

# EVOLUTION AND TAXONOMY OF THE POPULATIONS OF EREMINA (GASTROPODA, PULMONATA: HELICIDAE) IN MOROCCO

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**Abstract** The taxonomy and nomenclature of Moroccan *Eremina* (Helicidae) is revised, mainly on the basis of extensive new collections made in 1986 and 2016. Molecular data from the recent collections supplemented interpretations based on study of shells and genital anatomy. Four Moroccan species are recognised here: the localised *E. dillwyniana* s.s. (S. of El Ouatia [= Tan-Tan Plâge] to Tarfaya) and the widespread *E. duroi* (near Sidi Ifni southwards to N. Mauritania) have rounded shells with low spires and live in a relatively humid zone prone to sea mists just inland of the Atlantic coast. *E. vermiculosa* has a subglobular shell and occurs further inland around the range of *E. dillwyniana* and the northern part of that of *E. duroi* (from near Guelmim to region SW. of Tan-Tan). *E. inexpectata* with keeled shells has a small range in rocky sandstone hills from the Oued Draa southwards to near Tan-Tan, separating two groups of populations of *E. vermiculosa*. Populations comprised mainly of intergrades (presumed hybrids) occur in a narrow zone where the ranges of *E. duroi* and *E. vermiculosa* meet. Intergrades of *E. inexpectata* with *E. vermiculosa* occur within populations of the former species. Subfossil (Quaternary) shells show that the ranges of both *E. duroi* and *E. vermiculosa* formerly extended further inland, into desert regions now too arid and sparsely vegetated to support either taxon; fossils also demonstrate past occurrence of *E. vermiculosa* at a site that now has living *E. inexpectata*. Subfossil shells of the apparent hybrid of *E. duroi* with *E. vermiculosa* suggest that hybridization occurred when they met in the past, far outside the modern range of either species. Treatment of all four forms at species rank is based on the very narrow modern hybrid zones between *E. duroi* and *E. vermiculosa* and evidence that their hybridization elsewhere during the Quaternary did not lead to widespread introgression. Nevertheless, lack of sympatry, evidence of repeated hybridization where forms meet, the rather small differences in habitats, lack of differences in genital morphology and sometimes unresolved DNA sequences may imply that the speciation process in these taxa is incomplete. Possible explanations for the evolution of different shell shapes are discussed: the clearest environmental correlation of shell type being with high humidity near the coast (low-spired shells) and much lower humidity inland (subglobular shells with larger apertures). The narrow zones of hybridization apparently imply that intermediate shell types are at a disadvantage.

**Key words** *Eremina*, Helicidae, Morocco, Sahara, shell shape, genital anatomy, DNA, phylogeny, taxonomy, species limits, hybridization, distribution, habitats

## INTRODUCTION

The genus *Eremina* (Helicidae) comprises a few species of landsnails living mainly in desert or semi-desert habitats of north Africa and the Near East. They occur along the Atlantic coast of NW. Africa from SW. Morocco to Mauritania (Germain, 1908), and apparently in the Cape Verde Islands (Groh, 2005, 2012). The genus is unknown in E. Morocco and Algeria, but reappears beyond a large range gap in S. Tunisia, Libya and Egypt (Pallary, 1939; Biggs, 1959), extending southwards through Arabia to Somalia (Verdcourt, 1960; Neubert, 1998: 428) and northwards into the deserts of Israel (Heller, 2009).

The present study deals mainly with the Moroccan populations, including those of Western Sahara (Saquiati Al-Hamra and Oued Ad-Deheb), which became part of Morocco in

1976, although the territory is also claimed by the 'Saharoui Arab Democratic Republic' (since 1991 the United Nations has scheduled a referendum to decide on the future of the area).

These western *Eremina* have attracted attention because of their conspicuous shells and often abundant populations in regions that have few or no other living land snails. Over almost all of this range none of the coexisting snails is as large, and only *Theba* is equally widespread. Shells from the Atlantic coastal regions fringing the Sahara reached Europe and were given new names from the mid-nineteenth century onwards (Pfeiffer, 1851; Hidalgo, 1886). Anatomical and other data were presented by Boettger (1915), Hesse (in Pallary, 1936: 17–18) and Steenberg (1949). Cossignani (2014: 83–86) provided good illustrations of the varied shell forms. Nevertheless, there has been no modern taxonomic revision based on adequate shell and anatomical material.

Molecular data on Moroccan *Eremina* are also few (in Neiber & Hausdorf, 2015: table S1), but a detailed study of *E. desertorum* in Egypt has recently been published (Ali *et al.*, 2016).

