjustified according to modern ICZN Codes. Furthermore, as noted above, Hesse (1921) introduced the currently accepted genus-group name *Ponentina* as a tautonym based on *Helix ponentina*.

Helix lisbonensis L. Pfeiffer 1846 was another replacement name for *H. ponentina* Morelet provided because the latter was regarded as invalid on the basis that it was formed from the Portuguese word *ponente* (Rossmässler, 1854: 23, no. 827). According to Kennard & Woodward (1919: 134–135) the name was founded on a specimen in the Cuming collection, but this is incorrect since Pfeiffer subsequently (*Mon. Helic.*, 1, p. 131, 1848) acknowledged it to be a synonym of Morelet's species which he accepted under Récluz's amended name of *occidentalis*.

Thirty-two years later, Morelet (1877: 245–246) claimed that his *Helix ponentina correspond, sans le moindre doute, à l'H. revelata de Férussac. Les spécimens des environs de Lisbonne se distinguent à peine de ceux qui proviennent de l'Ouest de la France*. He went on to say that shells from Cintra [Sintra] and the Algarve were different in being thicker, and when adult, more yellowish-green, in losing their transparency and hairiness, and having a peristome that develops a callus. Nevertheless, he ended by stating *Mais c'est toujours la même coquille, comme on peut s'en covaincre en observant les degrés successifs de cette transformation.* However, our own experience in comparing shells from W. France with those from around Sintra and around Lisbon is different to this, as set out above, although the differences can be subtle. Also, the anatomical differences between those populations are clear.

The figure of genital anatomy in Manga (1980: 45, fig. 1) attributed to *Ponentina ponentina* from Prov. León, Spain, clearly represents *P. revelata*. However, Arrébola & García (1999: 28, figs 10–13) gave good figures of the anatomy of *P. ponentina* from Prov. Sevilla named as *P. subvirescens*.

Geographical range Our records show occurrence throughout much of Portugal from the coast near Porto southwards to the W. Algarve (Fig. 12). As noted above, Arrébola & García (1999) gave a clear figure of the anatomy of this species from Prov. Sevilla (Spain).

Simões (2006: 9, fig. 3) figured shells of *P. ponentina* from Serra de Montejunto (Estremadura) as

P. subvirescens. Reported from N. Spain by Raven (1984), but apparently in error for *P. revelata*.

Etymology Morelet (1845: 66) stated the species was *nommée* Ponentina *parce qu'elle semble emprunter ses caractères à l'extrême Occident et se rattacher à certaines formes des îles Canaries*. Kennard & Woodward (1919: 134) suggested it was based on a Portuguese word, *ponente*, meaning evening but this appears to be incorrect. Instead, the Italian *pónente*, meaning West or West-wind was the likely source. The rejection of the epiphet *ponentina* by some nineteenth century malacologists because of its non-Latin origin is discussed above.

P. subvirescens (Bellamy 1839)

Figs 2D, 5F, 8A–E, 10

Helix subvirescens Bellamy 1839, *Natural History of South Devon*, p. 420, pl. 18. Type locality: near Mevagissey, Cornwall (type probably lost).

Helix subviridis Bellamy: Gray, 1857, *A manual of the land & fresh-water shells of the British Islands* [by W. Turton], new ed., p. 139, in synonymy (orthographic error, cf. Kennard & Woodward, 1919: 134, 1926: 244).

Helix ptilota Bourguignat 1860, *Malacologie terrestre et fluviatile de la Bretagne*, p. 55, pl. 1, figs 5–8. Type-locality *3 kilomètres de Vannes, sur la route d'Auray, le long des haies qui bordent le chemin*. Kennard & Woodward (1919: 135) noted that "save for its black apex, agrees closely with the British form, of which it is in all probability only a local variation"; hence treated here as probably a syn. of *P. subvirescens*.

Helix ptylota Bourguignat: Tryon, 1887, *Manual of Conchology* (2)3, p. 181, pl. 41, fig. 79; *H. ptylota* [sic] Bourguignat: Pilsbry, 1895, *Manual of Conchology* (2)9, p. 274; an erroneous spelling of *ptilota* (*fide* Kennard & Woodward, 1919: 135).

Fruticicola (*Ponentina*) *montivaga* Westerlund: Germain, 1930, *Faune de France* 21, p. 246.

Description of shell 96 examined, from four localities (Cornwall and France; all live-collected specimens from sites where this species was confirmed by dissection). Convex to depressed-convex above, slightly flattened below; height 4.2–5.2 mm, breadth 6.9–8.5 mm, with 3.3–3.6 whorls. Whorls rounded, the body-whorl somewhat flattened above; sutures moderately deep. Umbilicus very narrow (0.6–0.7 mm, representing *ca* 7–9% of shell breadth, occasionally larger), partly overlapped by reflected peristome in adults, symmetrical and deep, with upper whorls visible. Mouth almost round to round except where interrupted by penultimate whorl, the last part of the body whorl not or slightly descending, but widening, especially outwards and downwards. Mouth edge thin, strongly reflected over umbilicus and usually slightly reflected on rest of lower lip, not or occasionally slightly reflected outwards and upwards; interior of mouth lacking any thickening. Shells thin, not or weakly calcified, translucent, light brown to light greenish-brown. Most shells clean or with thin sparse covering of tiny soil particles. Periostracum with waxy lustre, sometimes glossy on penultimate whorl near shell mouth. Spiral lines start at whorl 0.3, often relatively conspicuous up to whorl 1.3 because other sculpture commonly weak there, inconspicuous elsewhere on shell except near aperture. Spiral ridges low and difficult to see, visible mainly on body whorl. Transverse ribs start at about whorl 1.0, rather irregular, usually low and somewhat discontinuous around periphery of shell. Shell hairs start as low papillae around whorl 1.3 with tiny hairs from whorl 1.5–1.7; short, rather dense, often curved apically; on body whorl length 107–184 μm (mean 148.4 μm), width 11–16 μm (mean 13.7 μm). Populations differ slightly in shell size, relative height and average width of the umbilicus.

External features of body Top of head and forepart of body pale cream to pale grey or grey; lower sides of body, tail and sole of foot whitish to cream. Mantle pale cream to whitish with very variable dark markings even within the same population: occasionally unmarked; some snails with few small blackish or grey spots; others with many spots; some with spots replaced by larger blotches and short lines; a few with black blotches and irregular lines becoming confluent. Anterior edge of mantle with narrow unmarked whitish band, rarely fringed anteriorly with light grey line. Upper whorls cream and pale brown to brown without markings, with few blackish spots, or with numerous bold black blotches. The dark markings show through the translucent shell. (Based on 96 bodies and 30 whole specimens preserved in alcohol from three sites in Cornwall and one in France, all from localities where this species was confirmed by dissection).

Genital anatomy Ten mature specimens dissected (three from Bryher, Isles of Scilly; four from two localities in Cornwall, England; three from F199, Maine-et-Loire, France; fourth specimen in F199 figured because it died with penis fully everted) and numerous immatures. Flagellum 33–50% length of epiphallus; vas deferens slender throughout, with only short, small swelling at junction with epiphallus. Penis nearly twice length of epiphallus; pe1 medium length to long (as long as pe2 + pe3 in one specimen), narrow; pe2 ovoid, containing thick muscular verge with deep, narrow median groove that reaches to middle (pe2 externally with soft surface and thin wall, pale cream, without gloss); pe3 conical, thick-walled, muscular, tapering from epiphallus into pe2 (externally with firm, shiny, whitish surface; demarcated from pe2 by distinct oblique line). Extruded penis (Fig. 8D, E) 3.3 mm in length, comprising verge with pe3 everted over pe2 and possibly over distal part of epiphallus, the verge with crescentic hollow within a spoon-like apical depression. Penis retractor muscle a broad band, inserting on pe3/epiphallus junction, ending on body wall. Genital atrium very short, passing proximally into distal end of vagina with pe1 arising laterally. Vagina long, with narrow distal half and broader, cylindrical proximal half (widest near dart sacs or somewhat distal to them). Dart sacs two, hemispherical, muscular, rather small, symmetrically located on almost opposite sides of vagina (slightly approached) close to its proximal end, each containing small dart. Accessory sacs lacking. Mucus glands two, arising as short or very short slender common duct just proximal to base of dart sac, apparently in its axil, each with two branches of unequal length (short and very short), the branches thickening abruptly after they separate. Free oviduct very short, appearing to arise laterally from broader base of duct of spermatheca. Spermatheca duct slender in middle section, less often broad (as in Fig. 8B). Spermatheca ovoid or ovoid-spherical, flattened, resting on middle of spermoviduct.

Schileyko (2005: 1930) gave detailed figures and description of the distal genital anatomy of a specimen from Pembrokeshire, Wales, generally very similar to those of our Cornish material. He mentioned "short, conic darts" and figured a spermatheca duct that becomes more slender at its narrowest part than in our figure (as in another of our specimens from Isles of Scilly), and interior of the vagina with duct from each mucus gland entering alongside slit-like pores exiting from the dart sacs.

Species recognition Shells differ from those of *P. revelata*, which has an overlapping range in France, mainly in the much shorter hairs (undamaged hairs <200 μm in *P. subvirescens*, >300 μm in *P. revelata*; cf. Figs 5F and 5M, Table 2). Several Iberian species are much more similar to *P. subvirescens* in shell characters (Tables 1, 2), but the present study confirms that it has distinctive genital anatomy, with a pair of small dart sacs and no accessory sacs. The short mucus glands are also distinctive, although immature specimens of congeners also have them short.

Taxonomic history The only other species of the genus occurring within its known geographical range (S. Wales to C. France) is *P. revelata*. As noted above, Falkner *et al*. (2002: 147) argued that two shell types occur in W. France, comprising *P. subvirescens* (with short and strongly curved shell hairs and a greenish shell) and *P. revelata* (with long and tousled ["embroussaillés"] hairs and a corneous tint to the shell colour). During the present study, specimens collected from separate localities near Angers (Maine-et-Loire) represented both species and allowed descriptions of the anatomical characters of each of them that are presented here. Differences in shell hairs much as noted by Falkner *et al*. can be confirmed from our Angers material, as well as through comparisons of numerous English samples with additional French material of *P. revelata*: the hairs being consistently shorter in *P. subvirescens*, allowing every fresh shell to be allocated to one species or the other. Germain (1930: 245–247) long ago recognised that there were two species in France, although he adopted incorrect nomenclature as pointed out by Falkner *et al*. (*op. cit.*). Kerney & Cameron (1979) were evidently incorrect in recognising only *P. subvirescens* and regarding other French material as synonymous with it.

Within *Ponentina*, only *P. revelata* has an older name than *P. subvirescens*. Since the type-locality of *P. subvirescens* is in Cornwall and only one taxon with distinctive genital anatomy is known in England and Wales, there can be little doubt over application of the name, despite apparent loss of the types and the possibility that the species no longer occurs at the precise type locality (near Mevagissey). Our failure to refind it there in 2004 was apparently because of coastal development and increased scrub-cover on the sea-cliffs now that most of the coastline nearby is not grazed. However, K.N.A. Alexander recorded it on 3 May 1995 at Pabyer Point (U.K. grid ref. SX024427) which is *ca* 2 km SSE. of Mevagissey (ERICA Database, *fide* Dr C.N. French).

Geographical range Anatomically confirmed records of *P. subvirescens* extend from Pembrokeshire (S. Wales) (Schileyko, 2005: 1930) and the Isles of Scilly and Cornwall (England) to near Angers in the French Dept. of Maine-et-Loire (Fig. 10). Falkner *et al*. (2002: 147) reidentified nineteenth century shells as this species rather than *P. revelata* from the coastal regions of Finistère and Morbihan (Morlaix, Brest, Lorient, Vannes, La Roche-Bernard; at last two localities occurring sympatrically with the more widespread *P. revelata*). We were unable to find *P. subvirescens* along the S. Brittany coast during a brief visit in 2011, locating only a few populations of *P. revelata*, but much coastal habitat there has now changed due to reduction of coastal grazing and developments. A report of this species new to Tunisia (Abbes & Nouira, 2007) is presumably based on misidentification of some other species of Hygromiidae.

P. subvirescens has been reported many times from Spain and Portugal, but apparently always in error for other species. Those Iberian accounts with good figures of the genital anatomy along with locality data allow confident reidentification, e.g. Puente (1994: 663) evidently figured *P. revelata* from N. Spain whereas Arrébola & García (1999: 28, figs 10–13) clearly figured *P. ponentina* as their "*P. subvirescens*". No such certainty is possible with older Portuguese records; Nobre's (1941) single variable species listed for scores of localities was clearly a composite of several species (including *P. platylasia*, *P. ponentina* and *P. revelata*).

P. rosai (Castro 1887)

Figs 4, 5L, 7K–M, 11

Helix Rosai Castro 1887, *Jornal de Sciencias mathematicas, physicas, e naturaes, Lisboa* 11(44): 237. Type locality: "environs de Coimbra". Types perhaps lost.

Helix Rosai var. *declivis* Locard 1899, *Archives du Muséum d'Histoire Naturelle de Lyon*, 7: 71. Type locality: les bords du Douro à Roncão [Portugal]. Type: possibly in Locard Colln. at MNHN.

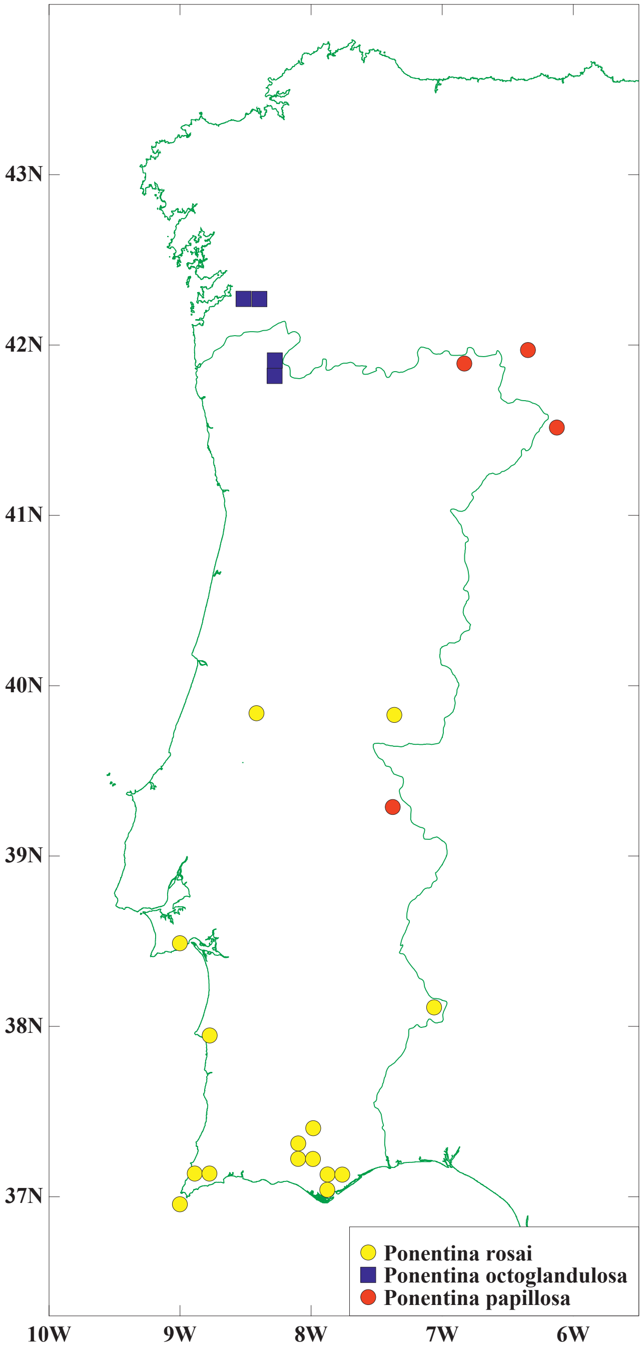

Figure 11 Distribution of *Ponentina rosai*, *P. octoglandulosa* and *P. papillosa* based on specimens studied by the authors, mapped by ten-kilometre squares of the U.T.M. grid.

Henkia mariannae E. Gittenberger 2012, *Basteria* 76: 73, figs 1, 3, 5, 6. Type locality: Portugal, Faro (Algarve): rocky slope 1 km N. of Lagos along road N125. Holotype RMNH 260563.

? *Henkia antoni* E. Gittenberger 2012, *Basteria* 76: 74, figs 2, 4, 7. Type locality: Spain, Prov. Málaga:

Alozaina, near Coin, among humus on igneous rocks. Holotype RMNH 260565.

Description of shell 88 examined, from 15 localities (see Appendix 1). Very depressed convex to almost discoid (except for descending body whorl) above, strongly flattened below; height 1.9–2.7 mm, breadth 3.5–4.6 mm, with 3.2–3.4 whorls. Whorls with rounded periphery but strongly flattened above and below; sutures moderately deep to deep. Umbilicus relatively very wide (0.6–0.9 mm, representing *ca* 15–20% of shell breadth), slightly overlapped by reflected peristome, symmetrical, deep, exposing upper whorls of spire. Mouth broadly oval to rounded except where interrupted by penultimate whorl, but somewhat asymmetrical with flattened top and often a tendency to be slightly angled below; the last part of the body whorl descending more steeply than the rest of this whorl and widening below and outwards. Mouth edge thin, reflected over umbilicus, plane elsewhere; interior of mouth lacking any thickening. Shells thin, translucent when immature, becoming calcified and more opaque at some localities but not others, light brown to brown. Many shells with most of surface covered by thin layer of fine soil particles (fine sand, silt or clay), which may be reddish or light grey-brown depending on the local soil colour; heavily coated shells may have the umbilicus plugged but clean shell hairs normally project far beyond the covering on the body whorl. Periostracum glossy when exposed. Spiral lines on body whorl fine, with close spacing; apparently absent on top of whorl, but present and sometimes strong on underside near parietal part of shell mouth, where spiral ridges absent. Spiral ridges begin at whorl 1.3–1.7; on body whorl very conspicuous, wavy, subparallel but variable (even and parallel on tops of whorls near sutures, more wavy and irregular towards periphery of whorl where attracted to hair bases), (19) 23–30 (45) μm apart, sometimes with a weaker intermediate ridge, the ridge crests low (<10 μm), very narrow. Transverse ribs begin around whorl 0.7; on body whorl forming low rounded ridges or ribs, often rather closely spaced and giving decussate effect with the spiral ridges. Shell hair bases begin at whorl 0.2, continuing as tubercles/papillae to whorl 1.3 where a few hairs appear; hairs on body whorl long, length 381–636 μm (mean 489 μm), very slender, width 6–14 μm (mean 10.2 μm); in detail, hairs relatively very long compared to shell breadth, mostly directed outwards from periphery of shell with few rising upwards from top of whorls, very slender above the conical thickened base, not consistently curved in any direction, often straight and perpendicular to shell surface; hair rows on body whorl 8–9 (the low number probably related to small size of shell mouth and perhaps also to great length of hairs relative to shell breadth). Minor differences between populations occur in shell size, height of spire and calcification of shell (some but by no means all populations living on limestone having stronger shells than those living over base-poor rocks).

External features of body Top of head, tentacles, top of forepart of body and upper one-third of sides grey to blackish-grey; lower sides, tail and foot white to pale grey (sometimes whitish with broad foot-fringe of pale grey). Mantle mainly whitish, with irregular blackish or greyish blotches and lines of variable extent; the anterior fringe grey or brownish, with narrow unpigmented band behind. Upper whorls dark brown and whitish, with small black blotches. The dark markings show through the translucent shells of those individuals lacking a covering of soil. (Based on three live animals and photos of them; also six bodies in spirit from three sites and eleven specimens in spirit from four sites).

Genital anatomy One dissected (site P88), fully mature; several other dissections incomplete. Flagellum of medium length, slender, cylindrical, tapering to point. Vas deferens moderately slender, not thickened at distal insertion on epiphallus/flagellum, passing distally alongside penis, not descending far into angle between distal penis and distal vagina, then returning proximally alongside vagina and free oviduct; linked to proximal end of vagina by narrow muscle slip. Epiphallus cylindrical, stout, muscular, nearly as long as penis, bent in curve near middle. Penis narrow distally, otherwise broadly cylindrical; interior of penis not studied. Penial retractor muscle membranous, apparently inserting extensively on proximal end of penis but details unclear. Genital atrium short, narrow. Vagina short, in two parts; va1/2 narrow at distal end, widening rapidly proximally to give triangular outline; va3 remaining wide proximal to dart sacs and ending where free oviduct and spermatheca duct separate, bending sharply through 90º; distal parts of free oviduct and spermatheca duct both almost in line with proximal end of vagina. Two dart sacs located symmetrically on almost opposite sides (slightly approximate) at proximal end of va1, each sac shortly cylindrical with blunt rounded tip. Smaller accessory sac located inside and attached to proximal edge of each dart sac, rounded apically. Mucus glands two, rather small, unbranched, very narrow at insertion points which are close together (but apparently separate) on va2 just above one dart sac, mucus glands small, soon thickening proximally; other dart sac lacks associated mucus glands. Free oviduct long (>150% length of vagina), rather wide, cylindrical. Spermatheca duct rather wide throughout, moderately long. Spermatheca almost triangular with long apical point, adhering to middle part of spermoviduct.

Species recognition The very small shell (mature at 3.5–4.6 mm breadth) provides an immediate distinction from all other species of the genus, as soon as it is realised that mature snails are involved (with 3.2–3.4 whorls) rather than immatures of a larger species (Table 1). This is indeed one of the smallest of all Hygromiidae. Other distinctive features of the shell are the low spire, relatively wide umbilicus (15–20% of shell breadth: Table 1) and relatively very long but often nearly straight and slender shell hairs (Fig. 5L, Table 2). Dissection of the small bodies proved difficult but revealed a basic similarity to other *Ponentina*. However, it showed various anatomical peculiarities, including the slender flagellum, two unbranched mucus glands present on only one side of vagina (none on other side) inserting remote from accessory sac, and the pointed triangular shape of the spermatheca. Other characters unique in combination are presence of two small dart sacs, two small accessory sacs, long free oviduct and stout spermatheca duct.

Taxonomic history Shells of this distinctive species were well described by Castro (1887: 237), Westerlund (1889: 52) and Locard (1899: 71). Nobre (1888: 602) noted that Moller collected a large number near Coimbra. Subsequently it has been almost completely overlooked, apparently because it was never figured and Nobre (1913, 1941) omitted it from his reviews of Portuguese land snails even as a synonym.

Gittenberger (2012) has recently described *Henkia mariannae* and *H. antoni* as new species, from the Algarve and Prov. Málaga respectively. *H. mariannae* clearly corresponds closely if not exactly to *Helix rosai* Castro 1887 in shell characters. The latter taxon was apparently overlooked by Gittenberger, since he claims in the protologue of *H. mariannae* (*op. cit*., p. 73) that "The species is not shown in Locard's (1899) often neglected monograph" when it is in fact there as *Helix Rosai* on p. 71. The genital anatomy of *H. mariannae* (*op. cit*., pp. 71–72, fig. 5) closely matches our figures for *Ponentina rosai* (Fig. 7K–M). Furthermore, we have collected *P. rosai* from similar habitats on rocky slopes in the Algarve both east and west of the type locality of *H. mariannae* near Lagos, as well as in Beira Litoral *ca* 30 km to the south of the Coimbra type locality of *H. rosai* (Fig. 11, Appendix 1). *H. antoni* was described only from shells, differing from *H. mariannae* "most clearly by its smaller, nearly entirely flattened shells, with a more widely open umbilicus". Since adult shells of *P. rosai* from some Portuguese populations are almost discoid (and some subadults have the spire completely flat), only 3.5 mm broad and match the long shell hairs and prominent sculpture figured for *H. antoni*, further evidence is needed to confirm it is specifically distinct.

