

# A REVISION OF THE LAND-SNAIL GENERA *OTALA* AND *EOBANIA* (GASTROPODA, HELICIDAE) IN MOROCCO AND ALGERIA

DAVID T. HOLYOAK & GERALDINE A. HOLYOAK

Quinta da Cachopa, Rua da Barcoila no. 274, Barcoila, 6100-014 Cabeçudo, Portugal

**Abstract** A taxonomic revision is presented of the genera *Otala* and *Eobania* in Morocco and Algeria based mostly on large collections of shells and anatomical specimens made in 1984, 1986 and 2016. Both genera, but especially *Otala*, show remarkably wide variations in shell coloration, size and form between local populations but often also much variation within the same population. Both genera have suffered from recognition of far too many species, resulting from the remarkably variable shell characters of local populations and acceptance of narrowly defined «morphological species». During the nineteenth century J.-R. Bourguignat dominated this work in Algeria and during the early twentieth century it was continued in Morocco by P. Pallary who was active as a shell dealer. For *Otala sensu lato* this resulted in a total of about 130 species names from the W. Maghreb region placed in five genera, frequently causing difficulties in reaching secure identifications. The present study reassesses variability in shells and genital anatomy from a total of 329 population samples and attempts to apply a biological rather than a morphological species concept. We recognise only five species of *Otala* in the region (*O. lactea*, *O. punctata*, *O. xanthodon* (syn. *dupotetiana*), *O. tingitana*, *O. hieroglyphicula*), and a single species of *Eobania* (*E. vermiculata*), present a key for their identification, synonymies, distribution maps and illustrations of their shells and genital anatomy. The ranges and ecology of these species are discussed and their morphological evolution is reconsidered in the light of recently published molecular phylogenies. A neotype is designated for *O. lactea* and the type localities are restricted for *O. punctata* and *O. xanthodon*.

**Key words** *Otala*, *Eobania*, *Helicidae*, taxonomy, nomenclature, shells, genital anatomy, Morocco, Algeria, habitats, distribution, evolution, intraspecific variation, hybridization

## INTRODUCTION

The large handsomely coloured shells of the land-snail genus *Otala* and allied *Helicidae* have delighted collectors over several centuries. During the nineteenth century large numbers of species were named on the basis of small differences in shell size, form and coloration by J.-R. Bourguignat and his followers (the “Nouvelle École”: see Dance, 1970a, 1970b; Heller, 2009: 256). For example, Westerlund (1889: 411–427, 430–442) listed 69 species for what would nowadays be regarded as *Otala*, and 8 of *Eobania*. The list for *Otala* had increased further by the time of the review by Pallary (1914) and this author named still more from Morocco in later years (Pallary, 1939b).

Nevertheless, the wide variability within populations of at least the Iberian *Otala* and the lack of anatomical differences between most of them implied to subsequent workers that most of these names should be relegated to synonymy. Hence, over the past few decades there has been near unanimity in recognising just two variable species of *Otala* in Spain and Portugal, *O. lactea* (O.F.

Müller 1774) and *O. punctata* (O.F. Müller 1774), representing a return to the treatment adopted by Hidalgo (1875, 1884) who illustrated the wide variability in their shells. The conchologically rather similar *Helix vermiculata* O.F. Müller 1774 was placed by some early authors with *Otala* in *Helix* (*Macularia*) (e.g. Tryon, 1888) or *Helix* (*Archelix*) (e.g. Germain, 1908), but shown to be anatomically distinct and separated generically as *Eobania vermiculata* (O.F. Müller 1774) by Hesse (1920: 25–32), whose treatment has persisted.

The representatives of *Otala*, *Eobania* and allied genera in the western part of the Maghreb region of north-west Africa (Morocco, Algeria and Tunisia) suffered especially badly from the fashion of splitting by the Nouvelle École. Bourguignat’s (1863–1864) early monograph *Malacologie de l’Algérie* gave detailed descriptions of species (some of them finely split) and numerous good illustrations, but most of his later publications dealing with them had poorer descriptions and no figures. The absence of illustrations from the later works appears to have been associated with his acrimonious responses to criticism by Kobelt (1882, *Iconographie*, (2) 1 (1/2), pp. 29–31, cf. Bourguignat [in Péchaud],

1883: 54–56) of his splitting, which focused on the genus *Otala*, as discussed below. Bourguignat also sought to confuse his critics on *Otala* in two co-authored publications (Servain, 1880; Péchaud, 1883) which were in fact largely written by him (Dance, 1970a, 1970b). Both works contained references to original descriptions mainly of new *Helix* [*Otala*] cited as “*Bourguignat*, Spec. noviss. moll. n° ..., 1878)” with numbers from 101 upwards to 125. However, that publication never existed as shown by Connolly (1934); the 25 original descriptions in fact having appeared in the co-authored works cited.

Paul Pallary (b. 1869, d. 1942) lived for much of his life in Oran, Algeria, working as a school-teacher. During his spare time he collected and studied shells, taking full advantage of the opportunities to explore and collect the previously almost unknown faunas of inland districts of Morocco, which gradually became accessible as French military expeditions subdued the indigenous tribes. Pallary was the last of the great splitters of western Palearctic snail species (Fischer & Fischer-Piette, 1946; Dance, 1970a: 81), carrying the tradition of the Nouvelle École forward into the 1930s: he named and described over 900 species and named an even larger number of varieties, often without descriptions. He was also a shell dealer, and issued regular lists of snail shells available for purchase (Heller, 2009: 256). Unfortunately, it appears that he understood very well that “A shell with a new name is more valuable in a pecuniary point of view than one with an old and well-known name” (Gray, 1868).

Even during the nineteenth century the multiplication of species names by Bourguignat, Westerlund and others led to considerable difficulties in identification in what had become a finely divided matrix of character combinations. These problems arose not only with their newer species (e.g. Locard, 1899: 39, “correcting” misidentifications by Kobelt, 1884; cf. Kobelt, 1881, 1892, Dance, 1970a: 74), but also with those species having older descriptions (e.g. Locard, 1899: 37–38).

The problems in correcting the finely split and muddled taxonomy left behind by the Nouvelle École and by Pallary are considerable (Dance, 1970a: 82). The collections were mostly of shells, with few anatomical specimens. Their shells were not collected as representative samples of

typical populations, on the contrary, undamaged shells of extreme forms appear to have been prized. Localities were sometimes vague. Material from drift deposits of lengthy ephemeral river systems such as the Oued Moulouya and from Mediterranean sea-shores was often collected, as were subfossil shells. Descriptions in the contemporary literature were commonly poor and illustrations lacking (or, with Pallary, reproductions of half-tone photographs varying in quality). The historic specimens are now scattered as single exemplars or small samples among the museums of the world (with local concentrations, especially at MHNG and MNHN, with Pallary’s material also well represented at ANSP, NHMUK, NMW.Z, SMF). Type specimens were often not labelled as such; occasionally though, other specimens were labelled as “type” that were collected after the name was published.

Judging the limits of biological species from the old material is thus difficult or sometimes impossible. Realisation of this led to fieldwork in 1984, 1986 and 2016 to collect new population samples or at least typical representative specimens from a large number of widespread localities in Morocco and Algeria, including anatomical specimens where possible. This paper is based on study of the *Otala* and *Eobania* from that material, along with the reinterpretation of old literature and specimens that is essential to establish correct nomenclature.

In the meantime, Razkin *et al.* (2015) have provided a more detailed molecular phylogeny of the Helicoidea than was hitherto available, with sufficient sampling of Iberian and Maghreb taxa of Helicidae to provide useful guidelines for taxonomic rearrangements. Although many more taxa need to be studied, the new insights provided by the molecular data provide a helpful framework for revisions at species-level based on morphological studies.

The present study therefore attempts to produce a usable classification into species of the W. Maghreb taxa of *Otala* and *Eobania* based on a biological species concept. A fuller explanation of the criteria used in judging species status is set out in the Discussion later in this paper. However, it has been taken as axiomatic that the species recognised should be identifiable from morphological characters, of shells, genital anatomy, or both. The most recent faunal list reported 421 species of terrestrial molluscs from Morocco

(Rour, Chahlaoui & Van Goethem, 2002), but that total was based on a compilation that did not revise many of the finely split species named by Pallary (e.g. 1939b). Walther, Neiber & Hausdorf (2016) have recently used a combination of morphological and molecular studies to argue that the mainly Moroccan genus *Rossmassleria* (Helicidae) comprises one polytypic species, rather than the up to 12 nominal species into which it had hitherto been classified. More such revised classifications remain necessary for comparative faunistic and zoogeographical studies and in assessing the conservation status of taxa. The intention here is to make a further contribution to replacing the current confusion over the limits of some of the species of *W. Maghreb* helicid land snails and their generic treatment.

## METHODS

During the summers of 1984 and 1986 extensive fieldwork was carried out in Morocco and Algeria to collect land snails. 296 of the numbered sites that were sampled yielded *Otala* or *Eobania*. These locations were widely scattered across the Mediterranean zone and its desert fringes in both countries. Each site represented an area of <1km<sup>2</sup>, usually much less and typically collecting was from within a radius of <300m of our vehicle. An attempt was made to collect all land snail species present, with a good representative sample of each, although the oldest and most damaged shells were discarded when large quantities of better material were accumulated by the three collectors involved. Locations were recorded on the basis of vehicle mileage readings and study of contemporary Michelin (1: 1 million scale) road maps; coordinates of latitude and longitude were added from these notes soon after the fieldwork was completed. Altitudes were estimated during the fieldwork using a barometric altimeter which was reset regularly at known altitudes. Habitats were described in the field at all sites; on the infrequent occasions when drifted material (e.g. from beside wadi beds) was collected this was always noted. Living specimens were lacking at many sites and often scarce and elusive where they were present. They were always collected where possible, those of the large Helicidae being killed the same evening using boiling water, a method which unfortunately resulted in hard brittle bodies that are difficult to dissect. The

bodies or a sample of them were then preserved in 70% industrial methylated spirit (ims). The material involved has been housed at NMW.Z since 1988 and is listed in a compressed form in the Appendix (available online).

Supplementary fieldwork focussed on large Helicidae was carried out by the authors during March and May 2016 at 67 sites in Morocco, 33 of which yielded samples of *Otala*. Localities and altitudes were recorded using a hand-held GPS (Garmin Etrex High Sensitivity, accurate to within <10m). Habitat notes including bedrock type and vegetation were recorded at all sites. Living specimens were sought at all sites and their diurnal resting places were recorded. Samples of these were mostly drowned in water for 24 hours, then preserved in 80% ims for later anatomical study.

In order to map species distributions in a meaningful manner, it is necessary to distinguish living populations from old or fossil shells. To achieve this, the specimens were categorised (see Appendix) as: (a) living or fresh dead shells, (b) old shells, or (c) subfossil or fossil. The "fresh" dead shells category comprised only those shells retaining most of the original coloration (with little or no bleaching) and much of the periostracum. Subfossil shells were those recorded as such in the field notes, mostly where their origin from stratified deposits was evident. The "old shells" category has thus become a large residue, varying from worn bleached shells of no great age (but lacking a live occupant) to shells from the ground surface that might sometimes have been unearthed from a Holocene deposit. Selected additional locality records from published sources are mapped for four of the species; those used being restricted to records where the species identification appears reliable, the locality was at least reasonably precisely stated and the place could be located using available maps, gazetteers, or Google Earth.

Shell descriptions in the species accounts are intended to be brief, so they do not account for every uncommon variant. Only the main characters that vary between the species are covered, but others are noted under the generic heading. Adult shells were distinguished from those of immatures by presence of a markedly thickened and reflected edge to the peristome. Shell breadth and height were measured with vernier callipers accurate to *ca* 0.05mm, but the measurement

of height is approximate because the greatest height from lower lip of aperture to apex of spire is widely offset laterally from the columellar axis. Whorls were counted following the method shown by Kerney & Cameron (1979: 13).

Up to five dark bands are often present on the shell, as in many genera of Helicoidea. We follow a system for describing the bands devised by G. von Martens, and described, e.g., by Taylor (1910: 290–294), that has been widely used with *Cepaea nemoralis* (Linnaeus 1758). Thus the bands are numbered from the uppermost downwards as 12345 (bands 1–3 being above the periphery, 4 and 5 beneath it); missing bands being denoted by 0, e.g. 00305 would represent a shell with only the middle and lowest bands present. Bands are often fused and this is denoted by parentheses in the formula, e.g. 1(23)45 has bands 2 and 3 fused to form a single broader band. Since fusion of bands can occur at any point, it was assessed on the body whorl at 90° to the aperture.

Shells and genital anatomy were examined using Meiji RZ series stereo-microscopes and high intensity illumination via twin fibre-optic swan necks. The drawings of anatomy were made with a Meiji drawing tube from genitalia removed from the bodies. Anatomical descriptions refer to proximal and distal in relation to the gonad.

Although forming part of the methodology adopted, criteria used for distinguishing species from local forms or variants and some of the observations underlying them were refined as this study progressed. They are therefore considered in the Discussion following the species accounts. Our reasons for not recognising subspecies are also considered there.

Synonymies given below for each species are intended to give all species-group names. To save space, they do not cover all citations of species-group names, all their uses in combination with different generic names, or every published misidentification or spelling error, although the aim has been to include all of the more important literature for Morocco and Algeria. For countries other than Morocco and Algeria only valid species-group names and the treatment from a few major works are listed. Most of the many old published “reidentifications” seeking to transfer citations or figures from what we regard as one synonym to another synonym of the same species are also ignored (e.g. from Pallary, 1914: 22–23).

The synonymies list many varietal names that have never been used at species or subspecies rank, but give few additional details of them. Such varietal names were produced in large numbers by Bourguignat, Pallary and other malacologists studying Helicidae in the W. Maghreb. These names are almost invariably names of variant individuals so they are regarded as infrasubspecific here, not names of variant populations which would be regarded as subspecific. Hence it is clear under the *ICZN Code of Zoological Nomenclature*, Art. 45.6.1. and 45.6.4, “it is infrasubspecific if ... the content of the work unambiguously reveals that the name was proposed for an infrasubspecific entity”. Infrasubspecific names are unavailable for zoological nomenclature, unless “either adopted as the valid name of a species or subspecies or ... treated as a senior homonym” prior to 1985 and other requirements are met (Art. 10.2, 45.6.4.1); this applies to very few of the names considered in this paper and those few are treated fully. The book of shell photographs by Cossignani (2014) created trinomial names for some taxa by using an earlier varietal name as a subspecies epithet, e.g. with *Tingitana laffitteana cretata* (Pallary 1928) (*op. cit.*, p. 107); the subspecies epithet involved is nevertheless unavailable in all of those instances since its adoption for a subspecies occurred after 1985.

Many of the varietal names had little or no description associated with them. Thus, for *O. lactea*, Locard (1899: 38) added “des var. *major*, *minor*, *alta*, *depressa*, *grisea*, *fusca*, *albida*, etc., qui se définissent d’elles-mêmes”. The last phrase, which can be translated as “which define themselves”, was also used repeatedly by Pallary in the early twentieth century. Using the modern *ICZN Code* most such names would be disregarded as *nomina nuda* because there is no description. In the residue where there is a description, many of the oft-repeated names such as *major*, *minor*, *alta* and *depressa*, must nowadays be discounted as junior homonyms. That situation arises quite often because both Bourguignat (e.g. 1863–1864) and Pallary evidently followed the older practice of regarding varietal names of each species in a genus as independent of those of the other species (cf. Pilsbry, 1939: xvi), so that they created numerous homonyms, occasionally even on the same page. Pallary also frequently separated “Variétés ex forma” from “Variétés ex colore” and it is likely that a single specimen sometimes

served as the basis for new names in both categories (e.g. *Tingitana tingitana* var. *minor-pullata* of Pallary, 1919: pl. 2 fig. 2).

Taxa treated amongst *Otala* in the literature as *Archelix Pallaryi* A. Koch 1909 (in Kobelt, 1909: 134–135; Hesse, 1911: 68–70, 94, 100, 111, pl. 442 figs 14–19; Pallary, 1914: 20, pl. 1 fig. 5; 1920b: 36) and *Archelix Le Chatelieri* Pallary 1917 (Pallary, 1917: 133, pl. 5 fig. 1) are regarded here as species of other genera of the Otalini, which will be reviewed in a separate publication.

Abbreviations: ANSP Academy of Natural Sciences, Philadelphia, U.S.A.; B greatest shell breadth; BP years before present; CGAH Private collection of G.A. and D.T. Holyoak; H greatest shell height; H&S Holyoak & Seddon Collection at NMW.Z; Icon. *Iconographie* (of Rossmässler, continued by Kobelt); ims industrial methylated spirit; Ma millions of years before present; MHNG Muséum d'Histoire Naturelle, Ville de Genève, Switzerland; MMM Museo Malacologico Piceno, Cupra Marittima, Italy; MNHN Muséum National d'Histoire Naturelle, Paris, France; NHMUK The Natural History Museum, London, U.K.; NMW.Z Department of BioSyB, National Museums and Galleries of Wales, Cardiff, U.K.; n.v. original not verified; SMF Forschungsinstitut Senckenberg, Germany; syn. synonym; t. tome; TL type locality; UTM Universal Transverse Mercator (map grid).

## TAXONOMY, DESCRIPTIONS AND DISTRIBUTION

### FAMILY HELICIDAE Rafinesque 1815

#### Subfamily Helicinae Rafinesque 1815

#### Tribe Otalini G. Pfeffer 1930 (p. 138 (288)) (as Otalae)

Recognition of this tribe follows the molecular-phylogenetic study by Razkin *et al.* (2015), who assigned the following genera to it: *Alabastrina* Kobelt 1904, *Atlasica* Pallary 1917, *Cantareus* Risso 1826, *Cornu* Born 1778, *Eobania* P. Hesse 1913, *Maurohelix* P. Hesse 1917, *Otala* Schumacher 1817, *Rossmässleria* P. Hesse 1907.

#### Genus *Otala* Schumacher 1817

Essai nouv. syst. Vers test., pp. 58, 191–192. Type species (by subsequent designation of Pilsbry, 1895, Man. Conch., (2) 9, p. 323) *Otala atomaria*

Schumacher 1817 (= *Helix lactea* O.F. Müller 1774) (*vide* Bank, Groh & Ripken, 2002: 139). The generic name is treated as a feminine noun.

syn. *Archelix* Albers 1850, Die Heliceen ..., p. 98 (type species *Helix lactea* O.F. Müller 1774, by subsequent designation of Schileyko 2006, Treatise 13, p. 1796).

*Dupotetia* Kobelt 1904, Iconogr., (2) 11, p. 132 (as subgenus of *Iberus*) (type species *Helix dupotetiana* Terver 1839, by monotypy according to I.C.Z.N. Code art. 68.3 since Kobelt's p. 132 lists only this species, although his p. 195 lists additional species).

*Deserticola* P. Hesse 1911, Iconogr., (2) 16, pp. 95, 102 (as section within *Archelix* (*Dupotetia*) (type species "*Helix tigris* Gervais" i.e. Marès 1857, by original designation; see below for authorship of species name).

*Tingitana* Pallary 1918, Bull. Soc. Hist. nat. Afr. Nord, 9 (7), p. 145 (as section of *Archelix*) (type species *Archelix Minettei* Pallary 1917 by original designation).

*Michaudia* Pallary 1926, J. Conchyl., 70 (1), p. 15 (as section of *Helix*) (type species *Helix hieroglyphicula* Michaud 1833 by original designation), non *Michaudia* Locard 1883, Annales de l'Academie de Macon, (2) 6, pp. 80. 81.

*Joleaudiella* Pallary 1926, J. Conchyl., 70 (1), p. 18 (as section of *Helix*) (type species *H. Vanvinciquia* Crosse by original designation).

*Pachydupotetia* G. Pfeffer 1930, Geol. Paleont. Abh., (N.F.), 17 (3), p. 185 (335) (type species *Helix jobaeana* Crosse 1861 following I.C.Z.N. Code art. 68.3 because Pfeffer, *loc. cit.*, stated that the three species previously recognised from the Algerian "Miocene" are conspecific; i.e. *P. jobaeana* (Crosse) (p. 186 (336)), *P. dumortieriana* (Crosse) (p. 186 (336)), and *P. subsenilis* (Crosse) (p. 187 (337)).

*Platyotala* G. Pfeffer 1930, Paleont. Abh., (N.F.), 17 (3), p. 188 (338) (type species *Helix vanvinciquia* Crosse 1861 by monotypy).

Razkin *et al.* (2015) provided molecular data on a wide range of taxa of Helicoidea, with a phylogenetic tree showing *Dupotetia* and *Tingitana* are apparently nested within *Otala s.l.*, so not worthy even of subgeneric rank, unless both *O. punctata* and *O. lactea* are also separated subgenerically. Three morphological synapomorphies also tend to differentiate this enlarged genus *Otala* from other Otalini: (1) a free oviduct longer than the vagina; (2) presence of a peculiar gland at the edge of the mantle (Hesse's Gland: see below);

(3) brown coloration inside the shell aperture that contrasts markedly with the whitish ground-colour of the underside of the shell just outside the aperture (secondarily lost only in a few populations of *O. xanthodon*, but present also in *Loxana punica* (Morelet 1851)).

Descriptions given below give characters of the shells that vary between the species. In the genus as a whole, shells are dextral (very rarely sinistral: Fig. 4A), moderately large to large, strong, with umbilicus covered, aperture downturned in last part of body whorl and the peristome interrupted on parietal area of shell mouth (normally without a parietal callus).

Germain (1930: 189) commented on a "glande de Hesse" (Hesse's Gland) that appeared to be peculiar to this genus (Hesse, 1911: 94), although we have recently confirmed its presence also in *Loxana rerayana* (Mousson 1873) (CGAH M35). Hesse (1909: 29, pl. 427 fig. 4, pl. 428 fig. 6, pl. 430 figs 21, 22) described it as resembling a whitish bean sliced in half, located on the left side of the body adjacent to the front outer edge of the mantle. The white or yellowish glandular structure measured up to 23mm long, 10mm high and 5mm thick in the largest snails; the outer side is convex, the inner side deeply concave. His microscopic study of sections revealed intermixed mucus-gland-cells (Schleimdrüsenzellen) with homogenous contents and albumen-gland-cells (Eiweissdrüsenzellen) with granular contents. The function of the secretions from the gland was uncertain.

We have confirmed occurrence of Hesse's Gland in all our *Otala* specimens which were deliberately dissected to check for it: *O. punctata* (four; with large glands), *O. lactea* (five; glands respectively 5.5 and 9.5mm long, 11.5×4, 12×3, 13×6mm), *O. xanthodon* (nine; 4–8.5mm long, the shortest on specimen with very small distal genitalia) and *O. tingitana* (two; lengths 6.5 and 8mm long). Its shape when viewed dorsally varied from ovoid-cylindrical to elliptical, curved around outline of left edge of mantle and tapered to a point at each end. Longitudinal sections revealed that the empty inner lumen of the gland passes into a slit like opening to the outside of the left flank of the body, under the overhanging mantle-collar.

The genital anatomy is mainly similar in all the species studied, as became apparent long ago from studies by Hesse (1909, 1910, 1911,

1934), although these did not report on structures inside the genital atrium, penis and vagina. Hence, this section defines the terminology used and gives a generalised description, with only those characters which vary interspecifically and are of potential value for species identification being discussed under the separate species headings. Fig. 7 illustrates the genital anatomy of representative specimens studied by us; Fig. 8 shows internal structures of the distal genitalia of *O. lactea*, and Table 1 compares these in other *Otala* species.

Other Helicidae are known to show considerable individual and geographical variations in measurements and proportions of the distal genitalia (Madec & Guiller, 1994; Van Osselaer & Tursch, 2000), and at least individual variability is also apparent in *Eobania* and *Otala*. Additional variation results from the stage of maturation of individual specimens, probably their reproductive history, and methods used to kill and fix specimens, which may produce artefacts. It is clear therefore that basing descriptions on single exemplars of a species greatly increases the risk of them being unrepresentative of the species as a whole. For this reason we record the number of (mature adult) individuals dissected by us and the number of populations represented by them. Samples studied remained very small for fully mature *O. tingitana*; *O. hieroglyphicula* is described largely from two published accounts.

The general structure of the genitalia is of semi-diaulic monotrematic type ("incomplete triaulic" monotrematic condition of Giusti *et al.*, 1995: 74). The gonad (ovotestis) is located inside the upper lobe of the digestive gland on its inner (columellar) side. From it arises the thin hermaphroditic duct that functions as a seminal vesicle; it is nearly straight proximally, twisting and convoluted in the middle, ending distally in a small concealed talon. The albumen gland is large, long, somewhat flattened, narrowly tongue-shaped; at its base the spermoviduct (second hermaphroditic duct) arises, with a single lumen that comprises the female channel (with seminal groove) fused with the prostate gland. The convoluted spermoviduct passes distally along the columellar side of the body.

The vas deferens is a long thin tube, initially following the sperm groove in the prostate gland along the spermoviduct, passing deep into the angle between the distal vagina and distal penis

**Table 1** Internal structure of distal genitalia of *Otala* species. Abbreviations: *O. hie.*, *O. hieroglyphicula*; *O. lac.*, *O. lactea*; *O. pun.*, *O. punctata*; *O. tin.*, *O. tingitana*; *O. xan.*, *O. xanthodon*. See Figs 7 and 8 and text for terminology used. Information on *O. hieroglyphicula* is based on Schileyko (2006: 1793–1794, fig. 2297B).

	<i>O. hie.</i>	<i>O. lac.</i>	<i>O. pun.</i>	<i>O. tin.</i>	<i>O. xan.</i>
<b>ATRIAL FLAP</b>					
Relative size	no data	medium	small	large	large
Length (mm)	no data	3.0	2.5	2.0	3.0
Basin margin	no data	raised	raised	involute	raised
Orientation, of apex <i>in situ</i>	no data	only across upper atrium	only across upper atrium	also entering distal vagina	also entering distal vagina
Extension on to wall of vagina	no data	none	none	as thickened band	as raised lamella
<b>DISTAL PENIS INNER WALL OF DISTAL HALF</b>					
	no data	low transverse ridges & some longitudinal pattern	5–7 raised nearly longitudinal ridges	almost smooth	nearly smooth, or low weak ribs, or 1 or 2 stronger longitudinal ribs
<b>DISTAL VERGE</b>					
	well developed, ±cylindrical	shortly cylindrical	shortly cylindrical	shortly cylindrical	short to inconspicuous
<b>CHAMBER OF PROXIMAL PENIS</b>					
Lumen	meandering	±straight	± straight	strongly meandering	± straight
Inner wall structures	smooth?	close, irregular, transverse ridges	tall, transverse folds	no data	tall to flatter transverse ridges

(and loosely attached to both of these by connective tissues), ending in the penial complex where it passes subterminally into the wider epiphallus.

A long or moderately long penial flagellum is present, continuing as a thinner tube beyond the proximal end of the epiphallus and frequently convoluted or coiled *in situ*. The epiphallus is well developed, connecting the junction of the vas deferens with the proximal end of the penis; it is thick-walled with a narrow central lumen (showing two high internal ridges in sections), usually somewhat shorter than the penis, sometimes about as long, and distinctly narrower than the proximal penis. The penial retractor muscle forms a moderately long and slender to rather short and stout strap, inserting on the epiphallus towards its distal end, the other end being attached to the inside of the wall of the mantle.

Externally, the penis usually appears to consist of two cylindrical parts, a *distal* part comprising up to about one-half of the total length is thinner, a *proximal* part comprising up to about

two-thirds of the total length is up to twice as wide. The entire penis has a thin membranous elastic *outer sheath*. Longitudinal sections (e.g. Schileyko, 2006: 1797–1798, fig. 2304C; Fig. 8) reveal that the middle part of the penis contains two verges, each of them muscular and cylindrical with central lumen and apical (distal) pore; the *proximal verge* formed by the distal end of the epiphallus where it enters the proximal part of the penis is usually smaller than the *distal verge* located at the junction of proximal and distal parts of the penis. The distal penis has a rather thin and elastic muscular wall around a relatively wide empty lumen. The proximal penis has an *inner sheath* enveloping a thicker muscular *penis wall*, surrounding a lumen (the *chamber*). In *O. lactea*, *O. punctata* and *O. xanthodon* the muscular wall of the proximal penis is roughly cylindrical, surrounding a rather large and almost straight chamber, which has transverse folds or ridges on its inner surface (Fig. 8). In *O. tingitana* (based on the single mature specimen available)

and perhaps *O. hieroglyphicula*, the interior of the proximal penis comprises a markedly meandering chamber with thinner muscular walls (Table 1). It is unclear whether this difference has arisen through simplification of a formerly convoluted structure to give the straight chamber of *O. lactea*, or *vice versa*. Functional aspects are also uncertain but potentially significant: in *O. lactea* the proximal penis might be eversible during mating so that the proximal verge extends the overall penis length by passing through the distal verge (as reported by Alonso & Ibáñez, 2007 for *Hemicycla*), whereas the complex convolutions of the chamber would appear to preclude its eversion in *O. tingitana*.

The external genital pore is low on the front of the body, close to and below the base of the right ommatophore. The genital atrium is a short to very short cylinder, dividing proximally into the distal penis and the distal end of the vagina. Schileyko (*loc. cit.*) noted and figured for *O. lactea* a “tubercular stimulator” at the atrium just distal to the exit from the lumen of the distal penis. Our study of specimens of four *Otala* species shows instead that this *atrial flap* is a flattened, muscular, more or less broadly ovate and tongue-shaped structure (resembling a conical tubercle only in a lateral view), with a concave depression in its proximal surface and convex distal surface. Its base is broadly attached to the upper wall of the atrium, below the exit from the distal penis (Fig. 8). The relative size of the flap varies between different *Otala* species (Table 1), being largest in *O. tingitana* and *O. xanthodon*, where it is longer than the diameter of the upper part of the atrial lumen and the tip of the atrial flap is directed proximally into the most distal part of the vagina. Those two species also have the thickened muscular base of the flap continuing proximally along the wall of the vagina, respectively as a thickened band (*O. tingitana*) or raised lamella (*O. xanthodon*).

Alonso & Ibáñez (2007: 16) argued that the “tubercular penial stimulator” described by Schileyko (2006) is unlikely to function in producing stimuli, because of the presence of the dart sac complex. Instead (*op. cit.*: 5, 16) they suggested it may be a “contact organ”, this presumably facilitating positioning or synchronisation of the partners during mating when the atrium is everted. While that interpretation may be correct, the complex structure and large size of the flap in

*Otala* suggests it might also have additional functions, since when the snails are not mating (or at early and late stages during mating) it largely closes access to the penial lumen from the atrium, and depending on its position, it could obstruct access to and from the vagina.

Schileyko (*loc. cit.*) also described and figured a “well-developed sphincter” on the distal penis of *O. lactea* just before its lumen passes into the genital atrium. However, our material shows that the thickened muscular wall passing from the base of the atrial flap to the distal vagina does not fully encircle the distal exit of the penis.

The vagina is shorter than the penis, nearly cylindrical distally, more ovoid and often somewhat flattened proximally, with more or less muscular walls that are mainly smooth internally. A single shortly elliptical to ovoid dart sac (“stylophore”) composed mainly of muscles arises from the wall of the vagina distal to the mucus glands; it has a narrow central lumen that enters the vagina from a prominent tubercle. The dart is nearly straight to rather strongly curved, tapering apically to a sharp point, basal crown with *ca* 12–14 grooves; middle part of dart with four longitudinal wings of similar height, set at right angles to each other, each wing widened apically to give T-shape in transverse section.

There are two large mucus glands (“digitiform glands”), each arising on opposite sides of the upper end of the vagina just distal to separation of the free oviduct, each with a pore entering the inner wall of the vagina just proximal to the exit from the dart sac. Each mucus gland is forked in its lower half (into two or sometimes three branches), then forked again into two or more branches nearer the apex, before dividing approximately palmately into numerous long slender cylindrical processes (glandular sacs); the basal branches of the glands are thick-walled and muscular, the processes thin-walled and fragile. The number and position of the branches and the detailed arrangement of the processes shows considerable variation between individual snails.

The free oviduct is a rather long tube, much longer than the vagina and variably convoluted *in situ*, its distal end is defined by insertion of the bursa copulatrix duct which appears to continue proximally in line with the vagina, whereas the closest part of the free oviduct diverges at right angles before returning to a proximal course



towards the junction with the distal end of the spermoviduct.

The bursa copulatrix (gametolytic gland) is a thin-walled sac, subspherical except where it tapers into the duct. Although positioned close to the proximal end of the spermoviduct, it does not touch the other genital organs, lying among connective tissue close to the diaphragm. The bursa copulatrix duct is long, slender and cylindrical throughout most of its length, widening  $\pm$  progressively into the bursa near the proximal end, and into the free oviduct close to its distal end; when *in situ*, the duct is loosely attached to the spermoviduct and although variably sinuous it follows its course proximally, leaving it abruptly near the distal end of the albumen gland. The duct of the bursa always has a long and often wider diverticulum, which diverges from near its distal end, terminating alongside the proximal end of the spermoviduct at about the same level as the bursa sac; the diverticulum is longer than the duct, its greater length being accommodated in more sinuous folds and loops as it passes proximally alongside the spermoviduct.

The right ommatophore passes through the angle between the distal parts of penis and vagina as in many other genera of Helicoidea.

There is very little published information on mating in *Otala* to guide interpretation of functional aspects of the genital anatomy, although the main features appear to correspond to those in other Helicidae which have been studied in detail (*Helix pomatia* Linnaeus 1758 – Lind, 1973; *Theba pisana* (O.F. Müller 1774) and *Cantareus apertus* (Born 1778) – Giusti & Andreini, 1988; *Hemicycla* – Alonso & Ibáñez, 2007). Our own observations and subsequent dissection of a mating pair of *O. lactea* confirm some aspects and also add to what is known, although there were peculiar features as described below.

The snails studied were collected near Palmela, Estremadura, Portugal on 6 Sept. 2016 (CGAH P432), and kept alive in a plastic box with several conspecifics. They were found *in copula* positioned head to head at 14:20 hours on 11 Sept. (both having penis everted and inserted into partner), at 14:40 they were still head to head but with penises retracted, at 15:40 there was no obvious change, so they were separated and immediately drowned in cool water. They were dead by 09:00 on 12 Sept., when they were transferred to 80% ims. The bodies were carefully pulled from

the shells on 13 Sept. and transferred to new ims, then dissected on 14 Sept. They are retained in CGAH.

These snails showed that during mating the atrium is everted, the distal penis is everted through it, and the proximal penis passes outwards through both (it was unclear whether the proximal penis was itself everted). The everted penis of each partner was seen to be simultaneously present in the female tract of the other and a spermatophore is transferred by each of them. Surprisingly, dissection of both snails revealed no trace of a spermatophore in the diverticulum of the bursa copulatrix, which functions as the site of spermatophore uptake during mating in Helicoidea (Lind, 1973; Alonso & Ibáñez, 2007) and which has been shown in *Arianta arbustorum* (Linnaeus 1758) to function in dissolving or at least partly breaking down the wall of the spermatophore (Beese, Beier & Baur, 2006). Instead, both of these *O. lactea* had a spermatophore occupying the proximal half of its free oviduct, this part of the organ having been forced into three or four helical coils with distended walls, through which the spermatophore was partly visible by translucence. One snail had a short section of its free oviduct close to the proximal end double the width of the other distended part with three projections from the outer wall (resembling two papillae and a short caecum), these apparently being artefacts produced by the spermatophore pushing outwards. There seems little doubt that passage of the incoming spermatophores in both partners from the vagina into the free oviduct rather than the diverticulum via the bursa copulatrix duct was abnormal, presumably caused by drowning the snails in water. Unfortunately, we have been unable to find other *Otala* spermatophores during routine dissections of preserved specimens. Future investigation should seek to check the “normal” location of spermatophore uptake after killing mated *Otala* in a different manner, e.g. by rapid freeezing.

The fragile and perishable spermatophores of these *O. lactea* were not removed from the respective free oviducts, although several small holes were cut to allow investigation of fragments, which provide some new information on spermatophore morphology. The observations fit in with the general assumption that the long, slender, cylindrical, curved structure involved was formed inside the epiphallus (the slightly wider

head portion of spermatophore) and the flagellum (the longer tapering tail portion). The spermatophore fragments recovered and observed were translucent when moist, becoming whitish as they flattened or collapsed on drying. Those found in the more proximal part of the free oviduct (i.e. head of spermatophore) were *ca* 0.5mm in diameter, in section broadly oval with several low ridges running along the length of each of the longer faces. Fragments from more distal locations in the free oviduct (of tail of spermatophore) were 0.45–0.5mm in diameter, round in section or flattened along one edge.

*Otala punctata* (O.F. Müller 1774) Figs 1E–G, 2A, 7A, 9, 11

*Helix punctata* O.F. Müller 1774, Verm. terr. fluv., 2, p. 21, no. 220, TL Italia (error, as pointed out by Pallary, 1914: 14–16, who demonstrated that the type material matches specimens “ziemlich häufig im Departement Oran”; accordingly, the type locality is herewith restricted to Wilaya of Oran in NW. Algeria) – Name placed on Official List of Specific Names in Zoology by Opinion 1996 (I.C.Z.N., 2002); Rossmässler (1854: 14–15, fig. 3 dart); Bourguignat (1864: t. 1, 117–119, pl. 12 figs 1–4), with var. *major* (p. 119), distributional data (p. 119); Bourguignat (1864: t. 2, 319, 329, 357, 362), in Morocco at Sidi-Merzoug, près de la frontière algérienne (p. 319); Hidalgo (1875: t. 1, 205, 222, pl. 11 figs 100–106), Spain, Balearic Is.; Paladilhe (1875: 79), Route de Tanger à Meknès [perhaps an error; there are no recent records in the region]; Morelet (1880: 20), Sidi Merzoug (Bourg.), etc.; *H. punctata* vars., Kobelt (1882: 29–31, pl. 9 figs 73–80, pl. 10 figs 81–88); Hidalgo (1884: t. 2, pl. 37 fig. 435, pl. 44 figs 518–519); Pilsbry (1895: 324), with syn. *myristigmæa* (Bgt.) Péch., f. *galena* (Bgt.) Péch., vars *punctatissima* Jen., *bredeana* Deb., *apalolena* Bgt.; Hidalgo (1909: 211–212); Pallary (1914: 13, 14–17), nomenclatural history; *Helix* (*Macularia*) *punctata*, Albers & Martens (1860: 133); Tryon (1888: 131–132, pl. 39 figs 99, 100), range listed included Canary Is. [error], and “introduced into Cuba and other Spanish colonies”; *Macularia punctata* var. *maurula* Kobelt (1904: 63–65, pl. 296 figs 1897), the var. newly described from westlichen Theile der Provinz Oran; *Archelix punctata*, Hesse (1909: 32–42, pls 427–432); Hesse (1911: 94, 95, 97–98, 103, 105, 109, 110); *Archelix punctata melanostoma*

Hesse 1909, Iconogr., (2) 16 (1/2), pp. 39–40, TL Tetuan [named as new subspecies; according to Hesse the anatomy mainly matched *A. punctata*, but with a rather long penial flagellum, slightly longer than penis or epiphallus on both snails dissected; therefore in our view a form of *O. lactea* could perhaps have been involved]; Hesse (1911: 109); Pallary (1929a: 50), Tétouan; Borrero & Rosenberg (2015), lectotype designated; *Archelix punctata globosa* Pallary (1914: 18, pl. 2 fig. 3), apparently intended as a new var. rather than subsp., since Pallary commented “Diese Form ist ausserordentlich selten in der Umgebung von Oran; *Archelix punctata*, Pallary (1920b: 31, 35–36), with Var. *melanostoma* P. Hesse reported from Tétouan [incorrectly?] despite a strong resemblance to *A. galena* Bgt., with suggestion that same var. occurs at other localities in NW. Morocco; *A. punctata*, Pallary (1922c: 250, 1939b: 107); Pallary (1923b: 280), Berkane; with var. *polita* from Islas Chafarinas and Tatsfachs (Oulad Settout); Llabador (1952: 108–109); *Otala punctata*, Rour *et al.* (2002: 195); Beckmann (2007: 126, fig. 154); Barbara & Schembri (2008); De Mattia & Mascia (2011); Irikov & Gerdzhikov (2013: 3), reported from near El Hajeb (NC. Morocco) and incorrectly claimed as new to Morocco [the identification apparently needs confirmation]; *Otala* (*Otala*) *punctata*, Puente (1994: 805–814, fig. 150); Falkner, Ripken & Falkner (2002: 54).

*Helix punctatissima* Jennison in Rossmässler 1837, Icon., (1) 1 (5/6), p. 8, pl. 22 fig. 302 b, TL von Barcellona; Bourguignat (1863–1870: pl. 35 figs 6–8, n.v.), Prov. Oran in der Küstenzone von Rio Salado bis Mostaganem (*fide* Hesse, 1911: 97); Tryon (1888: 130, 131), listed as syn. of both *O. lactea* [in error] and *O. punctata*; Pallary (1914: 16); *Archelix punctatissima*, Pallary (1914: 17).

*Helix lactea* (pars; non O.F. Müller 1774), Rossmässler (1837: 7–8, pl. 22 figs 302a, 403b only); Rossmässler (1839: 1–2, pl. 41 fig. 548 only). *Helix lactea* var. *polita* Gassies 1856, Descr. Coquilles Cap. Mayran, p. 7 [in offprint], n.v., TL voisinage de Nemours; Pallary (1914: 16); *Archelix polita*, Hesse (1911: 109); *Archelix polita* Gassies, Pallary (1914: 19), Nemours, with var. *minor* from Marnia, Nemours, Tlemcen und la Tafna; *Archelix polita* Var. *mahroufiana* Pallary (1917: 137–138), from: plaine du Mahrouf entre Debdou et la Moulouïa (Maroc); *Archelix polita*, Pallary (1920b: 36), Taforalt; Foum Sefrou dans les Beni Znassen; Taourirt; Pallary (1939b: 107);



**Figure 1** Shells of *Eobania vermiculata* (A–D) and *Otala punctata* (E–G); A Algeria, 35°17'N 6°38'E, NMW.Z 1993.051.1248; B Algeria, 36°21'N 5°39'E, NMW.Z 1993.051.880; C Portugal, Baixo Alentejo, edge of Montijo service area on A13 motorway (UTM: 29S 052874/428658), 27 Oct. 2014, CGAH PT 414; D Malta, SW. of Il-Quattara (UTM: 33SW 425/694), 18 Mar. 2005, CGAH; E Algeria, 35°34'N 0°00'E, NMW.Z 1993.051.1678; F ditto; G Algeria, 35°07'N 1°36'W, NMW.Z 1993.051.1745. See Appendix for additional details of N. African specimens. Scale bar 20mm.

Llabador (1936: 200), Massif des M'Sirdas au sud-ouest de Nemours; *Archelix polita mahroufi-ana*, Pallary (1939a: 64–65); *Otala polita*, Rour et al. (2002: 195); Cossignani (2014: 91), figs of two shells, from Berkane.

*Helix dupotetiana* (non Terver 1839) vars *aspera*, *fasciata*, Gassies (1856: 107, figs 13, 14), n.v.

*Helix calendyma* Bourguignat 1864, Malac. Alg., 1, pp. 126–127, pl. 11 figs 10–13, TL l'île de Rachgoun, à l'embouchure de la Tafna; Bourguignat (1864: t. 2, 333); Servain (1880: 39–40), "Echantillons identiques à ceux de l'Algérie. – Environs de Malaga"; Bourguignat [in Péchaud] (1883: 77), Plain de Tlelat, près Oran; environs de Malaga, en Espagne; Westerlund (1889: 434); *Archelix calendyma*, Pallary (1914: 18, pl. 1 fig. 2), zwischen Cap Lindlès und der Grenze des Departements Oran, an der ganzen Küste auf sandigen Terrain.

*Helix myristigmaea*, Bourguignat 1867, Moll. Nouv. Litig., pl. 35 figs 6–8, n.v. [very well figured according to Pallary 1899a: 104]; Bourguignat [in Péchaud] (1883: 57–58), Sud de l'Espagne; Maroc; province d'Oran [it is argued that this taxon is not a form of *O. punctata*, but this author adopted very narrow species limits]; Westerlund (1889: 419–420), with vars *punctatissima* Jenisson and *bredeana* Deb.; Pallary (1899a: 103–104), au Maroc [noted as one of "formes de la série de l'*H. lactea*", so allocation to *O. punctata* uncertain]; Pallary (1914: 14); *Macularia myristigmaea* vars, Kobelt (1903: 42–43, pl. 286 figs 1835, 1836), both sent by Pallary, fig. 1836 as typical *myristigmaea*, fig. 1835 as var. *incrassata*; *Helix (Marmorana) myristigmaea*, Pallary (1901: 133–134, 191, 194, 197), Algerian fossils, "= *H. punctata* auct. non Müller"; Pallary (1904: 49), "localités diverses" in Morocco; *Archelix myristigmaea*, Hesse (1909: 36–37, pl. 429 fig. 18, 430 fig. 19) (based on *Helix myristigmaea* from Cap Falcon, *op. cit.*, p. 32); Pallary (1939b: 107); *Otala myristigmae* [sic], Rour et al. (2002: 195).

*Helix apalolena* Bourguignat 1867, Moll. Nouv. Litig., [8<sup>th</sup> Déc.], p. 233, no. 74, pl. 35 [or 25?], figs 1–5, n.v.; Servain (1880: 36), bords de la mer à Del Prat, près de Barcelone; Bourguignat [in Péchaud] (1883: 57), Le Rousillon, les Baléares et toute la région orientale espagnole des Pyrénées à Valence [it is odd that this species was treated in the "groupe de *lactea*"; Westerlund (1889: 421); Pallary (1914: 16); *Helix (Macularia) punctata* var. *apalolena*, Tryon (1888: 132, pl. 64 figs 4, 5); *Archelix punctata apalolena*, Hesse (1909:

37–38, pl. 431; 1910: pl. 432 figs 33A–D) (based on *Helix apalolena* from Valencia und Korsika, *op. cit.*, 1909: 33); *Archelix apalolena*, Hesse (1911: 109, 110); Pallary (1914: 17); Germain (1930: 189, fig. 159, pl. 4 figs 97–98); Pallary (1939b: 107).