Different authors have adopted widely varying approaches to classification within *Eremina*: some named numerous taxa as species (e.g. Bourguignat, 1882) or recognised numerous varieties based on shell characters (e.g. Germain, 1908, 1910; Llabador, 1969); for Morocco, Cossignani (2014) recognised four species and several additional subspecies. However, Boettger (1915) demonstrated clearly that recognition of varieties in Moroccan material based on shell size, form and colouration within coexisting populations serves no useful purpose, and almost all modern workers have abandoned the practice. Biggs (1959) showed that *Eremina* previously recognised as species in Egypt were often connected by intermediate and apparently hybrid populations, suggesting that fewer species should probably be recognised with an “*Eremina* complex” comprising a “catenation” (chain) of intergrading forms. Ali *et al.* (2016) confirmed this for the two widespread Egyptian taxa through combined molecular and morphological studies. Verdcourt (1960) synonymised several of Bourguignat’s finely split “species” from NE. Africa.

Here we present a revision of Moroccan *Eremina*, based on large general collections made in 1986, supplemented by more selective collecting in 2016 to address areas of particular interest such as apparent zones of hybridization. A better interpretation of species limits among the Moroccan populations is sought through a combination of morphological and molecular analyses, paying special attention to zones of hybridization. The latest checklist of Moroccan land snails (Rour, Chahlaoui & van Goethem, 2002: 194) uses incorrect names for some *Eremina* and other literature uses species-group names which appear to be nomenclatorally incorrect, so full synonymies are given and discussed here. Notes are also recorded on evidence of more extensive past ranges and past hybridization based on fossil assemblages. Interpretation of patterns of variation in shell form and their ecological correlates in the genus appears to be complicated (Ali *et al.*, 2016). Hence we give details of the rather limited information currently available on the habitat preferences, general ecology, annual cycle, behaviour and predators of living populations, since

fuller information on these apparently needs to be obtained to provide adequate explanations of the morphological differences.

## METHODS

During the summer of 1986 extensive fieldwork to collect all landsnails encountered was carried out in Atlantic coastal regions of Morocco southwards to Ad-Dakhla; 75 samples of *Eremina* were collected covering much of the Moroccan range of the genus. 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. Habitats were described in the field at all sites; on the infrequent occasions when shells that may have drifted (e.g. from beside wadi beds) were collected this was always noted. An attempt was made to collect a good representative sample of shells at each locality, although the oldest and most damaged shells were discarded once large quantities of better material were accumulated by the three collectors involved. Living specimens were collected where they were found, although these were lacking at many sites and often scarce and elusive where present. They were killed the same evening using boiling water. 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 the Appendix.

Supplementary fieldwork was carried out during March 2016 at 30 sites in regions of SW. Morocco between Tiznit and Al-’Ayun (see Appendix). This visit concentrated on collecting *Eremina* from localities where ranges of different taxa meet, especially where intergrades (apparent hybrids) were detected in the material from 1986 or noted as the new fieldwork progressed. 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. In anticipation of the need to present unbiased counts of shell types from mixed populations, care was taken to collect shells of *Eremina* at random, discarding only those that were incomplete, badly damaged or immature. 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, with tails of representative individual drowned specimens being removed and placed in absolute ethanol for DNA studies.

Seven additional sites visited in October 2016 (see Appendix) provided more data on northern populations of *E. duroi* localities and habitats, with a few representative specimens being retained.

To map species distributions in a meaningful manner, 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 colouration (with little or no bleaching) and much of the periostracum. Subfossil shells were those recorded as such in the fieldnotes, 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 the body of a live snail) to shells from the ground surface that might sometimes have been unearthed from a Holocene deposit.

Only the main characters that vary between the taxa are described (see Key below) and illustrated (Fig. 1). Adult shells were easily 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. Shell whorls were counted following the method illustrated by Kerney & Cameron (1979: 13).

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

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”. Many of the varietal names had little or no description associated with them and early workers evidently regarded the varietal nomenclature of each species as independent from that of other related species. Hence, many of the most frequently used varietal epithets such as *major*, *minor*, *alta* and *depressa*, must nowadays be discounted as junior homonyms. Furthermore, using the current *ICZN Code* most such names would be disregarded as *nomina nuda* because there is no description.

Moroccan *Eremina* specimens used for DNA sequencing are listed in Table 1. Total genomic DNA was extracted from the foot using the DNeasy Tissue kit (Qiagen, Valencia, CA, U.S.A.). Three gene fragments were selected for multi-locus analyses: two mitochondrial markers [678 bp of the cytochrome c oxidase subunit I (*COI*) and around 431 bp of the 16S ribosomal RNA gene] and one nuclear marker [the complete *ITS2* region (864 bp)]. The general PCR cycling conditions used for DNA amplification were: (1) 1 min at 96°C, [30 s at 94°C, 30 s at 50°C, 1 min at 72°C] (repeated for 35 cycles) and 10 min at 72°C for *COI* and nuclear fragment, and (2) 20 s at 94°C, [20 s at 94°C, 30 s at 55°C, 30 s at 72°C] (repeated for 40 cycles) and 30 s at 72°C for 16S rRNA. The primers used are listed in Table 2. PCR products were purified and sequenced at Macrogen in Korea using an ABI3730XL sequencer. Genbank accession numbers are provided in Table 1.