Castro (1887: 237) noted that *H. rosai* was not allied to *Helix revelata*, but a close ally of the larger (5 mm diameter) *Helix anasina* Servain (1880: 56) from near Badajoz in Spain. Locard (1899: 71) stated it was the only Portuguese form of the species group containing *Helix becasis* Rambert 1868 and allied also to *H. martorelli*, *H. bofilliana* and *H. anasina*. However, *H. anasina* is of uncertain identity (Pilsbry, 1894: 275), never figured and poorly described. Germain (1930: 243) suggested *H. becasis*, from the E. Pyrenees, may be the same as *Trochulus hispidus* (Linnaeus 1758). The other two taxa mentioned as allies by Locard (*loc. cit.*) are endemic to Catalonia and now placed in the genus *Montserratina* Ortiz de Zárate López 1946, as *M. bofilliana* (Fagot 1884) and *M. martorelli* (Bourguignat 1870). The genital anatomy of *M. bofilliana* described by Giusti & Manganelli (1988) and Schileyko (2005: 2008) is clearly very different to that described here for *P. rosai*.

Gittenberger (2012) introduced the generic name *Henkia* with *H. mariannae* as its type species; that species is regarded here as a synonym of *Ponentina rosai*, as discussed above. In introducing and differentiating the genus *Henkia*, Gittenberger compared it with various genera of Hygromiidae, but not with *Ponentina* or *Trochulus*, despite considerable similarities to them in both shells and genital anatomy. However, reduction of various organs of the female genital tract in several species of *Ponentina* was unrecorded until the present study, so there would have been no reason to suspect that *H. rosai* provided one of several apparently comparable examples of it. On present evidence classification of *H. rosai* as a diminutive species of *Ponentina* now seems secure in view of the combination of similarities in genital anatomy, shell structure (including details of microsculpture) and external colouration of the body that are set out above. Its occurrence in a region with several other endemic species of *Ponentina* also suggests its allocation to the genus is appropriate. Nevertheless, as pointed out by Gittenberger (2012), molecular data are certainly needed to better understand and test the phylogeny of Hygromiidae genera, as well as evolution of their genital tracts and shell characters.

Geographical range Known by recent records only in central and southern Portugal (Fig. 11), although older records (see above) imply that it occurs north to Coimbra and “Roncão” on the R. Douro. If *Henkia antoni* is conspecific (see above) the range includes Prov. Málaga in S. Spain.

Etymology When Castro (1887: 237) introduced the new name *Helix Rosai* he noted that the species was discovered by M.[onsieur] J.M. Rosa de Carvalho; *rosai* is a noun in the genitive [of Rosa], so it remains unchanged in combination with *Ponentina*.

P. octoglandulosa sp. nov., D.T. Holyoak & G.A. Holyoak
Figs 2E, 5E, 8F, 11, 14F

Types Holotype NHMUK 20120215 (shell + body in spirit); eight paratypes from type locality in CGAH (one shell + body in spirit; seven shells).

Type locality Spain, Prov. Pontevedra, just N. of PO255 at *ca* 2 km NW. of Piñeiro, 29T 05499/46820; granitic slopes with much exposed rock, patchy *Ulex* scrub and sparse short grassland; 550 m alt. Coll. GAH & DTH E184, 28 Aug. 2011.

Description of shell Nine examined (only two mature, the larger shell being the holotype), from type locality (of which two were confirmed by dissection). Shells from five other localities for which anatomical confirmation lacking (see Appendix 1) probably of this species (see below) also studied but not regarded as paratypes. Shell depressed convex above, somewhat flattened below; heights 4.4, 5.1 mm, breadths 6.2, 7.1 mm, with 3.3 whorls. Whorls rounded, the body whorl flattened above towards the suture; sutures moderately deep. Umbilicus very narrow (0.4 and 0.6 mm, representing 7% and 9% of shell breadth), partly overlapped by reflected peristome in both adults, symmetrical, deep so that upper whorls can be seen. Mouth nearly round except where interrupted by penultimate whorl, the later parts of the body whorl descending slightly and gradually widening. Mouth edge thin, mainly plane but strongly reflected in small area of columellar margin; interior of mouth lacking any trace of thickening. Shells very thin, not or slightly calcified, translucent, light greenish brown. Periostracum without or with only slight cover of soil particles, glossy. Spiral lines begin about whorl 0.4, mainly inconspicuous, but clearly visible in parietal area of shell mouth where other sculpture absent. Spiral ridges apparently present from whorl 1.5 onwards, but rather inconspicuous on early whorls, better developed on later whorls. Transverse ribs start at whorl 0–0.1, rather strong but irregular so tending to obscure other types of sculpture. Hair bases evident as papillae from whorl 0.4 onwards and hairs present from whorl 1.3 onwards; hairs rather short, sometimes stout, often hooked apically; on body whorl, length 85–180 μm (mean 142.1 μm), width 15–29 μm (mean 21.3 μm).

External features of body Top of head and body not seen; lower sides of body, tail and sole of foot whitish. Mantle whitish to cream with greyish blotches, spots and occasional short lines; anterior fringe of mantle lacking dark line. Upper whorls missing. (Based on partly withdrawn bodies of holotype and one paratype, preserved in spirit).

Genital anatomy Two mature specimens were dissected. Flagellum short (*ca* 20% of epiphallus length), conical, spirally twisted near pointed proximal end. Vas deferens slender, remaining narrow at point where it enters wall of epiphallus/flagellum junction, sharply recurved close to that point, passing distally alongside penis and under right ommatophore retractor, then returning proximally alongside vagina and free oviduct. Epiphallus cylindrical, long (almost as long as pe2 + pe3 combined), with strong muscular walls and sharp bend near distal end. Penis composed of three parts; pe1 distal, cylindrical, moderately long; pe2 large, ovoid to almost spherical, thin-walled, containing large muscular verge (not investigated in detail); pe3 a well defined shortly cylindrical section, with muscular walls, narrowly oval (widened in middle), narrowing at junction with pe2. Penis retractor muscle inserted at or near pe3/epiphallus junction, rather long, slender, attached to body wall. Genital atrium very short or even absent, with pe1 and distal end of vagina diverging close to genital pore. Vagina long (nearly as long as penis), cylindrical in distal half, widening slightly along proximal half. Paired dart sacs symmetrically placed on opposite sides of distal vagina, each sac rather large, shortly cylindrical, spreading outwards from vagina, bluntly rounded at tip, apparently with muscular walls. Smaller accessory sac arising on inner proximal side of each dart sac, joined to dart sac basally and similar to it in shape, although shorter. Two mucus glands (both very large for the genus), each arising from single slender duct originating low on inner side of accessory sac, this basal duct soon bifurcating, after which each branch widens into cylindrical gland which then soon divides again (thus each mucus gland with four branches); branches of mucus glands swollen, somewhat folded and twisted when *in situ*, the inner pair of branches somewhat shorter than the outer pair. One individual with one branch of one mucus gland more slender and apparently shorter than other branches. Free oviduct shorter and narrower than vagina, cylindrical, its distal end continuing in almost same line as proximal vagina. Spermatheca duct cylindrical, slightly longer than vagina, narrowing proximally but remaining of medium width throughout, the distal end continuing in almost same line as proximal vagina. Outer surface of distal end of spermatheca duct lacking any muscle attachments. Spermatheca asymmetrically ovoid/shortly elliptical, flattened, lying on spermoviduct.

Species recognition The shell differs from that of *P. revelata* in the relatively narrow umbilicus (7–9% of adult shell breadth, cf. 8–16% of shell breadth, but usually 9–13%: Table 1) and shorter hairs (85–180, mean 142.1 μm; cf. 335–726, mean 571 μm, their length thus being outside the range of variation of *P. revelata*; cf. Figs 5E and 5M, Table 2).

Anatomically it differs markedly from that species in having eight not four branches in the mucus glands. Despite there being dissections of only two mature *P. octoglandulosa*, there are several other anatomical differences from *P. revelata* that leave no real doubt that a different species is at hand rather than a few individuals with unusual mucus gland structure. Thus, the accessory sacs are shorter than the large dart sacs, not *vice versa*; the mucus glands arise low on the inner side of each accessory sac, not towards its tip; the vagina is remarkably long; the vas deferens lacks any thickening where it joins the epiphallus/flagellum junction; the genital atrium is remarkably short if not absent.

Geographical range Recorded from NW. Spain (Prov. Pontevedra) and NW. Portugal (Minho), on hills of base-poor rock (Figs 11, 14F).

Etymology The epiphet *octoglandulosa* refers to the presence of eight mucus gland branches.

P. excentrica sp. nov., G.A. Holyoak & D.T. Holyoak
Figs 3C, 5D, 8G, 12

Types Holotype NHMUK 20120216 (shell + body in spirit); 16 paratypes from type locality in CGAH (11 shells + bodies; one immature spm; four sh).

Type locality Spain, Prov. Badajoz: by Castelo de Miraflores (N. of Alconchel), 29S 06683/42656; hillslope with crags (hard sandstone, quartzite), patchy scrub and walls; 370 m alt. Coll. GAH & DTH E240, 9 Apr. 2012.

Description of shell 32 examined (17 from type locality of which two confirmed by dissection; 15 from two localities in eastern Baixo Alentejo). Depressed convex to very depressed convex above, strongly flattened below; height 4.2–4.9 mm, breadth 7.6–10.1 mm, with 3.6–3.9 whorls. Whorls rounded, distinctly flattened above and below, the body whorl usually with a slight angle at periphery; sutures moderately deep. Umbilicus wide (1.0–1.9 mm, representing

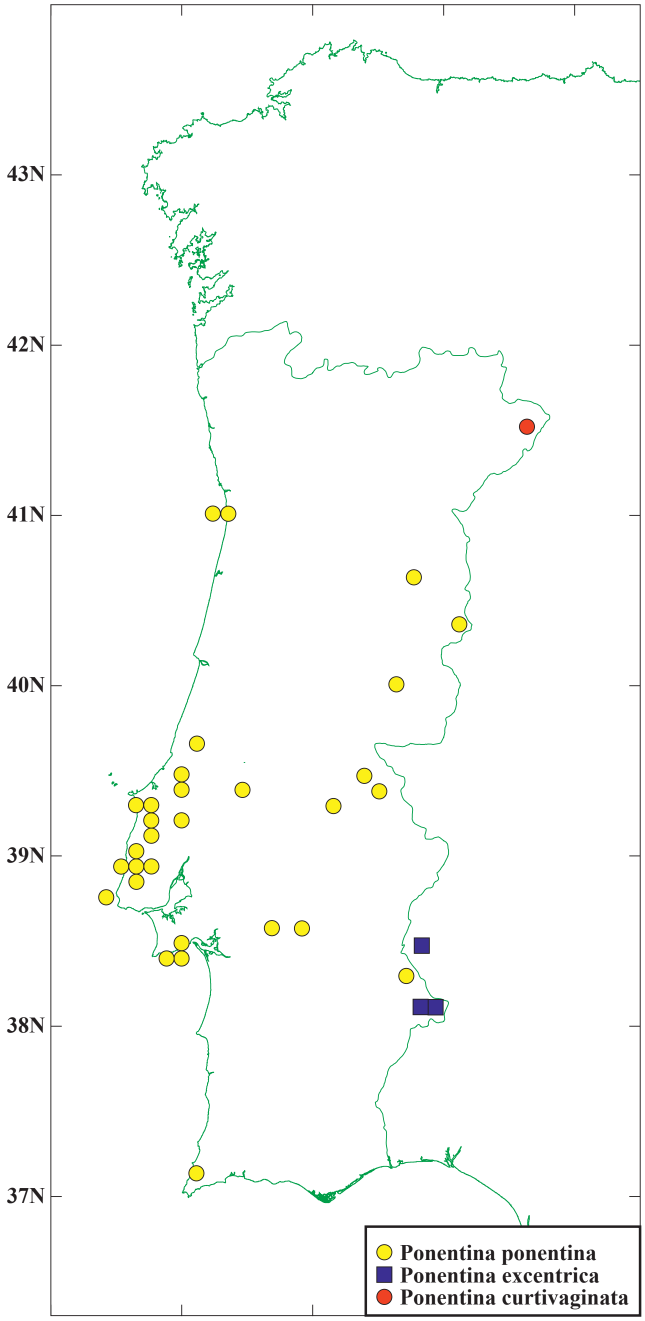

Figure 12 Distribution of *Ponentina ponentina*, *P. excentrica* and *P. curtivaginata* based on specimens studied by the authors, mapped by ten-kilometre squares of the U.T.M. grid.

13.2–19.0% of shell breadth), but strongly asymmetrical because of enlarged body whorl (with small overlap by reflected edge of peristome), the umbilicus of immatures being very narrow and deep, at maturity remaining open on some shells but closed off by body whorl on others. Mouth wider than high, interrupted by penultimate whorl, rounded above, more gently curved to almost straight on lower edge; the last part of body whorl descending or not near mouth, contracting just behind mouth then widening abruptly to peristome. Mouth edge thin, strongly reflected below, moderately reflected outwards, slightly reflected upwards; inside mouth of adults at type locality with thickened white rib, slightly set back from peristome edge, well developed on lower palatal and columellar sides of mouth, weak on upper palatal side, with slight whitish thickening also extending back into body whorl and across parietal side of mouth. The three shells with strongest development of a white internal rib also with a conspicuous low rounded tooth on middle part of rib. Shell thin and rather weakly calcified, remaining translucent ± throughout except for thickening around mouth (*q.v.*) of mature shells at type locality; light brown, sometimes with well defined narrow lighter (translucent) band at upper periphery (which in one shell is edged by ill-defined brown bands). Soil covering slight or lacking on live-collected snails, on the most heavily soiled individuals sealing deep part of umbilicus and tending to infill the sutures. Periostracum with waxy lustre. Spiral lines present by whorl 0.2 and visible on underside of body whorl near parietal edge of mouth, but mainly lost among other sculpture. Spiral ridges present by whorl 1.3, but difficult to see amongst other sculpture; on body whorl often strongly developed, subparallel, (13) 18–38 μm apart. Transverse ribs sometimes present but weak by whorl 0.2, on later whorls forming more obvious low ribs, irregularly spaced, often discontinuous, weak on underside of shell. Shell hairs start (at least as low basal papillae) from whorl 0; on body whorl hairs short, relatively stout, stiff, straight or curved or hooked with apex pointing away from shell mouth, brownish; on body whorl length 70–133 μm (mean 97.2 μm), width 22–33 μm (mean 26.6 μm). Hairs apparently brittle as shells of mature living snails have only the "foot-plates" remaining as rows of low papillae. Shells from the type locality are larger and relatively flatter with lower spires than those from Baixo Alentejo. As noted above, mature shells from the type locality also differ in having a well developed white rib inside the mouth which is weak or absent in the small samples from Baixo Alentejo.

External features of body Top of head and body pale grey (with darker tentacles) to grey; lower sides of body, tail and sole of foot usually whitish, in one snail pale grey throughout, in another pale grey towards and on foot fringe, in a third snail light grey with grey foot-fringe. Mantle light cream with individually variable grey to blackish spots or small blackish blotches that may enlarge to form short or long and irregular lines; anterior edge of mantle whitish, its posterior edge often bordered with a thin grey line. Upper whorls brown with variable blackish spots and blotches. The dark markings show through the translucent shells. (Based on 12 bodies in spirit from type locality and two from Baixo Alentejo).

Genital anatomy Two mature specimens and two immatures from type locality dissected and two additional immatures from Baixo Alentejo. Flagellum long (70–100% of epiphallus length), stout, tapering proximally to slender recurved point. Vas deferens narrow with conical thickened area adjoining junction with flagellum/ epiphallus, passing distally alongside penis, close alongside pe1 behind right ommatophore retractor, then returning proximally alongside vagina and free oviduct. Epiphallus stout, muscular, shorter overall than penis, strongly curved proximally. Penis in three parts: pe1 moderately long, distal, slender, cylindrical; pe2 longer than pe1, broadly oval, thin-walled, apparently containing muscular verge but not opened; pe3 a very short sheath over distal end of epiphallus. Penial retractor muscle inserted broadly onto wide sleeve of pe3 at its junction with epiphallus, strap-like, strong, attached to body wall. Genital pore a small slit below and behind right ommatophore. Genital atrium short, cylindrical. Vagina moderately long, in three parts: va1 distal, cylindrical, approximately equal in length to va2; va2 triangular or narrowly triangular, widening proximally to widest point at dart sacs; va3 shorter than va2, cylindrical, dividing proximally into spermatheca duct and free oviduct (at same level as apices of accessory sacs), the distal parts of which are approximately in line with each other and va3. Dart sacs two, oval, muscular, on approximately opposite sides of va2 and diverging slightly from line of vagina. Accessory sacs two, each united with inner basal one-third of subtending dart sac, separate from but tightly appressed to inside of dart sac, with rounded apex extending proximally to that of dart sac. Dart sacs and accessory sacs closely sheathed together across proximal part of va2 inside a thin common membrane. Mucus glands two, each inserting on inside of an accessory sac near its apex as a very slender tube, dividing almost immediately into two wider branches which are convoluted when *in situ*. Free oviduct cylindrical, moderately long (approximately equal to va2). Spermatheca duct slender throughout most of length, tapering proximally into wider section adjoining spermatheca and tapering distally into wider section adjoining va3; wider distal part with thin sheet of muscle attached in line along one side. Spermatheca broadly oval, thin-walled, lying on spermoviduct.

Species recognition Shells resemble those of *P. ponentina* and *P. martigena* in tending to have moderately numerous whorls (3.6–3.9: Table 1), the whorls of the spire slightly flattened, often a slight peripheral keel, and sometimes a pale band on the upper periphery of the body whorl. *P. excentrica* differs from both of those species in the lower spire, somewhat deeper sutures, more expanded body whorl giving an oval shape, the mouth wider than high rather than nearly round and a markedly asymmetrical and excentric umbilicus that is almost or fully closed. The development of a small white tooth close to the palatal edge of the peristome in some mature *P. excentrica* is a unique feature in the genus. The shell hairs are shorter than in *P. ponentina* (length 70–133 μm, compared to 141–236 μm; cf. Figs 5D and 5H, Table 2), appearing as tall slender brownish papillae rather than the whitish hairs of that species. They also average much shorter than in *P. martigena* (hairs 117–218 μm), although there is some overlap in hair length. The distal genital anatomy is similar to that of *P. ponentina*, differing only in the relatively larger dart sacs and accessory sacs; hence it is very different to that of *P. martigena*.

Geographical range Known only from hill areas with base-poor rocks at the type locality in western Prov. Badajoz and two localities in eastern Baixo Alentejo (Fig. 12). Typical *P. ponentina* have been collected at a site in the middle of the overall range of *P. excentrica*, by the old customs post at São Leonardo in easternmost Baixo Alentejo (site P241).

Etymology The epiphet is derived from the latin *excentricus* (adjective A), meaning eccentric or placed out of the centre, referring to the upper part of the spire and the umbilicus being in off-centre positions as a result of the wide expansion of the body whorl near the shell mouth.

P. grandiducta sp. nov., G.A. Holyoak & D.T. Holyoak

Figs 1A, 2F, 5I, 8H–K, 13, 14 A, B

Types Holotype NHMUK 20120217 (shell + body in spirit); 11 paratypes from type locality in CGAH (3 shells + bodies, 6 spm, 2 sh, collected on various dates: see Appendix 1) and 257 additional paratypes from four localities confirmed by dissection (37 shells + bodies, 7 spm, 213 sh in CGAH).

Type locality Portugal, Beira Baixa: Barcoila, near Sertã, 29S 05741/44096; on painted wall of house, with garden beneath; 410 m alt. Coll. GAH P36, 21 Apr. 2010.

Description of shell 303 examined, from five localities (including seven individuals confirmed by dissection, representing all the localities). Convex to depressed-convex above, somewhat flattened below; height 3.5–4.9 mm, breadth 6.4–8.3 mm, with 3.2–3.4 whorls. Whorls rounded, the body whorl somewhat flattened above near suture; sutures moderately deep. Umbilicus very narrow (0.5–0.7 mm, representing *ca* 7–10% of shell breadth), partly overlapped by peristome in adults, symmetrical and deep, exposing upper whorls. Mouth round to broadly rounded-oval except where interrupted by penultimate whorl, the last part of body whorl near mouth not or slightly descending, but widening, especially below. Mouth edge thin, strongly reflected below at least over peristome, not usually reflected outwards or upwards; interior of mouth lacking any thickening. Shells very thin to thin, not or slightly calcified, translucent to slightly translucent, light greenish brown or occasionally brown without green tinge. Some populations have no soil on shells or only a trace around sutures, several have thin patchy cover of particles, a few have almost complete but thin soil cover. Periostracum with rather waxy lustre to somewhat glossy (especially below), less often with only slight lustre because of strong ornamentation. Spiral lines are present from whorl 0–0.1 onwards but mainly inconspicuous. Spiral ridges present at least from whorl 1.8 onwards, becoming prominent on later whorls in some populations but very inconspicuous in others. Transverse ribs occur from whorl 0 onwards, but vary considerably in height, with low and often discontinuous ribbing commonest. Shell hairs short and rather slender, often lost, so evidently tending to be brittle or caducous; on body whorl, length 171–308 μm (mean 216.9 μm, sample P36), length 93–217 μm (mean 155.5 μm, sample P85), width 17–28 μm (mean 20.8 μm, sample P36), width 21–30 μm (mean 26.8 μm, sample P85). Local populations differ slightly in size, thickness/ translucence and apparently in length and persistence of the hairs. Those from high elevation are rather small and thin (maximum breadth 7.4 mm in P85 from 1370 m) with sparse hairs; shells from a very dry locality with granitic bedrock are also small and thin (maximum breadth 6.9 mm in P209 from 814 m).

External features of body Top half of body including head and tentacles light grey to blackish-grey; lower sides of body, tail and foot pale greyish-cream to pale grey or whitish. Mantle pale or whitish with very variable markings (often differing greatly between individuals within same population): of sparse grey to black spots; of bolder spots and blotches with some lines; or bold black blotches that join to form irregular longitudinal lines or a partly reticulate pattern; anterior margin often with thin light to dark grey line, bordered behind by narrow unmarked band. Upper whorls pale to dark brown, often with some whitish marks, lacking dark markings or with variable blackish markings much as on mantle. Dark markings on body are usually visible through the translucent shell. (Based on study of several live individuals, including some photographed (e.g. Fig. 1A) and 40 bodies preserved in alcohol).

