NEW SYSTEMATICS OF PARMACELLIDAE P. FISCHER 1856 (GASTROPODA, PULMONATA), WITH THE RECOVERY OF THE GENUS-NAME *DRUSIA* GRAY 1855 AND THE DESCRIPTION OF *ESCUTIELLA* SUBGEN. NOV.

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Abstract *This paper compares two western Mediterranean species so far included in the genus* Parmacella, P. deshayesii *from North Africa and* P. valenciennii *from the south of the Iberian Peninsula. These show many distinctive features that we believe are sufficient to consider them not only as separate species but also to be in different subgenera. Arguments about their conspecificity are clarified and neotypes designated for both. Taxonomic studies of the species of* Parmacella *has allowed us to propose a revision of the systematics of the family Parmacellidae and to restructure it into two genera:* Parmacella *and* Drusia*, the latter an available old genus-name, which in turn is divided into two subgenera* Drusia *s. str. and* Escutiella *subgen. nov. We also include a taxonomic key to the family Parmacellidae using the proposed new systematic scenario.*

Key words Parmacellidae, *Parmacella, Drusia, Escutiella,* nov. subgen., systematic, Iberian Peninsula, Morocco, Algeria.

INTRODUCTION

The family Parmacellidae P. Fischer 1856 includes large slugs with a rough skin, a large and grainy mantle, keeled back and sole lacking a caudal gland. The pneumostome is at the posterior end of the right mantle edge. The shell is characteristic, internal and situated under the posterior part of the mantle. It consists of a spire attached to a flat plate, the limacella.

The growth and development of these slugs is curious and remarkable and illustrates in some way a limacisation process, or, in simple terms, part of the evolutionary process by which snails involved into slug-like descendants. Therefore, as has been commented by Morelet (1845), Tryon (1885) or in our times South (1992) or Castillejo (1997), just after hatching, small slugs of this family have an external spiral shell that hosts the whole animal and thus gives it the appearance of a typical snail. As the body grows the shell can no longer accommodate the animal (semi-slug), and during subsequent ontogeny, the shell (limacella) remains inside the body as in a typical slug. Wiktor (1983) described the area inhabited by the family Parmacellidae as a band bordering the Mediterranean Sea and stretching from the Canary Islands to Afghanistan, being absent or not having been found in a vast area roughly running from Egypt to the Caucasus. Therefore we can distinguish two disjoint areas in their distribution: the western, from the Canary Islands to Egypt; and the eastern from the Caucasus to Afghanistan, each having distinct faunas. The species of the eastern zone have been studied jointly by Likharev & Wiktor (1980) and those of the western area by Wiktor (1983).

This family as so far defined includes three genera: *Parmacella* Cuvier 1804, with several species in both the eastern and the western areas, *Cryptella* Webb & Berthelot 1833 from the Canary Islands, and *Candaharia* Godwin-Austen 1888 from the oriental region.

In this paper we deal with western species of the genus *Parmacella*, and particularly with *P. valenciennii* Webb & Van Beneden 1836, from the southwest quadrant of the Iberian Peninsula and *P. deshayesii* Moquin-Tandon 1848, from northern Morocco and Algeria. There remains confusion about thespecies limits of these two taxa which we will try to clarify.

Two other species were described in southern France, *P. moquini* Bourguignat 1859 and *P. gervaisii* Moquin-Tandon 1850, both of La Crau, near Arles, in Provence. It seems that these refer to a single taxon, as *P. moquini* is not generally considered a valid species and there may be some confusion with the name *P. gervaisii,* which is the only one that appears in the checklist of

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France and in CLECOM I (Falkner, Ripken & Falkner (2002); Falkner, Bank & Proschwitz, 2002), respectively. Falkner, Ripken & Falkner (2002) and Gargominy & Ripken (1999) argue that the validity of this species, which has not been found since 1874, and its origin, are controversial with the possibility that it may have been introduced from Spain or North Africa. Despite this, the presence of fossil shells of *Parmacella* from the Pliocene in southern France (Germain, 1930; Falkner *et al*., 2002) suggests that it may be native to this area. The review by De Winter of the "historical" specimen of 1874 deposited in the MNHN of Paris does not resolve the issue. On the other hand, Groenenberg and De Winter have worked in the Ancient DNA Laboratory (ADL) of the IBL at the University of Leiden on the analysis of DNA from a sample of that specimen to compare it to the Iberian and North African species. Germain (1930) drew the shells of *P. moquini* and *P. gervaisii* and the genitalia of *P. moquini* (= *P. gervaisii* as mentioned above). The morphology of the shells, the dissimilar atrial appendices and, especially, the presence of a protuberance on the surface of the penis suggests that it could correspond to *P. deshayesii* (see below).

Comparison between Parmacella valenciennii and Parmacella deshayesii. Historical background The systematic position of these two taxa, and even their nomenclature, has always been confused, so, some authors such as Alonso *et al.* (1986) suggest the possibility of them being conspecific. In this paper we give sufficient data to justify not only that they are different species, but that the differences are so great that inclusion in separate subgenera can be justified. On their nomenclature, there has been considerable confusion. We will use the original names of the authors who described, in agreement with the criterion of Falkner *et al*. (2002) i.e. *P. deshayesii* and *P. valenciennii.*

Webb & Van Beneden (1836) proposed the new species, *Parmacella valenciennii* dedicated to the naturalist Achille Valenciennes, but with the name indicated, never as "*valenciennesii*", as quoted in some cases, although technically the latter might be more correct. The species was described from Portugal, from the limestone hills of Alcantara, Lisbon, on the right bank of the Tajo River. They comment that *Parmacella* seems to belong particularly to North Africa, this being the only species found in the extreme southwest of Europe. From materials collected at Alcantara they described in detail the external and internal anatomy of the animal.

Morelet (1845) discusses and describes *Parmacella* species known at that time, including one from the province of Oran and not yet described, which is undoubtedly *P. deshayesii*. He says that it resembles *P. valenciennii* from Portugal, but quotes clear differences such as the presence of lines and dark spots on the mantle of the Portuguese species, the darker background colour in the Algerian species, the very thin and crescent-shaped jaw of the Algerian species and the thicker, horseshoe-shaped jaw in the Portuguese with the curious feature of the nauseating smell produced by specimens collected in the Maghreb, which is absent in *P. valenciennii*. Moquin-Tandon (1848) later made a comparative study of the jaw of *P. deshayesii*, without citing any locality. Cockerell (1887) focused on the external features, describing olivaceous brown specimens and others reddish mottled with black spots and bands colour patterns from Tangier and Gibraltar. These were given the name *P. valenciennii*. Nobre (1941) described the external anatomy and the shell of *P. valenciennii* from several localities in southern Portugal, with no description of the internal organs. He noted that they were very abundant in the region of El Alentejo and in Vila Viçosa. Regarding this last locality, he mentioned that it was very abundant in the spring and was collected as pig food. Seixas (1976) also described *P. valencienii* and said that it exhibits, especially the young specimens, black pigmented bands on the mantle with a symmetrical pattern in the posterior lateral border of the mantle, while in the anterior part the pigmentation is reduced to little black lines. He also discusses and illustrates the existence of one or two glands in the atrium, which this author calls "prostatic glands". Alonso & Ibáñez (1981) produced a fairly exhaustive anatomical study of *P. valenciennii* (as *P. valenciennesii*), adding new information about its distribution and discussing its ordination and other issues. Wiktor (1983) offered a dichotomous key for *Parmacella* of the Mediterranean and the Canary Islands and differentiated the species considered here by the genitalia. *P. valenciennii* possesses, in the atrium, only one, straight, and horn-shaped appendix,

while *Parmacella deshayesi* is shown to have two horn-like appendices of different sizes, the largest usually straight and the smaller curved and thinner, although his description of *P. valenciennii* is based on a single juvenile specimen (20 mm in ethanol). In a later paper Alonso *et al.* (1986) give another key in which, they work towards "correcting the path followed by Wiktor (1983) to identify *P. valencienni*". They note that both species have two accessory appendices in the genital atrium and the only distinguishing character indicated is the presence of bright dark spots and bands in the mantle of *P. valenciennii*, which are absent in *P. deshayesi,* suggesting the possibility of conspecificity, with *deshayesi* a junior synonym of *valenciennii*. Parejo (1986) shows a drawing of the genitalia of *P. valenciennii* in which, while not visible, there appears to be two very dissimilar atrial appendices, the larger of which is strongly curved. Rodríguez Hermida & Outeiro (1993) describe an atrial horn-like body with two ends tapered where the farthest is curved and horn-shaped. They also report that the thick central part of this horn-like organ is attached to the vestibular gland. In the figures provided, of exemplars from southern Portugal, there is a large difference in size between the two ends of the appendix, and according to the position from which they are observed it may appear as if there are either just one, or two appendices. Garrido (1995) indicates that in the small genital atrium of *P. valenciennii* an elongated, curved structure enters at its free end, called the corniform organ. In his drawings there is a distinct horn-like body but also a small protuberance that could be the second atrial appendix.

