

SELENOCHLAMYS YSBRYDA SP. NOV. FROM WALES, UK: A TESTACELLA-LIKE SLUG NEW TO WESTERN EUROPE (STYLOMMATOPHORA: TRIGONOCHLAMYDIDAE)

B. ROWSON¹ & W. O. C. SYMONDSON²

¹Dept. Biodiversity & Systematic Biology, National Museum Wales, Cathays Park, Cardiff CF10 3NP, UK

²School of Biosciences, Biomedical Science Building, Cardiff University, Museum Avenue, Cardiff CF10 3US, UK.

Abstract The subterranean, carnivorous slug *Selenochlamys ysbryda* sp. nov. is described from a breeding population in an urban garden in Cardiff, Wales, UK. The species was probably introduced recently among garden plants. *Selenochlamys* is a distinctive and little-known genus of the Trigonochlamydidae, a family endemic to the Caucasus and neighbouring countries, hitherto unrecorded east of Turkey. Cardiff material differs from specimens and descriptions of the sole previously recognised species *S. pallida* O. Boettger, 1883 in having vestigial eyes, in greater body size, in musculature, in small differences in the genitalia, and in other features. In colour and vestigial eyes, *S. ysbryda* resembles certain troglobitic (cave-dwelling) molluscs of the Caucasus but may simply be a deeply edaphobitic (soil-dwelling) animal. We describe the living animal and aspects of the behaviour of *S. ysbryda*, including the consumption of earthworms. In size, morphology and behaviour there are numerous and striking convergences between *S. ysbryda* and the West Palearctic genus *Testacella* (Testacellidae), probably indicating a similar ecology. *Testacella* is known to have been widely spread by man, as have several earthworm-eating terrestrial planarians. In the light of these comparisons, we speculate on whether *S. ysbryda* is likely to occur elsewhere undetected or spread further.

Key words British Isles, Caucasus, slugs, introductions, earthworms, predation

INTRODUCTION

According to Kerney (1999) and Cameron & Killeen (2000), more than 20% of the extant terrestrial mollusc species of Britain and Ireland are established anthropogenic introductions. This includes several of the most familiar and widespread slugs, with at least 33% of the British slug species plausibly being introductions based on careful interpretation of census data and the fossil record (Kerney, 1999). As more species are introduced or detected the exotic proportion of the fauna is increasing (cf. Anderson, 2005). Land molluscs are liable to be introduced when plants are transplanted with soil around the roots, a mechanism that also aids their local spread once imported. Recently recorded British mollusc introductions include examples of introduction without establishment (e.g. the subulinid *Rumina decollata*; Seddon & Pickard, 2005), establishment without spread (e.g. the clausiliid *Papillifera papillaris*; Ridout Sharpe, 2007) and establishment followed by gradual spread (e.g. the limacid *Lehmannia valentiana* and the hygromiid *Hygromia cinctella*; Kerney, 1999). The risk of exotic slugs or snails becoming pests, or threats to native fauna, is considerable. A perpetual concern is that new introductions may belong to a fourth category, that of establishment followed by rapid spread. A

now classic example of this is shown by the slug *Boettgerilla pallens* Simroth, 1912 (Boettgerillidae). First noted in the British Isles in 1972 (Colville *et al.*, 1974) it now occurs nearly throughout in a wide range of habitats, a spread that has been paralleled in continental Europe (Kerney, 1999; Cameron & Killeen, 2000).

Unlike the other species mentioned above, each of which is originally Mediterranean, *B. pallens* was originally endemic to the Caucasus and South-east Europe (Colville *et al.*, 1974; Likharev & Wiktor, 1980). The Caucasus and neighbouring countries (Armenia, Azerbaijan, Georgia, northern Iran, southern Russia and eastern Turkey) form a region of considerable climatic and habitat diversity that is rich in endemic slug taxa, some of which represent highly specialised and presumably ancient lineages (e.g. Simroth, 1901; Likharev & Wiktor, 1980; Wiktor, 1994; Schileyko, 1988, 2003; Suvorov, 2003; Schutt, 2005). The genus *Boettgerilla* Simroth, 1910 is itself an example: a group of small vermiform ground and soil-dwelling slugs that constitutes the endemic monogeneric family Boettgerillidae (Likharev & Wiktor, 1980; Bouchet & Rocroi, 2005). The same region is also home to the endemic Trigonochlamydidae, a small but diverse family of carnivorous slugs whose biology is poorly known (Hesse, 1882, 1926; Simroth, 1901; Likharev & Wiktor, 1980; Barker & Efford,

2004). Their evolution has apparently been driven by extreme specialisation to soil-dwelling (edaphobitic) or cave-dwelling (troglobitic) habitats as well as various modifications associated with carnivory (Likharev & Wiktor, 1980; Schileyko, 1988; 2003; Barker & Efford, 2004). One trigonochlamydid genus, *Selenochlamys* O. Boettger, 1883 can be considered particularly specialised, having a greatly enlarged buccal mass and a reduced mantle displaced to the rear of the body (Likharev & Wiktor, 1980). It is this genus, which until now has been considered monotypic (e.g. Schileyko, 2003), that we here report as established in Britain.

Selenochlamys is a little-known slug, even in its original range, with little new data on the genus reported since Likharev & Wiktor (1980). Few specimens have been recorded and it appears to be restricted to the western Caucasus of Georgia and southern Russia, and the adjacent parts of Turkey (Simroth, 1901; Likharev & Wiktor, 1980; Forcart, 1983; Schutt, 2005). Both the genus *Selenochlamys* and the species *S. pallida* O. Boettger, 1883 were described from a single specimen from "Kutais" (probably Kutaisi, Georgia) (Böttger, 1883; Likharev & Wiktor, 1980). A second species, *S. plumbea* Simroth, 1912 was described, again from a single specimen, from Vilayet Çoruh, Ardanuç, Turkey (Simroth, 1912) but was synonymised with *S. pallida* by Likharev & Wiktor (1980), who suggested that the key differences were artefacts of preservation. According to Forcart (1983), Böttger's holotype of *S. pallida* is lost. However, Forcart (1983) provided a photograph of a preserved specimen of *S. pallida* from Vilayet Samsun, Turkey, which we have been able to examine on loan (see below). The general lack of observations and material of *Selenochlamys* has two implications. Firstly, that we are in a position to add to the knowledge of the genus; but secondly, that definitive identification to species is difficult. In the following Description we present evidence that the Cardiff population differs from previous descriptions and specimens of *S. pallida* to the extent that it should be considered a separate species. In the Discussion we also include published observations on the ecology and habitat of *Selenochlamys* in its original range, and make special mention of the numerous and striking similarities between *Selenochlamys* and the West Palearctic (and British) genus *Testacella* Cuvier, 1800 (Testacellidae). Such comparisons

may be important in predicting whether *S. pallida* is likely to spread elsewhere and how it might interact with other British fauna.

MATERIALS & METHODS

LOCALITY & HABITAT

The type locality for *S. ysbryda* is an urban domestic garden, here defined as "United Kingdom: Wales: Glamorgan (Watsonian vice-county 41): Cardiff: Canton: domestic garden (ST1676), 10-15m alt.". We do not wish to disclose the exact address, but with the permission of the donor have supplied the full locality data to the Conchological Society of Great Britain & Ireland (CSGBI), to be made available in accordance with their Data Policy. The suburb of Canton consists mainly of late Victorian residences, with gardens, built during a time when the port of Cardiff grew rapidly as an industrial centre. The first edition small-scale Ordnance Survey map of 1880 shows a large plant nursery very near the locality in question, when the house was not in existence but the garden plot is clearly marked out. By the third edition map of 1920, the nursery had been completely built over with houses of a similar age to that at the collection locality. The garden appears to have retained its original boundaries. At present, the garden has several soil beds supporting, among other garden plants, a large fig tree, two apple trees, and several shrubs of box. The soil is dark and well-tilled, has occasionally been manured and small amounts of metaldehyde have been applied in the past. Other molluscs present were the snails *Cornu aspersum*, *Cepaea hortensis*, *Hygromia cinctella*, *Trochulus striolatus* and *Oxychilus draparnaudi*, and the slugs *Arion ater*, *Arion hortensis*, *Deroceras reticulatum* and *Tandonia budapestensis* (all common in gardens in southwest Britain). On the date of collection (8th October 2007), after a period of relatively dry and mild weather, six living specimens of *S. ysbryda* were found resting under pots or potting trays standing on stone slabs or on the soil and removed to captivity. The donor had seen adult specimens on two previous occasions crawling on the soil and other ground surfaces in the garden (one as early as February 2007). We note that 2007 saw an unusually wet and cool summer (June-August), albeit with an unusually dry and warm spring (April-May).