*Helix lucentumensis* Bourguignat in Servain 1880, Étude Moll. Espagne Port., pp. 34–36, TL montagne du Pelop, près d'Alcoy, à 10 lieues d'Alicante; also reported près d'Elche entre Alicante et Murcie; with Var. B *Helix Pelopica* Bourguignat in Servain 1880, TL [same as for typical form] at montagne du Pelop, près d'Alcoy, à 10 lieues d'Alicante; earlier work cited here as "Bourguignat, Spec. Noviss. Moll. n° 103, 1878" is fictitious (Connolly, 1934); Bourguignat [in Péchaud] (1883: 46), entre Tlemcen et Lalla Maghnia [again citing fictitious work by "Bourguignat, Spec. Noviss. Moll. n° 103, 1878"]; Westerlund (1889: 422–423), with var. *pelopica*; Pilsbry (1895: 326); *Archelix punctata lucentumensis*, Hesse (1909: 38–39, 1910: pl. 432 figs 34–37); (based on *Helix lucentumensis*, from Lalla Marnia, *op. cit.*, 1909: 22); *A.[r]helix lucentumensis* Bgt., Pallary (1914: 19), treated as syn. of *A. polita* Gassies, with suggestion that name "richtiger *lucentensis*".

*Helix acanonica* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afrique, pp. 46–47, TL environs d'Oran; earlier work cited there as "Bourguignat, Spec. Nov., n° 104, 1878" is fictitious (Connolly, 1934); Westerlund (1889: 423); Pilsbry (1895: 326); *Helix (Macularia) acanonica*, Pallary (1901: 134, 191, 197), Algerian fossils.

*Helix eugastora* Bourguignat in Servain 1880, Étude Moll. Espagne Port., p. 38, TL abondante aux environs d'Oran; une variété un peu plus petite de cette espèce, dans les alluvions du Tage, près de Lisbonne; the earlier work cited there as "Bourguignat, Spec. noviss. moll., n° 108, 1878" is fictitious (Connolly, 1934); Bourguignat rather than Servain appears to be author of the short description published in 1880 because the wording is very similar to that by Bourguignat [in Péchaud] (1883: 54) that follows; Bourguignat [in Péchaud] (1883: 54, 60), très abondante dans toute la région qui avoisine Oran; en Espagne; acclimatée dans l'Amérique du Sud; with var. *zonulata* aux environs de Mascara, and variété *albinos*, named by Berthier as *Helix Victoriana* (p. 60); the earlier work cited there again as "Bourguignat, Spec. noviss. moll., n° 108, 1878" is fictitious (Connolly, 1934); Westerlund (1889: 421–422); [*Helix*] *eugastoria* [sic], Pilsbry (1895: 326); Locard

(1899: 39, Portugal [but unlikely to be *O. punctata* at the alluvions du Tage and Lisbonne localities cited]; *Helix (Macularia) eugastora*, Pallary (1901: 134, 193, 194, 197), Algerian fossils; *Archelix punctata eugastora*, Hesse (1909: 35–36, pl. 429 figs 16, 17) (based on *Helix eugastora* from El Aricha, *op. cit.*, p. 33); *Archelix eugastora*, Pallary (1939b: 107).

*Helix galena* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afrique, p. 59, TL environs d'Oran; signalée encore aux environs de Madrid et de Saragosse; with var *cincta*, from environs de Oran, de Tlemcen et de Mascara; earlier work cited there as "Bourguignat, Spec. noviss., n° 107, 1878" is fictitious (Connolly, 1934); Westerlund (1889: 421); *Helix (Marmorana) galena*, Pallary (1901: 133, 191, 197), Algerian fossils; Pallary (1904: 49), "localités diverses" in Morocco; *Archelix punctata galena*, Hesse (1909: 31, 33–35, pls 427–429 figs 12–15, 430), (based on *Helix galena*, from Oran and Boghari, *op. cit.*, p. 32); *Archelix galena*, Pallary (1939b: 107); *Otala galena*, Rour *et al.* (2002: 195).

*Helix baudotiana* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afrique, p. 60, TL Djebel Filauoucen, dans le massif das Trara, à l'est de Nedroma (province d'Oran); the earlier work cited there as "Bourguignat, Spec. noviss. moll., n° 112, 1878" is fictitious (Connolly, 1934); Westerlund (1889: 422); Pallary (1901: 4); [*Helix*] *bandotiana* [sic], Pilsbry (1895: 326); Pallary (1914: 16); *Archelix Baudotiana*, Pallary (1914: 17–18, pl. 2 fig. 2), bei Oran, Arzew, Le Sig und Pérregaux; Pallary (1939b: 107); *bandotiana* aucts., Richardson (1980) [error for *baudotiana*].

*Helix bouthyana* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afrique, pp. 49–50, TL environs de Perregaux; a larger variety (not named): alentours de Sebdou; Westerlund (1889: 433–434); Pilsbry (1895: 326); *Archelix Boutyi* Bgt., Pallary (1914: 18, pl. 2 fig. 4), unjustified emendation of name [cited as "Péchaud, l. c., S. 49–50", confirming that *H. bouthyana* was the species concerned]; *Archelix Bouthyana*, Pallary (1939b: 107).

*Helix Parisotiana* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afrique, pp. 50–51, TL dans la vallée d'Oum-el-Adham, près du ksar Boughrana, à 20 kilom. de Lalla-Maghnia [in NW. Algeria, near Moroccan border]; Westerlund (1889: 434); Pilsbry (1895: 326); *Archelix Parisotiana*, Pallary (1939b: 107).

*Helix Hermieri* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afrique, pp. 51–52, TL dans

la vallée d'Oum-el-Adham; sur les rochers, aux alentours de Lalla-Maghnia [in NW. Algeria near Moroccan border]; Westerlund (1889: 434); Pilsbry (1895: 326); *Archelix Hermieri*, Pallary (1939b: 107).

*Helix (Macularia) Duriezi* Debeaux mss. in Kobelt 1884, Nachrbl. d. malak. Ges., 16, p. 27, TL Oglat Tamestouta prov. Oranensis; *Helix duriezi* Deb., Westerlund (1889: 433); Pilsbry (1895: 326); *Archelix Duriezi*, Hesse (1911: 110); Pallary (1914: 19, pl. 2 fig. 5), Oglat Tamestouta (Sud oranais). *Helix rhummelensis* Tournouér MS., *nomen nudum* in Tournouér Collection, n.v.; *Helix (Macularia) rhummelensis* Pallary 1901, Mém. Soc. Géol. France, 22, pp. 135, 191, 197, pl. 1 fig. 22, with new var. *minor*, TL [fossil] calcaire lacustre d'Ain-el-Bey et de la base nord du dj. Tigmertz où elle est très commune [Algeria]; the name is validated by Pallary's description and fig.; he noted that it is allied to *Helix calendyma*.

*Archelix Cataloniensis* Pallary 1914, Nachrbl. d. malak. Ges., 46(1), p. 17 no. 3, pl. 1 figs 4, TL spanischen Küste von Valencia bis Barcelona, und auf den Balearen; new name along with brief description and figure validating *Helix lucentumensis* var. *H. pelopica* Bourguignat [in Péchaud] (1833: 46) (nom. nud.).

*Archelix Roselloi* Pallary 1914, Nachrbl. d. malak. Ges., 46(1), p. 17 no. 4, TL Carthagera [described only as "klein, mit dicker Lippe" ... "Sie ist die f. minor der vorhergehende", i.e. of *A. Cataloniensis*].

Sources of the following names that have appeared in the literature as synonyms of this species have not been traced; many of them are likely to be *nomina nuda* or errors; they are listed in alphabetical sequence of the epithets: *bredeana* Debeaux in Kobelt 1882; *globosa* Kobelt 1913; *Helix lactea*, A. Férussac (non O.F. Müller 1774); *Helix lactea* Bourguignat 1883 (not O.F. Müller 1774); *H. punctata* var. *magna* Schmidt 1855; *victoriana* Berthier in Westerlund 1889; *zonulata* Bourguignat in Westerlund 1889. For other synonyms and fuller citations of names from outside the W. Maghreb see Germain (1930: 189), Richardson (1980), Beckmann (2007: 126) and De Mattia & Mascia (2011).

*Shell* 314 shells examined from 39 localities (also comparative material from Portugal and Spain). Usual ranges, B 28.6–45.5, H 16.8–24.4mm, H/B 0.54–0.59, with 4.4–4.8 whorls. Shape low-depressed conical, flattened below, with rapidly

increasing whorls, the body whorl often relatively large; immatures and adults with rounded periphery; suture of moderate depth. Aperture oval (except where interrupted by penultimate whorl), with peristome slightly to rather strongly reflected; lower lip with small tooth variably evident near middle. Ground-colour whitish to cream or light brown, with up to five dull or dark brown or blackish-brown bands, type 1(23)45 being commonest, the bands often weak; dark areas of shell (especially the bands) usually with whitish spots. Peristome white, inside of aperture dull brown (varying to deep chestnut or purplish-brown), becoming gradually paler along parietal edge. Protoconch small, glossy, smooth or with weak radial ribs; teleoconch with irregular radial-tangential low ribs and lines, intersected by closely spaced fine spiral grooves; the underside somewhat smoother.

*Genital anatomy* Six specimens dissected from three localities (plus comparative material from Spain and Portugal). The species is usually distinctive in having the penial flagellum relatively shorter than in *O. lactea*, although it varies from shorter than the epiphallus (e.g. Puente, 1994: 814 fig. 850) to slightly longer (De Mattia & Masca, 2011: 41–42 figs 1, 3–6) or 1.5× its length (our Fig. 7A). Overall, the penis, epiphallus, flagellum and vagina may all appear relatively shorter in *O. punctata* than in *O. lactea*, when compared to their respective spermoviduct, dart sac and mucus glands (cf. Fig. 7A and 7B). However, individual and intrapopulation variability in proportions of organs of the distal genitalia is well known among other Helicidae (e.g. Van Osselaer & Tursch, 2000) and detailed study may be necessary for reliable comparisons of species. Internal structures of the genital atrium and penis provide a few more characters (Table 1), but none of them clearly separate *O. punctata* from *O. lactea*. For additional figures of genital anatomy of *O. punctata* see Hesse (1909: pls 427–430, 1910: pls 431–432) and Germain (1930: 189 fig. 159).

*Variation and taxonomy* Formerly split into several nominal species, as set out in the synonymy above, although Hidalgo (1875, 1884) recognised it as a single variable species in Iberia. Kobelt (1882, Icon., (2) 1 (1/2), pp. 29–31, pls 9, 10) clearly interpreted it as a variable and polytypic species for which he figured numerous forms as

varieties. This produced a lengthy and sarcastic response from Bourguignat (in Péchaud, 1883: 54–56), commencing: “qu’il n’a fait que montrer une fois de plus son ignorance; il n’est pas possible, en effet, d’accumuler, en aussi peu de pages et de figures, un si grand nombre d’erreurs.” Pilsbry (1895: 324) recognised several forms as varieties rather than separate species, apparently following Kobelt’s treatment.

Rossmässler (1854, Icon., (1) 3 (1/2), p. 14, quoting information from A. Schmidt) noted that the penial flagellum is longer in *H. lactea* than it is in *H. punctata*. This anatomical difference has been amply confirmed by later workers, as noted above. Hesse (1909) confirmed that anatomical differences are small or lacking between several forms he treated as subspecies or forms of *Archelix punctata* (see synonymy above; also Hesse, 1911: 97–98). However, his newly named *Archelix punctata melanostoma* had a relatively long penial flagellum, so that it could perhaps have been based on a form of *O. lactea*.

Through the latter part of the nineteenth century almost all studies recognised *H. punctata* as distinct from *H. lactea*, but the additional “species” associated with each of them varied considerably. The arrangements probably depended to a large extent on the weight attached to particular characters, sometimes the shell shape, sometimes the coloration in the aperture, sometimes the prominence of spotted patterns of coloration. Pallary (1939b: 107) recognised four sections in *Archelix* subgenus *Archelix*, the first “A. Punctatiana” mainly comprising forms we place in *O. punctata*, the other three (B. Nigriana, C. Lucasiana, D. Agadirensis) with forms we treat together as *O. lactea*. However, *A. maura* was listed twice, in groups A and B, while *A. punctata melanostoma* was in group B separated from *A. punctata* of group A, suggesting careless compilation. The Key below sets out the characters we regard as most useful in separating *O. punctata* from *O. lactea*, but occasional populations are difficult to place, especially if only a few shells are available without anatomical data.

Matos (1989a, 1989b, 1992, 2014: 230) reported results of hybridization experiments carried out in captivity, leading her to conclude that there was no indication that *Otala lactea* (O.F. Müller 1774) and *O. punctata* (O.F. Müller 1774) should be treated as different species. Furthermore, it was claimed that hybrids between *O. lactea*

and *Eobania vermiculata* (O.F. Müller 1774) were obtained before her genetic studies were interrupted. However, from the account by Matos (1989b) it would appear that all the snails she studied came from Portugal, where *O. punctata* was unknown before 2013. The descriptions given of shell characters suggest instead that two forms of *O. lactea* differing in shell coloration and pattern might have been involved (such as those figured by Matos, 2014: 229 figs 185 and 186, where the shell in the latter figure shows some resemblance to *O. punctata* except for the coloration around the aperture). At the only site where *O. punctata* is now known in Portugal, near Serpa in Alentejo (Holyoak *et al.*, 2014), it coexists in plenty with *O. lactea* without any evidence of interbreeding.

*Range in W Maghreb.* NE. Morocco, NW. Algeria (Fig. 11).

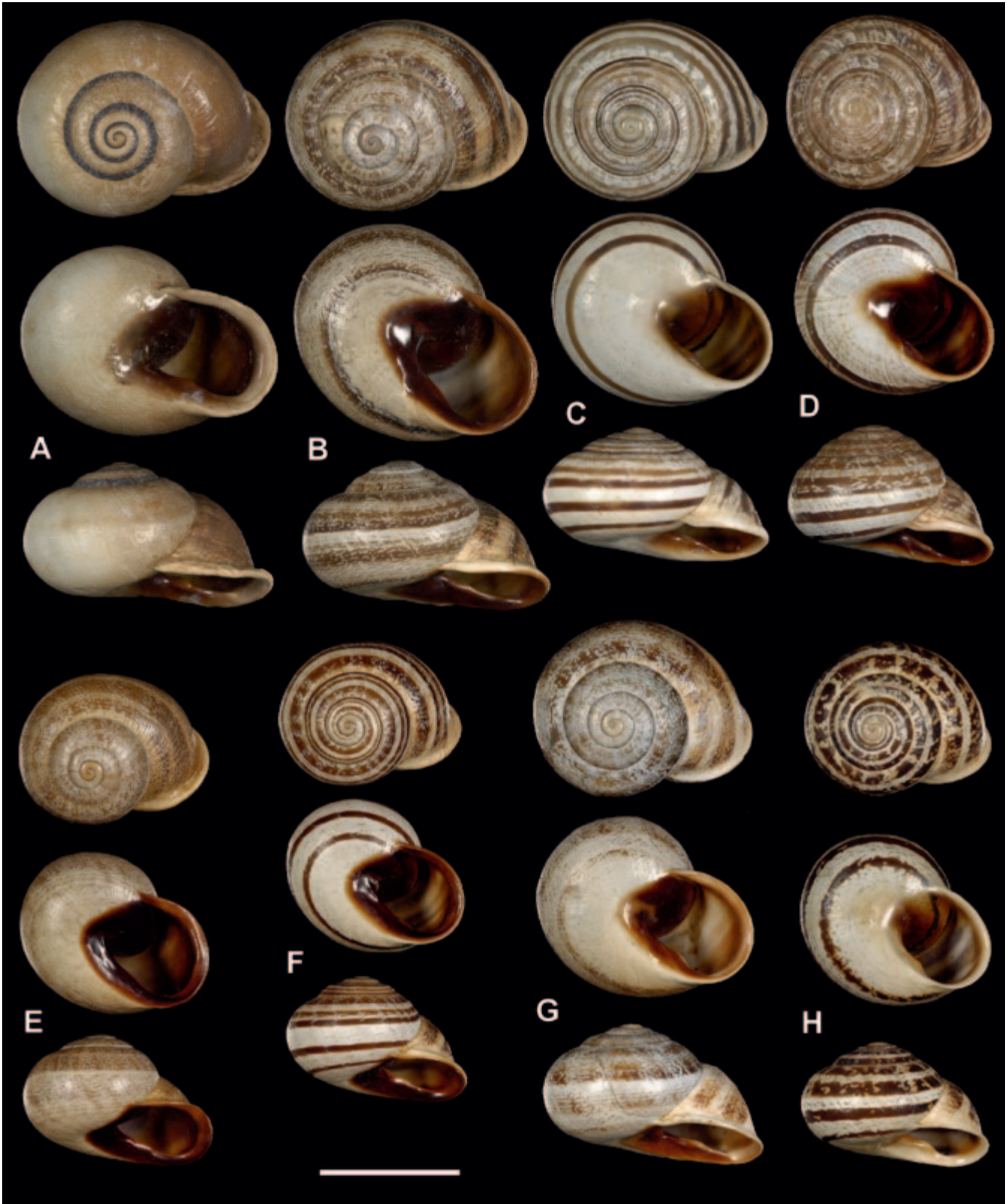
*Global range* Apparently native in NE., E. and S. Spain and Balearic Is. (Altonaga *et al.*, 1994: 303; Puente, 1994: 813; Beckmann, 2007: 126). Well established but apparently of introduced origin in SW. France (Depts Pyrénées-Orientales and Aude: Germain, 1930: 190; Kerney & Cameron, 1999: 307; Falkner, Ripken & Falkner, 2002: 54; Clanzig & Bertrand, 2001) and SE. Portugal (Serpa) (Holyoak *et al.*, 2014). Almost certainly introduced in Corsica (Rogliano on Cap Corse: Germain, 1930: 190), in NW. Sardinia (De Mattia & Mascia, 2011) and Malta (Barbara & Schembri, 2008).

The species has been widely introduced, perhaps in part as a food item and is now present in South Africa, North America and South America (Herbert & Sirgel, 2001; Cowie, Dillon, Robinson & Smith, 2009; Herbert, 2010: 52; Araya, 2015: 17).

*Otala lactea* (O.F. Müller 1774) Figs 2B–H, 3A–E, 4A, B, 7B, 8–10

*Helix lactea* O.F. Müller 1774, Verm. terr. fluv., 2, pp. 19–20, no. 218, TL not given [accompanied by four vars named with descriptive phrases], Neotype designated here (see Nomenclature below); *Helix lactea*, Müll., Gmelin (1790: 3629–3630, species 237), (non Müller, according to Pallary, 1914: 14), “Habitat in Jamaica et Lusitania” (Jamaica being an error); *Helix lactea* Gm., Röding (1798: 74, no. 942), given only as an indication for *Pomatia atomaria*; *Pomatia lactea*, Röding (1798: 73, no. 938),

*nom. nud.*; Michaud (1833: 2), n.v.; Rossmässler (1837: 7–8, pl. 22 figs 302c, 302d, 302 e, only); Forbes (1838: 251), Thickets about Algiers, common; d’Orbigny in Webb & Berthelot (1839: t. 2, p. 2, fig. 55), n.v., Canary Islands; Terver (1839: 15), province d’Oran; Tremecen; dans l’Atlas; à Ain-el Haout; Rossmässler (1839: 1–2, pl. 41 figs 545–547, 549–551), bei Bona [= Annaba, Algeria]; Rossmässler in Wagner (1841: t. 2, 249, 260; Atlas pl. 12 figs 9, 11), n.v.; Wagner (1841: t. 2, 265), n.v.; Erdl in Wagner (1841: t. 2, 269; Atlas pl. 13), n.v.; Morelet (1845: 68–70), Portugal; Morelet (1853: 285); Pfeiffer (1853: 194); Morelet (1854: 614–618), with Var. A from midi de l’Espagne, Var. B from environs de Malaga, Var. C from Almería, Var. D from Gibraltar; also Maroc et les Canaries (without localities); mention of form with white shell including aperture from Oran might refer to some other species; Rossmässler (1854: 12–13, pl. 64 figs 802, 803, 806–808), from Spain; Gassies (1856: 108), n.v.; Debeaux (1857: 321), n.v.; Morelet (1860: 152), n.v., Azores, where very similar to examples from Portugal and probably imported; Lowe (1861: 196, 200), from Mogador “plentifully, up the river, towards the Emperor’s Garden”; also Canary Is.; Aucapitaine (1862: 151), n.v.; Bourguignat (1862: 46), Algerian fossils; Bourguignat (1864: t. 1, 122–125, pl. 11 figs 1–9), with vars *albida*, *bifasciata*, *nigra*, *rufescens*, *griseo-lutescens*, *albido-atomata*, *omnino candida* & two others named with descriptive phrases (p. 124), *maxima*, *parvula* (p. 125) distributional data from Algeria (pp. 124–125); Bourguignat (1864: t. 2, 319, 332, 340, 356, 362), abundant partout [in Morocco] (p. 319); Hidalgo (1875: t. 1, 198, 221, 222, pl. 10 figs 92–99), Portugal, Spain, Balearic Is.; Morelet (1880: 19–20), Maroc [the country; “commune sur le littoral des deux mers”]; albino race, “localité ... au sud-ouest d’Oran ... Aïn-bou-Hhadjar”; Servain (1880: 36), Environs d’Alicante, de Saragosse, de Lisbonne et de Cintra; Kobelt (1881b: 158, 165), Tanger; near Tetouan; etc.; *H. lactea* var., Kobelt (1882: 29, pl. 8 figs 71), Tetouan; Bourguignat [in Péchaud] (1883: 52–53, 56), environs de Nemours, de Pereregaux, de Lalla-Maghnia et d’Aïn-Tolba à 18 kilom. de cette localité, sur la route de Nedroma; le Maroc; Hidalgo (1884: t. 2, pl. 28 figs 309–320, pl. 38 figs 437–445); Westerlund (1889: 414–415), with vars *ezquerriana*, *turturina*, *maura*, *sevillensis* and *sevilliana*; Pilsbry (1895: 324), with syn. *irrorata* Say and *atomaria* Schm., f. *bertheri* Bgt. (albino)



**Figure 2** Shells of *Otala punctata* (A) and *O. lactea* (B–H); A Morocco, 35°06'N 2°45'W, NMW.Z 1993.051.4182; B Morocco, 35°33'N 5°21'W, NMW.Z 1993.051.4240; C Algeria, 34°51'N 0°06'W, NMW.Z 1993.051.621; D Algeria, 34°48'N 1°05'W, NMW.Z 1993.051.603; E Algeria, 34°51'N 0°06'W, NMW.Z 1993.051.163; F ditto; G Morocco, 35°37'N 5°29'W, NMW.Z 1993.051.1925; H ditto. See Appendix for additional details of specimens. Scale bar 20mm.



and vars *ezquerriana* Bgt., *turturina* (Guirao) Rm., *maura* (Guirao) Rm. (syn. *simocheila* (Bgt.) Serv.), *sevillensis* Serv., *sevilliana* (Grat.) Mss., *murcica* Rm., *axia* Bgt., *malacensis* Anc., *bleicheri* Palad. (syn. *stomatodea* Bgt.), *ibrahimi* Bgt., *sphaeromorpha* Bgt., *plestiasteia* Bgt., *bathylæma* Bgt., *alybensis* Kob., *tagina* Serv.; Mabilie (1897: 84), environs de Mogador; Locard (1899: 37–38), with vars *major*, *minor*, *alta*, *depressa*, *grisea*, *fusca*, *albida*, etc.; Pallary (1901: 4); Hidalgo (1909), Beni-Bu-Fruor [but Llabador (1952: 113, *fide* Rutllant) suggested this record was an error for *Archelix* (*Dupotetia*) *Russadirensis*, a taxon treated here as part of *O. xanthodon*]; Hesse (1910: 43), Mahon (Menorca), Valencia, Sarasota (Portugal), Casablanca, Saffi; Pallary (1914: 8–14, 17), nomenclatural history; Pallary (1922c: 249), “groupe de l’*Helix lactea* des auteurs”; *Helix* (*Archelix*) *lactea*, Albers (1850: 98); *Helix* (*Tachea*) *lactea*, Adams & Adams (1855: 195); *Helix* (*Macularia*) *lactea*, Albers & Martens (1860: 133); Mousson (1874: 88–89), with var. *Sevilliana* Grat. (from: Gilishügel bei Marocco; Rabat; bei Tanger; also Gibraltar; Xeres; Sevilla) and new var *albescens* (p. 89, from: bei Schiodma und bei Ain Umest); Martens (1875: 99), citing Mogador report from Lowe (1861); Wollaston (1878: 31, 338–339), Azores: Sta. Maria, S. Miguel (p. 31), Canary Is.: Grand Canary, Teneriffe, Hierro (p. 338); Tryon (1888: 130, pl. 39 figs 89–96); *Helix* (*Macularia*) *lactea*, var. *punctata* (non *punctata* O.F. Müller, 1774), Martens (1900: 122), Drenkat (SW. Morocco); Pallary (1901: 133, 193, 197), Algerian fossils; *Archelix lactea*, Hesse (1910: 43–57, pls 433–438); Hesse (1911: 94, 95, 98–99, 109); *Otala lactea*, Irikov & Gerdzhikov (2013: 3); Limondin-Lozouet *et al.* (2013: 65, 66, 69 fig. 6 no. 13, 73), Holocene fossils from detailed studies of stratified deposits near Ksabi in Middle Moulouya basin (NE. Morocco); Matos (2014: 228, figs 185–186); Cossignani (2014: 91), figs of shells from Gibilterra and from Libia; *Otala* (*Otala*) *lactea*, Backhuys (1975: 249–251, fig. 94, map 95); Puente (1994: 796–804, figs 147–149); Schileyko (2006: 1798 figs 2304A–C), figs of shell and genital anatomy, based on specimen from Casablanca, Morocco; *Otala lactea lactea*, Beckmann (2007: 126, fig. 153); *Otala* (*Otala*) *lactea lactea*, Bank, Groh & Ripken (2002: 129, 139, 171), Azores, Madeiran Is., Canary Is.

*Helix* (*Marmorana*) *atlantica* var. *sevilliana* (Grat.) Mousson, Pallary (1904: 49), listed for Morocco; *Helix sevilliana*, Hesse (1910: 43), Sevilla; *Helix*

*lactea sevilliana*, Hesse (1910: 50–51, 54); *Archelix sevilliana*, Hesse (1910: pl. 437 figs 29–33) (making the name available; earlier usage of the name appears to have been as a *nom. nud.* or infraspecific taxon); Hesse (1911: 109); *Otala lactea sevillana*, Horst (1967: 166, n.v.).

*Helix faux nigra* Chemnitz 1786, Conchyl. Cab., 9, 2, p. 127, pl. 130, fig. 1161, n.v. (Unavailable because this work was rejected as not consistently binominal in Opinion 184 and Direction 1 of I.C.Z.N., 1944, 1954); *H. faux nigra*, Chemn., Rossmässler (1837: 7) (unavailable, name listed only as syn.); *H. fauci-nigra* [sic], Tryon (1888: 130, as syn.); *Helix faux nigra* “Chemnitz” Pallary 1914, Nachrbl. d. malak. Ges., 46(1), pp. 12, 13, 14, TL Portugal (based on Chemnitz, fig. 1161); the name *Helix fauxnigra* was thus made available only from 1914 with Pallary as author (its correction to *fauxnigra* not *faux-nigra* is based on Chemnitz’ work being rejected); *Archelix faux nigra*, Pallary (1920b: 31–33), with new vars *unicolor-alba* from Merada (p. 32), *minor* from Fès, Meknès (p. 33) and Var. without name from Guercif, Merada, Fès, Dj. Zehroun; Pallary (1922a: 141–142, with figs), pont des Atamna entre les Aït Attab et Bezou; Ouled Berahil, dans la vallée du Sous; Pallary (1922c: 250; 1923b: 279; 1935a: 354); Pallary (1929a: 48, 49), djebel bou Hellal (Ouezzan); Pallary (1939b: 107), =*lactea* auct.; *Otala fauxnigra*, Rour *et al.* (2002: 195); *Otala faux nigra* (Chemnitz 1786) [sic=*fauxnigra*], Cossignani (2014: 90), figs of shell, from Agadir.

*Pomatia atomaria* Röding 1798, Museum Boltenianum, p. 74 (no. 942), TL not given, regarded as validly published (cf. Dall, 1915: 48), and available by indication of *Helix lactea* of Gmelin (1791: 3692, species 237) and Chemnitz (1786: pl. 130 fig. 1161); *Otala atomaria*, Schumacher (1817: 191); Pallary (1914: 13, 14, 1920b: 32).

*Helix irrorata* Say 1822, Journ. Acad. Nat. Sci. Philad., 2, p. 370, TL Northumberland county, Pennsylvania; Say (1838: cover, p. 4; n.v., *fide* Binney, 1858: 240); Binney (1858: 23, 225); Tryon (1888: 130); Pilsbry (1939: 11).

*Helix Juilleti* Terver 1839 [Feb.], Cat. Moll. nord Afr., pp. 17–18, pl. 2, figs 3, 4, TL sur une montagne, près de Mascara [Algeria]; Rossmässler in Wagner (1841: t. 2, 249, 260; Atlas pl. 12 fig. 12), n.v.; Wagner (1841: t. 2, 265), n.v.; Morelet (1853: 285), n.v.; Pfeiffer (1853: 199); Bourguignat (1864: t. 1, 130–131, pl. 13 figs 16), with vars. *conoidea*, *minor*, *trifasciata*, and distributional data



**Figure 3** Shells of *Otala lactea* continued; A Morocco, 35°09'N 3°58'W, NMW.Z 1993.051.4471; B ditto; C Morocco, 30°39'N 9°53'W, NMW.Z 1993.051.2444; D ditto; E Morocco, 31°31'N 7°33'W, NMW.Z 1993.051.2218. See Appendix for additional details of specimens. Scale bar 20mm.

(p. 131); Bourguignat (1864: t. 2, 306), Environs de Chellalah, à 25 lieues au sud de Boghar [Algeria]; Ancey (1882: 288); Bourguignat [in Péchaud] (1883: 72), suggested *Helix chottica* Ancey 1882 is a syn.; Algerian distributional data given; Kobelt (1887: 19–20, pl. 74 figs 390–393); Westerlund (1889: 425); Pilsbry (1895: 324), with syn. *chottica* Anc., *saidana* Deb., vars *marguerit-tei* (B.) Pch., *heliophila* (B.) Pch.; Pallary (1901: 4); Pallary (1901: 195), Algerian fossils; Pallary (1939a: 65); *Helix (Archelix) Juilleti*, Albers (1850: 98); *Helix (Tachea) Juilleti*, Adams & Adams (1855: 195); *Helix (Macularia) juilleti*, Albers & Martens (1860: 133); Tryon (1888: 134–135, pl. 41 figs 26, 27), Mascara and Said [“Algiers” i.e. Algeria]; listed *H. chottiana* Ancey as syn.; *Archelix Juilleti*, Hesse (1911: 70–73, 94, 95, 100, 103, 111, pl. 443 figs 1–4), Aïn Fares bei Mascara [Algeria]; [sent by Pallary as *Helix wagneri*]; Pallary (1914: 20–21), Umgebung von Freuda und Franchetti; stated it is well known that *A. Juilleti* Terv.=*Wagneri* Rssm. [but latter name has the later publication date]; var. *minor* (*Helix Marguerit-tei* Bgt.) recorded from Ain Sfisifa, El May and Ksel; also from Asla (as misidentified *H. Seguyana*); Pallary (1939a: 66; 1939b: 107); *Archelix Marguerit-tei*, Pallary (1939b: 107); *Otala juilleti*, Rour *et al.* (2002: 195).

*Helix lactea* var. *hispanica* Michaud in Potiez & Michaud 1838 (before 28<sup>th</sup> Oct.), Galerie des Mollusques, t. 1, p. 16, TL Valencia, Sevilla, Palma (Spain) (non *Helix hispanica* Rossmässler 1838 (June)); *Helix hispanica* Mich., Terver (1839: 16–17, pl. 1 figs 7, 8), Masagran, entre cette ville et la mer, et sur toute la côte jusqu’à la Macta; Oran, à la batterie basse, près d’Al-Oudja; Erdl in Wagner (1841: t. 2, 271; Atlas pl. 13), n.v., [syn. *fide* Bourguignat, 1864: 127, as non Partsch in Rossmässler 1854]; *Helix lactea*, Müller Var. *Hispanica*, Morelet (1845: 68); Paladilhe (1875: 79–80), “Alluvions de la rivière Souani, à son embouchure, près de Tanger”; “aussi dans les environs de la ville de Maroc (Mousson)”; *Helix (Archelix) lactea* var. *hispanica*, Albers (1850: 98).

*Helix wagneri* Rossmässler 1839 [Sept.], Iconogr., (1) 2 (3/4), pp. 3, 43, pl. 42 fig. 554, TL Mascara [Algeria] [treated as syn. of *H. juilleti* by Bourguignat, 1864: t. 1, 130]; Bourguignat [in Péchaud] (1883: 71–72); Westerlund (1889: 425); Pilsbry (1895: 324); Pallary (1901: 5; 1939a: 65); *Helix (Macularia) wagneri*, Tryon (1888: 136, pl. 41 figs 30, 31); Pallary (1901: 136, 193, 197), Algerian fossils; *Helix Wagneri* (Terver MS.) Rossm., Kobelt

(1887: 18–19, pl. 74 figs 389), Boghar [Algeria]; *Otala wagneri*, Rour *et al.* (2002: 195).

*Helix Lucasi* Deshayes in A. Férussac & Deshayes 1848, Hist. génér. Moll., 1, p. 122, pl. 96, figs 8–12, n.v.; *Helix Lucasii* [sic], Pfeiffer (1853: 198); Bourguignat (1864: t. 1, 127–129, pl. 12 figs 5–15), with five vars named with descriptive phrases (p. 128), one var. named with descriptive phrase & vars *unifasciata*, *marmorata*, *bicolor* (p. 129), distributional data (pp. 128–129); Bourguignat (1864: t. 2, 319, 329), [in Morocco:] sur toute la côte, de la frontière algérienne à Tanger (p. 319); *Helix Lucasi* var. *Marmorata* (Paladilhe, 1875: 81–82), “Route de Tanger à Meknès” [but perhaps in error for *O. lactea* according to Kobelt, 1881b: 158]; Morelet (1880: 20), autour de Mazagran; à la embouchure de la Macta; environs de Tanger (*fide* Grasset, but perhaps in error for *O. lactea* according to Kobelt, 1881b: 158); etc.; Kobelt (1881b: 158), suggested reports from “bei Tanger” and “am Weg nach Mekines” are errors for black-mouthed form of *lactea*; Bourguignat [in Péchaud] (1883: 64–65, 86), environs de Nemours; rochers de la vallée de la Macta; Kobelt (1888: 51–52, pl. 86, figs 479, 480), bei Mostaganem, Mazagran, um Oran, Ain Turk, Nemours, etc.; *Helix lucasii* [sic], Westerlund (1889: 418); Pilsbry (1895: 324); Pallary (1899a: 107), Melilla (leg. Pallary); not found by Pallary at Tanger; locality “route de Tanger à Meknès” regarded as suspicious because species is restricted to within 10km of the coast; Pallary (1901: 5); Hidalgo (1909: 211); *Helix (Macularia) lactea* var. *Lucasii* [sic] Albers & Martens (1860: 133); *Helix (Macularia) lucasii* [sic], Tryon (1888: 132–133, pl. 40 figs 14, 15); *Helix (Macularia) lucasi*, Pallary (1901: 136, 195, 197), Algerian fossils; *Helix (Marmorana) Lucasi*, Pallary (1904: 28, 50), Oued Kiss; Mélilla; *Helix (Marmorana) Lucasi* var. *marmorata* B., Pallary (1904: 50), de Tanger à Meknès; *Archelix Lucasi*, Hesse (1909: 31; 1911: 94, 95, 99); *Archelix lucasii* [sic], Hesse (1910: 57–62, pl. 439; 1911: 103, 105, 110, 111); *Archelix Lucasi*, Pallary (1920b: 35), habitat une bande littorale très étroite, entre Mostaganem et Nemours; Llabador (1952: 110), Melilla; Restinga et Zeluán; *Archelix Lucasi* var. *discolor* Pallary (1926: 39), from Aïn-el-Turk (Oran) [Algeria]; Pallary (1939b: 107); *Otala lucasi*, Rour *et al.* (2002: 195); *Otala lucasii* [sic], Cossignani (2014: 91), figs of two shells, from Zaidia; Tistoutin.

*Helix senilis* Morelet 1851, J. Conchyl., 2, p. 353, pl. 9 figs 5, 6, TL sur les collines arides du

Tachondah, dans la direction de Constantine à Sétif; Pfeiffer (1853: 198); *Helix senilis* Morel., Pilsbry (1895: 325); *Helix (Tachea) senilis*, Adams & Adams (1855: 195); *Helix (Macularia) senilis*, Albers & Martens (1860: 133); Tryon (1888: 140, pl. 42, figs 54, 55), between Constantine and Setif ["Algiers", i.e. Algeria].

[*Helix lactea* var.] *maura* [Guirao in] Rossmässler 1854, Iconogr., (1) 3 (1–2), p. 14, pl. 64 fig. 804, TL bei Mazarron; Bourguignat [in Péchaud] (1883: 53, 57), Environs de Nemours et d'Aïn-Tolba [Algeria]; Sud de l'Espagne; Portugal; province d'Oran; acclimatée ... dans l'Uruguay (p. 53); Locard, (1899: 38, Spain and Portugal); Hesse (1911: 105); *Archelix maura*, Pallary (1939b: 107).

*Helix lactea* var. *murcica* Rossmässler 1854, Icon., (1) 3 (1/2), pp. 13–15, pl. 64 figs 800, 801, 804, 805, Königreich Murcia (Cartagena, Mazarron, Lorca und Totana), Almeria; *Helix murcica*, Westerlund (1889: 415–416); *Archelix murcica*, Hesse (1909: 31; 1910: pl. 435 figs 16–20; 1911: 109); *Archelix lactea murcica*, Hesse (1910: 47–49, 54); Pallary (1914: 19), with var. *minor* from Las Herrerias de Cuevas (Almeria).

[*Helix lactea* var.] *turturina* [Guirao in] Rossmässler 1854, Iconogr., (1) 3 (1–2), p. 14, pl. 64 fig. 805, TL bei Mazarron; var. *turturina*, Caziot & Thieux (1911: 123).

*Helix (Marmorana) atlantica* Pallary, Pallary (1904: 49), regarded as "= *lactea* auct. (non Müller)" from "localités diverses" in Morocco (non *Helix atlantica* Morelet & Drouët 1857=*Oxychilus (Drouetia) atlanticus* Morelet & Drouët 1857); *Helix atlantica* Pallary (1914: 14); *Otala atlantica*, Rour et al. (2002: 195).

*Helix hieroglyphicula* (non Michaud 1833), Debeaux (1857), Boghar [Pallary, 1929b: 123 pointed out that this was an error of identification].

*Helix hieroglyphicula* (non Michaud 1833), Aucapitaine (1862: 150), Djurdjura [Pallary, 1929b: 123 pointed out that this was an error of identification].

*Helix asteia* Bourguignat 1863, Moll. nouv. lit., (1<sup>re</sup> décade), pp. [11]-12, pl. 3 figs 5–8, TL les landes des environs de Madrid, en Espagne; also published in Rev. Mag. Zool., (2) 15, pp. 100–111; Bourguignat [in Péchaud] (1883: 64), cited original description as n° 5, pl. III-VIII [apparently in error]; Westerlund (1889: 422); Hesse (1911: 105); *Helix (Macularia) asteia*, Tryon (1888: 140, pl. 42 fig. 53), originally said to be from Madrid, but

referred to *H. bonduelliana* by Hidalgo who considered it to be an African species.

*Helix lactea* var. *canariensis* [Villa in litt.] Graëlls 1846, Catálogo Moluscos terrestres ... España, pp. 4–5, nom. nud.; *Helix canariensis*, Mousson (1872); *Helix lactea* var. *canariensis*, Hesse (1910: 43), Teneriffa; *Archelix lactea canariensis*, Hesse (1910: 52–53); *Archelix canariensis*, Hesse (1910: pl. 435 figs 13–15); *Archelix canariensis* Mss. [= Mousson], Pallary (1914: 20).

*Helix Bleicheri* Paladilhe 1875, Rev. Mag. Zool., (3) 3, pp. 80–81, pl. 6, figs 1–3, TL "Route de Tanger à Meknès"; Morelet (1880: 21–22), collines de la province d'Abda, etc.; Servain (1880: 37–38), Environs de Saragosse, de Madrid, de Valence; commune dans la partie occidentale de la province d'Oran; vit également au Maroc [*Helix stomatodæa* Bourguignat, in sched., 1870 is listed in synonymy]; Kobelt (1882: 28–29, pl. 8 figs 70, 70a), Tanger in Morocco; Bourguignat [in Péchaud] (1883: 53), environs de Tanger; Bourguignat [in Péchaud] (1883: 61–62), Tanger; Mogador; Rabat; Anq-el-Gemel; près Maroc; etc. [also listed for province d'Oran; Spain; Portugal]; Westerlund (1889: 417); Locard (1899: 40), Portugal; with vars *minor*, *alta*, *depressa*, *globulosa*, *grisea*, *luteola*, *subalbida*; var. *Subconica* Paladilhe 1875; var. *Candida* Paladilhe 1875; var. *Candida* subvar. *Subcarinata* Paladilhe 1875; Pallary (1901: 4); Hesse (1910: 43), Tanger; *Helix (Macularia) Bleicheri*, Tryon (1888: 132, pl. 39 fig. 98); *Helix (Marmorana) Bleicheri*, Pallary (1904: 28, 49, pl. 1 figs 16, 17), Nord du Maroc; with new var. *tenuis* (pl. 1 fig. 18) from l'ouad Ouarne dans l'Atlas [given as Agagour on p. 49]; vars *subconica*, *candida*, *subcarinata* listed for Morocco (p. 49); *Archelix bleicheri*, Hesse (1910: pl. 438 figs 34–37; 1911: 109); Pallary (1914: 19), von den Balearen; Pallary (1922a: 96, 145–146), sur les plateaux de la base de l'Atlas entre Demnate et Mogador; with vars *minor* and *tenuis*; Pallary (1929a), v. *minor*, djebel bou Hellal (Ouezzan) (pp. 48, 49); Moulay Bouchta (p. 53); Pallary (1939b: 107); *Archelix lactea bleicheri*, Hesse (1910: 51–52); *Archelix bleicheri*, Hesse (1910: 54–55); *Otala bleicheri*, Rour et al. (2002: 195).

*Helix Jourdaniana* Bourguignat 1867 [8 Dec.], Moll. nouv. lit., n° 75, pl. 38 figs 1–4, n.v.; *Helix jourdaniana* Kobelt (1875: 4–5, pl. 92 figs 979, 980), bei Tlemecen [Algeria]; Ancey (1882: 289), with var. *albina*, from: les rochers des cascades de la Saf-Saf; *Helix jourdaniana* var. *major* Kobelt (1882: 32, pl. 11 figs 94, 95), Tlemcen; Bourguignat [in Péchaud]

(1883: 66–67, 70), Mazagran; Mostaghanem; environs d’Oran; environs de Sayda et de Daya; forme *minor* dans les ruines de Mansourah, près de Tlemcen; Westerlund (1889: 423–424), with var. *propeda* Bgt.; Pilsbry (1895: 324); Hesse (1911: pls 441, 442), figs of genital anatomy; *Helix* (*Macularia*) *jourdani*, Tryon (1888: 136–137, pl. 41 figs 32, 33); *Helix* (*Macularia*) *jourdani* [sic] B., Pallary (1901: 135, 193, 197), Algerian fossils; *Macularia jourdaniana* vars, Kobelt (1903: 41–42, pl. 285 figs 1828–1833), with *M. jourdaniana* var. *lellae* newly described (figs 1830, 1831), Umgebung von Lella Marnia in der Provinz Oran, nahe der marokkanischen Grenze zwischen Tlemcen und Nemours; *Archelix Jourdaniana* Bgt., Pallary (1914: 20), noted that *Helix jourdani* Michaud 1862 (J. Conchyl., (3) 10, p. 62, pl. 3 figs 12–13) is the valid name of a different species, so proposed replacement name for *jourdani* of *A.[rchelix] agadirensis* [based on an old name for Tlemcen, Agadir=Citadelle]; Pallary (1921: 145), repetition of information from Pallary (1914: 20); *Archelix Agadirensis*, Pallary (1939b: 107); *Archelix Jourdaniana*, Hesse (1910: 65–67; 1911: 68, pl. 441 figs 8–10, pl. 442 figs 11–13), nähere Umgebung von Tlemcen; Hesse (1911: 94, 95, 99, 103, 106, 111); Pallary (1939a: 65, 1939b: 107); *Otala jourdaniana*, Rour *et al.* (2002: 195).

*Helix gibboso-basalis* Wollaston 1878, Testacea Atlantica, pp. 339–340, TL Teneriffam borealem, i.e. northern part of Teneriffe in Canary Islands; *gibbosobasalis*, Hesse (1911: 104); *Helix* (*Macularia*) *gibboso-basalis*, Tryon (1888: 131); *Helix gibbosobasalis*, Pilsbry (1895: 324).