Materials & Methods

Parmacella valenciennii Webb & Van Beneden 1836

Spain, Province of Cádiz: Algeciras, outskirts (UTM=TF70) (8/05/2006, Vicent Escutia leg.) (MVHNnº1628); Bornos, Villamartín-Arcos road (UTM=TF57) (15/04/1991, Juan S. Espín leg.) (MVHNnº010210RT04): Matalascañas, Coto de Doñana (UTM=QB10) (16/4/1991, Juan S. Espín leg.) (MVHNnº010210RT05); Puerto Serrano, path to Ermita (UTM=TF79) (26/04/1988). (MVHNnº010210RT06). Province of Seville: Constantina Mountains (UTM=TG7793) (15/05/2003) (MVHNnº1627). Province of Málaga: Antequera, El Torcal track (UTM=UF69) (4/12/05, Vicent Escutia leg.) (MVHNnº040610BA03).

For collections prior to 1992 see Castillejo & Rodríguez (1991), while the later collections are detailed in the following papers: Rodríguez, Hermida & Outeiro (1993); Garrido (1995); Bech *et al.* (2005); and Bragado, Araujo & Aparicio (2010).

Parmacella deshayesii Moquin-Tandon 1848

Algeria: Oran, Ain Franin, Oran-Kristel road, near the cliff (UTM=YE2765) (16/03/2009, 17/03/2010, Vicent Escutia and Alberto Martínez-Ortí col.) (MVHNnº010210RT01, 14 specimens); Tlemcen (UTM=XD7372) (10/3/2008, Errol Vela leg.) (MVHNnº010210RT02). Morocco: Taforalt-Berkane (UTM=WD9374) (29/12/2006, Vicent Escutia leg.); Beni Sicar (UTM=WD0707) (Collection Rutllant, MVHNnº040610BA04). Spain: Melilla, close to Spanish Legion Barracks (UTM = WE0215) (27/12/2006, Vicent Escutia leg.) (MVHNnº010210RT07).

Moquin-Tandon (1848) described this species using the jaws of specimens, but without mentioning the origin of the specimens. Bourguignat (1861b), in his work on slugs of Algeria, gave no clear citations of this species or its localities. Mousson (1874) describes the Atlas Mountains in Morocco as *terra typica* for the species. Rechaud (1883) cited *Parmacella dorsalis* between Tlemcen and Sidi Ben Abbes (Algeria) (UTM = YD1191) and Tangier (Morocco) (UTM = TE4766). Torres-Mínguez (1926) cited *P. deshayesii* from Tangiers, Melilla and Algeciras, saying that it was not *P. valenciennii*. Wiktor (1983) recorded the species in several locations in Morocco: Sidi Slimane (UTM = TC3095); Kasbah Tadla (UTM = QS5511); Oued Elhadar (3 km south of Taza Haut) (UTM = VC0577); and the mountains of Beni Hozman, about 5 km south of Tetouan (UTM = TE7832).

Results

From a detailed anatomical study of the two morphospecies, *P. deshayesii* and *P. valenciennii,* we have found the following common and differentiating features.

Common morpho-anatomical features

Shell (*Fig. 1)* In both taxa shells are characteristic for the genus, with the convex spiral part,

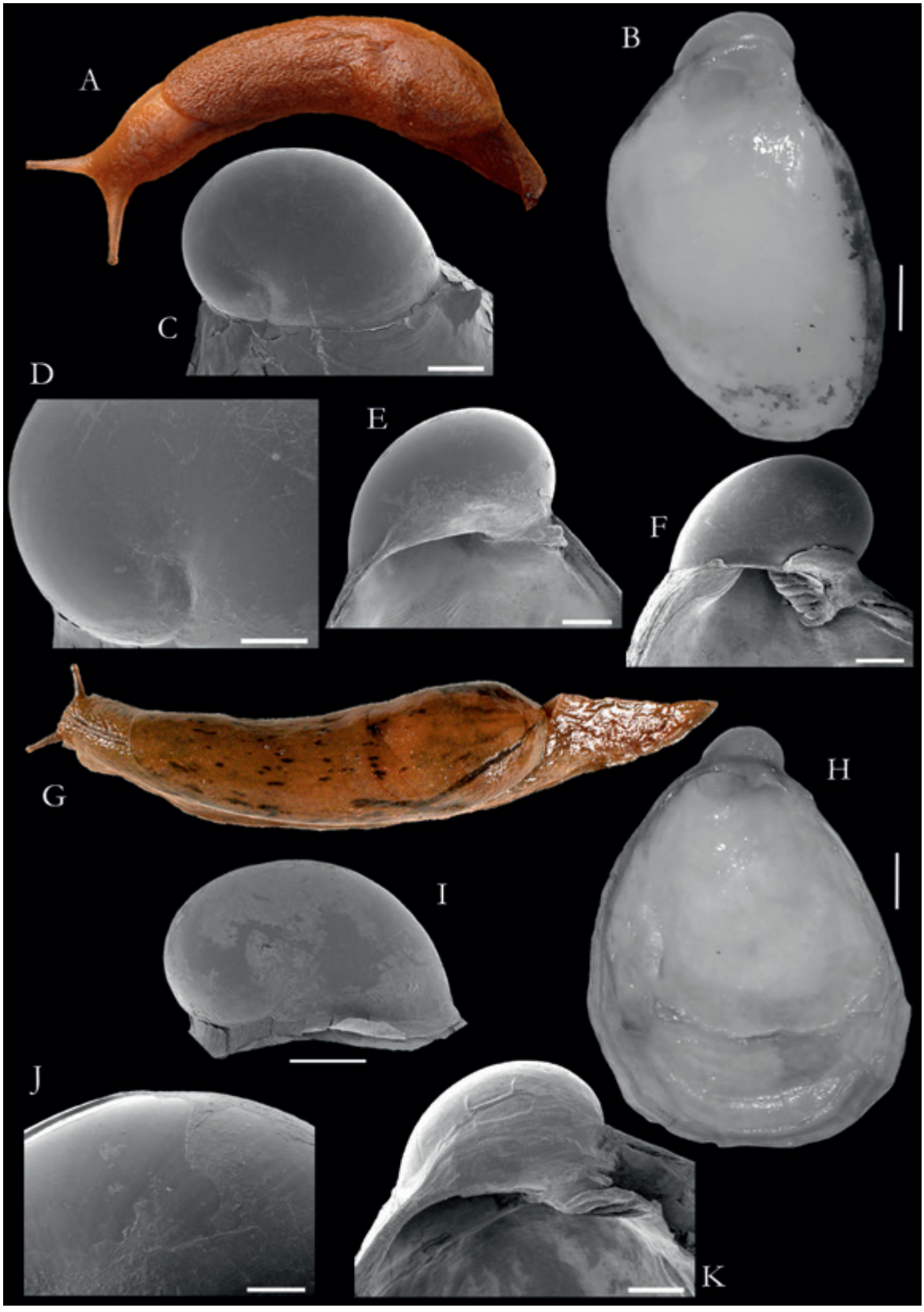

Figure 1 External morphology and shells. A–F *Drusia (Escutiella* subg. nov.*) deshayesii*. Ain-Franin, Oran (Algeria). A Neotype (Length= 52 mm). B Shell. C Dorsal view of protoconch (Oran). D Detail of the nucleus of the protoconch. E–F Ventral view of the protoconch: E Morocco; F Oran. G–K *Drusia (D.) valenciennii*: G Neotype. Mountains of Constantina (Seville, Spain) (length= 81 mm); H Shell (Bornos, Cádiz, Spain); I Protoconch; J Detail of the protoconch; K Ventral view. Scales: B, C, E, F, H, I, K = 1 mm; D = 600 µm; J = 400 µm.