Genital anatomy Seven dissected (from five localities), plus four additional immature individuals. Flagellum rather short (*ca* 33% length of epiphallus), conical with point recurved in hook. Vas deferens slender, lacking much thickening at junction with epiphallus/flagellum, slender throughout, passing distally alongside penis and under right ommatophore retractor to reach pe1/ vaginal angle, then returning proximally alongside vagina and free oviduct. Epiphallus shorter than penis (*ca* 50% its length), muscular. Penis divided into three parts; pe1 distal, cylindrical,

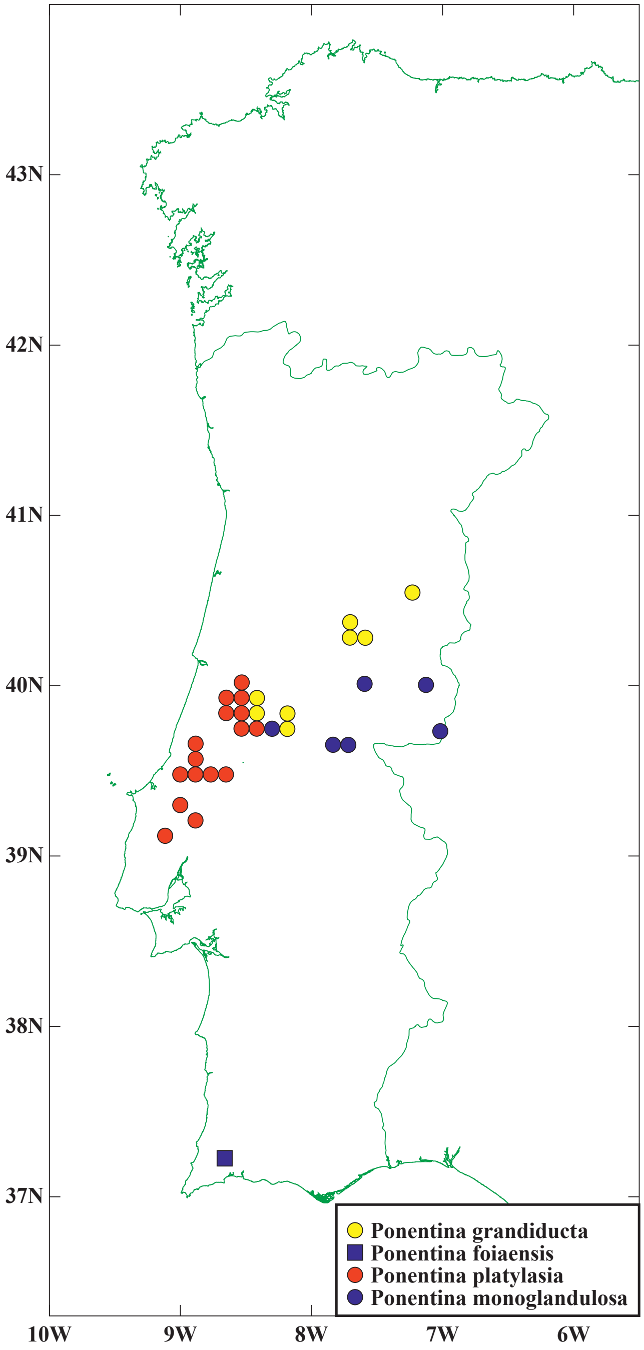

Figure 13 Distribution of *Ponentina grandiducta*, *P. foiaensis*, *P. platylasia* and *P. monoglandulosa* based on specimens studied by the authors, mapped by ten-kilometre squares of the U.T.M. grid.

approximately as long as pe2; pe2 ovoid, thin-walled, containing large muscular verge with bluntly rounded end near opening into pe1; verge with narrow longitudinal groove in distal half; pe3 short, firm, conical, tapering into epiphallus. Penis retractor muscle inserted as collar around pe3/epiphallus junction, rather short and broad but variable, attached to body wall (sometimes looped under vas deferens). Genital atrium very short, soon dividing into pe1 and distal vagina. Vagina short (about equalling pe1), cylindrical. No dart sacs. Pair of accessory sacs symmetrically located on opposite sides of proximal end of vagina (arising just distal to separation of free oviduct and spermatheca duct), each sac rather small, cylindrical with bluntly rounded tip, often recurved distally (dark central line visible internally in sac by translucence, but apparently not a dart). Mucus glands usually two, each arising inside axil at proximal side of base of accessory sac; each mucus gland with slender basal duct, soon dividing into two subequal branches that are wider, especially near the tips. One individual with somewhat immature genitalia (site P140) atypical, with second mucus gland on each side, arising close to first, the second gland unbranched on one side, two-branched on other side (Fig. 8J, K). Free oviduct moderately long (longer than vagina), the distal end continuing in line with proximal vagina. Spermatheca duct with ovoid-cylindrical muscular enlargement near distal end, wider than vagina (length 100–250% that of vagina), this distal part continuing almost in line from proximal vagina, remainder of spermatheca duct moderately wide (wider than epiphallus), rather short. Distal part of spermatheca duct often with thin line of muscle inserted longitudinally along outer side in position proximal to insertion of mucus gland bases. Spermatheca large, elongate-ovoid, tapering gradually into duct, resting on middle part of spermoviduct.

Species recognition The thin, uncalcified or weakly calcified shell is moderately small with few features to distinguish it from that of *P. monoglandulosa* (Table 1) other than the shell hairs averaging shorter and thinner (mainly 100–270 μm long, 17–32 μm wide, cf. 186–481 μm long, 18–48 μm wide in *P. monoglandulosa*; cf. Figs 5I and 5J, Table 2), the hairs often being broken or lost. *P. octoglandulosa* has a different range in NW. Portugal and neighbouring parts of Galicia, but is very similar in the small, thin, narrowly umbilicate shell (Table 1), with short hairs (85–180 μm long, 15–29 μm thick, Fig. 5E, Table 2). *P. grandiducta* is much more distinctive from both species in its genital anatomy, with narrow vagina, prominently swollen distal part of spermatheca duct, pair of small cylindrical accessory sacs (that are often recurved) and mucus glands arising inside base of the accessory sacs.

Geographical range Hill and mountain areas of C. Portugal (Fig. 13).

Etymology The epiphet *grandiducta* refers to the greatly enlarged distal end of the spermatheca duct.

P. curtivaginata sp. nov., D.T. Holyoak & G.A. Holyoak

Figs 1E, 2G, 5K, 9A, B, 12

Types Holotype NHMUK 20120218 (shell + body in spirit); 14 paratypes in CGAH (shells + bodies in spirit).

Type locality Portugal, Trás-os-Montes e Alto Douro, *ca* 1 km S. of Vale de Águia (NE. of Miranda do Douro), 29T 0729638/4600096; exposed low and flat granitic rocks with boulders, patchy scrub and low evergreen *Quercus* trees; 672 m alt. Coll. DTH P172, 1 July 2011.

Description of shell 15 examined (including five adults), all from type-locality (including two confirmed by dissection). Depressed-convex above, somewhat flattened below; height 4.4–4.6 mm, breadth 8.2–8.4 mm, with 3.2–3.4 whorls. Whorls rounded, the body whorl somewhat flattened above; sutures moderately deep. Umbilicus narrow (0.7–1.0 mm, representing *ca* 8–12% of shell breadth), asymmetrical and slightly overlapped by reflected peristome in adults, but deep with upper whorls visible in oblique view. Mouth nearly round except where interrupted by penultimate whorl, the last part of the body whorl descending and widening, especially below. Mouth edge thin, strongly reflected below, slightly reflected outwards; interior of mouth lacking any trace of thickening. Shells very thin, not or very slightly calcified (no dead empty shells were found, this apparently being a unique feature of this population), translucent, light greenish-brown. Most shells with a thin or sometimes thicker covering of soil (e.g. Fig. 1E), restricting study of shell sculpture to minority of cleaner specimens. Periostracum glossy. Spiral lines start at whorl 0.5, on body whorl *ca* 9–10 μm apart, visible only locally, where bright light is reflected. Spiral ridges 49–57 μm apart. Transverse ribs start at whorl 0.8 but indistinct until after 1.0, on body whorl present as low rounded ridges or ribs, irregularly spaced (e.g. 83–318 μm apart), variable in amplitude. Shell hairs start at whorl 0.7, medium length; on body whorl, length 279–431 μm (mean 382.8 μm), width 19–30 μm (mean 24.0 μm); in 12–13 rows on body whorl.

External features of body Top of head and body grey to dark grey; lower sides of body, tail and sole of foot varying from whitish to light grey in different individuals. Mantle whitish with variable blackish spots, blotches and irregular lines forming a bold pattern; the anterior fringe usually with a grey to dark grey line, with an irregular blackish line always present just behind fringe. Upper whorls light brown with blackish markings similar to those on mantle, or larger. The dark markings show through the translucent shells of those individuals lacking a thick covering of soil. (Based on 15 bodies from type locality preserved in alcohol and several live individuals, e.g. Fig. 1E).

Genital anatomy Two dissected, both mature. Penial flagellum very short (*ca* 10% length of epiphallus), conical, slightly curved. Vas deferens slender, not thickened at junction with epiphallus, passing distally alongside penis, under right ommatophore retractor, then back proximally alongside vagina and free oviduct. Epiphallus a little shorter overall than penis, sharply bent at point distal of middle. Penis divided into three parts; pe1 distal, shortly cylindrical, rather wide; pe2 in middle, large, stout, shortly cylindrical, containing large muscular verge that apparently ends in blunt point near opening into pe1; pe3 short, tapering rapidly from pe2 to junction with epiphallus. Penial retractor muscle with wide insertion at pe3/epiphallus junction, rather broad, short, ending on body wall. Genital atrium shortly cylindrical, dividing proximally into pe1 and distal end of vagina. Vagina short overall, <67% penis length and less wide than penis at its widest point which is close to proximal end, narrowing markedly towards distal end. Dart sacs lacking. Pair of shortly cylindrical accessory sacs inserting symmetrically on opposite sides of vagina at its widest point near proximal end, but clearly distal to separation of free oviduct and spermatheca duct, each sac usually orientated proximally alongside female tract (one sac in one snail recurved distally, alongside vagina), with a bluntly rounded end. Two mucus glands, each with two branches, arising as short common duct in axil of each accessory sac. Free oviduct short, cylindrical, continuing in line with proximal end of vagina and parallel to distal end of spermatheca duct. Spermatheca duct wide at distal end, nearly as wide as vagina, from which it continues proximally in straight line, moderately wide in middle, length relatively short (less than penis length); distal end of spermatheca duct with line of small muscle attachments on its outer surface. Spermatheca ovoid, tapering gradually into spermatheca duct, lying on middle part of spermoviduct.

Species recognition The shell is generally rather similar to those of *P. revelata*, *P. monoglandulosa* and *P. grandiducta* (Table 1), all of which occur in Portugal, but none of them are recorded from Trás-os-Montes e Alto Douro. Shells of *P. curtivaginata* differ mainly in having medium length hairs (279–431 μm), their length overlapping those of some populations of *P. monoglandulosa* but tending to average narrower (cf. Figs 5K and 5J, Table 2). The hairs are considerably shorter than those of *P. revelata*, considerably longer than those of *P. grandiducta*. The genital anatomy is markedly different from that of *P. revelata*, with no dart sacs and mucus glands arising in axils of accessory sacs, not directly from them, and penial flagellum much shorter. *P. monoglandulosa* differs in its reduced mucus glands, etc., *P. grandiducta* in the enlarged distal part of the spermatheca duct and other characters.

Geographical range Known only from the type locality (Fig. 12). 12 shells collected in the same region at 4 km NW. of Vimioso (site P171) perhaps represent the same species, but the shells are slightly thicker (weakly calcified), with stronger sculpture on the first two apical whorls and hairs on the later whorls appearing shorter and finer, so in the absence of anatomical data their identity remains uncertain.

Etymology The epiphet *curtivaginata* refers to the short vagina (Curtus/-a/-um, short; Vaginatus/-a/-um, sheathed).

P. papillosa sp. nov., G.A. Holyoak & D.T. Holyoak

Figs 1B, 3E, 5A, B, 9C–E, 11, 14D

Types Holotype NHMUK 20120219 (shell + body in spirit); 217 additional paratypes in CGAH (13 spm + 25 sh from type locality; 24 spm + 155 sh from other localities).

Type locality Portugal, Alto Alentejo [Dist. Portalegre], Pico de São Mamede, 29S 06413/43527; beneath boulders on sparsely vegetated N.-facing hillside near crags; *ca* 1015 m alt.; Colls. GAH & DTH site P5, 15 May 2007.

Description of shell 218 examined, from seven localities. Convex to somewhat depressed-convex above, somewhat flattened below; height 4.3–5.6 mm, breadth 5.8–8.1 mm, with 3.2–3.4 whorls. Whorls rounded, the body whorl somewhat flattened above; sutures moderately deep. Umbilicus narrow (0.4–0.9 mm, *ca* 7–12% of shell breadth), slightly to moderately overlapped by reflected peristome in adults, almost symmetrical and deep, with upper whorls visible. Mouth nearly round to broadly rounded-oval, except where interrupted by penultimate whorl; the last part of the body whorl not or slightly descending, but widening somewhat, especially below. Mouth edge thin, strongly reflected below in largest shells, weakly reflected in others; interior of mouth lacking any trace of thickening. Shells very thin, not or slightly calcified, translucent, light brown, with slight green tinge when fresh. Shells usually with soil cover thin (when often concentrated in sutures) or lacking. Periostracum with mainly weak gloss, strongest on underside. Spiral lines present on whorl 0–1 and underside of body whorl, but not evident elsewhere. Spiral ridges inconspicuous among other types of sculpture, but present on later whorls. Sculpture of transverse ribs strong from whorl 0–1.3, consisting of ± regularly spaced riblets formed by transversely elongate papillae or short lamellae; on later whorls ribs lower, less regular, forming elongate transversely orientated elements among the more conspicuous papillae. Shell hairs lacking, represented only by closely-spaced low-conical papillae which are apparently homologous with hair bases of congeners; on body whorl length of papillae 21–45 μm (mean 32.9 μm). Differences between populations appear slight and mainly to involve size, the few shells from E216 (Prov. Zamora) being relatively small compared to those from the type locality, with breadth up to 6.3 mm.

External features of body Top of head and fore-part of body grey to light grey; lower sides of body, tail and foot whitish or pale cream. Mantle whitish to pale cream with variable pattern: of grey spots and small blotches; or large dark grey to blackish blotches some of which are elongated to form short irregular lines; or large black blotches forming netted pattern; anterior margin of mantle with thin grey or light grey line, behind which is narrow band without markings. Upper whorls pale brown with blackish spots or blotches, sometimes forming a bold pattern. The dark markings show through the translucent shells of individuals lacking much soil on the shell. (Based on 18 bodies from four localities preserved in alcohol and study of several live individuals, e.g. Fig. 1B).

Genital anatomy Six dissected, from four localities (P5 Type locality; P168 in Trás-os-Montes e Alto Douro; E216 and E217 in Prov. Zamora). Flagellum medium-long (>50% length of epiphallus, but latter relatively short), conical, ending in blunt to rounded point. Vas deferens with prominent conical thickening at junction with flagellum/epiphallus, otherwise slender, passing distally alongside penis, beneath right ommatophore retractor to pe1/vaginal angle, then back proximally alongside vagina and free oviduct. Epiphallus relatively short (<50% total length of penis), stout, muscular. Penis in three parts; pe1 distal, cylindrical, nearly as long as pe2 to slightly longer; pe2 widely ovoid (tapering into pe1) to asymmetrically narrowly ovoid, much wider than pe1 and pe3, thin-walled, containing large, muscular, shortly conical verge that terminates near opening into pe1; apical 67% of verge with deep, narrow longitudinal groove that ends in furrow at tip, opens proximally into epiphallic pore in transverse slit; pe3 conical, muscular, tapering into epiphallus. Penis retractor muscle inserts widely around pe3/epiphallus junction (or apparently more proximally on epiphallus in individual from P5), ends on body wall, the muscle varying from short and wide (P5) to relatively narrow and longer (P168). Genital atrium short, cylindrical, soon dividing into pe1 and distal vagina. Vagina medium to long (67–100% total length of penis), divided into narrow cylindrical distal half, wider proximal half that is subcylindrical to subconical (widest proximally); proximal half of vagina internally with few muscular longitudinal ridges, lacking any obvious papilla where accessory sac/mucus gland pore enters. Dart sacs apparently lacking. Pair of rather large accessory sacs located symmetrically on opposite sides of vagina near its proximal end, each subcylindrical, bluntly rounded at tip, with dark longitudinal line along middle visible by translucence (apparently not a dart, but few sacs dissected). Two mucus glands, one arising inside axil at proximal end of base of each accessory sac (mainly attached to base of accessory sac rather than to proximal vagina), each gland with two medium to long branches arising from very near base (P168, E216, E217) or at base (P5), the basal parts thinner than much of length of branches but not conspicuously slender. Free oviduct of medium length (*ca* 50% length of vagina or slightly more), its distal end continuing approximately in line with proximal vagina, cylindrical. Spermatheca duct rather long (equal to total penis length or slightly shorter), about width of free oviduct at distal end, but soon tapering; medium to narrow in middle, tapering more or less gradually into spermatheca. Spermatheca ovoid, resting on middle part of spermoviduct.

Species recognition Shells are distinctive in always lacking hairs, having hair bases prominent as lines of papillae (Fig. 5A, B; Table 2). Mature shells are also relatively small (Table 1). The genital anatomy has a distinctive combination of features, with rather long vagina, no dart sacs, single pair of accessory sacs at proximal end of vagina, relatively long free oviduct and spermatheca duct and prominent conical swelling on vas deferens where it joins epiphallus/flagellum.

Geographical range Hill and mountain regions of NE. and EC. Portugal, in Trás-os-Montes e Alto Douro and Alto Alentejo (at Pico de São Mamede), extending into W. Spain in Prov. Zamora (Fig. 11).

Etymology The epiphet is derived from *papillosus*, covered with papillae, referring to the papillose rather than hairy surface of the shell.

P. foiaensis sp. nov., G.A. Holyoak & D.T. Holyoak

Figs 3D, 5C, 9F, 13

Types Holotype NHMUK 20120220 (shell and mature body in spirit); additional paratypes in

Figure 14 Habitats of *Ponentina* in Portugal and Spain: A *P. grandiducta* sp. nov., Portugal, Beira Alta, CGAH P209, granitic slopes with much bare rock; B *P. grandiducta* sp. nov., Portugal, Beira Alta, CGAH P53, inside mature *Betula* wood on N.-facing rocky granitic slope at *ca* 1375 m alt.; C *P. platylasia*, Portugal, Beira Litoral, CGAH P40, cultivated grove of *Olea* trees on hill of Mesozoic limestone (aestivating snails 0.5–1.0 m above ground on trunks); D *P. papillosa* sp. nov., Portugal, Trás-os-Montes e Alto Douro, CGAH P166, granitic slopes with much bare rock near hill tops at *ca* 1311 m alt.; E *P. revelata*, Portugal, Estremadura, CGAH P93, coastal dunes of calcareous sand with patchy low scrub; F *P. octoglandulosa*, Spain, Prov. Pontevedra, E 184 (type locality), granitic slope with much exposed rock, the scrub is mainly of *Ulex* and often burnt. See Appendix 1 for detailed information on localities and dates of photography.

CGAH (16 immature spm with bodies in spirit; 27 dead shells).

Type locality Portugal, Algarve: W. slope of Fóia, 29S 05347/41292; hillslopes with low metamorphic crags (Foyaite: coarse-grained hornblende-nepheline-syenite rock) and patchy cover of *Erica* and *Cistus*, grassland locally; 810 m alt. Colls. GAH and DTH, 5 Feb. 2011.

Description of shell 44 examined, all from type locality (including five adults, of which only the holotype had mature genital anatomy checked by dissection). Convex above, somewhat flattened below; height 5.4–6.1 mm, breadth 7.6–8.5 mm, with 3.6–3.7 whorls. Whorls rounded, only slightly flattened above, suture moderately deep. Umbilicus narrow (0.6–0.7 mm, representing 7–8% of shell breadth), very narrow in immatures, in adults partly overlapped by peristome and asymmetrical so that upper whorls not visible inside. Mouth nearly round except where interrupted by penultimate whorl, the last part of the body whorl descending slightly and widening, especially below. Mouth edge thin, strongly reflected below, slightly reflected outwards and sometimes upwards; interior of mouth lacking any trace of thickening. Shells thin, not calcified or sometimes weakly calcified, translucent, light brown with little or no greenish tinge; an inconspicuous paler band just above periphery of body whorl of a few shells. Shell surfaces with little or no soil adhering. Periostracum not or slightly glossy, except in and around shell mouth. Protoconch usually partly overlapped by first whorl of spire, so appearing narrow. Spiral lines begin on whorl 0.6, often inconspicuous on early whorls, later evenly spaced, fine. Spiral ridges evident from whorl 2.0 onwards, on body whorl *ca* 29–37 μm apart, parallel but not wavy, with weaker intermediate ridges sometimes present between pairs of main ridges. Transverse ribs often begin on whorl 0.2, often strong and discontinuous. Shell papillae/hairs develop from whorl 0.6 onwards but are inconspicuous on early whorls; on later whorls consisting of conical tubercles, some of them ending as very short stout cylindrical hairs, which are erect or hooked; on body whorl length 43–77 μm (mean 55.9 μm), in 12–13 rows, but rows difficult to count.

External features of body Top of head and body light grey; sides of body, tail and sole of foot white. Mantle whitish with blackish markings of variable extent in different individuals, some lightly marked with scattered spots and small blotches, others heavily marked with large blotches and irregular lines forming coarse barring or an irregular reticulate pattern, others with markings of intermediate extent. Anterior edge of mantle fringed by thin grey line, behind which is a narrow unmarked whitish band. Upper whorls pale or light brown with mainly bold, irregular, blackish bars or blotches. The dark markings show through the translucent shell. (Based on 17 bodies from type locality preserved in alcohol).

Genital anatomy One mature specimen dissected (holotype) and three others with small immature genitalia. Penial flagellum long (slightly >50% length of epiphallus), stout, cylindrical but tapering proximally and slightly flattened, ending in short curved, conical point, whitish. Vas deferens mainly slender, but wide close to insertion onto epiphallus, passing distally close behind insertion of penial retractor muscle [where apparently trapped] and behind right ommatophore retractor before returning proximally parallel to vagina and passing to proximal end of free oviduct. Epiphallus broadly cylindrical but tapering proximally, sharply bent towards proximal end, whitish, glossy, obviously muscular. Penis with three parts; pe1 distal, short, cylindrical, narrowing proximally, somewhat muscular, whitish with few small blackish spots; pe2 large, whitish, ovoid-elliptical, with thin flexible wall through which large opaque whitish verge visible inside, the verge bluntly pointed at its distal end which reaches nearly to opening into pe1; pe3 very short, strongly tapering proximally to junction with epiphallus. Penial retractor muscle short, wide, flat, inserting near distal end of epiphallus, apparently double, ending in wide attachment to body wall. Genital atrium very short, with fine blackish marks. Genital pore an obvious opening behind base of right ommatophore. Vagina slender relative to penis, but slightly longer overall than penis, white throughout, composed of three distinct parts; va1 distal, narrow, cylindrical; va2 in middle, the longest and widest part, widening proximally to greatest width at proximal end, thick-walled; va3 cylindrical but narrowing proximally to junction of free oviduct and duct of spermatheca, almost as long as va2, thick-walled. Paired dart sacs on either side of va2/

va3 junction, symmetrically located but slightly approximated, each dart sac consisting of inconspicuous, low, slightly elongated projection from outline of vagina; possible presence of darts not investigated in unique specimen available. Accessory sacs lacking. Two mucus glands, both rather small, both with two slender branches of unequal length, the division into two branches occurring proximal to a very short basal common duct; insertion of each mucus gland in line with collateral dart sac, but some distance proximal to it, the narrowly cylindrical basal duct seen (by transparency) to continue distally as thin tube that reaches axil of dart sac within the wall of va3. Free oviduct cylindrical, narrower than most of spermatheca duct, its distal end leaving junction of va3 and spermatheca duct at wide angle. Spermatheca duct short (shorter than flagellum), moderately wide distally, conspicuously narrower for short section proximally near spermatheca. Spermatheca ovoid, widest proximally, tapering into duct, thin-walled, light brown, lying on middle part of spermoviduct.