MAINTENANCE IN CAPTIVITY

Living slugs were maintained in captivity at 15°C with 16h:8h light:dark cycle for up to 18 weeks. Individuals were isolated in ventilated plastic boxes containing 20-40mm topsoil from a South Wales garden kept moist with distilled water. Live earthworms (mainly small *Lumbricus rubellus* Hoffmeister and *Allolobophora chlorotica* [Savigny]) from the same garden were added every 2-5 days, and habitually created burrows throughout the soil in the box. Soil was replaced every few weeks and searched for eggs or uneaten worms. Stray spiders, centipedes or other potentially harmful invertebrates were removed. There was no evidence that these conditions adversely affected the slugs' health, behaviour or appearance and all (except those killed for study) are presently still alive. Growth appeared to be slow and specimens did not increase much in size over the captive period. One individual laid eggs (see below). For behavioural comparison, two live specimens of *Testacella scutulium* Sowerby, 1820 were kept under the same conditions.

PRESERVATION & EXAMINATION

Live slugs were drowned separately for 12h in boiled and cooled tap water and preserved in 80% ethanol at ambient temperature. Small pieces of the body wall of each specimen were removed to 96% ethanol and stored at -15°C for future DNA extraction. Drawings were made from living animals, from photographs, or from dissected specimens with a microscope and camera lucida. Radulae were removed manually from the buccal mass, cleaned for 1h in 10% potassium hydroxide solution, rinsed in distilled water and air-dried on stubs before gold-coating for scanning electron microscopy.

ABBREVIATIONS

NMW National Museum of Wales, Cardiff, UK
 NMB Naturhistorisches Museum, Basel, Switzerland
 BMNH Natural History Museum, London, UK

MATERIAL EXAMINED

S. ysbryda sp. nov., Holotype (one adult, dissected): UK: Wales: Glamorgan: Cardiff: domestic garden in Canton (ST1676), 10-15m alt., leg. P. Thomas 28 Sep 2007, det. B. Rowson & W. O. C. Symondson (NMW.Z.2008.005.00001; 80% ethanol).

S. ysbryda sp. nov., Paratype 1 (one adult, dissected): UK: Wales: Glamorgan: Cardiff: domestic garden in Canton (ST1676), 10-15m alt., leg. B. Rowson 8 Oct 2007, det. B. Rowson & W. O. C. Symondson (NMW.Z.2008.005.00002; 80% ethanol).

S. ysbryda sp. nov., Paratype 2 (one adult, dissected): UK: Wales: Glamorgan: Cardiff: domestic garden in Canton (ST1676), 10-15m alt., leg. B. Rowson 8 Oct 2007, det. B. Rowson & W. O. C. Symondson (NMW.Z.2008.005.00003; 80% ethanol).

S. ysbryda sp. nov., Paratype 3 (one adult): UK: Wales: Glamorgan: Cardiff: domestic garden in Canton (ST1676), 10-15m alt., leg. B. Rowson 8 Oct 2007, det. B. Rowson & W. O. C. Symondson (NMW.Z.2008.005.00004; 80% ethanol).

S. ysbryda sp. nov., (several juveniles, excluded from the type series, collection data as above, maintained in captivity and to be accessioned or distributed on preservation).

S. pallida O. Boettger, 1883 (one juvenile, dissected): Turkey: Vilayet Samsun, near Çukurbük railway station, under stones and moss, leg. L. Forcart, 4 May 1936, det. L. Forcart (figured in Forcart, 1983) (NMB.4662a; drowned, preserved in 80% ethanol/IMS, probably ex. 10% formalin).

Testacella haliotidea Draparnaud, 1801 (four adults, three dissected): UK: England: Essex: Stisted (TL799246), leg. W. M. Webb, det. B. Rowson & W. O. C. Symondson (BMNH.1899.11.9.12-14; drowned, preserved in 80% ethanol/IMS, probably ex. 10% formalin).

T. scutulium Sowerby, 1820 (two adults): UK: England: MIDDLESEX: London: Kensall Green Cemetery (TQ233827), leg. R. A. D. Cameron & B. M. Pokryszko, 10 Nov 2007, det. B. Rowson (maintained in captivity and to be accessioned on preservation).

DESCRIPTION

CLASSIFICATION

Higher classification, following Bouchet & Rocroi (2005): Gastropoda: Pulmonata: Stylommatophora: Sigmurethra: Superfamily Parmacelloidea P. Fischer, 1856. Family and genus-level classification, following Likharev & Wiktor (1980) and Schileyko (2003):

Family TRIGONOCHLAMYDIDAE Hesse,
1882

Subfamily SELENOCHLAMYDINAE I. M.
Likharev & Wiktor, 1980

Genus *Selenochlamys* O. Boettger, 1883

Type species *S. pallida* O. Boettger, 1883;
monotypy.

Selenochlamys ysbryda sp. nov.

Derivation of name Specific epithet *ysbryda*, from Welsh "*ysbryd*", a ghost or spirit, latinized by the addition of a feminine ending "*a*" and to be treated as a noun in apposition. The name alludes to the species' ghostly appearance, nocturnal, predatory behaviour and the element of mystery surrounding its origin.

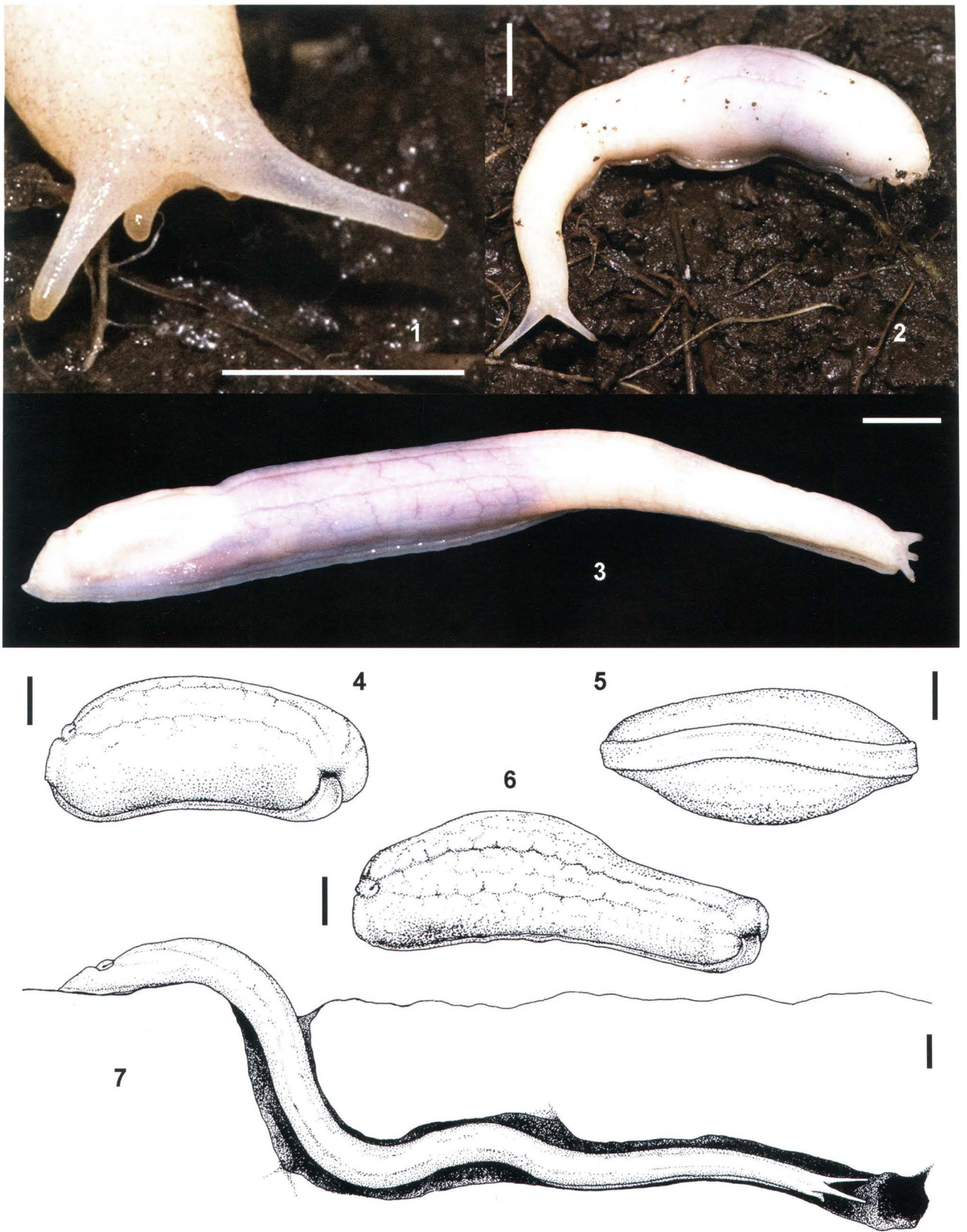
BEHAVIOUR (Figs 1-7)