Sequences were aligned with Mafft v.7 online version (Kato & Standley, 2013). We used the Q-INS-i algorithm for rRNA, which considers the secondary structure of RNA, and the Auto algorithm for *COI*. Default values were assigned to the remaining parameters. *COI* protein coding sequences were translated into amino acids using DnaSP v.5.10.1 (Librado & Rozas, 2009) to check for stop codons. Evolutionary models were estimated independently for each of the gene partitions using jModelTest v.2.1.1 (Darriba





**Figure 1** Shells of Moroccan *Eremina* species: A, *E. dillwyniana* s.s., Syntype, no locality, Ex. Collection of Hugh Cuming, NHMUK 20150074; B, ca 40km SW. along road from Tan-Tan Plage, NMW.Z 1993.051.06; *E. inexpectata*, C, ca 19km NE. along road from Tan-Tan, NMW.Z 1993.051.00014; D, *E. inexpectata*×*E. vermiculosa*, ca 8km NE. of Tan-Tan, NMW.Z 1993.051.02709; E, *E. duroi*, ca 256km NE. along track from Ad-Dakhla, NMW.Z 1993.051.02836; F, 10km S. of Daoura, NMW.Z 1993.051.07; G, *E. duroi*×*E. vermiculosa*, ca 48km SW. along road from Tan-Tan, NMW.Z 1993.051.02896; H, *E. vermiculosa*, ca 14km SW. along road from Goulimine, NMW.Z 1993.051.02675. See Appendix for additional details of localities.

*et al.*, 2012) applying the Bayesian information criterion (BIC) to select among models (Table 3). For phylogenetic reconstruction, both Bayesian inference (BI) and maximum likelihood (ML) methods were used on the combined data set partitioned by genes, through the CIPRES Science Gateway (Miller *et al.*, 2010), allowing

each one to evolve at different rates. For COI, the data set was divided into three partitions according to codon positions. Bayesian inference analyses were conducted with MrBayes v.3.2.2 (Ronquist *et al.*, 2012). Two independent runs were conducted for  $20 \times 10^6$  generations saving trees each 100 generations with a burn-in value

**Table 1** Site field numbers and GenBank accession numbers of specimens used for DNA sequencing.

Taxon	Site field number	GenBank accession number		
		COI	16S	ITS-2
<i>E. duroi</i>	M3	KY304081	KY197727	KY304094
<i>E. duroi</i>	M4	KY304082	KY197728	KY304095
<i>E. vermiculosa</i>	M7	KY304083	KY197729	KY304096
<i>E. vermiculosa</i>	M9	KY304084	KY197730	KY304097
<i>E. vermiculosa</i>	M10	KY304085	KY197731	KY304098
<i>E. vermiculosa</i>	M11	KY304086	KY197732	KY304099
<i>E. inexpectata</i>	M12	KY304087	KY197733	KY304100
<i>E. vermiculosa</i>	M13	KY304088	KY197734	KY304101
<i>E. vermiculosa</i>	M14	KY304089	KY197735	KY304102
<i>E. dillwyniana</i>	M17	KY304090	KY197736	KY304103
<i>E. duroi</i>	M18	KY304091	KY197737	KY304104
<i>E. duroi</i>	M19	KY304092	KY197738	KY304105
<i>E. duroi</i> × <i>E. vermiculosa</i>	M20	KY304093	KY197739	KY304106

**Table 2** List of primers used for DNA amplification and sequencing.

Gene	Primer	Sequence	Reference
COI	LCO1490 (5')	5' GGTCAACAAATCATAAAGATATTGG 3'	Folmer <i>et al.</i> (1994)
	HCO2198 (3')	5' TAAACTTCAGGGTGACCAAAAATCA 3'	Folmer <i>et al.</i> (1994)
16S rRNA	16sar (5')	5' CGCCTGTTTATCAAAAACAT 3'	Palumbi <i>et al.</i> (1991)
	16sbr (3')	5' CCGGTCTGAACTCAGATCACGT 3'	Palumbi <i>et al.</i> (1991)
ITS2	LSU-1 (5')	5' CTAGCTGCGAGAATTAATGTGA 3'	Wade <i>et al.</i> (2006)
	LSU-3 (3')	5' ACTTTCCTCACGGTACTTG 3'	Wade <i>et al.</i> (2006)

**Table 3** Evolutionary model selected for each partition analysed in *Eremina* under BIC criterion implemented in jModelTest2 (Darriba *et al.*, 2012).