Species recognition Fresh shells are distinctive because of the very short hairs which arise from basal papillae (total length 43–77 μm, Fig. 5C, Table 2), but the hairs are lost from most mature shells. The globular shape, narrow umbilicus (Table 1), brown rather than greenish colour and occasional presence of a pale peripheral band are otherwise suggestive of *P. ponentina*, although apertural thickening is absent. The distal female genitalia are unique for the genus in the much longer va3 than in other species, combined with very small dart sacs, lack of accessory sacs and the short but rather stout spermatheca duct. The distal male genitalia combine a relatively large flagellum and pe2 being relatively long, ovoid-elliptical.

Geographical range Known only from the type locality on Fóia (Algarve) (Fig. 13).

Etymology The epiphet is an adjective derived from the name of the type-locality, Fóia.

P. monoglandulosa sp. nov., D.T. Holyoak & G.A. Holyoak

Figs 2H, 5J, 9G–M, 13

Types Holotype NHMUK 20120221 (shell + body in spirit); 116 paratypes from type locality in CGAH (23 shells + bodies in spirit; 93 shells); 79 additional paratypes from three other localities confirmed by dissection in CGAH (33 shells + bodies in spirit; 46 shells).

Type locality Portugal, Beira Baixa, *ca* 2 km W. of Vila Velha de Ródão, 29S 061177/439016; rocky (quartzite) ridge and slopes with patchy low scrub and herbs; 321 m alt. Colls. GAH & DTH P87, 19 Dec. 2010.

Description of shell 207 examined, from five localities (including 11 confirmed by dissection, representing all five localities). Convex to depressed-convex above, somewhat flattened below; height 3.6–4.7 mm, breadth 6.4–8.7 mm, with 3.1–3.3 whorls. Whorls rounded, the body whorl somewhat flattened above; sutures deep. Umbilicus narrow (0.6–0.9 mm representing *ca* 9–10% of shell breadth), partly overlapped by reflected peristome in adults, symmetrical or nearly symmetrical and deep, with upper whorls visible. Mouth broadly rounded-oval to nearly round, except where interrupted by penultimate whorl, the last part of the body whorl descending ± markedly and widening, especially below. Mouth edge thin, strongly reflected below (especially over umbilicus), often somewhat reflected outwards, occasionally also narrowly reflected upwards; interior of mouth lacking any trace of thickening. Shells very thin or thin, not or slightly calcified, translucent, light brown to light greenish-brown. Periostracum commonly with soil particles adhering, sometimes almost covering shell as a thin layer and tending to fill sutures. Exposed periostracum with waxy lustre, or more glossy near shell mouth. Spiral lines start at whorl 0–0.1 but mainly inconspicuous, except at parietal edge of shell mouth where other sculpture weak or lacking. Spiral ridges start at around whorl 1.4, becoming conspicuous on later whorls where subparallel, often rather wavy and irregular. Transverse ribs start at around whorl 0.7, rather irregular, usually low and discontinuous around whorl periphery. Shell hairs start as low tubercles at whorl 0.1 with short hairs present at whorl 0.2; on body whorl moderately short, length 186–481 μm, width 18–48[62] μm (in three populations, see Table 2 for details). Individual hairs typically straight to gently curved, few or many hooked apically, remaining rather wide even near tips. Shells differ somewhat in size between populations, being relatively small at P84 and P87, larger at P135.

External features of body Colouration variable, differing between individuals in the same population. Top of head and upper forepart of body light grey to grey (occasionally pale grey); sides of body and tail whitish, pale grey (especially along and above foot-fringe), or occasionally grey throughout; sole of foot whitish to light grey. Mantle of lighter snails whitish to dull cream with irregular blackish (or deep grey) spots, blotches and short lines; in darker snails blackish (or deep grey) with irregular spots and blotches of whitish. Anterior edge of mantle unmarked or fringed with grey, behind which is narrow unmarked pale band. Upper whorls pale brown, light brown to brown, with blackish blotches; in darker snails blackish ± throughout. The dark body markings show clearly through the translucent shell of those individuals lacking a covering of soil. (Based on 53 bodies preserved in alcohol from P84, P87, P101 and E244).

Genital anatomy Nine mature individuals dissected (from five localities: P84, P86, P87, P135, E244); also 13 immature snails from same localities. Flagellum short overall, with shortly conical base giving rise to slender, cylindrical appendage of approximately similar length that is often curved or twisted. Vas deferens narrow, with only small thickening at junction with epiphallus/flagellum, passing distally alongside penis to pe1/vaginal angle, then returning proximally alongside vagina and free oviduct. Epiphallus of medium length (somewhat shorter than penis), white, with strong muscular walls, curved or more sharply bent in proximal half. Penis with three parts; pe1 distal, very short or not differentiated from pe2, although penis narrowing at junction with vagina/genital atrium; pe2 the widest part, ovoid-cylindrical, forming 67% or more of penis length, with muscular verge internally; pe3 short, <33% length of pe2, cylindrical or tapering proximally towards junction with epiphallus. Verge partly extruded from genital pore of one specimen, its distal part white, bluntly rounded at tip, with shortly cylindrical protuberance (not a spermatophore) with rounded apex arising laterally near tip. Penis retractor muscle inserted as collar approximately around junction of pe3/epiphallus, muscle short and wide, attached to body wall. Genital atrium very short, forming a narrower distal continuation of junction of pe1/vagina, just inside genital pore. Vagina short to very short (*ca* 20–33% length of penis), cylindrical to broadly cylindrical or funnel-shaped (narrowing proximally). Dart sac (or perhaps a greatly reduced accessory sac: no dart seen) single (not paired), a small to tiny hemispherical protuberance (rounded or slightly pointed at tip, appearing white, firm and somewhat muscular), on one side only of the proximal part of the penis (Fig. 9G, H, M), sometimes reduced to a tiny rudiment visible in the surface of the vaginal wall only by translucence (Fig. 9J). Mucus gland single (eight snails: P84, P86, P87, P135), when usually two-branched (seven snails: P84, P86, P87, E244, e.g. Fig. 9G, H, M), less often unbranched (two snails: P86, P87, e.g. Fig. 9J), the gland arising as short common duct from or close to axil on inner proximal side of dart sac, the branch or branches of moderate (often unequal) length, becoming wider proximally, especially towards tip(s). Single individual (from P84) also with second unbranched mucus gland on opposite side of vagina, arising opposite two-branched mucus gland inserting in axil of dart sac in usual manner (Fig. 9I). Free oviduct short, cylindrical, narrower than distal spermatheca duct, continuing approximately in line from proximal end of vagina or somewhat offset to side. Spermatheca duct of medium width distally, soon tapering proximally, arising distally almost in line with proximal end of vagina; at least sometimes with thin line or translucent sheet of muscle inserting on outside of distal part of duct, starting at proximal end of vagina and continuing distally, attached to other thin tissues inside mantle cavity. Spermatheca not seen.

Species recognition The rather small, thin shells with a narrow umbilicus (Table 1) and relatively short hairs are generally similar to those of *P. grandiducta*, which occurs close to the range of *P. monoglandulosa* to the west and north, sometimes at higher elevations. The principal difference in their shells is that *P. monoglandulosa* tends to have longer shell hairs (186–481 μm long, 18–48 μm wide, cf. mainly 100–270 μm long, 17–32 μm wide in *P. grandiducta*; cf. Figs 5J and 5I, Table 2). Also, the body whorl tends to descend more markedly near the shell mouth in *P. monoglandulosa*. The genital anatomy of *P. monoglandulosa* is much more distinctive, with only a single small dart sac that has a branched or unbranched mucus gland arising in its axil; the opposite side of the proximal vagina always lacks a dart sac; in one individual it had a second, unbranched mucus gland.

Geographical range Central Portugal (S. and E. Beira Baixa) and edge of Spain (Prov. Cáceres), occurring on hills of base-poor rock (Fig. 13).

Etymology The epiphet *monoglandulosa* refers to the single mucus gland present in most individuals.

Multi-access key to European species of *Ponentina*

An attempt is made here to provide an "artificial" key to aid identification of as many specimens as possible of European *Ponentina*. It includes characters from both shells and the distal genital anatomy. Compared to a traditional bipartite key, it may be more useful in dealing with characters which are difficult to observe, such as precise measurements of hairs on fresh shells or structure of distal female genitalia when mature specimens may be unavailable. However, detailed study of the species descriptions and data on geographical ranges should provide further checks on determinations and help establish whether the specimens involved are complete and mature enough to allow an accurate identification.

Character states Note that alternative states of characters are identified by different letters, capitals for shell characters, lower-case for characters from the genital anatomy.

Shell always lacking hairs (which very often wear off in other spp.!), but with conical papillae <50 μm high (Fig. 5A, B) A
Shell with all hairs very short, arising from conical papillae <100 μm high (Fig. 5C, D) B
Shell with longest hairs 100–250 μm (Fig. 5E–I) C
Shell with longest hairs 250–450 μm (Fig. 5J–L) D
Shell with majority of hairs >450 μm (Fig. 5M–O) E

Shell often with narrow paler peripheral band (as in Fig. 3A, B) F
Shell lacking narrow paler peripheral band G

Shell breadth of mature snails <4.5 mm H
Shell breadth of mature snails 4.5–8 mm I
Shell breadth of mature snails 8–15 mm J

Mature shell with umbilicus wide (>13% of shell breadth); spire low K
Mature shell with umbilicus narrower (<13% of shell breadth); spire high or low L

Shell with spire having somewhat shallower sutures M
Shell with spire having deeper sutures N

Paired dart sac and accessory sac present, only on one side of proximal vagina a
Dart sac alone present on both sides of proximal vagina (not accompanied by accessory sac) b
Paired dart sac and accessory sac present, on both sides of proximal vagina c

Mucus glands arising on both sides of proximal vagina from a slender base (or inside the inner surface of an accessory sac) d
Mucus glands arising on both sides of proximal vagina from a markedly thicker base (i.e. an accessory sac) e
Mucus gland(s) arising only on one side of proximal vagina f

Mucus glands with total of one, two or three branches g
Mucus glands with total of four branches h
Mucus glands with total of eight branches i

Vagina short (<0.5 × penis length) j
Vagina longer (>0.5 × penis length) k

Spermatheca duct broad at distal end adjoining vagina (>60% of width of vagina) l
Spermatheca duct narrower at distal end adjoining vagina (<60% of width of vagina) m

Penis with distal cylindrical part (pe1) equal to or longer than swollen central part (pe2) n
Penis with distal cylindrical part (pe1) shorter than swollen central part (pe2) o

Flagellum long (>⅓ length of epiphallus) p
Flagellum of medium length (<⅓ but >⅛ length of epiphallus) q
Flagellum short (<⅛ length of epiphallus) r

Vas deferens with elongate and markedly swollen portion at its insertion onto epiphallus s
Vas deferens with markedly swollen portion at its insertion onto epiphallus lacking or short t

Species Where both of two character states can occur in the same species both letters identifying them are listed.

P. papillosa	A G I L N b d h k m n q s
P. excentrica	B C F I J K N c d h k m n p s t
P. foiaensis	B F G I L N b d h k m o p q t
P. ponentina	C F G I J L M c d h k m n p s t
P. martigena	C F I J L M c d i k m o q r t
P. grandiducta	C G I L N b d h k l n q t
P. subvirescens	C G I L N b d h k m o p q t
P. octoglandulosa	C G I L N c d i k m o q t
P. rosai	D E G H K N c f g j l m o p t
P. monoglandulosa	D G I L N a d f g j l m o r t
P. curtivaginata	D G I L N b d h j l o r t
P. platylasia	E F G I J K N c e h k m n p s t
P. revelata	E G I J K L N c e h k m o p q t

Nominal species of *Ponentina* from Morocco

Helix agardhi Pallary 1898

Helix ponsonbyi Westerlund 1888, *Bulletins de la Société Malacologique de France* 5, pp. 57–58. Pilsbry (1892, *Manual of Conchology* (2) 8, p. 190) pointed out that this is a junior homonym of *H.* (*Jacosta*) *ponsonbyi* Kobelt.
Helix (Section *Fruticicola*) *ponsonbyana* Pilsbry 1895, *Manual of Conchology* (2) 9, p. 274, as new name for *Helix ponsonbyi* Westerlund 1888 (pre-occupied).
Helix Agardhi Pallary 1898, *Journal de Conchyliologie, Paris* 38, p. 70, pl. 5, fig. 7 (proposed as new name for *Helix ponsonbyi* Westerlund 1888, and the erroneous emendation of it to *Helix* (Section *Fruticicola*) *ponsonbyana* Pilsbry 1895, both junior homonyms of *H. ponsonbyi* Kobelt).
Treated as valid species by Pallary (1898) from "le Djebel, à l'ouest de Tanger (Ponsonby, Vaucher)" [Morocco] and by Pallary (1904, *Journal de Conchyliologie, Paris* 52, p. 10) from "Charf Lakàab", Morocco. Shell figures in Pallary (1898) show a globular-conical shell with a round mouth and very small umbilicus, so possibly a form of *P. martigena*.

Fruticicola riatana Pallary 1920

Fruticicola riatana Pallary 1920, *Bulletin de la Société d'histoire naturelle d'Afrique du Nord* 11, p. 18. Type-locality: in NE. Morocco, "Sidi-Abdallah, à une trentaine de kil. a l'Ouest de Taza, sur l'Innaouen". Apparently a small, conical-globular form (cf. Pallary 1928, *Journal de Conchyliologie, Paris* 71, pp. 199–200, pl. 3, fig. 26), of uncertain identity.

Fruticicola russoi Pallary 1928

Fruticicola russoi Pallary 1928 [March], *Journal de Conchyliologie, Paris* 71 (3), pp. 200–201, pl. 3, fig. 25. Type locality: "djebel Bou Hellal, à 2 kil. S.-E. d'Ouezzan" [Morocco]. Described by Pallary (*loc. cit.*) as allied to *H. ponentina*, but easily distinguished by its less globular shape, more elongated ("plus allongée"), and by the stronger furrow of the lip ("sillon du labre bien plus marqué"). The figure shows a shell with a low spire.

Nominal species of *Ponentina* from Algeria and Tunisia

P. sordulenta (Morelet 1851)
Figs 3F–I, 10

Helix sordulenta Morelet 1851, *Journal de Conchyliologie, Paris* 2, p. 356, pl. 9, figs 9, 10. Type-locality: aux alentours de Constantine dans les cimetières musulmans [Algeria].
Helix sordulenta Morelet: Bourguignat, 1864, *Malacologie de l'Algerie* 1, p. 187, pl. 18, figs 17–19.
Helix sordulenta var. *conoidea* Bourguignat 1864, *Malacologie de l'Algerie* 1, p. 187, pl. 18, fig. 20. Type-locality: Constantine.
Helix sordulenta Morelet: Tryon, 1887, *Manual of Conchology* (2) 3, p. 177, pl. 39, figs 1, 2.
Helix lasia Bourguignat 1864, *Malacologie de l'Algerie* 1, pp. 188–190, pl. 18, figs 26–29. Type-locality: environs de Constantine ... Bou Mécid ... ravin du Rummel, non loin des Cascades [Algeria].
Helix lasia Bourguignat: Tryon, 1887, *Manual of Conchology* (2) 3, p. 179, pl. 40, figs 47–49.
Helix chnoodia Bourguignat 1864, *Malacologie de l'Algerie* 1, pp. 190–191, pl. 18, figs 30–33. Type-locality: environs de'Hammam-Mescoutin, ... province de Constantine [Algeria].
Helix chnoodia Bourguignat: Tryon, 1887, *Manual of Conchology* (2) 3, p. 179, pl. 40, figs 53–55.
?*H. glischra* Bourguignat in Letourneux & Bourguignat 1887, *Prodrome malacologie terrestre et fluviatile Tunisie* p. 10. Type-locality: Tunisie ... Guelaat-es-Snam.
?*H. persordida* Bourguignat in Letourneux & Bourguignat 1887, *Prodrome malacologie terrestre*

et fluviatile Tunisie p. 10. Type locality: Tunisie ... Djebel Reças.
?*H. rypa* Bourguignat in Letourneux & Bourguignat 1887, *Prodrome malacologie terrestre et fluviatile Tunisie* p. 11. Type-locality: Tunisie ... Guelaat-es-Snaam.
?*H. zaritosi* (H. Berthier) Bourguignat in Letourneux & Bourguignat 1887, *Prodrome malacologie terrestre et fluviatile Tunisie* p. 11. Type locality: Tunisie ... Lac Bizerte.

Description of shell 85 examined (including 13 adults, but only 4 of the adults and 4 immatures with intact periostracum and hairs) from nine localities. Slightly depressed to strongly depressed convex above, distinctly flattened below; height 4.1–5.7 mm, breadth 7.6–8.6 mm, with 3.7–4.1 whorls. Whorls rounded, the body whorl somewhat flattened above, resulting in bluntly rounded keel towards upper side of periphery; sutures deep. Umbilicus relatively wide for the genus (1.1–1.6 mm, representing 13.4–18.9% of shell breadth), the width varying between populations as discussed below, ± asymmetrical depending on expansion of body whorl, but deep and exposing upper whorls, slightly to widely overlapped by reflected peristome. Mouth nearly round except where interrupted by penultimate whorl (shape often somewhat wider than high), averaging proportionately smaller than in most species of genus, the body whorl gradually descending towards mouth or not, the last part of body whorl widening, especially below. Mouth edge thin, slightly to strongly reflected below, not reflected outwards or upwards; interior of mouth lacking any thickening. Shells thin, but becoming ± calcified when mature, when fresh translucent, light brown. Fresh shells mainly with cover of clayey or silty soil which is often nearly complete and filling umbilicus. Study of periostracum and its sculpture thus possible on few specimens; periostracum glossy in these, at least below near mouth. Spiral lines present at whorl 1.3, indistinct or lacking amongst other sculpture on much of shell, but clear on underside of body whorl in parietal edge of mouth. Spiral ridges present from whorl 1.7 onwards, prominent and continuous as parallel lamellae (higher than in most congeners) on upper and outer surfaces of body whorl. Transverse ribs present at least from whorl 0.3–1.3 onwards, often rather strong but irregular on upperside of later whorls, weaker on underside. Well developed shell hairs present from whorl 0.5 onwards (although sometimes persisting only as low hair bases). On body whorl hairs of medium length to long, typically rather thin, varying somewhat between populations (SE. of Alger 1984.338.13 with hairs 311–635 μm long, 16–19 μm wide, straight to curved; ENE. of Bouira 1984.325.5 one subadult shell with hairs 341–356 μm long, 20–31 μm wide, strongly curved).

Shells vary considerably in size and in relative height (H/B 0.53–0.67), but some samples show variability even at the same locality. Width of the umbilicus differs between populations, small samples giving 1.1–1.3 mm (U × 100/B 13.4–16.0%) (N. of Sétif: Fig. 3G) and 1.3–1.6 mm (U× 100/B 17.7–18.9%) (ENE. of Bouira: Fig. 3H). Three shells from WNW. of Batna (one immature, two subadult) have the umbilicus very narrow (Fig. 3I), at least partly because of the wide overlap of the reflected peristome. Length and thickness of the shell hairs also appears variable between populations (see above) but shortage of material in good condition prevents any detailed comparisons.

External features of body, Genital anatomy no information

Species recognition The combination of shell characters in *sordulenta* is different to that of any European species of *Ponentina*. The rather high number of shell whorls (3.7–4.1) overlaps almost completely with that in the two species of *Ponentina* with the southernmost ranges in Spain (*P. martigena*, *P. ponentina*), one of which occurs in N. Morocco (*P. martigena*), but the umbilicus is normally much larger than in those species (Table 1) and the shell hairs are longer. The number of whorls also overlaps that in two other European species, of which the relatively large umbilicus in some *sordulenta* populations and rather long shell hairs are suggestive of the Portuguese *P. platylasia* whereas other populations with a smaller umbilicus are more like *P. revelata*, although the shell mouth is proportionately smaller than in both of these and the body whorl differs in having a bluntly keeled periphery (Fig. 3F, G). Because the genital anatomy is unknown, the generic placement of *sordulenta* remains tentative.

Taxonomic history The description and figures by Morelet (1851) leave no doubt about the identity of this species; it was compared with *H. ponentina* and the first of the genus to be described from N. Africa. Bourguignat (1864) gave a good description and figures of the species. In addition, he named the new "var. *conoidea*" in the *Explication* to his pl. 18 and figured it (pl. 18, fig. 21), but without any description. In the same publication, *Helix lasia* Bourguignat 1864 appears to be a flatter form of *sordulenta* with a proportionately larger umbilicus; *H. chnoodia* Bourguignat 1864 may be another form with a low spire, but with less prominent transverse ribs and much shorter shell hairs.

The four taxa from Tunisia named by Bourguignat (in Letourneux & Bourguignat, 1887; see Bourguignat, 1891: 142 for recognition of him alone as author of the names) are even more difficult to assess because they have short descriptions in latin and no figures, as usual in that publication. They were listed again by Westerlund (1889: 60) but largely ignored by subsequent authors.

Geographical range N. Algeria (type was from near Constantine; other localities were listed by Bourguignat, 1864, as cited in synonymy above; collections made in 1984 are listed in our Appendix and mapped on Fig. 10). Probably also N. Tunisia, since *Helix lasia* and *H. sordulenta* were listed by Bourguignat (in Letourneux & Bourguignat, 1887).

Etymology The epiphet *sordulenta* apparently derives from combination of the latin adjectives *sordidus* (dirty-looking, soiled) and *lentus* (clinging, tenacious, sticky), and is appropriate because the fresh shell normally has a covering of soil.