Most of our behavioural observations were made on captive animals (Figs 1-7). *S. ysbryda* shows strong positive geotaxis and was found only on, in, or very near the ground, and captive animals were only rarely observed crawling on the sides or lids of their shallow containers. Its climbing ability appears to be weak, probably related to the narrowness of the foot. At temperatures of 12-25°C, it is highly active when disturbed or exposed, but is normally only active and mobile in darkness or for 1-2h in the morning or evening. The animal rests in a characteristic, cylindrical, partially or fully contracted position (Figs 4-6), in which the head and forebody are invaginated like the finger of a glove, and the mantle and tail are contracted, with the ends of the sole slightly upturned. The sole may partially enfold on itself and the middle of the body may be swollen in a spindle shape (Fig. 5). Dissection of contracted specimens indicates that the tentacles are withdrawn as far as the odontophore, the

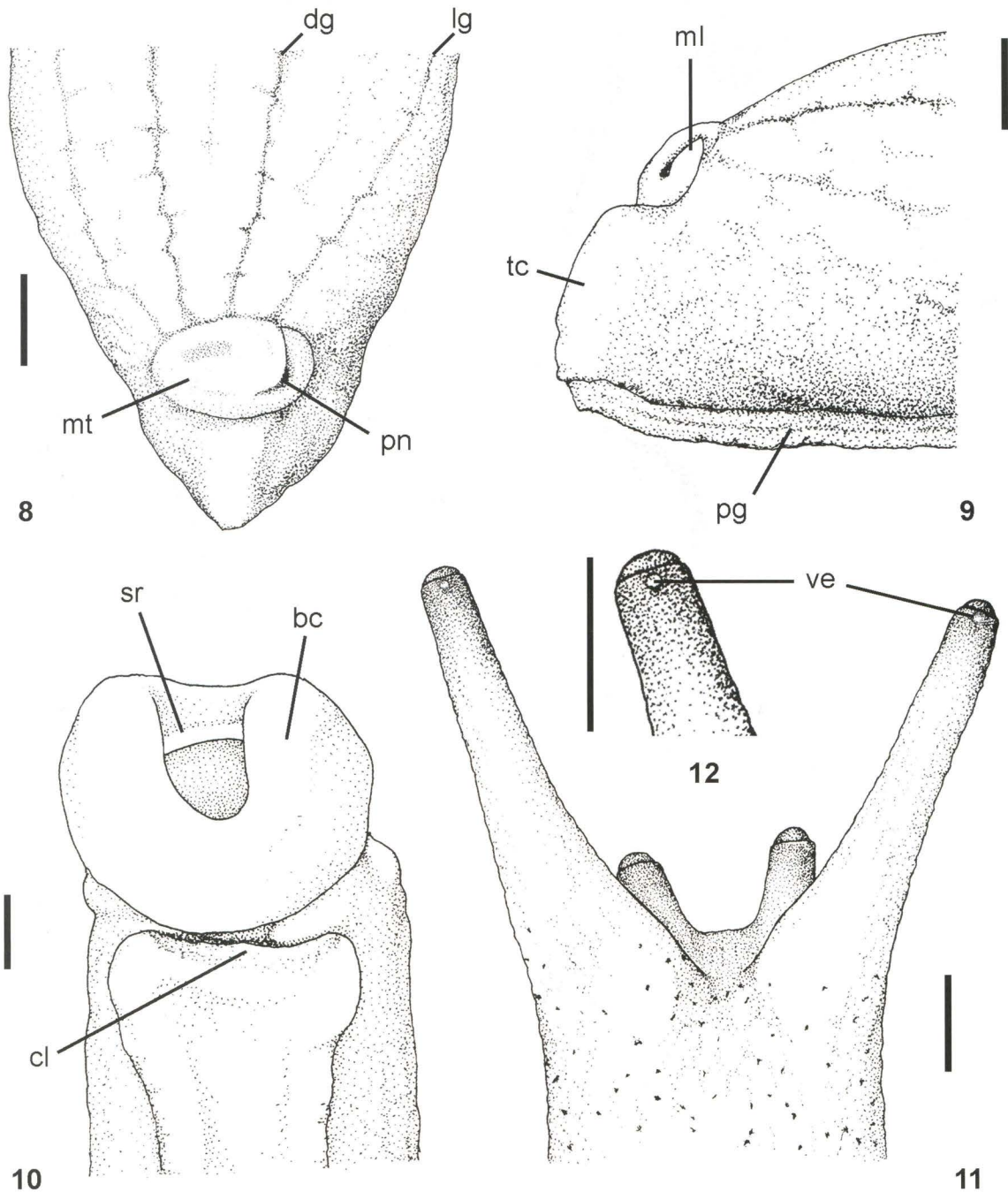
head and neck being so extensible that they are turned fully inside-out.

When extending, the head is evaginated and crawling may begin before the rear end begins to unfurl (Fig. 2). Crawling is slow relative to many slugs, but the tapering forebody appears to help the animal disappear rapidly below the soil surface or under stones when disturbed. Alternatively, the animal may reach its maximum extension before crawling begins, amounting to a forward movement of the head of up to 80mm without the rear end moving. Fig. 3 shows how slender the slug may appear while active under normal or photographic light. However, we only observed it reaching its maximum extension under red light during the hours of darkness. This showed that *S. ysbryda* is exceptionally extensible (perhaps even more so than *Boettgerilla pallens*) and adopts such a slender and flexible form when fully extended it could be mistaken for a pale earthworm (Fig. 7). While thus extended, *S. ysbryda* is able to crawl slowly forward and spends much of its time hidden in earthworm burrows. On several occasions, slugs on the surface kept the hind end stationary with the head probing deep into burrows. Under red light in darkness, they repeatedly withdrew the head and then probed down other, nearby burrows with the hind end remaining on the surface. Likharev & Wiktor (1980) alluded to similar behaviour in the trigonochlamydid *Troglolestes* Ljovushkin & Matiokin, 1965 but it does not seem to have been documented in *Selenochlamys*.

Like other Trigonochlamydidae, *Selenochlamys* is said to prey upon earthworms, including whiteworms/potworms (Enchytraeidae) (Likharev & Wiktor, 1980; Barker & Efford, 2004; Schutt, 2005). We know that captive *S. ysbryda* fed on the lumbricid earthworms we supplied because earthworms regularly disappeared from the containers, and faeces appeared every 2-6 days. These were small (2-5mm) pale yellow or white piles conspicuous against the dark soil surface. They contained numerous sigmoid earthworm chaetae, soil grains, and fragments of tissue, but were mainly composed of an almost pure paste of minute 1-10µm white granules, strongly resembling the crystalline calcium carbonate spherites produced by the calciferous glands of lumbricid earthworms (A. J. Morgan, pers. comm.; Canti & Pearce, 2003). Each pile of faeces contained several hundred granules, very roughly the same number of calcospherites found in a single small



Figs 1-7 *Selenochlamys ysbryda* sp. n., living animals. 1-3 holotype in life; 4-7 typical positions. 4 fully contracted; 5 fully contracted, ventral view; 6 semi-contracted (a common resting position); 7 fully extended, probing earthworm burrow. Scalebars = 5mm.



Figs 8-12 *Selenochlamys ysbryda* sp. n., external morphology. **8-9** hind end, dorsal and lateral view; **10** head, ventral view of Paratype 1; **11-12** head and tentacles, dorsal view of holotype in life. bc, buccal cavity (everted); cl, cleft at anterior end of sole; dg, dorsolateral groove; lg, lateral groove; ml, mantle lobe; mt, mantle; pg, peripodial groove; pn, pneumostome; sr, semilunar ridge; tc, tail crest; ve, vestigial eyes. Scalebars: 1mm.

earthworm. Presumably the slugs do not metabolise these. However, we are yet to observe the feeding behaviour or the capture of earthworms. Earthworms appeared to be ignored and even avoided under normal light, so is possible that *S. ysbryda* will only feed during strict darkness and without the disturbance needed to inspect the

container. Our captive specimens of *T. scutulium* behaved similarly (although we could not find faeces from *T. scutulium*). We did not observe *S. ysbryda* regurgitating earthworms on handling, as has been documented for *Testacella* (e.g. Taylor, 1907). As the slugs were kept in isolation to prevent cannibalism we did not observe mating in *S.*

ysbryda. On one occasion we found a clutch of 22 colourless spherical eggs approximately 2mm in diameter, loosely clumped in the soil. These were laid by a medium-sized specimen of *S. ysbryda* that had been in isolation for eight weeks (Paratype 2). 16 juveniles hatched from these five weeks later and are being maintained on small whiteworms (*Enchytraeus* sp.) at the time of going to press. In external features (vestigial eyes, body colour etc.) these resemble the adults.

EXTERNAL MORPHOLOGY (Figs 8-12)

Body size and shape Body subcircular in cross-section, whether extended, contracted or preserved. In life, when contracted swollen cylindrical or spindle-shaped, 28-36mm long x 7-16mm wide, compact, with mantle somewhat contracted, head and forebody deeply invaginated, and anterior and posterior ends of sole upturned. In life, when extended vermiform, very elongate (52-75mm long, or up to 110mm undisturbed in darkness) and very narrow (6.5-10mm wide, or as little as 3-6mm undisturbed in darkness). For measurements of holotype and paratypes under preservation see Table 1.