*Helix axia* Bourguignat in Servain 1880, Étude Moll. Espagne Port., pp. 36–37, TL Minorque; Majorque; midi de l’Espagne; Malaga; las Aquilas (Murcie) et San Roque, près de Gibraltar; alentours de Valence; earlier work cited as “Bourguignat, Spec. noviss., N° 106, 1878” is fictitious (Connolly, 1934); Bourguignat [in Péchaud] (1883: 53, 59), Baléares (Minorque et Majorque), de Valence, de Las Aquilas et de San Roque (Espagne); environs d’Oran et de Mascara (Algérie); alentours de Tanger; Djebel Takreda et des collines d’Anq-el-Gemel, près de la ville de Maroc; earlier work cited as “Bourguignat, Spec. nov., n° 106, 1878” is fictitious (Connolly, 1934); Westerlund (1889: 416); Pallary (1898d: 561), le nord du Maroc [Algerian localities at Mascara and Oran given by Bourguignat (in Péchaud, 1883 p. 59) were errors]; Pallary (1899a: 104), alentours

de Tanger; Fez; etc.; Locard (1899: 39), with vars *minor*, *depressa*, *luteola*, *alba*; range includes Portugal; Hesse (1910: 43, 46); Hesse (1911: 105); Pallary (1914: 14); *Helix* (*Marmorana*) *axia*, Pallary (1904: 49), Morocco at Tanger, Chechaouen, Fez; *Archelix axia*, Pallary (1939b: 107); Hesse (1910: pls 433–435 figs 11, 12), with mut. *albina* (pl. 438 fig. 40); *Archelix lactea axia*, Hesse (1910: 54).

*Helix simocheila* Bourguignat in Servain 1880, Étude Moll. Espagne Port., p. 38, TL aux alentours d’Alicante; à las Aquilas, près de Murcie; very short description just avoids this being regarded as a *nom. nud.*; the earlier work cited as “Bourguignat, Spec. noviss. moll., n° 111, 1878” is fictitious (Connolly, 1934); Bourguignat [in Péchaud] (1883: 61), environs d’Alicante et de las Aquilas [Spain]; province d’Oran; only slightly fuller description than that given in 1880; the earlier work cited again as “Bourguignat, Spec. noviss., n° 111, 1878” is fictitious (Connolly, 1934); Hesse (1910: 43), Cuevas (Südspanien); Hesse (1911: 105); *Archelix simocheila*, Pallary (1914: 19, pl. 1 fig. 3), with *forma minor* from: bei Aguilas und in der Sierra Cabreras bei Cuevas; Pallary (1939b: 107).

*Helix tagina* Servain 1880, Étude Moll. Esp. Port., pp. 38–39, TL Alluvions de Tage, au-dessous de Lisbonne; Algésiras; environs d’Oran, en Algérie; Kobelt (1882: 28, pl. 8 figs 68, 79), bei Algesiras; Bourguignat [in Péchaud] (1883: 65, 66), vallée de la Macta; environs d’Oran et d’Arzew [Algeria]; Westerlund (1889: 419); Locard (1899: 40–41); Hesse (1911: 104); *Helix* (*Macularia*) *lactea* var. *tagina*, Tryon (1888: 130), Spain.

*Helix Chottica* Ancey 1882, Naturalisto Siciliano, 1, pp. 288–289, TL sur un des versants qui dominants a rivièrè de Saïda, province d’Oran, et dans le lit même de la rivièrè [Algeria]; Hesse (1911: pl. 444), figs of genital anatomy; *Archelix chottica*, Hesse (1909: 31); Hesse (1911: 73–74, 94, 100, 111, pl. 444 figs 1–6), from: Mecheria und Bossuet-Daya; also as *Helix charieia* from Bossuet-Daya.

*Helix lactea* var. *alybensis* Kobelt 1882, Icon., (2) 1 (1/2), p. 28, pl. 8 figs 67, Felsen von Gibraltar; Kobelt (1883: 6), Gibraltar; Bourguignat [in Péchaud] (1883: 66); *Helix alybensis* Kobelt, Westerlund (1889: 419); Pallary (1899a: 108), Tanger; Ceuta; also Gibraltar and Algésiras (*vide* Kobelt); Pallary suggested the epithet should probably be corrected to *abylae* or *abylaensis*, but did not amend the name; *Helix* (*Macularia*) *lactea* var. *alybensis*, Tryon (1888: 130), Gibraltar; *Helix*

(*Marmorana*) *alybensis*, Pallary (1904: 50); *Archelix alybensis*, Hesse (1911: 109); Pallary (1939b: 107); *Otala abyblae* (Pallary, 1898), Rour *et al.* (2002: 195) (see above for apparent source of this name).

*Helix bathylaema* Bourguignat, Kobelt (1882, Icon., (2) 1 (1/2), p. 29, pl. 8 figs 72), Balearen; *Helix* (*Macularia*) *lactea* var. *bathylæma*, Tryon (1888: 130), Balearic Is.

*Helix Juilleti* var. *Beguirensis* [Debeaux in litt.] Kobelt (1882, Icon., (2) 1 (1/2), p. 31, pl. 11 figs 89), Dschebel Beguira in der Provinz Oran; Bourguignat [in Péchaud] (1883: 70–71); *Helix Beguirana*, Kobelt (1887: 17–18, pl. 74 figs 388), Dschebel Beguira in der Nähe von Mascara; Westerlund (1889: 426); *Helix beguirensis*, Pilsbry (1895: 324), syn. *beguirana* auct.; Pallary (1899a: 109); *Helix* (*Macularia*) *beguirana*, Tryon (1888: 135–136, pl. 41 figs 28, 29); *Helix* (*Marmorana*) *beguirana*, Pallary (1904: 50), in Morocco at Dj. Sidi el Abed; *Beguirana*, Pallary (1939a: 65), in list of *Otala* species but without generic name; *Archelix Beguirensis*, Pallary (1939b: 107); *Otala beguirana*, Rour *et al.* (2002: 195).

*Helix berthieri* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afrique, pp. 47–48, TL la plaine de Thelat près d’Oran; earlier work cited here as “Bourguignat, Spec. nov., n° 105, 1878” is fictitious (Connolly, 1934); Pallary (1901: 4); ? *Helix berthieri*, Westerlund (1889: 416); *Archelix Berthieri* (albinos), Pallary (1939b: 107).

*Helix Ezquerriana* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afrique, pp. 56–57, TL Algèsiras, environs d’Oran; the description is very brief; the name is followed by “Bourguignat, 1882” but no publication earlier than 1883 has been located.

*Helix ibrahimi* [“Bourguignat 1879”] Bourguignat [in Péchaud] 1883, Exc. malac. Nord Afrique, pp. 58–59; TL les collines d’Anq-el-Gemel (tribu des Ahmar), à 40 lieues de Mogador dans la direction de Maroc; acclimatée à Ténérife”; Pallary (1899a: 105–106, pl. 8 fig. 1); Westerlund (1889: 417); *Helix* (*Marmorana*) *Ibrahimi*, Pallary (1904: 49); *Archelix ibrahimi*, Hesse (1911: 109); Pallary (1914: 10); Pallary (1920b: 34), Guercif, Taza, Bab Moroudj, El Menzel, Aït Ibrahim; with var. *minor* from Fès; a form intermediate between *A. Ibrahimi* and *A. ahmarina* reported from between Meknassa and Sidi bel Kaçem au S.O. de Bab Moroudj; Pallary (1939b: 107); *Archelix ahmarina* var. *Ibrahimi*, Pallary (1922a: 143); *Otala ibrahimi*, Rour *et al.* (2002: 195).

*Helix malacensis* [Ancey mss.] Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afrique, pp. 60–61, TL environs de Malaga (Espagne); Westerlund (1889: 416).

*Helix ahmarina* [Bourguignat 1879] Bourguignat [in Péchaud] (1883), Exc. malac. Nord Afrique, p. 61, TL les collines d’Anq-el-Gemel, dans la tribu des Ahmar, à 40 lieues de Mogador, dans la direction de Maroc; Westerlund (1889: 417); Pilsbry (1895: 324); Pallary (1899a: 104–105, pl. 7 fig. 10), dans les forêts d’arganier, au Sud-Ouest de Mogador (leg. Buchet); etc., including Canary Is.; Pallary suggested it is a syn. of *H. eugastora* from NW. Algeria, although differing in apertural coloration; Hesse (1910: 43), Mogador; *Helix* (*Macularia*) *ahmarina*, Tryon (1888: 131, pl. 40 fig. 13), Ins. Grand Canary [perhaps an error, but see below under Pallary, 1914]; *Helix* (*Marmorana*) *ahmarina*, Pallary (1904: 49), Anq el djemel; *Archelix ahmarina*, Pallary (1914: 20), identified figure in Mabile (1884: pl. 16 fig. 16) from Canary Is. as this taxon, apparently a small form of the type introduced from Mogador; *Archelix Ahmarina* Var. *ksebiana* Pallary (1915: 27), described briefly as new var. from: vallée de l’oued Kseb (Grand Atlas); *Archelix ahmarina*, Hesse (1909: 31); Hesse (1910: pls 436, 437 fig. 28); Hesse (1911: 109); *Archelix lactea ahmarina*, Hesse (1910: 49–50, 54); Pallary (1920b: 34), Taza, Col de Touahar, Bab Moroudj, Fès, Sefrou, Dar Khelloch, El Menzel; répandu dans le sud-ouest du Maroc, notamment dans la banlieue de Mogador; with Var. *minor* Ply., from Fès; Pallary (1922a: 95, 96, 142–144), with vars *kesebiana* [sic], *Ibrahimi*, *albescens*, *plestiasteia* and subvar. *minor* of the last [*Ibrahimi* and *plestiasteia* were often treated previously at species rank]; localities listed in region of Grand Atlas; Pallary (1939b: 107); *Otala ahmarina*, Rour *et al.* (2002: 195); *Otala ahmarina kebesiana* (Pallary, 1920) [sic], Cossignani (2014: 90), figs of shell, from Sidi Kouki [?= *O. lactea*; the name given has not been traced in Pallary’s publications, but it appears to be a mis-spelling of *ksebiana* with an incorrect date].

*Helix agenna* [Bourguignat 1880] Bourguignat [in Péchaud] 1883, Exc. malac. Nord Afr., pp. 62–63, TL Sud et centre du Maroc, notamment sur les collines autour de la ville du même nom [i.e. now the city of Marrakech]; Westerlund (1889: 422); Pallary (1899a: 105); Pilsbry (1895: 326); Hesse (1911: 105); *Helix* (*Marmorana*) *agenna*, Pallary

(1904: 49); *Archelix agenna*, Pallary (1939b: 107); *Otala agenna*, Rour *et al.* (2002: 195).

*Helix sphaeromorpha* Bourguignat [in Péchaud] 1883, Exc. malac. Nord Afrique, p. 63, TL Tanger [also reported from Baléares and Mascara]; earlier work cited as “Bourguignat, Spec. noviss., N° 109, 1878” is fictitious (Connolly, 1934); Westerlund (1889: 417); Pallary (1899a: 104, pl. 7 fig. 8), Tanger; Fez; Hesse (1910: 43), Tanger; *Helix (Marmorana) sphaeromorpha*, Pallary (1904: 49), Tanger, Rabat, Fez; *Archelix sphaeromorpha*, Pallary (1920b: 33–34, pl. 3 fig. 7), Souk el Arba de Tissa, Fès, Moulaï Idriss du Zehroun, Sefrou; with new vars *albicans*, *quinque-fasciata*, *lineolata* (pl. 3 fig. 7), *minor* (all p. 33), *depressa*, *subangulata* (p. 34); Pallary (1939b: 107); *Archelix lactea sphaeromorpha*, Hesse (1910: 51–52); *Archelix sphaeromorpha*, Hesse (1910: pl. 438 figs 38, 39); *Otala sphaeromorpha*, Rour *et al.* (2002: 195); *Otala sphaeromorpha* [sic] (Bourguignat 1883), Cossignani (2014: 92–93), figs of two shells, from Sidi Kacem.

*Helix plesiasteia* [Bourguignat 1879] Bourguignat [in Péchaud] 1883, Exc. malac. Nord Afr., pp. 63–64, TL sud du Maroc, entre Mogador et Aghadyr; with Var. *minor* (*Helix plesiasteilla*) Bourguignat [in Péchaud] (p. 64), from: près la ville de Maroc [= Marrakech], sur les collines d’Anq-el-Gemel [the species name *H. plesiasteilla* was apparently newly published here]; Westerlund (1889: 417–418); Pallary (1899a: 106–107), sud du Maroc entre Mogador et Agadir; *Helix plesiasteia* Bourguignat Var. *minor* (*H. plesiasteilla*, B.), Pallary (1899a: 107), près la ville de Maroc, sur les collines d’Anq-el-Gemel (*fide* Bourguignat); *Helix (Marmorana) plesiasteia*, Pallary (1904: 49), with var. *minor*; *Archelix plesiasteia*, Pallary (1914: 19–20), noted that *H. lactea* var. *albescens* in Mousson (1874) from Saffi is identical and latter name has priority; *Archelix ahmarina* Var. *plesiasteia*, Pallary (1922a: 144), with subvar. *minor*; *Otala plesiasteia*, Rour *et al.* (2002: 195).

*Helix sevillensis* Servain 1880, Étude Moll. Esp. Port., pp. 39, TL dans les détritits du Guadalquivir, à Seville “est une miniature de la *Juilleti* d’Algérie”; Bourguignat [in Péchaud] (1883: 71).

*Helix Galiffetiana* [Bourguignat 1870] Bourguignat [in Péchaud] 1883, Exc. malac. Nord Afr., p. 66, TL dans les oasis du sud du Maroc, à Ras-el-aïn des Beni-Mattar; Westerlund (1889: 419); Pallary (1899a: 107), Pallary commented that it is strange to find this species reported by Bourguignat from

Ras-el-Aïn des Beni-Mattar in central Morocco since the three allied species are restricted to the southern coast of Spain and to Algeria; Pilsbry (1895: 326); Pallary (1904: 50); *galiffetiana* [sic], Hesse (1911: 104); *Otala galiffetiana*, Rour *et al.* (2002: 195).

*Helix propeda* [Bourguignat 1882] Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afrique, pp. 67, 70, TL environs de Sayda; la plaine de Terni, près d’Oran; *Archelix propeda*, Pallary (1939b: 107).

*Helix charieia* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afrique, pp. 67–68, 72, TL Sur les rochers, aux environs de Daya (province d’Oran); *Helix charieia*, Kobelt (1888: 49–50, pl. 86 figs 475, 476), in den Bergen von Daya an den Quellen des Sig in der Provinz Oran; Westerlund (1889: 424); Pilsbry (1895: 324); *Helix (Macularia) charieia*, Tryon (1888: 136, pl. 46 figs 4, 46); ? *Charrieria* [sic], Pallary (1939a: 65), in list of *Otala* species but without generic name; *Archelix Charieria* [sic], Pallary (1939b: 107), in list; *Otala charieria*, Rour *et al.* (2002: 195).

*Helix Marguerittei* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afrique, pp. 72–73, TL les contrées au sud de Géryville, dans la province d’Oran; earlier work cited as “Bourguignat, spec. noviss., N° 110, 1878” is fictitious (Connolly, 1934); Westerlund (1889: 426).

*Helix heliophila* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afrique, pp. 73–74, TL dans le sud la province d’Oran, vers la région des grands Chotts; earlier work cited as “Bourguignat, spec. noviss., N° 113, 1878” is fictitious (Connolly, 1934); Westerlund (1889: 426–427).

*Helix Ghazouana* [Debeaux in litt.] Kobelt 1888, Icon., (2) 3 (5/6), pp. 50–51, pl. 86 figs 478, TL um Nemours (Djemâa Ghazouan der Araber) [Algeria]; Westerlund (1889: 418); Pilsbry (1895: 324); Pallary (1899a: 107), Sidi Merzoug, sur la frontière algérienne” [regarded as var. of *H. Lucasi* by Pallary]; *Helix (Macularia) ghazouana*, Tryon (1888: 133, pl. 46 figs 47–48); *Helix (Marmorana) Lucasi* var. *ghazzouana* [sic], Pallary (1904: 50), Sidi Merzoug; *Archelix lucasii ghazouana*, Hesse (1910: 59–61); *Archelix ghazouana*, Hesse (1911: 111); *Archelix ghazzouana* [sic] Pallary (1939b).

*Helix Denansi* Kobelt 1888, Icon., (2) 3 (5/6), p. 50, pl. 86 figs 477, TL not known; Pilsbry (1895: 324); *Helix (Macularia) denansi*, Tryon (1888: 135, pl. 46 figs 61, 62); Westerlund (1889: 427).

*Helix (Macularia) leucochila* Westerlund 1892, Nachrbl. d. malak. Ges., 24(11/12), p. 191, TL

Spanien bei Sevilla; "Gehört der Gruppe *H. myristigmaea* Bgt. (*punctata* Auct.) zu und steht vielleicht der *H. asteia* Bgt. am nächsten"; *Helix leucochila* Pilsbry (1892: 240); *Helix leucochilops* Pilsbry 1895, Man. Conch., (2) 9, p. 325, "*leucocheila* [sic] W., not Cox" [i.e., although including a spelling error while being rather too briefly stated, a new name for *Helix leucochila* Westerlund 1892 non J.C. Cox 1868]; Hesse (1911: 104).

*Helix proelongata* Pallary 1898(d), Comptes r. Assoc. franç. Avanc. Sci., 27(2), pp. 560–561, pl. 5 figs 5, 6 [figure details *vide* Pallary 1899d, p. 106, not figs 6–8 as given in the text of the protologue], TL sur la plage de l'O. Hallouf, ... charriées par les rivières marocaines; M. Gentil ... rapportée fossile d'une couche argileuse sous les basaltes de Ténikrent; environs de Tétouan; the species epithet was clearly printed as PROELONGATA with the OE as a diphthong, but apparently amended to *praelongata* by Pallary (1899d p. 106); *Helix praelongata*, (Pallary, 1899a: 106, pl. 7 fig. 9), origin of this species remained uncertain (see Pallary 1898d: 560–561; also recorded amongst unlocalised Moroccan shells); he speculated that the shells from the coast of NW. Algeria were carried by currents from around Tétouan; *Helix proelongata*, Pily var. *magnifica* Pallary (1898d: 560–561, pl. 5 figs 7, 8; figure details *vide* Pallary, 1899d: 106); *Helix praelongata* var. *magnifica*, Pallary (1899a: 106); *Helix (Macularia) praelongata*, Pallary (1901: 134, 193, 197), Algerian fossils; *Helix (Marmorana) praelongata*, Pallary (1904: 49) "Riff?"; *Archelix praelongata*, Pallary (1920b: 35), Alluvions de la Moulouïa à Guercif ... Elle paraît provenir de la lisière sud du Riff; *Archelix (Dupotetiana) praelongata*, Pallary (1939a: 64), no explanation is given for the novel [and apparently incorrect] subgeneric treatment; *Archelix (Dupotetiana) praelongata*, Llabador (1952: 114), Dagamur (Oulad Settout); *Otala praelongata*, Rour *et al.* (2002: 195).

*Helix (Macularia) grossularia* Martens 1900, Nachrbl. d. malak. Ges., 32, pp. 122–123, TL Südwestliches Marokko, bei Drenkat, 2 Tagmärsche südlich von Marrakesch; Kobelt (1901: 52–53, pl. 258 figs 1671); Pallary (1904: 27, 49, pl. 3 figs 18, 19); *Archelix grossularia*, Hesse (1911: 109); *Otala grossularia*, Rour *et al.* (2002: 195).

*Macularia (lukasii* [sic] subsp.) *riffensis* ["Pallary"] Kobelt 1903, Icon., (2) 10 (3/4), pp. 37–38, pl. 284 figs 1822–1823), TL um das spanische Presidio Melilla an der Nordküste von Marocco [not

marked as a new species at the reference cited, but apparently newly described; it seems likely that Pallary provided the specimens and the name whereas Kobelt prepared the description]; *Helix (Marmorana) Lucasi* Var. *riffensis*, Pallary (1904: 28–29, 50, pl. 2 figs 8, 9), Mélilla au pied du dj Gourougou; Hidalgo (1909: 211), Melilla; Llabador (1952: 110–111), Taurirt (Beni Sicar); Monte Arruit (Beni bou Yahi); Islas Chafarinas; *Archelix lucasii riffensis*, Hesse (1910: 60–62, pl. 440; 1911: 105); *Archelix Lucasi riffensis*, Pallary (1939a: 64); *Archelix riffensis*, Hesse (1911: 111); Pallary (1914: 20), with var. *minor*; Pallary (1920b: 35), Cheràa, Berkane, Taforalt; L'espèce est localisée entre Mélilla et la frontière algérienne qu'elle n'atteint pas; Pallary (1939b: 107); *Otala riffensis*, Rour *et al.* (2002: 195); Cossignani (2014: 92), figs of five shells, from Ras el Ma.

*Archelix gebiletana* Pallary 1918, Bull. Soc. Hist. nat. Afr. Nord, 9(7), p. 146, TL chez les Serarna, sans indication précise de localité; Dans les Djebilet, au N. de Marrakech; Pallary (1919: 55–56, pl. 2 figs 11–13), figs show var. *minor* from El Klàa, à la lisière des Djebilet (he claimed that species is "une forme du groupe *punctata*", but this seems unlikely from examination of the figs); *Otala gebiletana*, Rour *et al.* (2002: 195).

*Archelix Barbini* Pallary 1918, Bull. Soc. Hist. nat. Afr. Nord, 9(7), p. 147, TL Tléta, tribu des Azails, cercle de Marnia; with vars *coloria* (locality not stated) and *persimilis* (from: le Kef, sur la rive droite de la Tafna); Pallary (1926: 37–39, pl. 7 figs 1–7), with vars *coloria* (p. 38, pl. 7 fig. 5) and *persimilis* (p. 38, pl. 7 figs 6, 7) and new vars *major* (p. 38, pl. 6 fig 11, pl. 7 figs 1, 2) and *minor* (p. 38); Pallary (1939a: 65, 1939b: 107); *Archelix persimilis*, Pallary (1939b: 107).

*Archelix Derenica* Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11(2), p. 21, no. 57, fig., TL dar Goundafi, au coeur du Grand Atlas; Pallary (1922a: 96, 144–145 with fig.), Dar Goudafi, Tanant; Pallary (1939b: 107); *Otala derenica*, Rour *et al.* (2002: 195); Richardson (1980); Cossignani (2014: 90) figs of shell from Goundafa.

*Archelix liocephala* Pallary 1923(a), Bull. Soc. Hist. nat. Afr. Nord, 14(3), p. 114, TL Les Kiffans (Maroc); Pallary (1926: 36–37, pl. 7 fig. 8); *Otala liocephala*, Rour *et al.* (2002: 195).

*Archelix Freydieri* Pallary 1923(a), Bull. Soc. Hist. nat. Afr. Nord, 14(3), p. 114, TL Outat-el-Hadj, dans la haute Moulouya (Maroc); Pallary (1923b: 279; 1939b: 107); *Otala freydieri*, Pallary (1926:



35–36, pl. 5 figs 5, 6), with vars *minor*, *unifasciata* (p. 36); Rour *et al.* (2002: 195); Cossignani (2014: 91), figs of shell, from Outat el Hadj; *Archelix Freydieri*, Pallary (1939a: 64–65).

*Archelix Ceardi* Pallary 1924, Bull. Soc. Hist. nat. Afr. Nord, 15(3), p. 112, TL Colomb-Béchar [= Béchar], dans une dépôt de Pléistocène récent; Pallary (1926: 33–34, pl. 6 figs 9, 10); Pallary (1939b: 107); *Otala ceardi*, Rour *et al.* (2002: 195), erroneously listed as Moroccan.

*Archelix Solignaci* Pallary 1926, J. Conchyl., 70(1), pp. 34–35, figs, TL Dans les brèches calcaires (Pontien) du dj. Mendjel Hédil.

*Archelix Huotiana* Pallary 1926, J. Conchyl., 70(1), pp. 39–40, pl. 6 figs 1, 2, TL Bou Hellou (Maroc oriental); Djebel Azrou Akchchar, à 80 kil. environ N. de Taza; Pallary (1939b: 107); *Otala huotiana*, Rour *et al.* (2002: 195); Cossignani (2014: 91) figs of shell, from Morocco.

*Archelix Connollyi* Pallary 1926, J. Conchyl., 70(1), pp. 40–41, pl. 6 figs 3–5, TL Bou Hellou; Ouled Haddou; Les Kiffans et Safsafat dans le Maroc orientale (région septentrionale); Pallary (1929a: 48, 49), djebel bou Hellal (Ouezzan); Pallary (1939a: 64–65, 1939b: 107); Llabador (1952: 109), Vila Alhucemas (Bokkoya); Amaïer (Beni Itef); *Otala connollyi*, Rour *et al.* (2002: 195); Cossignani (2014: 90), figs of two shells, from Al Hoceima.

*Archelix De Gouttesiana* Pallary 1928, J. Conchyl., 72(1), pp. 11–12, pl. 1 figs 4, 13, TL Talzent et la cascade d'Immouzer des Marmoucha, dans la tache de Taza (Maroc); with vars *minor* and *pallida* (p. 12); Pallary (1929a: 51, 53), Gorges du Meskedal; Moulay Bouchta; *Otala degouttesiana*, Rour *et al.* (2002: 195).

*Helix faux-nigra sanctae-galdanae* Aguilar-Amat 1933 (pp. 327–328), Menorca.

*Otala punctata*, Cossignani (2014: 92), figs of two shells from Marrakesh represent misidentified *O. lactea*.

Sources of the following names that have appeared in the literature as synonyms of this species have not been traced; many of them are likely to be *nomina nuda* or errors (although names marked ‡ apparently represent Miocene fossils from Algeria from Jodot, 1955, n.v.); they are listed in alphabetical sequence of the epiphets: *aecouria* Letourneux & Bourguignat 1887 (name listed by Pilsbry, 1895: 326); *albinos* Westerlund 1889; “*areia* Bourguignat” (in Richardson, 1980); *argentina* Holmberg 1909 (apparently in Holmberg, 1909a or 1909b, n.v.); *atavora* Mabille 1885 (listed

as *H. atavorum* Mab., by Pilsbry, 1895: 324); “*bathytera* Bourguignat” (in Richardson, 1980); ‡*betieri* David & Jodot 1955; *concolor* Westerlund 1889; ‡*conica* David & Jodot 1955; *crassidens* Pallary 1898; *depressa* Bourguignat in Westerlund 1889; *expansa* Kobelt 1913; *fasciata* Rossmässler in Westerlund 1889; *houtiana* Pallary 1926; *H. Jacquementana* Bourg. (listed by Tryon, 1888: 130, as syn. from Canary Is.); *Helix lactea* var. *magna* Schmidt 1855; *mentonensis* Sidebotham 1880; *Helix lactea* var. *minor* Schmidt 1855; *minor* Pallary 1928; *pallida* Pallary 1928; “*parvula* Bourguignat” (in Richardson, 1980); *quinquefasciata* Westerlund 1889; *ramisi* Bourguignat 1883 (listed by Pilsbry, 1895: 326); *saidana* Debeaux in Kobelt 1887 (listed as syn. of *juilleti* by Tryon, 1888: 134–135); *Helix sublactea* Caziot & Thieux 1911 (p. 123); “*submaura* Deveaux & Fagot, Bourguignat” (in Richardson, 1980); *stomatodaea* Bourguignat in Kobelt 1882; *subseguyana* Kobelt 1903; *tafnensis* Kobelt 1903; ‡*tectiformis* David & Jodot 1955; ‡*tioukaensis* David & Jodot 1955; *Helix transitana* Caziot & Thieux 1911 (pp. 124, 125); *trarensis* Kobelt 1913; *trifasciata* Bourguignat in Westerlund 1889; *unicolor* Westerlund 1889; *unicoloralba* Pallary 1920. *Helix efferata* Mousson 1872 has been listed as a syn. of *O. lactea* but it is now treated as *Hemicycla efferata* (Mousson 1872) (Bank *et al.*, 2002). For fuller citations and a few additional synonyms from outside the W. Maghreb see Richardson (1980) and Beckmann (2007: 126).

*Shell* 2145 shells examined from 170 localities (also comparative material from Canary Islands, Portugal and Spain). Usual ranges, B 22.9–47.1, H 14.1–28.6mm, H/B 0.53–0.62 (0.67), with 4.2–4.7 whorls. Shape depressed conical to very depressed conical, somewhat flattened below, with gradually increasing whorls, the body whorl relatively larger in many populations; immatures and adults with rounded periphery; suture of moderate depth. Aperture broadly to rather narrowly oval (except where interrupted by penultimate whorl), with peristome slightly to strongly reflected in different populations; lower lip with tooth near middle that is low and inconspicuous to tall in different populations. Ground-colour whitish, with up to five dark brown bands; common banding forms are 12345 and 1(23)45, others seen rarely being 00305 (with 5 weak), 00345 (1 and 2 being present only at peristome edge), 02345 and 10340 (with 1 and 4 very

faint); the dark bands vary markedly in width and they often have whitish spots or blotches; some populations and individuals in others have broad but faint bands that are almost obscured by pale speckling; locally in NC. Morocco a few populations have all-white shells except for dark coloration inside the aperture (e.g. Fig. 4B). Dark area normally present inside aperture, brown to blackish, with sharp demarcation across parietal area; peristome varying from white with brown lower lip to mainly dark like coloration inside aperture. Protoconch small, glossy, nearly smooth with weak radial ribs variably developed; teleoconch with irregular radial-tangential low ribs and lines, intersected by closely spaced fine spiral grooves; the underside generally smoother.

*Genital anatomy* Eight specimens dissected from six localities (plus comparative material from Portugal). See account of *O. punctata* above for differences. For additional figures of genital anatomy see Hesse (1910: figs 433–438, 1911: pl. 443), Castillejo (1986: 47), Puente (1994: 803–804), Schileyko (2006: 1798) and De Mattia & Mascia (2011: 43). Internal structures of the genital atrium and penis in fully mature snails provide a few additional characters (Fig. 8, Table 1), none of them clearly separating *O. punctata* from *O. lactea*, while *O. xanthodon* and *O. tingitana* are apparently more distinctive.

*Variation and taxonomy* Formerly split into numerous species, as set out in the synonymy above. See the account of *O. punctata* above for comments on the separation of that species in earlier studies. Kobelt (1882, Icon., (2)1 (1/2), pp. 27–29) evidently thought that *O. lactea* was a variable species that should include other nominal species, since he placed three of them as varieties. Bourguignat (in Péchaud, 1883: 54–56) contested this, suggesting repeatedly that Kobelt misunderstood or misidentified the segregate species (as with *O. punctata*, *q.v.*). Pilsbry (1895: 324) listed 15 taxa as varieties, evidently because he was more inclined to follow Kobelt's approach than that advocated by Bourguignat.

Hesse (1909–1911) treated several but not all forms previously regarded as distinct species as subspecies or forms (for list see Hesse, 1911: 98–99), although he used the nomenclature somewhat inconsistently. He found only small

differences between named populations in the anatomy of the distal genitalia (Hesse, 1910: 54), which might at least in part have been due to variation between individuals rather than populations.

Shell characters vary markedly within populations, especially size. As examples, ranges of shell breadth among samples of fresh adult shells were 25.9–33.5mm (1993.051.191) and 24.5–37.5mm (1993.051.4515); even larger ranges occur in samples of old shells that are likely to represent many different generations, e.g. 21.5–39.0mm (1993.051.1867).

Marked differences in other characters occur between different regional populations, these having led to recognition of numerous additional species in the past. Nevertheless, our study of large samples from numerous populations reveals intermediates between some of the most differentiated local forms. Thus:

*O. juilleti* looks very distinctive in samples from eastern parts of its Algerian range (e.g. 1993.051.621, -635, -666; Fig. 2C), with up to 4.7 slowly expanding whorls, a low spire and rather flat base to the shell, peristome with white upper and outer edges, prevalence of morphs with four and five well defined narrow bands, and weak spiral microsculpture on the periostracum. Nevertheless, these distinctive characters are less marked in samples from the Monts de Tlemcen in NW. Algeria (1993.051.603, -590) (Fig. 2D).

*O. riffensis* from the eastern Riff is also distinctive, with large size (B 41–44mm), low spire, a relatively large body whorl, a large narrow aperture, strongly reflected peristome, blackish coloration inside aperture and a large tooth on the lower lip (Fig. 3A, B). However, old shells from within its range include striking series of intergrades with much smaller (28–34mm), high-spired, pale forms (in 1993.051.215, -1860), and other populations nearby have the distinctive characters less developed (e.g. 1993.051.4462).

A sample from the NW. Riff (1993.051.1925, comprising 41 shells from *ca* 3km S. of Souk Sebt el Kdim, NW. of Tétouan), has shells that seem to be of two main types (Fig. 2G cf. 2H), one small (B 27.0–28.7mm) with white upper and outer lips and reduced amount of mid-brown in the aperture (ending before reaching parietal area), the other larger (B 38.5mm) with blackish-brown in the aperture that extends outwards beyond the parietal area. Nevertheless, these two types

are accompanied by a few clearly intermediate shells.

Some populations in dry regions of NE. Morocco resemble *O. xanthodon* in having shells that are all-white (or dark-banded with white background coloration) and in a tendency towards globular shape (e.g. Fig. 4B), but these also show the more extensive and darker apertural coloration, single low tooth placed centrally on the lower lip and proportionately large body whorl more typical of *O. lactea*.

In Europe, treated as a polytypic species with five subspecies by Beckmann (2007: 126). In Andalusia, Spain, Ruiz *et al.* (2006: 170) recognised ssp. *murcica* in Prov. Almeria and ssp. *lactea* elsewhere in Andalusia.

**Nomenclature** Pallary (1914: 8–14) drew attention to serious inconsistencies in the original description of *O. lactea* by Müller (1774: 19–20, no. 218), most notably that the indications of published figures from Petiver and Lister show other species, comprising *O. punctata* (O.F. Müller, 1774) and banded shells of unrelated snails from Jamaica or perhaps Ceylon. Pallary also commented on the atypically small shell size of forms  $\alpha$  and  $\beta$  described by Müller, with diameters respectively of 12 lin. (27mm) and 10 lin. (22.5mm), and the large shell size of form  $\delta$  of 18 lin. (40.6mm), although the range of adult shell size in our material is 22.9–47.1mm, many shells from southern Iberia are below 27mm in diameter, and samples from the E. Riff of Morocco are mostly 41–44mm. Nevertheless, the remainder of Müller's description is consistent with *H. lactea* as currently understood, and of course, Müller himself named *O. punctata* in the same publication. Unfortunately, Müller gave no locality for *H. lactea* and Pallary's enquiries to the Copenhagen Museum revealed that they no longer had a type specimen. Thus, there are reasons to be doubtful whether the original description by Müller (1774) refers entirely to the species that later authors have regarded as this taxon, but no clear proof that it was all or mainly incorrect. Firm evidence of its correctness now seems unlikely to be forthcoming from painstaking analysis of the historic literature and illustrations, especially in the absence of a type-locality or type specimen.

His findings led Pallary to propose that the name *H. lactea* auct. should be replaced by *H. faux nigra* Chemnitz 1786. The reasons for this do

not appear fully convincing and only two publications by authors other than Pallary himself have since adopted the latter name (see above), and those that did so gave no explanations: they do not make it clear that they were intentionally using the name to replace *H. lactea* rather than merely citing what they believed to be a different segregate species. The name *H. faux nigra* based on Chemnitz (1786) anyway cannot now be used because the publication involved is unavailable for zoological nomenclature, it having been rejected as not consistently binominal in Opinion 184 and Direction 1 of I.C.Z.N. (1944, 1954). It was apparently not until Pallary (1914) himself wrote on the subject that this name was eventually validated.

Currently, *Otala lactea* (O.F. Müller, 1774) is generally used as the name for the species in the principal contemporary authoritative checklists covering its native range (Bank, Groh & Ripken, 2002: 128; Animalbase [edited by F. Welter-Schultes; accessed 2017]; Fauna Europaea [edited by R.A. Bank; accessed 2017]), in addition to the modern illustrated handbooks for these regions (Backhuys, 1975: 249–251; Seddon, 2008: 86; Cadevall & Orozco, 2016: 558). The species is important commercially in the Maghreb and south-west Europe where it is traded internationally as a food item (see below), and widely known elsewhere as a potentially invasive introduction on several continents (see below).

If the familiar and now almost universal usage of the name *O. lactea* needs to be changed, the oldest available synonym is *Pomatia atomaria* Röding 1798, a name based on an unlocalised shell or shells that has remained unused except in synonymy for 200 years – adoption of this name to replace *O. lactea* is in our view undesirable. The broadened taxonomic definition of *O. lactea* proposed in this paper may diminish the need for clarification of its nomenclatural basis. However, in case other workers wish to recognise subspecies or segregate species within *O. lactea*, we are proposing a Neotype here in order to support and maintain existing usage. The neotype chosen is from southern Iberia (SW. Portugal), since shells of the species from southern Iberia are rather small, as in parts of Müller's description, the first published locality data for *H. lactea* was given by Gmelin (1791: 3630) as "Jamaica et Lusitania" (Jamaica being an error), and the recent literature from southern Iberia

has regarded the nominotypical form as occurring over most of the region with *O. l. murcica* further east (Ruiz *et al.*, 2016: 61, 170; Bank, 2011: 34; Cadevall & Orozco, 2016: 558). It is unclear whether assigning the populations ranging from central Andalucia to Portugal as *O. l. lactea* is really warranted, but this is now fixed by our neotype designation:

NEOTYPE collected alive on 27 October 2014; Portugal, Baixo Alentejo: N. of Porto Covo (UTM: 29S 051767/419559), low sand dunes with grasses and patchy herbs on slope between head of beach and car parking at roadside, ca 12m altitude; collectors G.A. and D.T. Holyoak site P413; shell B 26.9, H 18.2mm, now housed in NMW.Z.2017.012.1. The shell was selected as typical from a sample of 11 adult and 5 immature shells from the same locality in CGAH; the adult shells have B 24.7–29.6mm; one of several bodies preserved in ims was dissected, revealing distal genitalia typical for *O. lactea*.

*Range in W Maghreb.* Morocco (S. to Anti Atlas and slightly beyond in coastal region), NW. Algeria (regions near Tlemcen, Oran, Mascara, Saida, El Bayadh and Laghouat) (Figs 9, 10). Limondin-Lozouet *et al.* (2013: 65, 66, 69 fig. 6 no. 13, 73) record Holocene fossils from numerous levels through a stratified succession <sup>14</sup>C dated from 9450 to <2725 years B.P. near Ksabi in Middle Moulouya basin (NE. Morocco).

*Global range* Widespread and appearing to be native in S. and E. Spain, Balearic Is. (Beckmann, 2007: 126), C. and S. Portugal (Matos, 2014: 228–230). An old report from Italy (Argentarola in Tuscan Archipelago) may be based on misidentification (De Mattia & Mascia, 2011: 39). Shells of Neolithic age were reported from C. Portugal by Matos (2014: 228).

The species is widely collected and transported as a food item and it may also be introduced with garden plants. It has been widely introduced within and near the limits of its native European range and is probably of introduced origin also in the Madeiran Is. (Seddon, 2008: 86); its populations in the Azores and Canary Is. (Backhuys, 1975: 249–251; Bank *et al.*, 2002: 128) may similarly have originated from anthropogenic introductions according to early malacological visitors (d’Orbigny in Webb & Berthelot, 1839; Morelet, 1860). It is certainly an introduction in Arizona,

Florida, Pennsylvania (since Say, 1822: 370), Cuba, Bermuda, Uruguay and SE. Australia.

*Otala xanthon* (Anton 1838) Figs 4C–H, 7E, 9, 12

[*Helix*] *xanthon* Anton 1838 (“1839”), Verzeichniss der Conchylien ..., p. 39, no. 1432, TL not stated, here restricted to Oran (NW. Algeria); *Helix xanthon* Anton mss., Rossmässler (1839: 6, pl. 43 fig. 563), Oran; Rossmässler in Wagner (1841: t. 2, 260; Atlas pl. 13 fig. 8), n.v.; Morelet (1843: 290); Pfeiffer (1853: 198); Bourguignat (1864: t. 1, 140–142, pl. 14 figs 10–16), with vars *major*, *obesa*, *albinos*, *picta* (p. 141) and distributional data; Bourguignat (1864: t. 2, 319, 333, 357, 362), Oudjdah [in Morocco; p. 319]; *H. xanthon* var., Kobelt (1876: 55–56, pl. 114 fig. 1129 [“1130” in text]), bei Oran; Morelet (1880: 22), Oudjdah, sur la frontière du Maroc et de l’Algérie (*vide* Bourguignat); Ancey (1882: 287); Bourguignat [in Péchaud] (1883: 75, 79–80), environs d’Oran, de Mascara; Ras-el-Aïn, chez les Beni Mattar (Maroc) [location uncertain; three places in Morocco with this name are all far to the west of the range of the species]; Westerlund (1889: 435); Pilsbry (1895: 325), with vars *ema* Bgt., *pseudoemia* Bgt.; Pallary (1899a: 115), Ras el Aïn, chez les Beni Mattar, also plaine d’Ouchda; Hidalgo (1909: 212), Melilla, Zeluán, Beni-Bu-Fruor; Hesse (1911: 106, 112); *Helix (Archelix) Xanthon*, Albers (1850: 98); *Helix (Tachea) xanthon*, Adams & Adams (1855: 195); *Helix (Macularia) xanthon*, Albers & Martens (1860: 133); Tryon (1888: 139, pl. 41 figs 42, 43); *Helix (Marmorana) xanthon*, Pallary (1904: 51); *Archelix xanthon*, Pallary (1914: 21), identified shells figured by Bourguignat (1864, t. 1, pl. 14 figs 10–16) as *A. abrolena*; also commented on synonymy of Bourguignat [in Péchaud] (1883); var. *major* Pallary zwischen Marnia und Udschda (*nomen nudum*); new var. *subcarinata* Pallary from Marnia (*nomen nudum*); Pallary (1920b: 37), Cheràa; Oued Tagma (Beni Znassen); *Archelix xanthon*, Hesse (1911: 85–86, pl. 447 figs 1–3), bei Lalla Marnia; *Archelix (Dupotetia) xanthon*, Hesse (1911: 95, 101); Pallary (1939b: 107); Llabador (1952: 112); *Otala xanthon*, Rour *et al.* (2002: 195); *Dupotetia xanthon* Anton, Cossignani (2014: 82–83), figs of two shells, from Ras el Ma.

*Helix Dupotetiana* Terver 1839 [Feb., *vide* Bourguignat, 1864: t. 1 p. 130; June, *vide* Sherborn, 1925: 1329, under *Helix cirtae*], Cat. Moll. Nord



**Figure 4** Shells of *Otala lactea* continued (A, B) and *O. xanthodon* (C–H); A Morocco, 31°31'N 7°33'W, sinistral individual, NMW.Z 2218; B Morocco, 34°59'N 3°12'W, NMW.Z 1993.051.1852; C Morocco, 35°06'N 2°45'W, NMW.Z 1993.051.4181; D ditto; E Morocco, 34°00'N 2°29'W, NMW.Z 1993.051.2017; F Morocco, 34°12'N 3°31'W, NMW.Z 1993.051.526; G Morocco, 34°17'N 3°11'W, NMW.Z 1993.051.531; H Morocco, 34°51'N 2°52'W, NMW.Z 1993.051.4548. See Appendix for additional details of specimens. Scale bar 20mm.

Afr., pp. 13–14, pl. 1 figs 4–6, TL Oran, près le fort Saint-Grégoire, Santa-Cruz, dans les montagnes entre la ville et la fort de Mers-el-Kebir, Viel-Arzew, montagnes aux environs de Mascara [Algeria]; Albers (1850: 98) acted as first reviser and gave precedence to this name over *H. zaffarina* Terver 1839 (under ICZN Code Art. 24) [although Westerlund (1889: 430) subsequently gave precedence to *H. zaffarina* over *H. dupotetiana* he was not the first reviser]; Rossmässler (1839: 2–3, pl. 41 figs 552, 553), Oran [Algeria]; Rossmässler in Wagner (1841: t. 2, 249, 255, 259; Atlas pl. 12 figs 6, 7), n.v.; *Helix Dupotetiana* var. *β alba* Saint-Simon (1848: 20–23), from “environs d’Alger”; Morelet (1853: 283); Pfeiffer (1853: 198); Servain (1880: 34), shells reported from Spain (see below); *Helix dupotetiana* var. *rugosa* Kobelt (1882: 26, pl. 7 figs 64), Nemours [Algeria]; *H. Dupotetiana* varr., Kobelt (1882: 31–32, pl. 11 figs 90, 91), nächsten Nahe von Oran; *Helix dupotetiana* var. *albina* Kobelt (1882: 32, pl. 11 fig. 92), Markthalle von Oran; Bourguignat [in Péchaud] (1883: 39); Pilsbry (1895: 325); Pallary (1899a: 111–112); *alba* Gassies 1856, p. 107 (non Beck 1837), n.v.; *Helix dupoteti* var. *alba*, Hesse (1911: 106); *Helix (Archelix) Dupotetiana*, Albers (1850: 98); *Helix (Tachea) Dupotetianus*, Adams & Adams (1855: 195); *Helix (Macularia) dupotetiana*, Albers & Martens (1860: 133); Tryon (1888: 138, pl. 41 fig. 39); *Helix (Macularia) dupoteti* [sic], Pallary (1901: 136, 194, 198), Algerian fossils; *Macularia dupotetiana*, Kobelt (1904: 65, pl. 296 figs 1898–1904), Gebiet zwischen der Macta und der Muluja, figs 1898–1900 zwischen Lella Marnia und Tlemecen (var. *scissilabrum*), figs 1901–1902 Umgebung von Oran (var. *microstoma*), fig. 1904 sent by Debeaux as *Helix zaffarinoides* nov. from Lella Marnia; *Helix (Marmorana) Dupoteti* [sic], Pallary (1904: 50), Mélilla; “with var. *alba* P. = *zaffarina* auct.”; *Archelix Dupotetiana*, Hesse (1909: 31); Hesse (1911: 77–83, 106, 110, 111, 112, pl. 445 figs 1–7), also as Pleistocene fossil (p. 103); Pallary (1920b: 32); *Archelix (Dupotetia) Dupotetiana*, Hesse (1911: 100–101); *Dupotetia Dupotetiana*, Llabador (1936: 200), Massif des M’Sirdas au sud-ouest de Nemours; Pallary (1939b: 107); *Archelix (Dupotetia) Dupoteti* [sic] var. *alba*, Llabador (1952: 111–112), Tatsfachs (Oulad Settout); embouchure de la Moulouya (Kebdana); *Otala dupotetiana*, Rour et al. (2002: 195); *Otala (Dupotetia) dupotetiana*, Schileyko (2006: 1797 figs 2302 A, B), figs of shell and genitalia (after Hesse, 1911).