HABITATS AND ECOLOGY

An analysis of the habitat data on *Ponentina* collected during fieldwork by the authors is given in Table 3 and Fig. 14 illustrates the wide range of habitat types occupied by the genus in Portugal and W. Spain. There appears to be a clear distinction between eight species confined to base-poor habitats (*P. curtivaginata*, *P. excentrica*, *P. foiaensis*, *P. grandiducta*, *P. monoglandulosa*, *P. octoglandulosa*, *P. papillosa*, *P. subvirescens*), one confined to base-rich habitats on limestone (*P. platylasia*) and four which occur in both base-poor and base-rich places (*P. ponentina*, *P. revelata*, *P. rosai*, *P. sordulenta*). Our few data on *P. martigena* are evidently insufficient to show its full habitat tolerance, since we collected it only on base-poor sandstones (twice) and conglomerate (once), although a single immature shell presumably of this species was found on limestone. However, detailed studies in Prov. Málaga by J.S. Torres Alba (pers. comm.) have shown that the species often occurs in limestone habitats (13 sites, mainly on Triassic marble or Jurassic limestone) and often in acidic habitats (10 sites, mainly on shale), so it clearly belongs among the species tolerating both base-rich and base-poor sites.

The eight species restricted to base-poor sites include six with small or very small geographical ranges, only *P. papillosa* and *P. subvirescens* being more widespread. Except for the northern *P. subvirescens*, they are restricted mainly to hill or montane areas. All of these species live in places with few if any other Mollusca, often with no other snails or at most with rare individuals of one or two other species. The five species occurring in both base-poor and base-rich places include four with large geographical ranges mainly in the lowlands (a very large range in *P. revelata*), only that of *P. martigena* being rather small. These sometimes live with several other species of snail. The calciphile *P. platylasia* has only a moderately large range, restricted to the Mesozoic limestone hills and adjoining alluvial lowlands of west-central Portugal, where it often occurs at rather high densities in places with several other snail species (e.g. Fig. 14C).

Instances of two species of *Ponentina* coexisting were recorded by us only twice, on each occasion involving the diminutive *P. rosai* living alongside a larger species (*P. excentrica*, *P. ponentina*). Falkner *et al*. (2002: 147) reported *P. subvirescens s. str*. as having been collected along with the more widespread *P. revelata* at two French localities. However, it is not made clear whether this was based only on shells of both species being mixed together in old collections, which may have been accumulated from large areas and labelled only with the name of the nearest town, as was common practice in the nineteenth century.

A high proportion of habitats of all of the species are in open places that are not or only slightly shaded by vegetation. The only record deep inside shady woodland was of *P. grandiducta*, which was found living at low density inside mature woodland of *Betula pubescens*

Table 3 Analysis of habitat data on *Ponentina* species. Based only on specimens collected by the authors that were securely identified to species. Totals and subtotals are given in round brackets. Several localities included two rock types. Base-status of sites was judged from the flora, coexisting Mollusca and rock type.

Ponentina species:	*curtivaginata*	*excentrica*	*foiaensis*	*grandiducta*	*martigena*	*monoglandulosa*	*octoglandulosa*	*papillosa*	*platylasia*	*ponentina*	*revelata*	*rosai*	*sordulenta*	*subvirescens*
No. of localities	1	3	1	7	3	8	6	7	25	21	20	16	7	14
Altitude in metres a.s.l.														
minimum	672	196	810	250	370	143	550	770	40	30	7	15	130	22
maximum	–	370	–	1375	525	734	986	1338	651	554	890	462	1570	247
Analysis by rock types														
No rock exposed:	–	–	–	–	–	–	–	–	(3)	(7)	(11)	–	–	(9)
soil only	–	–	–	–	–	–	–	–	1	2	3	–	–	–
dune sand/blown sand	–	–	–	–	–	–	–	–	–	–	8	–	–	3
siliceous china-clay spoil	–	–	–	–	–	–	–	–	–	–	–	–	–	6
concrete/basic masonry	–	–	–	–	–	–	–	–	2	5	–	–	–	–
Sedimentary rocks:	–	(2)	–	–	(3)	–	–	–	(22)	(8)	(4)	(13)	(8)	(1)
sandstone	–	2	–	–	2	–	–	–	–	–	2	1	1	1
conglomerate	–	–	–	–	–	–	–	–	–	–	–	–	1	–
shale	–	–	–	–	1	–	–	–	–	–	1	2	–	–
limestone	–	–	–	–	–	–	–	–	22	8	1	10	6	–
Igneous rocks:	(1)	–	–	(4)	–	(4)	(5)	(5)	–	(5)	(4)	–	–	(2)
granitic	1	–	–	4	–	4	5	5	–	5	4	–	–	1
other	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Metamorphic rocks:	–	(3)	(1)	(3)	–	(4)	(1)	(4)	–	(2)	(3)	(6)	–	(2)
slate	–	2	–	1	–	1	1	1	–	2	2	5	–	1
schist/mica schist	–	–	–	–	–	–	–	1	–	–	–	1	–	–
quartzite	–	1	–	2	–	3	–	1	–	–	–	–	–	–
Foyaite	–	–	1	–	–	–	–	–	–	–	–	–	–	–
serpentinite	–	–	–	–	–	–	–	–	–	–	–	–	–	1
unidentified metamorphic	–	–	–	–	–	–	–	1	–	–	1	–	–	–
Analysis by base status														
% sites base-rich	–	–	–	–	–	–	–	–	100%	62%	45%	63%	75%	–
% sites base-poor	100%	100%	100%	100%	100%	100%	100%	100%	–	24%	25%	31%	–	100%
% sites uncertain [base]	–	–	–	–	–	–	–	–	–	14%	30%	6%	25%	–
Analysis by vegetation type														
% in closed woodland	0%	0%	0%	14%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% in open woodland/groves	0%	0%	0%	14%	0%	0%	0%	0%	12%	14%	15%	0%	0%	0%
% amongst scrub	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% unshaded by scrub/trees	100%	100%	100%	72%	100%	100%	100%	100%	88%	86%	85%	100%	100%	100%

Ehrh. with a closed canopy on a montane slope in the Serra da Estrela (Fig. 14B). Another record of it was from rocky slopes in open woodland of *Quercus* and *Pinus* in Beira Baixa, but its five other localities were open or only slightly shaded (e.g. Fig. 14A). This species may also reach the highest altitudes, judging from shells apparently of this species found at 1725 m in the Serra da Estrela in a site that regularly has deep snow cover in winter.

In Britain *P. subvirescens* has been regarded as occurring exclusively in coastal locations, "on cliffs by the sea (occasionally inland along estuaries)" (Kerney, 1999: 198) and Falkner *et al*. (2002: 147) implied that it has an essentially coastal range in western France. However, Holyoak (2000) reported it from seven localities inland in Cornwall on very acidic china-clay spoil, 1.9–19.5 km from the sea and at altitudes up to 250 m, so the species is certainly not limited to coasts. Also, the only French locality at which we have found it is inland near Angers (Maine-et-Loire), over 80 km inland even of the nearest estuary.

Resting and aestivation sites of all species are often on the ground amongst the base of low vegetation, in the soil surface, or beneath loose rocks. However, *P. platylasia* and *P. ponentina* sometimes also occur in quantity up to two metres above the ground on tree bark (e.g. Figs 1C, 14C) or walls. The same was true of *P. revelata* at one locality (on *Populus* and *Eucalyptus* trees in park beside lake, P247). Small numbers of *P. grandiducta* have also been found resting on walls of a house at the type locality.

NOTES ON EVOLUTION WITHIN THE GENUS *PONENTINA*

Shells Those species of *Ponentina* which occur in both basic and base-poor habitats commonly have thinner, less calcified shells in the base-poor sites. The species which are restricted to areas with base-poor rocks tend to have even thinner shells, sometimes with little if any calcification. They also tend to have fewer whorls and smaller overall size than related species in base-rich habitats. Their minimal calcium requirements presumably allow survival in habitats that support few or no other land snails, although it is rather surprising that one of the few frequent associates in western Iberia is *Oestophora barbella* (Servain) (see Holyoak & Holyoak, 2012) which has a more substantial shell.

Many living *Ponentina* have layers of dirt on the shell, apparently consisting mainly of fine particles of soil (Fig. 1C–F), although strands of spiders' web are also common. These layers are so consistently present in some species (see shell descriptions above) that they are likely to be of adaptive significance, perhaps as camouflage from predators by improving the colour match to substrata, perhaps also in providing a hygroscopic moisture reservoir (cf. Yanes *et al*., 2010, 2011: 401), possibly even strengthening very thin shells by providing a siliceous outer layer and plugging the umbilicus. The elaborate periostracal sculpture (see notes under genus heading and under each species) may be involved in providing surfaces suitable for adhesion of the right kind and quantity of particles.

The size of shell hairs varies very widely between species (Table 2), as in the allied genus *Trochulus*. Indeed, the length and thickness of shell hairs afford some of the best characters for identifying shells of *Ponentina* to species level, as shown in the Key above and in Fig. 5. In *P. papillosa* hairs have evidently been lost, with only the papilla-like "foot-plate" (21–45 μm high) remaining (Fig. 5A, B). *P. foiaensis* has tiny hairs (up to *ca* 30 μm) emerging from the "foot-plate" (Fig. 5C), suggesting a similar process of reduction has almost been completed. At the other extreme, *P. platylasia* from the Serra de Montejunto have hairs up 1235 μm long (*ca* 13% of shell breadth) (Fig. 5O) and the diminutive *P. rosai* has hairs of similar relative length in proportion to its small shell size (mean 489 μm long, *ca* 12% of shell breadth; Fig. 5L).

The adaptive significance of hairs of widely differing length is largely unknown. Pfenninger *et al*. (2005) argued that different *Trochulus* species from three lineages have tended to lose hairs as they shifted from humid to dry habitats. They demonstrated experimentally that the long hairs of *T. villosus* (S. Studer) facilitate adherence to herbaceous food plants during foraging when humidity levels are high. From this, they inferred that absence of hairs in some *Trochulus* species could be explained as a loss of the potential adaptive function linked to habitat shifts.

Ponentina differs from *Trochulus* in showing no consistent correlation between humidity of habitats and length of hairs. Some individual species show wide discrepancies, notably *P. octoglandulosa* with mean hair length short (142 μm) which inhabits a region with high rainfall (mean of *ca* 2750 mm annually), whereas *P. rosai* has long hairs (mean 489 μm) but inhabits regions with low rainfall (mean of *ca* 600 mm). Indeed, when the 14 species recognised here are ranked in order of mean length of shell hairs (from data presented in Table 2, corresponding to the arrangement of species in Fig. 5) and also ranked in terms of the mean annual rainfall in their ranges (based mainly on Daveau *et al*., 1977), the value of Spearman's Rank Correlation Coefficient (R) = -0.0725, implying a slight negative correlation exists. The explanations of hair function and hair loss presented by Pfenninger *et al*. (2005) therefore seem inapplicable to *Ponentina*, or at least to some of the species. Additional functions of shell hairs seem likely, including capture of water droplets (by providing foci for condensation of dew), provision of a larger surface area to aid retention of a water film around the shell, preventing adhesion of large particles to the shell by inhibiting close contact, excluding some predators, and possible roles in obtaining and storing soil particles on the shell, none of which need be mutually exclusive.

Behaviour The southern populations of *Ponentina* live in regions with the long dry summers characteristic of a mediterranean climate. Some of the hottest and driest areas occupied are in eastern Portugal and adjoining regions of western Spain on open rocky hillsides. *P. curtivaginata*, *P. excentrica*, *P. monoglandulosa* and *P. papillosa* are endemic to this region and *P. grandiducta* extends into it from higher and moister hills further west, all of them usually living at low densities. They apparently aestivate throughout the hot summer months, typically either attached to the underside of boulders or shaded in the soil surface at the base of herbaceous plants, often *Dianthus* or *Digitalis*. Both mature adults and immatures aestivate, apparently often for months at a time, forming one or more epiphragms that seal the shell mouth. Many of the aestivation sites are in habitats rocky enough to offer protection from brush fires, which are frequent in much of the region.

Reduction of distal female genitalia The genus *Ponentina* shows remarkable variability in the development of accessory organs on the distal female genitalia, with interspecific variability as great as that characterising different genera among other Hygromiidae. Thus, different *Ponentina* species show loss of one or both dart sacs, one or both accessory sacs and variable numbers of mucus glands, with no corresponding reduction of size of the vagina, spermatheca, or the distal male genitalia. Since some of the species involved are otherwise very similar to those *Ponentina* with fully developed genitalia, there is little doubt that recent evolutionary reduction has been involved, rather than misjudgement of evolutionary relationships on our part resulting in misleading taxonomy.

It is noteworthy that reduced female genitalia occur mainly in species restricted to base-poor sites, such reduction characterising six of the eight species of these habitats, with only *P. excentrica* and *P. octoglandulosa* not showing much reduction. In contrast, the only calciphile species (*P. platylasia*) and three of the four base-tolerant species for which the genitalia are known (*P. martigena*, *P. ponentina*, *P. revelata*) have female genitalia showing little or no reduction. The only species with apparently reduced genitalia that occurs in both base-rich and base-poor places is the diminutive *P. rosai*, in which the reduction might be associated with its very small body size.

Very little is known of the reproductive biology of any *Ponentina*, the species with reduced female genitalia being virtually unknown in this respect. Explanations of the reduction in the female genitalia of several species can therefore only be tentative, although the loss seems likely to be an example of phenotypic regression (i.e. trait simplification) due to the loss of adaptive function (see Porter & Crandall, 2003 for a review of this phenomenon). One possible cause of reduction is that extreme shortage of calcium in base-poor habitats has not only lead to virtually calcium-free shells, but that it also precludes production of the calcareous darts that occur in the species of basic habitats. This might have led to loss of dart sacs along with a tendency to lose the accessory sacs and mucus glands that relied at least partly on darts for transport of their glandular products. Another possibility, that need not exclude the first, is that very low population densities may lead to a predominance of self-fertilization, or mating only with close kin, so that the elaborate hormonal mechanisms to control fertility during mating hypothesized for the dart-sac and related structures in other Helicacea (e.g. Koene & Schulenberg, 2005) are no longer selected for and thus prone to evolutionary loss. However, a sound and conclusive understanding is likely to require much more knowledge of population genetics and reproduction in the genus.

ACKNOWLEDGEMENTS

Thanks are due to the Dept. of BioSYB at National Museum and Gallery of Wales, Cardiff, U.K. (NMW.Z) for loan of specimens and Jennifer Gallichan and Dr Graham Oliver for helping with arrangements for this. Jonathan Ablett of the Natural History Museum, London, U.K. (NHMUK) and Adrian Norris helped with information and Álvaro de Oliveira, Rui da Costa Mendes and J. Sebastián Torres Alba provided distributional or habitat data, access to specimens in their collections and helpful comments. Tom Blockeel is thanked for advising us on nomenclatural matters. Dr Colin French and Mrs Stella Turk provided records from Cornwall from the ERICA Database; Rui da Costa Mendes and Mark Pool helped in obtaining literature. The maps were prepared using the DMAP software written by Dr A.J. Morton. A referee is thanked for helpful comments.

REFERENCES

ABBES I & NOUIRA S 2007 Contribution to the revision of the biodiversity of Tunisian terrestrial malacofauna. *In* JORDAENS K, VAN HOUTE N, VAN GOETHEM J & BACKELJAU T (eds) World Congress of Malacology, Antwerp Belgium, 15–20 July 2007, *Abstracts*: 1.

ALBUQUERQUE DE MATOS RM 2004 Non-marine testaceous Gastropoda of continental Portugal and Berlengas Islands 1. Catalogue and bibliography. *Arquivos do Museu Bocage* N.S. **4** (1): 1–158.

ALLGAIER C 2011 A hairy business– periostracal hair formation in two species of helicoid snails (Gastropoda, Stylommatophora, Helicoidea). *Journal of Morphology* **272** (9): 1131–1143.

ANIMALBASE WEBSITE: www.animalbase.uni-goettingen/de/zooweb/servlet/AnimalBase/home/genus?id=699 Accessed 4 Feb. 2012.

ARRÉBOLA BURGOS JR 1995 *Caracoles terrestres (Gastropoda, Stylommatophora) de Andalucia, con especial referencia a las Provincias de Sevilla y Cadiz*. Thesis for Doctor en Biología, Universidad de Sevilla, Unpublished. 589 pp.

ARRÉBOLA JR & GARCÍA FJ 1999 Redescripción de *Helix martigena* Férussac (1832) como perteneciente al género *Trichia* Hartmann, 1840 (Gastropoda: Pulmonata: Hygromiidae). *Iberus* **17** (1): 21–30.

BELLAMY JC 1839 *The natural history of South Devon*. Jenkin Thomas, Plymouth & London. i-xxvi, i-ii, i-viii, 1–456 pp., 18 pls, 5 maps.

BOURGUIGNAT J–R 1860 *Malacologie terrestre et fluviatile de la Bretagne.* J.B. Baillière, Paris. xxiv + 179 pp., 2 pls.

BOURGUIGNAT J–R 1864 *Malacologie de l'Algérie ou histoire naturelle des animaux Mollusques terrestres et fluviatiles recueillis jusqu'à ce jour dans nos possessions du nord de l'Afrique.* Challamel Aine, Paris: **1**: xii + 294 pp., 32 pls.

BOURGUIGNAT J–R 1891. *Œuvres scientifiques de M. J.-R. Bourguignat ... précédées d'une preface biographique par le Dr. Georges Servain*. D. Dumoulin et cie, Paris. vii + 256 pp.

CASTRO J DA S 1887 Contributions à la faune malacologique du Portugal. II. Hélices du groupe de la *revelata*. *Jornal de Sciencias mathematicas, physicas e naturaes, Lisboa* **11** (44): 232–238.

DAVEAU S, COELHO C, COSTA VG & CARVALHO L 1977 Répartition et rhythme des précipitations au Portugal. *Memórias do Centro Estudos Geográficos*, Lisbon **3**: 1–189.

DESMARS J 1873 *Essai d'un catalogue méthodique et descriptif des mollusques terrestres, fluviatiles et marins, observés dans l'Ille-et-Vilaine, les départements limitrophes de l'Ouest de la France, et sur les cotes de la Manche, de Brest a Cherbourg. Première partie.* Redon: P. Chauvin. 94 pp.

DUPUY D 1848 *Histoire naturelle des mollusques terrestres et d'eau douce qui vivent en France.* V. Masson, Paris, fasc. 2: 107–226, pls 5–10.

ELLIS AE 1926 *British snails. A guide to the non-marine Gastropoda of Great Britain and Ireland, Pleistocene to Recent.* Oxford University Press, Oxford. Reprint with additions, 1969, Clarendon Press, Oxford. 298 pp., 14 pls.

FALKNER G, RIPKEN TEJ & FALKNER M 2002 *Mollusques continentaux de France. Liste de réference annotée et bibliographie*. Muséum national d'Histoire naturelle–Laboratoire de biologie des invertébrés marins et de malacologie, Paris.350 pp.

FÉRUSSAC AÉJPJF D'AUDEBARD DE [fils] 1821–1822 *Tableaux systématiques des Animaux Mollusques classés en familles naturelles, dans lesquels on a établi la concordance de tous les systèmes; suivis d'un prodrome générale pour tous les mollusques terrestres et fluviatiles, vivants et fossiles*. Paris. Tableaux systématiques généraux, pp. i-xlviii (1822); **1** (Tableau de la famile des Limaces): 1–27 (1821), **2** (Tableau de la famile des Limaçons): 1–94 (1821), **3** (Tableau de la famile des Auricules): 95–114 (1821).

FÉRUSSAC AÉJPJF D'AUDEBARD DE [fils] & Deshayes GP 1819–1851 *Histoire naturelle générale et particulière des Mollusques terrestres et fluviatiles*. Paris. vols. **1–4**: 247 pls.

GARGOMINY O, PRIE V, BICHAIN J–M, CUCHERAT X & FONTAINE B 2011 Liste de référence annotée des mollusques continentaux de France. *MalaCo* **7**: 307–382.

Gassies J-B 1849 *Tableau méthodique et descriptif des mollusques terrestres et d'eau douce de l'Agenais.* J.-B. Baillière, Paris. 209 [+4 unpaginated] pp., 4 pls.

Germain L 1930 *Mollusques terrestres et fluviatiles*. Faune de France. Paul Lechevalier, Paris **21**: 1–477, i-viii, pls: 1–13. (Facsimile reprint, 1962).

Gittenberger E 1978 On two nominal *Ponentina* species (Helicidae, Hygromiinae). *Basteria* **42** (1–3): 14.

Gittenberger E 2012 An Iberian surprise, *Henkia mariannae* gen. & spec. nov. and *H. antoni* gen. & spec. nov. (Gastropoda, Pulmonata, Hygromiidae). *Basteria* **76** (1–3): 71–74.

Giusti F & Manganelli G 1989 ["1988"]. *Montserratina* Ortiz de Zárate López, 1946 (Pulmonata, Hygromiidae): a redescription. *Iberus* **8** (1): 89–100.

Hesse P 1921 Beiträge zur näheren Kenntnis der Subfamilie Fruticicolinae. *Archiv für Molluskenkunde* **53** (1/2): 55–83.

Holyoak DT & Holyoak GA 2012 A taxonomic revision of *Oestophora barbula* (Rossmässler, 1838) and *O. barbella* (Servain, 1880), two Iberian endemic land-snail species (Gastropoda: Trissexodontidae). *Iberus* **30** (1): 15–40.

Holyoak GA 2000 Occurrence of *Ponentina subvirescens* (Helicidae) inland in Cornwall on spoil from china clay quarries. *The Conchologists' Newsletter* **9** (3) [no. 154]: 386–388.

Janus H 1965. *The young specialist looks at land and freshwater molluscs.* Reprinted 1979, Burke Books, London & Toronto. 180 pp.

Kennard AS & Woodward BB 1919 On *Helix revelata* Britt. auctt. (*non* Férussac, *nec* Michaud), and the validity of Bellamy's name of *Helix subvirescens* in lieu of it for the British mollusc. *Proceedings of the Malacological Society of London* **13** (5–6): 133–136.

Kennard AS & Woodward BB 1926. *Synonymy of the British non-marine Mollusca (Recent and post-Tertiary).* British Museum, London: xxiv + 447 pp.

Kerney M 1999 *Atlas of the land and freshwater molluscs of Britain and Ireland*. Harley Books, Colchester, 261 pp.

Kerney MP & Cameron RAD 1979 *Land snails of Britain and north-west Europe*. Collins (Collins Field Guide), London. 288 pp., 24 pls.

Kobelt W 1892 *Iconographie der Land- & Süsswasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten*. C.W. Kreidel's Verlag, Wiesbaden (2) **5**: 118 pp., 30 pls (nos. 121–150).

Koene JM & Schulenberg H 2005 Shooting darts: coevolution and counter-adaptation in hermaphroditic snails. *BMC Evolutionary Biology* **5**: **25**, 13 pp.

Letourneux A & Bourguignat J–R 1887 *Prodrome de la Malacologie terrestre et fluviatile de la Tunisie*. Imprimerie Nationale, Paris (published as part of series entitled: Exploration scientifique de la Tunisie). 166 pp.

Locard A 1882 *Prodrome de Malacologie Française. Catalogue général des Mollusques vivants de France, Mollusques terrestres, des eaux douces et des eaux saumâtres.* Henri Georg, Lyon & J.-B. Baillière et fils, Paris. vi + 462 pp.

Locard A 1894 *Conchyliologie Française. Les Coquilles terrestres de France. Description des familles, genres et espèces.* J.-B. Baillière et fils, Paris. 370 pp.