Body surface In life, body colourless to milk-white, almost devoid of pigment save for minute pale brown speckles scattered on dorsum and mantle and in a row along dorsal edge of sole. Pale brown pigment also suffuses tips of tentacles (Figs 1, 11-12). Body and sole mucus colourless, not copious. Body wall thin, in places translucent, sometimes flaccid, smoothish, of large, little-raised polygonal tubercles. Body wall becoming opaque white upon preservation. Two shallow dorsolateral grooves arising almost symmetrically from near anterior mantle edge and running length of body, becoming obscure towards head. Two even shallower, more lateral grooves running likewise from near anteriolateral mantle edge. Lateral edges of body lacking clear oblique minor grooves running down from lateral grooves. Sole narrow, comprising less than half width of body when body extended, and even less when body retracted, appreciably tripartite beneath and with strong peripodial groove. Anterior end of sole with a broad bow-shaped medial cleft (Fig. 10). Posterior end of sole just reaching posterior tip of body, this being marked by a short raised

dorsoposterior keel or crest running along body midline to posterior edge of mantle. Sole not visible when posterior end of body viewed from above. Sole lacking a slit at posterior end. Mantle very small, subovoid, broader than long, slightly sunken, lacking strong lobes and with pneumostome exposed and open to right dorsolateral side. No horseshoe-shaped groove visible on mantle. Upper tentacles slender, tapering, with pale brown pigment suffused near tip. Upper tentacles distinctive in nearly meeting at the base (*i.e.*, forehead very narrow) and having minute, colourless, vestigial eyes (Figs 11-12). Lower tentacles stouter, suffused near tip with pale brown pigment, lacking any appreciable palps or division into two parts. Common genital pore on right side, below and just behind right upper tentacle, but lying anterior to it when fully contracted.

INTERNAL MORPHOLOGY (Figs 13-24, 28)

Shell Shell minute (1.8-2.1mm long), situated entirely within mantle and not exposed, colourless, calcified, irregular and variable in form but consisting of virtually uncoiled nucleus and concave spatula, with remnant of columellar visible (Figs 13-15).

Free muscle system Lateral retractor muscles of buccal mass (Fig. 17) posterior, obtaining symmetrically from left and right body walls some distance above sole, becoming more ventral posteriorly, attached to ventral surface of buccal mass. These muscles numerous, six on each side, some becoming bifid near attachment to body wall. Posterior retractor muscles of buccal mass less numerous (three), obtaining almost symmetrically from posterior end of body cavity ventral to pallial septum, attached to ventral surface of buccal mass. Anterior protractors of buccal mass rather weak. Left and right tentacular retractors bifid (*i.e.* attaching to both ocular and lower tentacles), obtaining from body wall about a third of the way to posterior end of body (Fig. 28). Right tentacular retractor passing below both penis and vagina. Vestigial eyes not visible when tentacles retracted.

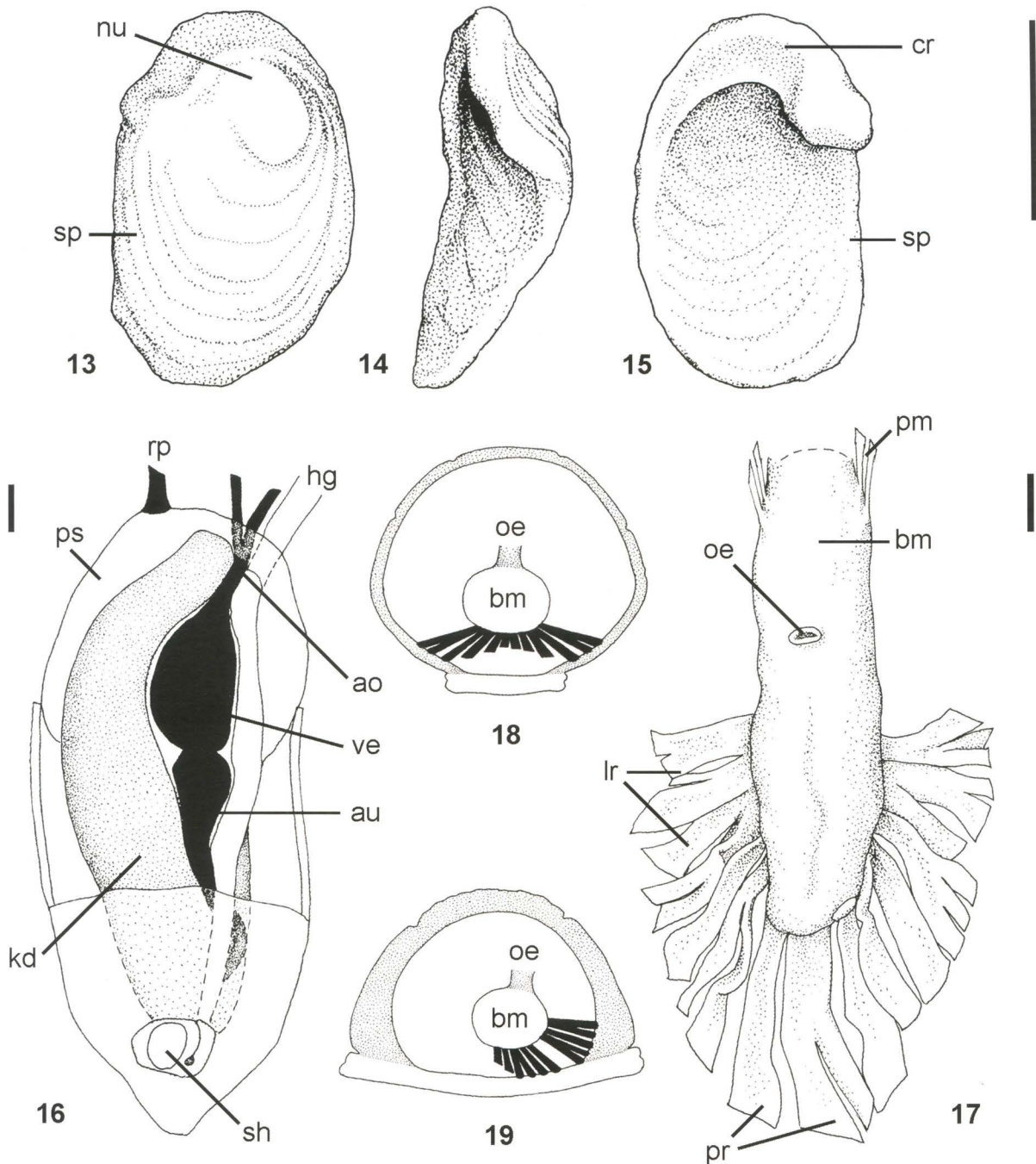
Buccal mass, radula and alimentary system Buccal cavity (when partially everted under preservation) voluminous, thin-walled, with a stiff, semi-

lunar dorsomedial ridge corresponding to position of jaw but lacking any internal jaw vestige (Fig. 10). Buccal mass thick, elongate, occupying much of body cavity in small specimens, about a third in larger specimens. Buccal mass attached symmetrically by retractors as described above. Dorsal surface of buccal mass with slightly sinuous groove corresponding to channel of odontophoral cartilage, visible through circular muscle in posterior half. Opening of oesophagus dorsomedial, about half-way towards posterior end of buccal mass. Odontophoral cartilage

forming a tube, U-shaped in cross-section, slightly pointed anteriorly. Radula belongosan, lacking central tooth and with a narrow toothless central strip, with V-shaped rows of 38-42 teeth (19-21 in each half-row) (Figs 20-22). Laterals 10-15 reaching nearly 500µm long, marginals smaller in the mid-part of the radula but long and needle-like towards the radula sac (Figs 20-21). All teeth aculeate, unicuspid, laterals typically with spearhead-like cusps, rounded above and with a cutting blade below (Fig. 22). Radula and teeth colourless. Oesophagus broad,

Specimen (s)	Living		Preserved		Mature
	Length x width (mm) (extended)	Length x width (mm) (contracted)	Condition	Length x width (mm)	
Kutais, Georgia, 1881 (Böttger, 1883; holotype of <i>S. pallida</i>)	-	-	Semi-contracted	13.0 x 5.5	-
Vilayet Çoruh, Ardanuç, Turkey, 10 Nov 1907 (Simroth, 1912; holotype of <i>S. plumbea</i>)	-	-	Semi-contracted	18.0 x 6.5	-
Vilayet Samsun, Turkey, 4 May 1936 (Forcart, 1983; <i>S. pallida</i>)	-	-	Semi-contracted	15.0 x 3.9	No
Voyenno-Sukhumskaya road, Georgia, 7 Jul 1974 (Likharev & Wiktor, 1980; <i>S. pallida</i>)	-	-	Semi-contracted	22.0 x ?	Yes
Cardiff, UK, 28 Sep 2007 (holotype of <i>S. ysbryda</i>)	75.0 x 10.0	36.0 x 16.0	Contracted	34.5 x 13.0	Yes
Cardiff, UK, 8 Oct 2007 (Paratype 1 of <i>S. ysbryda</i>)	52.0 x 7.0	24.0 x 7.0	Semi-contracted	25.0 x 6.5	Yes
Cardiff, UK, 8 Oct 2007 (Paratype 2 of <i>S. ysbryda</i>)	55.0 x 6.5	25.0 x 7.0	Contracted	25.0 x 7.0	Yes (laid eggs)
Cardiff, UK, 8 Oct 2007 (Paratype 3 of <i>S. ysbryda</i>)	73.5 x 8.0	28.0 x 14.5	Semi-contracted	43.0 x 11.0	Yes
Cardiff, UK, 8 Oct 2007 (<i>S. ysbryda</i> , two small juveniles)	9.0 x 1.0 (mean)	5.0 x 2.0 (mean)	-	-	No
Hatchlings (offspring of Paratype 2 of <i>S. ysbryda</i>)	7.0 x 1.0 (mean)	4.0 x 1.5 (mean)	-	-	No