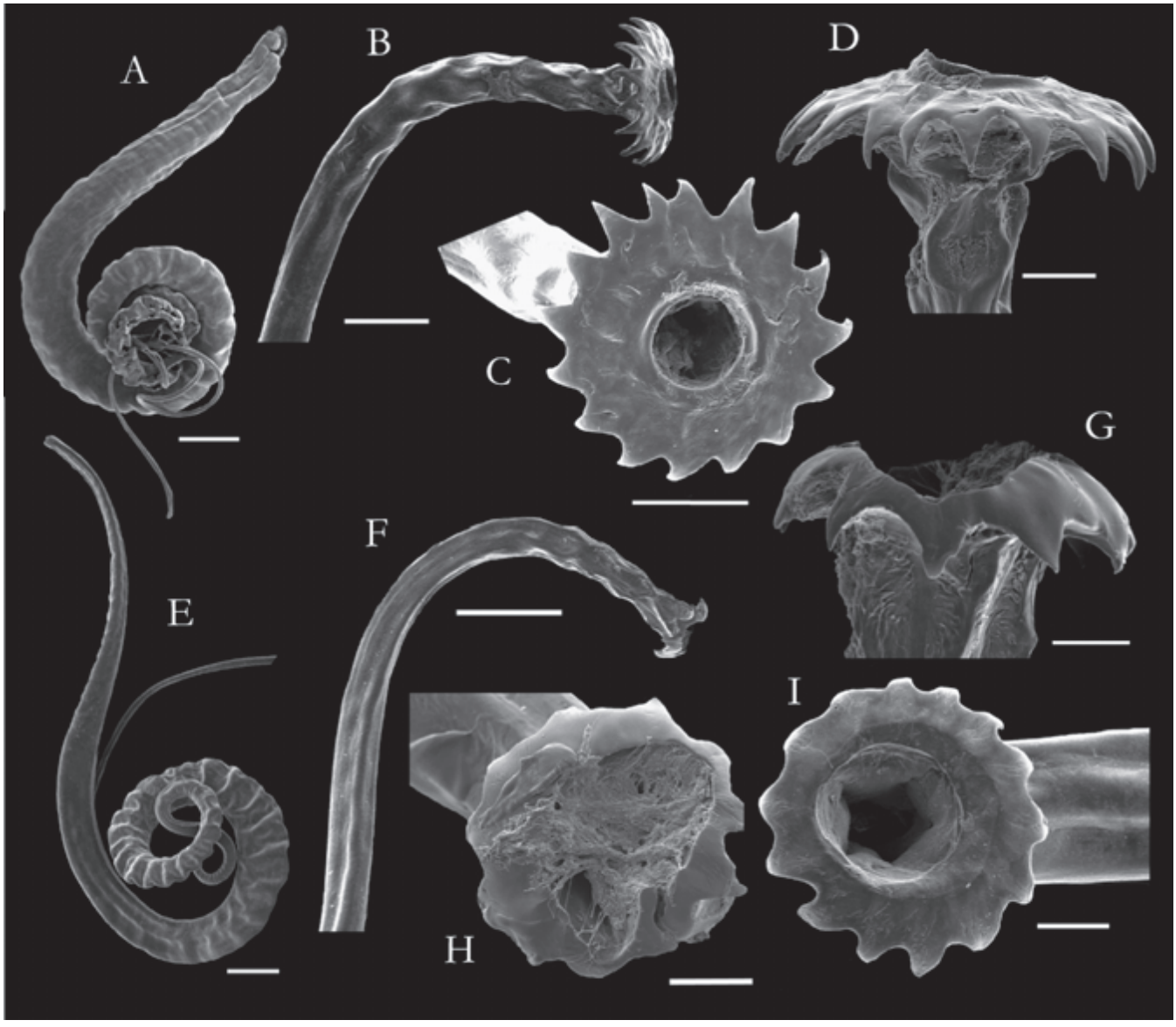

Figure 2 Spermatophores. A–D *Drusia (Escutiella* subg. nov.*) deshayesii* (Oran, Algeria): A General view (scale = 1 mm); B Terminal portion; C Anchoring disc; D Lateral view of the anchoring disc. E–I *Drusia (D.) valenciennii* (Algeciras, Cádiz, Spain): E General view; F Terminal portion; G–I Frontal and lateral views of the anchoring disc; I Puerto Serrano (Cádiz). Scales: A, E = 1 mm; B = 300 µm; C = 200 µm; D, H, I = 100 µm; F = 500 µm; G = 70 µm.

having a smooth yellow-green or brown, shiny surface, attached to a spatula or limacella, which is flat, oval and wide, of a white colour and covered with a yellowish periostracum that forms a membranous rim.

Reproductive system (*Figs 3 and 4)* The morphology of the genital tract is similar in both taxa with a few exceptions commented upon below. They have a medium-sized hermaphrodite gland (about 10 mm in diameter), consisting of two lobes with irregular acini, in among and covered by, the digestive organs. The hermaphroditic duct is very long (up to 25 mm) and winding. Albumen gland, triangular, white, appearing well developed with acini of unequal sizes. The spermoviduct is relatively short and the distal part appears entangled with a large bursa copulatrix, united to it by small fibres. The male and female ducts enter the spermoviduct distally. The male has a vas deferens and an epiphallus, both quite long. The epiphallus widens slightly in its distal part, which may contain within it a ligula that consists of two or three folds. The epiphallus forms an elbow that leads to a thicker penis, which internally contains densely crowded

tubercles and the penial papilla, an evaginable structure that is also covered with dense tubercles. The area where the penis and the atrium connect is narrower, tube-shaped and lacks tubercles. At the level of the elbow, a retractor muscle is attached. The epiphallus and penis are connected by a membranous muscular sheet that keeps them folded and together. The female part begins with a relatively short cylindrical free oviduct which ends in a bulky structure coinciding with the channel of the bursa copulatrix which is also very widened at this level. The bursa copulatrix is large and thin-walled, ovoid and elongate but often wrinkled and partly intertwined with the spermoviduct. Its duct is short and has a roughly spherical lump on its distal part. Here it joins the free oviduct with the vagina beyond this bulging, spherical and smooth, then another widening to form a large bean-shaped, swollen and glandular organ, the perivaginal gland. Internally until the atrium, the entire vagina is covered with longitudinal folds. The genital atrium is of variable size and attached to the same one or two accessory appendices of different sizes, which form the corniform organ, single or double, sometimes croissant-shaped of unequal tips and inside which there is a thick fold evaginable during copulation as a stimulator. The total length of the genitalia, from the atrium to the end of the albumen gland is 40 mm, of which the distal genitalia, well developed, occupies more than half.

The spermatophore (Fig. 2) of both species, like others of the genus, is long (up to 40 mm in length), chitinous and of shiny amber appearance. It comprises two parts, a proximal spiral starting broad but narrowing to join the distal part, a very long and thin tail ending in a small star-shaped disk (less than 1 mm in diameter), whose hooked tips serves as anchor into the expanding end of the bursa copulatrix duct.

Differential morpho-anatomical features These two taxa show many differences discussed below and summarized in Tables 1 and 2.

1. *Parmacella valenciennii* is the larger of the two with live specimens exceeding 10 cm. *Parmacella deshayesii*, according to our observations, rarely exceeds 6 cm. A notable exception is provided by a specimen of *P. deshayesii* collected in the vicinity of Oran in March 2010. This *in vivo* length was 115 mm and weight 19.5 g. The dimensions obtained from specimens preserved in ethanol can be seen in Table 1.
2. *P. deshayesii* is reddish-brown with orange and chocolate over-tones, and a relatively uniform appearance, lacking spots and streaks of darker colour. *P. valenciennii* is light brown but may have many blackish spots on the mantle, sometimes elongated as bands. From our observations and the literature we observe that European specimens invariably possess dark spots, but these are absent in specimens of N. African origin (Fig. 1A, 1G).
3. As pointed out by Morelet (1845), and confirmed here, live specimens of Algerian origin exude an unpleasant smell. This has not been observed in European specimens. This odour disappears when preserved in ethanol.
4. The shell shows several differences: The protoconch is very smooth, greenish yellow in *P. deshayesii* but amber brown and lightly ornamented in *P. valenciennii*. The spiral part appears more dominant in *P. deshayesii*, but its curvature is longer in *P. valenciennii*. There is a slight difference in size: 4 mm to the junction with the limacella in *P. deshayesii;* 3.5 mm in P. valenciennii. Total shell size (protoconch + limacella): larger in *P. valenciennii*, 17×13 mm on maximum dimensions; smaller in *P. deshayesii*, 15×8 mm. The limacella of *P. valenciennii* is clearly wider (13 mm versus 8 mm), and shows a more pronounced membranous ridge which gives it a broader palette appearance. The angle of separation of the protoconch and the limacella is also much more closed in *P. valenciennii*. The limacella of this species is flatter and therefore less convex than that of *P. deshayesii*. We have observed a much greater development of the teeth of insertion at the inner

Table 1 Dimensions of *D. deshayesii* and *D. valenciennii* preserved in ethanol 70%.