Locard A 1899 Conchyliologie Portugaise. Coquilles terrestres, des eaux douces et saumâtres. *Archives du Muséum d'Histoire Naturelle de Lyon* **7**: i-vi, 1–303.

Maltzan H von 1885 Diagnosen neuer Arten. *Jahrbücher der deutschen malakozoologischen Gesellschaft* **12**: 235.

Manga González MY 1980 Notas sobre *Ponentina ponentina* (Morelet, 1845) y *Euomphalia* (*Mengoana*) *brigantina* (Da Silva Mengo, 1867) (Gastropoda, Helicidae) en la provincia de León. *Comunicaciones al Primer Congreso Nacional de Malacología*, Madrid, 1980: 41–45.

Michaud ALG 1831 *Complément de l'histoire naturelle des Mollusques terrestres et fluviatiles de la France, de J. P. R. Draparnaud*. Lippmann, Verdun. xvi + 116 pp., 3 pls (nos. 14–16).

Moquin-Tandon A 1855. *Histoire naturelle des Mollusques terrestres et fluviatiles de France* ... J.-B. Baillière, Paris **2**: 646 pp.

Morelet A 1845 *Description des Mollusques terrestres et fluviatiles du Portugal.* J.-B. Baillière, Paris. 115 pp., 14 pls.

Morelet A 1851 Appendice à la conchyliologie de l'Algérie; descriptions d'espèces nouvelles. *Journal de Conchyliologie* **2**: 351–361, pl. 9.

Morelet A 1877 Révision des mollusques terrestres et fluviatiles du Portugal. *Journal de Conchyliologie* **25** (3): 242–261.

Nobre A 1888 Contribuições para a fauna malacologica de Portugal. *O Instituto*, Coimbra (2nd ser.) **35**: 600–604.

Nobre A 1913 *Moluscos de Portugal. I. Moluscos terrestres, fluviais e das águas salobras.* Part 2. Memórias publicadas pela Sociedade Portuguesa de Sciências Naturals, Lisboa. Pp: 131–343.

Nobre A 1941 Fauna Malacológica de Portugal. II. Moluscos terrestres y fluviais. *Memòrias e Estudos do Museu Zoológico da Universidade de Coimbra* **124**: 1–277, pls 2 & 30.

Ortiz de Zárate Rocandio A & Ortiz de Zárate Lopez A 1961 Moluscos terrestres recogidos en la provincia de Huelva. *Boletín de la Real Sociedad española de Historia natural (Sección Biológica)* **59**: 169–190.

Pallary P 1898 Deuxième contribution à l'étude de la faune malacologique du nord-ouest de l'Afrique. *Journal de Conchyliologie* **46** (2): 49–170, pls 5–9.

Pallary P 1904 Quatrième contribution à l'étude de la faune malacologique du nord-ouest de l'Afrique. *Journal de Conchyliologie* **52** (1): 5–58.

Pallary P 1920 Description d'une nouvelle cinquantaine de mollusques terrestres nouveaux du Nord-ouest de l'Afrique. *Bulletin de la Société d'Histoire naturelle de l'Afrique du Nord* **11** (2): 18–34.

Pallary P 1928 [March] Compléments à la faune malacologique de la Berbérie (suite). *Journal de Conchyliologie* **71** (3) [for 1927]: 197–277, pls 1–7.

PFEIFFER L 1846 *Symbolae ad Historiam Heliceorum*. Th. Fischer, Cassellis **3**: 100 pp.

PFEIFFER L 1847–1848 *Monographia Heliceorum viventium. Sistens descriptiones systematicas omnium huius familiae generum et specierum hodie cognitarum*. Brockhaus, Leipzig **1** (1): 1–160 (1847), **1** (2) 161–320, **1** (3): 321–484, I-XXXII (1848).

PFENNINGER M, HRABÁKOVA M, STEINKE D & DÈPRAZ A 2005. Why do snails have hairs? A Bayesian inference of character evolution. *BMC Evolutionary Biology* **5**: **59**, 11 pp.

PILSBRY HA 1892 *Manual of Conchology, structural and systematic, with illustrations of the species. By George W. Tryon, Jr. Second series: Pulmonata.* vol. **8**. Helicidæ:– vol. VI. Conchological Section, Academy of Natural Sciences, Philadelphia. 314 pp., 58 pls.

PILSBRY HA 1894–1895. *Manual of Conchology, structural and systematic, with illustrations of the species. By George W. Tryon, Jr. Second series: Pulmonata.* vol. **9**. (Helicidæ, vol. 7). Guide to the study of Helices. Conchological Section, Academy of Natural Sciences of Philadelphia, Philadelphia. xlviii + 366 pp., 71 pls.

PORTER ML & CRANDALL KA 2003 Lost along the way: the significance of evolution in reverse. *Trends in Ecology and Evolution* **18** (10): 541–547.

POTIEZ VLV & MICHAUD ALG 1838 *Galerie des mollusques, ou catalogue méthodique, descriptif et raisonné des mollusques et coquilles du Muséum de Douai.* J.-B. Baillière, Paris **1**: xxxvi + 564 pp.

PROĆKÓW M 2009 The genus *Trochulus* Chemnitz, 1786 (Gastropoda: Pulmonata: Hygromiidae) – a taxonomic revision. *Folia Malacologica* **17** (3): 101–176.

PUENTE MARTINEZ AI 1994 *Estudio taxonómico y biogeográfico de la Superfamilia Helicoidea Rafinesque, 1815 (Gastropoda: Pulmonata: Stylommatophora) de la Península Ibérica e Islas Baleares*. Unpublished Doctoral Thesis, Universidad del País Vasco, Facultad de Ciencias, Departamento de Biologia Animal y Genetica.

RAVEN JGM 1984. Notes on Spanish non-marine molluscs 2. New data on the distribution of some species. *Basteria* **48** (1–3): 17–21.

RÉCLUZ C 1845 Review of: Description des Mollusques terrestres et fluviatiles du Portugal, par Arthur Morelet, ... *Revue Zoologique, par La Société Cuvierienne* **8** (8): 306–312.

RICHARDSON L 1980 Helicidae: Catalog of species. *Tryonia* **3**: iii + 697 pp.

ROSSMÄSSLER EA 1854. *Iconographie der Land- und Süsswasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten.* Hermann Costenoble, Leipzig (1) **3** (1–2), viii + viii + 140 pp., 18 pls.

RUIZ RUIZ A, CÁRCABA POZO Á, PORRAS CREVILLEN AI & ARRÉBOLA BURGOS JR 2006 *Caracoles terrestres de Andalucía. Guía y manual de identificación.* Fundación Gypaetus, Sevilla. 303 pp.

SACCHI CF 1957 Lineamenti biogeografici della Spagna mediterranea su basi malacofaunistiche. *Publicaciones del Instituto de Biología Aplicada, Barcelona* **25**: 5–48.

SCHILEYKO AA 1991 Taxonomic status, phylogenetic relations and system of the Helicoidea *sensu lato* (Pulmonata). *Archiv für Molluskenkunde* **120** (4/6): 187–236.

SCHILEYKO AA 2005 Treatise on Recent terrestrial pulmonate molluscs. Part 14. Helicodontidae, Ciliellidae, Hygromiidae. *Ruthenica*, Supplement 2: 1905–2047.

SERVAIN G 1880 *Étude sur les mollusques d'Espagne et de Portugal.* D. Bardin, Saint-Germain (Paris). 172 pp.

SIMÕES JMM 2006 Notas sobre a espécie *Ponentina subvirescens* (Bellamy, 1839) (Helicidæ: Hygromiinæ). *Portugala* **8**: 7–9.

TAYLOR JW 1916 *Monograph of the land & freshwater Mollusca of the British Isles.* Taylor Bros, Leeds. Part 22: 64 pp., 5 pls.

TRYON GW JR 1887. *Manual of conchology, structural and systematic, with illustrations of the species. Second series: Pulmonata.* vol. 3. Helicidæ:– vol. I. Published by the author, Philadelphia. 313 pp., 63 pls.

TURTON W 1840 *A manual of the land & fresh-water shells of the British Islands*. New ed., by J.E. Gray, London. ix [i] + 324 pp., 12 pls.

TURTON W 1857 *Manual of the land & fresh-water shells of the British Islands*. . . . New ed., by J.E. Gray, with additions, Longman, Brown, Green, Longmans, and Roberts, London. xvi + 335 pp., 12 pls.

WESTERLUND CA 1876 *Fauna Europaea Molluscorum extramarinorum prodromus. Sistens descriptiones systematicas et criticas omnium generum et specierum horum animalium in Europa viventium et hodie cognitarum*. Berlingia, Lundae Fasc. 1: 160 pp.

WESTERLUND CA 1888 Species et varietates nonnullas minus cognitas vel novas. *Bulletins de la Société Malacologique de France* **5**: 55–64.

WESTERLUND CA 1889 *Fauna der in der Paläarktischen region ... Lebenden Binnenconchylien.* II. Genus *Helix*. R. Friedländer & Sohn, Berlin & Håkan Ohlsson's Buchdruckerei, Lund. **2**: 473 pp. + index 31 pp.

YANES Y, MARTÍN J, DELGADO JD, ALONSO MR & IBÁÑEZ M 2010 Active disguise in land snails: *Napaeus badiosus* (Gastropoda, Pulmonata, Enidae) from the Canary Islands. *Journal of Conchology* **40** (2): 143–148.

YANES Y, MARTÍN J, SANTANA J, HOLYOAK GA, HOLYOAK DT, ARTILES M, DENIZ F, ALONSO MR & IBÁÑEZ M 2011 Four new *Napaeus* species (Gastropoda: Pulmonata: Enidae) from La Gomera (Canary Islands). *Journal of Conchology* **40** (4): 393–407.

APPENDIX 1

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), habitat description, altitude, date, collectors' initials and collector's field number, Determined or Confirmed by (with date), collection where housed, registration number if any, number of shells or specimens (immature or adult), 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: ÁDO = Á. de Oliveira, bod = bodies in spirit, CGAH = Collection of G.A. and D.T. Holyoak, Conf. = confirmed, CRCM = Collection of R. da Costa Mendes, Det. = determined, DTH = D.T. Holyoak, GAH = G.A. Holyoak, incl. = including, MH = M. Holyoak, MBS = M.B. Seddon, NHMUK = The Natural History Museum, London, U.K., NMW.Z. = Department of BioSYB, National Museum and Gallery of Wales, Cardiff, U.K., RCM = R. da Costa Mendes, sh = number of shells, spm = number of specimens in alcohol.

***P. curtivaginata* sp. nov., Portugal, Trás-os-Montes e Alto Douro,** *ca* 1 km S. of Vale de Águia (NE. of Miranda do Douro), 29T 0729638/4600096, exposed low and flat granitic rocks with boulders, patchy scrub and low evergreen *Quercus* trees, 672 m, 2011.07.01, DTH P172, CGAH (14 sh & bod: paratypes), NHMUK (1 sh & bod: holotype); ***P. curtivaginata*?, Portugal, Trás-os-Montes e Alto Douro,** by N218 *ca* 4 km due NW. of Vimioso, 29T 070334/460939, slopes of river gorge with crags (slate, schist), screes and patchy scrub, 447 m, 2011.06.30, GAH & DTH P171, CGAH (12 sh [1 imm live; 11 dead]).

***P. excentrica* sp. nov., Portugal, Baixo Alentejo,** by Rio Murtega on road to Noudar (N. of Barrancos), 29S PC7662/2455, rocky river bank (slaty) with patchy scrub and trees, springs locally, 196 m, 2012.04.10, GAH & DTH P243, CGAH (2 sh & bod [imm], 12 sh [dead, 8 ad, 4 imm]); near Castelo de Noudar, 29S PC698/272, rocky (slate and sandstone) slopes and banks, with patchy scrub and scattered *Quercus* trees, 243 m, 2012.04.10, GAH & DTH P242, CGAH (1 sh [dead]); **Spain, Prov. Badajoz,** Castelo de Miraflores (N. of Alconchel), 29S PC683/656, hillslopes with crags (hard sandstone and quartzite), patchy scrub and walls, 370 m, 2012.04.09, GAH & DTH E240, CGAH (11 sh & bod, 1 spm [imm], 4 sh [dead]: paratypes), NHMUK (1 sh & bod: holotype).

***P. foiaensis* sp. nov., Portugal, Algarve,** W. slope of Fóia, 29S 05347/41292, hillslopes with low metamorphic crags (Foyaite) and patchy cover of *Erica* and *Cistus*, grassland locally, 810 m, 2011.02.05, GAH & DTH P120, CGAH (16 sh & bod, 27 sh: paratypes), NHMUK (1 sh & bod: holotype).

***P. grandiducta* sp. nov., Portugal, Beira Alta,** by N338 high in Vale glaciário do Zêzere, 29T 06209/44650, mature *Betula* wood by streams on N.-facing granitic slope, *ca* 1375 m, 2010.07.02, GAH P53, CGAH (1 sh & bod, 28 sh [dead]: paratypes); by N338 high in Vale glaciário do Zêzere, 29T 06208/44649, mature *Betula* wood on rocky slope with streams, *ca* 1375 m, 2010.08.10, GAH P66, CGAH (2 spm [1 died 2010.10.05], 11 sh [dead, 4 ad, 7 imm]: paratypes); by N338 high in Vale glaciário do Zêzere, 29T 062091/446496, floor of mature *Betula* wood on rocky N.-facing granitic slope, *ca* 1370 m, 2010.12.17, GAH & DTH P85, CGAH (9 sh & bod, 3 sh [dead]: paratypes); 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 P209, CGAH (14 sh & bod, 124 sh [dead]: paratypes); **Beira Baixa,** Barcoila, near Sertã, 29S 05741/44096, walls of house, 410 m, 2010.04.21, GAH P36, CGAH (2 sh & bod, 2 sh: paratypes; 3 spm killed 2010.10.09: paratypes), NHMUK (1sh & bod: holotype); Barcoila, near Sertã, 29S 05741/44096, walls of house, with garden beneath, 410 m, 2011.02.22, GAH & DTH P134, CGAH (3 spm: paratypes); Barcoila, near Sertã, 29S 05741/44096, walls of house, with garden beneath, 410 m, 2011.04.29, GAH P142, CGAH (1 sh & bod: paratype); Rio Zêzere valley W. of Pedrógão Pequeno, 29S 05737/44176, rocky granitic slopes of valley side, with open *Pinus* and *Quercus* woodland, 250 m, 2011.04.27, GAH & DTH P140, CGAH (9 sh & bod [1 ad, 8 imm], 18 sh [dead]: paratypes); just S. of N339 at *ca* 1.5 km NW. of Penhas da Saúde, 29T 06225/44635, rocky (granitic) slope with patches of short grassland and low bushes, 410 m, 2011.03.30, GAH P139, CGAH (6 sh [dead]); **Beira Litoral,** Casal de São Simão (NE. of Aguda), 29S 05582/44188, quartzite crags, slopes and walls of chapel, 385 m, 2011.09.06, GAH & DTH P192, CGAH (4 spm [imm], 6 sh [dead]); *ca* 2 km NE. of Favacal, 29S 05576/44272, quartzite rocks and slopes of hill-top, with grassland and bushes, 755 m, 2011.09.06, GAH & DTH P191, CGAH (9 sh & bod [5 ad, 4 imm], 29 sh [dead]: paratypes); ***P. grandiducta*?, Portugal, Beira Alta,** E. of N339

SW. of Lagoa Comprida, 29T 06141/44679, low granitic rocks with patchy grassland and low scrub, *ca* 1635 m, 2010.07.09, GAH P54, CGAH (6 sh [dead]); Sabugeiro, 29T 06149/44733, bases of low granite crags and walls near river, 1050 m, 2010.08.31, GAH & DTH P71, CGAH (1 sh); by N16 at 2 km NE. of Arrifana, D. Guarda, 29T PE59, hillside with much bare granitic rock, grasses, herbs and shrubs, few *Pinus* trees, *ca* 770 m, 1984.08.25, DTH, MH & MBS, Det. DTH 2011.10.03, NMW.Z.1993.052.10381 (47 sh [dead]); **Beira Baixa,** by N339 S. of Cântaro Raso (*ca* 2 km E. of Torre summit), 29T 06195/44642, slopes with granitic crags and boulders, *ca* 1725 m, 2010.07.02, GAH P52, CGAH (9 sh [dead, 3 ad, 6 imm]).

***P. martigena,* Morocco, Er Rif,** by S304 at *ca* 6 km NE. of Taounate, 34º34′N., 4º36′W., sandstone crags by road, grasses and herbs on ledges, *ca* 370 m, 1984.07.20, DTH, MH & MBS, Det. DTH 2011.10.03, NMW.Z.1993.051.00090 (24 sh [23 dead, 1 live: bod listed on label but not found in collection]); **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, Conf. DTH 2011.10.03, CGAH (5 sh & bod, 4 spm); **Prov. Málaga,** by C339 at *ca* 8 km NW. of S. Pedro de Alcántara, UF2, rocky (shale) road cutting with partial shade from low bushes, *Quercus* trees nearby, *ca* 525 m, 1984.07.11, DTH, MH & MBS, Det. DTH 2011.10.03, NMW.Z.1993.052.10075 (5 sh [dead]); ***P. martigena?*, Spain, Prov. Málaga,** by C339 at 20 km SE. of Ronda, UF1, rocky limestone slopes, partly shaded by *Pinus*, with grass, herbs and few bushes, *ca* 1135 m, 1984.07.11, DTH, MH & MBS, Det. DTH 2011.10.03, NMW.Z.1993.052.10082 (1 sh [dead, imm]).

***P. monoglandulosa* sp. nov., Portugal, Beira Baixa,** by Rio Zêzere and N238 ENE. of Dornes, 29S 05644/44037, steep rocky (slate) roadside cuttings near reservoir, 143 m, 2011.08.05, GAH & DTH P177, CGAH (36 sh [dead]); Portas de Almorão (NE. of Foz do Cobrão), 29S 060681/439902, rocky (quartzite) slopes with patchy scrub and herbs, 275 m, 2010.12.19, GAH & DTH P86, CGAH (2 sh & bod, 26 sh [dead]: paratypes); *ca* 2 km W. of Vila Velha de Ródão, 29S 061177/439016, rocky (quartzite) ridge and slopes with patchy low scrub and herbs, 321 m, 2010.12.19, GAH & DTH P87, CGAH (26 sh & bod, 93 sh [dead]: paratypes), NHMUK (1 sh & bod: holotype); W. edge of Castelo Novo, 29T 06276/44374, rocky granitic slopes with patchy herbs and low scrub, *ca* 725 m, 2010.06.08, GAH & DTH P50, CGAH (19 sh [dead]: paratypes); 0.5 km W. of Castelo Novo, 29T 062769/443741, rocky granitic slopes with patchy herbs and low bushes, *ca* 705 m, 2010.12.17, GAH & DTH P84, CGAH (15 sh & bod [7 ad., 8 imm.], 8 sh [dead]: paratypes); 1 km E. of Moreirinha (3 km N. of Monsanto), 29T 066166/443619, flat and sloping granitic rocks with sparse low bushes and herbs, 505 m, 2011.01.15, GAH & DTH P101, CGAH (10 sh & bod, 1 sh: paratypes); just NE. of Cidral (NNE. of Monsanto), 29T 066166/443619, low granitic rocks with sparse bushes and herbs, 518 m, 2011.03.10, GAH & DTH P135, CGAH (7 sh & bod, 10 sh [dead]: paratypes); Campo Frio (E. of Salvador), 29T 066329/443971, under quartzite boulder on open rocky ridge (sparse low vegetation and few *Pinus* saplings), 734 m, 2011.01.15, GAH & DTH P102, CGAH (1 sh [freshly dead]); **Spain, Prov. Cáceres,** just E. of Portuguese frontier above Rio Erges *ca* 2 km S. of Segura, 29S 067285/440956, rocky granitic slopes above river with patchy scrub, 206 m, 2012.05.06, GAH & DTH E244, CGAH (9 sh & bod, 31 spm, 11 sh [dead]).

***P. octoglandulosa* sp. nov., Portugal, Minho,** due S. of Várzea (Serra da Peneda), 29T 056521/463750, open heathy area on hilltop with much exposed mica-schist rock, sparse low *Ulex* and heathers, 619 m, 2011.08.29, GAH & DTH P189, CGAH (2 sh [dead]); N. edge of Peneda village, 29T 056447/464734, rocky granitic slope with old walls, patchy grasses and herbs, 688 m, 2011.08.29, GAH & DTH P187, CGAH (3 sh [live, imm], 4 sh [dead]); S. of Gavieira (Serra da Peneda), 29T 056234/464321, roadside bank and slope with granitic rocks, grasses and patchy scrub, 640 m, 2011.08.29, GAH & DTH P188, CGAH (2 sh [dead]); **Spain, Prov. Pontevedra,** just N. of PO255 at *ca* 2 km NW. of Piñeiro, 29T 054999/468206, granitic slopes with much exposed rock, patchy *Ulex* scrub and sparse short grassland, 550 m, 2011.08.28, GAH & DTH E184, CGAH (2 sh & bod [1 ad. & 1 imm], 7 sh: paratypes), NHMUK (1 sh & bod: holotype); *ca* 1 km N. of Porto de Moncelos (N. of A Cañiza), 29T 05578/46801, granitic slopes with much bare rock, patchy grasses, herbs and burnt *Ulex,* 758 m, 2011.08.28, GAH & DTH E185, CGAH (14 sh [dead]); just N. of Faro de Avión (NE. of

Prado), 29T 055960/468430, rocky granitic slope with patchy grassland and low scrub, 986 m, 2011.08.28, GAH & DTH E186, CGAH (2 sh [dead]).

***P. papillosa* sp. nov., Portugal, Alto Alentejo,** at summit of Pico de São Mamede, 30º19´N., 7º22´W., under boulders on slopes, *ca* 1020 m, 2001.05.28, GAH 2001/13, CGAH (5 spm, 2 sh & bod: paratypes); Pico de São Mamede, 29S 06413/43527, beneath boulders on sparsely vegetated N.-facing hillside near crags, *ca* 1015 m, 2007.05.15, GAH 2007/05, CGAH (7 spm [3 ad, 4 imm], 1 sh: paratypes), NHMUK (1 sh & bod: holotype); Pico de São Mamede, 29S 064132/435289, slopes of slaty/quartzite rock near outcrops, with patchy herbs, 1020 m, 2010.07.14, GAH & DTH P55, CGAH (6 spm, 24 sh: paratypes); **Trás-os-Montes e Alto Douro,** *ca* 5 km NW. of Montezinho (P.N. de Montezinho), 29T 068333/464830, rocky granitic slopes with patchy low bushes and bare rock, 1311 m, 2011.06.27, GAH & DTH P166, CGAH (6 sh [1ad, 5 imm] & 4 bod, 12 sh: paratypes); by NW. edge of Barragem de Serra Serrada, NNW. of Montezinho, 29T 068444/464854, rocky granitic slope with patchy low scrub, bare rock and few loose boulders, 1270 m, 2011.06.28, GAH & DTH P167, CGAH (3 sh & bod, 89 sh [dead]: paratypes); *ca* 5.5 km NW. of Montezinho (P.N. de Montezinho), 29T 068334/464904, rocky granitic slopes with patchy low scrub and bare rock, 1338 m, 2011.06.28, GAH & DTH P168, CGAH (9 sh & bod (4 ad, 5 imm), 17 sh [dead]: paratypes); *ca* 1.5 km N. of Montezinho (P.N. de Montezinho), 29T 06855/46468, slope with much bare rock (granitic, schistose) and patchy low bushes, recently burnt in parts, 1220 m, 2011.06.29, GAH & DTH P169, CGAH (13 sh dead [1 live imm, 12 dead]: paratypes); **Spain, Prov. Zamora,** by N631 at Embalse Nostra Senora de Argavanzal (S. of Rionegro del Puente), 29T 072914/465153, slopes above reservoir edge with outcrops of metamorphic rock, patchy grassland, bushes and saplings, 797 m, 2011.10.17, GAH & DTH E216, CGAH (5 sh & bod [2 ad, 3 imm], 23 sh [dead]: paratypes); just N. of N122 just SW. of Cerezal de Aliste, 29T 074522/460772, low outcrops of granitic rock (with few patchy herbs) in grassland with sparse low *Quercus* trees and scrub, 770 m, 2011.10.17, GAH & DTH E217, CGAH (1 sh & bod, 1 sh [dead]: paratypes).