*Helix zapharina* Beck 1837, Index. Moll., p. 39 no. 13 (unavailable: most probably a *nom. nud.*; refers only to “Webb et B[erthelot] t. f”, which could refer to any fig in any of several papers); *Helix Zaffarina* Terver 1839, Cat. Moll. Nord Afr., pp. 12–13, pl. 1 figs 2, 3, TL Iles Zaffarines [= Islas Chafarinas], sur les côtes de Barbarie, se trouve communément dans la province d’Oran, etc.; Wagner (1841: t. 2, 266), n.v.; *Helix zaffarina*, Beck, Pallary (1899a: 111), Iles Zaffarines et des côtes avoisinantes, also Mélilla (*fide* Bourguignat); *Helix Dupotetiana* (Var. *Zaffarina*), Terver, Morelet (1880: 22), Melilla (*fide* Bourguignat); Bourguignat (1864: t. 1, 119–122, pl. 10, fig. 8), with vars *minor* (p. 120), *5-fasciata*, *4-fasciata*, *trifasciata*, *bifasciata*, *aspera*, *atro-castanea*, *fulvescens* (p. 121), distributional data (pp. 120–122); Bourguignat (1864: t. 2, 319, 333, 357, 362) in Morocco, Iles Zaffarines, environs de Melilla (p. 319); Servain (1880: 34), entre Ronda et Malaga [errors?]; Ancey (1882: 286–287); Kobelt (1882: 32, pl. 11 fig. 93); Bourguignat [in Péchaud] (1883: 38–39); Bourguignat [in Péchaud] (1883: 86), in list as *Zapharina*; Westerlund (1889: 430–431), with vars *zelleri*, *dupotetiana* and *Tingitana* Palad. [the last of these clearly misplaced here]; Pilsbry (1895: 325), with var. *zelleri* Kob., f. *doubletti* Bgt.; Hesse (1911: 77), Oran; *H. zaffarina* var. *Zelleri* Kobelt (1882: 32–33, pl. 12 figs 96, 96a), Markte zu Mascara [Algeria]; *Helix zelleri*, Hesse (1911: 77, 111), Mascara; *Helix (Archelix) Dupotetiana* var. *Zaffarina*, Albers (1850: 98); *Helix (Macularia) Dupotetiana* var. *Zaffarina*, Albers & Martens (1860: 133); *Helix (Macularia) zaffarina*, Tryon (1888: 137–138, pl. 41 fig. 37), with var. *zelleri* (p. 138, pl. 41 fig. 38); Pallary (1901: 136, 193, 194, 198), Algerian fossils; *Helix (Marmorana) zaffarina*, Pallary (1904: 30–31), discusses confusion over identity of *H. zaffarina* Terver, suggesting it should be replaced by *H. Dupoteti* Terver var. *alba* Pallary [contrary to Westerlund, 1889: see above]; *Archelix zaffarina*, Hesse (1911: 111, pl. 445 figs 8–10); *Archelix dupotetiana zaffarina*, Hesse (1911: 80–81), also as Pleistocene fossil (p. 103); *Archelix (Dupotetia) Zaffarina*, Pallary (1939b: 107). *Helix arabica* Terver 1839, Cat. Moll. Nord. Afr., pp. 14–15, pl. 2 figs 1, 2, TL dans l’Atlas, au col des Beni-ou-Assan ... dans les rochers qui forment presque toute la crête de la montagne; [non *Helix arabica* Forskal 1775; renamed as *H. abrolena* Bourguignat 1864, see below; = *H. mea* Bgt according to Pallary 1899a: 115]; Rossmässler in Wagner (1841: t. 2, 249, 255, 259; Atlas, pl. 13 fig.

3), n.v.; Morelet (1853: 281); Pfeiffer (1853: 198); Kobelt (1876: pl. 114 fig. 1130 ["1131" in text]), Habibas-Inseln; Westerlund (1889: 435); Ancey (1882: 285–286); Pilsbry (1895: 325), with var. *abrolena* Bgt.; Hidalgo (1909), Chafarinas; *Helix* (*Archelix*) *arabica*, Albers (1850: 98); *Helix* (*Tachea*) *Arabicus* Terv., Adams & Adams (1855: 195); *Helix* (*Macularia*) *arabica*, Albers & Martens (1860: 133); Tryon (1888: 139, pl. 42 figs 47, 48), "Province of Oran and Adjacent Islands"; *Archelix arabica*, Hesse (1911: 89–90, 107, 112, pl. 448 figs 7, 8), Taforalt im östlichen Marokko; *Archelix* (*Dupotetia*) *arabica*, Hesse (1911: 101). [*Helix*] *aspera* Gassies, 1856, n.v.; *Archelix* (*Dupotetia*) *aspera*, Pallary (1939b: 107). *Helix Tigri* P. Gervais mss., in Mus. Monspeussul. (unavailable: not published), n.v., [*fide* Bourguignat, 1864: t. 1, 144]; *Helix tigri* [P. Gervais] Marès 1857 [in report on *Séance du 6 juillet 1857*], Rev. Mag. Zool., (2) 9, p. 330, TL Le bas-fond de Tigré, situé au sud du Maroc (this publication provides a description and makes the name available); *Helix Tigri* Fischer 1857 (October), J. Conchyl., 6(2), pp. 189–190, pl. 6, fig. 3, province d'Oran; *maresi* Crosse in Pfeiffer 1859, n.v.; *Helix Maresi* Crosse 1862 [April], J. Conchyl., 10, p. 154; replacement name for *Helix Tigri* P. Gervais 1857, "invalid because a noun"; Morelet (1880: 23), chott de Tigri; noted that locality denoted by the name, chott de Tigri, is on the border of Morocco in territory that might be disputed and that the name given is invalid being a noun and should be replaced by *H. Maresi* Crosse 1862; *Helix tigri*, Pilsbry (1895: 325), syn. *tigriana* Bgt., *maresi* Cr., vars *stereodonta* Bgt., *dicallistodon* Bgt.; *Helix Tigriana* Bourguignat 1862 [May], Paléont. Alg., p. 53, pl. 1, figs. 4–5; [Morelet (1880: 23) noted that this name was published later than *Helix Maresi* Crosse 1862, so it is an invalid junior synonym]; Bourguignat (1863: Moll. nouv. lit., p. 6, pl. 1 figs 4–8); also published in Rev. Mag. Zool. (2) 15, pp. 100–111, 1863; Bourguignat (1864: t. 1, 144–145, pl. 15 figs 6–12), with var. *crassidens* & locality data; Bourguignat (1864: t. 2 p. 319), in Morocco, Plaines des hauts plateaux, près du chott de Tigr; Kobelt (1875: 2–3, pl. 91 figs 975), du Bas-fond di Tigri frontière sud du Maroc; Bourguignat [in Péchaud] (1883: 85, 86, 91), with locality data (p. 91); Westerlund (1889: 441); Pallary (1899a: 117–118), Pallary adopted the name *tigriana* in preference to *H. Maresi* Morelet, which has priority; *Helix* (*Macularia*) *tigri*, Albers

& Martens (1860: 133); Tryon (1888: 141–142, pl. 42 figs 63–65); with *H. stereodonta* (p. 142, pl. 43 figs 68, 69) treated as syn.; *H. dicallistodon* (p. 142, pl. 42 figs 66, 67) treated as syn.; *H. surrodonta* (p. 142, pl. 43, figs 70, 71) treated as syn.; *Helix* (*Marmorana*) *tigriana*, Pallary (1904: 51), in Morocco at Chott Tigri; *Archelix tigri*, Hesse (1911: 92–94, 107, pl. 449 figs 4–8), Süden der Provinz Oran; *Archelix* (*Dupotetia*) *tigri*, Hesse (1911: 102); *Deserticola tigriana*, Pallary (1939a: 64); *Otala tigriana*, Rour *et al.* (2002: 195); *Otala* (*Deserticola*) *tigri*, Schileyko (2006: 1798: fig. 2303A, B), figs of shell and genital anatomy (after Hesse, 1911); *Otala tigri*, Limondin-Lozouet *et al.* (2013: 65, 67, 68 fig. 6:5), several well preserved Holocene fossils found loose [not stratified] during studies of deposits near Ksabi in Middle Moulouya basin (NE. Morocco).

*Helix embia* Bourguignat 1863, Moll. nouv. lit., (1<sup>re</sup> décade), pp. [3]-4, pl. 1 figs 1–3, TL île Habibas, près de la côte algérienne, entre Cherchell et Oran; also published in Rev. Mag. Zool. (2) 15, pp. 100–111; Bourguignat (1864: t. 1, 143–144, pl. 15 figs 17–20); Ancey (1882: 290); Bourguignat [in Péchaud] (1883: 82); *H. embia* var.?, Kobelt (1888: 45–46, pl. 84 figs 467), am Strand von Nemours [Algeria]; Westerlund (1889: 437), with var. *apista*; Pilsbry (1895: 325); Hesse (1911: 107); *Helix* (*Macularia*) *embia*, Tryon (1888: 140–141, pl. 42 figs 56, 57).

*Helix burini* Bourguignat 1863, Moll. nouv. lit., (1<sup>re</sup> décade), pp. [5]-6, pl. 1 figs 9–12, TL assez abondamment dans le chott de Tigri au sud de la province d'Oran, près de la frontière du Maroc; also published in Rev. Mag. Zool. (2) 15, pp. 100–111, 1863; Bourguignat (1864: t. 1, 146–147, pl. 15, figs 13–17; t. 2, 319), in Morocco, chott de Tigri; près du Djebel-Doug; Ancey (1882: 290); Bourguignat [in Péchaud] (1883: 85, 86, 87), chott de Tigri (TL), Lambelt entre Ain-Defla et Figuig, vallée de Chegguet-Kradya, dans le Dough; Kobelt (1887: 24–25, pl. 26 figs 399, 399a), in der oranesischen Sahara, in der Umgebung des Schott el-Tigri; Westerlund (1889: 438); Pilsbry (1895: 325); Pallary (1899a: 116), type from chott Tigri; Lambelt entre Ain Delfa et Figuig; vallée longitudinale de Chegguet Kradya, dans le Dough; *Helix* (*Macularia*) *burini*, Tryon (1888: p. 141, pl. 42 figs 60–62); *Helix* (*Marmorana*) *Burini*, Pallary (1904: 51); *Otala burini*, Rour *et al.* (2002: 195).

*Helix dastuguei* Bourguignat 1863, Moll. nouv. lit., (1<sup>re</sup> décade), pp. [7]-8, pl. 2 figs 1–5, TL

Redjem-el-Mouilah, à 5 kilomètres au nord d'Aïn-Safra, oasis du sud de la province d'Oran; also published in *Rev. Mag. Zool.* (2) 15, pp. 100–111, 1863; Bourguignat (1864: t. 1, 147–148, pl. 15 figs 18–22); Ancey (1882: 290); Bourguignat [in Péchaud] (1883: 85, 86, 88); Kobelt (1887: 25–26, pl. 26 fig. 399b), in der südoranesischen Sahara, nach Bourguignat nur bei Bedschem-el-Mouilah nördlich von Aïn-Safra; Kobelt (1888: 47, pl. 85 figs 470, 471); Westerlund (1889: 439–440); *Helix dastugui* [sic], Pilsbry (1895: 325); *Helix (Macularia) dastugui* [sic], Tryon (1888: 142, pl. 43 fig. 72); *Helix (Macularia) dastuguei*, Pallary (1901: 129, 197), hamada de la rive gauche de l'oued Safra; doubtful whether a Quaternary fossil or not, since it is living at the locality; *Archelix (Dupotetia) dastuguei*, Hesse (1911: 102).

*Helix odopachya* Bourguignat 1864, *Malac. Alg.*, 1, pp. 142–143, pl. 14 figs 17–20, TL Fritis, entre Geryville et le Chott de Tigri, au sud de la province d'Oran; *Helix odopachya*, Bourguignat (1864: t. 2, 319), in Morocco, Plaines des hauts plateaux; près du chott de Tigri; Morelet (1880: 22–23), chott de Tigri; Ancey (1882: 290); Kobelt (1882: 33, pl. 12 figs 97), bei Asla in der Sebcha Namaa in der oranesischen Sahara; Bourguignat [in Péchaud] (1883: 81–82, 86); Westerlund (1889: 436–437); Pilsbry (1895: 325); Pallary (1899a: 116), Sud oranais [may also extend to “centre du Maroc, car nous l'avons trouvée avec les bidentées charriées par la Tafna”]; *Helix (Macularia) odopachia* [sic], Tryon (1888: 140, pl. 42 figs 49–52), “Oran, Algiers” [i.e. Prov. Oran, Algeria]; *Helix (Marmorana) odopachya*, Pallary (1904: 51), Sud Est Maroc; *Archelix odopachia* [sic], Hesse (1911: 90–92, pl. 449 figs 1–3), Aïn Sefra; Sebka Naama, zwischen Aïn Sefra und Mecheria; *Archelix (Dupotetia) odopachia* [sic], Hesse (1911: 102); *Archelix (Dupotetia) odopachya*, Pallary (1939b: 107); “*odopachya* aucts.”, Richardson (1980); *Otala adopachya* [sic], Rour *et al.* (2002: 195).

*Helix abrolena* Bourguignat 1864, *Malac. Alg.*, 1, pp. 138–140, pl. 14 figs 1–9; nom. nov. for *Helix arabica* Terver 1839 (preoccupied), with vars *albidula*, *microstoma* and distributional data; Ancey (1882: 286); Bourguignat [in Péchaud] (1883: 75, 77–78, 86), ile de Rachgoun; Westerlund (1889: 434–435); Pallary (1899a: 114), Iles Zaffarines, with vars. *minor* Bourguignat, *microstoma* Bourguignat, *albidula* Bourguignat; *Helix (Macularia) abrolena*, Tryon (1888: 139, pl. 42 figs 44–46); *Helix (Marmorana) abrolena*, Pallary (1904:

50), with vars *minor*, *microstoma*, *albidula*; *Archelix abrolena*, Hesse (1911: 87–89, 107, 112, pl. 448 figs 1–6), Habibas-Inseln; *Archelix abrolena* var. *incrassata* Pallary (1920a: 21), from iles Habibas, Rachsgoun, Zaffarines; *Archelix (Dupotetia) abrolena*, Hesse (1911: 101); Pallary (1939b: 107); *Otala abrolena*, Rour *et al.* (2002: 195).

*Helix Flattersiana* Ancey 1882, *Naturalisto Siciliano*, 1, p. 290, TL Sebcha Namaâ, dans le Sahara Oranais [Algeria]; Westerlund (1889: 437); Pilsbry (1895: 326); *Helix (Macularia) flattersiana*, Kobelt (1898: 42, pl. 223 figs 1422), in der oranesischen Sahara an der Sebcha Namoâ und bei Ain Sefra; *Helix (Macularia) Flattersi*, Ancey, Pallary (1900: 733), unjustified emendation of name; *Archelix (Dupotetia) Flattersi*, Pallary (1939b: 107).

*Helix acatergastra* Bourguignat [in Péchaud] 1883, *Exc. Malac. Nord Afr.*, pp. 39–40, TL environs d'Oran, entre cette ville et Bou-Sofer; “M. Bourguignat possède cette espèce de Malaga, en Espagne” [which seems unlikely, unless it was found as a drifted shell on the beach]; Westerlund (1889: 431); Pilsbry (1895: 326).

*Helix speiratopa* Bourguignat [in Péchaud] 1883, *Exc. Malac. Nord Afr.*, pp. 40–41, TL sur les rochers, entre Beni-Aïad et la frontière marocaine; aux alentours de Lalla-Maghnia, une variété tout blanche, à spire moins élevée; Westerlund (1889: 431); Pilsbry (1895: 326); Pallary (1899a: 112); Hesse (1911: 106); *Helix (Marmorana) speiratopa*, Pallary (1904: 50), in Morocco at Beni Aïad; *Otala speiratopa*, Rour *et al.* (2002: 195).

[*Helix*] *catodonta* Bourguignat [in Péchaud] 1883, *Exc. Malac. Nord Afr.*, pp. 45–46, 86, 88, TL l'extrême sud de la province d'Oran, au midi du chott R'arbi, d'Aïn ben Rheld; the only description (p. 46, consists merely of: très remarquable par son ouverture relativement fort petite, rétrécie par une énorme lamelle columellaire dentiforme brusquement coupée à son extrémité.”; the earlier work cited (p. 45) as “Bourg., *Spec. noviss.*, N° 102, 1878” is fictitious (Connolly, 1934); *Helix arichensis*, Debeaux var. *catodonta* Bourguignat: Pallary (1899a: 113), les oasis du S. de Maroc dans le région du Chott R'arbi, à Aïn ben Kheld; *Archelix (Dupotetia) catodonta*, Hesse (1911: 102).

*Helix ema* [Bourguignat, sp. nov. 1880] Bourguignat [in Péchaud] 1883, *Exc. Malac. Nord Afr.*, pp. 75, 79, 81, new name for *Helix xanthodon* Bourguignat 1864 (non Anton), *Malac. Alg.*, 1, p. 140, pl. 14 figs 10–16; from Ile de Rachgoun;



environs de Nemours; îles Zaffarines; Habibas; Westerlund (1889: 435–436); Pallary (1899a: 115), Îles Zaffarines [Pallary considered it to be almost a var. of *H. abrolena*, from which it differed only in characters of slight importance]; with vars *albinos* Bourguignat, *major* Bourguignat; *Helix* (*Marmorana*) *ema*, Pallary (1904: 51), with vars *albinos*, *major*; *Otala ema*, Rour *et al.* (2002: 195).

*Helix surrodonta* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 86, 88, TL Oglat-Mazer, près du chott de Tigri; Djebel-Galloul, non loin de Fratis; défile de Kradya, au sud de la région de Tigri; the earlier work cited as “Bourguignat, spec. noviss., N° 117, 1878” is fictitious (Connolly, 1934); Kobelt (1887: 27–28, pl. 26 figs 401, 401a, 401b), in der südoranesischen Sahara – Bourguignat nennt Oglat-Mazer, den Dschebel Galloul und da Defilé von Kradya, sämtlich in der Nahe des Schott el-Tigri gelegen; Westerlund (1889: 438–439); Pilsbry (1895: 325); Pallary (1899a: 116), Oglat Mazir, près du Chott Tigri; Dj. Galloul, non loin de Fratis; défilé de Kradya, au Sud de la région du Tigri; *Helix* (*Marmorana*) *surrodonta*, Pallary (1904: 51); *Archelix* (*Dupotetia*) *surrodonta*, Hesse (1911: 102); *Archelix surrodonta*, Hesse (1911: 107); *Deserticola surrodonta* [sic], Pallary (1939a: 64); *Otala surrodonta*, Rour *et al.* (2002: 195).

*Helix romalæa* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 86, 89–90, TL chez les Beni-Mattar (Maroc), aux environs de Ras-el-Aïn; the earlier work cited as “Bourguignat, spec. noviss., N° 116, 1878” is fictitious (Connolly, 1934); Westerlund (1889: 440); Pallary (1899a: 117, pl. 8 fig. 4); Pilsbry (1895: 326); *Macularia romalæa*, Kobelt (1903: 38, pl. 284 figs 1824); *Helix* (*Marmorana*) *romalæa*, Pallary (1904: 51), in Morocco at Beni Mattar; *Archelix* (*Dupotetia*) *romalæa*, Hesse (1911: 103); *Deserticola romalæa*, Pallary (1939a: 64); *Otala romalæa*, Rour *et al.* (2002: 195); *Dupotetia romalæa* Bourguignat 1878 [sic], Cossignani (2014: 81–82), figs of two shells, from Berguent.

*Helix mattarica* [Letourneux, in litt., 1872] Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 86, 94, TL environs de Ras-el-Aïn, chez les Beni-Mattar au Maroc; the earlier work cited as “Bourguignat, spec. noviss., N° 120, 1878” is fictitious (Connolly, 1934); Westerlund (1889: 442); Pilsbry (1895: 326); Pallary (1899a: 118); *Helix* (*Marmorana*) *mattarica*, Pallary (1904: 51), in Morocco at Beni Mattar; *Archelix mattarica*, Hesse

(1911: 107); *Deserticola mattarica*, Pallary (1939a: 64); *Otala mattarica*, Rour *et al.* (2002: 195).

*Helix brocha* [Bourguignat 1882] Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 86, 90–91, TL chez les Beni-Mattar au Maroc; Westerlund (1889: 440–441); Pilsbry (1895: 326); Pallary (1899a: 117); *Helix* (*Marmorana*) *brocha*, Pallary (1904: 51), in Morocco at Beni Mattar; *Archelix* (*Dupotetia*) *brocha*, Hesse (1911: 103); *Otala brocha*, Rour *et al.* (2002: 195).

*Helix dicallistodon* [Bourguignat, in coll. 1872] Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 86, 91–92, TL la plaine de Tambelt, au sud de Tigri, entre Aïn-Delfa et Figuig; environs d’Aïn-ben-Khelil au nord de Taoussera; Kobelt (1887: 28, pl. 26 figs 402, 402a, 402b), in der südoranesischen Sahara ... Umgebung von Aïn-ben-Khalil nördlich von Taoussera; Westerlund (1889: 441); Pallary (1899a: 118), la plain de Tambelt, au S. de Tigri, entre Aïn Defla et Figuig; *Helix* (*Marmorana*) *dicallistodon*, Pallary (1904: 51), in Morocco at Tambelt; *Deserticola dicallistodon*, Pallary (1939a: 64); *Otala dicallistodon*, Rour *et al.* (2002: 195).

*Helix mea* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 78–79, 86, new name for *Helix arabica* Terver 1839 (non Forskal 1775, nec Roth 1839), TL dans les montagnes du col des Beni-Ouassan; also environs de Mascara et de Lalla-Maghnia; alentours d’Oran et de Nemours; earlier work cited as “Bourguignat, spec. noviss., N° 115, 1878” is fictitious (Connolly, 1934); Pallary (1899a: 115), Entre Lalla Marnia et Ouchda; *Helix* (*Marmorana*) *mea*, Pallary (1904: 51); *Otala mea*, Rour *et al.* (2002: 195).

*Helix Seignetti* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 86, 93–94, TL à peu près dans les mêmes régions que la précédente, i.e., *H. stereodonta*, [Oglat-Moussa, dans la région de Tigri; Galloul près de Fratis (sud province d’Oran)]; earlier work cited as “Bourguignat, spec. noviss., N° 119, 1878” is fictitious (Connolly, 1934); Westerlund (1889: 442); Pilsbry (1895: 326); Pallary (1899a: 118), dans la même région de la précédente (i.e. Oglat Moussa, près du Chott Tigri et de Galloul); *Helix* (*Marmorana*) *Seignettei* [sic], Pallary (1904: 51), in Morocco at Oglat Monça; unjustified emendation of name; *Archelix seignetti*, Hesse (1911: 107); *Archelix Seignettei* [sic], Pallary (1914: 21); *Deserticola Seignettei* [sic], Pallary (1939a: 64); *Otala seignettei*, Rour *et al.* (2002: 195).

*Helix stereodonta* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 86, 92–93, TL Oglat-Moussa, dans la région de Tigri; Galloul près de Fratis (sud province d’Oran); earlier work cited as “Bourguignat, spec. noviss., N° 118, 1878” is fictitious (Connolly, 1934); Kobelt (1887: 26–27, pl. 26 figs 400, 400a, 400b), oranesischen Sahara in den Umgebung des Schott-el-Tigri ... Galloul bei Fratis; Westerlund (1889: 441–442); Pallary (1899a: 118), Oglat Moussa, près du Chott Tigri et de Galloul; *Helix (Marmorana) stereodonta*, Pallary (1904: 51), in Morocco at Oglat Monça; with var. *sublaevis* W.; *Otala stereodonta*, Rour et al. (2002: 195).

*Helix euglyptolena* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 41–43, new name for and redescription of *H. Dupotetiana* var. *rugosa* Kobelt 1882 (see above; non *rugosa* Lamarck, Anton, Férussac, etc.), TL Environs de Nemours; Benisaf, près de l’embouchure de la Tafna (une autre forme); Westerlund (1889: 431–432); Pallary (1899a: 112), commune sur le littoral, au voisinage de la frontière algérienne [after examining types in Colln. Bourguignat, Pallary treated it as syn. of *H. Brevieri*]; *Helix (Marmorana) euglyptolena*, Pallary (1904: 50), in Morocco at Adjéroud; *Otala euglyptolena*, Rour et al. (2002: 195).

*Helix brevieri* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 44–45, new name for and redescription of *Helix Dupotetiana* var. *aspera* Gassies 1856 (Coq. Mayran, p. 5, fig. 13) (non *Helix aspera* Férussac 1821, nec Grateloup 1840), TL sur les rochers, aux environs de Nemours; dans les vallées de l’oued Mouilah, affluent de la Tafna; also var. *minor* in the same localities; Kobelt (1887: 23, pl. 75 figs 397, 398), bei Nemours, anscheinend mehr nach Osten von diesen Hafem; Westerlund (1889: 432); Pilsbry (1895: 325), with syn. *dopet[etiana]* v. *aspera* Gass., vars *rugosa* Kob. (syn. *euglyptolena* Bgt.), *subbrevieri* Bgt.; Pallary (1899a: 112), ça et là dans les vallées de l’O. Mouilah, affluent de la Tafna; with var. *minor* Pallary 1899a (p. 112) [but this var. previously named and described by Bourguignat in Péchaud 1883: 45], ça et là dans les vallées de l’O. Mouilah, affluent de la Tafna; *Helix Brevierei* [sic], Hesse (1911: 77, 106), Lalla Marnia; *Archelix dupotetiana brevieri* [sic], Hesse (1911: 81); *Helix (Macularia) Brevierei* [sic], Tryon (1888: 139, pl. 41 figs 40, 41), with *H. dupotetiana* var. *rugosa* Kobelt, *D. dupotetiana* var. *aspera* Ancey and *H. subbrevieri* Bourg. treated as syn.; *Helix (Macularia) Brevieri*,

Pallary (1901: 137, 194, 198), Algerian fossils; *Helix (Marmorana) Brevierei* [sic], Pallary (1904: 50), in Morocco at O. Mouilah, O. Kiss; apparently an unjustified emendation of name; *Archelix brevieri* [sic], Hesse (1911: pl. 446 fig. 15), also as Pleistocene fossil (p. 103); *Archelix (Dupotetia) Brevieri*, Pallary (1939b: 107); *Otala brevieri*, Rour et al. (2002: 195).

*Helix doubleti* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 76–77, 81, 86, 91, TL sur les rochers entre la Maghnia et Tlemcen; sur les montagnes près de la plage de Beni-Saf; alentours de Nemours, d’Oran, ... ile de Rachgoun; *H. doubletti* [sic], Tryon (1888: 138), regarded as syn. of *Helix (Macularia) zaffarina*; Westerlund (1889: 436); Pallary (1899a: 116), la plaine entre Marnia [Lalla Marnia?] et Ouchda, also sur les rives de l’O Kiss; Hesse (1911: 77), Mascara und Remchi; *Helix (Marmorana) Doubleti*, Pallary (1904: 51); *Archelix dupotetiana doubleti*, Hesse (1909: 31); *Archelix doubleti*, Hesse (1911: 112, pl. 446 fig. 16); Pallary (1914: 21, pl. 2 fig. 1), shell measurements in original description (*op. cit.*, p. 76) corrected to breadth 26, height 16mm; *Archelix (Dupotetia) Doubleti*, Pallary (1939b: 107); *Otala doubleti*, Rour et al. (2002: 195).

*Helix chydopsis* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 80–81, TL au sud du Chott-el-R’arbi, vers la frontière du Maroc; earlier work cited as “Bourguignat, spec. noviss., N° 114, 1878” is fictitious (Connolly, 1934); Westerlund (1889: 436); Pilsbry (1895: 326); Pallary (1899a: 115), Sud du chott R’arbi sur la frontière [Pallary examined the Holotype at MHNG and reidentified it as *H. abrolena* “déformé, de teinte unicolore”]; Hesse (1911: 107).

*Helix anoterodon* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 82–83, 86, 87, TL dans les gorges des montagnes voisines de Lalla-Maghnia, sur les frontières du Maroc; also Var. *minor* described; Kobelt (1888: 44–45, pl. 84 figs 466), Umgebung von Lella Marnia an der marokkanischen Gränze ... an Felsen oberhalb der Barrage der Mouila; Pilsbry (1895: 325); Westerlund (1889: 438), with new var. *variosculpta* from “Algerian bei Lella Marnia” (Kobelt, 1888: pl. 84 figs 466); *Helix (Macularia) anoterodon*, Tryon (1888: 138, pl. 46 figs 43, 44); *Helix (Marmorana) anoterodon*, Pallary (1904: 51), O. Mouilah; *Archelix anoterodon*, Hesse (1911: 83–85, 112, pl. 446 figs 17, 18), Lalla Marnia, Udschda im östlichen Marokko; *Archelix (Dupotetia) anoterodon*, Hesse

(1911: 101); Pallary (1939b: 107); *Otala anoterodon*, Rour *et al.* (2002: 195).

*Helix alabastra* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 83–84, 86, 89, TL dans la plaine des Andalouses, près d’Oran; alentours de Lalla-Maghnia; Westerlund (1889: 440); Pilsbry (1895: 326); Pallary (1898d: 562–563); Pallary (1899a: 116, gave pl. 5 figs 24–25, correcting the figs 9, 10 given in text of Pallary 1898d), suggested that “plage des Andalouses” locality from Bourguignat [in Péchaud] (1883: 83–84, as plaine des Andalouses) resulted from shells drifted down-river from localities inland in NE. Morocco (his Marnia [= Lalla Marnia] locality is likely to be correct); Pallary (1899a: 116–117), see above under Pallary (1898d), vivant sur la rive de l’O. Isly [supposition?]; chez les Beni Iznaten; Pallary (1901: 194), Algerian fossils; *Helix (Marmorana) alabastra*, Pallary (1904: 51), in Morocco at Beni Iznaten; *Archelix (Dupotetia) alabastra*, Hesse (1911: 103); *Archelix alabastra*, Hesse (1911: 112); *Archelix alabastra* Var. *Zonata* Pallary (1920a: 21), from Merada, Mokla Debdeba\*, Aïn bou Meçad\*, Guettara\*, Taourirt, Safsafat, Midelt [\*these places not located by present authors; “Guettara” was presumably not the town in the Algerian Sahara at 4°41'E.]; Pallary (1920b: 37–38), with slightly different listing of localities; with “sous-variété minor” (p. 38); Pallary (1923b: 279); Pallary (1926: 47, pl. 7 fig. 14, showing var. *zonata*); *Deserticola alabastra*, Pallary (1939a: 64), with var. *zonata*; *Otala alabastra*, Rour *et al.* (2002: 195); *Dupotetia alabastra*, Cossignani (2014: 81), figs of shell, from Hassi-Berkane; *Dupotetia alabastra zonata* (Pallary 1920), Cossignani (2014: 81), figs of two shells, from Hassi-Berkane; Taourirt.

*Helix (Macularia) Arichensis* Debeaux mss. in Kobelt 1884, Nachrbl. d. malak. Ges., 16, p. 26, TL el Arischa prov. Oranensis; *Helix Arichensis* [Debeaux in litt.], Kobelt 1887: 20–22, pl. 75, figs 394, TL bei el Arich südlich von Sebdou, bereits im Gebiet der Muluja; Westerlund (1889: 432–433), with vars *crassidens* and *catodonta*; Pilsbry (1895: 324–325), with vars *crassidens* Deb., *catodonta* (B.) Pech., *lobethana* Deb.; Pallary (1899a: 112–113), dj. Sidi el Abed qui s’étend entre El Aricha, du département d’Oran, et Ras el Aïn, du Maroc; *Helix arichensis* var. *crassidens* [Debeaux in litt.] Kobelt (1887: 22, pl. 75 figd 395), bei el Arich südlich von Sebdou, bereits im Gebiet der Muluja; *Helix arichensis*, Debeaux var. *crassidens*: Pallary (1899a: 112–113), dj. Sidi el Abed qui

s’étend entre El Aricha, du département d’Oran, et Ras el Aïn, du Maroc; *Helix (Macularia) arichensis*, Tryon (1888: 137, pl. 41 figs 34, 35), with var. *crassidens* (pl. 41 fig. 36); *Helix (Marmorana) arichensis*, Pallary (1904: 50), in Morocco at Dj. Sidi el Abed; with vars *crassidens* and *catodonta*; *Archelix (Dupotetia) arichensis*, Pallary (1939b: 107); *Otala arichensis*, Rour *et al.* (2002: 195).

*Helix lobethana* [Debeaux in litt.] Kobelt 1887, Icon., (2) 3 (5/6), pp. 46–47, pl. 84 figs 468, 469), TL am Dschebel Sidi Lobeth, etwa 12 Kilometer östlich von el-Aricha im südlichen Oran [NW. Algeria]; Westerlund (1889: 433); Pallary (1899a: 114), dj. Sidi el Abed, qui est une montagne que la frontière algérienne partage en deux; *Helix (Macularia) lobethana*, Tryon (1888: 137, pl. 46 figs 49, 50); *Otala lobethana*, Rour *et al.* (2002: 195).

*Helix pseudoembia* [Debeaux in litt.] Kobelt 1887, Icon., (2) 3 (3/4), pp. 22–23, pl. 75 figs 396, TL in der Umgebung von Lella Marnia an der marokkanischen Gränze, zwischen Tlemcen und Nemours; Westerlund (1889: 437–438); *Helix (Macularia) pseudoembia*, Tryon (1888: 141, pl. 42 figs 58, 59).

*Helix subjobaeana* Kobelt 1888, Icon., (2) 3 (5/6), pp. 47–48, pl. 85 figs 472, TL am Chott el-Tigri an der marokkanischen Gränze; Westerlund (1889: 439); Pilsbry (1895: 325); Pallary (1899a: 117), Chott Tigri [from the published figure, Pallary thought it very similar to *H. alabastra*, if not identical]; *Helix (Macularia) subjobaeana*, Tryon (1888: p. 142, pl. 46 figs 54–56); *Helix (Marmorana) subjobaeana*, Pallary (1904: 51); *Otala subjobaeana*, Rour *et al.* (2002: 195).

*Helix (Macularia) kebiriana* var. *minor* Pallary 1896, Comptes r. Assoc. franç. Avanc. Sci., Congrès de Carthage, offprint, p. 2, text fig.; *Helix (Macularia) kebiriana* Pallary, Kobelt (1898: 42, pl. 223 figs 1423; in fig. legend as *Helix punctata* var. *kebiriana* Pall.), aus den Dünen von Ain-turk bei Oran; *Helix (Macularia) kebiriana*, Pallary (1900: 733); Pallary (1901: 134, 191, 197), Algerian fossils; *Macularia kebiriana* var. *minor* Pall., Kobelt (1903: 42, pl. 286 figs 1834), Cap Falcon, westlich von Oran; *Archelix kebiriana*, Pallary (1939b: 107).

*H.[elix] microzaffarina* Pallary 1898(d), Comptes r. Assoc. franç. Avanc. Sci., 27 (2), pp. 561–562 [pl. 5 figs 10–12 *fide* Pallary 1899a, p. 114, not figs 16–18 as given in text of Pallary 1898d], TL sur la plage de l’O. Hallouf avec d’autres coquilles charriées par la Tafna ou la Moulouïa (reidentified [?] by Pallary as a syn. of *H. chydopsis* Bourguignat

from Chott Tigri); Pallary (1899a: 114), Sud-Est marocain d'où il a été charrié par la Moulouïah et rejeté sur les côtes algériennes; Hesse (1911: 77), Beni-Znassen; *Helix (Marmorana) microzaffarina*, Pallary (1904: 50), Est Maroc; *Archelix dupotetiana* f. *microzaffarina*, Hesse (1911: 82); *Archelix microzaffarina*, Hesse (1911: 112, pl. 446 figs 11–14); *Archelix (Dupotetia) microzaffarina*, Pallary (1939a: 64); *Otala microzaffarina*, Rour et al. (2002: 195).

*Helix stereodonta* Bourguignat Var. *sublaevis* Westerlund, Pallary (1899a: 118).

*Helix Aidæ* Pallary 1899(a), J. Conchyl., 46, pp. 119–120, pl. 9, figs 2, TL sur la plage de l'O. Hallouf, sur le littoral de l'Oranie [NW. Algeria], où elle a été portée par les courants [perhaps via the Moroccan river Tafna or the Moulouïah]; Forme *minor* Pallary 1899 (1899a: 119–120), sur la plage de l'O. Hallouf, sur le littoral de l'Oranie [NW. Algeria], où elle a été portée par les courants [perhaps via the Moroccan river Tafna or the Moulouïah]; Kobelt (1903, Icon., (2) 10 (3/4), p. 39, pl. 284 figs 1826); *Helix (Marmorana) Aidæ*, Pallary (1904: 51), Est Maroc; with var. *minor*; *Archelix (Dupotetia) aidæ*, Hesse (1911: 103); *Archelix aidæ*, Hesse (1911: 112); *Otala aidæ*, Rour et al. (2002: 95).

*Helix lariollei* Pallary 1899(a), J. Conchyl., 46, p. 113, pl. 8 fig. 3, TL Rar el Maden, non loin de la frontière; Sur les rives de l'Oued Kiss, à la lisière des Traras; Kobelt (1903: 34–35, pl. 283, figs 1816–1818) [figs suggest a form of *O. xanthodon* but *O. tingitana* might also be a possible identification]; Hesse (1911: pl. 447), fig. of genital anatomy; *Helix lariollei* Pallary 1899, Var. *crassidens* Pallary 1899 (1899a: 113, fig. 1), Sur les rives de l'Oued Kiss, à la lisière des Traras (perhaps collected with type of species at Rar el Maden, non loin de la frontière); *Archelix Lariollei*, Hesse (1911: 75–77, 94, 100, 111, pl. 447 figs 4–8), Rar el Maden im Travas-Massiv; *Archelix Lariollei* Pallary var. *expansa* Pallary (1914: 21–22, pl. 1 fig. 1), with typical form, bei Rar el Maden, im Herzen des Traras-Gebirges; also a *forma minor*; *Tingitana Lariollei*, Pallary (1939a: 65); *Otala lariollei*, Rour et al. (2002: 195).

*Helix (Marmorana) labettrana* Deb., Pallary (1904: 50), Morocco at Dj. Sidi el Abed (*nomen nudum*).

*Archelix Cavelliana* Pallary 1917, J. Conchyl., 63(2), p. 136, TL Moulay Taïeb, entre El Aioun et Moul el Bacha, sur les rives de l'oued el Ksob affluent de la rive droite de la Moulouïa [also on plages de l'Oranie, as drifted shells]; Pallary

(1926: 46–47, pl. 8 figs 5, 6), Son habitat parait être restreint entre Safsafat et Guercif; with vars *minor*, *depressa*, *major* (p. 46); *Otala cavelliana*, Rour et al. (2002: 195); *Dupotetia cavelliana*, Cossignani (2014: 81), figs of shell, from Guercif.

*Archelix galiyana* Pallary 1917, J. Conchyl., 63(2), pp. 140–141, pl. 5 figs 11, 12, TL Tribu des Guelaïa, au voisinage de Mèlilla; with vars *minor*, *bidenticulata*, *vernica*; *Archelix (Dupotetia) galiyana*, Llabador (1952: 114), embouchure de la Moulouya (Kebdana), no explanation is given for the novel subgeneric treatment; *Otala galiyana*, Rour et al. (2002: 195).

*Archelix maurusiana* Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11(2), p. 21, TL Berkane et à Taforal, dans les Beni Znassen [Morocco]; Pallary (1926: 41–42, pl. 7 figs 9–199), with vars *major*, *minor* and *subcarinata* (p. 42); *Archelix (Dupotetia) maurusiana*, Pallary (1939b: 107); *Otala maurusiana*, Rour et al. (2002: 195).

*Archelix aposa* Pallary 1923(a), Bull. Soc. Hist. nat. Afr. Nord, 14(3), p. 114, TL “? Trouvée sur les plages de l'Oranie dans les radeaux de détritiques charriés par la mer et provenant très probablement du bassin de la Moulouïa” [i.e. found on beaches of NW. Algeria which it very probably reached with debris floated from the basin of the Oued Moulouya in NE. Morocco]; Pallary (1926: 43–44, pl. 6 figs 6–8), with new var *minor*; *Archelix (Dupotetia) aposa*, Pallary (1939a: 64, 1939b: 107); *Otala aposa*, Rour et al. (2002: 195).

*Archelix Lafayei* Pallary 1923(a), Bull. Soc. Hist. nat. Afr. Nord, 14(3), pp. 114–115, TL Berguent (Maroc); Pallary (1926: 45–46, pl. 8 figs 3, 4), with new var. *minor* (p. 46); *Deserticola Lafayei*, Pallary (1939a: 64); *Otala lafayei*, Rour et al. (2002: 195).

*Archelix alvisetiana* Pallary 1926, J. Conchyl., 70(1), pp. 44–45, pl. 8 figs 1, 2, TL Guefait, à 45 kil. N.-O. de Berguent, chez les Beni Mattar (Maroc oriental); *Deserticola alvisetiana*, Pallary (1939a: 64); *Otala alvisetiana*, Rour et al. (2002: 195); *Dupotetia alvisetiana*, Cossignani (2014: 81), figs of two shells, from Guefait.

*Archelix depageana* Pallary 1926, J. Conchyl., 70(1), pp. 47–49, pl. 5 figs 13–15, TL dans les oliveraies d'Outata el Hadj (moyenne Moulouïa) [Morocco], with new var. *rhorgiana* (p. 48), from Rhorgia, au N.-O. de Guettara, moyenne Moulouïa; Pallary (1939b: 107); *Deserticola Depageana*, Pallary (1939a: 64); *Otala depageana*, Rour et al. (2002: 195).

*Archelix steppica* Pallary 1926, J. Conchyl., 70(1), pp. 42–43, pl. 7 figs 12, 13, TL dans les steppes

qui s'étendent de Marnia (plaine des Angads) à Oudjda et El Aïoun; *Deserticola steppica*, Pallary (1939a: 64); *Archelix (Dupotetia) steppica*, Pallary (1939b: 107); *Otala steppica*, Rour *et al.* (2002: 195); *Dupotetia steppica* (Pallary 1926), Cossignani (2014: 82), figs of shell, from Ouxda.

*Archelix (Dupotetia) Russadirensis* Pallary 1933, Bull. Soc. Hist. nat. Afr. Nord, 24(7), pp. 246–247, TL Les Kebdana, entre Melilla et la rive gauche de la Moulouya; with vars *major*, *minor*, *subdentata*, *lucida*; Pallary (1936: 44–45, pl. 2 fig. 6); *Archelix (Dupotetia) Russadirinsis* [sic] Pallary (1939a: 64); *Archelix (Dupotetia) Russadirensis*, Pallary (1939b: 107); Llabador (1952: 113), Dar Drius (Metalza); Tastataf (Beni Tuzin); Aïn-Zorah (Metalza); suggested record of *Helix lactea* from Beni bou Frior by Hidalgo (1909) was this taxon (*vide* Rutllant); *Otala russadirensis*, Rour *et al.* (2002: 195); *Dupotetia russadirensis* Pallary 1933, Cossignani (2014: 82), figs of two shells, from Kebdana Mountains; *Dupotetia russadirensis minor* Pallary 1933, Cossignani (2014: 82), figs of two shells, from Kebdana Mountains.

*Archelix (Dupotetia) Vanrossomi* Pallary 1933, Bull. Soc. Hist. nat. Afr. Nord, 24(7), p. 247, TL Région des Kebdana, dans le Maroc oriental, sur la rive gauche de la Moulouïa; with vars *major*, *minor*, *depressa*, *fusca*, 5–6 *lineolata*; Pallary (1936: 45–47, pl. 2 fig. 5), with vars *depressa*, *major*, *minor*, *conica*, *fusca*, *bizonata* (all p. 46); *unifasciata*, *lacticolor*, *quinquefasciata* (all p. 47); Pallary (1939a: 64, 1939b: 107); Llabador (1952: 113); *Otala vanrossomi*, Rour *et al.* (2002: 195).

*Archelix (Dupotetia) kebdanensis*, Pallary (1939b: 107), in list (apparently a *nomen nudum*); *Otala kebdanensis*, Rour *et al.* (2002: 195).

*Otala astcia* Terver, Cossignani (2014: 90), figs of shell, from Saidia [non *Helix asteia* Bourguignat 1863, apparently a form of *O. xanthodon*].

Other names of uncertain status that have been regarded as synonyms of this species are (in alphabetical order): “*andromicas* Monterosato”, Richardson (1980); *meknensis* Jodot 1954 (apparently a lower Pliocene fossil named in Jodot, 1954, n.v.); *sahariensis* Mares in Kobelt 1876; *subbrevieri* Debeaux in Kobelt 1911; *subcarinata* Pallary 1897; *xanthodontoides* Debeaux in Hesse 1911.

*Shell* 1117 shells examined from 59 localities. Usual ranges, B 22.9–34.8, H 14.8–18.0mm, H/B 0.52–0.65, with 4.2–4.7 whorls. Shape depressed conical, flattened below, with gradually

increasing whorls; immatures and adults with rounded periphery; suture of moderate depth. Aperture broadly oval (except where interrupted by penultimate whorl), with peristome not or slightly reflected above and outwards; tooth near outer end of lower lip variably raised and prominent; often a second tooth forming short raised lamella (frequently curved inwards) on outer palatal area inside peristome, the second tooth low in some populations, or present only on few shells, high in other populations and present on all shells. Populations consist entirely of white shells lacking bands (with or without brown inside aperture), shells all banded, or a mixture. The banded shells have whitish ground colour and usually four continuous narrow or broad brown bands in pattern 1(23)45 and no other markings other than dark coloration inside aperture. Peristome white with lower lip brown; inside of aperture white in a few populations, with most usually brown, the colour sometimes present only on small area in mouth, more often extensive with rather gradual transition, but sometimes with abrupt transition; apices of both teeth usually brown. Fresh shell rather glossy and usually thick and strong, especially around aperture. Protoconch small, glossy, smooth with variable development of weak radial ribs; most fresh shells appear rather smooth, the teleoconch with irregular radial-tangential very low ribs and lines, intersected by closely spaced fine spiral grooves; the underside generally with weaker sculpture.