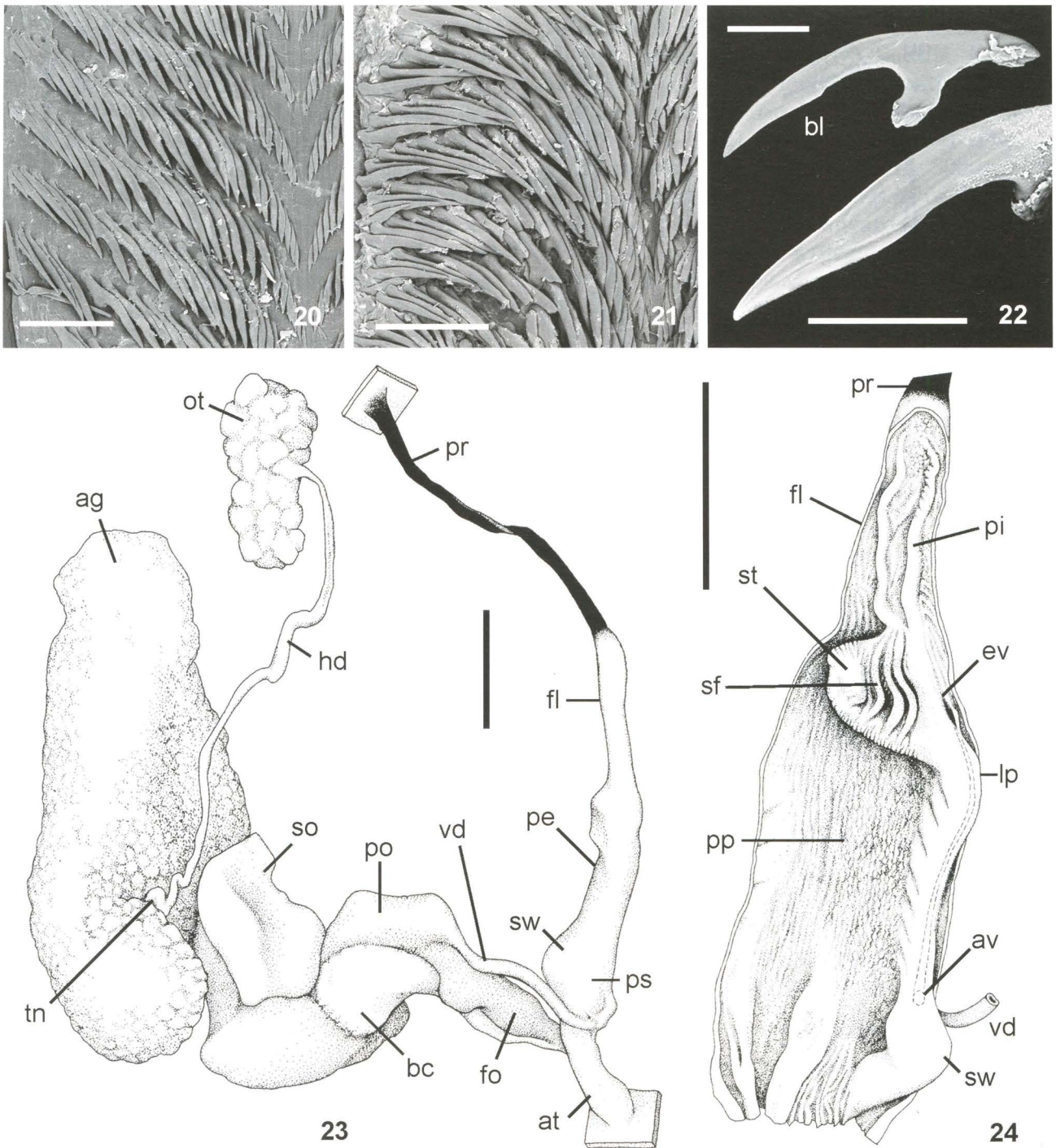
Table 1 Body measurements recorded for specimens of *Selenochlamys*. Measurements of living *S. ysbryda* were made from captive animals in October 2007. For living animals, "extended" refers to extension under normal light (e.g. Fig. 3); maximum extension in darkness is longer and narrower (e.g. Fig. 7).



Figs 13-19 *Selenochlamys ysbryda* sp. n., internal morphology. 13-15 shell of Paratype 1; 16 pallial organs of holotype; 17 buccal mass of holotype, dorsal view; 18 diagrammatic cross-section. 19 *Testacella haliotideae* Draparnaud, 1801, diagrammatic cross-section. ao, aorta; au, heart auricle; bm, buccal mass; cr, remnant of columella; hg, hindgut; kd, kidney; nu, shell nucleus; oe, entry to oesophagus; pm, protractor muscles of buccal mass; ps, pallial septum; pr, buccal mass posterior muscles of buccal mass; rp, penial retractor muscle; sh, position of shell; sp, shell spatula; ve, heart ventricle. Scalebars: 1mm.

attended by paired salivary glands entering buccal mass posteriorly, internally with numerous, irregular papillae not obviously arranged in rows. Hindgut pale, with two lateral diverticulae

entering lobes of hepatopancreas anterior to loop of hindgut. Posterior hindgut straight, tapering and passing through pallial septum on right of heart and kidney towards anus. Hepatopancreas



Figs 20-24 *Selenochlamys ysbryda* sp. n., internal morphology. 20 middle part of radula; 21 radula from sac; 22 two lateral radula teeth in different orientations; 23 genitalia; 24 interior of penis. ag, albumen gland; at, atrium; av, attachment of vas deferens to penis; bc, bursa copulatrix; bl, cutting blade; ev, entry of vas deferens to lumen of penis; fl, flagellum; fo, free oviduct; hd, hermaphroditic duct; lp, longitudinal pilaster; ot, ovotestis; pe, penis; pi, minor pilasters; po, prostate; pp, penial pads and papillae; pr, penial retractor muscle; ps, penial sheath; sf, longitudinal folds on stimulator; st, stimulator; sw, swelling of pilaster or penis; tn, talon; vd, vas deferens. Scalebars = 500 µm (20-21); 100µm (22); 5mm (23-24).

colourless or pinkish-brown, coarsely acinose, with two strong, just subequal lobes, effectively free in body cavity but usually lying on the right

side posteriorly, reaching septum. Suprapedal gland elongate, narrow, attached to foot.

Pallial complex Pallial complex (Fig. 16) separated anteriorly from viscera by a pallial septum stretching obliquely from dorsal surface to posterior ventral surface. Mantle small, exposed and without lobes as described above. Pulmonary cavity sunken below mantle, its volume difficult to establish, and without obvious venation. Rectum and ureter opening into pulmonary cavity. Kidney large, elongate, pale yellow, anteriorly meeting dorsal part of septum. Heart large, attending right dorsolateral side of kidney, rotated (ventricle anterior to auricle), with aorta becoming bifid a short distance after passing through septum.