	COI			16S rRNA	5.8S-ITS2-28S
	1 <sup>st</sup>	2 <sup>nd</sup>	3 <sup>rd</sup>		
Evolutionary model selected	TrNef	F81	HKY	HKY+G	JC

of 25%. Convergence between runs was assessed using Tracer v1.6 (Rambaut & Drummond, 2007). Maximum likelihood analyses were conducted using RAxML v.8.0.24 (Stamatakis, 2014) under the GTRGAMMA model, with 1000 nonparametric bootstrap replicates to assess node support. In general, we interpreted bootstrap values above 75% in the ML analyses as well supported and in the BI analyses a posterior probability value of 0.95 was taken as a threshold. *Iberus gualtieranus* and *Otala lactea* were used as outgroups. Uncorrected pairwise p-distances were calculated with PAUP v. 4.0b10.

Abbreviations: AB shell aperture breadth; AH aperture height; ANSP Academy of Natural

Sciences, Philadelphia, U.S.A.; B greatest shell breadth; BI Bayesian inference; BS bootstrap values; CGAH Private collection of G.A. and D.T. Holyoak; H greatest shell height; H&S Holyoak & Seddon Collection at NMW.Z; Iconogr. *Iconographie* (of Rossmässler, continued by Kobelt); juv juvenile (immature) snail; MHNG Muséum d'Histoire Naturelle, Ville de Genève, Switzerland; ML maximum likelihood; 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 National Museum Wales, Cardiff, U.K.; n.v. original not verified; PP posterior

probability; syn. synonym; t. tome; TL type locality.

The systematic treatment below covers all taxa and synonyms recorded for the western Maghreb (Morocco, Algeria, Tunisia). Full and detailed literature citations are provided only for Moroccan reports.

### MORPHOLOGY AND TAXONOMY

This section presents data on genital anatomy, shells and other morphological characters, and a key to shells intended to give brief morphological diagnoses of the species recognised. This is followed by a formal nomenclatural listing for the *Eremina* of the W. Maghreb in a revised classification with five species (four of them in Morocco). Subsequent sections present the Molecular Results, and discuss Distribution, habitats and ecology, and Evolution of shell form, leading to an analysis of hybridization and (biological) species limits among the nominal taxa involved. This arrangement simplifies discussion and presentation of the information, since (a) nomenclature used for them in the existing literature is often incorrect or muddled so that it needs clarification before considering taxonomy, and (b) all of the relevant data needs to be presented and discussed before judging species limits.

#### FAMILY HELICIDAE Rafinesque 1815

##### Subfamily Helicinae Rafinesque 1815

##### Tribe Otalini G. Pfeffer 1929 (p. 138) (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, and *Rossmassleria* P. Hesse 1907. Allocation of *Eremina* to this tribe remains tentative for reasons discussed here.

Razkin *et al.* (2015) placed *Eremina* in the Tribe Helicini, apparently as sister-group to *Levantina* Kobelt 1871, along with *Helix* Linnaeus 1758, on the basis of sequence data from GenBank for “*Eremina desertorum* (Forskål, 1775), Location Unknown, Collector Unknown” (AY841335) obtained by Wade *et al.* (2007: 412).

However, comparison of AY841335 with other sequences published in GenBank implies

the specimen was misidentified. A Blast search reveals that the most similar sequences are for *Levantina hierosolyma* (Mousson 1854), with 99% of identity for a nucleotide length of 2447 base pairs. That species occurs very close geographically to *E. desertorum* e.g. in Israel and shows similarities in shell characters (Heller, 2009: 338, 340). We have been unable to locate the voucher specimen for AY841335, which was received at Nottingham University by the late Bryan Clarke in October 1998.

Neiber & Hausdorf (2015) have since shown that *Eremina dillwyniana* from Sidi Ifni in SW. Morocco (i.e. *E. duroi* of our treatment) gives sequence data (16S and 5.8S+ITS2+28S) implying *Eremina* belongs in a group consisting of the tribes Otalini and Thebini. They could not resolve the relationships within this group. Trying to go further in the resolution of the phylogenetic relationships of *Eremina* within the Helicinae, we have made some new phylogenetic reconstructions, adding Moroccan *Eremina* sequences to the Helicinae sequences published by Razkin *et al.* (2016). Phylogenetic reconstructions (results not shown) with *Arianta arbustorum* and *Marmorana muralis* as outgroups, joined *Eremina* together with Thebini and Otalini, as a full polytomy when considering partial 5.8S, complete ITS-2 and partial 28S nuclear DNA sequences. *Eremina* was grouped as the sister group of all the Otalini genera studied by Razkin *et al.* (2016) (enumerated above), when COI and 16S mitochondrial DNA sequences were also included, but without PP support.