Dimensions (in mm)	n	Length (max-$\bar{x}$-min)	Wideness mantle area (max-$\bar{x}$-min)	Height mantle area (max-$\bar{x}$-min)
D. deshayesii (Tlemcen, Oran, Algeria)	11	34.3–26.73–17.2	19.0–13.47–10.5	18.6–14.05–7.5
D. valenciennii (Cádiz, Spain)	8	61.0–40.50–36.0	22.8–20.47–16.0	20.0–15.39–13.5

Table 2 Morpho-anatomical differences between *Drusia (Drusia) valenciennii* and *Drusia (Escutiella* nov. subgen.) *deshayesii.*

Character	*Drusia (Drusia) valenciennii*	*Drusia (Escutiella) deshayesii*
Average size (long×wide×high) in mm	40.50×20.47×15.39	26.47×13.47×14.05
Colour of dorsum	Light brown	Reddish chocolate
Spots and/or strips on the mantle	Always present. Black colour	No
Nauseating smell	No	Yes
Protoconch. Colour and texture	Amber.Lightly ornamented surface	Greenish. Very smooth
Protoconch. Spiral	Spiral less marked but longer	Spiral more marked but shorter
Protoconch. Wideness in the edge of limacella	3.5 mm	4 mm
Shell (Spiral protoconch + limacella). Higher dimensions (in mm)	17×13	15×8
Limacella. Shape and maximum wideness (in mm)	Elongated paddle. 8 mm	Wide paddle. 13 mm
Angle of separation. Protoconch – limacella	Closed	Open
Limacella	More convex	Flat
Jaw	Thick, more closed, horse-shoe shape	Thin. Open crescent shape
Radular formula	65 + C + 65 (118rows)	70 + C + 70 (120rows)
Morphology of central tooth	Without basal notch	Deep basal notch
Mesocone of central tooth	Short	Long
Wing-shape expansion of the external ectocone of central tooth	Small	Large
Hermaphrodite gland	Black	Light greyish
Ep /Cd	1.08(17/18 mm)	0.92(20/18 mm)
Penis	Smooth, without protuberance	With an elongated protuberance
Interior of penis	Thick papilla solid and elongated, sometimes accompanied by other accessory swellings	Three little swelling with other accessory staying into the protuberance
Interior of the epiphallus	No reticulated, Only rows of parallel folds	Reticulated, with longitudinal folds that set a kind of ligula
Atrial accessory appendices	One or two, very unequal, Length ratio : 2.42	Two unequal. Length ratio: 1.45
Interior of atrium	A big fold, fleshy, solid and thick	Two narrow and flexuous folds
Spermatophore. Number of tips of the anchoring plate	11–14	16
Spermatophore. Shape of the tips of the anchoring disc	Narrow, clearly curved downwards	Wider and less curved
Spermatophore. Diameter of the anchoring plate	0.35	0.54
Spermatophore. Distal portion of tail	Longitudinal ridges	Longitudinal ridges less marked

edge of the protoconch in *P. deshayesii* (Fig. 1B–F, 1H–K).

5. The jaw in *P. deshayesii* is thin and of an open crescent shape, while in *P. valenciennii* it is thicker and less open. Morelet (1845) describes the jaws as crescent-shaped and horseshoe-shaped, respectively (Fig. 5A, 5F).

6. The radular formulae are similar, over an average of four radulae per species, but not identical: *P. deshayesii*, 120 rows, with radular formula 70 + C + 70; *P. valenciennii*, 118 rows with radular formula 65 + C + 65.

Despite the different body sizes, the sizes of the radula are very similar. Dimensions: *P.*

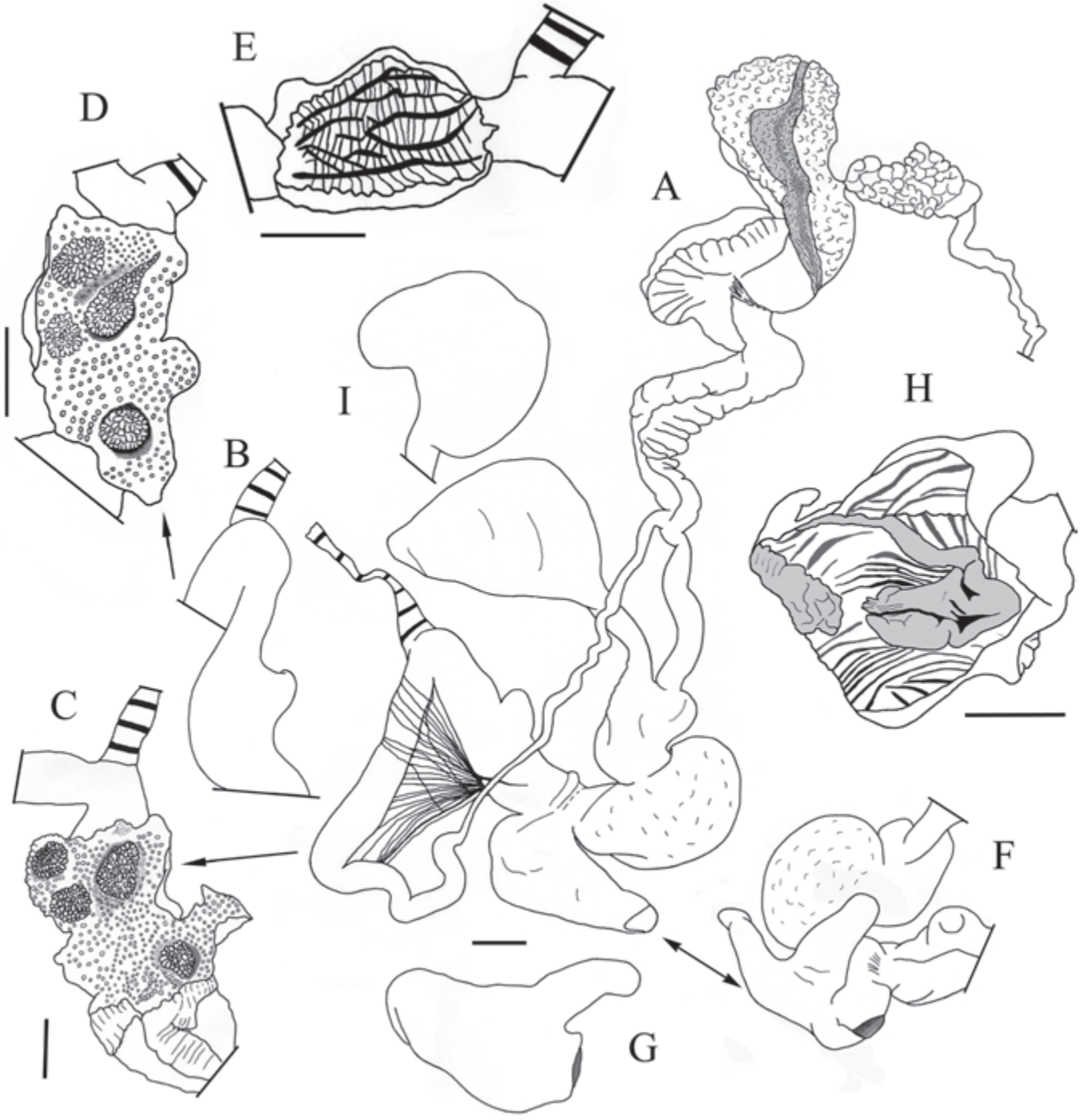

Figure 3 Reproductive system of *Drusia (Escutiella* subg. nov.*) deshayesii.* A General view. B Penis and insertion of the retractor muscle. C–D Interior of the penis from two different specimens. E Interior of the epiphallus. F Distal genitalia. G Distal genitalia (atrium) of another specimen. H Stimulator folds inside the atrium. I Bursa copulatrix of another specimen. Scales = 1 mm.

deshayesii, 6.75×3.95 mm; *P. valenciennii,* 7.0×4.0 mm.

7. There are differences in the morphology of radular teeth (Figs 5B–E, 5G–J). In *P. deshayesii*, the central tooth has a deep notch in the form of an isosceles triangle at the base of the mesocone, which is long, its base nearly reaching the apex of the triangle. Likewise, the base of the ectocones have winged expansions. The rest of the teeth have similar winged expansions at the base of the external ectocone but directed outwards.