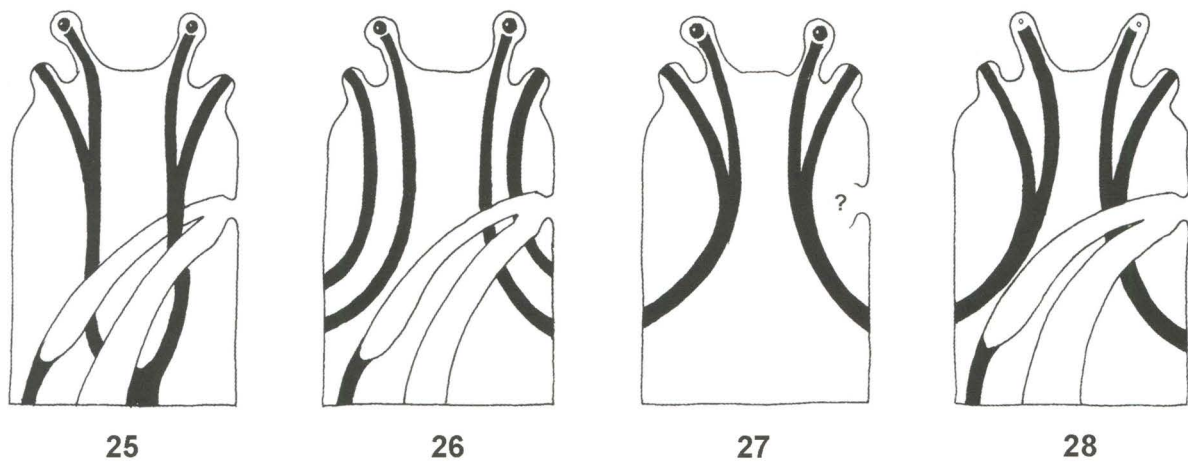
Genitalia Proximal genitalia (ovotestis to free oviduct; Fig. 23) white, lying free on left or right side of body. Ovotestis large, subhemispherical, cupped in a lobe of hepatopancreas some distance anterior to pallial septum. Hermaphroditic duct slender, not convoluted, with small bulbous talon at junction with albumen gland. Albumen gland large, wedge-shaped, of coarse acini. Spermoviduct broad, strongly folded; prostate little distinguished from other components of duct. Free oviduct long, with stout bursa copulatrix duct entering near atrium; thus vagina short. Bursa copulatrix voluminous, subrectangular, thin-walled. Bursa copulatrix and duct tightly bound to spermoviduct. Free oviduct and vagina weakly pigmented pale brown. Atrium rather long, simple. Vas deferens short, thick, bound to penis by thin sheath, directed apically with respect to penis and entering main body of penis near base, without papilla. Penis and flagellum together (phallus) rather long, almost as long as distance from atrium to albumen gland. Phallus with a strong basal swelling near entry of vas deferens and a second swelling halfway along total length. Flagellum slender, a little clavate, flattened. Penial retractor muscle contiguous with sheath at apex of flagellum, slender, obtaining from midline of dorsal body wall near anterior edge of pallial septum. Internally, penis with a basal rounded muscular pilaster corresponding to basal swelling of penis, connected to an enrolled tongue-like structure (stimulator) corresponding to second swelling by a single longitudinal pilaster (Fig. 24). Vas deferens continues apically through longitudinal pilaster, opening to lumen of phallus above stimulator.

Interior surface of flagellum with two lesser longitudinal pilasters branching from main penial pilaster. Surface of stimulator with several deep longitudinal grooves. Interior surface of penis (excluding pilasters) with numerous elongated rhombic raised pads in longitudinal rows, supplanted first by smaller, less elongated papillae, then by substantial, irregular longitudinal pilasters towards atrium.

DISCUSSION

COMPARISONS WITH *S. PALLIDA* AND OTHER TRIGONOCHLAMYDIDAE

According to Likharev & Wiktor (1980) and Schileyko (2003), *Selenochlamys* is unique among Trigonochlamydidae in having the following characters: i) a very small mantle at the hind end of the body; ii) an enlarged buccal mass with strong posterior and lateral retractors independent of the tentacle retractors; iii) the heart ventricle anterior to the auricle; iv) the vas deferens entering the phallus ("penis") laterally, *i.e.* subapically; and v) a tongue-like penial stimulator rather than the "penial ampullae" (sensu Schileyko, 2003) of other Trigonochlamydidae. These characters are all seen in the new species *S. ysbryda* so we are certain it ought to be included in *Selenochlamys*. However, as both authorities considered *Selenochlamys* monotypic, certain other characters they included in their descriptions can now be seen to apply only to the species *S. pallida* and not to *S. ysbryda*. This is complicated by the general lack of data and the fact that the sole type specimen of *S. pallida* is lost (Forcart, 1983). The most thorough description of *S. pallida* is given by Likharev & Wiktor (1980), based on material from Georgia. We here presume this description represents authentic *S. pallida* and recommend that any future neotype designation should be based on their material. Forcart's (1983) specimen from Turkey is unsuitable as neotype on the grounds of immaturity. We also noticed differences in musculature between it and Likharev & Wiktor's description of *S. pallida*, so Turkish specimens may yet prove to represent a third species of *Selenochlamys*, requiring a reinvestigation of the name *plumbea* Simroth, 1912. For the time being, however,



Figs 25-28 Trigonochlamydidae, tentacle retractors (diagrammatic). **25** *Troglolestes* / *Drilolestes* after Likharev & Wiktor (1980), modified; **26** *Selenochlamys pallida* O. Boettger, 1883 after Likharev & Wiktor (1980), modified; **27** *S. pallida* from Turkey (NMB.4662a), original; **28** *S. ysbryda* sp. n., original.

we provide the following list of the characters distinguishing *S. ysbryda* from *S. pallida*, noting how each was treated in earlier descriptions. Some of these characters may ultimately affect how *Selenochlamys* is classified in relation to other Trigonochlamydidae. Although Likharev & Wiktor (1980) and Schileyko (2003) granted *Selenochlamys* a monotypic Selenochlamydinæ, Hesse (1926), Hausdorf (1998) and Bouchet & Rocroi (2005) have proposed different patterns of relationships.

Vestigial eyes and subterranean habit All specimens of *S. ysbryda* have minute, colourless, vestigial eyes. Eyes are seldom mentioned in descriptions of Stylommatophora. In contracted specimens of *Selenochlamys*, such as those illustrated by Böttger (1883), Simroth (1912) and Forcart (1983), eyes are not visible externally. It seems reasonable, however, that their absence (or presence as vestigial eyes) would be commented on if noticed. Thus, although Likharev & Wiktor (1980) do not mention the eyes of *S. pallida* we can assume that normal, pigmented eyes were present in their material. Furthermore, their anatomical figure of *S. pallida* (p.329) indicates large circular structures in the appropriate position and their figure of tentacle retractors (p.96, albeit diagrammatic) shows eyes like other trigonochlamydidids. Three other (presumably secondary) sources on *Selenochlamys* do not mention the eyes (Schileyko, 2003; Barker & Efford, 2004; Schutt, 2005), although the latter two include eyes in their figures. We found two conspicuous, black,

apparently normally developed eyes in Forcart's Turkish specimen of *S. pallida*. Thus we conclude that *S. ysbryda* is unique among *Selenochlamys* in having vestigial eyes.

Vestigial eyes have been described in the trigonochlamydid *Troglolestes sokolovi* Ljovushkin & Matiokin, 1965 and *Lesticulus nocturnus* Schileyko, 1988. Along with the daudebardiid *Daudebardia nivea* Schileyko, 1988, a predatory semi-slug also with vestigial eyes, all three are "snow-white" coloured animals less than 32mm long when extended (Schileyko, 1988; 2003). All three were collected deep (e.g. 1.5km) within caves in western Georgia and according to Schileyko (1988) are obligate troglobionts (as opposed to merely troglobites, i.e. organisms that are found in caves but can survive outside). Whether these species reflect a propensity of carnivorous pulmonates to become troglobionts or simply reflect the age and diversity of cave systems in the Caucasus is not clear. For them to evolve in caves there must be some input of worms, other animals or organic matter such as bat guano. The white body and vestigial eyes of *S. ysbryda* suggest it might also be a troglobite, but if so it is not easy to explain how it could be imported to Britain, unless guano or similar from caves is routinely used as a nursery fertiliser in the country of origin. Perhaps more likely is that *S. ysbryda* is a deeply edaphobitic (soil-dwelling) species in which the eyes and body pigment have been reduced as in the troglobionts. Such a species could arise by peripatric speciation among isolated patches or drifts of specific soil types, in

much the same way as can happen in caves (*e.g.* Barr & Holsinger, 1985; Schiltuizen *et al.*, 2004). The few available observations on the habitat of *S. pallida* suggest that a strongly edaphobitic slug that seldom comes to the surface. This could in part explain the rarity of sightings and difficulty in finding specimens, commented upon by Simroth (1912) and Likharev & Wiktor (1980). The natural habitat is said to be subterranean or under stones in deep, rich, calcareous soil amongst "Mediterranean-type" vegetation or in woods (Likharev & Wiktor, 1980; Jungbluth *et al.*, 1985). Simroth's (1912) single Turkish specimen (the holotype of *S. plumbea*) was found beneath a heavy stone block that the collector was "scarcely able to lift". Schutt (2005) generalised further, suggesting that the habitat was loose, rich soil with earthworm burrows. These conditions match those of the Cardiff locality and are likely to be met in many European gardens.

Body size and shape *S. ysbryda* reaches a substantially larger size than has been recorded for *S. pallida*, even allowing for small differences attributable to preservation (Table 1). This makes them the second largest trigonochlamydid species yet recorded, after *Trigonochlamys imitatrix* O. Boettger, 1881 (up to 38mm contracted; Schileyko, 2003). According to Schileyko (2003), 22mm is the maximum contracted length of *S. pallida*, and according to Schutt (2005), *S. pallida* measures "barely 30mm when fully stretched". These sizes are far exceeded by *S. ysbryda*.