*Genital anatomy* Fourteen specimens dissected from six localities. The species shows few consistent or obvious anatomical differences from *O. lactea* except in size. However, in fully mature individuals the atrial flap appears to be relatively larger in *O. xanthodon*, its apex being directed proximally into the distal vagina. Also, a seemingly distinctive raised lamella runs proximally from the base of the flap along the inner wall of the distal vagina. The value of these features for species identification nevertheless needs checking in more populations than the two investigated (M48, M50). For other figures of genital anatomy see Hesse (1911: pls 445–446 *dupotetiana*, 447 *xanthodon*, 448 *abrolena*, 446 *anoterodon*, 448 *arabica*, 449 *odopachia*, 449 *tigri*) and Schileyko (2006: 1797, 1798, with copies of Hesse's figures).

*Variation and taxonomy* As noted under the genus heading, molecular data imply that the genus *Dupotetia* is nested within *Otala*. Although treated as a subgenus by Schileyko (2006: 1796), recognition of subgenus *Dupotetia* is also unnecessary on morphological grounds because some forms of this group have a less thickened, less chalky shell with colour bands visible, so that they come close to other *Otala* in shell characters. The genus *Deserticola* was introduced for forms having shells with a second (palatal) tooth, often termed “Bidentata” in the literature; it was recognised as a subgenus by Schileyko (2006: 1797). However, as noted in our description above and discussed further below, development of the palatal tooth is very variable both within and between populations.

The varied development of apertural teeth in different populations coupled with marked differences in shell size and coloration (see e.g. Fig. 4C–H) led to many species being named in the nineteenth century, by Kobelt as well as by Bourguignat. Their new species based on typological concepts were often named on the basis of few shells with imprecise locality data and rather scanty comparative material. Nevertheless, by the late nineteenth century larger samples often showed that within some populations only a minority of shells have any trace of a palatal tooth, other populations consist partly of mature shells lacking teeth and partly of shells with more strongly developed teeth, whereas in yet other populations this tooth is strongly developed in all shells (as noted by Bourguignat [in Péchaud] 1883: 85, Pallary 1898d: 562, 1899d). Bourguignat (*op. cit.*, 82) remarked of his *Helix embia*, that: “dont la denticulation, *seulement péristomale*, ne se prolonge pas dans l’intérieur, forme le passage de ce groupe à celui des Bidentées.” Pallary (1899d: 317) emphasised that “il faut réunir des séries considérables pour bien apprécier les variations de l’espèce ...”. However, his assertion that bidentate forms are no more than aberrations from the type of the species (p. 317), present in a minority within a single population (p. 316), does not correspond to many of our collections of specimens where all adult shells from several of the localities are bidentate. Possible he was too strongly influenced by accumulations of shells of mixed provenance in river deposits or on coastal beaches.

Hesse (1910–1911) made studies of the genital anatomy of *Dupotetia* which did not reveal

any significant differences among them, but he nevertheless continued to recognise ten separate species. Despite this, he proposed a considerable reduction from the number of species recognised previously, giving a list in which many of them were regarded as forms or synonyms (Hesse, 1911: 100–103).

Samples we have studied show that shells having similar combinations of size, shape, coloration, mouth colour and tooth development are repeated in different scattered localities, so that consistent recognition even of subspecies would be difficult. Furthermore, populations with intermediate shells link the more extreme forms to those with less pronounced characters. Large samples from some localities also show that variability in shell form and coloration within populations is often great. Together, these considerations imply that only a single variable species (*O. xanthodon*) is involved.

Kadolsky (1971: 193) showed that the publication date of Anton’s *Verzeichniss der Conchylien* was in 1838, not 1839 which was printed in the book. Hence, [*Helix*] *xanthodon* Anton 1838 is the oldest name available for the species, rather than the more widely used *Helix dupotetiana* Terver 1839 (or *H. zaffarina* Terver 1839).

*Range* Endemic in W. Maghreb, where restricted to NE. Morocco and NW. Algeria (S. of Oran, occurring to edge of Sahara and near Moroccan border; Zaffarine Is.) (Figs 9, 12). Eight empty shells found on the eastern coast of the western Riff (on sandy ground above the beach, 1km N. of Mdiq; NMW.Z 1993.051.4526) had presumably drifted there from much further east. In summer there is a westbound current in the Mediterranean offshore along the north Moroccan coast, forming part of the West Alboran Gyre current system (Hogan, 2013). Servain (1880: 34) reported shells identical to those from Algeria from Spain (“entre Murviedro et Valence”), presumably in error. A few Spanish records might, however, be correct but based on drifted shells from Mediterranean beaches.

*Ecology* See “Habitats” below. Large populations of this species occur locally in NE. Morocco in dry regions with patchy cover of shrubs or bushes. At some localities (e.g. 2016: M50) they were found by roadsides resting on branches of thorn bushes (*Paliurus*) where scores were massed

together conspicuously; nearby, others were clustered on varied herbs, and in smaller numbers several metres above ground on *Eucalyptus* trees. Numerous other sites where this species occurs are on open plains, without rocks or bushes or other obvious means of concealment. The snails rest there by day on low shrubs or herbs (e.g. at 2016: M58). Many other sites with old shells of *O. xanthodon* are nowadays arid and open, without live snails, perhaps as a result of overgrazing or climate change.

TERTIARY FOSSILS ALLIED TO *OTALA XANTHODON*  
(ANTON 1838)

The following taxa were named from fossils from ca 5km W. of Constantine (Aïn-el-Hadj-Baba) in NW. Algeria.

*Helix Jobæana* Crosse 1861, J. Conchyl., 9, p. 356; Crosse (1862b: 153–155, pl. 7 figs 3, 4); Bourguignat (1862: 52, pl. 1 figs 6–8); Coquand (1862: 260, pl. 29 figs 3, 4); Kobelt (1888: 48, pl. 85 figs 473), fossilen Form von Constantine; Pilsbry (1895: 325); Pallary (1899b: 60; 1899c: 375; 1899d: 315), with spellings *Jobæana* and *Jobæ* or *Jobæ* [sic]; *Helix (Macularia) jobæana*, Tryon (1888: 142–143, pl. 46 figs 57–59), Constantine, Algiers [i.e. Algeria], fossil; *Helix (Macularia) Jobæ* [sic], Pallary (1901: 132–133, 189, 190, 197), with new vars *bleicheri* [Tourn. in litt.] (pl. 1 fig. 18) and *minor* (pl. 1 fig. 20); *Archelix jobæana*, Hesse (1911: 103); Pfeffer (1930: 186), n.v., fossil from Algerian Miocene; *H.[elix] Jobai* [sic], Pallary (1939a: 64), temps tertiaires, les steppes constantinoises.

*Helix Semperiana* Crosse 1861, J. Conchyl., 9, p. 357; Crosse (1862b: 155–156, pl. 7 figs 7, 8).

*Helix Desoudiniana* Crosse 1862, J. Conchyl., 10, pp. 84–85; Crosse (1862b: 157–158, pl. 7 figs 1, 2); Bourguignat (1862: 51–52, pl. 1 figs 1–3); Coquand (1862: 261, pl. 29 figs 1, 2); *H.[elix] Desoudiana* [sic], Pallary (1899b: 60, 1899c: 375); *Helix (Macularia) desoudini* [sic], Pallary (1901: 128, 189, 190, 197), with new var. *minor*; *Archelix desoudini* [sic], Hesse (1911: 103); *desoidini* [sic] aucts., Richardson (1980).

*Helix Dumortieriana* Crosse 1862, J. Conchyl., 10, p. 85; Crosse (1862b: 160–162, pl. 7 figs 5, 6); Bourguignat (1862: 47–48, pl. 3 figs 4–6); Coquand (1862: 262, pl. 29 figs 5, 6); Pallary (1899b: 60, 1899c: 375, 1899d: 315), with spellings *Dumortieriana* and *Dumortieri* [sic]; *Helix (Macularia) Dumortieri*, Pallary (1901: 130–131,

189, 197); *Archelix subsenilis* var. *dumortieri* [sic], Hesse (1911: 103); Pfeffer (1930: 186), n.v., fossil from Algerian Miocene.

*Helix subsenilis* Crosse 1862, J. Conchyl., 10, p. 85; Crosse (1862b: 162–164, pl. 7 figs 12, 16); Bourguignat (1862: 48–50, pl. 2 figs 1–5); Coquand (1862: 263, pl. 29 figs 12–14); Pilsbry (1895: 325); Pallary (1899b: 60, 61; 1899c: 375, 376; 1899d: 315); *Helix (Macularia) subsenilis* Pallary (1901: 129–130, 189, 190, 191, 197); *Archelix subsenilis*, Hesse (1911: 103); Pfeffer (1930: 187), n.v., fossil from Algerian Miocene.

*H.[elix] senilis* Pallary (1899b: 60; 1899c: 375) non *H. senilis* Morelet 1851 (apparently an unintentional slip, since Pallary's accompanying text makes it clear that he was referring to a form allied to *H. subsenilis*, not Morelet's species which is placed here as a form of *O. lactea*).

*Helix lamprozona* Bourguignat MS., *nomen nudum* for fossils from Coudiat-Aty, housed in Bourguignat Collection at MHNG; *Helix (Macularia) lamprozona* [Bourguignat] Pallary 1901, Mém. Soc. Geol. France, 22, pp. 131, 197; very short description by Pallary validates the name; he suggested it is a form allied to *H. Dumortieri*.

*Affinities and age of fossils* The fossils from Aïn-el-Hadj-Baba listed above all seem to be of *Otala* closer to *O. xanthodon* than to other species of the genus. All of them have strongly incrassate shells, which might reflect an adaptation to local conditions with abundant calcium. While the commonest of the fossils (*H. subsenilis*: "excessivement abondante") is a close match for some forms of *O. xanthodon*, some of the others (all either "Très-rare" or "Assez rare") have an additional apertural tooth or other peculiarities such as a well developed parietal callus and further investigation may be needed to show whether aberrant individuals or distinct taxa are involved. Joba (1862) gave an account of the deposits producing these fossils ("argiles fossilifères et gypseuse") and assigned a Pliocene age to them, but the basis for that age determination is unclear and there appears to be no certainty that all of the shells involved were stratified when found. The living Algerian "bidentate" *Otala* were almost unknown when Crosse (1862: 167–172) wrote his interpretation of the significance of the faunal assemblage. This lack of similar forms known nearby doubtless led to him wrongly regarding

the Constantine shells as closest to West Indian snails, and consequently providing evidence of a former "Atlantide" continent.

Pfeffer (1930: 126) unaccountably gave a Miocene age when basing his new genus *Pachydupotetia* on them. Pallary (1899d) regarded them as "Oligocène", again without any explanation. Later, in an extensive review of Algerian fossiliferous deposits and their snails he named the authorities giving the age as "Oligocène (Tongrien)" (Pallary, 1901: 9, 15, 189), but gave no other justification for it. Hesse (1911: 103) changed this to "oberen Tertiär" which seems more likely, but again no explanation is given. Pallary (1901) gave various other fossil records of "bidentate" *Otala* fossils, assigned to various epochs younger than Oligocene (*op. cit.*, pp. 26–27, 28–29, 198).

Pallary (1899d: 315) suggested that if series of specimens are examined, Crosse's species may represent "une seule et même espèce qui a varié suivant certaines conditions". He also hinted (*op. cit.*, p. 316) that the wide development of apertural teeth and peristome thickening in living forms of the group (which we regard as the single species, *O. xanthodon*) may imply that Crosse's rarer fossil forms are merely extreme individual variants.

There appears to be nothing about the shell characters of the commonest form (*H. subsenilis*) or the limited information recorded about the stratigraphy or lithology of the deposits to discount reinterpretation of the fossils as being merely incrassate *O. xanthodon* of Quaternary age.

Similar *Otala* taxa named as Tertiary or Quaternary fossils from different localities are as follows:

*Helix euthygyra* Bourguignat 1868(a), Ét. géol. et paléont. des hauts plat. de l'Atlas, entre Boghar et Tiharet, p. 21, pl. 1 figs 1–4, TL Dans les marnes rouges à Hélices de la gara d'El goléa (Doui Hasseni); *Helix (Macularia) euthygyra*, Pallary (1901: 129).

*Helix fossulata* Pomel 1890, Explication 2<sup>nd</sup> édit. Cart. géol. Algérie, pp. 169, 180, n.v.; *H.[elix] fossulata* Pomel, Pallary (1899b: 60; 1899c: 375), as fossils from Algeria; Wenz (1923: 560); *Helix (Iberus) fossulata minor* Pallary 1901, Syntype MNHN-F-B37803 (MNHN online catalogue).

*Helix macarita* Bourguignat MS., *nom. nud.* for fossils (internal casts) in Bourguignat Collection at MHNG; *Helix (Macularia) macarita*, Pallary (1901: 131, 197).

*Helix velaini* Munier Chalmas MS., *nom. nud.* for fossil in Paris Collection (now MNHN); *Helix (Macularia) velaini* Pallary, 1901, Mém. Soc. Géol. France, 22, pp. 137, 198, pl. 3 fig. 34, TL sables quaternaires de Rachsgoun ou de Camerata [Algeria], name validated with description and fig.; *Archelix velaini*, Hesse (1911: 103), im Pleistocaen.

*Otala tingitana* (Paladilhe 1875) Figs 5A–G, 6D–H, 7D, 9, 13

*Helix Tingitana* Paladilhe 1875, Rev. Mag. Zool., (3)3, pp. 78–79, pl. 6, figs 4–6, TL Route de Tanger à Meknès (non *H. Tingitana* Beck 1837, Index Moll., p. 14, *nom. nud.*); Morelet (1880: 22), route de Tanger à Mékinez; Bourguignat [in Péchaud] (1883: 39), environs de Tanger; Pilsbry (1895: 324); Hesse (1911: 104); *Helix dupotetiana* var. *tingitana* Paladilhe 1875, Bourguignat [in Péchaud] (1883: 39); Pallary (1899a: 111); *Helix (Macularia) tingitana*, Tryon (1888: 132, pl. 64 figs 1–3); *Helix zaffarina* var. *tingitana* Palad., Westerlund (1889: 431); *Tingitana tingitana* Paladilhe 1875, Pallary (1919: 52–55, pl. 2 fig. 1), depuis Agouraï, au sud, jusqu'à Meknès, Kalâa des Sless et Souk el Arba de Tissa au nord; Taza; "plésiotype" figured from Kalâa des Sless (*ibid.*, pl. 2 fig. 1) may be tantamount to restriction of the type locality; new vars *minor* (p. 53, single shell figured as var. *minor-pullata* on pl. 2 fig. 2, from Kalâa des Sless), *lacunata*, *angulosa*, *pullata*, *punctulata*, *lacticolor*, *interrupta*; Pallary (1920b: 30), djebel Zehroun; lists names of vars from 1919 paper, adding var. "*major=slessica*" and var. *globulosa*; Pallary (1923b: 278); Pallary (1929a: 48–49, 53), djebel bou Hellal; Moulay Bouchta; Pallary (1936: 32–34, 35), with list of localities and vars (p. 35); Pallary (1939a: 63; 1939b: 107); Irikov & Gerdzhikov (2013: 2), near El Hajeb (NC. Morocco); Rour *et al.* (2002: 195); Cossignani (2014: 110), figs of two shells, from Volubilis; *Tingitana tingitana pullata*, Cossignani (2014: 110), figs of two shells, from El Kalaa. *Helix seguyana* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 69–70, 74, TL aux alentours de Tanger; also reported (p. 74) from NW. Algeria, "sud de la province d'Oran, ... Mécheria"; Westerlund (1889: 425); Pilsbry (1895: 326); Pallary (1899a: 108, pl. 8 figs 2), brousailles de la pointe Malabatta (leg. Pallary); environs de Tanger (Bourguignat [in Péchaud]); *Helix (Marmorana) seguyi*, Pallary (1904: 50), Tétouan,





**Figure 5** Shells of *Otala tingitana* (A–G) and hybrid *O. tingitana* × *O. lactea* (H); A Morocco, 33°27'N 4°51'W, NMW.Z 1993.051.359; B ditto; C Morocco, 33°46'N 4°45'W, NMW.Z 1993.051.400; D ditto; E Morocco, 33°46'N 4°45'W, NMW.Z 1993.051.401; F Morocco, 35°06'N 2°45'W, NMW.Z 1993.051.4178; G ditto; H Morocco, 34°36'N 6°09'W, NMW.Z 3322. See Appendix for additional details of specimens. Scale bar 20mm.

Ouled Ras près de Tanger [unnecessary emendation of name]; *Macularia seguyana*, Kobelt (1903: 40–41, pl. 285 fig. 1827), bei Tanger in Felslöchern; *Archelix seguyana*, Hesse (1911: 99, 106, 109); *Tingitana Seguyana*, Pallary (1929a: 50), Tétouan; Pallary (1936: 34, 35); Rour *et al.* (2002: 195); *Helix Seguyana* Var. *minor* Pallary 1899 (1899a: 108, pl. 8 figs 2).

*Helix (Macularia) Pauli* Dautzenberg 1915, J. Conchyl., 62(3), pp. 158–160, with 2 figs, TL Kebibicha (Maroc oriental) [location details from Pallary 1917: 137 are that Col de Kebibicha was the scene of combat on 18 mars 1917, “à 12 kilomètres environ au sud-ouest du poste de Mahiridja qui est lui-même situé entre Debdou et la Moulouïa”; additional location details are given in Pallary 1920b: 31]; *Archelix Pauli*, Pallary (1917: 137), interpreted here as *Archelix Lariollei* var. *Pauli* (nom. inval. when transferred to *Archelix*, non Bourguignat); *Tingitana Pauli*, Pallary (1920b: 31), “Cette espèce est vraiment une Tingitane, car les premiers tours sont bordés”; Pallary (1926: 33), “Il est probable que, par analogie, cette espèce fait également partie du groupe *Tingitana*. Mais n’ayant pu examiner l’unique spécimen qui a servi de type, je ne peux qu’avancer cette probabilité”; Pallary (1936: 32, 34, 36, 42), “Col de Kebibicha (?), Berkane” (p. 36); Rour *et al.* (2002: 195); Cossignani (2014, 110), figs of shell, from Beni Snassen.

*Archelix (?) Minettei* Pallary 1917, J. Conchyl., 63(2), pp. 130–131, pl. 5 figs 2, 3, TL Tarzout-du-Guigou; Pallary (1920b: 25–26), Tazouta, à l’est de Anoœur; descriptions of new vars: *major*, *elata*, *minor*, *depressa*, *crustaria*, *zonata*; *Tingitana minettei*, Pallary (1926: 26); Pallary (1936: 33, 34, 38–39), lists of localities (pp. 38–39) and seven vars (p. 39) with “new” var. *decussata* from Peineta (chez les Keddana), rive gauche de la Moulouïa; Pallary (1939a: 63, 1939b: 107); Rour *et al.* (2002: 195); *Tingitana minetti minetti* [sic], Cossignani (2014: 109), figs of shell, from Tazouta; *Tingitana minetti* [sic] *depressa*, Cossignani (2014: 109), figs of shell, from Skoura; *Tingitana Minettei* var. *decussata* Pallary (nom. nud.), Llabador (1952: 107–108, pl. 5 figs 18, 19) from Djebel Zamzog (La Peineta), à 900 mètres d’altitude; *Tingitana minettii* [sic], Schileyko (2006: 1796 fig. 2301); *Tingitana minetti* [sic] *decussata*, Cossignani (2014: 109), figs of four shells, from Ras el Ma; Tazouta [Pallary, 1936: 33, 39 named the var *decussata* but gave no real description beyond “Une très jolie

variété” and no figure; Llabador, 1952: 107–108 and Cossignani, 2014: 109 also gave no description, only figures; so following the ICZN Code Art. 13(a), the name remains unavailable as a *nom. nud.*).

*Archelix gharbiana* Pallary 1917, J. Conchyl., 63(2), pp. 131–132, pl. 5 figs 5, 6, TL Tarzout-du-Guigou; Cossignani (2014: 106), figs of two shells, from Begnanes; *Archelix gharbiana* var. *minor* Pallary 1917 (p. 132); *Tingitana gharbiana*, Pallary (1920b: 26–27), with var. *major* (from Bessabis); Pallary (1936: 33, 34, 38, 40, 43), with list of localities and vars (var. *minor* listed as new, p. 40, which was incorrect); Pallary (1939a: 63); Rour *et al.* (2002: 195).

*Archelix slessica* Pallary 1917, J. Conchyl., 63(2), pp. 138–140, pl. 5 figs 7–10, TL El Kelàa des Sless, à 72 kil. au nord de Fès, près de l’Ouerghia, affluent du Sebou; Pallary (1919: 53), placed this taxon as *H. tingitana* var. *slessica*.

*Tingitana anoœurensis* Pallary 1918, Bull. Soc. Hist. nat. Afr. Nord, 9(7), p. 145, TL Anoœur, à 20 kilom. environ au sud de Sefrou; Pallary (1920b: 27, pl. 1 figs 7, 8), Anoœur; Bessabis; Pallary (1926: 26); Pallary (1936: 33, 34, 38), with new vars listed as *major* (from Bessabis), *conica* (from Anoœur), *lerouafensis* (from Ich Lerouaf), *minor* (from Anoœur); Rour *et al.* (2002: 195); Cossignani (2014: 106), figs of shell, from Anoœur; *Archelix (Tingitana) anoœurensis*, Hesse (1934: 47, 57, pl. 8 figs 68a, b), genital anatomy and jaw described and figured.

*Tingitana Bessabisana* Pallary 1918, Bull. Soc. Hist. nat. Afr. Nord, 9(7), p. 145, TL dans les Bessabis, à l’est d’Anoœur; Pallary (1920b: 29–30, pl. 1 figs 10–12), dans les Bessabis; Aït Brahim; with new vars *angulosa*, *concolor*; Pallary (1936: 34, 37), with vars listed; Rour *et al.* (2002: 195); Cossignani (2014: 106), figs of two shells, from Bessabis.

*Tingitana orientalis* Pallary 1918, Bull. Soc. Hist. nat. Afr. Nord, 9(7), pp. 145–146, TL Berkane; Pallary (1923b: 277); Pallary (1926: 31–33, pl. 5 figs 10–12), Berkane, dans la partie supérieure des Beni Snassen, localisée dans le vallon du Zegzel; Pallary (1936: 32, 34, 36, 42; 1939a: 64; 1939b: 107); Rour *et al.* (2002: 195); Cossignani (2014: 109–110), figs of two shells, from Berkane.

*Archelix (?) Liasana* Pallary 1918, Bull. Soc. Hist. nat. Afr. Nord, 9(7), pp. 146–147, TL Aït Lias (Moyen Atlas); *Tingitana liasana* Pallary (1926: 30–31, pl. 4 figs 3, 4), recorded also from Dayat Achlef; Pallary (1936: 33, 34, 35–36), with new

var. *inflata* (from Ziar in région de Khénifra, pp. 36, 39); Pallary (1939a: 63); Rour *et al.* (2002: 195); Cossignani (2014: 108), figs of two shells, from Khouribga; *Tingitana* cf. *liasana* (Pallary 1918), Cossignani (2014: 108), figs of shell, from Khouribga.

*Tingitana keblina* Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11(2), p. 20, TL Aïn-Leuh; with new var. *conglobata*; Pallary (1926: 26–27, pl. 4, figs 9–11), type from Aïn Leuh (fig. 9), var. *conglobata* from Aïn Leuh (fig. 10), new var. *major* from Immouzer (fig. 11); Pallary (1936: 33, 34, 36), with list of localities and vars (p. 36), including new vars *minor* (from Azrou), *angulata* from Taounza; Pallary (1939a: 63); Rour *et al.* (2002: 195); Cossignani (2014: 106–107), figs of two shells, from Azrou and Immouzer.

*Tingitana Mangini* Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11(2), p. 20, TL Col de Begnanas, entre Almîs du Guigou et Anoœur; Pallary (1920b: 28–29); Pallary (1926: 28–29, pl. 5 figs 3, 4); Pallary (1936: 33, 34, 37, 40), with new var. *depressa* (from Tilmirat, p. 40); Rour *et al.* (2002: 195); Cossignani (2014: 108), figs of shell, from Begnanas.

*Tingitana Lyauteyi* Pallary 1923(a), Bull. Soc. Hist. nat. Afr. Nord, 14(3), p. 113, TL Anoœur (Moyen Atlas), with var. *minor*; Pallary (1926: 27–28, pl. 2 fig. 7, pl. 5 figs 1, 2), from Anoœur, with var. *minor*; Pallary (1936: 33, 34, 38); *lyantyei* [sic], Richardson (1980); *T. lyauteyi*, Rour *et al.* (2002: 195); Cossignani (2014: 108), figs of two shells, from Annoœur.

*Tingitana bonjeani* Pallary 1923(a), Bull. Soc. Hist. nat. Afr. Nord, 14(3), pp. 113–114, TL Timhadit; Taghzout du Guigou; Pallary (1926: 29–30, pl. 5 figs 7–9), fig. 7 is captioned “type de Tarzout du Guigou” [given as Taghzout du Guigou in text on p. 30]; Pallary (1936: 33, 34, 37), with new vars (p. 40) *major* (from Col de Tigoulmamine, Aït Seghrouchen), *minor* (from El Mers des Aït Seghrouchen); Pallary (1939a: 63); Rour *et al.* (2002: 195).

*Tingitana laffitteana* Pallary 1928, J. Conchyl., 72(1), pp. 9–10, pl. 1 figs 8–10, TL Skoura (Moyen Atlas), with new vars *minor*, *major*, *cretata*, *umbilicata* (fig. 10), 3 *et* 4 *fasciata*; Pallary (1936: 34, 37), with list of vars; *T. Laffitteana*, Pallary (1939a: 63); *T. Laffiteana* [sic], Pallary (1939b: 107); *T. laffitteana*, Rour *et al.* (2002: 195); Cossignani (2014: 107), figs of shell from Skoura; *Tingitana laffitteana cretata*, Cossignani (2014: 107), figs of two shells, from

Skoura; *Tingitana laffitteana minor*, Cossignani (2014: 107), figs of two shells, from Skoura.

*Tingitana Le Rochana* Pallary 1928, J. Conchyl., 72(1), pp. 10–11, pl. 1 figs 11, 12, TL Tilmirat, ‘Aderj et le Nif de l’Aderj, entre Immouzer des Marmoucha et Skoura, dans le moyen Atlas septentrional; Pallary (1936: 34, 36); *T. lerochana*, Rour *et al.* (2002: 195); *Tingitana le rochana* [sic], Cossignani (2014: 108), figs of shell, from Aderj.

*Tingitana Lapiierrei* Pallary 1933, Bull. Soc. Hist. nat. Afr. Nord, 24(7), p. 246, TL Maroc oriental sans indication de localité; Pallary (1936: 34, 41–42, pl. 1 fig. 7); Rour *et al.* (2002: 195); Cossignani (2014: 107), figs of two shells, from Sierra de Quebdana.

*Tingitana martinae* Cossignani & Ahuir 2012, Malacologia, Cupra Marittima, 75(2), p. 27, TL sud-ouest e sud-est di Mechra Benabbou, Morocco; Cossignani (2014: 108), figs of holotype shell, from Mechra Benabbou, MMM.

Cossignani (2014) also figured three unidentified taxa that appear to be conspecific with *Otala tingitana*, as follows: *Tingitana elenae* (Rutllant) (*nom. nud.*?), Cossignani (2014: 106), figs of two shells from Taforalt (the name does not appear to have been published before; Rutllant may have been the collector); *Tingitana* sp. 1, Cossignani (2014: 110), figs of shell from Ras el Ma; *Tingitana* sp. 2, Cossignani (2014: 110) figs of shell from Ras el Ma. The latter two taxa are discussed below under Variation and taxonomy.

*Shell* 483 shells examined from 27 localities. Characters of Rounded shells are described separately from those of Keeled shells.

Rounded shells with usual size ranges B (19.1) 24.1–34.4, H (12.8) 15.0–24.7mm, H/B 0.60–0.74, with 4.3–4.5 whorls. Shape rounded conical to depressed conical, flattened below, with gradually increasing whorls except for more rapid expansion of body whorl; immature shell of most populations sharply keeled, body whorl rounded, so suture shallow (a few populations have upper edge of immature whorls bluntly shouldered, so suture deeper). Aperture broadly oval (except where interrupted by penultimate whorl), with peristome slightly to strongly reflected; lower lip with tooth near middle low to absent. Ground-colour whitish (to cream above), with up to five bands of dark brown or brown. Banding patterns vary between populations, sometimes 12345, often 1(23)45, the bands unmarked or rather heavily speckled or blotched with whitish (some

populations lack shells with unmarked bands); other populations have bands weakly indicated or lacking, with upperside of shell pale brown, underside whitish (the palest, most uniformly coloured shells are whitish throughout, often with close ribbing and a weak peripheral keel on body whorl, suggesting introgression from keeled forms, although a few shells are entirely whitish above but lack evidence of any keel). Peristome white on upper and outer lips, pale brown on at least inner part of lower lip; inside of aperture brown to dark brown, with gradual to rather abrupt edge near parietal edge of aperture. Protoconch smooth or with weak radial ribs; teleoconch with rather irregular radial-tangential low ribs and lines, intersected by weaker spiral grooves; the underside generally with weaker sculpture. The strength of sculpture on the upperside varies between populations.

Keeled shells with usual size ranges B 25.5–33.8, H 14.5–16.7mm, H/B 0.49–0.57, with 4.3–4.5 whorls. Shape low-conical (almost discoid) to depressed conical, flattened below, with gradually increasing whorls; immature shell sharply keeled, adult body whorl with sharp keel, so suture nil to very shallow. Aperture oval with peristome slightly reflected upwards and outwards; lower lip with small tooth near middle; outer lip with small sinus at keel. Peristome and coloration in aperture similar to those in rounded shells. Remainder of shell entirely whitish (without bands). Protoconch smooth except for weak radial ribs; teleoconch with close, somewhat irregular radial-tangential ribs, intersected by weaker spiral grooves that vary in depth on different shells; shell generally much smoother below.

*Genital anatomy* Ten specimens dissected from three localities, although fully mature specimens were from only one locality. The specimen used for our Fig. 7D has a short vagina but another mature individual from the same site (CGAH M56) has it longer, about equal to length of middle plus distal parts of penis. Three specimens with immature genitalia (CGAH M46) have the vagina 0.7–1.0× length of proximal plus distal parts of penis. The genital anatomy was first described by Hesse (1934), who commented that it did not differ from that typical for *Archelix* (i.e. *Otala*), leading him to place the taxon in that genus while retaining Section *Tingitana* on the

basis of shell characters. In fully mature individuals the internal structure of the proximal penis appears to be distinctive with the chamber meandering strongly, a feature perhaps shared with *O. hieroglyphicula*. However, this character and features of the atrial flap need checking on more populations to assess their value for species identification.

*Variation and taxonomy* Numerous local forms differ markedly from nominate *tingitana* and some of these may be worthy of subspecific separation. Keeled and rounded shells of markedly different appearance occur in different populations (e.g. Fig. 5A, 5D), but other populations at some of the same locations are intermediate (e.g. Fig. 5B, C). The most divergent form is *minettei* with the shell keeled and white. However, it is connected to globular forms by intermediate populations in the Moyen Atlas that may be of hybrid origin. The late J.F.M. de Bartolomé (pers. comm., *ca* 1985) obtained hybrids from keeled and globular parents kept in captivity in England. The hybrids were fertile and produced a second generation.

Populations of rounded shells may show marked variability in size within a single population; e.g., a sample from *ca* 8km SE. of Souk el Arba du Rharb (1993.051.192) had rather old shells varying (B) from 19.1–35.2mm (Fig. 6E, F), suggesting different opportunities for growth at different times in the past at the same site. Variation in coloration within the same population may also be large (e.g. Fig. 6D, G, H).

A single shell collected with a sample of *O. lactea* (1993.051.3322) is clearly a hybrid between *O. tingitana* and that species, combining the upper whorls without a suture of the latter with the typical apertural coloration of the former (Fig. 5H); a second shell in the sample might also be hybrid.

*Range in W Maghreb* (endemic). Confirmed only for N. Morocco, where widespread S. of the Riff, in the Moyen Atlas, extending towards the Atlantic coast and north-eastwards to Berkane and Beni Snassen mountains in NE. (Figs 9, 13). The species may extend into the northwestern corner of Algeria, but we have no confirmed records.

Cossignani (2014) figured four peculiar sharply keeled shells with malleate sculpture from Ras el Ma (on the coast of NE. Morocco) as *Tingitana*

*minetti decussata* (Pallary 1936) (*op. cit.*, p. 109) and two from the same place with a slight spiral cord at the periphery as *Tingitana* sp. 1 and sp. 2 (*op. cit.*, p. 110). Our material includes comparable shells from nearby (coastal salt marsh on shore of Sabkhat Bou Arg), including shells from a strand-line (1993.051.4178), one keeled (Fig. 5G), two with a peripheral cord (e.g. Fig. 5F). Both sites are far outside the known range of keeled *O. tingitana minettei*, but they are near the estuary of the Oued Moulouya, whereas the original locality of *Tingitana minettei decussata* (Pallary, 1936: 39, *nomen nudum*) was far inland at "Peineta (Kebdana), rive gauche de la Moulouïa". It therefore seems likely that these were shells that had drifted down the O. Moulouya from the Moyen Atlas, although it is just possible that living populations are established in this coastal region following dispersal down-river.

*Ecology* See "Habitats" below. Pallary (1919: 52, 1920b: 26) noted that *Archelix* (i.e. *Otala lactea* and *O. punctata* of our taxonomic treatment) are diurnal and live amongst the vegetation, the *Tingitana* (i.e. *O. tingitana* of our treatment) are essentially nocturnal and live among rocks. Several local forms appear to have shell coloration matching the rocks among which they live.

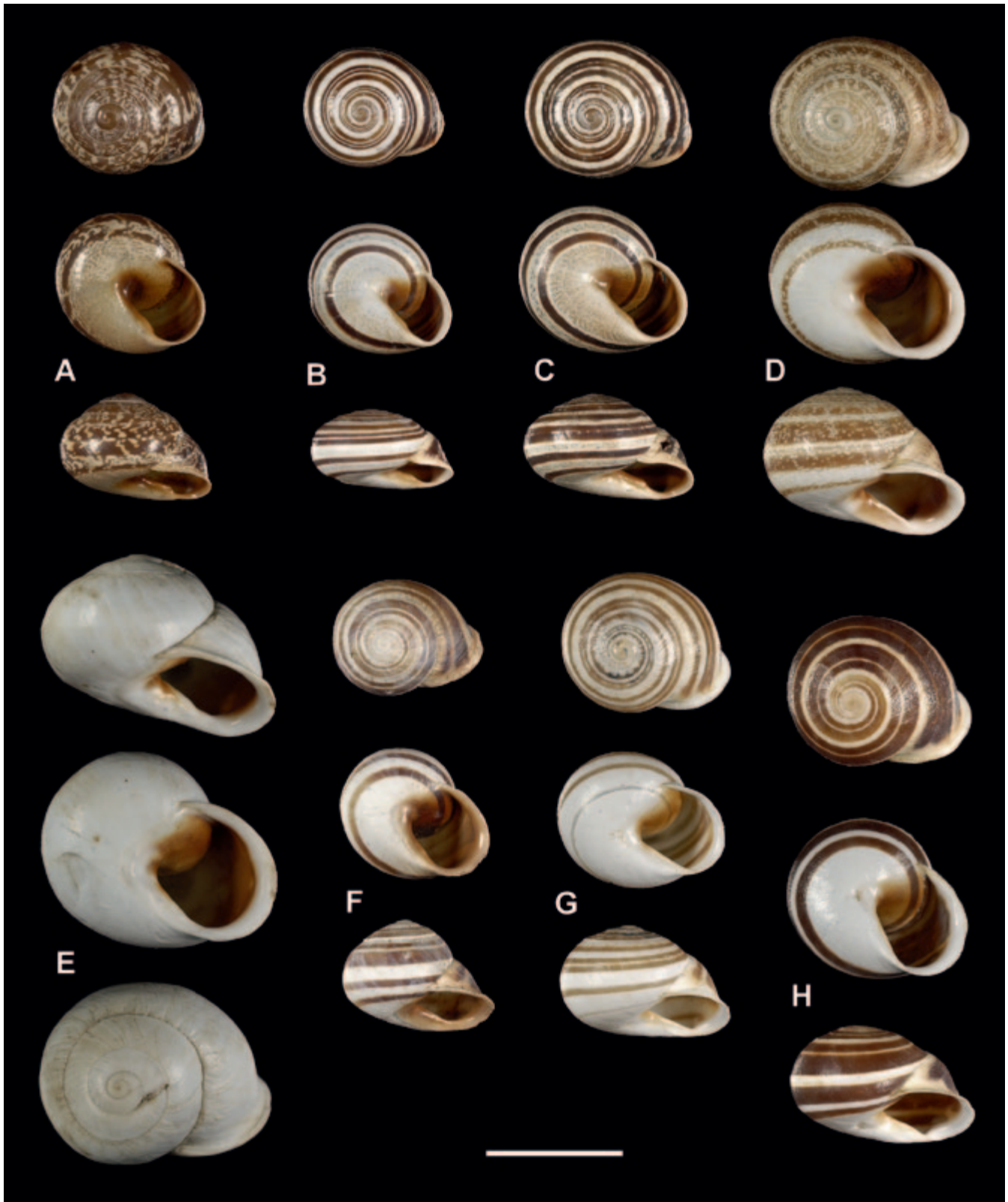
Pallary (1926: 26) presented the following notes on *T. minettei* and *T. anoceurensis*: They aestivate from the end of June onwards, sticking themselves onto the rock and resting there until September. When aestivating they are not sensitive to humidity and stay in place even when wetted. Mating takes place after aestivation ends in September and October. *T. minettei* kept in his garden laid eggs at the end of September, after the first rainfall, and around 10<sup>th</sup> October very young snails were seen on the plants. Two *T. anoceurensis* were seen mating on 20<sup>th</sup> October. Species of this group selected plants with fibrous leaves ("Buis de Mahon, les Iris, Ruscus, Aspidistras et Strelitzia"). Pallary (1936: 33) noted that *T. tingitana* occurs mainly on sandstone terrain, under stones, also near streams and (*ibid.*, p. 43) that the occurrence of *T. gharbiana* shows a close relationship with the presence of the shrub Buis de Mahon (i.e. *Buxus*).

We found adults of *O. tingitana* at Skoura (2016.M46) in considerable numbers in May resting during the day on branches of shrubs and bushes on dry calcareous slopes, not far from

small streams, suggesting differences between populations may exist in the extent to which vegetation is used.

*Otala hieroglyphicula* (Michaud 1833) Figs 6A–C, 9, 14

*Helix hieroglyphicula* Michaud 1833, Mém. Soc. Hist. nat. Strasbourg, 1, offprint pp. 3–4, figs 1–5, n.v.; Terver (1839: 17, pl. 4 figs 4–6), Oran, autour du fort Saint-Grégoire; dans les montagnes de Mers-el-Kebir; du fort et de l'intermédiaire de St-Philippe; près du marabout de Monley-Lo dans l'Atlas; Rossmässler (1839: 3–4, pl. 42 figs 555, 556), Oran [Bône (= Annaba, Algeria) was apparently an error]; Rossmässler in Wagner (1841: t. 2, 249, 256, 259; Atlas pl. 12 fig. 5), n.v.; Wagner (1841: t. 2, 264), n.v.; Erdl in Wagner (1841: t. 2, 270; Atlas pl. 13), n.v.; Morelet (1853: 284); Mostaganem; two vars described in descriptive phrases; var. *fasciis albo maculatis*, var. *fasciis integris*, var. *major*, var. *minor* Morelet 1853; [the polynomial phrases cannot enter nomenclature]; Pfeiffer (1853: 199); Gassies (1856: 108), with vars from Morelet and new var. *lactata* from ruines de Touent près de Djemâa Ghazaouat (Nemours); Bourguignat (1864: t. 1, 131–134, pl. 13 figs 7–11); with vars *major*, *4-fasciata*, *lactata* and var. named with descriptive phrase [var. *fasciis integris ornata* Bourguignat 1864: invalid polynomial phrase] and distribution data (p. 133); var. *major* from environs de Mostaganem; other localities at Boghar; Nemours; environs d'Oran; Touent [localities at Alger and Bône probably erroneous]; Kobelt (1904: 66, fig. 1912), var. *compacta* from Tlemcen; Ancy (1882: 287–288), with new var. *integrivittis* (p. 288); Bourguignat [in Péchaud] (1883: 70, 74), montagne de Nedroma (alt. 1.114m.) à 18 kilomètres S. E. de Nemours; Westerlund (1889: 424–425); *oranica* Debeaux in Westerlund 1889, n.v. [Tryon 1888: 133 cited *H. oranica* Bourg. as syn.]; Pilsbry (1895: 324), syn. *oranica* Bgt., with f. *integrivitta* Anc.; *Helix hieroglyphicula*, Pallary (1899a: 108), Très commune entre la frontière et l'embouchure de la Moulouïah; Pallary (1901: 4); *Helix (Archelix) hieroglyphicula*, Albers (1850: 98); *Helix (Tachea) hieroglyphiculus*, Adams & Adams (1855: 195); *Helix (Marmorana) hieroglyphicula*, Pallary (1904: 50), Ksar Adjeroud; *Helix (Macularia) hieroglyphicula*, Albers & Martens (1860: 133); Tryon (1888: 133, pl. 40 figs 17–19), with var. *integrivittis* (pl. 40 fig. 16); Pallary



**Figure 6** Shells of *Otala hieroglyphicula* (A–C) and *O. tingitana* continued (D–H); A Algeria, 34°43'N 1°33'W, NMW.Z 1993.051.560; B Algeria, 34°58'N 1°55'W, NMW.Z 1993.051.1775; C Algeria, 35°38'N 0°44'W, NMW.Z 1993.051.1714; D Morocco, 34°14'N 5°39'W, NMW.Z 1993.051.3361; E Morocco, 34°37'N 5°58'W, NMW.Z 1993.051.192; F ditto; G Morocco, 34°14'N 5°39'W, NMW.Z 1993.051.3361; H ditto. See Appendix for additional details of specimens. Scale bar 20mm.

(1901: 136, 191, 195, 197), Algerian fossils; *Helix* (*Marmorana*) *hieroglyphicula*, Pallary (1904: 50), in Morocco at Ksar Adjeroud; *Macularia hieroglyphicula* var. *compacta* Kobelt (1904: 66, pl. 197 figs 1912), newly described var. from "an der Strasse von Oran nach Tlemcen"; *Archelix hieroglyphicula*, Hesse (1910: 63–65, pls 440, 441 figs 3–7), from Oran; Hesse (1911: 94, 99, 103, 110); Pallary (1920b: 31–32); *Archelix hieroglyphicula compacta*, Hesse (1910: 64–65, pl. 441 figs 7, 7a), from Rar el Maden; *Archelix hieroglyphicula* var. *compacta*, Hesse (1911: 110); *Helix* (sect. *Michaudia*) *hieroglyphicula*, Pallary (1926, J. Conchyl., pp. 15–16, n.v.); *Michaudia hieroglyphicula*, Pallary (1929b: 122–130, pl. 6), detailed review of species and its history; detailed treatment of vars, those previously named listed as *minor* Mrlt, *major* Mrlt, *compacta* Kobelt, *integrivittis* Ancey (pl. 6 fig. 8), *lactata* Gassies 1856; new vars named as var. *achatina* (from Oran), *compacta minima* (from Rar-el-Maden), *crassa* (from Batterie espagnole près Oran), *decorata* (from Oran; but named differently as *lucida unifasciata* in legend to pl. 6 fig. 15 on p. 130), *depressa* (from Oran), *egregia* (from Aïn Acheb), *integra*, *lucida*, *quinquefasciata*, *subcarinata*, *trifasciata* (last 5 vars all from Oran); Pallary (1939a: 65), Le Massif des Traras, with vars *compacta* and *egregia*; Rour *et al.* (2002: 195).