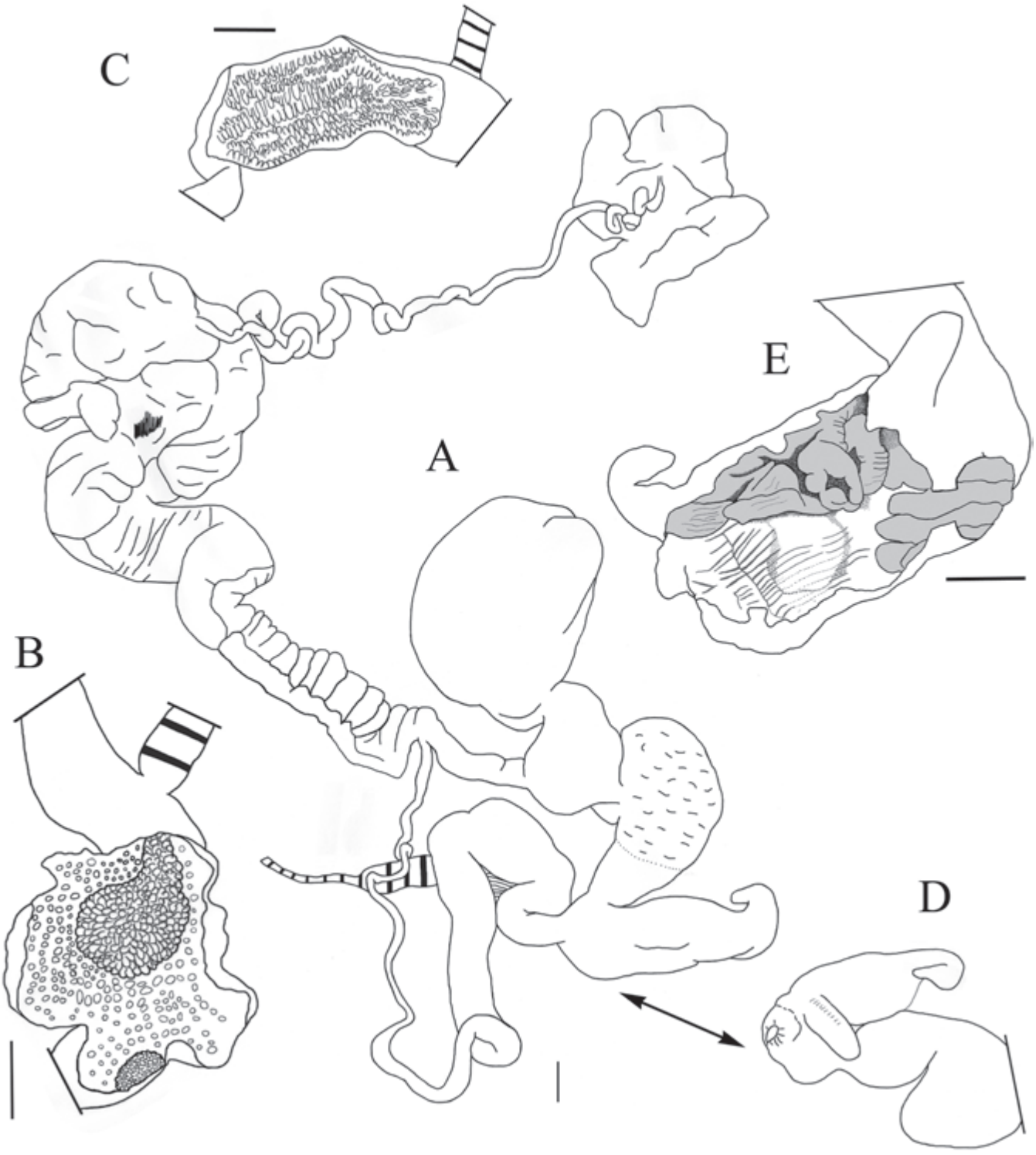

Figure 4 Reproductive system of *Drusia (Drusia) valenciennii*. A General view. B Interior of the penis. C Interior of the epiphallus. D Distal genitalia. Atrium with accessory appendices. E Interior of the atrium with large stimulator fold. Scales= 1 mm.

Parmacella valenciennii does not possess the notch, or it is barely visible. Wing shaped expansions of the central tooth ectocones are much smaller so the central tooth as a whole is lance-shaped. The mesocone is considerably shorter, reaching only the beginning of the ectocones. The other teeth have a slight outward expansion wing, far smaller than in *P. deshayesii*.

8. At least in the specimens we have dissected, the hermaphrodite gland of *P. deshayesii* is clear, gray, sometimes slightly greenish while that of *P. valenciennii* is very dark or black. The hermaphrodite duct is completely black in *P. valenciennii* and only dark with black areas in *P. deshayesii*.
9. The ratios between the length of epiphallus (Ep) and vas deferens (Cd) were taken in four exemplars of each taxon. *P. valenciennii*: 1.08; maximum length, Ep, 20 mm; Cd, 18 mm. *P. deshayesii*: 0.92; maximum length, Ep, 17 mm; Cd, 18 mm. Although the differences are not significant, we can state that the epiphallus is somewhat longer in *P. valenciennii.*
10. The inner wall of the penis is covered in both species with dense tubercles, but in *P. valenciennii* there is a long, thick and solid papilla inserted near the entrance of the epiphallus, with another accessory small swelling, present only in some individuals and located slightly above the free edge of the papilla. The internal structure of the penis in *P. deshayesii* differs from that of *P. valenciennii* with the papilla resolved into three small swellings, and the accessory swelling being present in all individuals studied. The accessory swelling is present in a long protuberance protruding from the wall of the penis to the outside (Figs 3C–D, 4B).
11. There are also notable differences in the epiphallus (Figs 3E, 4C). In *P. deshayesii* its internal walls have a few longitudinal, conspicuous folds (ligula), which form a kind of reticulum along with other small, transverse or oblique folds. In *P. valenciennii* the internal ornamentation of the epiphallus consists of several homogenous rows of pleats each with a rough surface; the rows are longitudinal developed and parallel.
12. According to the literature and our own observations, the atrium of *P. deshayesii* always has two corniform appendices somewhat uneven in size, with some curved edges and whose shape resembles a *croissant*. In *P. valenciennii* there are individuals with one or two appendices and in this case there are great differences in size, the shortest is straight and the longest is curved at the end (Figs 3F,G, 4A,D,E).

The average length ratio of both appendices, calculated from four individuals of each taxon (showing two appendices) is: *P. valenciennii*, 2.32; *P. deshayesii,* 1.45.

Of the eight samples of *P. valenciennii* studied, six had double-horned appendices (with very unequal tips as just noted) and two single appendices. In the latter, single appendices, were very long.
13. Within the atrium, *P. deshayesii* has two laminar and flexuous stimulator folds, one bigger than the other, while *P. valenciennii* has a single, large, fleshy, flexuous, fold which occupies much of the interior volume of the atrium (Figs 3H, 4E).
14. The full length of the genitalia and the relative length of the distal genitalia is very similar as a whole, if not almost identical in both taxa, but given the larger size of *P. valenciennii* we note that the proportional size of the genitalia of *P. deshayesii* is greater than that of *P. valenciennii.*
15. The spermatophore is proportionately larger in *P. deshayesii* and less twisted in its broad part. The number of points or hooks on the anchor disc is greater in *P. deshayesii* (Fig. 2C) than in *P. valenciennii* (Fig. 2H, 2I), being much broader and less curved backwards. The diameter of the anchoring disc is considerably wider in *P. deshayesii* (0.54 mm) than in *P. valenciennii* (0.35 mm). The distal spermatophore in *P. valenciennii* also has sinuous longitudinal ridges on the anchoring disk, these being less marked in *P. deshayesii.*

Taking into account all the differences above we regard *P. deshayesii* and *P. valenciennii* to be different at the species level. The respective ranges are, predominantly Algeria and Morocco for *P. deshayesi,* the southwest quadrant of the Iberian Peninsula for *P. valenciennii* (Table 2). Their areas of distribution appear well separated on both sides of the Strait of Gibraltar. Due to the huge traffic of goods between the two shores of the Mediterranean, it is possible that *P. deshayesii* could occur on the Iberian Peninsula, as suggested by Torres Mínguez (1926), or *P. valenciennii* in northern Africa. The differences between the two taxa are such that we consider them to belong to separate subgenera, which we will now define.

Update of the systematics of Parmacellidae Currently the family Parmacellidae comprises three genera (Schileyko, 2003): *Candaharia*, in Central Asia, with two subgenera and three species; *Cryptella* in the Canary Islands, with seven species lacking subgeneric divisions; and *Parmacella*, in North Africa, the Canary islands, southern Iberian Peninsula and southern France plus an area between the Black and Caspian seas, and comprising six or seven species without subgeneric division.

Gray (1855), in his catalogue of the pulmonates of the British Museum collection, includes up to 13 different genera within the family Arionidae in a systematic group that is currently invalid. Three of these genera, *Drusia, Parmacellus* and *Girasia*, include species within current concepts of the Parmacellidae. That author listed four species in the genus *Girasia* of which the second one, from Candahar (Afghanistan), was listed doubtfully, as *G.? rutellum* Hutton and currently corresponds to *Candaharia (Candaharia) rutellum* (Hutton 1849).