***P. platylasia*, Portugal, Beira Litoral,** Leiria: Encosta Norte do Castelo, 29S ND19, 2011.09.24, RCM, Det. DTH 2011.05.25, CRCM (16 sh [14 ad incl. 5 fresh, 9 old; 2 imm fresh])**; above Grutas de Alvados (W. of Mira de Aire), 29S 05220/43768, limestone rocks and scrub-covered slopes, *ca* 535 m, 2009.11.18, GAH P14, CGAH (2 sh & bod, 14 sh [dead]); *ca* 1.5 km SE. of Almagreira, 29S 05304/44267, *Olea* grove with grassland, 40 m, 2012.07.30, DTH P256, CGAH (2 sh & bod, 3 sh [dead]); Pombal Castle, Pombal, 29S NE3218, limestone soil, 2008.04.24, ÁDO (10), CGAH (1 spm, 2 sh & bod, 2 sh [dead]); Pombal: junto ao Castelo de Pombal, 29S NE31, 2011.08.13, RCM, Det. DTH 2011.05.25, CRCM (15 sh [13 ad, 2 imm]); Serra de Sicó (summit area), 29S 053909/441909, rocky limestone slopes with patchy low scrub and grassland, 548 m, 2011.01.13, GAH P98, CGAH (2 sh & bod, 4 sh [dead]); Serra de Sicó (summit area), 29S 05390/44191, rocky limestone slopes with patchy low scrub, 542 m, 2011.02.24, GAH & DTH P132, CGAH (2 spm, 4 sh [dead]); SE. of Almoster, 29S 05497/44096, scrub covered limestone hillside with low walls and scree, 2009.12.09, GAH P18, CGAH (3 sh [dead]); *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 near dried river, *ca* 190 m, 2010.09.26, GAH & DTH P73d, CGAH (2 sh [dead]); by IC8 just NE. of Ansião, 29S 054915/441926, sparse grassland on road verge/ditch over limestone, 210 m, 2011.04.29, GAH & DTH P141, CGAH (2 sh [dead]); Alvaiázere: Vale da Couda, Almoster, 29S NE41, 2011.08.13, RCM, Det. DTH 2011.05.25, CRCM (5 sh [ad, 1 fresh, 4 old]); *ca* 1 km SW. of Ateanha village (E. of Alvorge), 29S 05498/44262, low limestone walls in small fields/*Olea* groves, 310 m, 2010.05.29, DTH P46, CGAH (1 sh & bod, 9 sh [dead]); Capela de Nossa Senhora de Covões (near Covões), 29S 05511/44073, on low limestone rock and on trunks of *Olea,* 2008.09.01, GAH 2008/P8, CGAH (2 sh & bod, 7 spm, 9 sh [dead]); by Capela de Nossa Senhora de Covões (near Covões), 29S 05511/44070, low limestone boulders in managed ‘park’ area, *ca* 345 m, 2009.11.23, GAH P16, CGAH (2 sh & bod, 12 sh [dead]); Conimbriga (near Roman ruins), 29T 05434/44388, walls of building and trunks of trees in open grassy area, *ca* 100 m, 2010.02.23, GAH & DTH P25, CGAH (5 sh & bod [4 ad, 1 imm]); by Ruínas de Conimbriga, 29T 054352/443878, on bark of *Olea* trees in open olive-grove with grassland and herbs beneath, *ca* 100 m, 2010.04.27, GAH & DTH P39, CGAH

(2 spm, 31 sh & bod); Castelo do Rabaçal, 29T 05489/44309, on bark of *Olea* trees in open olive-grove with grassland and herbs beneath, *ca* 315 m, 2010.04.27, GAH & DTH P40, CGAH (10 sh & bod); **Estremadura,** Serra de Montejunto, 29S 04937/43365, on bare face of steep limestone crag, *ca* 500 m, 2010.04.19, GAH P32, CGAH (11 sh [dead], 2 sh & bod [killed 2011.02.28]); Serra de Montejunto, 29S 049299/433625, on limestone bank with patchy grassland and herbs, *ca* 445 m, 2010.04.19, DTH P33, CGAH (8 sh [dead]); Serra de Montejunto (near summit), 29S 049487/433620, walls of ruins, limestone rocks & slopes, *ca* 651 m, 2012.03.24, DTH & GAH P237 & RCM, CGAH (74 sh & bod, 10 spm, 31 sh [dead]); Montejunto: junto à Capela de Nossa Senhora das Neves, 29S MD93, sobre musgos, 2011.10.28, RCM, Det. DTH 2011.05.25, CRCM (62 sh [55 ad incl. 53 fresh, 2 old; 7 fresh imm])**; Cadaval: junto ao Centro de Interpretação Ambiental da Serra de Montejunto, Quinta da Serra, Serra de Montejunto, 29S MD93, 2011.05.28, RCM, Det. DTH 2011.05.25, CRCM (28 sh [17 ad, 11 imm])**; junto à Estrada de acesso à Serra de Montejunto, 29S MD93, solo, 2011.09.03, RCM, Det. DTH 2011.05.25, CRCM (4 sh [old]); Alcoa River Springs, Alcobaça, 29S ND0576, limestone soil, 2009.05.08, ÁDO (12), CGAH (1 sh & bod); source of Alcoa River at Chiqueda de Cima (E. of Alcobaça), 29S 050476/437631, rocky limestone slopes with saplings, scrub, low crags and walls, 54 m, 2012.03.24, GAH & DTH P238 & RCM, CGAH (2 sh & bod, 6 sh [dead]); Serro Ventoso, Porto de Mós, 29S ND1479, limestone soil, 2008.02.12, ÁDO (13), CGAH (1 spm, 2 sh & bod); by N243 near Alcaria, 29S 05177/43799, concrete walls by open ground with grasses and herbs, *ca* 215 m, 2010.05.02, GAH & DTH P42, CGAH (7 sh & bod); Fórnea (SE. of Alcaria), 29S 05170/43789, limestone crags, screes and slopes, patchy scrub, *ca* 275 m, 2010.05.02, GAH & DTH P43, CGAH (1 sh & bod, 24 sh [dead])**; 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 P59, CGAH (20 sh & bod, 61 sh [dead]); *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 P62, CGAH (7 spm, 10 sh [dead]); Porto de Mós: junto à Estrada de Serro Ventoso para Mendiga (à saída de Serro Ventoso), 29S ND17, debaixo de pedras, 2011.04.09, RCM, Det. DTH 2011.05.25, CRCM (35 sh [4 ad, 31 imm]); Porto de Mós: junto à Lagoa Grande, Arrimal, 29S ND17, debaixo de pedras, 2011.04.09, RCM, Det. DTH 2011.05.25, CRCM (12 sh); Porto de Mós Castle, Porto de Mós, 29S ND1583, limestone soil, 2009.05.08, ÁDO (11), CGAH (5 spm, 3 sh & bod); Parque Verde da Vila, at Porto de Mós, 29S 05154/43831, public park with old trees, damp lawns and walls, 130 m, 2011.10.09, GAH, DTH P207 & RCM, not kept (1 sh [ad]); *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 (1 sh & bod, 10 sh [dead]); *ca* 1 km SE. of Livramento, 29S 05170/43809, low limestone rocks in rough grassland, 247 m, 2010.07.30, GAH & DTH P63, CGAH (4 spm, 31 sh [dead]); *ca* 0.5 km SE. of Livramento, 29S 05170/43809, rocky limestone slope with grassland and scrub, 238 m, 2011.03.22, GAH P136, CGAH (2 sh & bod, 24 sh [dead, 3 ad, 21 imm]); **Estremadura & Ribatejo,** *ca* 4 km NNW. of Serra de Santo António, 29S 05223/43759, grassland, limestone rocks and low walls, 494 m, 2012.02.18, GAH, DTH P227 & RCM, CGAH (6 sh & bod, 64 sh [dead]); **Ribatejo,** by N1 at 3 km NW. of Rio Maior, 29S ND05, limestone slopes with quarried rocks, bushes locally, elsewhere grasses and herbs, *ca* 130 m, 1984.08.24, DTH, MH & MBS, Det. DTH 2011.10.03, NMW.Z.1993.052.10374 (2 sh [dead]); Rio Maior: São João da Ribeira (junto a uma fonte), 29S ND14, muros and sobre ervas, 2011.04.02, RCM, Det. DTH 2011.05.25, CRCM (2 sh); SE. of Moitas Venda, 29S 05311/43717, limestone crags and rocky slopes with scrub, *ca* 195 m, 2010.05.02, GAH & DTH P41, CGAH (7 sh).

***P. ponentina*, 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 P124, CGAH (1 sh & bod); **Alto Alentejo,** by Ribeira de Sôr, SE. of Comenda, 29S 000622/435974, roadside verges with grasses and herbs, some near concrete of bridge wall, *ca* 229 m, 2010.07.14, GAH & DTH P57, CGAH (6 sh [dead]); by Ribeira de Sôr, *ca* 4 km NW. of Monte da Pedra (NW. of Crato), 29S 06062/43597, concrete walls of bridge near small river, in dry rocky area, 225 m, 2007.05.15, GAH 2007/07, CGAH (32 sh & bod); by Ribeira de Sôr, *ca* 4 km NW. of Monte da Pedra (NW. of Crato), 39º23´N., 7º46´W., granite rocks with sparse scrub near river, 2001.05.30, GAH, CGAH (6 sh); by N370 SW. of Nossa Senhora da Graça do Divor, 29S 058567/427601, open roadside verge with short and long herbs and grasses, 357 m, 2011.01.27, GAH & DTH P103, CGAH (21 sh [8 live imm, 13 dead]); just N. of Barragem da Póvoa, 29S 062432/437100, low exposures of granitic rock in open grassland area in valley, 286 m, 2012.02.05, GAH & DTH P225, CGAH (31 sh [dead]); by N246–1 just SW. of Portagem, 29S 063882/436024, widespread, in grasses and *Populus* litter at base of old tree and at foot of concrete wall and on bark 1–2 m up on *Populus*, 2010.07.14, GAH & DTH P56, CGAH (14 sh & bod, 53 sh [dead])**; Montemor-o-Novo (by the castle), 29S NC67, 2012.04.28, RCM, Conf. DTH 2012.04.30, CRCM; **Baixo Alentejo,** by N256.1 at São Leonardo, E. of Mourão, 29S PC520/494, unshaded concrete walls around disused customs post, with low grasses and herbs, few trees, 242 m, 2012.04.09, GAH P241, CGAH (3 sh & bod [imm], 16 sh [dead]); **Beira Alta,** W. edge of Moinhos de Aveia (W. of Alverca da Beira), 29T 06518/45071, rocky granitic slopes with patchy low scrub, 554 m, 2011.06.26, GAH P165, CGAH (2 sh & bod [ad], 6 sh [dead, imm]); Sabugal: Aldeia da Ponte (margem esquerda do Rio Cesarão), 29T PE87, sobre muros, 2011.06.23, RCM, Det. DTH 2011.05.25, CRCM (1 sh); **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 P100, CGAH (1 sh & bod, 3 sh [dead]); **Douro Litoral,** just E. of São Félix da Marinha, 29T 05325/45427, on wall at edge of woodland, *ca* 100 m, 2007.05.20, GAH 2007/18, CGAH (13 sh & bod); Granja, Gaia, 29T NF2043, granitic soil, 2007.03.21, ÁDO (6), CGAH (2 spm, 2 sh & bod); Miramar, Gaia, 29T NF2946, granitic soil, 2008.09.13, ÁDO (5), CGAH (7 spm, 4 sh & bod); Francelos, Gaia, 29T NF2947, on wall facing E. (between road and agricultural field), 20 m, 2010.10.25, ÁDO [49], CGAH (4 spm, 3 sh & bod [ad]); **Estremadura,** 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 P130, CGAH (1 sh [live]); Serra da Arrábida, 29S 050117/425874, base of S.-facing limestone road-cutting, with herbs and grasses, 131 m, 2011.02.12, GAH & DTH P131, CGAH (1 sh [dead]); Serra da Arrábida, 29S 05020/42602, N.- and S.-facing rocky limestone slopes with patches of scrub, 388 m, 2011.02.12, GAH & DTH P129, CGAH (1 sh [dead]); Serra da Arrábida, 29S 05032/42604, on exposed boulders on limestone pavement, 300–350 m, 2007.05.17, GAH 2007/11B, CGAH (31 sh & bod); Serra da Arrábida, 29S 05032/42604, high on rocky S.-facing limestone slope with patchy low scrub, 351 m, 2011.02.12, GAH & DTH P128, CGAH (14 sh & bod, 8 sh [dead]); Serra da Arrábida, 29S 05033/42604, low limestone rocks with patchy cover of low bushes on hill top, *ca* 350 m, 2010.04.12, GAH P30, CGAH (22 sh & bod; 2 spm [killed 2010.09.26]); Setúbal: Arrábida (Convento), 29S MC95, 2011.07.05, RCM, Det. DTH 2011.05.25, CRCM (6 sh [2 near fresh, 4 old]); Setúbal: Portinho da Arrábida, 29S NC05, 2010.12.11, RCM, Det. DTH 2011.05.25, CRCM (2 sh); *ca* 5 km NE. of Portinho da Arrábida, 29S NC06, rocky limestone slopes with low crags, partly shaded by tall maquis scrub, partly open with herbs, *ca* 310 m, 1984.08.24, DTH, MH & MBS, Conf. DTH 2011.10.03, NMW.Z.1993.052.10341 (2 sh [dead, old]); by school on Rua Mártires do Tarrafal, Leiria, 29S 05161/43996, aestivating on concrete wall around garden of school, 94 m, 2011.10.09, GAH, DTH P208 & RCM, CGAH (7 sh & bod [ad]); beside Caminho da Fonte, Atalaia, Colares, Sintra, 29S MC59 (38º46′50.6″N., 9º28′32.9″W.), found alive on walls, 2012.01.21, RCM, CGAH (7 sh & bod); 7 km NE. of Sesimbra, 29S MC95, limestone crags and slopes by river, partly shaded by *Hedera*, trees and bushes, elsewhere grasses and herbs, *ca* 80 m, 1984.08.23, DTH, MH & MBS, Conf. DTH 2011.10.03, NMW.Z.1993.052.10310 (4 sh [dead]); 6 km S. of Vila Nogueira de Azeitão, 29S MC95, limestone crags, with grasses and herbs on ledges, bushes nearby, *ca* 230 m, 1984.08.24, DTH, MH & MBS, Conf. DTH 2011.10.03, NMW.Z.1993.052.10326 (1 sh [dead]); Mafra: Picanceira (junto ao Lavadouro), Sto. Isidoro, 29S MD61, 2011.04.30, RCM, Det. DTH 2011.05.25, CRCM (85 sh [74 ad, 11 imm])**; Mafra: Picanceira, Sto. Isidoro, 29S MD61, 2011.10.25, RCM, Det. DTH 2011.05.25, CRCM (25 sh [20 ad, 5 imm]); Mafra: Carapinheira, 29S MD70, 2010.11.27, RCM, Det. DTH 2011.05.25, CRCM (1 sh); Mafra: Abrunheira, 29S MD70, 2010.11.27, RCM, Det. DTH 2011.05.25, CRCM (5 sh [4 ad, 1 imm, all old]); Mafra: Cheleiros (margem esq. do Rio Lizandro), 29S MD70, 2011.02.20, RCM, Det. DTH 2011.05.25, CRCM (11 sh [10 ad, 1 imm])**; Mafra: Salgados, 29S MD71, debaixo de pequenas pedras, 2010.11.26, RCM, Det. DTH 2011.05.25, CRCM (10 sh [6 ad, 4 imm])**; Mafra: entre Salgados e A-Da-Perra, 29S MD71, 2010.12.27, RCM, Det. DTH 2011.05.25, CRCM (12 sh [ad, 11 fresh, 1 old]); Mafra: junto à margem direita do Rio do Cuco, 29S MD71, 2011.06.10, RCM, Det. DTH 2011.05.25, CRCM (5 sh [old]); Torres Vedras: Castelo de Torres Vedras, 29S MD72, 2010.11.06, RCM, Det. DTH 2011.05.25, CRCM (60 sh [ad, 6 fresh, 54 old])**; Torres Vedras: Castro do Zambujal, Ribeira dos Pedrulhos, 29S MD72, sobre ervas, 2010.11.13, RCM, Det. DTH 2011.05.25, CRCM (42 sh [41 ad incl. 35 fresh, 6 old; 1 imm fresh]); Torres Vedras: Estrada da Serra da Vila (junto à Escola EB3 São Gonçalo), 29S MD72, junto à margem esquerda de um pequeno riacho, 2010.12.01, RCM, Det. DTH 2011.05.25, CRCM (2 sh [nearly ad]); Torres Vedras: Miradouro do Forte de São Vicente, 29S MD72, 2011.04.21, RCM, Det. DTH 2011.05.25, CRCM (60 sh [57 ad, incl. 53 fresh, 4 old; 3 imm fresh])**; Torres Vedras: Termas dos Cucos, 29S MD72, 2011.03.19, RCM, Det. DTH 2011.05.25, CRCM (43 sh [39 ad incl. 37 fresh, 2 old; 4 imm fresh])**; Termas dos Cucos, Torres Vedras, 29S 047917/432686, park with old trees, buildings and lawns (on concrete flower pots), 43 m, 2012.07.18, DTH, GAH, RCM P254, CGAH (1 sh & bod, 2 sh [dead]); Torres Vedras: EN 115–2 (Cadaval-Maxial-Ermegeira-T. Vedras), km 11.6, 29S MD83, 2010.12.26, RCM, Det. DTH 2011.05.25, CRCM (3 sh [1 ad, 2 imm]); Peniche: Albufeira de São Domingos, Atouguia da Baleia, 29S MD75, 2011.04.30, RCM, Det. DTH 2011.05.25, CRCM (3 sh); Ruínas de Salvador (junto ao cemitério) Estrada Cabêda – Sobral de Monte Agraço – Sobral de Monte Agraço, 29S MD81, Debaixo de pedras, 2010.12.04, RCM, Det. DTH 2011.05.25, CRCM (11 sh [8 ad, 3 imm]); Bombarral: Qta. dos Loridos, Carvalhal, 29S MD84, 2010.10.09, RCM, Det. DTH 2011.05.25, CRCM (7 sh); Óbidos: Parque da Vila, 29S MD85, 2011.01.08, RCM, Det. DTH 2011.05.25, CRCM (3 sh); Óbidos: Estrada 8 de Dezembro (da Estrada Real para Trás do Outeiro), 29S MD85, no solo, 2011.10.25, RCM, Det. DTH 2011.05.25, CRCM (7 sh [6 ad old; 1 imm fresh])**; Cadaval: na Estrada de Cercal, para Alcoentre (à saída de Cercal), 29S ND04, sobre muros, 2011.02.12, RCM, Det. DTH 2011.05.25, CRCM (15 sh [10 ad, 5 imm]); Castelo de Alcobaça, Alcobaça, 39º33′2.7″N., 8º58′57.4″W., under stones, 2012.05.26, RCM, Conf. DTH 2012.07.10, CGAH (3 sh & bod, 4 spm), CRCM (9 spm); Cabo da Roca, 29S 04568/42926, dry bank by road edge near car park, with sparse low herbs and grasses, 136 m, 2012.07.17, DTH, GAH, RCM P250, Conf. DTH 2012.07.20, not kept (2 dead sh [1 ad, 1 imm]); 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, GAH, RCM P251, CGAH (7 sh [dead]); **Ribatejo,** R.N. de Paúl de Boquilobo (SW. of Golegã), 29S 05403/43622, dry banks with grassland and *Olea*, *Eucalyptus* grove, 30 m, 2011.07.27, GAH & DTH P173, CGAH (15 sh & bod [8 ad, 7 imm]); Rio Maior: junto ao Olho de Água de Alcobertas, 29S ND06, sobre muros, 2011.02.12, RCM, Det. DTH 2011.05.25, CRCM (6 sh [3 ad, 3 imm]); Rio Maior: junto à Estrada de Alcobertas para Casais Monizes, Alcobertas, 29S ND06, debaixo de pedras, 2011.02.12, RCM, Det. DTH 2011.05.25, CRCM (9 sh [7 ad, 2 imm]); ***P. ponentina?*, Portugal, Estremadura,** Mafra: Salgados, 29S MD71, 2010.04.26, RCM, Det. DTH 2011.05.25, CRCM (2 sh [imm]).