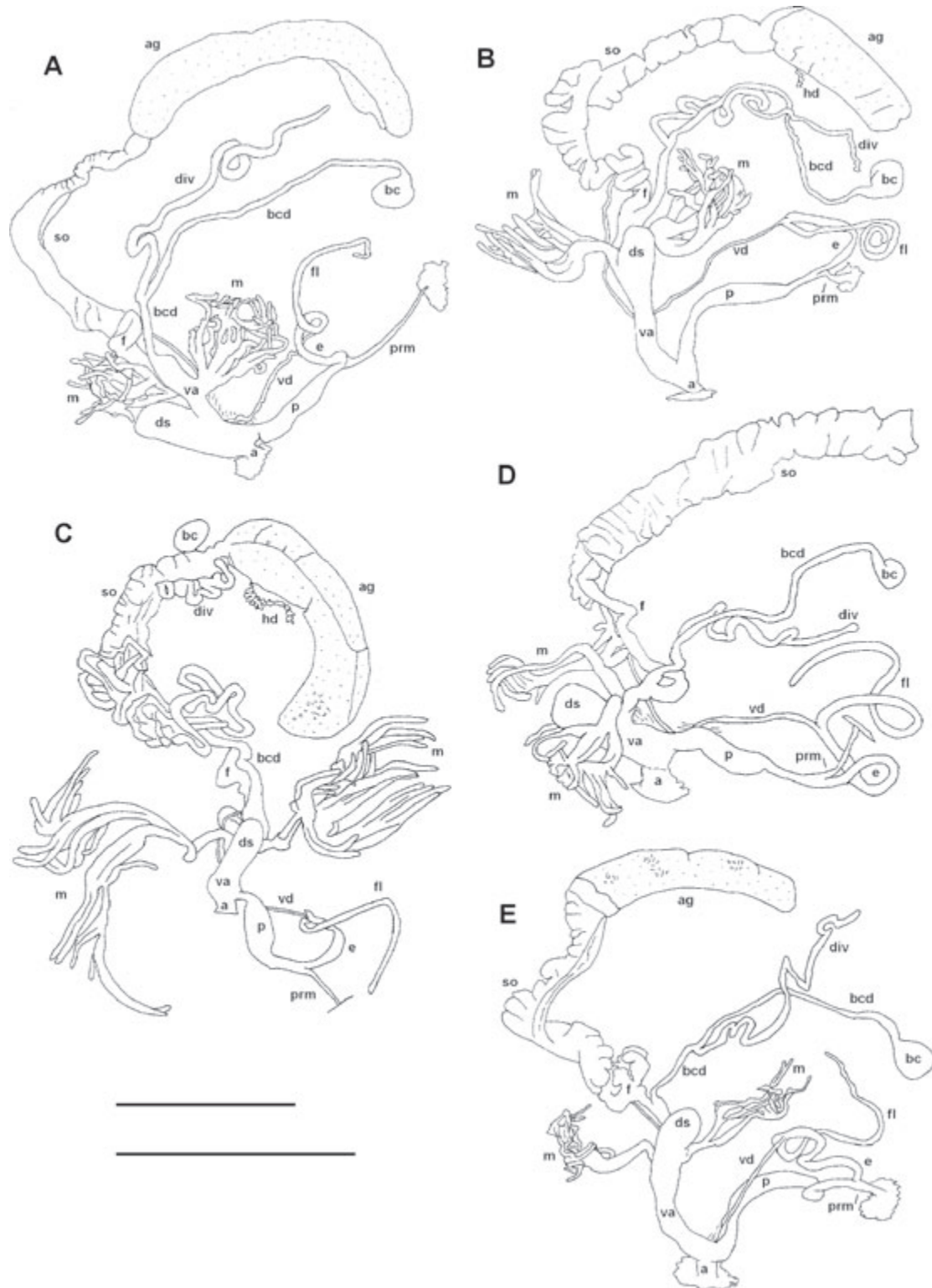
**Shell** 38 shells examined from 4 localities. Usual ranges, B 21.5–25.6, H 12.5–16.7mm, H/B 0.58–0.69, with 4.2–4.6 whorls. Shape rounded conical to depressed conical, flattened below, with rather gradually increasing whorls; immature shell sharply keeled, adults with penultimate and body whorls rounded; sutures of spire shallow. Aperture oval (except where interrupted by penultimate whorl), with peristome at most slightly reflected; lower lip with small tooth near middle. Ground-colour whitish to cream, with up to five narrow to broad blackish-brown to brown bands, banding pattern sometimes 12345, more often 1(23)45, or with broad bands on upperside almost concealing ground-colour giving (123)45; the darker shells often with prominent whitish blotches and short streaks. Peristome white or whitish on upper and outer lips, brown on lower lip; inside of aperture brown, becoming gradually paler near parietal edge. Fresh shells very glossy. Protoconch almost smooth or with faint radial ribs that are often strongest near suture; teleoconch with rather weak radial-tangential

growth lines or faint ribs, intersected by finer closely spaced spiral grooves; sculpture generally weaker below.

**Genital anatomy** One dissected by DTH in 1987 has not been relocated at NMW.Z. The genital anatomy was first described by Hesse (1910: pl. 440, 1911: pl. 441) and it evidently led to him moving the species into the genus *Archelix* (i.e. *Otala*); his figures show the penial flagellum distinctly longer than the epiphallus. Schileyko (2006: 1793–1794 fig. 2297) dissected a different specimen (Vienna No. 56.175) and provided clear illustrations similar to those by Hesse, except that the penial flagellum is clearly shorter than the epiphallus. Schileyko treated the taxon as *Alabastrina* (*Michaudia*) *hieroglyphicula*, but it differs from *Alabastrina* and resembles *Otala* in several anatomical characters, especially the proportionately long free oviduct and large vaginal mucus glands with numerous branches, as well as in the brown interior of the shell aperture. We therefore follow Hesse in allocating it to *Otala*. Indeed, *O. hieroglyphicula* shares most of the characters of *O. tingitana*, to the extent that it might be better placed as a small subspecies of it (see Key below). More information is needed on the apparent similarity of *O. hieroglyphicula* to *O. tingitana* in the internal structure of the proximal penis; the atrial flap also remains undescribed for *O. hieroglyphicula*.

**Variation and taxonomy** *Michaudia aenigmatica* (Pallary 1918) (Based on *Archelix* (?) *aenigmatica* Pallary 1918, Bull. Soc. Hist. nat. Afr. Nord, 9(7), pp. 147–148; syn. *enigmatica* Pallary 1929b: 129, apparently a spelling error) is of uncertain identity. Pallary (1926: 16, pl. 3 fig. 9; 1929b: 129) knew of three shells, from Ravin de Noiseux (Oran). He thought it was probably based on a hybrid between *H. hieroglyphicula* and *Alabastrina* (or *Massylaea*) *soluta* (Michaud 1833), but this seems less likely to us in view of anatomical differences between these species (see above).

**Range** Endemic in W. Maghreb where almost restricted to NW. Algeria, with range limits on the coast from estuary of Chélif to that of the Oued Kiss; in west it reaches Marnia (Maghnia), Tlemcen, and in the east, to Mascara and Mostaganem (Pallary, 1929b: 129) (Figs 9, 14). It also occurs in extreme NE. of Morocco at Ksar Adjeroud (Pallary, 1904: 50). Older records



**Figure 7** Genital anatomy of representative specimens of *Eobania vermiculata* and *Otala* species from NW. Africa; A *Otala punctata*, Morocco, 34°02'N 2°38'W, CGAH M62; B *O. lactea*, Morocco, 34°09'N 4°01'W, CGAH M51; C *Eobania vermiculata*, Algeria, 35°17'N 6°38'E, NMW.Z 1993.051.1248; D *Otala tingitana*, Morocco, 33°34'N 5°07'W, CGAH M56; E *O. xanthodon*, Morocco, 33°24'N 3°39'W, CGAH M48. See Appendix for additional details of specimens. Both scale bars represent 20mm, the upper applies to A, B and C, the lower to D and E. Abbreviations: a genital atrium, ag albumen gland, bc bursa copulatrix, bcd duct of bursa copulatrix, div diverticulum on bcd, ds dart sac, e epiphallus, f free oviduct, fl flagellum, hd hermaphrodite duct, m mucus gland, p penis, prm penis retractor muscle, so spermoviduct, va vagina, vd vas deferens.



further east in Algeria are errors, as is “tout le département d’Oran” given by Bourguignat (1864). Pallary (1929b: 129) recorded it as a fossil in Pliocene sandstones at Saint-Eugène d’Oran and reported a record from Quaternary deposits (grès tendres, i.e. soft sandstones) under the “fortin du cap Figalo” (*vide* feu Gentil).

*Ecology* See “Habitats” below. Terver (1839: 17) recorded it on escarpments of a fort, in gardens, on trees and on prickly-pear *Opuntia*. According to Pallary (1929b: 129) it is found only in calcareous regions, where it lives on dwarf palms (*Chamaerops*) and “les diss”. In hot weather it takes refuge on shaded rocks, hiding in cavities and fissures, where several individuals may be found fixed to each other in groups. In the same paper he noted that at Oran the species lays eggs after the first rains of the autumn, at the start of November. At the end of May the young snails measure 13–15mm in diameter (Pallary, 1929b: 125).

#### Genus *Eobania* P. Hesse 1913

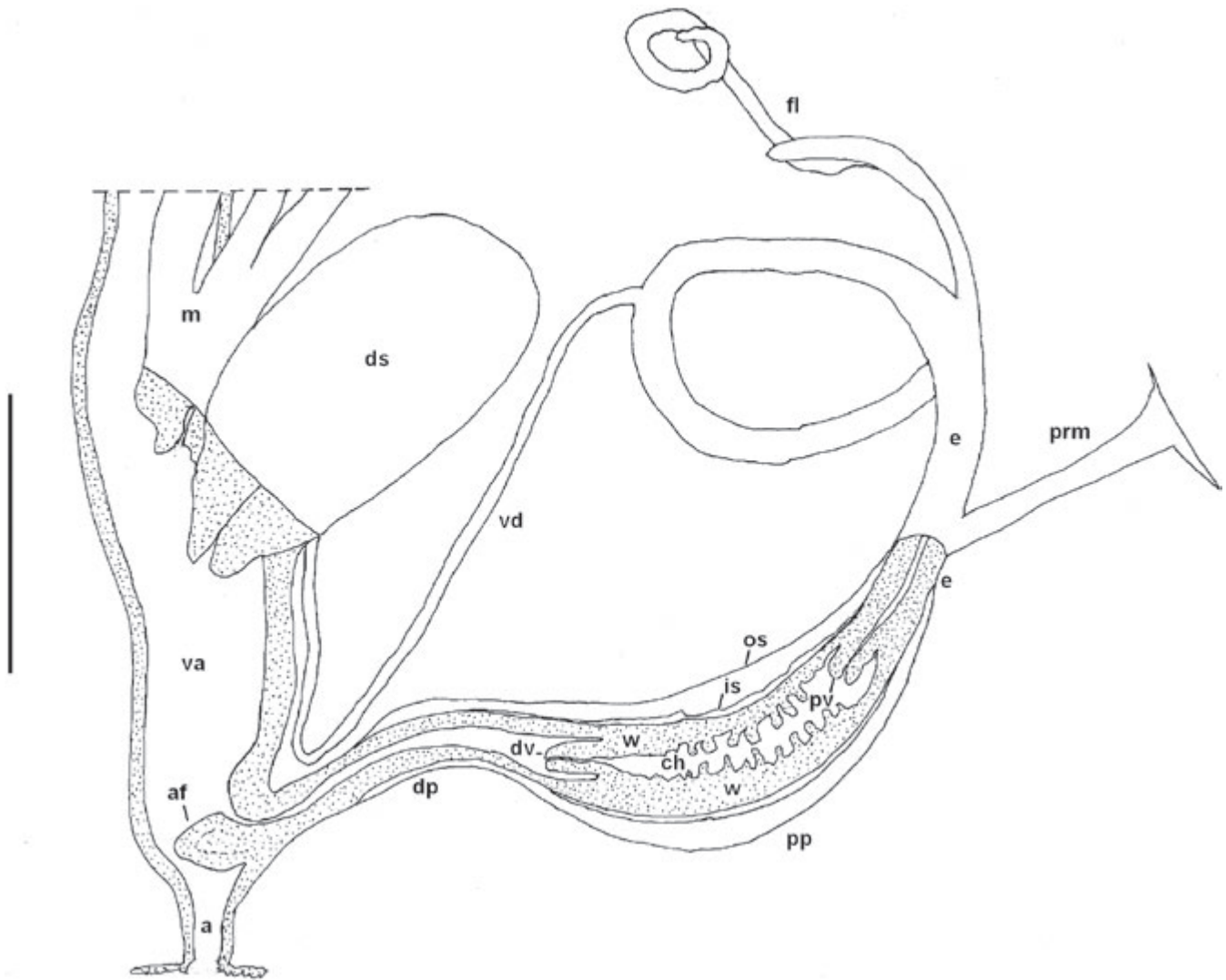
Nachrbl. d. malak. Ges., 45(1), p. 13. Type species: *Helix vermiculata* O.F. Müller, 1774, by monotypy. The genus name is treated as a feminine noun.

#### *Eobania vermiculata* (O.F. Müller 1774) Figs 1A–D, 7C, 9, 15

*Helix vermiculata* O.F. Müller 1774, Verm. terr. fluv., 2, pp. 20–21, no. 219, TL In Italiae [accompanied by 3 vars named with descriptive phrases]; Michaud (1833: 6); Rossmässler (1837: 6–7, pl. 22 fig. 301; 1838: 28, pl. 36 figs 499, 500); Terver (1839: 11), Alger; Rossmässler in Wagner (1841: t. 2, 249, 259; Atlas pl. 12 fig. 2), n.v.; Erdl in Wagner (1841: t. 2, 272; Atlas pl. 14), n.v.; Morelet (1853: 290, pl. 4); Pfeiffer (1853: 195); Moquin-Tandon (1855: t. 2, 159, pl. 12 figs 27–28), France; Bourguignat (1862: 50), fossils from Algeria; Bourguignat (1864: t. 1, 111–113, pl. 8 figs 7–11), vars *albida*, *expallescens*, *trizonata*, *aspersa*, *minuta* (p. 112); listed localities in N. Algeria (pp. 112–113); Bourguignat (1864: t. 2, 319, 322, 332), in Morocco, “Sur tous les rochers du nord du Maroc” (p. 319; information apparently incorrect or at best exaggerated); in régence de Tunis, “Abondante presque partout” (p. 322); *Helix vermiculata* var. *subangulata* Issel (1868: 18, pl. 2 fig. 3); Bourguignat (1868b: 11–12), Tunisia: environs de Tunis; versant du Djebel-Ahmar;

Vallée de l’Oued-Melianah; Environs de Porto-Farina; Hidalgo (1875: t. 1, 210, 221, 223, pl. 19 figs 197–203), Spain, Balearic Is. [listing of Portugal (pp. 210, 221) may be erroneous];

*Helix vermiculata* var. *pygmaea* Kobelt (1879: 8, pl. 182 figs 1830, 1831), Marseille; Morelet (1880: 19), Tanger et tout le littoral méditerranéen du Maroc; Kobelt (1881b: 158), bei Tanger und längs der ganzen Küste; *Helix vermiculata* var. *saharica* Kobelt (1882: 9, pl. 66 figs 343–345), subfossil in der Umgebung von Biskra [Algeria]; *H. vermiculata* var., Kobelt (1882: 9, pl. 66 figs 346–347), Insel Lampedusa; Bourguignat [in Péchaud] (1883: 36), Bords de la Mafrag, près de Bone, et environs de Cherchell; Hidalgo (1884: pl. 37 fig. 436); Kobelt (1887: 8, pl. 65 figs 335–337), bei Bu Nuara (fig. 335), zwischen el Guerrah und der Quelle des Bu Merzug (figs 336, 337); Letourneux & Bourguignat (1887: 6), with list of localities; var. *minuta*; var. *pelagosana*, from Îles de Kerkenna [based on *Helix Pelagosa* Stossich]; Pilsbry (1895: 324), syn. *muraloides* Chier., vars *thalassina* Porro, *grimaldiensis* Nev., *uticensis* Kob., *gaidurina* Bl. & W., *saharica* Kob., *linusina* Ben. (syn. *linusæ* Calc.), *subangulata* Iss., *pelagosana* (Stoss.) West.; Pallary (1899a: 103), suggested the reports from “N. du Maroc” (Bourguignat) and Tanger are errors based on misidentification of *Helix sphaeromorpha* which looks similar, since neither Pallary nor six other collectors had found it; Westerlund (1889: 411–412), with vars *uticensis* and *gaidurina*; Germain (1908: 131); Hidalgo (1909: 212), Melilla; Pallary (1914: 11); Hesse (1915: 25); *Helix (Archelix) vermiculata*, Albers (1850: 98); *Helix (Tachea) vermiculatus*, Adams & Adams (1855: 195); *Helix (Macularia) vermiculata*, Albers & Martens (1860: 133); Paulucci (1882: 62–63), Sardinia; Tryon (1888: 128, pl. 37 figs 54–57), with var. *saharica* (p. 128, pl. 37 fig. 59), var. *linusæ* (p. 129, pl. 37 fig. 58), and vars *subangulata*, *minuta*, *pelagosana* (p. 129); Pallary (1901: 135, 195), Algerian fossils; *Helix (Archelix) vermiculata*, Germain (1908: 170–173), Ile de Tabarka, with var. *albida* (p. 172); *Eobania vermiculata*, Hesse (1915: 26–29, pl. 634 figs 3–11), from: Ramleh in Ägypten, San Remo, Nizza, Menorca, Valencia, Murcia und Cerigo; Germain (1930: 190, fig. 160, pl. 2 figs 56, 57); Pallary (1939b: 107); Llabador (1952: 108), var. *expallescens* from Farhana (Beni Sicar); Puente (1994: 728); Giusti *et al.* (1995: 479, figs 602–607); Falkner, Ripken & Falkner (2002: 54); Rour *et al.* (2002: 194); Schileyko (2006: 1799 fig. 2305A–C),



**Figure 8** Distal genitalia of *Otala lactea*, Morocco, 35°12'N, 6°7'W, CGAH M39. Drawn with penis, distal epiphallus, vagina and genital atrium in longitudinal sections to show internal structures. Scale bar represents 5mm. Abbreviations additional to those used for Fig. 7: af atrial flap, ch chamber, dp distal penis, dv distal verge, is inner sheath, os outer sheath (of penis), pp proximal penis, pv proximal verge, w wall of proximal penis.

figs of shell and genitalia (with internal structure of penis drawn incorrectly); Beckmann (2007: 127, fig. 155); Cossignani (2014: 83), figs of three shells, from Saidia and Marrakesh.

*Helix Linusae* Calcara 1846, *Catalogo molluschi terr. fluv. Sicilia*, p. 2 (name only), p. 4 note (1) (description) [apparently offprint from: *Atti 8<sup>a</sup> Riun. Sc. It. Genova*, p. 524], TL rupi vulcaniche dell'isole di Linosa e Pantellaria, in Sicilia; Calcara (1851: 26); *Helix vermiculata* var. (*Linusiana*), Benoit (1857: 82; 1862: pl. 1 fig. 17); *Helix vermiculata* var. *linusiana* [sic] Issel 1868 (p. 18); *Helix vermiculata* var. *linusina* Ben. [sic], Pilsbry (1895: 324); *Helix vermiculata* var. *Linusiana*, Kobelt (1876: 55, pl. 114 fig. 1128 ["1129" in text]), auf der Insel Linosa, zwischen Malta und Lampedusa; *Helix*

(*Macularia*) *vermiculata* var. *linusæ* Tryon (1888: 129, pl. 37 fig. 58), Ins. Linosa, near Malta; listed *H. linusiana* [sic] Benoit as syn.

*Macularia vermiculata* var. *filfolensis* Despott undated, Exchange list of marine, land, fresh and brackish water shells from the Maltese Islands, (p. 2), n.v.

*Helix Constantina* Forbes 1838, *Ann. nat. Hist.*, 2(10), p. 251, & *Suppl.*, 1839, pl. 11 fig. 1, TL In waste places among nettles at Bougia [Algeria]; Morelet (1853: 283); Pfeiffer (1853: 198); *Helix constantinæ*, Bourguignat (1864: t. 1, 113–116), with vars *maxima*, *minima*, *depressa*, *conoidea*, *trifasciata*, *bifasciata*, *omnina candida*, and two vars named with descriptive phrases (pp. 114–115); distributional data (pp. 114–115); Bourguignat (1864:

t. 2, 305, 322), distributional data from Algeria (p. 305); in régence de Tunis, Pays monueux, sur les frontières, entre le Calle et le cap Roux (p. 322); Bourguignat (1868: 12), Tunisia: environs de Tunis, surtout dans la partie sud et sud-est; la Mohammedia; ruines d'Oudena; with vars *unifasciata* (ruines d'Utique; Xamart), *candida* (Environs de Tunis), *conoidea* (Près de la colline de Sidi ben Hassen), *minima* (portes de Tunis; près du marabout Mahoubia; Ruines d'Utique; *Helix Constantina* var., Kobelt (1875: 5, pl. 92 figs 981), locality unknown; *Helix Constantinae* var. *minor*, Kobelt (1876: 55, pl. 114 fig. 1125 ["1126" in text]), in den nächsten Umgebung von Tunis; *Helix Constantinae* varr., Kobelt (1876: 55, pl. 114 figs 1126, 1127 ["1127.1128" in text]); Bourguignat [in Péchaud] (1883: 37–38), Hammam-Meskhoutin; environs de Constantine; Pilsbry (1895: 324), syn. *cirtæ*, with var. *fleurati*; Germain (1908: 131); *Helix Constantinae*, Kobelt (1887: 7–8, pl. 64 figs 328, 329, pl. 65 figs 330–334), Algeria, from Beni Mansur (figs 328, 329), Bône (fig. 330), Bougie (figs 332–334); Letourneux & Bourguignat (1887: 7), with list of localities; var. *minima* recognised; Westerlund (1889: 413); *Helix (Archelix) constantina*, Albers (1850: 98); *Helix (Tachea) Constantinus*, Adams & Adams (1855: 195); *Helix (Macularia) constantina*, Albers & Martens (1860: 133); *Helix (Macularia) Constantinae*, Tryon (1888: 129, pl. 37, figs 60–62); Pallary (1901: 135, 190, 191, 193, 197), Algerian fossils; *Helix (Archelix) constantinae*, Germain (1908: 174–178, pl. 23 figs 1, 2), Tunisia: Région de Aïn-Draham; Dunes de Tabarka; Environs de Aïn-Cherchera; with new var. *coalita* (p. 175) from région de Aïn-Cherchera; *Eobania constantinae*, Hesse (1915: 29–30, pl. 634 fig. 12), Tebessa in Algerien; Tunis; *E. boghariensis* studied from Boghar treated as syn. (*op. cit.*, pl. 634 figs 13–15); Pallary (1939b: 107).  
*Helix Cirtæ* Terver 1839, Cat. Moll. Nord Afr., p. 11, pl. 1, fig. 1, TL Bone, surtout près d'Hippone; aussi à Drian, à Guelma, à Constantine, à Bougie et dans l'intérieur ... ; Wagner (1841: t. 2, 266), n.v.; *H. vermiculata* var. *Cirtæ* Rossmässler (1839: 12, pl. 46 figs 592a, 592b), bei Bona [=Annaba, Algeria]; Wagner (1841: t. 2, 249, 258; Atlas pl. 13 fig. 1), n.v.  
*Helix boghariensis* Debeaux 1857, Recueil travaux Société agric., sci. et arts d'Agen, 8(2), n.v.; *H. Cirtæ* var. *boghariensis* Debeaux 1863 (p. 13), n.v.; *Helix boghariensis*, Kobelt (1887: 6–7, pl. 64 figs

323–327), Boghar und Boukhrari; Pilsbry (1895: 324); Westerlund (1889: 413); *Helix (Macularia) boghariensis*, Tryon (1888: 129, pl. 39 figs 1–2), "Very near to *H. constantinae*"; *Eobania boghariensis*, Pallary (1939a: 66).

*Helix Bonduelliana* Bourguignat 1863, Moll. nouv. lit. (1<sup>er</sup> décade), pp. [9]–10, pl. 3 figs 1–4, TL Province d'Oran (Algeria), exact locality unknown; also published in Rev. Mag. Zool., (2) 15, pp. 100–111, n.v.; Bourguignat (1864: t. 1, 116–117); Letourneux & Bourguignat (1887: 8), Environs de la gare de Ghardimaou [Tunisia]; Pilsbry (1895: 325), with var. *asteia* Bgt.; Westerlund (1889: 414); *Helix (Macularia) bonduelliana*, Tryon (1888: 140, pl. 37 figs 67, 68), "Oran, Algiers" [i.e. Province of Oran, Algeria].

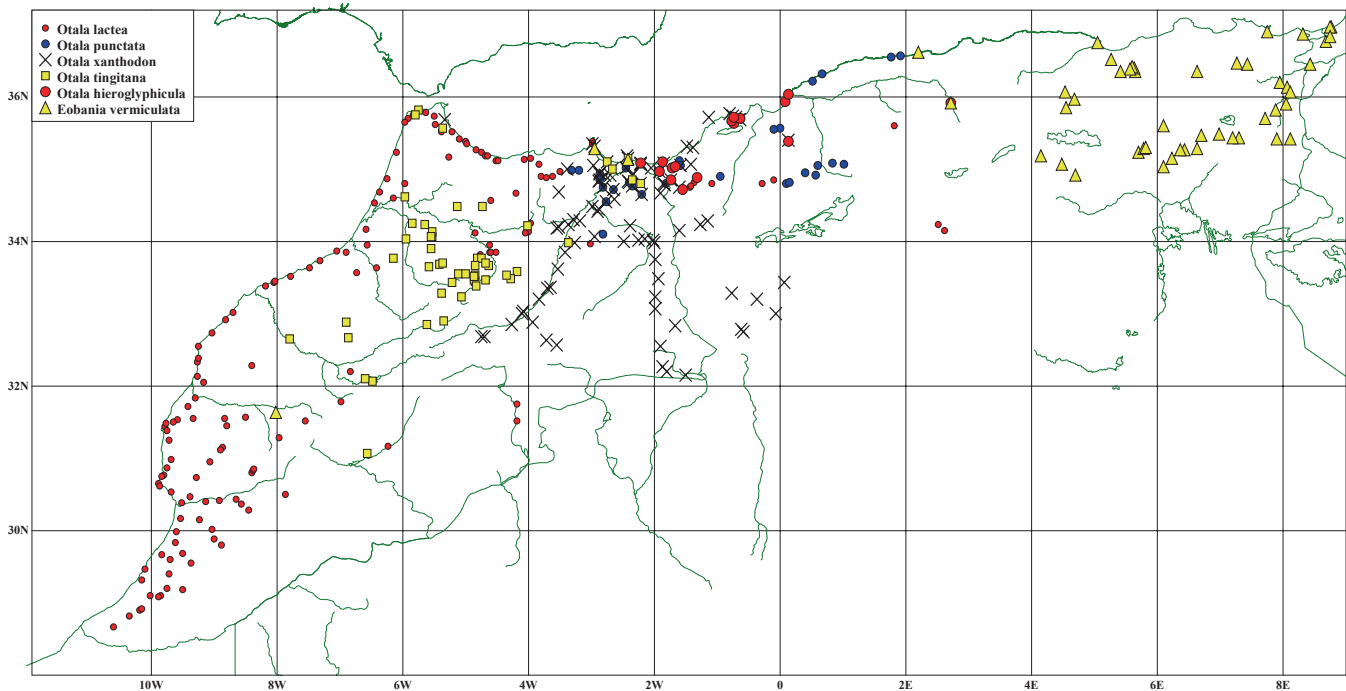
*Helix fleurati* Bourguignat 1868(b), Hist. Malac. Régence Tunis, pp. 12–14, 35, 36, pl. 1 figs 1–4, TL environs de Tunis ...; Ruines d'Oudena, Ruines d'Utique et du Carthage, non loin de la chapenne Saint-Louis; with vars *subcarinata* and *obesa*; *H. Fleurati*, Kobelt (1887: 8–9, pl. 66 figs 338–342), bei Beja; in der Nähe von Porto Farina; Letourneux & Bourguignat (1887: 8), with list of localities; vars *subcarinata* and *obesa* listed; Westerlund (1889: 413); *Helix (Macularia) Constantinae* var. *fleurati*, Tryon (1888: 129, pl. 37, fig. 66); *Helix (Macularia) fleurati* var., Westerlund (1892: 191) Tunis; the var. is not named; *Eobania Fleurati*, Hesse (1915: 31–32, pl. 634 figs 16, 17), von Tunis; Pallary (1939b: 107).

*Helix vermiculata* var. *crassilabris* G. Rigacci & E. Rigacci 1874, Catal. conch. coll., p. 46, n.v.; Haas (1929: 259).

*Helix Catharolena* Bourguignat 1876, Spec. nov. moll., no. 100, n.v.; Servain (1880: 34), entre Madrid et l'Escurial; Bourguignat [in Péchaud] (1883: 37), alentours d'Oran; Pilsbry (1895: 326); Westerlund (1889: 412).

*Helix Toukriana* Bourguignat [in Péchaud] 1883, Exc. Malac. Nord Afr., pp. 37–38, TL Coteaux des hauts plateaux du Sersou, entre Aïn-Toukria et la Nahr-Ouassel, dans la direction de Sebain-Aïoun; work cited there as "(Bourg., Test. noviss., n° 101, 1878)" is fictitious (Connolly, 1934); Letourneux & Bourguignat (1887: 8), Environs de la gare de Ghardimaou [Tunisia]; Pilsbry (1895: 326); Westerlund (1889: 414).

*Helix aecouria* Letourneux & Bourguignat 1887, Prodr. Malac. terr. fluv. Tunisie, p. 7, TL environs d'Houmt-Souk dans l'île de Djerba [Tunisia]; *H. aecouria*, Westerlund (1889: 412).



**Figure 9** Overview map of distribution of *Otala* and *Eobania* in Morocco and Algeria.

*Helix vermiculata* var. *Vilassarum* E. Caziot 1905, Butll. Inst. Cat. Hist. Nat., 5, p. 89 fig. 2, p. 90 fig. 3, n.v.; Haas (1929: 259).

*Helix vermiculata* var. *minor* Romani 1917, Butll. Inst. Cat. Hist. Nat., 4, pp. 45–48. n.v.; Haas (1929: 259).

*Helix vermiculata sarcostomopsis* Bofill & Aguilar-Amat 1924, Trabajos Museo Cienc. Nat. Barcelona 10(3), pp. 28–29, pl. 2 figs 2, 3, n.v.; Beckmann (2007: 127).

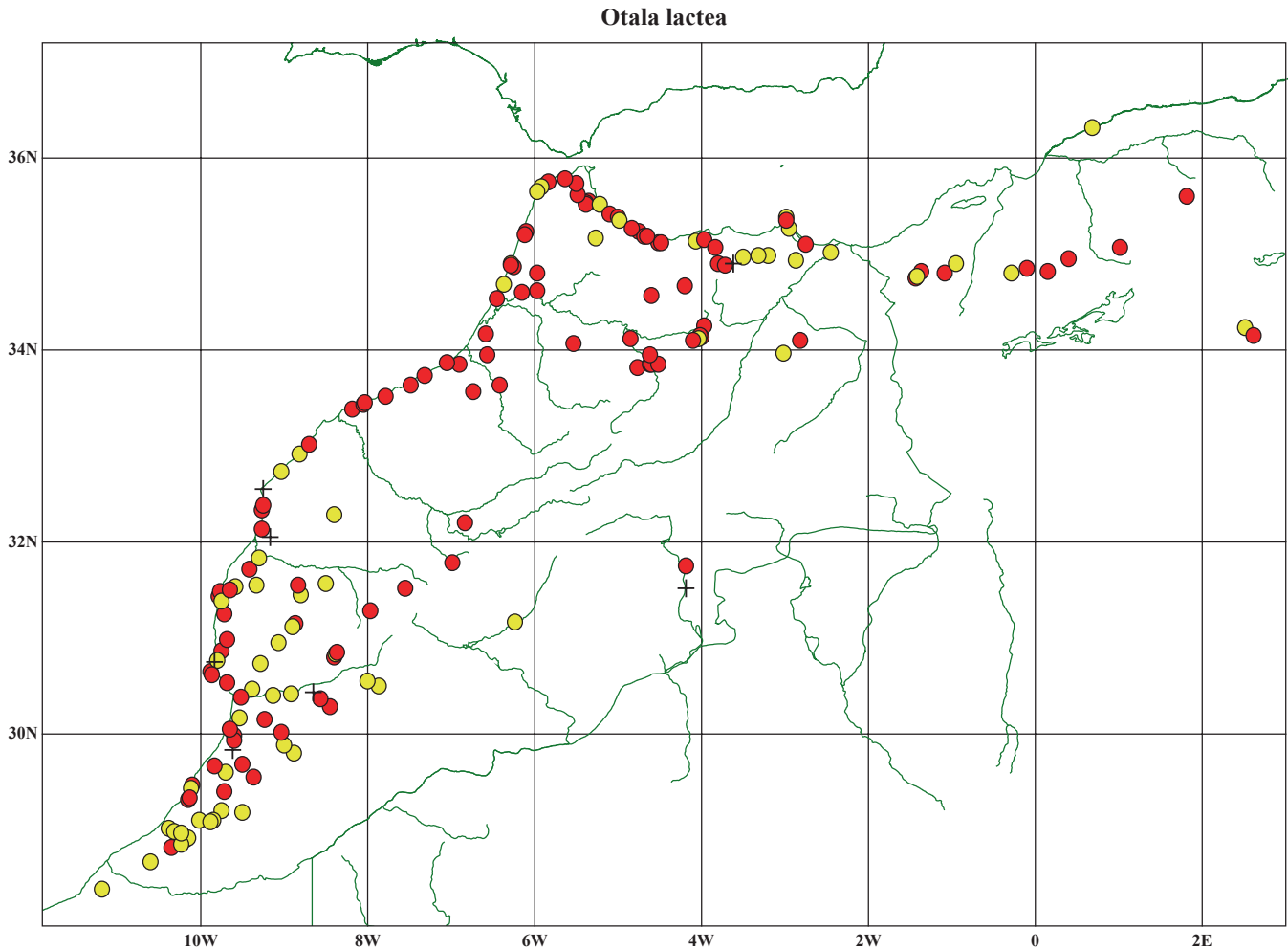
*Helix (Otala) protovermiculata* Trechmann 1938, Geological Magazine (4<sup>th</sup> ser.) 75, pp. 18, 19–20, pl. 1 figs 4–7, TL Marfa Point, Armier Bay, St Paul's Bay, bottom of cliff, Marsascirocco Bay, Valletta shore, in Malta; Cala Dueira in Gozo; based on Quaternary fossils.

See Alzona (1971: 215) and Giusti *et al.* (1995: 479) for bibliographical details of the following additional nominal taxa from Italy and adjacent islands (*concolor* De Cristofori & Jan 1832; *figarolae* Rensch 1928; *linosae* Calcara 1846; var. *linusina* Benoit 1857; *minuta* Issel 1880; *pelagosana* Westerlund 1894; *rugulosa* Risso 1826; var. *solidior* Monterosato 1892; *subangulata* Issel 1868; var. *thalassina* Villa 1841; var. *umbilicata* Castriota 1899; *usticensis* Monterosato 1892).

**Shell** 227 shells examined from 31 localities (also comparative material from Portugal and Malta

not used in preparing this diagnosis). Usual ranges, B (27.2) 28.8–40.9 (42.6), H 18.0–28.2mm, H/B 0.63–0.69, with 4.4–4.9 whorls. Shape depressed conical, somewhat flattened below, with rapidly increasing whorls; immatures and adults with rounded periphery; suture of moderate depth. Aperture almost round (except where interrupted by penultimate whorl); peristome reflected; lower palatal lip with slight hint of a tooth. Ground-colour whitish to pale cream; normally with dark brown bands that are usually narrow and well defined, patterns 12345 and 1(23)45 being common, rare shells have variable interrupted bands or all-white coloration. Peristome white, inside of aperture white. Protoconch nearly smooth, with fine radial grooves; teleoconch with irregular radial-tangential growth lines or weak ribs, and shallow variably irregular and discontinuous spiral grooves; the underside less sculptured.

**Genital anatomy** Twelve specimens dissected (six with distal genitalia mainly intact, six others with body broken away at the spermoviduct) from three localities in Algeria (also two from different localities in Portugal, in CGAH). The genital anatomy of *E. vermiculata* from Malta was described in detail and figured by Giusti *et al.* (1995: 482–484, figs 606–607). Schileyko (2006:

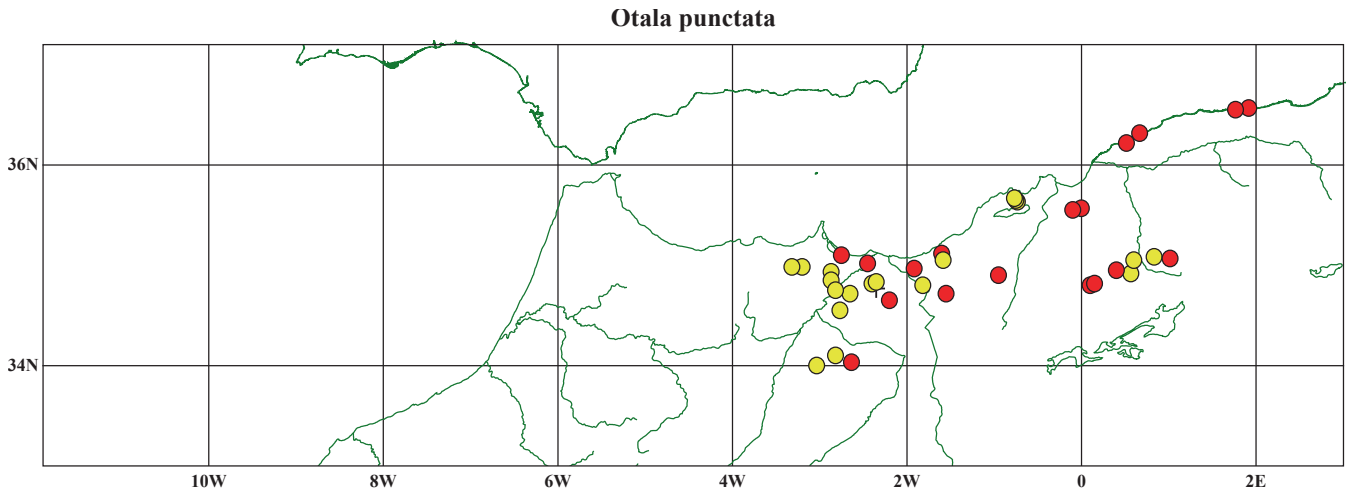


**Figure 10** Map of distribution of *Otala lactea* in Morocco and Algeria. Red circles: living, or fresh shells; yellow circles: old shells; + subfossil.

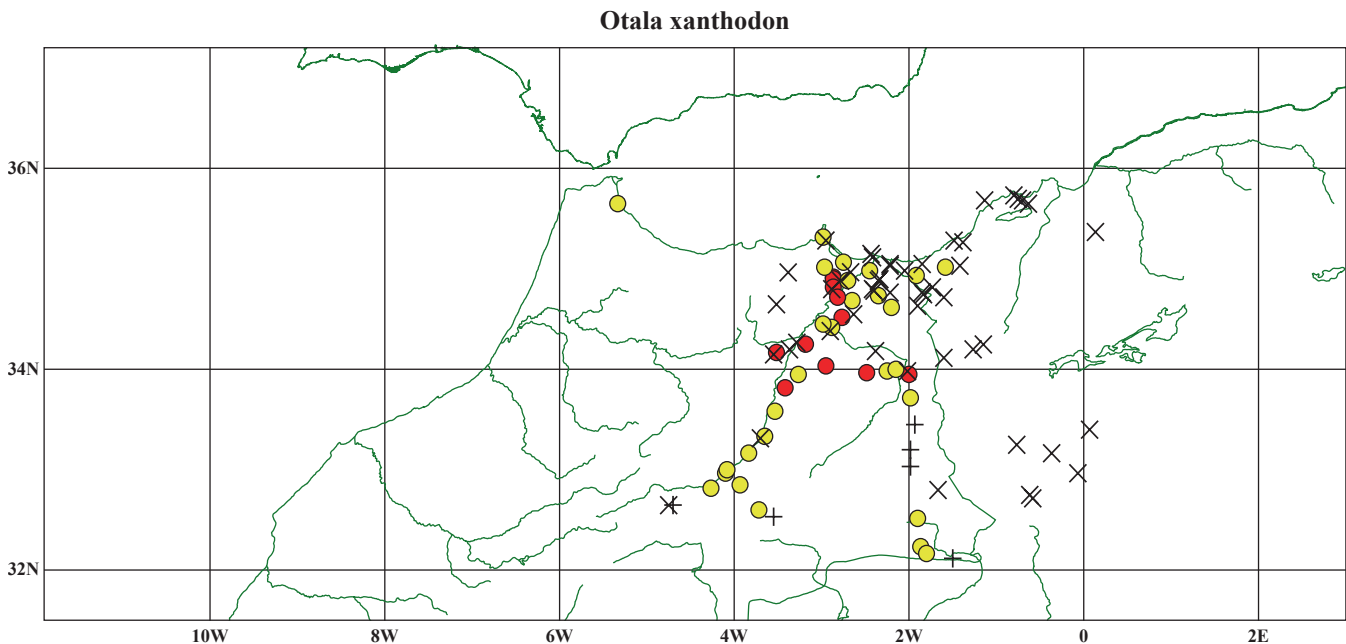
1799, fig. 2305) also gave a description and figures, but with incorrect information on the internal structure of the penis. The Algerian specimens of "*E. constantinae*" (Fig. 7C) had larger bodies than the Portuguese material, but otherwise matched them closely and also matched the account by Giusti *et al.* (*loc. cit.*). In particular, the diverticulum on the duct of the bursa copulatrix was very long (>twice length of "free" part of duct), wider than the rest of the duct and highly convoluted *in situ* (studied from six snails from three sites). The internal structure of the penis (studied in three snails from different sites and compared with one from each of the two Portuguese sites) was also similar in all the specimens studied, with a long cylindrical false verge ("false penial papilla" of Giusti *et al.*, 1995: 484–485 fig. 607) inserted on the side wall of the lumen of the wider proximal part of the penis near its proximal end.

For other figures of genital anatomy see Hesse (1915: pl. 634), Germain (1930: 191 fig. 160), Puente (1994: 735), Giusti *et al.* (1995: 483), Schileyko (2006: 1799B, C, with interior of penis drawn incorrectly) and Neubert & Bank (2006: 104–105).

*Variation and taxonomy* Bourguignat (1864: 111, 113) treated *E. constantinae* and *E. vermiculata* as two valid species, both of which occur widely in Algeria. He separated them (*op. cit.*, p. 116) as follows: "*L'Helix Constantinae* se distingue de la *vermiculata* par sa coquille plus convexe, plus globuleuse, plus forte; par son péristome très évasé et bien plus réfléchi; par son bord columellaire plus calleux, plus sinueux, moins droit; par sa suture un peu moins profonde; etc." Neither species was figured. Bourguignat (*op. cit.*, pp. 112, 114) gave shell measurements of *H. vermiculata* as H 16–28, B 24–35mm, those of *H. Constantinae* as H 20–24, B 32–36mm, but its var. *C minima* from



**Figure 11** Map of distribution of *Otala punctata* in Morocco and Algeria. Red circles: living, or fresh shells; yellow circles: old shells; + subfossil.



**Figure 12** Map of distribution of *Otala xanthodon* in Morocco and Algeria. Red circles: living, or fresh shells; yellow circles: old shells; + subfossil; × selected records from literature.

Bône [= Annaba] as H 15, B 29mm; thus they overlap broadly in shell size.

Germain (1908) repeated Bourguignat's (1864) account of the differences between the two taxa, but added (pp. 176–177): "En réalité, on observe des termes de passage assez nombreux entre les deux espèces, et le seul caractère réellement appréciable est l'élévation de la spire, l'*Helix constantinae* étant la forme elevata. D'ailleurs les caractères anatomiques des deux espèces sont identiques." Summarising (p. 178), that the two are "tres voisin" and *Helix constantinae* is an "espèce représentative".

We compared shells of *E. constantinae* (Fig. 1A, B) with samples of *E. vermiculata* (e.g. Figs 1C, D) from Portugal (P313, P414) and Malta (two samples). The differences in shell form claimed by Bourguignat (1864: 116) simply do not exist in the material examined. The *E. vermiculata* studied were mainly smaller (B 26.4–30.4mm) and of different general appearance, lacking clear narrow dark bands and instead having broad fused bands or no evident banding, darker ground colour and commonly spotted or blotched patterns. However, Giusti *et al.* (1995: 481) figured shells from Malta that have similar banding

patterns to those normal in Algerian *E. constantinae*, although the shell breadth given for Malta by them is much smaller (B 20.3–28.2mm).

Detailed information and figures of the genital anatomy of *E. constantinae* and *E. vermiculata* were provided by Hesse (1920: 25–32). He noted (*op. cit.*, p. 29) in the account of *E. constantinae* that “Die Art ist in anatomischer Hinsicht der *E. vermiculata* so ähnlich, dass ich mich darauf beschränken kann, die wenigen Unterschiede kurz zu besprechen.” Continuing (*op. cit.*, p. 30), “Durchgreifende Unterschiede gegenüber den bei *E. vermiculata* beobachteten Verhältnissen konnte ich nicht konstatieren; am auffallendsten ist das Vorkommen von relativ kurzen Blasenstieldivertikeln, von 45 und 70mm, die ich bei *E. vermiculata* nie gefunden habe. Auch die stärkere Berippung des Kiefers kann vielleicht als Unterscheidungsmerkmal gelten.”

The occurrence of a rather short diverticulum on the duct of the bursa copulatrix [“Blasenstieldivertikel”] might be significant, since Hesse (*op. cit.*, p. 28) gave the diverticulum length as 134–271mm in European specimens of *E. vermiculata*, based on at least seven specimens from four localities. However, our dissections show that his specimens from Algeria with a short diverticulum were atypical (if not immature, or broken) and our material generally provides a close match for that of *E. vermiculata*. It therefore appears that *E. constantinae* should be ranked as at most a subspecies of *E. vermiculata*. Because of the wide overlap in shell size and banding patterns we prefer to treat them as synonyms.

Puizina *et al.* (2013) studied two mitochondrial genes in populations from the Croatian coast and islands, finding relatively high haplotype diversity in both 16S rDNA and COI sequences. They interpreted this diversification as evidence of long historical presence of the species in that region.

*Range in W Maghreb.* Morocco (apparently scarce and local: Saidia; Marrakech); Melilla; N. Algeria (Bourguignat 1864: 112–113; Bourguignat [in Péchaud] 1883: 36); N. and E. Tunisia and coastal islands (Letourneux & Bourguignat, 1887). The main range of this species in the Maghreb appears to replace that of *Otala lactea* to the east (Fig. 9); the few records from Morocco and Melilla within the range of the latter species might result from recent introductions.

*Global range* Widespread in Mediterranean Europe and islands, in NE., E. and S. Spain and Balearic Is. (Altonaga *et al.*, 1994: 302), S. France (mainly in Mediterranean zone: Kerney & Cameron, 1999: 302, cf. Germain, 1930: 192), Corsica, Italy, Balkans, Bulgaria, Turkey (mainly in Mediterranean regions, occasionally adventive elsewhere: Schütt, 2005: 476), Cyprus, Crimea; also reported from Canary Islands (Neiber *et al.*, 2011), Israel (Heller, 2009: 342), and Egypt. Recorded as introduction in C. Portugal (Holyoak *et al.*, 2014), Hungary, Odessa region of Ukraine (Sysoev & Schileyko, 2009: 167), Israel (Roll *et al.*, 2009), Turkmenistan (Izzatullaev, 1996), Saudi Arabia (in gardens at Taif: Neubert, 1998: 430), S. Africa (widespread: Herbert, 2010: 48), U.S.A., SE. Australia.