The same author included five species within *Parmacella*, incorrectly transcribed in the original paper as *Parmacellus*. The first to be listed was *P. olivieri* Cuvier. Eight species were included in *Drusia*, five of them doubtful. The first listed is *D. valenciennii*, which therefore should be considered as the type species of *Parmacella* according to Wiktor (1983). Schileyko (2003) indicated that there is no type species for *Drusia*, although the study of Wiktor (1983) was not taken into account.

Drusia as a name has not been used for over 150 years, except occasionally when it was cited as a junior synonym of *Parmacella*. The five doubtful *Drusia* mentioned above and listed by Gray (1855) do not correspond to current members of the Parmacellidae. But of the remaining three, two, *D.? deshayesii* Moquin-Tandon and *D.? alexandrinus* Ehrenberg (*sic*), are listed in fourth and fifth place respectively. corresponding without a doubt to the hitherto mentioned as *Parmacella deshayesii* and *Parmacella alexandrina* Ehrenberg, 1831, actually synonyms of *P. olivieri*. Later, Adams & Adams (1858) indicated that Gray, in a personal communication, reconsidered his classification and proposed to include the species assigned to *Drusia* and *Girasia* in the genus *Cryptella*. In consequence, *Drusia* became a junior synonym of *Cryptella* as well.

Within the genus *Parmacella* Cuvier 1804 subgeneric divisions have been applied. Zilch (1960) proposed three subgenera, *Proparmacella* Simroth 1912, *Kandaharia* Godwin-Austen 1914 (*sic*) and *Parmacella* s.str. He considered *Cryptella* Webb & Berthelot 1833, *Phosphorax* Webb & Berthelot 1833, *Clathropodium* Westerlund 1897 and *Drusia* as synonyms of *Parmacella*. Later, Wiktor (1983) proposed two subgenera, *Parmacella* s. str. and *Cryptella*. This system was by Alonso *et al*. (1985, 1986), among others. Finally Hutterer & Groh (1991) re-erected *Cryptella* as a genus, a decision followed by Schileyko (2003). After analyzing thoroughly the bibliography and comparing in depth samples of *P. deshayesii* and *P. valenciennii,* we believe that the existing schema for the six species currently recognised in *Parmacella* should be modified.

Two of these six species, *Parmacella olivieri* Cuvier 1804 and *P. festae* Gambetta 1925, both from the eastern North Africa (Libya and Egypt), differ from the others in: possessing an extended atrial entrance, running from the genital opening to the insertion of the atrial appendices; the lack of intra-atrial stimulators; and the presence of two atrial accessory appendices of very similar size. The other species have a shortened atrium, internal folds developed as stimulators, some of them very thick, and two atrial appendices differing in size, or else only one. We believe that these features are sufficient to assign them to two separate genera. So, *P. olivieri* and *P. festae*, would remain in the genus *Parmacella* because *P. olivieri* was described first (first ascribed to *Parmacella*) and has priority over *P. valenciennii* (first ascribed to *Drusia*). According to ICZN rules (Arts. 11 and 12) the name *Drusia* is available, so the remaining four species of *Parmacella* can be assigned here. We therefore propose *Drusia* for the species currently included in *Parmacella* minus *P. olivieri* and *P. festae*. Within it we propose two subgenera, *Drusia* s. str. with three species and *Escutiella* nov. subg. with one species. We illustrate this with an updated taxonomic key to the family Parmacellidae.

The proposed differentiation into two genera bears some resemblance to what was proposed by Wiktor (1981) for the family Milacidae Ellis 1926, which is close to the Parmacellidae. In this are two genera, *Milax* Gray 1855 and *Tandonia* Lessona et Pollonera 1882. According to Wiktor, these genera are scarcely distinguishable by their external appearance and even the general organization of their genitalia, but they differ in the large atrium of *Milax* with stimulator appendix (known as a corniform organ), and atrial accessory glands, while *Tandonia* has a small atrium, no corniform organ, at most one papilla, and the accessory glands open into the vagina.

Genus *Drusia* Gray 1855

Type species: Drusia valenncienii (Webb & Van Beneden 1836).

Table 3 Main morpho-anatomical differences between *Drusia (Drusia)* and *Drusia (Escutiella* nov. subg.). For further information see Table 2.

	Drusia (Drusia)	*Drusia* (*Escutiella* nov. subg.)
Average size	Bigger	Smaller
Spots and strokes on the mantle	Always	No
Limacella. Shape	Elongated paddle	Wide paddle
Separation angle Protoconch – limacella	Closed	More open
Penis	No protuberance	With protuberance
Interior of penis	Thick and solid papilla sometimes with other accessory lump	Some little swellings with other accessory lump joining the protuberance
Interior of epiphallus	No reticulated, rows of parallel folds	Reticulated,with longitudinal folds constituting a kind of ligula
Atrial accessory appendices	One or two, very unequal	Two unequal
Interior of the atrium	A big, solid and thick fold, except to *D. ibera*	Two flexuous and rather thin folds

Diagnosis Slugs of the family Parmacellidae with the dorsum and mantle light brown with black patches and/or bands, at least on the mantle. Animal large or very large. Vagina without caecum and with a swollen and bean-shaped perivaginal gland. Duct of the bursa copulatrix with a distal thickening. Genital atrium short, with one or two horn-like accessory appendices of very different sizes, which enter near the genital pore. One or more well-developed fleshy stimulator folds present in the atrium.

The new genus comprises four species: *Drusia ibera* (Eichwald 1841) in various parts of Central Asia (Schileyko, 2003); *D. tenerifensis* (Alonso, Ibáñez & Díaz 1985) from La Laguna, Tenerife, Canary Islands (Alonso, Ibáñez & Díaz, 1985); *D. valenciennii* from the southwest of the Iberian Peninsula; and *D. deshayesii* of northern Algeria and Morocco. Westerlund (1897) proposed the genus *Clathropodium* with the type species *C. vitrinaeforme* Westerlund 1897 for a type of slug, later identified (Wiktor, 1983) as *Parmacella ibera*. This does not affect the classification proposed here because the type species of *Drusia* is *D. valenciennii*. Similarly, Simroth (1912) proposed the genus *Euparmacella* for *Parmacella olivieri* sensu Simroth equivalent to *P. ibera* (= *D. ibera*) according to Wiktor (1983). For the same reason mentioned above, this last circumstance does not affect our proposed nomenclature.

It is our opinion that the first three species are closely related, with near identical appearance, except for the gigantism of *D. tenerifensis*, with colouration of a light brown tone with spots and dark bands on the mantle (Alonso *et al.*, 1985). *Drusia valenciennii* and *D. tenerifensis* possess stimulators with very thick and well-developed folds inside the atrium. Their limacellas appear to differ by being more spade-shaped in *D. tenerifensis* and their spermatophores by the anchoring plate appearing umbrella-shaped and somewhat curved in this species (Alonso *et al.*, 1985). It is possible that *D. tenerifensis* was originally an introduction of *D. valenciennii* from the Iberian Peninsula through the secular exchange of goods between the mainland and the Canaries. The other species, *D. deshayesi* is very different from *D. valenciennii*, as justified above, with uniform reddish brown colour, easily distinguishable on external features. Therefore, we propose the division of *Drusia* into two subgenera: *Drusia* s. str. and *Escutiella* nov. subgen. The list of the different morpho-anatomic features between these two subgenera is given in Table 3.

Subgenus *Drusia* Gray 1855

Diagnosis Dorsum and mantle light brown with black patches and/or bands, at least on the mantle. Animal large or very large (36 to 95 mm in *D. valenciennii* preserved in ethanol). One or two accessory atrial appendices, mainly of very different sizes (Tables 1, 2 and 3).