Free muscle system The tentacle retractors of *S. ysbryda* are bifid, obtaining from the body wall and with one branch of each travelling to the upper (ocular) and lower tentacle on each side of the body (Fig. 28). In contrast, Likharev & Wiktor (1980) describe the upper and lower tentacle retractors of *S. pallida* as arising independently on each side (Fig. 26). Forcart's (1983) Turkish specimen is more similar to *S. ysbryda* than Likharev & Wiktor's *S. pallida* in this respect (Fig. 27). According to Likharev & Wiktor (1980) and Schileyko (2003), the right (presumably upper) tentacle retractor does not pass between the penis and vagina in *S. pallida* (Fig. 26). The same state is seen in *S. ysbryda*, where the right tentacle retractor passes beneath both parts of the genitalia (Fig. 28). Forcart's (1983) Turkish specimen is

so immature that the genitalia are present only as a single bifid strand, although the right tentacle retractor does not pass between its branches. As Likharev & Wiktor (1980) suggested that the arrangement of retractor muscles was indicative of relationships within the Trigonochlamydidae, this information could be of systematic importance.

Genitalia The genitalia of *S. ysbryda* are very similar to those figured for *S. pallida* by Likharev & Wiktor (1980). Apart from the presence of the small, bulb-like talon that was not noted by Likharev & Wiktor (1980), and a less globular bursa copulatrix, the genitalia are macroscopically almost identical. Inside the penis of *S. ysbryda*, the penial stimulator, though tongue-like, is rolled rather than folded and possesses several very clear ridges, and the vas deferens opens to its upper surface (rather than the lower as in *S. pallida* according to Likharev & Wiktor [1980]). The main longitudinal pilaster is also substantially swollen distal to the attachment of the vas deferens, and there is a thin sheath around the penis not mentioned by Likharev & Wiktor (1980). These apparently minor inter-specific differences may reflect the genitalia in *Selenochlamys* being simplified relative to other Trigonochlamydidae. The genitalia of *Selenochlamys* also show a strong macroscopic resemblance to those of *Testacella* (see below).

Other features A vestigial, semilunar jaw, sometimes transparent, is present in several trigonochlamydid species but absent in others, including *S. pallida* according to Likharev & Wiktor (1980). We detected a stiff semilunar jaw ridge in *S. ysbryda*, although without any internal jaw vestige. We could not find this structure in Forcart's (1983) specimen of *S. pallida*. The radula of *S. ysbryda* shows a narrower toothless central strip than that of *S. pallida* as figured by both Likharev & Wiktor (1980) and Jungbluth *et al.* (1985). The heart and kidney of *S. ysbryda* also appear to be relatively much larger than those of *S. pallida*, judging by the figures of Likharev & Wiktor (1980). Lastly, *S. ysbryda* lacks the slit at the end of the sole figured by Likharev & Wiktor (1980).

COMPARISONS WITH *TESTACELLA* & CURRENT STATUS IN BRITAIN

Selenochlamys (both *S. pallida* and *S. ysbryda*) shows numerous morphological and behavioural similarities with the genus *Testacella* (Testacellidae). *Testacella* occurs in the British Isles and western Europe, Macronesia, and the western Mediterranean and is widely known to be edaphobitic and prey upon earthworms (see Rinaldi, 2003a, b for a recent review). As recent classifications (e.g. Schileyko, 2003; Bouchet & Rocroi, 2005) reject any close phylogenetic relationship between Trigonochlamydidae and Testacellidae, the similarities must be interpreted as convergences. As such these are likely to indicate a similar ecology, so the comparison is pertinent to the adaptability of *S. ysbryda* to British ecosystems and those of other countries to which it might be introduced. *Testacella* is also unusual among carnivorous slugs in that it is known to have been widely spread by man, becoming established as far afield as South Africa (Watson, 1915), North America (Pilsbry, 1946) and New Zealand (Barker, 1999). Conceivably, *S. ysbryda* might be similarly easily dispersed if it has now entered the garden plant supply network.

Morphological comparisons *S. ysbryda* resembles *Testacella* in the following: rearward displacement of the mantle, extensibility of head, enlargement and increased muscularisation of the buccal mass, shortened gut, elongate suprapedal gland, tapering ocular tentacles and apparent simplicity of the genitalia (e.g. compare Barker's [1999] figure of *T. haliotideia* with ours of *T. ysbryda*). Remarkably, *Testacella* and *Selenochlamys* share a detorsion of the pallial complex to the extent that the heart is rotated 180°, the endpoint of a transformation that does not appear to have been reached in other carnivorous slugs, including the other Trigonochlamydidae (Watson, 1915; Likharev & Wiktor, 1980). The enlarged and muscularised buccal mass of *Selenochlamys* operates in a similar way to that of *Testacella* judging by the description of Likharev & Wiktor (1980). It has a similarly robust, if more symmetrical, attachment to the body walls (Figs 18-19; Taylor, 1907). The size and form of the radula of *Selenochlamys* and *Testacella* are similar, although the teeth of *Selenochlamys* have spearhead-like points rather than the prominent barbs of *Testacella*. That *S.*

ysbryda comes closer in size to *Testacella* than most other Trigonochlamydidae suggests it might take similar-sized prey and show similar longevity. *S. ysbryda* differs from *Testacella* in the absence of an external shell, but that *Testacella* can survive without shells was demonstrated by Stokes (1957) for *T. scutulium* Sowerby, 1820, and shell-less individuals of this species have also been found in the wild in Britain (R. C. Preece, pers. comm.). Perhaps a more important difference is the much thicker body wall and broader sole of *Testacella* (Figs 18-19). This could mean *Testacella* is better able to dig in soil to withstand adverse conditions. However *S. ysbryda*, being much more extensible and unimpeded by a shell, may be able to utilise refuges or penetrate earthworm burrows more effectively.

Behavioural comparisons Behaviourally, *S. ysbryda* generally resembles *Testacella* in being nocturnal, spending most of its time in the soil, in the slow speed of movement, in extending down burrows and in feeding on earthworms. *Testacella* is said to kill between one earthworm per week (Edwards & Lofty, 1977) and one every two days (Quick, 1960). Our observations suggest *S. ysbryda* feeds with a frequency somewhere in this range, but more rigorous experiments are required to determine this with accuracy. Invertebrates other than earthworms have been recorded in the diet of *Testacella* (e.g. Taylor, 1907) but this may require confirmation. Three other differences we observed between *S. ysbryda* and *Testacella* in captivity might prove important. Firstly, the egestion of large volumes of earthworm spherites in faeces of *S. ysbryda*, but apparently not *Testacella* (*T. scutulium*), may indicate that the dietary calcium requirement of *S. ysbryda* is low. This could mean that it is able to exploit a wider variety of soils, and hence habitats, than *Testacella*. Secondly, one specimen of *S. ysbryda* laid 22 small, shell-less eggs. *Testacella* lays several clutches of up to thirteen large, shelled eggs (Stokes, 1957); production of egg-shells might induce a further calcium requirement. It is not clear how many such clutches an individual *S. ysbryda* might lay in its lifetime, or what the ensuing mortality might be, but one may be more fecund than the other under the right conditions. Thirdly, *S. ysbryda* appears to be reluctant to climb above ground, whereas *Testacella* has been recorded climbing ivy-covered walls after heavy rains (Latter, 1906). This could indicate differences in dispersal ability.

Status in the British Isles *S. ysbryda* was found with other introduced molluscs, in a heavily disturbed, urban garden in a port city. Coupled with the limited known natural range of *Selenochlamys* and other Trigonochlamydidae we can be confident that the species has been introduced, although we do not know the exact place of origin. The long (>100y) history of the area as a garden, and the past existence of a plant nursery nearby, mean we cannot rule out *S. ysbryda* being a long-established introduction that has failed to spread beyond a small area. However, *Selenochlamys* is highly distinctive, and to our knowledge has not yet been recorded elsewhere in western Europe. We thus favour the hypothesis that it is a more recent introduction, probably from soil around the roots of garden plants. It is not clear what the climatic and habitat requirements of *S. ysbryda* are, but again we can draw parallels with *Testacella*. Three species of *Testacella* occur in the British Isles (Anderson, 2005). All have been established since at least the early 19th century, although there is debate over their native status (e.g. Webb, 1895; Taylor, 1907; Quick, 1960; Kerney, 1999). The first record of *T. maugei* Férussac, 1812 was from a suburban plant nursery in Bristol (Taylor, 1907) and the majority of British records of all three species are from gardens or parklands, with the possible exception of parts of the south-west (Kerney, 1999). The association of *Testacella* with gardens was strong enough for Boycott (1934) to state that, in contrast to other British molluscs, their distribution was limited by resource (earthworm) density, which might decline away from cultivation. However, the area of potentially suitable habitat is very large, especially now with far more of the British landscape disturbed, improved or cultivated than even in Boycott's time. The apparent absence of *Testacella* from areas of suitable habitat may result from the animals' elusive behaviour but also from a lack of thorough searching (Barker & Efford, 2004). Alternatively, it may simply reflect their anthropogenic spread between localities. If so, their distribution pattern could be a model for that of *S. ysbryda* should it spread unchecked in future.