The incorporation of some additional DNA fragments could allow better resolution of the relationships of *Eremina* with Thebini and Otalini. However, the Thebini Wenz 1923 comprises only the genus *Theba* Risso 1826, which differs markedly in anatomy from *Eremina* and Otalini, so it seems unlikely that *Eremina* belongs there. Alternatively, *Eremina* might form a tribe independent of both the Otalini and Thebini. This possibility may receive some support from anatomical data (penis with proximal verge absent, although it is “very short, rosette like” in *Eobania vermiculata* (O.F. Müller 1774): Giusti, Manganelli & Schembri, 1995 and pers. obs; lack of diverticulum on duct of bursa copulatrix, but it is lacking also in *Maurohelix*: Schileyko, 2006: 1791). Nevertheless, for the time being the most parsimonious option is to consider *Eremina* as part



of the Otalini. Our sequence data on Moroccan *Eremina* tend to confirm that the genus does not belong in the Helicini. That tribe would also be a poor zoogeographical fit for the occurrence of *Eremina* in the extreme north-west of Africa and the *Eremina* genitalia having a penis with a single verge and lack of diverticulum on the bursa duct differ from characters of any of the Helicini.

Genus *Eremina* L. Pfeiffer 1855

Malak. Bl., 2, p. 139. Type species *Helix desertorum* Forskål 1775, by monotypy.

syn. *Erinna* Mörch 1865, J. Conchyl., 13, p. 387; type species *Erinna desertorum* Forskål 1775, by monotypy (not *Erinna* H. Adams & A. Adams 1858, The genera of Recent Mollusca, 2, p. 644, Lymnaeidae).

*Eremophila* Kobelt 1871, Catalog europ. Faunengebiet lebenden Binnenconch., p. 19; type species *Helix desertorum* Forskål 1775, by subsequent designation of Martens, 1873, Zool. Record for 1871, n.v. (not *Eremophila* F. Boie 1828, Aves).

*Eremiopsis* C.R. Boettger 1909, Nachrichtsbl. d. malakozool. Ges., 41 (1), pp. 10, 11; type species *Otala duroi* Hidalgo 1886, by monotypy.

*Hessea* C.R. Boettger 1911, Nachrichtsbl. d. malak. Ges., 43 (3), p. 128; type species *Hessea vermiculosa* Morelet 1874, by original designation.

*Nomma* Pallary 1924, Mém. Inst. Egypte, 7 (1), p. 9; type species *Eremina zitteli* Pallary 1909, by monotypy.

*Exiliberus* Iredale 1942, Rec. Australian Mus., 21 (2), p. 126; type species *Exiliberus jacksoni* Iredale 1942, by original designation.

*Eremia* auctt. (spelling error).

Steenberg (1949: 23) listed *Ereminella* Pallary 1919 as another synonym of *Eremina*. However, this was a slip because that genus is only distantly related; the name was introduced by Pallary (1919: 66) as *Xerophila* sect. *Ereminella*, with type species *Xerophila latastei* Letourneux, by monotypy. Later, Pallary (1939b: 105) listed "*Ereminella* Pllary 1919" as a genus with species *latastei*, *simulata*, *mesraniana*.

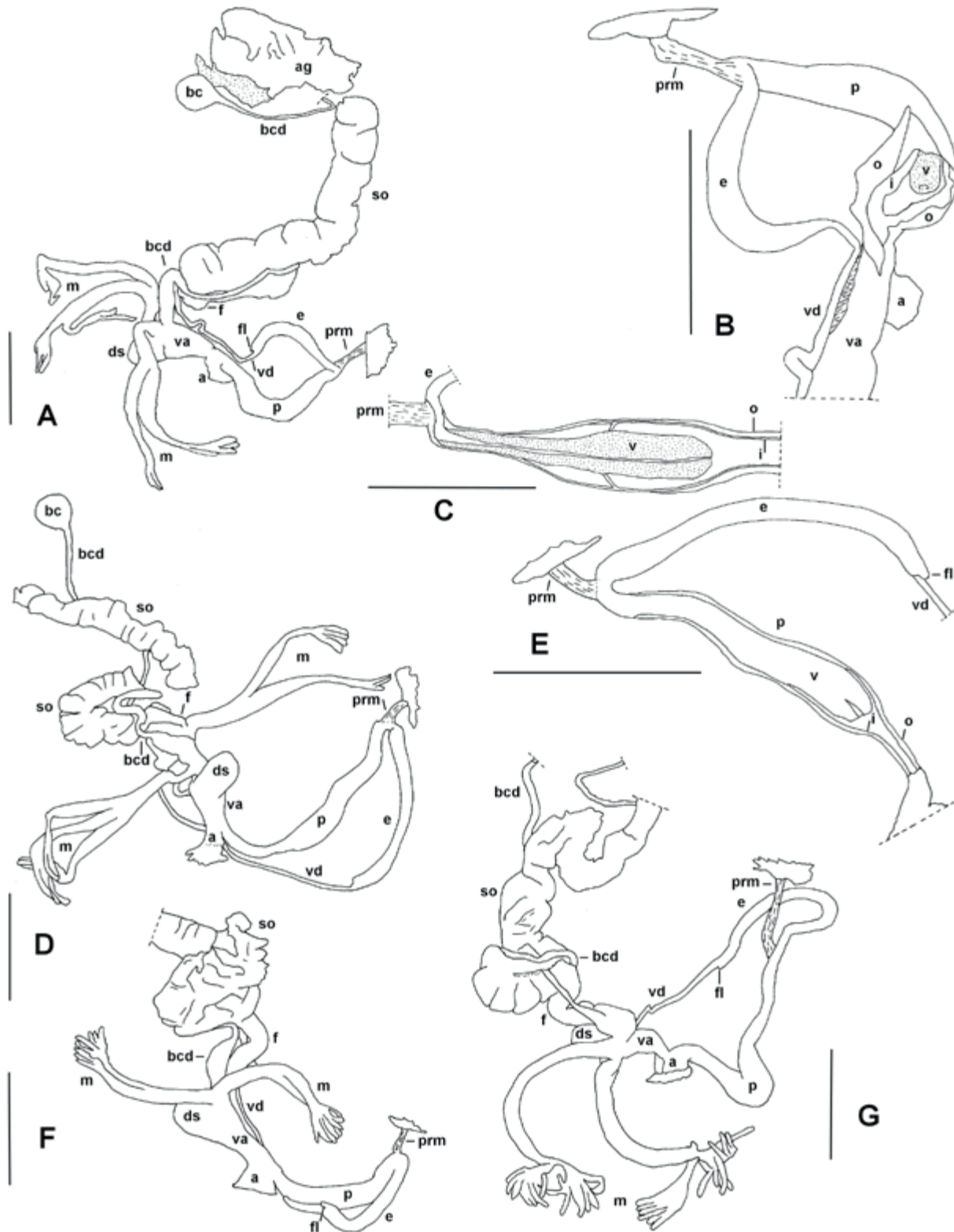
*Genital anatomy* During the present study the genital anatomy has been studied from specimens representing all of the more distinctive taxa named from Morocco: *E. dillwyniana* s.s. (five snails from two populations), *E. duroi*