Three species: *Drusia (Drusia) valenciennii* (Webb & Van Beneden 1836), *Drusia (Drusia) ibera* (Eichwald 1841) and *Drusia (Drusia) ten-*

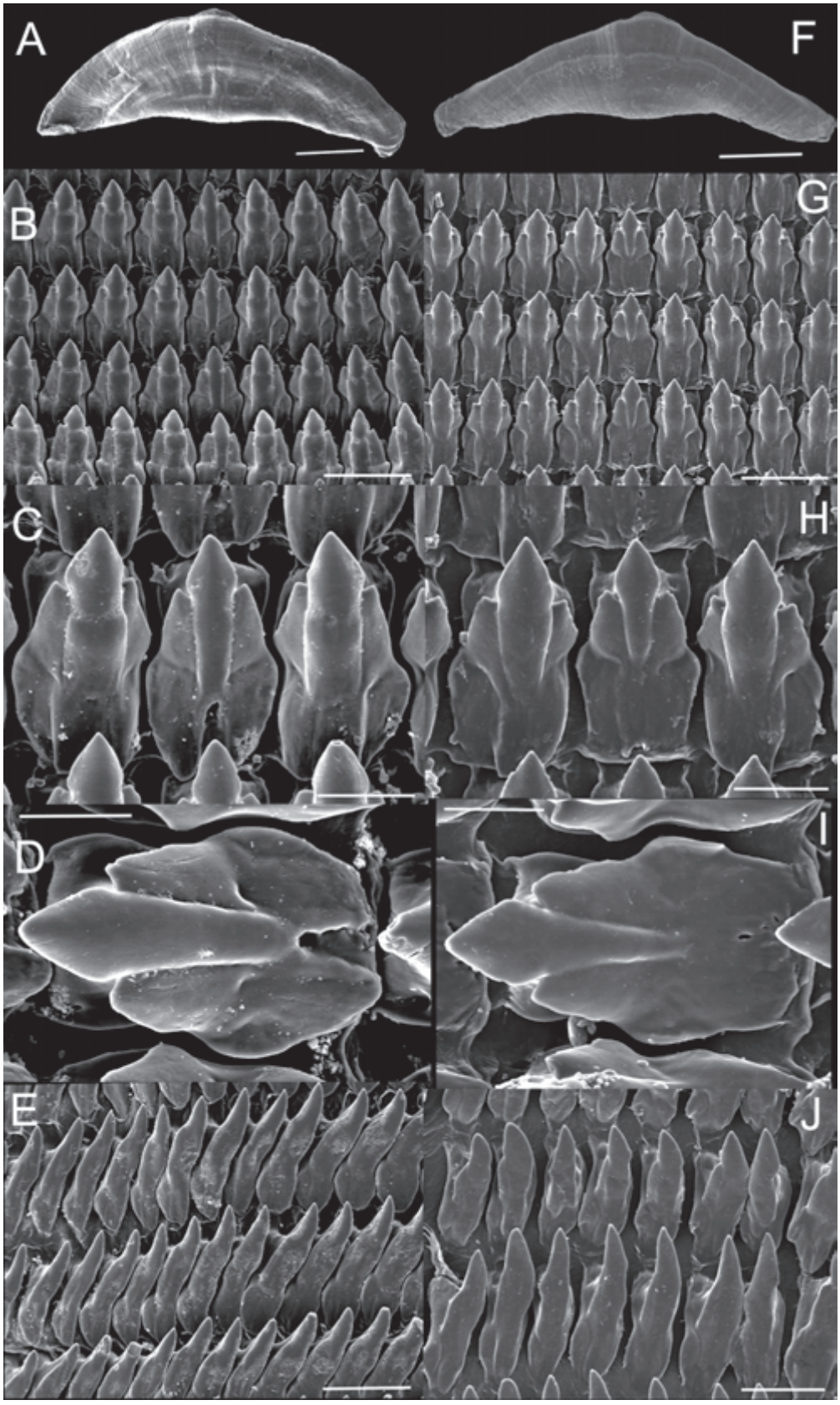

Figure 5 Comparison of radula and jaw of *Drusia (Escutiella* subg. nov.*) deshayesii* (A–E) and *D. (D.) valenciennii* (F–J): A, F Jaws; B, G General view of the central tooth and first laterals; C, H Central tooth and next laterals; D, I Detail of the central tooth; E, J Marginal teeth. Scales: A = 600 µm; B, G = 70 µm; C, H = 30 µm; D, I = 20 µm; E = 50 µm; F = 800 µm; J = 40 µm.

erifensis (Alonso, Ibáñez & Díaz 1985). At present nothing is known about the type series of any of the first two taxa: Wiktor (1983) states Spain and Portugal as *terra typical*; about *D. ibera* Kantor, Vinarski, Schileyko & Sysoev (2009) note that the types are unknown and referred to a type locality "in Iberia", Georgia, with quotation marks, as do Likharev & Wiktor (1980). The type range should however refer to the eastern part of the actual state of Georgia, the ancient kingdom of Iberia, as the Greeks named, a fact that generated much confusion enters the two "Iberia" among the ancient geographers. Therefore we designate. *D.(D.) valenciennii* (Webb & Van Beneden, 1836) as type species of *Drusia*, and select a neotype (Fig. 1G) according to the conditions required by the ICZN (Art. 75.3). Since we did not find specimens of this species in the locality of the nominal taxon, Alcantara (Lisbon, Portugal), one specimen from the mountains of Constantina (Seville, Spain) has been selected as neotype and so this locality is the new *locus typicus* for this taxon (Art. 76.3 ICZN). It is deposited in the collection of the Museu Valencià d'Història Natural (MVHN) of Valencia (Spain) with the code MVHNnº1627 (44 mm in ethanol 70%).

Subgenus nov. *Escutiella* Martínez-Ortí & Borredà

Diagnosis Dorsum and mantle a uniform reddish-brown, without darker spots or bands. Size medium (average length 27 mm preserved in ethanol). The penis has a protuberance in the middle and internally it contains several bumps, including one located in a more proximal position that is housed inside the protuberance while the others, slightly separated from it, are in a more distal position. Interior of the epiphallus with reticular ornamentation. Two accessory atrial appendices differ slightly in size.

Etymology Genus dedicated to Mr. Vicent Escutia, a mathematics teacher and a great amateur of malacology and collaborator of the authors, as well as co-collector of both species of *Drusia*.

One species: *Drusia (Escutiella) deshayesii* (Moquin-Tandon 1848). Type species designated by monotypy of *Escutiella* nov. subgen. (Article 68.3, ICZN). Since no one knows the whereabouts of the type series, we proceed to designate an appropriate neotype (Fig. 1A), which is deposited in the malacological collection of the MVHN in Valencia city (MVHNnº010210RT01-1) (31 mm in 70% ethanol), with type locality Oran, Ain Franin (Algeria).

Distribution and habitat *Drusia* Gray 1855 is distributed in the western Mediterranean: Iberian Peninsula and North Africa (Algeria and Morocco) (Fig. 6); Canary Islands; and an area of Central Asia that includes parts of Georgia, Transcaucasia and Iran. *Drusia* (*Drusia* s. str.), whose type species is *D. (D.) valenciennii* is distributed throughout the southwest quadrant of the Iberian Peninsula with very few localities north of the River Tagus, which may act as a natural barrier. In southern Portugal found in the regions of Algarve, Alto Alentejo and Baixo Alentejo, Estremadura and Ribatejo. In south-western Spain the provinces of Huelva, Cádiz, Seville, Córdoba, Málaga and Granada in Andalusia, the provinces of Cáceres and Badajoz in Extremadura, the provinces of Ciudad Real and Toledo in Castilla-La Mancha and in Gibraltar. *Drusia (D.) tenerifensis*, is only known in farmland on the outskirts of La Laguna (Tenerife, Canary Islands), and as we noted above could be an introduction of *D. (D.) valencienni* from the Iberian Peninsula. *Drusia (D.) ibera* occupies an area disjunct from the previous areas, centred between the Black Sea and the Caspian Sea. This is striking, but it is not the only case among slugs. So, recently Wiktor, Quintana & Beckmann (2007) have cited the genus *Gigantomilax* (O. Boettger 1883) in the Balearic Islands, with its known distribution area ranging from Albania to Armenia and Azherbajhan, focusing more or less in the Caucasus (Kantor *et al*., 2009; Dhora & Welter-Schultes, 1996). This results from *Limax majoricensis* Heynemann being reassigned to *Gigantomilax* as *Gigantomilax (Vitrinoides) majoricensis* (Heynemann), comparing it with *G. (V.) cecconi* Simroth 1916, of Israel. In a later work (Borredà & Martínez-Orti, 2008) we have adopted this nomenclature to describe a new species from Menorca, *Gigantomilax (Vitrinoides) benjaminus* Borredà & Martínez-Ortí 2008. Wiktor *et al*. (2007) compare the disjunct distribution of *Gigantomilax* with that of the family Parmacellidae. They also note similar fossil records. In fact, fossil or subfossil shells of Parmacellidae have been found in Italy, dating from the end of the Miocene to the Middle Pleistocene (Manganelli & Giusti,