More speculatively, we can compare *S. ysbryda* and *Testacella* with another introduced earthworm predator, the New Zealand flatworm *Arthurdendyus triangulatus* (Dendy, 1985). One

of several terrestrial planarians introduced to Britain, *A. triangulatus* was first noticed in the mid-1960s in botanical gardens, nurseries and gardens, but is now found throughout lowland Scotland and much of northern Ireland and is spreading southwards (see Boag & Yeates, 2001 for a review). In agricultural land it has been shown to occur at densities sufficient to diminish earthworm populations, which in turn may affect crop yields, and is on the quarantine pest lists of several European countries (Boag & Yeates, 2001). Pest species such as *A. triangulatus* emphasise the need to detect all introductions as early as possible. We note that *S. ysbryda* is the second new slug species to be detected in the British Isles recently. *Arion (Kobeltia) occultus* Anderson, 2004 (Arionidae) was first identified in Northern Ireland where it had been established for some time. Like *S. ysbryda*, it was an undescribed species thought to be an introduction of unknown origin (Anderson, 2004). It is unfortunate that the necessary fundamental research on such species is often done only after they are intercepted as introductions.

ACKNOWLEDGEMENTS

We are very grateful to Mr. Phil Thomas for bringing the slugs to our attention, and to Graham Oliver for advice and encouragement. Anatoly Schileyko and Adrian Norris commented on the manuscript. Edi Stöckli (NMB) kindly loaned Forcart's specimen of *S. pallida*. James Turner (NMW) took the photographs and Leonid Popov (NMW) helped with Russian translation. John Morgan (Cardiff University) examined earthworm remains. Jon Ablett and Fred Naggs (BMNH), Beata Pokryszko and Robert Cameron provided access to specimens of *Testacella*, and several members of CSGBI shared their observations on *Testacella* finds.

REFERENCES

- ANDERSON R 2004 *Arion occultus* sp. nov., a new slug in *Arion* subgenus *Kobeltia*, from Ireland. *Journal of Conchology* **38** (4): 13-26.
 ANDERSON R 2005 An annotated list of the non-marine Mollusca of Britain and Ireland. *Journal of Conchology* **38** (6): 607-637.
 BARKER GM 1999 Naturalised terrestrial

- Stylommatophora (Mollusca: Gastropoda). *Fauna of New Zealand* **38**. Manaaki, Whenua Press, Lincoln, New Zealand.
- BARKER G M & EFFORD MG 2004 Predatory Gastropods as Natural Enemies of Terrestrial Gastropods and Other Invertebrates. In: Barker GM (ed.) 2004 *Natural Enemies of Terrestrial Molluscs*. CABI Publishing, Wallingford, UK.
- BARR TC JR & HOLSINGER JR 1985 Speciation in Cave Faunas. *Annual Review of Ecology and Systematics* **16**: 313-337.
- BOAG B & YEATES GW 2001 The potential impact of the New Zealand flatworm, a predator of earthworms, in Western Europe. *Ecological Applications* **11** (5): 1276-1286.
- BÖTTGER O 1883 Siebentes Verzeichniss von Mollusken der Kaukasusländer. *Jahrbucher der Deutschen Malakozoologischen Gesellschaft* **X** (ii) 155-201, pls. 4-7.
- BOUCHET P & ROCROI J-P (eds.) 2005 Classification and nomenclator of gastropod families. *Malacologia* **47** (1-2): 1-397.
- BOYCOTT AE 1934 The Habitats of Land Mollusca in Britain. *Journal of Ecology* **22** (1): 1-38.
- CAMERON RAD & KILLEEN IJ 2000 Land slugs and snails. pp355-366 In: HAWKSWORTH DL (ed.) 2000 *The Changing Wildlife of Britain and Ireland*. Systematics Association Special Volume 62.
- CANTI MG & PEARCE TG 2003 Morphology and dynamics of calcium carbonate granules produced by different earthworm species. *Pedobiologia* **47**: 511-521.
- COLVILLE B, LLOYD-EVANS L, & NORRIS A 1974 *Boettgerilla pallens* Simroth, a new British species. *Journal of Conchology* **28** (4): 203-206, pl. VIIa.
- EDWARDS CA & LOFTY JR 1977 *Biology of Earthworms*. Chapman & Hall, London, UK.
- FORCART L 1983 Türkische Trigonochlamydidae und Taxonomie des Genus *Pseudomilax* O. Boettger 1881. *Archiv für Molluskenkunde* **114** (1-3): 45-57.
- HAUSDORF B 1998 Phylogeny of the Limacoidea sensu lato (Gastropoda: Stylommatophora). *Journal of Molluscan Studies* **64**: 35-66.
- HESSE P 1882 Miscellen. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft* **IX**: 29-38.
- HESSE P 1926 Die Nacktschnecken der palaearktischen Region. *Abhandlungen des Archiv für Molluskenkunde* **II**: 1-152, pls. 1-2.
- JUNGBLUTH JH, LIKHAREV IM & WIKTOR A 1985 Vergleichend morphologische Untersuchungen an der Radula der Landnacktschnecken. *Archiv für Molluskenkunde* **116** (1/3): 25-45.
- KERNEY M 1999 *Atlas of the Land and Freshwater Molluscs of Britain and Ireland*. Harley Books, Colchester, UK.
- LATTER OH 1906 *Testacella haliotidea* at Godalming. *Journal of Conchology* **11** (12): 365.
- LIKHAREV IM & WIKTOR A 1980 *The Fauna of Slugs of the USSR and Adjacent Countries (Gastropoda Terrestria Nuda)*. Fauna USSR, Mollusca III (5). Akademia Nauk USSR, Leningrad, Russia. [in Russian].
- PILSBRY HA 1946 Land Mollusca of North America (North of Mexico). *Monographs of the Academy of Natural Sciences Philadelphia No. 3* **II** (1).
- QUICK HE 1960 British Slugs (Pulmonata; Testacellidae, Arionidae, Limacidae) *Bulletin of the British Museum (Natural History) Zoology* **6** (3): 103-226.
- RIDOUT SHARPE J 2007 *Papillifera papillaris* (Müller, 1774) in Britain: a giant leap for a small snail. *Mollusc World* **14**: 12-14.
- RINALDI AC 2003a Notes on *Testacella* Cuvier, 1800 (Gastropoda, Pulmonata, Testacellidae). *La Conchiglia* **309**: 47-54.
- RINALDI AC 2003b Errata-Corrige. *La Conchiglia* **311**: 24.
- SCHILEYKO AA 1988 Two new troglobiont species of the terrestrial Pulmonata from Georgia (Daudebardiidae and Trigonochlamydidae). *Zoologicheskii Zhurnal* **67** (11): 1730-1735. [in Russian with English summary].
- SCHILEYKO AA 2003 Treatise on Recent Terrestrial Pulmonate Molluscs (Part 11): Trigonochlamydidae, Papillodermidae, Vitrinidae, Limacidae, Bielziidae, Agriolimacidae, Boettgerillidae, Camaenidae. *Ruthenica* Supplement 2, Moscow, Russia.
- SCHILTHUIZEN M, CABANBAN AS & HAASE M 2004 Possible speciation with gene flow in tropical cave snails. *Journal of Zoological Systematics and Evolutionary Research* **42**: 1-6.
- SCHUTT H 2005 *Turkish Land Snails* (4th, revised and enlarged edition). Verlag Natur & Wissenschaft, Soligen, Germany.
- SEDDON M & PICKARD M 2005 Another Mediterranean land-snail found in UK. *Journal of Conchology* **38** (6): 714.
- SIMROTH H 1901 *Die Nacktschneckenfauna des Russischen Reiches*. J. Glasunov, St. Petersburg, Russia.
- SIMROTH H 1912 Neue Beiträge zur Kenntnis der Kaukasischen Nacktschneckenfauna. *Mitteilungen des Kaukasischen Museums* **VI**: 1-140, pls. 1-10.
- STOKES BM 1957 The worm-eating slugs *Testacella scutululum* Sowerby and *T. haliotidea* Draparnaud in captivity. *Proceedings of the Malacological Society of London* **33** (1): 11-20, pls. 1 & 2.
- SUVOROV AN 2003 A new species and genus of carnivorous slugs (Pulmonata: Trigonochlamydidae) from West Transcaucasia. *Ruthenica* **13** (2): 149-152.
- TAYLOR JW 1907 *Monograph of the Land & Freshwater Mollusca of the British Isles 2: Testacellidae, Limacidae, Arionidae*. Taylor Bros., Leeds, UK.
- WATSON H 1915 Studies on the Carnivorous Slugs of South Africa, including a Monograph of the Genus *Apera*, and a Discussion on the Phylogeny of the Aperiidae, Testacellidae, and other Agnathous Pulmonata. *Annals of the Natal Museum* **III** (2): 108-267, pls. VII-XXIV.
- WEBB WM 1895 The British species of *Testacella*. *The Journal of Malacology* **IV** (4): 74-76, pls. II & III.
- WIKTOR A 1994 Contribution to the knowledge of the slugs of Turkey (Gastropoda terrestria nuda). *Archiv für Molluskenkunde* **123**: 1-47.