(thirteen snails from eight populations), *E. inexpectata* (eight snails from two populations), *E. vermiculosa* (eight snails from four populations), *E. duroi* × *E. vermiculosa* hybrids (three snails from one population). The distal genitalia were generally similar in all of them and resembled those reported in previous studies. Hence, this section defines the terminology used and gives a generalised description to avoid repetitive accounts under the species headings. Fig. 2 illustrates genitalia of representative Moroccan specimens studied by us.

The general structure of the genitalia is of semidiaulic 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. It consists of many minute tubes (acini), arranged in groups on separate short branches, but forming a rather compact elongate structure overall. It gives rise to a long hermaphroditic duct functioning as a seminal vesicle, nearly straight proximally, winding and convoluted in the middle, ending distally in a small talon. The albumen gland is large and long, tongue-shaped and somewhat flattened; from its base arises the spermoviduct (second hermaphroditic duct), consisting of a female channel (with a seminal groove) and prostate gland fused to define a single lumen. The spermoviduct is convoluted *in situ* as it passes distally along the columellar side of the body.

The vas deferens is a long and slender tube, following the sperm groove in the prostate gland of the spermoviduct, passing in a loop between the vagina and the penial complex (where there are several small folds), loosely attached to the distal end of the penis by connective tissues, ending in the penial complex where it passes subterminally into the wider epiphallus.

A penial flagellum is absent or very short (its length up to 2.0 × width), at most forming a small blunt tipped papilla continuing beyond the proximal end of the epiphallus. The well developed epiphallus connects the proximal end of the penis with the vas deferens junction; it is usually slightly shorter than the penis or about as long, and as wide or slightly wider than the distal penis but tapering to a slender neck at its distal end where penial retractor muscle inserts and also tapering proximally to union with vas deferens; it has thick muscular walls and a narrow



**Figure 2** Anatomy of distal genitalia of Moroccan *Eremina* species: A–C, *E. duroi* (A, B, site #163, NMW.Z 1993.051.7; C, semi-schematic longitudinal section of penis, site M3, CGAH); D, E, *E. vermiculosa* (site #208, NMW.Z 1993.051.2887; E, shows interior of penis); F, G, *E. inexpectata* (site #148, NMW.Z 1993.051.2704, genitalia of different individuals). See Appendix for additional details of localities. All scale bars represent 5mm. Abbreviations: a genital atrium, ag albumen gland, bc bursa copulatrix, bcd duct of bursa copulatrix, ds dart sac, e epiphallus, f free oviduct, fl flagellum, i inner sheath of penis, m mucus gland(s), o outer sheath of penis, p penis, prm penis retractor muscle, so spermoviduct, v verge, va vagina, vd vas deferens.



central canal with 4–5 longitudinal ridges. The epiphallus lies rather close alongside the penis but is not attached to it laterally; it bends sharply close to the distal end where the penis joins. The penial retractor muscle forms a slender to rather stout strap, inserting on or close to the outside of the distal end of the epiphallus, the other end being attached to the diaphragm.