***P. revelata*, France, 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 F206, CGAH (12 sh & bod, 10 spm, 20 sh [dead]); **Maine-et-Loire,** N. edge of D54 at *ca* 4 km E. of Angevine, 30T 067447/524549, S.-facing, rocky, sandstone bank above road-side ditch, below vineyard, with patchy low herbs and grasses, 63 m, 2011.09.23, GAH & DTH F198, CGAH (49 sh & bod, 5 spm [imm], 42 sh [dead]); **Morbihan,** by Fort de Penthièvre (*ca* 4 km N. of Quiberon), 30T 048977/526557, steep sandy slope above beach, with short herb-rich grassland, 12 m, 2011.09.24, GAH & DTH F203, CGAH (23 sh & bod, 5 spm [imm], 126 sh [dead]); 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 F205, CGAH (15 sh & bod, 6 spm [imm], 27 sh [dead]); **Portugal, Beira Litoral,** Ilha do Picoto, Avô, 29T 059294/446110, grassland and low granitic rocks near river, mainly shaded by *Acacia* and other young trees, 221 m, 2011.11.27, GAH & DTH P222, CGAH (47 sh & bod, 10 spm [imm])**; 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 P97, CGAH (35 sh & bod, 8 sh [dead]); Praia da Tocha, 29T 05134/44647, sand dunes with patches of low bushes, 14 m, 2010.11.18, GAH & DTH P83, CGAH (44 sh & bod)**; just S. of Praia de Mira, 29T 05171/44772, bark crevices and soil at base of *Populus* and *Eucalyptus* trees in park by lake, 26 m, 2012.07.05, DTH, GAH, RCM P247, CGAH (74 sh & bod, 1 spm [imm], 9 sh [dead]); by Paúl do Taipal near Montemor-o-Velho, 29T 05271/44481, limestone quarry with patches of short vegetation, 45 m, 2011.01.09, GAH P96, CGAH (41 sh & bod); Penedo da Saudade, Coimbra, 29T NE4950, limestone soil, 2010.02.02, ÁDO (8), CGAH (1 sh & bod); Santa Cruz Garden, Coimbra, 29T NE4951, limestone soil, 2010.03.22, ÁDO (9), CGAH (1 sh & bod); Cais do Puchadouro, 29T NF3120, sand, 2009.11.20, ÁDO (7), CGAH (2 sh & bod, 2 spm); **Douro Litoral,** Serralves Farm, Porto, 29T NF2856, granitic soil, 2007.03.13, ÁDO (3), CGAH (1 sh [live]); Leça da Palmeira, 29T NF2660, granitic soil, 2007.01.31, ÁDO (1), CGAH (4 sh & bod, 3 spm); Ribeira do Abade, Gondomar, 29T NF3654, granitic soil, 2008.01.18, ÁDO (4), CGAH (1 sh & bod); Botanical Garden, Porto, 29T NF3056, granitic soil, 2010.01.23, ÁDO (2), CGAH (2 sh & bod); left bank of Rio Ave near the railway station of Santo Tirso, Santo Tirso, 29T NF4477, on a bridge concrete wall facing SE., 35 m, 2010.12.12, ÁDO [50], CGAH (3 sh & bod, 4 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 P91, CGAH (3 sh & bod, 27 sh [dead]); just N. of Praia da Vieira, 29S 050275/441459, sand dunes with patchy low scrub, 7 m, 2010.12.25, GAH & DTH P93, CGAH (13 sh & bod, 82 sh [dead]); **Minho,** Ofir (SE. of Esposende), 29T 05175/45972, low sand dunes with patchy bushes, herbs and grassland, 9 m, 2011.08.30, GAH & DTH P190, CGAH (16 sh & bod, 86 sh [dead]); **Spain, Prov. Burgos,** by BU601 at *ca* 4 km SW. of Villadiego, 30T 041328/470532, dry grassland on road verge and low banks, with herbs and bare soil patches, 856 m, 2011.10.15, GAH & DTH E210, CGAH (20 sh & bod, 123 sh [dead]); **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 *Pinus* wood, 48 m, 2011.08.27, GAH & DTH E183, CGAH (26 sh [dead]); **Prov. León,** NW. of Almázcara, 29T 07035/47203, low banks between grassland and road, above shallow ditch, with patchy grasses and herbs, bushes locally, 672 m, 2011.10.16, GAH & DTH E212, CGAH (21 sh [dead]); by N536 at *ca* 1 km S. of Salas de la Ribera, 29T 06796/46993, low roadside cutting/crag/scree of slaty rock with sparse low grasses and herbs (bushes above), 393 m, 2011.10.16, GAH & DTH E213, CGAH (3 sh & bod, 44 sh [dead]); by N120 at 1 km S. of Salas de la Ribero, PH4, dry crag of slaty rock above road, with low herbs on ledges, *ca* 370 m, 1983.08.09, DTH & MBS, Det. DTH 2011.10.03, NMW.Z.1993.052.07710 (2 sh); **Prov. Ourense,** by OU533 near Cemiterio at *ca* 2 km S. of Santa Cruz, 29T 065406/468446, granitic rocks and slopes by road, with sparse herbs and few bushes, 648 m, 2011.10.17, GAH & DTH E215, CGAH (20 sh [dead]); **Prov. Palencia,** by P620 at *ca* 0.5 km NW. of Mave, 30T 03950/47330, rocky (sandstone and shale) slope with patchy grasses and herbs, few bushes, 890 m, 2011.10.15, GAH & DTH E211, CGAH (152 sh [dead]); **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 E182, CGAH (3 sh & bod, 17 sh [dead]); ***P. revelata?*, Spain, Prov. Ourense,** by OU533 at *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 E214, CGAH (10 sh [dead]).

***P. rosai*, Portugal, Algarve,** *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 P125, CGAH (3 sh [1 live, 2 dead]); 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 P124, CGAH (6 sh [4 live imm, 2 dead]); W. of N120 at 0.5 km SSE. of church at Bensafrim, D. Faro, 29S NB21, limestone crags and rocky slopes, partly shaded by bushes, elsewhere grasses and herbs, *ca* 50 m, 1984.08.23, DTH, MH & MBS, Det. DTH 2011.10.03, NMW.Z.1993.052.10280 (18 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 P121, CGAH (1 spm, 1 sh [live]); 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 P104, CGAH (3 sh [1 ad, 2 imm]); E. end of Rocha da Pena, 29S 058033/412344, nearly flat ground with patchy *Cistus* scrub and scattered low limestone rocks, 462 m, 2011.01.31, GAH & DTH P112, CGAH (17 sh [5 live imm, 12 dead]); by N2 at 4.5 km NW. along road from Ameixial, 29S 058988/413885, roadside cutting with steep slaty/shaly rock and patchy low herbs and grasses, 265 m, 2011.01.30, GAH & DTH P110, CGAH (2 sh & bod, 5 sh); by N124 W. of Quintã, 29S 059037/412121, road cuttings in slaty/schist rock, with sparse *Cistus*, grasses and herbs, 211 m, 2011.01.31, GAH & DTH P113, CGAH (4 sh [live, imm]); *ca* 3 km NNW. of Moncarapacho (just S. of A22), 29S 060695/410771, rocky limestone hillslope with patchy bushes, 131 m, 2011.02.04, GAH & DTH P118, CGAH (6 spm, 6 sh [3 live, 3 dead]); 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 P119, CGAH (3 spm, 3 sh [imm]; 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 P107, CGAH (1 sh [ad]); 5 km E. of Sta. Catarina, D. Faro, 29S PB11, rocky limestone hillslope with cover of low bushes, grasses and herbs, *ca* 120 m, 1984.08.22, DTH, MH & MBS, Det. DTH 2011.10.03, NMW.Z.1993.052.10228 (3 sh); **Alto Alentejo,** S. edge of Santiago do Cacém, 29S 052721/420649, limestone slope above quarry with short grasses and herbs, scattered loose stones, 239 m, 2011.02.08, GAH & DTH P126, CGAH (1 spm, 4 sh [live imm]); **Baixo Alentejo,** by N2 at *ca* 1.5 km SSE. of Dogueno, 29S 059045/414242, unshaded road cuttings with exposed shale, sparse low vegetation, 338 m, 2011.01.30, GAH & DTH P109, CGAH (1 sh & bod, 1 spm, 17 sh [mainly live imm]); by Rio Murtega on road to Noudar (N. of Barrancos), 29S PC7662/2455, rocky river bank (slaty) with patchy scrub and trees, springs locally, 196 m, 2012.04.10, GAH & DTH P243, CGAH (2 spm, 5 sh [dead, 1 ad, 4 imm]); **Beira Baixa,** 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 P88, CGAH (1 spm, 1 shell & bod, 3 bod [shells with P94]); by N240 on W. bank of Rio Pônsul, W. of Ladoeiro, 29S 06423/44133, steep S.-facing rocky (slaty) bank above road and river, 195 m, 2010.12.27, GAH & DTH P94, CGAH (11 sh & 1 bod [other bod with P88]); **Beira Litoral,** 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 P133, CGAH (3 sh [dead]); **Estremadura,** Castelo de São Filipe, Setúbal, 29S NC06, junto à entrada de acesso ao Castelo ... antes da entrada da muralha externa, 2011.09.10, RCM, Det. DTH 2011.10.12, CRCM (1 sh [no hairs, but fairly fresh]).

***P. sordulenta*, Algeria,** by N3 at 1.5 km NNW. of El Kantara (N. of Biskra), 35°14′N., 5°42′E., limestone crags and slopes near gorge, scanty herbs on ledges, *ca* 510 m, 1984.07.31, DTH, MH & MBS 1984.237.12, Conf. DTH 2011.10.04, NMW.Z.1993.051.00089 (50 sh); 7 km NW. of Batna (Mts. de Belezma), 35°35′N., 6°07E., limestone crags and slopes, with patchy cover of shrubs (*Juniperus*, evergreen *Quercus*) and herbs on ledges, *ca* 1200 m, 1984.07.31, DTH, MH & MBS 1984.241.9, Conf. DTH 2011.10.04, NMW.Z.1993.051.00098 (2 sh); by N9 at *ca* 4 km SE. of Amoucha (N. of Sétif), 36°21′N., 5°25′E., limestone crags and slopes, cover of grasses and herbs, locally shrubs and saplings, *ca* 940 m, 1984.08.01, DTH, MH & MBS 1984.251.10, Conf. DTH 2011.10.04, NMW.Z.1993.051.00096 (6 sh); SW. slopes of Djebel Babor (32 km due N. of Sétif), 36°29′N., 5°28′E., limestone/shale slope with low crags, grasses and herbs, with patches of *Juniperus*, *ca* 1040 m, 1984.08.01, DTH, MH & MBS 1984.252.7, Conf. DTH 2011.10.04, NMW.Z.1993.051.00092 (1 sh); *ca* 1 km SE. of Col de Telmet (11 km WNW. of Batna), 35°35′N., 6°04′E., sandstone crags and slopes, partly shaded by scrub of *Juniperus* and evergreen *Quercus*, grass tussocks, *ca* 1570 m, 1984.07.31, DTH, MH & MBS 1984.242.6, Conf. DTH 2011.10.04, NMW.Z.1993.051.00097 (3 sh); by N3 at 9 km NE. of El Kantara (N. of Biskra), 35°17′N., 5°47′E., rocky limestone slope with scattered patches of herbs, perhaps subfossil shells from head, *ca* 585 m, 1984.07.31, DTH, MH & MBS 1984.238.8, Conf. DTH 2011.10.04, NMW.Z.1993.051.00095 (4 sh [old]); Gorges de Beni Amrane by N5 at 6 km NW. of Lakhdaria (SE. of Alger), 36°36′N., 3°58′E., crags and rocky slopes (limestone and conglomerate) in gorge, partly shaded by low trees, bushes, herbs and grasses, *ca* 130 m, 1984.08.12, DTH, MH & MBS 1984.338.13, Conf. DTH 2011.10.04, NMW.Z.1993.051.00091 (12 sh); by N15 at *ca* 4 km N. of Col de Tirourda (ENE.

of Bouira), 36º31′N., 4º21′E., limestone crags and rocky slopes, patches of grasses and herbs, few low bushes, *ca* 1260 m, 1984.08.10, DTH, MH & MBS 1984.325.5, Det. DTH 2011.10.04, NMW.Z.1993.051.00094 (4 sh); 2 km W. of Col de Telmet (14 km WNW. of Batna), 35º36′N., 6º03′E., shady stream gully on steep hillside, sandstone rock exposed, shaded by *Ilex*, evergreen *Quercus* and few *Juniperus*, *ca* 1420 m, 1984.07.31, DTH, MH & MBS 1984.243.7, Det. DTH 2011.10.04, NMW.Z.1993.051.00093 (3 sh).

***P. subvirescens*, France, Maine-et-Loire,** *ca* 1 km N. of Denée, 30T 068066/525042, sandstone crags and banks with patchy bare rock, scrub and areas of sparse low herbs and grasses, 22 m, 2011.09.23, GAH & DTH F199, CGAH (27 spm, 38 sh & bod, 108 sh); **Great Britain, East Cornwall,** NW. of Melbur, UK grid reference SW916554, sparsely vegetated china-clay spoil, 1999.02.16, GAH, CGAH (2 sh); NW. of Melbur, SW916556, open vegetation near edge of low *Ulex* scrub on china-clay spoil, 1999.02.16, GAH, CGAH (1 sh); S. of Treviscoe, SW941546, clayey bank with short rough grassland and *Rumex obtusifolius* L., 1999.04.03, GAH, CGAH (2 sh); S. of Treviscoe, SW944551, grassy slope at edge of china-clay quarry, 1999.07.01, GAH, CGAH (1 sh); SE. of Roche, SW977582, short grassy vegetation on china-clay spoil-tip, *ca* 247 m, 1999.07.01, GAH, CGAH (19 sh); NNE. of St. Neot, SX197708, sparsely vegetated china-clay spoil, 1999.06.01, GAH, CGAH (3 sh); **South Devon,** Blackstone Point, S. of Dartmouth, SX888495, short turf and herbs on slope of sea-cliff [igneous rock], 1982.06.13, DTH, Conf. DTH 2011.10.03, NMW.Z.1993.052.06956 (5 sh [label states 6 sh & bod, but 6th shell & body not seen by DTH on loan in 2011]); **West Cornwall,** Kynance Cliff, SW677135, SW.-facing slope and tops of serpentinite sea-cliff, with patchy short vegetation, 60 m, 2011.04.06, GAH & DTH, CGAH (38 sh & bod, 24 sh)**; Bryher, Isles of Scilly, SV8762/1441, dune grassland (mainly *Festuca*), 2003.04.05, GAH, CGAH (7 sh & bod); Appletree Bay, Tresco, Isles of Scilly, SV8930/1369, dune grassland, 2003.04.03, GAH, CGAH (1 sh); St. Mary's, Isles of Scilly, SV9087/0977, herb-rich turf on coastal cliff, 2003.03.29, GAH, CGAH (17 sh); Great Bay, St. Martin's, Isles of Scilly, SV9216, blown-sand on slope, 1995.06.20, GAH (as G.A. Griffiths) & DTH, CGAH (25 sh); Trewellard Common, SW382335, sparsely vegetated china-clay spoil, with masonry and other debris, 1999.01.09, GAH, CGAH (2 sh); Hudder Down (*ca* 4 km NE. of Hayle), SW604429, patchy short grassland with herbs and very short *Calluna* at top edge of slaty sea-cliffs, 68 m, 2011.04.04, GAH & DTH, CGAH (13 sh & bod, 14 sh); Porthleven, SW62, 1954, H.B. Sargent, CGAH (ex S.M. Turk Colln.) (1 sh).

APPENDIX 2. OTHER NOMINAL TAXA FROM EUROPE WHICH ARE OR HAVE BEEN ASSIGNED TO *PONENTINA*

This section lists names (in bold type) that appear to be referable to European species of *Ponentina*, which cannot currently be securely placed as synonyms of any of the species recognised in this paper. Many of the names are invalid as homonyms or *nomina nuda*, but it remains possible that a few of them represent species that are as yet unrecognised.

Helix **aporina** Castro 1887, *J. Sci. math., phys., nat., Lisboa* 11(44): 237. Type locality: in Portugal at Familicão, Guimarães and Praia da Granja. According to Castro (1887), found only in autumn; he had previously distributed specimens under the name *Helix autumnalis* Castro, but changed the name becuse it was preoccupied. Listed as synonym of *P. revelata* by Nobre (1941). Apparently a *Trichia* sp. [i.e. *Trochulus*] according to Richardson (1980), but this is almost certainly incorrect as that genus is unknown in Portugal and the original description stated *anguste perforata, tenui, subpellucida, fragili, obscure corneo-viridula ... anfractibus 4 ... peristomate simplici*.

Helix **atachypora** Bourguignat MS. in Locard 1899, *Arch. Mus. Hist. Nat. Lyon*, 7: 69.

Helix **badiella** Ziegler. According to Kennard & Woodward (1919: 135) this name was listed by L. Pfeiffer (*Mon. Helic.*, 1, p. 65, 1848) as a syn. of *H. revelata* Férussac. However, Germain (1930: 242) regarded it as a synonym of *Fruticicola hispida* var. *plebeia* (Draparnaud, 1805), i.e. *Trochulus hispidus* (Linnaeus 1758).

Helix **conimbricensis** Castro 1887, *J. Sci. math., phys., nat., Lisboa* 11(44): 235. Type-locality Coimbra [Portugal] and a single shell from Bussaco [Buçaco] found by A. Neves e Mello. Perhaps a synonym of *P. revelata* or *P. platylasia*.

Helix **Cynetarum** Maltzan 1885, *Jb. d. malakozool. Ges.* 12: 235. Type-locality Boliqueime, Algarve. Listed as a synonym of *P. revelata* by Nobre (1941), but apparently *Trichia* sp. [i.e. *Trochulus*] according to Richardson (1980), although neither of these is known from the Algarve. Original description gave shell of 6½ whorls, which if correct is inappropriate for any *Ponentina*.

Helix revelata Var. B. ***major*** Castro 1887, *J. Sci. math., phys., nat., Lisboa* 11(44): 234. Type-locality "aux environs de Porto, à Gaya [= Gaia]" [Portugal]; the name is doubtless preoccupied.

Helix venetorum Bourguignat in Servain var. B. ***major*** Castro 1887, *J. Sci. math., phys., nat., Lisboa* 11(44): 234. Type-locality "à Povoa de Varzim" [Póvoa de Varzim] [Portugal]; name is preoccupied (if only by *H. revelata* var. *major*, named higher on same page).

Helix villula Bourguignat in Servain Var. B. ***major*** Castro 1887, *J. Sci. math., phys., nat., Lisboa* 11(44): 236. Type-locality "aux environs de Porto, à Gaya [Gaia]"; name is preoccupied (if only by *H. revelata* var. *major*, named earlier in same publication).

Helix revelata var. ***martigenopsis*** Servain 1880, *Etudes Moll. Espagne & Port.*, p. 56. Type-locality "alluvions du Tage, au-dessous de Lisbonne, ... , aux environs de Miranda de Ebro ..., en France dans le bois du Petit-Puy prés de Saumur et à Cormen et Chin dans l'Indre-et-Loire". Described only as differing from *H. revelata* in larger size, more open umbilicus and closely resembling *Helix martigena* A. Férussac (Servain, 1880: 55–56). It is likely that the specimens from the various Portuguese, Spanish and French localities listed by Servain represented more than one species.

Helix Salmurina var. ***minor*** Servain 1880, *Etudes Moll. Espagne & Port.*, p. 55. Type-locality: "çà et là en France, notamment dans le Morbihan et la Loire-Inférieure". Servain (1880: 55) noted that this var. (which he described) was published by Michaud (1831: 27, pl. XV, figs 6–8) as *Helix revelata* (non *H. revelata* A. Férussac), suggesting he was introducing a new name for it because he regarded Michaud's name as preoccupied. Since Férussac's name was a *nomen nudum* that was validated by Michaud (see under *revelata* Michaud below), Servain's var. *minor* is presumably only a form of *H. revelata* Michaud.

Helix ***montivaga*** Westerlund 1876, *Fauna europaea*, p. 66.

Helix montivaga West.: Westerlund, 1889, *Fauna Pal. Reg. Binnenconch., Helix*, p. 62. Given by Kennard & Woodward (1919: 135) as named by Westerlund (1889, *Fauna Palaärct. Region. Binnenconch., Helix*, p. 61), based on part of a gathering of *H. ponentina* sent by Morelet, but evidently named earlier by Westerlund.

Helix (*Trichia*) *montivaga* Westerlund: Kobelt, 1892, *Iconogr.*, 2 (5), p. 15, no. 749, pl. 124. Perhaps a syn. of *subvirescens*, as regarded e.g. in Kerney & Cameron (1979); treated as separate sp. by Germain (1930).

Helix ***Nevesiana*** Castro 1887, *J. Sci. math., phys., nat., Lisboa* 11(44): 232. Type locality "aux environs de Sernache dos Alhos" [just S. of Coimbra, Portugal]; the name is dedicated to A. des Neves e Mello.

Helix ***occidentalis*** Moquin-Tandon 1855

A homonym of, or error for, *occidentalis* Recluz 1845; probably based on *P. revelata* or *P. subvirescens*.

Helix ***occidentalis*** Nobre 1941 (part)

Presumably an error for *occidentalis* Recluz 1845.

Helix occidentalis [var.] *β* ***ornata*** Moquin-Tandon 1855, *Hist. nat. Moll. France*, 2, p. 222. Type locality not stated, but presumably France (only locality for which specimens confirmed given on p. 223 as Saint-Julien-de-Fargues), so on that basis likely to be a synonym of *P. revelata* or *P. subvirescens*.

Helix occidentalis var. B ***pellucida*** Castro 1887, *J. Sci. math., phys., nat., Lisboa* 11(44): 233. Type locality "aux environs de Coimbra" [Portugal].

Helix ***ponentina*** Dupuy 1850

A homonym of, or error for, *P. ponentina* Morelet 1845; perhaps based on *P. revelata* or *P. subvirescens*.

Helix ***salmurina*** Servain 1880, *Etudes Moll. Espagne & Port.*, p. 54. Type locality: "aux environs de Saumur (Maine-et-Loire), notamment dans le bois du Petit-Puy"; "un échantillon absolument identique [retrouvé] au Cacillas [Cacilhas] près de Lisbonne". *Helix salmurina* Servain: Tryon, 1887, *Man. Conch.* (2) 3, p. 181, pl. 41, figs 83–85. Servain (1880) described *H. revelata* Michaud as corresponding to his var. *minor* of this species (*q.v.*); hence the species as a whole is likely to be a syn. of *P. subvirescens* or *P. revelata*.

Helix (Zenobia) ***saxivaga*** Maltzan 1885, *Jb. d. malakozool. Ges.* 12: 235. Type-locality: "Boliqueime Olhao, Silves, Algarve" [i.e. Boliqueime, Olhao and Silves, three different localities in the Algarve]. Original description starts "Aff. *H. montivagae* West." and listed as synonym of *P. revelata* by Nobre (1941). Richardson (1980) regards it as a *Trichia* sp. [i.e. *Trochulus*], but probably incorrectly as that genus is unknown in Algarve.

Helix ***utriculina*** Locard 1899, *Arch. Mus. Hist. Nat. Lyon* 7: 128–129. Type locality: Estoy [Estói], Algarve. This taxon was reidentified as a *Ponentina* by Gittenberger (1978: 14) based on 12 syntypes in MNHN (in three samples). He figured two of the shells for which breadths were given as 9.8 and 10.2 mm. The illustrations (apertural view only) suggest *P. ponentina* might be involved, since the shells are conical and depressed conical with whorls somewhat flattened above, an almost round mouth and a thickened apertural rib, with "typical widely spaced hair scars all over the shell".

Helix ***venetorum*** Bourguignat MS. in Servain 1880, *Études Moll. Espagne & Port.*, p. 56, *nomen nudum*. *Helix venetorum* Bourguignat MS. in Locard, 1882, *Prodr. Malac. France*, 316–3177. Type locality: "Vannes, dans le Morbihan; Fontenay-le-Comte dans les Deux-Sèvres (col. Bourguignat" (*op. cit.* p. 74). Presumably a syn. of *P. subvirescens* or *P. revelata*. Castro (1887: 234) reported it from Portugal and gave a description that is partly different; the Portuguese material perhaps represented a different species.

Helix ***villula*** Bourguignat MS. in Servain 1880, *Études Moll. Espagne & Port.*, p. 56, *nomen nudum*. *Helix villula* Bourguignat MS. in Locard 1882, *Prodr. Malac. France*, 316–317. Type-locality: "Vannes, dans le Morbihan; Fontenay-le-Comte dans les Deux-Sèvres" [France](*ibid.*, p. 74). Presumably a syn. of *P. subvirescens* or *P. revelata*.