Reported as fossil in the Quaternary of Alpes-Maritimes, France (Germain, 1930: 192), Malta and Gozo (Giusti *et al.*, 1995: 480, 485) and Algeria (Bourguignat, 1862: 50).

*Ecology* See “Habitats” below. Occupies a wide range of lowland habitats in southern Europe, including roadsides and gardens. In Algeria it occurs in natural habitats, including rocky slopes of varied lithology, with patchy cover of grasses and herbs.

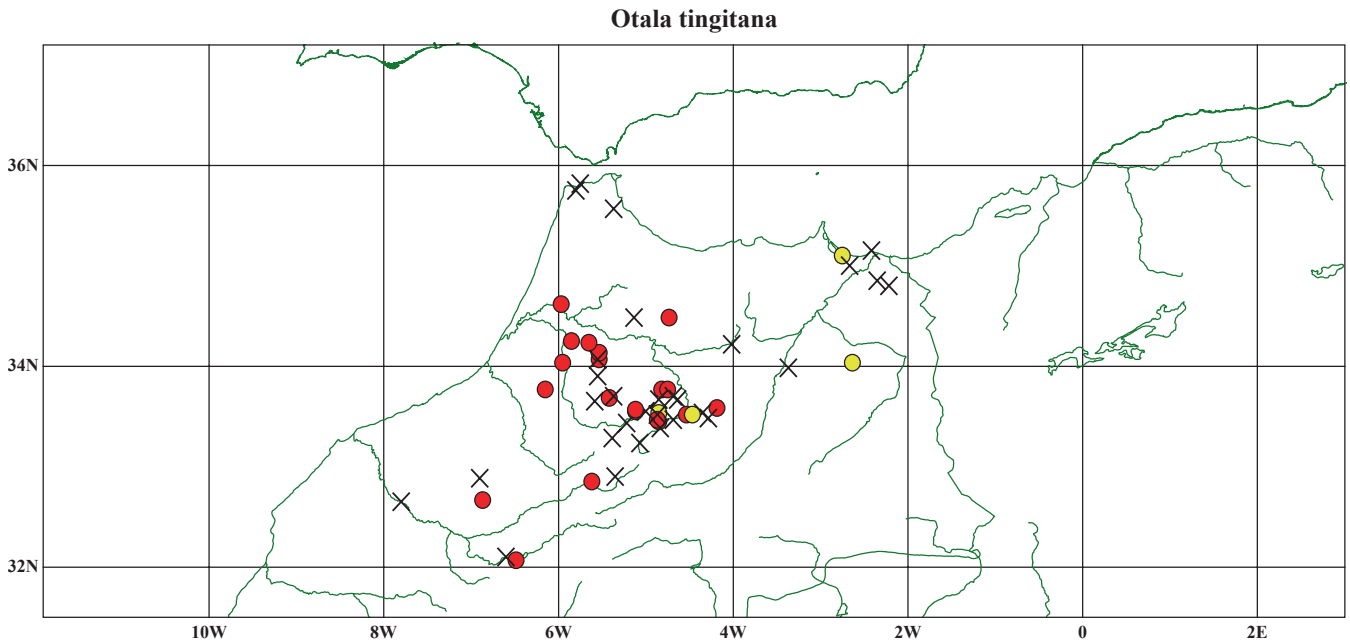
#### KEY TO SPECIES OF *OTALA* AND *EOBANIA* OCCURRING IN MOROCCO AND ALGERIA

1.

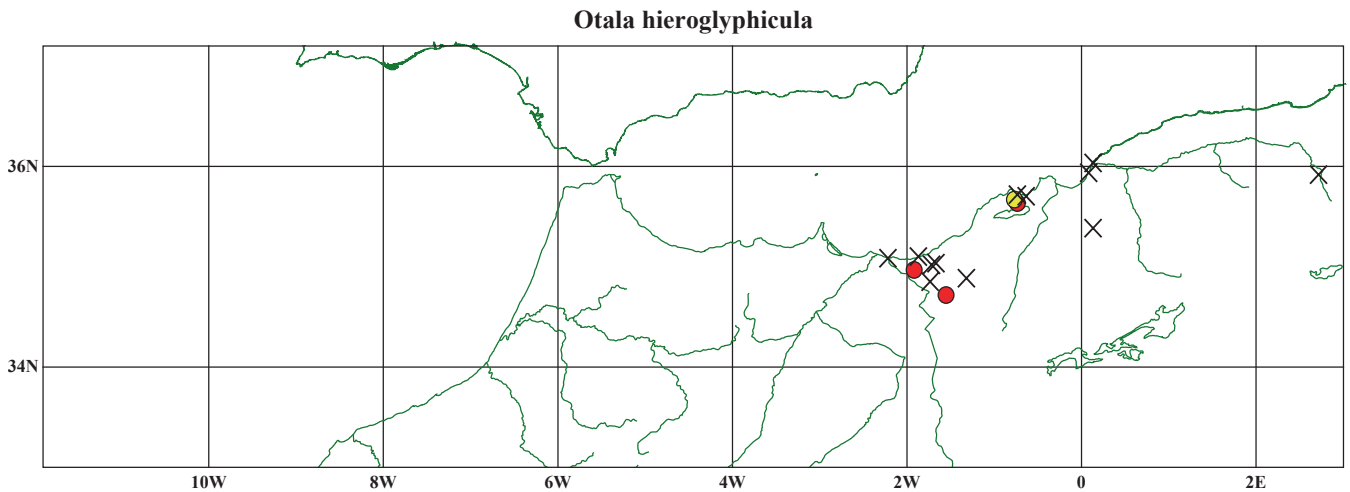
– Interior of shell aperture white or very pale on all or large majority of shells in population (brown in only one species that is restricted to east of 5°E. longitude) and shell always lacking second tooth on outer palatal area; free oviduct shorter than vagina; interior of proximal part of penis sometimes with short verge formed by distal end of epiphallus, with or without an additional false verge; Hesse’s Gland lacking at mantle edge except in *Loxana rerayana*

2

– Interior of shell aperture brown to nearly black, darker than rest of underside of shell on all or large majority of shells in population (white only in a few populations that possess a second tooth on outer palatal area); ranges west of 5°E. longitude; free oviduct as long as vagina or longer; interior of proximal part of penis with single



**Figure 13** Map of distribution of *Otala tingitana* in Morocco. Red circles: living, or fresh shells; yellow circles: old shells; x selected records from literature.



**Figure 14** Map of distribution of *Otala hieroglyphicula* in Morocco and Algeria. Red circles: living, or fresh shells; yellow circles: old shells; x selected records from literature.

short verge formed by distal end of epiphallus, lacking an additional false verge; Hesse's Gland always present on left edge of mantle

3 (*Otala*)

2.

– Diverticulum on duct of bursa copulatrix < twice length of remainder of duct; interior of proximal part of penis with short verge formed by distal end of epiphallus and sometimes an additional false verge that may be cylindrical

other genera of Otalini

– Diverticulum on duct of bursa copulatrix usually >twice length of remainder of duct; interior

of proximal part of penis with cylindrical false verge on wall of lumen in addition to very short verge formed by distal end of epiphallus

*Eobania vermiculata*

3.

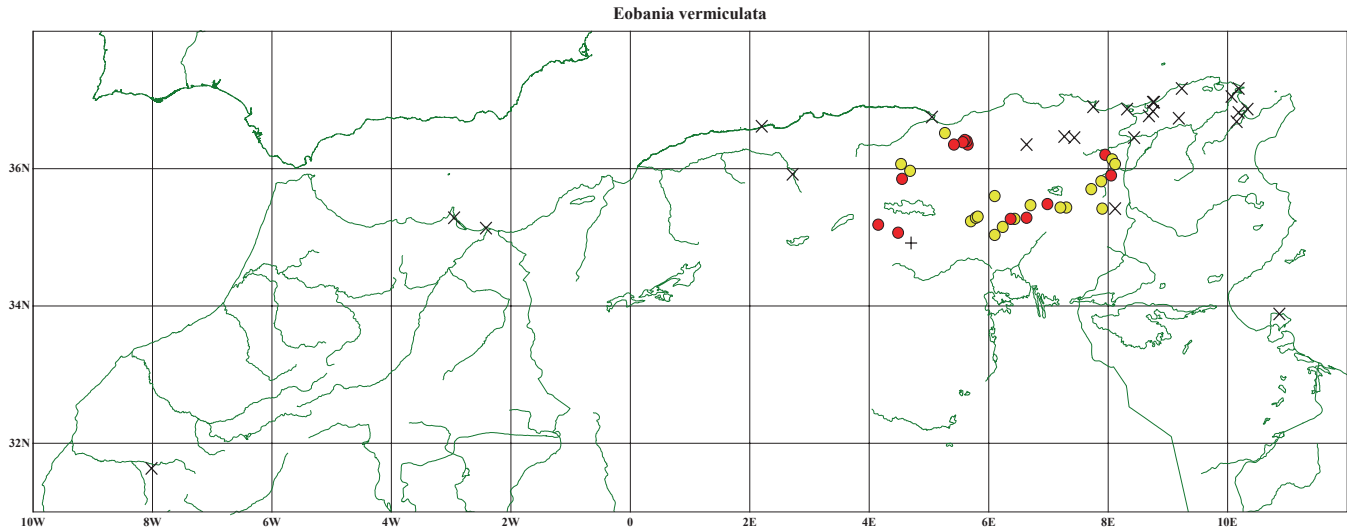
– Immature shell with sharply keeled periphery, resulting in very shallow suture on upper spire of adult shell (Figs 5, 6)

4

– Immature shell with rounded periphery, resulting in deeper suture on upper spire of adult shell (e.g. Figs 2–4)

5





**Figure 15** Map of distribution of *Eobania vermiculata* in Morocco, Algeria and Tunisia. Red circles: living, or fresh shells; yellow circles: old shells; + subfossil; x selected records from literature.

4.  
– Shell breadth <25mm; adult shell very glossy, subglobular (H/B 0.58–0.68) with rounded periphery; peristome only slightly reflected; tooth on lower lip often strong; almost endemic in NW. Algeria, just reaching NE. Morocco

*O. hieroglyphicula*

– Shell breadth 21–42mm; adult shell not very glossy, subglobular to almost discoid, with periphery rounded to keeled; peristome slightly to strong reflected; tooth on lower lip weak or lacking (especially in subglobular shells) to strong; endemic in C., NW. and NE. Morocco

*O. tingitana* (most populations)

5.  
– Shell aperture often with second tooth on outer palatal area, inside peristome; tooth on lower lip often high, commonly located close to outer edge of aperture; interior of aperture brown, partly brown or white; shells typically smaller or medium-sized with raised spire (B 19–35mm); all-white shells (except inside aperture) present in many populations, others usually with 4 (less often 3) well defined dark bands; restricted to NE. Morocco and NW. Algeria

*O. xanthodon*

– Shell aperture always lacking a second outer palatal tooth; with single tooth on lower lip, variable in size, usually located nearer middle of lip than to outer edge of aperture; interior of aperture brown to blackish; shells small to large (B 22–46mm), spire raised to low; populations of all-white shells rather rare (recorded only

from inland in NC. Morocco); banding types often very varied; includes more widespread taxa

6

6.  
– Parietal area of aperture with brown to blackish coloration of interior most often sharply distinct at its edge from pale coloration of exterior (e.g. Figs 2B–G, 3A–E, 4B); shells small or large; with or without well defined dark bands, very often lacking a pattern of pale spots; flagellum usually much longer than epiphallus; widespread in W. Maghreb (over most of W. and N. Morocco and NW. and NC. Algeria)

*O. lactea*

– Parietal area of aperture with brown coloration of interior blending gradually with pale coloration of exterior (e.g. Fig. 1E–G); shells small or large; with or without well defined dark bands, often with a pattern of pale spots; flagellum shorter than epiphallus or up to 1.5× its length; less widespread taxa (see next couplet)

7

7.  
– Shells typically large (B 28–46mm), most often with weakly defined dark bands and obvious pattern of pale spots; flagellum often shorter than epiphallus or about equal to its length; in W. Maghreb only in NE. Morocco (absent from Moyen Atlas) and NW. Algeria

*O. punctata*

– Shells usually smaller (B <35mm, often <28mm), variable in colour and pattern; flagellum longer

**Table 2** Habitats of *Eobania* and *Otala* in Morocco and Algeria, based on specimens collected in 1984, 1986 and 2016. Figures give numbers of sites with living snails or fresh shells of each species. Abbreviations: *E. ver.*, *Eobania vermiculata*; *O. xan.*, *Otala xanthodon*; *O. hie.*, *O. hieroglyphicula*; *O. lac.*, *O. lactea*; *O. pun.*, *O. punctata*; *O. tin.*, *O. tingitana*.

	<i>E. ver.</i>	<i>O. xan</i>	<i>O. hie.</i>	<i>O. lac.</i>	<i>O. pun.</i>	<i>O. tin.</i>
Altitudinal range (m above sea-level)	570–1500	210–1125	160–650	5–1410	13–1146	45–1520
Rock type:						
no rock exposed	-	7	1	25	3	6
limestone	6	1	2	37	7	11
clay	-	-	-	1	1	-
shale	1	-	-	7	-	1
sandstone	3	3	-	13	2	-
calcareous sandstone	3	4	-	13	4	-
quartzite	-	-	-	1	-	-
granitic	-	-	-	2	-	-
tufa	-	-	-	-	-	1
Topography:						
plains/nearly flat ground	-	9	-	26	2	6
slopes/banks	3	3	2	33	7	4
crag & slopes	10	3	1	40	8	9
Vegetation cover:						
mainly herbs or grasses	12	7	-	49	7	8
patchy shrubs or scrub	1	7	2	35	10	8
trees & bushes	-	1	1	12	-	2
woodland	-	-	-	2	-	1
marsh	-	-	-	1	-	-
irrigated cultivation	-	-	-	1	-	-
Other features:						
sand dunes & edges	-	-	-	5	-	-
Total N sites	13	15	3	100	17	19

than epiphallus (local forms known from Moyen Atlas and possibly also NE. Morocco)

*O. tingitana* (few atypical populations).

#### HABITATS AND ECOLOGY

Data on the habitats from which the *Eobania* and *Otala* specimens studied were collected are summarised in Table 2, based on notes made during the fieldwork. It is inevitable that information of this kind reflects the habitat preferences of the collectors as well as those of the snails, with a strong bias being likely towards searching in calcareous and stable sites which support rich faunas of land Mollusca. However, comparisons of species within these genera can reasonably be made using our data so long as some allowance is made for under representation of disturbed and species-poor habitat types.

All of the species were found to be most widespread and most abundant in sites with calcareous substrata, especially over limestone or calcareous sandstones. A small minority of records of most of the species (and usually rather few individuals) also came from calcium-poor districts, mostly over shales or sandstones, but all three sites for *O. hieroglyphicula* were probably calcium-rich. Habitats with plenty of hiding places among crags and other rock outcrops were used by all of the species. Open flat ground with no more than sparse low shrubs, herbs or grass vegetation was used only by some populations of *O. xanthodon*, although presence of cover among boulders, bushes, dwarf palms (*Chamaerops*) or large grass tussocks in relatively open places can provide suitable local conditions for all of the species. *O. xanthodon* is more tolerant than any of the other species of the arid steppe habitats inland

in eastern Morocco (although as noted above it also occurs in *Eucalyptus* plantations there, resting on trunks and branches, or in masses on thorny bushes), whereas *O. hieroglyphicula* and *O. punctata* prefer much more mesic local conditions while tolerating the dry Mediterranean climate of the W. Maghreb. *O. hieroglyphicula* is apparently restricted to lowland regions but all the others occur from the lowlands to moderate heights in hill or mountain areas (maximum recorded 1520m), although it is only with *O. tingitana* that a substantial proportion of the populations occurs in the uplands. Our Algerian material of *E. vermiculata* was entirely from the uplands (570–1500m), but there are published records there from lowland districts.

Most *Otala* populations in the W. Maghreb do not occupy habitats that are obviously isolated from those of adjacent populations, unlike the limestone crags or mountains to which many highly localised species of *Chondrina* (Chondrinidae) are restricted (Kokshoorn, 2008; Kokshoorn *et al.*, 2009; Kokshoorn & Gittenberger, 2010), although a few local forms of keeled *O. tingitana* are indeed restricted to crags. On the contrary, the larger *Otala* species are typically of rather widespread occurrence in open farmland, by roadsides, in gardens and in parks, and along valley bottoms, favouring moist places such as stream banks and sites with shelter which may be provided by scrub, thorn hedges, stands of introduced *Opuntia* cacti, dwarf palms (*Chamaerops*), tall herbs, grass tussocks, natural rocks, old walls, or masonry debris. The extent of habitat available to them has doubtless increased as a result of modern land use in many of the semi-arid regions they occupy, due to irrigation, cultivation and afforestation, while declining in other places due to overgrazing.

There is thus little reason to expect most local populations of *Otala* and *EoBANIA* to have been genetically isolated from each other for long enough to cause extensive subspeciation or speciation. While many of the obvious shell characters of size, overall shape, coloration and banding patterns may be adaptive responses to local factors, often reiterated wherever similar conditions occur, mixing of populations through accidental or deliberate introductions is likely to have confused the natural pattern. Consequently they may give a poor indication of the extent of genetic differentiation or degree of genetic

isolation of populations, factors on which there is anyway no direct evidence at present.

#### PREHISTORIC AND HISTORIC HUMAN USAGE OF LAND-SNAILS IN THE W. MAGHREB

Large land-snails are conspicuous elements in the modern fauna of the W. Maghreb and remains of their shells are spectacularly abundant at numerous archaeological sites, where they represent remains of prehistoric meals (Lubell, 2004: 78). There are also accounts from the colonial days of widespread transport and trade in live *Otala* and other snails for food (Pallary, 1936: 42). The evidence of *Otala* and other large snails being collected and carried from place to place is so strong and extensive that it is briefly reviewed here, since their natural ranges of dispersal of at most a few tens of metres per generation will undoubtedly have been greatly expanded at times through human activity. Accidental loss during transport of a single fertilised mature snail could easily have founded a new population, and even an unfertilised individual might have interbred with and thus affected the genotype of a different local population. Our ideas about genetic differentiation of their local populations or subspeciation based on very limited dispersal abilities therefore need to take account of the long history and large extent of interference by man.

Lubell *et al.* (1976) and Lubell (2004) have reviewed the archaeological evidence of prehistoric snail use in the W. Maghreb. Iberomaursian cultures occupied the region prior to 10,000 years BP and their accumulations of land-snail shells are known mainly from caves. They were replaced from 10,000 to 6000 years BP by Capsian cultures who left shells mainly in open air mounds. The review by Lubell (2004: 78) stressed that “The most dramatic and convincing evidence for prehistoric land snail consumption” in the whole circum-Mediterranean region are found in the W. Maghreb, with thousands of Capsian “escargotières” known inland in E. Algeria and S. Tunisia. Lubell *et al.* (1976: 910) noted that the “enormous numbers of land snail shells ... are the dominant visual element in most sites”. These included a large proportion of *Otala* shells at some sites (*op. cit.*, p. 915). It was noted that “While land snails may not have been the primary source of animal protein in the Capsian diet, they were certainly important” (p. 918). The archaeologists involved

even developed the thesis that the delay in development of agriculture in the W. Maghreb compared to the Near East may have been due to availability of snails for food during seasons when other natural foods were scarce.

The Romans are known to have exploited large Helicidae for food in Europe, where the arrival of *Cornu aspersum* (O.F. Müller 1774) coincided with the Roman occupation in both England (Kerney, 1999: 205) and C. Portugal (Matos, 2014: 10). They may have arrived due only to accidental transport with traded goods but it is quite likely there were also deliberate imports of snails for food (known as *escargot* when cooked), as is widely assumed in Britain for the “Roman Snail” (*Helix pomatia*) which arrived around the same time. Gaius Plinius Secundus (Pliny the Elder, b. AD 23, d. AD 79) wrote about snails in his *Naturalis Historia* (the whole work was finished in AD 77; see Bostock & Riley, 1855 for translation). He recorded that *escargot* were considered as an elite food and that Fulvus Lupinus raised snails in a garden (*cochlear*) which had separate sections for different species.

At the ruins of the Roman site of Volubilis in N. Morocco we found shells of *Otala lactea* (1993.051.3389) stratified in soil between the blocks of limestone of the wall of a Roman house. Hogan [2007] also reported independently that *Otala lactea* was recovered in excavations at Volubilis. Hence it is certain they were present when the Romans occupied the site, but we can only speculate on whether they were used as food or carried about by Romans in the W. Maghreb.

Pallary (1936: 42) reported that “Ces dernières années, il s’est fait un grand commerce d’escargots du Maroc oriental sur les marchés de l’Oranie: ce qui était d’autant productif que ces Mollusques

ne payaient aucun droit d’entrée en Algérie. Nous avons vu ainsi débiter par milliers: *Archelix polita*, *riffensis*, *alabastra*, *Vanrossomi*, *russadirensis* et la présente espèce [*Tingitana Lapierrae*]”.

A large trade in edible snails continues to the present day in southern Europe. For example in C. Portugal, living specimens of *Otala lactea* were regularly available at the fish counter in the Pingo Doço supermarket at Sertã (at 3,99 euros/kg) in 2015 and these were not of local origin. 13,000 tonnes of snails are imported annually to the EEC, including large quantities of them from Morocco and Algeria. Matos (2014: 228) noted that tons of edible snails are imported to Portugal from north Africa each year, including *Eobania vermiculata* and “non-indigenous species” of *Otala*. Evidence of widespread anthropogenic introduction of *O. lactea* and *O. punctata* is discussed above under the respective species headings.

#### DISCUSSION OF TAXONOMIC TREATMENT

Although a biological species concept has been adopted here, actual or potential interbreeding or lack of interbreeding mainly had to be inferred indirectly. The following criteria were used to assess this:

(1) At a single locality, the coexistence of two forms without interbreeding (or with very rare hybrids and no introgression) pointed to existence of two species. On the other hand, intergradation of two forms or wide variability in characters pointed to a single species being present.

Data on occurrence of each of the *Otala* species in Morocco and Algeria with and without other species of the genus are given in Table 3. Coexistence is less frequent than occurrence alone for all of the species. However, based on

**Table 3** Data on coexistence of populations of different species of *Otala* in Morocco and Algeria. The figures give the number of sites where each species occurred alone or in combination with each of the other species, based on specimens collected in 1984, 1986 and 2016 (see Methods). Figures in parentheses give the number of additional sites with more than one species where data for one or both of them is based only on old shells. Sites with any likelihood of shells having drifted to the collection locality (e.g. river edges, wadi beds, edges of lagoons) were excluded.

	<i>xanthodon</i>	<i>hieroglyphicula</i>	<i>lactea</i>	<i>punctata</i>	<i>tingitana</i>
<i>xan.</i>	10	0	0	0	0
<i>hie.</i>	(1)	2	0	1	0
<i>lac.</i>	(3)	(0)	86	3	2
<i>pun.</i>	(8)	(2)	(5)	12	0
<i>tin.</i>	(0)	(0)	(0)	(1)	15

living snails or fresh shells, three pairs of species were found to coexist: *O. lactea* with *O. punctata* at three sites (site field numbers 1984–166, -169, -172), *O. lactea* with *O. tingitana* at two sites (1984–91, 1986–264), and *O. hieroglyphicula* with *O. punctata* at one site (1984–351).

Table 3 also gives data separately on occurrence of more than one species at a site based on finds of old shells (i.e. excluding material known to be subfossil). These data can only point to a likelihood of the species involved having coexisted in the past, since they might sometimes have replaced each other without ever meeting. These records are of *O. punctata* with *O. xanthodon* (eight sites: 1984–350, -351, -352, -355; 1986–51, -52, -53, -392), *O. lactea* with *O. punctata* (five sites: 1984–161, -357, -358; 1986–57, -392), *O. lactea* with *O. xanthodon* (three sites: 1986–50, -389, -392), *O. hieroglyphicula* with *O. punctata* (two sites: 1984–348, -351), *O. hieroglyphicula* with *O. xanthodon* (one site: 1984–351) and *O. punctata* with *O. tingitana* (one site: 2016-M62). Hence, only two sites had three species represented: 1984–351 with *O. xanthodon*, *O. hieroglyphicula* and *O. punctata*; 1986–392 with *O. xanthodon*, *O. lactea* and *O. punctata*. Considered together, the data from fresh and old shells suggest almost all of the species pairs with ranges that overlap coexist somewhere, or have probably done so during the late Holocene. The only exception apparently being *O. hieroglyphicula* and *O. lactea*, but the former species was recorded from few sites.

The only clear instance of an interspecific hybrid involved *O. tingitana* and *O. lactea* at site 1986–259 (NMW.Z 1993.051.3322); one shell is perfectly intermediate (Fig. 5H), a second less convincing but possibly hybrid; seven other shells are of typical *O. lactea*.

Our finding that most localities have only one of our broadly defined species of *Otala*, with two species together in a small minority and three rarely, is in marked contrast to the old listings of distributional ranges of narrowly defined species (e.g. Bourguignat [in Péchaud], 1883: see our synonymies above), where some places such as îles Zaffarines, Île de Rachgoun or the vicinity of Nemours were supposed to have numerous species. We believe most of those extra species were based on atypical individuals or non-random selections from local subpopulations of the same species.

(2) With forms showing range overlap at a regional scale, presence of locally allopatric populations that show no signs of intergradation suggested two species are likely to be involved. However, presence of locally allopatric populations that intergrade suggested a single species is involved.

(3) Differences between forms in features of the distal genital anatomy likely to function as reproductive isolating mechanisms would suggest two species are involved. (e.g. penis morphology; flagellum and epiphallus length important in determining spermatophore size and structure: Lind, 1973; bursa tract diverticulum length: Beese, Beier & Baur, 2006). This is evident e.g. with penial flagellum length in *Otala punctata* compared to *O. lactea* (see above). Lack of such differences might be due to presence of a single species, or of several species reproductively isolated in other ways.

(4) With entirely allopatric forms, lack of intergradation in several independent characters suggested two or more species may be involved. However, if in the material as a whole all characters appeared to show intermediate and transitional states there was a presumption that only a single variable species is involved.

Admittedly, cryptic or sibling species might occur, and these might be identifiable only by comparison of combinations of multiple character states. Nevertheless, attempts to define species on the basis of combinations of multiple character states should be based on numerous large samples of specimens, i.e. sufficient to reveal contradictions, and the characters involved need to be clearly defined and readily recognisable. Otherwise, unidentifiable species will be proposed that are unhelpful to other biologists, and anyway likely to be contradicted as soon as fuller material is studied.

Despite the existence of large numbers of distinctive local populations, subspecies are not recognised here. This is because many of the populations show intergrading characters, the characters often vary independently, and some “forms” reappear at widely separated localities (e.g. *H. axia* Bourguignat 1878 occurs in Portugal, Spain, the Balearic Islands and Algeria: Locard, 1899: 39). At least some local populations have shell coloration that appears to match that of the rocks and soils among which they live (pers. obs.), so selection for camouflaging coloration

and patterns may account for convergence in appearance of geographically separated populations. Furthermore, the existence of complex colour and shell-banding polymorphisms in most populations makes interpretation difficult, with the likelihood that in the same population the banded individuals are best adapted for concealment among grasses and other plants, whereas the less patterned individuals are adapted for concealment against soil or rock.

#### NOTES ON EVOLUTION IN THE GENUS *OTALA*

Based on the molecular-phylogenetic analyses of Razkin *et al.* (2015: 108), the tribe Otalini of the Helicidae consists partly of genera and subgenera endemic to the Maghreb (*Maurohelix*, *Alabastrina*, *Atlasica*, *Dupotetia*, *Tingitana*) and partly of those occurring in both the Maghreb and southern Europe (*Cantareus*, *Cornu*, *Eobania*, *Otala* s. str., *Rossmassleria*; for confirmation of occurrence of the last of these at Gibraltar see Torres *et al.*, 2016). Thus, there are no European endemic (sub-) genera among those analysed. Indeed, at genus level, the southern European lineages can be seen as nested within north African clades, a situation found repeatedly by Husemann *et al.* (2013) through analyses of several animal groups. In fact, the imbalance of Otalini species numbers in favour of the Maghreb rather than southern Europe is much greater than implied by the lists of (sub-)genera used in molecular-genetic studies, since numerous endemic Maghreb taxa of *Rossmassleria* and (possibly subgeneric) groups allied to *Alabastrina* were not represented.

The same pattern is also clear within the genus *Otala* as broadly treated in this paper (including *Dupotetia* and *Tingitana*), since three of our five recognised species are west Maghreb endemics, whereas the other two are widespread in the western Maghreb and also present in SW. Europe, mainly in the Iberian Peninsula, the part of Europe also showing closest biogeographical affinities to the Maghreb in the other animal groups studied by Husemann *et al.* (2013).

Although good fossil evidence is not known the much greater diversity of Otalini in the W. Maghreb than in S. Europe provides a strong inference that the original diversification of the tribe occurred in the W. Maghreb. The existence there of several mountain ranges, sometimes wide rivers and evidence of large climatic

fluctuations during the Neogene and Pleistocene would appear to have offered ample opportunities for geographical speciation of land-snails. The Mediterranean Sea provided a potential barrier to colonisation northwards into Europe over much of this time, although the sea straits were closed at Gibraltar and (almost) closed to Sicily during the Messinian Salinity Crisis at 5.96–5.33 Ma (Krijgsman *et al.*, 1999; Duggen *et al.*, 2003). Because Tertiary and early Pleistocene fossils of Otalini are almost unknown, it is uncertain whether the tribe reached SW. Europe in that part of the Pliocene or whether its colonisation was more recent across sea gaps, or instead based mainly on anthropogenic introductions within the last few millennia. Lack of a modern revision of Neogene fossils of large Helicoidea from southern Europe might have concealed evidence of the past occurrence there of Otalini, although it is reasonable to question whether the shell characters of Tertiary fossils can allow discrimination of the tribes of Helicidae that have only become apparent recently on the basis of molecular data. Nevertheless, the lack of any endemic species of Otalini from the Iberian Peninsula (except, possibly, *Rossmassleria scherzeri* (Zeilebor 1867) at Gibraltar: Torres *et al.*, 2016, cf. Walther *et al.*, 2016) certainly suggests entirely recent colonisation. However, the Sicilian endemic genus or subgenus *Erctella* (Colomba *et al.*, 2011), allied to *Cornu*, may provide evidence of older links with the Maghreb in that region.

Madec, Bellido & Guiller (2003: 225) accepted that *Cornu aspersum* populations in W. Europe are a recent introduction from the W. Maghreb by man, with consequent loss of genetic variation (shown in earlier allozyme and mtDNA studies). They noted that its W. European populations are also characterized by high homogeneity in shell morphology and genital anatomy. This interpretation evidently supersedes that of Guiller, Madec & Daguzan (1994: 214–216) who also considered in detail the possibility that the species had spread naturally from NW. Africa during the Neogene, a theory based in large part on a few old and probably unreliable reports of “Pliocene” fossils from S. Europe (Taylor, 1910). As discussed above, *Cornu aspersum*, *Otala lactea* and *O. punctata* have all been used extensively for human food for millenia, including by the Romans, who apparently brought *Cornu* to both C. Portugal and England. Genetic studies of the

European *Otala* might shed an interesting light on the sources of the populations, although recent and apparently ongoing introductions for the food trade may confuse analyses.

Polymorphisms based on the basic five-banded (pentataeniate) pattern on shells occur in all the species of *Otala* and *Eobania*, and in other genera of Helicidae (e.g. Boettger, 1909). The pattern is evidently much more ancient than these genera and indeed of all Otalini, since it is present in *Pseudotachea splendida* (Draparnaud 1801), *Cepaea nemoralis*, *Caucasotachea vindobonensis* (C. Pfeiffer 1828) and *Macularia sylvatica* (Draparnaud 1801), all of which have been shown by Neiber & Hausdorf (2015: 146) to be rather distantly related to each other and to the genera of Otalini. However, *Theba* (tribe Thebini) show complicated banding polymorphisms that are judged to be based on a four-banded pattern (Heller, 2009: 120 fig. 87). It is tempting to speculate that their smaller shells cannot accommodate so many bands if similar adaptations for concealment among grasses are involved. Even the much larger *Otala lactea* is more often four banded with form 1(23)45, than five banded. However, *Eremina* also appears to be related to Otalini and its banding pattern is complicated and not obviously pentataeniate or four-banded (Holyoak *et al.*, in preparation).

As noted above, unlike the other *Otala* species, *O. xanthodon* inhabits numerous sites on open plains, sometimes without rocks or bushes or other obvious means of concealment for living snails as large as these. Unbanded white shells are dominant or exclusive in many of its populations and the shells are commonly thicker and stronger than those of other *Otala* of similar size. During fieldwork it was sometimes difficult to collect living specimens because the ground was littered with hundreds of apparently similar white shells, not only of conspecifics, but also of dead and occasionally also living *Sphincterochila* (which have all-white shells of similar size, but even thicker and stronger). From this it seems likely that the white shells of *O. xanthodon* mimic both dead shells of its own species and those of other snails, and also living *Sphincterochila*. Since chewed shells often occur in caches left by rodents it seems likely that these predators are important in maintaining the Müllerian mimicry (cf. Heller, 2009: 119–132), although concealment from avian predators might also be involved. The

four-banded pattern present in other accumulations of *O. xanthodon*, which frequently consist entirely of old dead shells, is presumed to have formerly offered concealment among grasses in areas now overgrazed and almost bare.

The interior of the shell aperture is brown to blackish-brown in almost all *Otala*, a character setting it apart from nearly all other Otalini where these areas of the shell are white or at least pale. The mantle-collar, which remains visible within the aperture when the rest of the body is retracted, is also often dark to blackish-grey in *Otala*, although sometimes whitish e.g. in some *O. xanthodon*. When the mantle-collar is dark, e.g. in *O. lactea* and *O. punctata*, its colour is frequently darker than either the sole of the foot or concealed areas of the mantle on the same snail. Although the adaptive significance of the dark coloration both of the aperture and mantle-collar has not been studied, matching the dark coloration of the shell aperture with a dark mantle-collar might hinder at least nocturnal predators wishing to find living snails by sight.

As noted in the species descriptions, *Eobania* and several species of *Otala* have a small tooth developed on the lower lip of the aperture, usually towards its middle. The tooth becomes very inconspicuous in some populations of *O. tingitana* (e.g. Figs 5A–C, 6D–H) whereas it is tall and strong in a few populations of *O. lactea* (notably “*riffensis*”) (Fig. 3A, B). *O. xanthodon* shows much more variable development of apertural teeth, many populations having a second tooth on the outer palatal area in addition to the tooth on the lower lip being larger and placed nearer the outside edge (e.g. Fig. 4E–H). Both teeth are developed only in adult or nearly adult shells and they are variable in size, especially between populations. When the teeth are large they significantly obstruct access into the shell aperture; when the outer palatal tooth is well developed it forms a curved lamella continuing inwards.

The function of the teeth was apparently misinterpreted in the early literature. Bourguignat [in Péchaud] (1883: 85) suggested “pourraient bien n’être qu’un cas pathologique résultant de certaines influences climatologiques ou produit par une cause accidentelle jusqu’à présent inconnue” [i.e. the larger teeth may represent no more than a pathological response to certain climatic conditions, or result from accidental causes as yet unknown]. Pallary (1898: 562) agreed with this

and he repeated the same opinion later (Pallary, 1899d: 315). Nonetheless, there seems little doubt that the apertural teeth, combined with a thick, strong shell, globular shape and smooth shell surface together form fortifications to reduce the likelihood of predation, most probably by rodents. There has been very little study of the ecology of Helicidae in the W. Maghreb, or of the influence of predators on them.

#### ACKNOWLEDGEMENTS

Marcel Holyoak and Dr Mary B. Seddon are thanked for their help with field collecting in 1984 and 1986. During the 1980s, facilities at the Department of Geography, University of Nottingham and Department of Geography at the College of St Paul and St Mary, Cheltenham were used in initial study of the collections, for which a grant from the Nuffield Foundation to DTH provided a microscope. The late J.F.M. de Bartolomé shared his observations on the *Otala tingitana* forms he bred and hybridized in captivity.

The Department of BioSyB at National Museum & Galleries of Wales, Cardiff allowed large loans of the specimens from 2015–2017 without which the completion of the study would not have been possible; thanks are due to Jennifer Gallichan and Harriet Wood for arranging these loans. Rui da Costa Mendes, J. Sebas Torres Alba, Dr Martin J. Willing and Harriet Wood helped with obtaining copies of literature; Miguel Carrillo Pacheco provided living specimens. We are also grateful to two anonymous referees for detailed and helpful comments.

#### REFERENCES

- ADAMS H & ADAMS A 1855 *The genera of Recent Mollusca arranged according to their organization*. J. Van Voorst, London, 2(part XXII): 189–220.
- AGUILAR-AMAT JB DE 1933 Observacions malacològiques. XIX. Contribució al coneixement de la malacofauna menorquina. *Butlletí de la Institució catalana d'història natural*, Barcelona 33: 324–338. n.v.
- ALBERS JC 1850 *Die Heliceen, nach natürlicher Verwandtschaft systematisch geordnet von Joh. Christ. Albers*. Th. Chr. Fr. Enslin, Berlin. 262 pp.
- ALBERS JC & MARTENS E VON 1860 *Die Heliceen, nach natürlicher Verwandtschaft systematisch geordnet von Joh. Christ. Albers*. Zweite Ausgabe. Wilhelm Engelmann, Leipzig. xviii + 359 pp.
- ALONSO MR & IBÁÑEZ M 2007 Anatomy and function of the penial twin papillae system of the Helicinae (Gastropoda: Helicoidea: Helicidae) and description of two new, small *Hemicycla* species from the laurel forest of the Canary Islands. *Zootaxa* 1482: 1–23.
- ALTONAGA K, GÓMEZ B, MARTÍN R, PRIETO CE, PUENTE AI & RALLO A 1994 *Estudio faunístico y biogeográfico de los Moluscos terrestres del Norte de la Península Ibérica*. Eusko Legebiltzarra [Parlamento Vasco], Vitoria-Gazteiz. 505 pp.
- ALZONA C 1971 Malacofauna Italica. Catalogo e Bibliografia dei Molluschi Viventi Terrestri e d'Acqua Dolce. *Atti della Società Italiana di Scienze Naturali & Museo Civico di Storia Naturale di Milano* 111: 1–433+[1].
- ANCEY CF 1882 Observations sur quelques *Macularia* accompagnées de descriptions de coquilles nouvelles d'Espagne et d'Algérie. *Il Naturalista Siciliano* 1: 285–295.
- ANIMALBASE WEBSITE: <http://www.animalbase.uni-goettingen.de/zooweb/servlet/AnimalBase/home/species?id=1366> (Accessed 13 April 2017).
- ANTON HE 1838 (“1839”) *Verzeichniss der Conchylien welche sich in der Sammlung von Hermann Eduard Anton befinden*. Eduard Anton, Halle. xvi + 110 pp.
- ARAYA JF 2015 Current status of the non-indigenous molluscs in Chile, with the first record of *Otala punctata* (Müller, 1774) (Gastropoda: Helicidae) in the country and new records for *Cornu aspersum* (Müller, 1774) and *Deroceras laeve* (Müller, 1774). *Journal of Natural History*, DOI: 10.1080/00222933.2015.1006703.
- AUCAPITAINE H 1862 (April) Mollusques terrestre et d'eau douce observés dans la haute Kabylie (versant nord du Djurjura). *Revue et Magasin de Zoologie* 25: 144–162.
- BACKHUYS W 1975 *Zoogeography and taxonomy of the land and freshwater molluscs of the Azores*. Backhuys & Meesters, Amsterdam. pp. xii + 350, 97 maps, 32 pls.
- BANK RA 1989 Die Veröffentlichungsdaten der Rossmässler'schen “Iconographie der Land- und Süßwasser-Mollusken” Europas (1835–1920). *Mitteilungen der deutschen Malakozoologischen Gesellschaft* 44/45: 49–53.
- BANK RA 2011 Checklist of the land and freshwater Gastropoda of the Iberian peninsula (Spain, Portugal, Andorra, Gibraltar). 35 pp. Fauna Europaea Project, PDF downloaded from: [http://www.nmbe.ch/sites/default/files/uploads/pubinv/fauna\\_europaea\\_-\\_gastropoda\\_of\\_iberian\\_peninsula.pdf](http://www.nmbe.ch/sites/default/files/uploads/pubinv/fauna_europaea_-_gastropoda_of_iberian_peninsula.pdf) (Accessed 13 Apr. 2017).
- BANK RA, GROH K & RIPKEN TEJ 2002 Catalogue and bibliography of the non-marine Mollusca of Macaronesia. In: Falkner, M., Groh, K. & Speight, M.C.D. *Collectanea Malacologica. Festschrift für Gerhard Falkner*. ConchBooks, Hackenheim. Pp: 89–235.
- BANK RA & MENKHORST HPMG 2009 A revised bibliography of the malacological papers of Paul Pallary. *Zoologische Mededelingen* 83(5): 537–546.
- BARBARA N & SCHEMBRI PJ 2008 The status of *Otala punctata* (Müller, 1774), a recently established



- terrestrial gastropod in Malta. *Bollettino Malacologico* **44**(5–8): 101–107.
- BARTOLOMÉ JFM DE 1982 Comments on some Mediterranean rockdwelling helicids. *Journal of Conchology* **31**(1): 1–6.
- BECK HH 1837–1838 *Index Molluscorum praesentis aevi Musei Principis Augustissimi Christiani Frederici ... Fasciculus primus et secundus Mollusca Gastropoda Pulmonata. Hafniae*. 124 (8) pp. [pp. 1–100 were issued in 1837 and pp. 101–124 with the eight pages of descriptions of new species in 1838].
- BECKMANN K–H 2007 *Die Land- und Süßwassermollusken der Balearischen Inseln*. ConchBooks, Hackenheim. 255 pp.
- BEESE K, BEIER K & BAUR B 2006 Bursa tract diverticulum in the hermaphroditic land snail *Arianta arbusatorum* (Stylommatophora: Helicidae): morphology, function, and evolutionary implications. *Journal of Morphology* **267**(8): 940–953.
- BENOIT L 1857, 1862 *Illustrazione sistematica critica iconografica de' testacei estramarini della Sicilia ulteriore e delle isole circostanti*. Cav. Gaetano Nobile, Napoli. Fasc. 2, pp. 53–116 (1857); pls 1–12 (1862).
- BINNEY WG (ed) 1858 *The complete writings of Thomas Say on the conchology of the United States*. H. Baillièrre, New York, etc. Pp. vi +249+48; pls 75.
- BOETTGER CR 1909 Ein Beitrag zur Erforschung der europäischen Heliciden. *Nachrichtsblatt der deutschen Malacozoologischen Gesellschaft* **41**(2): 49–68.
- BOFILL A & AGUILAR-AMAT JB DE 1924 Malacologia de les Illes Pitiuses. *Trabajos del Museo de Ciencias Naturales de Barcelona* **10**(3): 1–71, 2 pls.
- BORRERO F & ROSENBERG G 2015 The Paul Hesse Collection at the Academy of Natural Sciences of Philadelphia, with a review of names for Mollusca introduced by Hesse. *Proceedings of the Academy of Natural Sciences of Philadelphia* **64**(1): 43–100.
- BOSTOCK J & RILEY 1855 *The Natural History. Pliny the Elder*. Taylor & Francis, London. Original n.v., accessed online 3 June 2015 at: [www.perseus.tufts.edu/hopper/text?doc=Plin.+Nat+toc](http://www.perseus.tufts.edu/hopper/text?doc=Plin.+Nat+toc)
- BOURGUIGNAT J–R 1862 *Paléontologie des mollusques terrestres et fluviatiles de l'Algérie*. Baillièrre et fils, Paris. 126 pp., 6 pls. [Some bibliographical details of Bourguignat's publications have been obtained from Bourguignat, 1891 and Dance, 1970b].
- BOURGUIGNAT J–R 1863 *Mollusques nouveaux, litigieux ou peu connus*. F. Savy, Paris. Première Décade (March 1863), pp. 1–22, pls 1–4; originally published in *Revue et Magasin de Zoologie* (2) **15**: 100–111 (1863).
- BOURGUIGNAT J–R 1863–1864 *Malacologie de l'Algérie ou histoire naturelle des animaux Mollusques terrestres et fluviatiles recueillis jusqu'à ce jour dans nos possessions du nord de l'Afrique*. Challamel Aine, Paris. 2 vols, **1**: xi +294 pp., 32 pls; **2**: 380 pp., 26 pls (published in six fascicles between May 1863 and December 1864).
- BOURGUIGNAT J–R 1863–1870 *Mollusques nouveaux, litigieux ou peu connus*. F. Savy, Paris; Premier fascicule (1863) to Douzième décade (1870), as collected series of reprints from *Revue et Magasin de Zoologie* 2<sup>nd</sup> ser., **15**: 100–111 to **22**: 87–97, 166–171.
- BOURGUIGNAT J–R 1868a Etudes géologique et paléontologique des Hauts Plateaux de l'Atlas entre Boghar et Tiaret. In: *Souvenirs d'une exploration scientifique dans la Nord de l'Afrique*, **2**, Challamel Ainé, Paris. 35 pp., 3 pls.
- BOURGUIGNAT J–R 1868b Histoire malacologique de la Régence de Tunis. In: *Souvenirs d'une exploration scientifique dans le nord de l'Afrique*, **3**, Challamel Ainé, Paris. 36 pp., 1 pl.
- BOURGUIGNAT J–R 1876 *Species novissimae Molluscorum in Europaeo systemati detectae: notis diagnosticis succinctis breviter descriptae*. Paris. pp. 1–80. [Bourguignat in Péchaud, 1883 made many references to another part of this work dated 1878, but this never existed: see Connolly, 1934; Dance, 1970a: 76].
- BOURGUIGNAT J–R 1891 *Œuvres scientifiques de M.J.-R. Bourguignat ... précédées d'une préface biographique par le Dr. Georges Servain*. D. Dumoulin et cie, Paris. vii +256 pp. [Dance, 1970b: 95 established that Bourguignat himself wrote all but the preface of this work].
- CADEVALL J & OROZCO A 2016 *Caracoles y Babosas de la Península Ibérica y Baleares*. Nuevas Guías de Campo Omega, Barcelona. Pp. 817.
- CALCARA P 1846 *Catalogo dei molluschi terrestri e fluviali della Sicilia*. Palermo. pp. 4, pl. [1]. [Apparently an offprint from: *Atti 8<sup>a</sup> Riun. Sc. It. Genova*, pp. 524, etc.]
- CALCARA P 1851 *Descrizione dell'isola di Linosa*. P. Morvillo, Palermo & Georgio Franz, Monaco. 29 pp.
- CASTILLEJO J 1986 *Caracoles terrestres de Galicia. Familia Helicidae (Gastropoda, Pulmonata)*. Servicio de Publicacións e Intercambio Científico, Universidade de Santiago de Compostela, Spain. 65 pp., 23 pls. n.v.
- CAZIOT E 1905 Contribution à la faune malacologique de la Catalogne. Étude sur quelques *Helix*. *Butlleti de la Institució Catalana d'Història Natural* **5**: 88–93. n.v.
- CAZIOT E & THIEUX E 1911 Etude sur les *Helix* algériens et espagnols des groupes *lactea* Müller et *myristigma* Bourguignat. *Bulletin de la Société zoologique de France* **36**(10): 111–128. n.v.
- CHEMNITZ JH 1786 *Neues systematisches Conchylien-Cabinet ... durch Johann Hieronymus Chemnitz ... Bd 9* (2). Gabriel Nicolaus Raspe, Nürnberg. n.v.
- CLANZIG S & BERTRAND A 2001 *Otala punctata* (O.F. Müller, 1774) en France. *Documents Malacologiques* **2**: 47–48.
- COLOMBA MS, GREGORINI A, LIBERTO F, REITANO A, GIGLIO S & SPARACIO I 2011 Monographic revision of the endemic *Helix mazzullii* De Cristofori & Jan, 1832 complex from Sicily and re-introduction of the genus *Ercella* Monterosato, 1894 (Pulmonata, Stylommatophora, Helicidae). *Zootaxa* **3134**: 1–42.
- CONNOLLY M 1934 A Bourguignatian bluff! *Proceedings of the Malacological Society of London* **21**: 70–73.
- COQUAND H 1862 La Géologie et la Paléontologie de la région Sud de la province de Constantine. *Mémoires de la Société d'Émulation de Provence* **2**, Arnaud, Marseille. 365 pp.+Atlas 35 pls.