Externally, the penis usually appears to consist of three cylindrical parts, a *distal* part comprising about one-quarter of the total length is thinner and somewhat translucent, a *middle* part comprising up to about one-half of the total length is 2–3× wider, a *proximal* part comprising around one-quarter (to one-third) of the length is still opaque but somewhat thinner. Longitudinal sections (Fig. 2C) reveal that the entire penis has a thin elastic inner wall surrounded by a thinner outer sheath; the distal penis has a wide empty lumen with smooth walls; the middle penis contains a large muscular verge that is cylindrical, its distal end blunt with an arcuate apical pore, the muscular structure of the verge continues into the proximal penis, narrowing proximally, and its narrow central canal is continuous with that of the epiphallus; the eversible distal part of the verge is 2–3× as long as wide and it occupies the distal half of the middle penis, its proximal end being attached to the outer wall. There is no second verge or papilla inside the proximal penis. In mature snails the transition proximally into the epiphallus may be marked by a narrow neck with thinner walls, at or very close to where the penial retractor muscle inserts.

The genital atrium is a short to very short cylinder, dividing proximally into the distal penis and the distal end of the vagina. The external genital pore is located low on the front of the body, its position varying from directly below the base of the right ommatophore to below and slightly behind its base.

The vagina is shorter than the penis, cylindrical distally (internally with 6–7 low longitudinal ridges inside the somewhat muscular outer wall), subcylindrical to ovoid and often somewhat flattened proximally, with more or less muscular walls. A single rather small ovoid to very shortly elliptical dart sac (“stylophore”) with thick muscular walls arises from the wall of the vagina beneath the mucus glands; it has a narrow central lumen that enters the vagina. In the present study

only small fragments of the calcareous dart were found (up to 0.8mm in length). Steenberg (1949: 17, pl. 7 figs 4, 5) described and figured the dart of “*E. dillwyniana* var. *nounensis*” [= *E. duroi*×*E. vermiculosa*] as 2mm long, slightly curved, tapering to point from broad base, with four longitudinal ridges set at right angles to each other and extending over most of the length, each ridge T-shaped in cross-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 mucus gland is usually forked at around one-quarter to three-quarters of its total length, the basal “stem” and the main branches typically being swollen and thick-walled in mature snails, although the size of each gland often differs appreciably. Most often, each fork is into two branches (less often three; infrequently one gland is unbranched: see below). Sometimes there is another large branch just above the main fork, but more often the main branch terminates apically in a flattened, palmate array of up to five or six “fingers”.

The free oviduct is a moderately short tube, of similar length to the vagina or only slightly longer; 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 is bent back distally before another bend returns it 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. It does not touch the other genital organs, lying among connective tissue linking the intestine to the external lobe of the liver (as described by Steenberg, 1949: 17, not lying on the albumen gland as described for *E. desertorum* by Schileyko, 2006: 1787). The bursa copulatrix duct lacks any diverticulum; it is long, slender and cylindrical throughout most of its length, widening 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 follows its course proximally, leaving it abruptly near the distal end of the albumen gland.

No spermatophore has been seen (even after dissecting a mating pair) and apparently none are described in the literature. The right

ommatophore passes through the angle between the distal parts of penis and vagina as in many other genera of Helicidae *sensu lato*.

The main characters found to vary in our study were presence or length of penial flagellum, and the number and arrangement of the larger branches of the mucus glands. Development of the penial flagellum evidently showed individual rather than specific variation (*E. dillwyniana* s.s. had flagellum nil (1 snail), slight (1) or small (2); *E. duroi* had nil (5), slight (3), small (1); *E. inexpectata* had nil (2), slight (2), small (2); *E. vermiculosa* had nil (3), slight (1), small (1); *E. duroi* × *E. vermiculosa* had slight (1), small (2)). Likewise, variation in branching of the mucus glands did not correlate with specific identity, since departures from the commonest arrangement with two large branches on both glands were found in *E. duroi* (2 snails with one gland three-branched, 1 snail with one gland unbranched) and *E. vermiculosa* (2 snails with one gland three branched). The position of divergence of the main branches varied widely (e.g., Fig. 2A, D, F, G); however, it tended to be similar for each gland in the same snail, but to vary between individual snails within species rather than differ consistently between species.

*Hessea* has sometimes been treated as a subgenus of *Eremina* and it was regarded by Schileyko (2006: 1791) as an independent genus, endemic to Morocco and not closely related to *Eremina*, although he presented no anatomical data for *Hessea*, just shell characters. His treatment resembled that of Hesse (1920: 247, 256), but Hesse subsequently (in Pallary, 1936: 17–18, fig. 4) demonstrated that the anatomy of the type species of *Hessea*, *Helix vermiculosa* is similar to that of *Eremina desertorum*. Hesse (1915: pl. 634, fig. 2) had also described the genital anatomy of *E. duroi* and later Steenberg (1949) described and figured the genitalia of "*E. dillwyniana* var. *nounensis*" in greater detail and gave more information on that of *E. desertorum*, showing that all three taxa have virtually identical distal genitalia. Steenberg (1949) also described and figured genitalia of *E. hasselquisti zitteli* from "la Marmarique" (W. Egypt); which again has very similar distal genitalia to the other species, except that the cross-sectional shape of its dart differs markedly from the symmetrical maltese-cross arrangement of "*E. dillwyniana* var. *nounensis*", being asymmetrical, with one of the four longitudinal ridges greatly

reduced; darts of *E. desertorum* and *E. vermiculosa* have not been described in detail. However, there seems to be no anatomical reason to treat any of the species in separate subgenera, or indeed as separate species, except possibly the Libyan *E. hasselquisti zitteli* which was not studied by us.