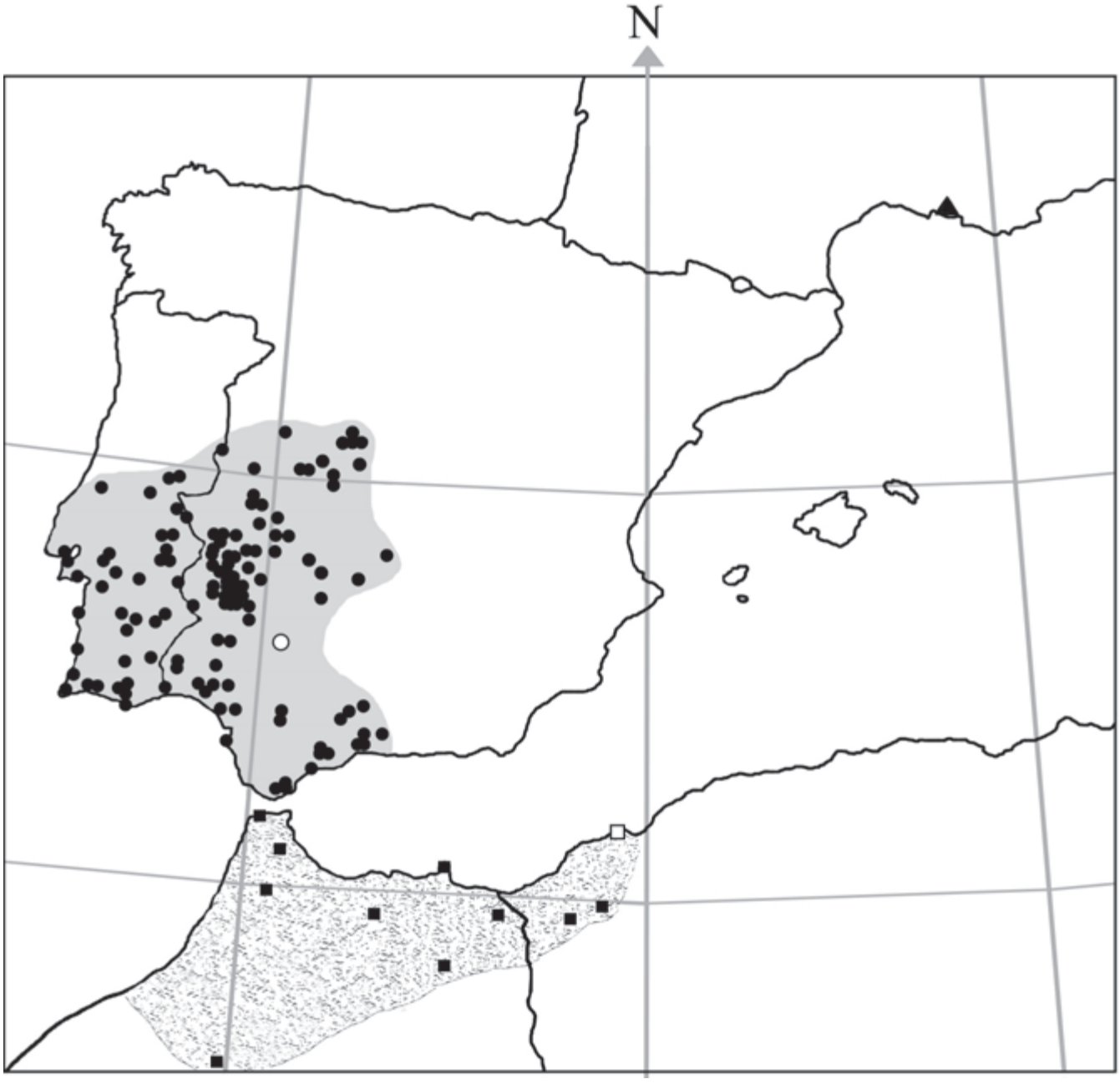

Figure 6 Geographical distribution of *Drusia* in the western Mediterranean. *Drusia (Drusia)* (shaded) and *Drusia (Escutiella* subg. nov.*)* (dot matrix). (●) *D. (D.) valenciennii*; (○) *Locus typicus* of *D. valenciennii*, mountains of Constantina, Sevilla (Spain); (■) *D. (E.) deshayesii*; (□) *Locus typicus* of *D. deshayesii*, Oran, Ain Franin (Algeria); (▲) *D.? gervaisii*, *locus typicus*, La Crau (Provence, France).

1993), and in France, as mentioned previously. Hutterer (1990) also cited this family in the Canary Islands (Pliocene), in Britain (Lower Pleistocene, Norfolk), in Ukraine (Late Pliocene) and in Poland (Eocene amber). It seems therefore that in the past the range of Parmacellidae was quite wide and that the gap between Georgia and the Iberian Peninsula actually is well within the former range.

In periods of the past, Parmacellidae were distributed from Afghanistan to the Canary Islands, including all of North Africa and most of Europe. The fossil record should be reviewed more thoroughly ina n attempt to identify the four existing genera, *Candaharia*, *Cryptella, Parmacella* and *Drusia*, with a view to properly explaining the current disjunct distribution. It also highlights the fact that the current distribution of the genus

Parmacella, in the sense applied here, is an area (Libya, Egypt) intermediate between the two areas occupied by *Drusia*, south of the Iberian Peninsula and Morocco-Algeria in the west and the Caucasus region in the east. In these two cases and according to the existing data there are gaps in both sides, one located in Tunisia and the main part of Libya, in the west, and the other in the Middle East and Turkey, in the east. Both areas exhibit notable xeric conditions, which may have acted as geographical barriers facilitating the process of speciation. Bourguignat (1877) noted that the different *Parmacella* species were found in the estuaries of large rivers such as the Tagus, Nile, Oued-el-Kebir (Oran), Rhone, Volga and Euphrates, sometimes extending to the limit of marine influence. *Escutiella* subgen. nov. is monospecific at present, with *D. (E.) deshayesii* the only species, and is confined to northern areas of Algeria and Morocco. In a recent study of slugs in Tunisia, Abbes *et al.* (2010) found no Parmacellidae. The parmacelles of Libya and Egypt as we have shown, belong to the *Parmacella*.

Drusia (D.) valenciennii is an herbivorous species of nocturnal habits, quite synanthropic, being abundant in cork oak pastures and olive groves, generally in large populations. The habits of *D. (E.) deshayesii* are very similar, and also fairly synanthropic. It lives in oak, pine, cork oak and olive groves and scrubland at low altitude and is often quite numerous. According to Bourguignat (1861a) this slug produces an extremely strong smell (nauseating in our experience), comparable to that of the Rubiaceae plant *Putoria tenella* (formerly *Putoria brevifolia*), common in North Africa and also living in Ain Franin (Oran) on which the slugs probably feed (personal observations). During our collection in March 2009 these slugs emitted a strong smell while in March 2010 after a very cold winter with the consequent delay in the arrival of spring, which influenced its activity, the smell was much weaker, probably because they had eaten less of the plant. We never perceived this smell in *D. (D.) valenciennii*, nor is there other evidence to that effect.

New Key to Family Parmacellidae

1. Vagina surrounded by an unthickened perivaginal gland and with a long digitiform caecum . . . . . *Candaharia* (2 subg., 4 spp.), Central Asia
– Vagina with a swollen perivaginal gland, well developed and bean-shaped, but without caecum 2
2. Genital atrium without accessory appendices; structure of the bursa copulatrix without thickening. . . . . *Cryptella* (7 spp.), Canary Islands
– Genital atrium with at least one accessory appendix, usually two; bursa copulatrix with a thickening where the spermatophore is anchored 3
3. Accessory atrial appendices of similar size; atrium with only small ridges in its wall, lacking fleshy stimulators. . . . .*Parmacella* (2 spp.), Libya, Egypt 4
– Accessory atrial appendices of very different size, sometimes only one; distal part of the atrium short; stimulators present as one or more large fleshy folds *Drusia* . . . . . (4 spp.) 5
4. Protoconch ornamented with small parallel spiral grooves; epiphallus very long, with two loops. . . . . .*P. festae*
– Protoconch smooth; epiphallus shorter and with a single loop. . . . . .*P. olivieri*
5. Mantle with dark spots and/or bands; body size larger than that of *Escutiella* subg. nov.; atrial appendices of evidently different sizes . . . . . .*D. (Drusia* s. str.)..6
– Mantle and dorsum of a uniform brown colour; body size medium (27 mm in ethanol on average); atrial appendices of similar size or at laest less evidently different; individuals often with a strong smell . . . . . *D.* (*Escutiella*) *deshayesii* . . . . . Morocco, Algeria
6. Shell with limacella shovel-shaped, very broad; body size large (70–95 mm in ethanol); spermatophore anchoring plate curved and umbrella-like in shape . . . . . *D. (D.) tenerifensis*. . . . . Tenerife
– shell with Limacella oval in shape, much narrower; body size small; spermatophore anchoring plate almost flat. 7
7. Limacella wide (length/width <1.60); stimulator fold inside the atrium thin and little developed. . .*D. (D.) ibera* . . Georgia, Kazakhstan and other countries east of the Caspian
– Limacella much narrower (length/width >1.85); atrial appendices of very different sizes, sometimes only one present; single very thick stimulator fold present inside the atrium, occupying most of the intra-atrial space . . . . . *D.(D.) valenciennii*. . . . . south-west Iberia.

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