- COSSIGNANI T 2014 *African landshells*. L'Informatore Piceno, Ancona. 207 pp. (mainly of col. pls).
- COSSIGNANI T & AHUIR GALINDO J 2012 Nuova *Tingitana* dal Marocco. *Malacologia* (Mostra Mondiale, Cupra Marittima) **75**: 27.
- COWIE RH, DILLON RT JR, ROBINSON DG & SMITH JW 2009 Alien non-marine snails and slugs of priority quarantine importance in the United States: A preliminary risk assessment. *American Malacological Bulletin* **27**(1–2): 113–132.
- CROSSE H 1861 Diagnoses d'Hélicéens fossiles des environs de Constantine (Algérie). *Journal de Conchyliologie* **9**: 356–357.
- CROSSE H 1862a Diagnoses d'Hélicéens fossiles des environs de Constantine (suite). *Journal de Conchyliologie* **10**: 84–85.
- CROSSE H 1862b Description des Mollusques terrestres du gisement de Coudiat-Aty et d'Aïn-el-Hadj-Baba, suivie de considérations sur les caractères de cette faune. *Journal de Conchyliologie* **10**: 152–172, pl. 7.
- DALL WH 1915 *An index to the Museum Boltenianum*. Smithsonian Institution, City of Washington (Publication 2360). 64 pp.
- DANCE SP 1970a "Le Fanatisme du Nobis": a study of J.-R. Bourguignat and the "Nouvelle École". *Journal of Conchology* **27**(2): 65–86.
- DANCE SP 1970b List of J.-R. Bourguignat's publications on molluscs. *Journal of Conchology* **27**(2): 87–95.
- DAUTZENBERG P 1915 Description d'un *Macularia* nouveau provenant du Maroc. *Journal de Conchyliologie* **62**(3): 158–160.
- DEBEAUX O 1857 Catalogue des Mollusques vivants observés aux environs de Boghar (Algérie). *Recueil des travaux de la Société d'agriculture, sciences et arts d'Agen* **8**(2): 317–329.
- DE MATTIA W & MASCIA F 2011 *Otala punctata* (O.F. Müller, 1774) (Stylommatophora: Helicidae) in Italy. *Iberus* **29**(1): 39–46.
- DESPOTT G [undated] *Exchange list of marine, land, fresh and brackish water shells from the Maltese Islands*. Malta. 3 pp. n.v.
- DUGGEN S, HOERNLE K, VAN DEN BOGAARD P, RÜPKE L & MORGAN JP 2003 Deep roots of the Messinian salinity crisis. *Nature* **422**: 602–606.
- FALKNER G, RIPKEN TEJ & FALKNER M 2002 *Mollusques continentaux de France. Liste de référence annotée et bibliographie*. Patrimoines naturels **52**: 1–350 (Muséum national d'histoire naturelle–Laboratoire de biologie des invertébrés marins et de malacologie, Paris).
- FAUNA EUROPAEA WEBSITE: [http://www.faunaeur.org/full\\_results.php?id=425958](http://www.faunaeur.org/full_results.php?id=425958) (Accessed 13 April 2017).
- FÉRUSAC AÉJPJF D'Audebard de [fils] & DESHAYES G–P 1819–1851 *Histoire naturelle générale et particulière des mollusques terrestres et fluviatiles, tant des espèces que l'on trouve aujourd'hui vivantes, que des dépouilles fossiles de celles qui n'existent plus; classés d'après les caractères essentiels qui présentent ces animaux et leurs coquilles*. J.-B. Baillière, Paris. T. 1: 8+184 pp.; T. 2(1): pp. [1–3], 1–402; 2(2): 1–260, 1–22, [1, 2], i–xvi; Atlas 1: 70 pls; Atlas 2: 166+5 pls.
- FISCHER P 1857 Description d'une espèce nouvelle du Genre *Helix*. *Journal de Conchyliologie* **6**(2): 189–190, pl. 6 fig. 3.
- FISCHER PH & FISCHER-PIETTE E 1946 [Obituary notice of] Paul Pallary. *Journal de Conchyliologie* **87**(1): 5–6.
- FORBES E 1838 On the land and freshwater Mollusca of Algiers and Bougia. *Annals of Natural History; or, Magazine of Zoology, Botany, and Geology*, London. **2**(10): 250–255, & Supplement, 1839, pls 11–12.
- GASSIES J–B 1856 Description des coquilles univalves, terrestres et d'eau douce envoyées à la Société Linnéenne de Bordeaux par M. le capitaine Mayran, correspondant. *Actes de la Société Linnéenne de Bordeaux* **21**: 104–114, 1 pl.
- GERMAIN L 1908 Étude sur les mollusques recueillis par M. Henri Gadeau de Kerville pendant son voyage en Khroumirie (Tunisie). In: Gadeau de Kerville, H. *Voyage zoologique en Khroumirie (Tunisie)*. J.-B. Baillière et fils, Paris. Pp. 129–297, pls: 22–30.
- GERMAIN L 1930, 1931 *Mollusques terrestres et fluviatiles*. Faune de France. Paul Lechevalier, Paris. **21**: 1–477, i–viii, pls: 1–13.; **22**: 478–897, ix–xiv, pls: 14–26. (Facsimile reprint, 1962).
- GIUSTI F 1970 Notulae Malacologicae, XII. L'isola di Pianosa e lo scoglio La Scola (Arcipelago Toscano). *Annali del Museo Civico di Storia Naturale di Genova* **78**: 59–148.
- GIUSTI F & ANDREINI S 1988 Morphological and ethological aspects of mating in two species of the family Helicidae (Gastropoda: Pulmonata): *Theba pisana* (Müller) and *Helix aperta* Born. *Monitore Zoologico Italiano (Nuova Serie)* **22**: 331–363.
- GIUSTI F, MANGANELLI G & SCHEMBRI PJ 1995 *The non-marine molluscs of the Maltese Islands*. Monografie Museo Regionale di Scienze Naturali, Torino **15**, 607 pp. [See Giusti & Schembri 2004 for confirmation that this work was published in December 1995].
- GIUSTI F & SCHEMBRI PJ 2004 The date of publication of the non-marine molluscs of the Maltese Islands. *Journal of Conchology* **38**(4): 457–458.
- GMELIN JF 1791–1792 *Caroli a Linné, Systema Naturae*, t. **1** pars 6. Beer, Lipsiae. Pp. 3021–3910 (1791), 3911–4120 (1792).
- GRAELLS MP 1846 *Catalogo de los Moluscos terrestres y de agua dulce observados en España y descripcion y notas de algunas especies nuevas ó poco conocidas del mismo pais*. Madrid & Lima. [Pp. 44 including covers & wrappers].
- GRAY JE 1868 Notes on the specimens of Calyptraeidae in Mr. Cumings' collection. *Proceedings of the Zoological Society of London* (for 1867): 726–748.
- GUILLER A, MADEC L & DAGUZAN J 1994 Geographical patterns of genetic differentiation in the landsnail *Helix aspersa* Müller (Gastropoda: Pulmonata). *Journal of Molluscan Studies* **60**(3): 205–221.
- HAAS F 1929 *Fauna malacológica terrestre y de agua dulce de Cataluña*. Imprenta Elzeviriana i Librería Camí, Barcelona. Facsimile with additional figures published 1991, *Treballs del Museu de Zoologia* **5**: i–xxiv, 1–491, xxvii–lxv.

- HELLER J 2009 *Land snails of the land of Israel. Natural history and a field guide*. Pensoft, Sofia & Moscow. 360 pp.
- HERBERT DG 2010 *The introduced terrestrial Mollusca of South Africa*. SANBI Biodiversity Series 15, South African National Biodiversity Institute, Pretoria. vi +108 pp.
- HERBERT DG & SIRGEL WF 2001 The recent introduction of two potentially pestiferous alien snails into South Africa and the outcomes of different pest management practices: an eradication and a colonization; research in action. *South African Journal of Science* **97**: 301–304.
- HESSE P 1909–1911 *Iconographie der Land- & Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten*. C.W. Kreidel's Verlag, Wiesbaden. Neue Folge, Band 16. Heft 1–2 (1909), pp. 1–42, pls 421–430; Heft 3–4 (1910), pp. 43–66, pls 431–440; Heft 5–6 (1911), pp. 67–119, pls 441–450.
- HESSE P 1913 Zur Kenntnis der Molluskenfauna von Ostrumelien. II. *Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft* **45**(1): 1–16, 69–74.
- HESSE P 1915–1920 *Iconographie der Land- & Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten*. C.W. Kreidel's Verlag, Wiesbaden. Neue Folge, Band 23. Heft 1–2 (1915), pp. 1–72, pls 631–640; Heft 5–6 (1920), pp. 153–262, pls 651–660.
- HESSE P 1934 Zur Anatomie und Systematik palaearktischer Stylommatophoren. Zweiter Teil. *Zoologica* **33** (85): 1–59, pls 1–9.
- HIDALGO JG 1875, 1884 *Catálogo iconográfico y descriptivo de los Moluscos terrestres de España, Portugal y las Baleares*. 2 vols. (unfinished). Imprenta de Segundo Martinez, Madrid. Part 1, pp. i–iv, 1–224, pls 1–24+portrait, 1875; Part 3, pp. 1–16, pls A, 25–44, 1884.
- HIDALGO JG 1909 Enumeración de los Moluscos recogidos por la Comisión exploradora de Marruecos. *Boletín de la Real Sociedad española de Historia Natural* **9**(4): 211–213.
- HOGAN CM [2007] *Volubilis*, in: *Mogador, The Megalithic Portal*, ed. A. Burnham. www.megalithic.co.uk/article.php?sid=14906, & pages.rediff.com/heliciculture/709508, both accessed 3 June 2015.
- HOGAN CM [2013] Oceans and seas. Alboran Sea. The Encyclopedia of Earth. www.eoearth.org/view/article/149961, accessed 24 April 2016.
- HOLMBERG E L 1909a *Mollusca Geophila Argentina Nova*. *Apuntes Historia Natural Buenos Aires* **1**: 19–22.
- HOLMBERG E L 1909b *Mollusca Argentina Varia*. *Apuntes Historia Natural Buenos Aires* **1**: 691–692.
- HOLYOAK DT, HOLYOAK GA & MENDES R DA COSTA 2014 New and noteworthy distributional records of land and freshwater Mollusca (Gastropoda) in Portugal. *Noticiario de la Sociedad Española de Malacología* **61**: 45–54.
- HORST D 1967 Malakologische Notizen aus Spanien. *Mitteilungen der deutschen Malakozoologischen Gesellschaft* **9**: 165–167.
- HUSEMANN M, SCHMITT T, ZACHOS FE, ULRICH W & HABEL JC 2013 Palaeartic biogeography revisited: evidence for the existence of a North African refugium for Western Palaeartic biota. *Journal of Biogeography* **41**(1): 81–94.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (F Hemmings, ed.) 1944 Opinion 184. On the status of names first published in volumes 1 to 11 of Martini (F.H.W.) and Chemnitz (J.H.), *Neues systematisches Conchylien-Cabinet*, Nürnberg, 1769–1795. *Opinions and Declarations rendered by the International Commission on Zoological Nomenclature* **3**(3): 27–35.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (F Hemmings, ed.) 1954 Direction 1. Addition to the “Official Lists” and “Official Indexes” of certain scientific names and of the titles of certain books dealt with in “Opinions” 182 to 194. *Opinions and Declarations rendered by the International Commission on Zoological Nomenclature* **3**(30): 403–415.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 2002 Opinion 1996. *Helix lucorum* Linnaeus, 1758 and *Helix punctata* Müller, 1774 (currently *Otala punctata*; Mollusca, Gastropoda): usage of the specific names conserved by the replacement of the syntypes of *H. lucorum* with a neotype. *Bulletin of Zoological Nomenclature* **59**(2): 135–136.
- IRIKOV A & GERDZHNIKOV G 2013 Mollusca (terrestrial and marine Gastropods et Bivalvia) from Morocco. *ZooNotes* **50**: 1–5.
- ISSEL A 1868 Dei molluschi terrestri e d'acqua dolce raccolti nell'Arcipelago di Malta. *Bullettino Malacologico Italiano* **1**: 1–6, 17–24, pl. 2.
- IZZATULLAEV ZI 1996 On a new terrestrial mollusk *Eobania vermiculata* (Pulmonata, Helicidae) brought to central Asia. *Zoologicheskii Zhurnal* **75**(5): 778–780. n.v.
- JOBA J 1862 Note sur un terrain tertiaire des environs de Constantine. *Journal de Conchyliologie* **10**: 150–152.
- JODOT P 1954 Gastéropodes continentaux du Pliocène inférieur de l'Oued Assermo n'Ait Zahrar (Sud du Haut Atlas marocain). *Notes et Mémoires du Service Géologique du Maroc*, Rabat, n° 120 (*Notes du Service Géologique du Maroc*, t. 8). n.v.
- JODOT P 1955 Gastéropodes tortoniens d'Aïn Toudja au SE de Gambetta. In: David L & Jodot P 1955 Quelques précisions sur la transgression miocène dans les environs de Gambetta (Est-Constantinois). *Bulletin de la Société d'Histoire naturelle de l'Afrique du Nord* **46**. n.v.
- KADOLSKY D 1971 Nomenklatorische Bemerkungen. *Archiv für Molluskenkunde* **101**(1/4) 191–193.
- KADOLSKY D 2012 Nomenclatural comments on non-marine Mollusca occurring in the British Isles. *Journal of Conchology* **41**(1): 65–90. [Appendix 3, pp. 84].
- KERNEY MP 1999 *Atlas of the land and freshwater molluscs of Britain and Ireland*. Harley Books, Colchester. 264 pp.
- KERNEY MP & CAMERON RAD 1979 *Land snails of Britain and north-west Europe*. Collins (Collins Field Guide),

- London. 288 pp., 24 pls. (reprinted 1987, 1994 by HarperCollins).
- KERNEY MP & CAMERON RAD 1999 *Guide des escargots et limaces d'Europe*. Delachaux & Niestlé, Lausanne & Paris (adaptation of Kerney & Cameron, 1979 by A. Bertrand). 370 pp., 28 pls.
- KOBELT W 1875–1876 *Iconographie der Land- & Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten*. C.W. Kreidel's Verlag, Wiesbaden. Band 4. Heft 1 (1875), pp. 1–12, pls 91–95; Heft 5–6 (1876), pp. 45–72, pls 111–120. [Publication dates, etc., for the *Iconographie* follow Bank, 1989].
- KOBELT W 1879 *Iconographie der Land- & Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten*. C.W. Kreidel's Verlag, Wiesbaden. Band 7. Heft 1–3, pp. 1–24, pls 179–193.
- KOBELT W 1881 *Catalog der im europäischen Faunengebiet lebenden Binnenconchylien*. 2<sup>nd</sup> ed. Cassel.
- KOBELT W 1882 *Iconographie der Land- & Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten*. C.W. Kreidel's Verlag, Wiesbaden. Neue Folge, Band 1. Heft 1–2, pp. 1–32, pls 1–10.
- KOBELT W 1884 Diagnosen neuer Arten. *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft* 16(1–2) 26–28.
- KOBELT W 1887–1888 *Iconographie der Land- & Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten*. C.W. Kreidel's Verlag, Wiesbaden. Neue Folge, Band 3. Heft 1–2 (1887), pp. 1–12, pls 61–70; Heft 3–4 (1887), pp. 13–36, pls 71–80; Heft 5–6 (1888), pp. 37–60, pls 81–90.
- KOBELT W 1892 [Obituary notice of J.-R. Bourguignat]. *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft* 24: 207.
- KOBELT W 1898 *Iconographie der Land- & Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten*. C.W. Kreidel's Verlag, Wiesbaden. Neue Folge, Band 8. Heft 3–4, pp. 41–72, pls 221–230.
- KOBELT W 1901 *Iconographie der Land- & Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten*. C.W. Kreidel's Verlag, Wiesbaden. Neue Folge, Band 9. Heft 3–4, pp. 25–56, pls 251–260.
- KOBELT W 1903–1904 *Iconographie der Land- & Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten*. C.W. Kreidel's Verlag, Wiesbaden. Neue Folge, Band 10. Heft 3–4 (1903), pp. 33–48, pls 281–290; Heft 5–6 (1904), pp. 49–77, pls 291–300.
- KOBELT W 1909 Diagnose einer neuen *Archelix*. *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft* 41(3): 134–135.
- KOKSHOORN B 2008 *Resolving riddles and presenting new puzzles in Chondrinidae phylogenetics*. Thesis, Leiden University. 188 pp.
- KOKSHOORN B, ERKELENS I, SCHOOR M VAN & GITTEBERGER E 2009 Extreme speciation on landlocked islands; Island-hopping *Chondrina* species. Poster, presented at the “Evolutionary Islands 150 years after Darwin. Evolution and turnover in isolated ecosystems” symposium, February 11–13, National Museum of Natural History (Naturalis), Leiden, The Netherlands. Downloaded 23 Aug. 2016 from: [http://www.baskokshoorn.nl/files/pdf/Kokshoorn\\_etal\\_2009-DarwinSymposium.pdf](http://www.baskokshoorn.nl/files/pdf/Kokshoorn_etal_2009-DarwinSymposium.pdf)
- KOKSHOORN B & GITTEBERGER E 2010 Chondrinidae taxonomy revisited: new synonymies, new taxa and a checklist of species and subspecies (Mollusca: Gastropoda: Pulmonata). *Zootaxa* 2539: 1–62.
- KRIJGSMAN W, HILGEN FJ, RAFFI I, SIERRO FJ & WILSON DS 1999 Chronology, causes and progression of the Messinian salinity crisis. *Nature* 400: 652–655.
- LETOURNEUX A & BOURGUIGNAT J-R 1887 *Prodrome de la Malacologie terrestre et fluviatile de la Tunisie*. Imprimerie Nationale, Paris (published as part of series entitled: Exploration scientifique de la Tunisie). 166 pp.
- LIMONDIN-LOZOUET N, HADDOUMI H, LEFÈVRE D, GHAMIZI M, ANOURAGHE H & SALEL T 2013. Holocene molluscan succession from NE Morocco: palaeoenvironmental reconstruction and biogeographical implications. *Quaternary International* 302: 61–76.
- LIND H 1973 The functional significance of the spermatophore and the fate of spermatozoa in the genital tract of *Helix pomatia* (Gastropoda: Stylommatophora). *Journal of Zoology*, London 169: 39–64.
- LLABADOR F 1935 *Les Mollusques testacés marins, fluviatiles et terrestres de l'ouest Algérien ...* Thèse pour le Doctorat en pharmacie. Imprimerie ‘La Typo-Litho’ et Jules Carbonel Reunies, Alger. 180 pp. n.v.
- LLABADOR F 1936 Notice sur la faunule malacologique du Massif des M'Sirdas au sud-ouest de Nemours. *Bulletin de la Société d'Histoire naturelle de l'Afrique du Nord* 36: 200–203.
- LLABADOR F 1952 Contribution à l'étude de la faune malacologique terrestre et fluviatile du Rif oriental. *Journal de Conchyliologie* 92(3): 93–142, pl. 5.
- LOCARD A 1899 Conchyliologie Portugaise. Coquilles terrestres, des eaux douces et saumâtres. *Archives du Muséum d'Histoire Naturelle de Lyon* 7: i-vi, 1–303.
- LOWE RT 1861 A list of the shells observed or collected at Mogador and in its immediate environs during a few days' visit to the place in April 1859; with notes and observations. *Journal of the Proceedings of the Linnean Society. Zoology* 5: 169–204.
- LUBELL D 2004 Prehistoric edible land snails in the circum-Mediterranean: the archaeological evidence. In: Brugall J-P & Dese J, Petits animaux et sociétés humaines du complément alimentaire aux ressources utilitaires. XXIV<sup>e</sup> *Rencontres Internationales d'Archéologie et d'Histoire de Antibes*. Editions ADDCA, Antibes. pp. 77–98.
- LUBELL D, HASSAN FA, GAUTIER A & BALLAIS J-L 1976 The Capsian escargotières. *Science*, New York 191: 910–920.
- MABILLE J 1884 Matériaux pour une faune malacologique des Iles Canaries. *Nouvelles Archives du*

- Muséum d'Histoire naturelle*, Paris, (2<sup>nd</sup> ser.) **6**: 201–284, pls 15–18.
- MABILLE J 1897 Notitiæ malacologicæ. *Bulletin de la Société Philomathique de Paris* (8<sup>th</sup> ser.) **9**(2): 78–102.
- MADEC L BELLIDO A & GUILLER A 2003 Shell shape of the land snail *Cornu aspersum* in North Africa: unexpected evidence of a phylogeographical splitting. *Heredity* **91**: 224–231.
- MADEC L & GUILLER A 1994 Geographic variation of distal genitalia in the landsnail *Helix aspersa* (Mollusca: Gastropoda). *Journal of Zoology* (London) **33**: 215–231.
- MARÈS P 1857 [Observations de météorologie et d'histoire naturelle faites dans le sud de la province d'Oran]. In: Séance du 6 juillet 1857, by Guérin-Méneville, II. Sociétés Savantes. Académie des Sciences de Paris. *Revue et Magasin de Zoologie pure et appliquée* (2<sup>nd</sup> ser.) **9**: 329–332.
- MARTENS E VON 1875 Bemerkungen über marokkanische Landschnecken. *Jahrbuch der deutschen Malakozoologischen Gesellschaft* **2**: 97–102.
- MARTENS E VON 1900 Ueber einige Landschnecken aus dem südwestl. Marokko. *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft* **32**: 121–123.
- MATOS, RM ALBUQUERQUE DE 1989a Polimorfismo de helicídeo *Otala lactea* (Müller 1774) em relação à sua genética. Posição sistemática desta espécie e afins. *Publicações Ocasionais da Sociedade Portuguesa de Malacologia*, Lisboa **13**: 1–12, pls 1, 2. n.v.
- MATOS, RM ALBUQUERQUE DE 1989b A note on *Otala punctata* and *Otala lactea* (also mention on *Otala apalolena*). *Conchologists' Newsletter* **109**: 187–189.
- MATOS, RM ALBUQUERQUE DE 1992 Novos resultados na genética do polimorfismo da concha de *Otala lactea*. *Cuadernos de Investigaciones Biológicas* (IX Congreso Nacional de Malacologia, Bilbao, Dezembro 1992) **17**: 66. n.v.
- MATOS, RM ALBUQUERQUE DE 2014 *Atlas dos Caracóis terrestres e de águas doces e salobras Portugal continental*. Published by the author, Portugal. iv +258 pp.
- MICHAUD A-L-G 1833 Catalogue des testacés vivants envoyés d'Alger, par M. Rozet (capitaine au corps royal d'état-major), au cabinet d'histoire naturelle des Strasbourg;— notice présentée à la Société d'histoire naturelle de la même ville. *Mémoires de la Société d'histoire naturelle de Strasbourg* **1**. Offprint, 22 pp.
- MOQUIN-TANDON A 1855–1856 *Histoire naturelle des Mollusques terrestres et fluviatiles de France ...* J.-B. Baillièrre, Paris. 2 vols +Atlas, published in 6 livraisons.
- MORELET A 1845 *Description des mollusques terrestres et fluviatiles du Portugal*. Baillièrre, Paris. 115 pp.
- MORELET A 1851 Appendice a la Conchyliologie de l'Algérie. *Journal de Conchyliologie* **2**: 351–361, pl. 9.
- MORELET A 1853 Catalogue Mollusques terrestres et fluviatiles de l'Algérie. *Journal de Conchyliologie* **4**: 280–305.
- MORELET A 1854 Notice sur quelques Hélices recueillis dans le midi de l'Espagne et au Maroc, par M. Tarnier. *Revue et Magasin de Zoologie pure et appliquée* (2<sup>nd</sup> ser.) **6**: 614–623.
- MORELET A 1860 *Notice sur l'histoire naturelle des Açores suivie d'une description des mollusques terrestres de cet archipel*. Baillièrre, Paris. Pp. 1–216, pls 1–5.
- MORELET A 1880 La Faune malacologique du Maroc en 1880. *Journal de Conchyliologie* **28**: 5–83, pls 1–3.
- MORELET A & DROUËT H 1857 Conchologiae Azoricæ prodromus novarum specierum diagnoses sistens. *Journal de Conchyliologie* (2) **2**: 148–153.
- MOUSSON A 1872 Revision de la faune malacologique des îles Canaries. *Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesamten Naturwissenschaften* **25**: 1–176, pls 1–6.
- MOUSSON A 1874 Bemerkungen über die von Hrn. Dr. von Fritsch und Dr. Rein aus West-Marocco 1872 zurückgebrachten Land- und Süßwasser-Mollusken. *Jahrbuch der deutschen Malakozoologischen Gesellschaft* **1**: 1–16, 81–107, pls 1, 4, 5.
- MÜLLER OF 1774 *Vermium terrestrium et fluviatilium, seu animalium infusoriorum, Helminthicorum et Testaceorum, non marinorum succincta historia*. 2. Havniae & Lipsiae. pp. xxxvi +214 [10].
- NEIBER MT & HAUSDORF B 2015 Molecular phylogeny reveals the polyphyly of the snail genus *Cepaea* (Gastropoda: Helicidae). *Molecular Phylogenetics and Evolution* **93**: 143–149.
- NEIBER MT, VEGA-LUZ R, VEGA-LUZ R & KOENEMANN S 2011 *Hemicycla (Adiverticula) diegoi* (Gastropoda: Pulmonata: Helicidae), a new species from Tenerife, Canary Islands, with a phylogenetic analysis of conchologically similar species in the genus *Hemicycla* Swainson, 1840. *Zootaxa* **2757**: 29–46.
- NEUBERT E 1998 Annotated checklist of the terrestrial and freshwater molluscs of the Arabian Peninsula with descriptions of new species. *Fauna of Arabia* **17**: 333–461.
- NEUBERT E & BANK RA 2006 Notes on the species of *Caucasotachea* C. Boettger 1909 and *Lindholmia* P. Hesse 1919, with annotations to the Helicidae (Gastropoda: Stylommatophora: Helicidae). *Archiv für Molluskenkunde* **135**(1): 101–132.
- PALADILHE A 1875 Étude sur les coquilles terrestres et fluviatiles rapportées du Maroc par le Dr. Bleicher. *Revue et Magasin de Zoologie, pure et appliquée* (3<sup>rd</sup> sér.) **3**: 75–101, pl. 9.
- PALLARY P 1896 Description de quelques nouvelles espèces d'hélices du département d'Oran. *Comptes rendus de l'Association française pour l'Avancement de Science* [Carthage] **25**(1): 196, **25**(2): 478–484. [Publication dates, etc., for Pallary's publications follow Bank & Menkhorst, 2009].
- PALLARY P 1898 Première contribution à l'étude de la faune malacologique de nord-ouest de l'Afrique. *Comptes rendus de l'Association française pour l'Avancement de Science* [Saint-Etienne] **27**(2) [1897]: 556–563, pl. 5.
- PALLARY P 1899a Deuxième contribution à l'étude de la faune malacologique du Nord-Ouest de l'Afrique. Supplément à "La faune malacologique du Maroc" de A. Morelet. *Journal de Conchyliologie* **46**(2) [1898]: 49–170, pls 5–9.
- PALLARY P 1899b Sur les faunes fossiles des mollusques terrestres et d'eau douce d'Algérie. *Comptes*

- rendus de l'Association française pour l'Avancement de Science **12**: 59–62.
- PALLARY P 1899c Sur les faunes fossiles des mollusques terrestres et d'eau douce d'Algérie. *Bulletin de la Société Géologique de France* (3) **27**(4): 374–376.
- PALLARY P 1899d Sur des Hélices bidentées de l'oligocène algérien. *Bulletin du Muséum national d'Histoire naturelle*, Paris **5**(6): 314–317.
- PALLARY P 1900 Troisième contribution à l'étude de la faune malacologique de nord-ouest de l'Afrique. *Comptes rendus de l'Association française pour l'Avancement de Science* [Paris] **29**(2): 731–735, pl. 11.
- PALLARY P 1901 Sur les mollusques fossiles terrestres, fluviatiles et saumâtres de l'Algérie. *Mémoires de la Société Géologique de France* **9**(1): 213 pp.+1 p. Errata, 4 pls. Offprint as *Mémoire* No. 22 with same pagination, C. Naud, Paris. [Also reprinted in 1970 by Swets & Zeitlinger, Amsterdam].
- PALLARY P 1904 Quatrième contribution à l'étude de la faune malacologique du Nord-Ouest de l'Afrique (Deuxième supplément à la "Faune malacologique du Maroc" d'Arthur Morelet). *Journal de Conchyliologie* **52**(1): 5–58, pls 1–3.
- PALLARY P 1914 Bemerkungen über einige Arten der Gattung *Archelix*. *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft* **46**(1): 8–23, pls 1, 2.
- PALLARY P 1915 Description de quelques mollusques nouveaux du Grand Atlas. *Bulletin du Muséum national d'Histoire naturelle*, Paris **21**(1): 21–28.
- PALLARY P 1917 Hélicidées nouvelles du Maroc. *Journal de Conchyliologie* **63**(2): 126–141, pl. 5.
- PALLARY P 1918 Diagnoses d'une cinquantaine de mollusques terrestres nouveaux du Nord de l'Afrique. *Bulletin de la Société d'Histoire naturelle de l'Afrique du Nord* **9**(7): 137–152.
- PALLARY P 1919 Hélicidées nouvelles du Maroc. 2<sup>e</sup> Partie. *Journal de Conchyliologie* **64**(2) [1918]: 51–69, pls 2–3.
- PALLARY P 1920a Descriptions d'une nouvelle cinquantaine de mollusques terrestres nouveaux du Nord-Ouest de l'Afrique. *Bulletin de la Société d'Histoire naturelle de l'Afrique du Nord* **11**(2): 18–34.
- PALLARY P 1920b Récoltes malacologiques du capitaine Paul Martel dans la partie septentrionale du Maroc. *Journal de Conchyliologie* **65**(1): 1–39, pls 1–3; **65**(2): 131–160, pls 4–5.
- PALLARY P 1921 Quelques rectifications de nomenclature concernant des mollusques de la faune paléarctique. *Proceedings of the Malacological Society of London* **14**(4): 141–147.
- PALLARY P 1922a Faune malacologique du Grand Atlas. *Journal de Conchyliologie* **66**(2) [1921]: 89–154, pls 3–5; **66**(3) [1921]: 185–217.
- PALLARY P 1922c Notes de zoogéographie-nord-Africaine. *Bulletin de la Société Géologique de France* (4) **21**: 247–252.
- PALLARY P 1923a Vingt mollusques terrestres nouveaux du Maroc. *Bulletin de la Société d'Histoire naturelle de l'Afrique du Nord* **14**(3): 112–118.
- PALLARY P 1923b Les origines de la faune marocaine. *Bulletin de la Société d'Histoire naturelle de l'Afrique du Nord* **14** (7): 275–290.
- PALLARY P 1924 Note sur quelques mollusques d'un dépôt Pléistocène de Colomb-Béchar. *Bulletin de la Société d'Histoire naturelle de l'Afrique du Nord* **15**(3): 111–113.
- PALLARY P 1926 Compléments à la faune malacologique de la Berbérie. *Journal de Conchyliologie* **70**(1): 1–50, pls 1–8.
- PALLARY P 1928 Notice sur seize mollusques nouveaux du Maroc découverts en 1926–1927. *Journal de Conchyliologie* **72**(1): 1–24, pls 1–4.
- PALLARY P 1929a Étude comparative de quelques faunules malacologiques du Maroc septentrional. *Journal de Conchyliologie* **73**(1): 47–55.
- PALLARY P 1929b Histoire de l'Hélice hiéroglyphique de Michaud. *Bulletin de la Société d'Histoire naturelle de l'Afrique du Nord* **20** (6): 122–130, pl. 6.
- PALLARY P 1933 Diagnoses de quinze mollusques continentaux du Maroc. *Bulletin de la Société d'Histoire naturelle de l'Afrique du Nord* **24**(7): 243–248.
- PALLARY P 1935a Resultats zoologiques d'une prospection dans les S. O. du Maroc. *Comptes rendus de l'Association française pour l'Avancement de Science* **68**(2): 351–355.
- PALLARY P 1936 Deuxième complément à la faune malacologique de la Berbérie. *Journal de Conchyliologie* **80**(1): 5–65, pls 1–4.
- PALLARY P 1939a Les milieux zoologiques au Maroc et en Afrique du Nord: le peuplement malacologique. *Journal de Conchyliologie* **83**(1): 61–69.
- PALLARY P 1939b Classification générique des mollusques terrestres et d'eau douce de la Berbérie. *Journal de Conchyliologie* **83**(2): 104–110.
- PAULUCCI M 1882 Note malacologique sulla fauna terrestre e fluviale dell'Isola di Sardegna. *Bullettino della Società Malacologica Italiana* **8**, offprint, vii +247 pp., 9 pls.
- PÉCHAUD J 1883 *Excursions malacologiques dans le Nord de l'Afrique de la Calle a Alger, d'Alger a Tanger*. No. 1. J. Tremblay, Paris. pp. 112. [Only the 1<sup>st</sup> fascicule of four that were proposed was published, owing to death of the "author". However, Dance, 1970a: 75–76 established that the entire text was apparently written by J.-R. Bourguignat not Péchaud].
- PFEFFER G 1930 Zur Kenntnis tertiärer Landschnecken. *Geologische und Paläontologische Abhandlungen*, Jena (N.F.) **17**(3): 3–230 (153–380).
- PFEIFFER L 1853 *Monographiae heliceorum viventium. Sistens descriptiones systematicas et criticas omnium huius familiae generum et specierum hodie cognitarum. 3 & Supplementum*. F.A. Brockhaus, Lipsiae. viii +711 pp. (see Kadolsky, 2012: 84 for publication date).
- PILSBRY HA 1892 *Manual of Conchology, structural and systematic, with illustrations of the species*. By George W. Tryon, Jr. Second series: Pulmonata. vol. 8. Helicidae:—vol. VI. Conchological Section, Academy of Natural Sciences, Philadelphia. 314 pp., 58 pls.
- PILSBRY HA 1895 *Manual of Conchology, structural and systematic, with illustrations of the species*. By George W. Tryon, Jr. Second series: Pulmonata. vol. 9. (Helicidae, vol. 7), part 36, pp. 161–366, pls 41–71, frontispiece. Guide to the study of Helices. Conchological Section,

- Academy of Natural Sciences of Philadelphia, Philadelphia.
- PILSBRY HA 1939 *Land Mollusca of North America (north of Mexico)*. Academy of Natural Sciences of Philadelphia, Monographs No. 3. Philadelphia. 1(1), xvii +573+ix pp.
- POTIEZ V-L-V & Michaud A-L-G 1838 *Galerie des mollusques, ou catalogue méthodique, descriptif et raisonné des mollusques et coquilles du Muséum de Douai*. Baillière, Paris, Londres. Tome premier, pp. i-xxxvi [= 1-36], 1-560,[1-4]; Atlas, pp. 1-56, pls i-xxxvii [= 1-37].
- PUENTE MARTINEZ AI 1994 *Estudio taxonómico y biogeográfico de la Superfamilia Helicoidea Rafinesque, 1815 (Gastropoda: Pulmonata: Stylommatophora) de la Península Ibérica e Islas Baleares*. Unpublished Doctoral Thesis, Universidad del País Vasco, Facultad de Ciencias, Departamento de Biología Animal y Genética.
- PUIZINA J, FREDOTOVIĆ Ž, ŠAMARIĆ I, ŠUŠNJARA T, KEKEZ L, CUKROV D & PLESLIĆ G 2013 Phylogeography of the land snail *Eobania vermiculata* (O.F. Müller, 1774) (Gastropoda: Pulmonata) along the Croatian coast and islands. *Journal of Entomology and Zoology Studies* 1(4): 23-31.
- RAZKIN O, GÓMEZ-MOLINER BJ, PRIETO CE, MARTÍNEZ-ORTÍ A, ARRÉBOLA JR, MUÑOZ B, CHUECA LJ & MADEIRA MJ 2015 Molecular phylogeny of the western Palearctic Helicoidea (Gastropoda, Stylommatophora). *Molecular Phylogenetics and Evolution* 83: 99-117.
- RICHARDSON L 1980 Helicidae: Catalog of species. *Tryonia* 3: iii +697 pp.
- RIGACCI G & RIGACCI E 1874 *Catalogo delle conchiglie componenti la collezione Rigacci*. Salviucci, Roma. n.v.
- RÖDING PF 1798 *Museum Boltenianum*. Hamburg. (1<sup>st</sup> ed., issued by Röding, with Latin introduction by Abbe Lichtenstein; reprint issued by Sherborn CD & Sykes ER, 1906, British Museum (Natural History), published by FW Reader, London). n.v.
- ROLL U, DAYAN T, SIMBERLOFF D & MIENES HK 2009 Non-indigenous land and freshwater gastropods in Israel. *Biological Invasions* 11: 1963-1972.
- ROMANI A 1917 Alguns moluscos de la Comarca de Capellades. *Butlletí de la Institució catalana d'història natural*, Barcelona 4: 45-48.
- ROSSMÄSSLER EA 1837 *Iconographie der Land- und Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten*. Arnoldische Buchhandlung, Dresden & Leipzig. Band 1, Heft 5 & 6, 70 pp., pls 21-30. [Publication dates, etc., for the *Iconographie* follow Bank, 1989].
- ROSSMÄSSLER EA 1838-1839 *Iconographie der Land- und Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten*. Arnoldische Buchhandlung, Dresden & Leipzig. Band 2, Heft 1-2 [7-8] (1838) 44 pp., pls 31-40; Heft 3-4 [9-10] (1839) iv +46 pp., pls 41-50.
- ROSSMÄSSLER EA 1854 *Iconographie der Land- und Süßwasser-Mollusken Europa's, mit vorzüglicher Berücksichtigung kritischer und noch nicht abgebildeten Arten*. Hermann Constenoble, Leipzig. Band 3, Heft 1-2 [13-14], viii +139 pp., pls 61-70.
- ROUR E, CHAHLAOUI A & VAN GOETHEM J 2002 Etat actuel des connaissances de la malacofaune terrestre du Maroc. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie* 72: 189-198.
- RUIZ A, CÁRCABA A, PORRAS AI & ARRÉBOLA JR 2006 *Guía y manual de identificación. Caracoles terrestres de Andalucía*. Consejería de Medio Ambiente, Junta de Andalucía & Fundación Gypaetus, Sevilla. 303 pp.
- SAINT-SIMON A DE 1848 *Miscellanées malacologiques. Première décade*. Aug. de Labouisse-Rochefort, Toulouse. 54 pp.
- SAY T 1822 Description of univalve terrestrial and fluviatile shells of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 2(2): 370-381.
- SAY T 1834 *American conchology; or, Description of the shells of North America*. 6. New Harmony, Indiana. n.v.
- SCHILEYKO AA 2006 Treatise on recent terrestrial pulmonate molluscs. Part 13. Helicidae, Pleurodontidae, Polygyridae, Ammonitellidae, Oreohelicidae, Thysanophoridae. *Ruthenica*, Suppl., Moscow 2: 1764-1906.
- SCHMIDT A 1855 Der Geschlechtsapparat der Stylommatophoren in taxonomischer hinsicht gewürdigt. *Abhandlungen des Naturwissenschaftlichen Vereins für Sachsen und Thüringen in Halle*, Berlin 1: 1-52, pls 1-14. n.v.
- SCHUMACHER CF 1817 *Essai d'un nouveau système des habitations des vers testacés*. Schultz, Copenhagen. [1-3] 1-287 pp., 22 pls.
- SCHÜTT H 2005 *Turkish Land Snails 1758-2005*. 4<sup>th</sup> ed. Verlag Natur & Wissenschaft, Solingen. 559 pp.
- SEDDON MB 2008 The landsnails of Madeira. An illustrated compendium of the landsnails and slugs of the Madeiran archipelago. *Studies in Biodiversity and Systematics of Terrestrial Organisms from the National Museum of Wales, Biotir Reports* 2: 1-204.
- SERVAIN G 1880 *Étude sur les Mollusques d'Espagne et de Portugal*. D. Bardin, Saint-Germain (Paris). 172 pp.
- SHERBORN CD 1925 *Index animalium sive index nominum quae ab a.d. MDCCLVIII generibus et speciebus animalium imposita sunt*. Sectio Secunda, Part VI. British Museum (Natural History), London. Pp: 1197-1452.
- SYSOEV A & SCHILEYKO A 2009 *Land snails and slugs of Russia and adjacent countries*. Pensoft, Sofia & Moscow. 312 pp. & 142 pls.
- TAYLOR JW 1910 *Monograph of the Land & Fresh-water Mollusca of the British Isles*. Taylor Bros, Leeds. Part XVII, pp. 225-304, pls 16, 17, 18, 20, 21, 22.
- TERVER A-P 1839 *Catalogue des mollusques terrestres et fluviatiles, observés dans les possessions françaises au nord de l'Afrique, publié par M. Terver...* J.-B. Baillière, Paris & Savy, Lyon. 40 pp., 4 pls.
- TRECHMANN CT 1938 Quaternary conditions in Malta. *Geological Magazine* (4<sup>th</sup> ser.) 75: 1-26, 2 pls.
- TORRES ALBA JS, VÁZQUEZ TORO FE, MENESES SORES V, HOLYOAK DT & HOLYOAK GA 2016 Status and

- redescription of *Rossmassleria scherzeri*, an overlooked land snail endemic on Gibraltar, with notes on *R. olcese* and other Moroccan species of *Rossmassleria* (Gastropoda: Helicidae). *Iberus* **34**(1): 1–17.
- TRYON GW JR 1888 *Manual of Conchology, structural and systematic, with illustrations of the species. Second series: Pulmonata*. vol. 4. Helicidæ:– vol. II. Published by the author, Philadelphia. 296 pp., 69 pls.
- VAN OSSELAER C & TURSCH B 2000 Variability of the genital system of *Helix pomatia* L., 1758 and *H. lucorum* L., 1758 (Gastropoda: Stylommatophora). *Journal of Molluscan Studies* **66**(4): 499–515.
- WAGNER M 1841 *Reisen in der Regentschaft Algier in den Jahren 1836, 1837 und 1838 nebst einem naturhistorischen anhang und einem Kupperatlas*. Leipzig. 3 vols & Atlas, 17 pls. n.v.
- WALTHER F, NEIBER MT & HAUSDORF B 2016 Species complex or complex species? Integrative taxonomy of the land snail genus *Rossmassleria* (Gastropoda, Helicidae) from Morocco and Gibraltar. *Systematics and Biodiversity* (2016) 1–23.
- WEBB PB & BERTHELOT S 1839 *Histoire Naturelle des Iles Canaries*. T. 2, Partie 2 Mollusques .... Béthune, Paris. n.v.
- WENZ W 1923 *Fossilium Catalogus, I: Animalia* (ed. C. Diener), Pars 18, *Gastropoda extramarina tertiaria* II. W. Junk, Berlin.
- WESTERLUND CA 1889 *Fauna der in der paläarktischen Region (...) lebenden Binnenconchylien*. Part 2 Genus *Helix*. R. Friedländer & Sohn, Berlin. 473+31 pp.
- WESTERLUND CA 1892 *Spicilegium Malacologicum. Neue Binnen-Conchylien in der paläarktischen Region*. *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft* **24**(11/12): 185–201.
- WOLLASTON TV 1878 *Testacea Atlantica, or the land and freshwater shells of the Azores, Madeiras, Salvages, Canaries, Cape Verdes, and Saint Helena*. L. Reeve & Co., London: xi +588 pp.

Appendix, available online from website of Conchological Society of Great Britain and Ireland.