For accounts of the external morphology, radula, jaw and other organ systems see Hesse (1915: 23–25, pl. 634) and, for more detail, Steenberg (1949). Biggs (1959) reported that the jaw of *E. desertorum* usually has two ridges, less often one or three, whereas three or four ridges are normal in *E. duroi* (Boettger, 1915; Steenberg, 1949). However, the original description of *E. desertorum tunetana* by Hesse (1915) recorded that it had four or five ribs, more than in Egyptian material of the species. It therefore seems likely that the number of ribs is not useful as an identification character.

External body colouration appears to be similar in all four Moroccan taxa (e.g. Fig. 10A, G), with sides of body, foot-fringe, tail and tentacles pale grey and somewhat translucent, top of head and dorsal surface of forepart of body brown to dark brown. The part of the mantle-collar exposed inside the shell aperture when live animals are collected is commonly light yellow but sometimes white.

Shells of adult snails are dextral, of 3.3–4.3 whorls, that expand rather rapidly. Shell shape varies from globular through low-conical to discoid (planorboid). The whorls are rounded or have a peripheral keel and the shell aperture is oval to rounded (except where interrupted by penultimate whorl), with an angled outer lip when the whorl profile is keeled. The body whorl descends more or less strongly near the aperture. The peristome varies from simple to widely expanded outwards. Adult shells are strong and opaque, but infrequently thick or heavy. The surface varies from nearly smooth (finely malleate with irregular radial growth lines) to roughly malleate with irregular radial-tangential ribs.

All W. Maghreb taxa and most of their populations include unmarked white shells. Shells with multiple spiral bands are also common in all Moroccan taxa except *E. inexpectata*. In many populations these bands show complicated and highly variable patterns (Figs 1, 10), some bands being continuous, others interrupted, very often with adjacent unmarked dark and pale bands, or speckled bands alternating. Within a population,

bands apparently split, fuse, or spread to cover large parts of the body-whorl. There is so much complex variation between individual banding patterns that we have been unable to establish whether there is a basic (“fundamental”) pattern of five bands as in many other Helicidae (e.g. Taylor, 1910: 290–294), of up to four bands that may be overlain with narrower stripes as in *Theba* (Heller, 2009: 120 fig. 87; Holyoak & Holyoak, 2016: 22), or neither of these (at least a few *Eremina* shells have six narrow dark bands, three above the periphery, three below it).

A key to taxa of *Eremina* occurring in the W. Maghreb follows; Fig. 1 illustrates their shells. Interspecific hybrids may complicate identification in certain small areas: thus, as discussed below, hybrids with *E. vermiculosa* occur within populations of *E. inexpectata*; hybrids between *E. vermiculosa* and *E. duroi* completely dominate some local populations.

1. Body whorl of adults with sharp peripheral keel; spire usually somewhat scalariform; surface of shell rough, whitish, usually lacking all trace of colour bands *E. inexpectata*

-. Body whorl of adults lacking peripheral keel; spire not scalariform; surface of shell moderately rough to almost smooth, whitish to cream or brownish, with or without dark colour bands

2

2. Adult shell globular or subglobular, with H/B >0.7, with 3.5–4.1 whorls; peristome lip not reflected or only narrowly reflected; shell surface often rather rough *E. vermiculosa*

-. Adult shell low conical to discoidal, with H/B <0.7, with 3.8–4.3 (mostly >4) whorls; peristome lip usually widely reflected; shell surface almost smooth

3

3. Adult shells with spire flat or very low; umbilicus widely open, but shallow (at least near peristome lip); coastal regions of SW. Morocco between El Ouatia [Tan-Tan Plâge] and Tarfaya

*E. dillwyniana* s.s.

-. Adult shells with umbilicus closed, a chink, or with narrow but deep opening partly overlapped by peristome lip

4

4. Adult shells with umbilicus closed, a chink, or with narrow, deep opening partly overlapped by peristome lip; shells white or more often with dark bands; range from SW. Morocco (near Mirleft) southwards to N. Mauritania

*E. duroi*

-. Adult shells with umbilicus closed; S. Tunisia eastwards *E. desertorum*

(Based on Hesse 1915: 21–22 and Pallary, 1926: 11, the shells from S. Tunisia are all white and lack colour bands. Shells from Egypt may closely resemble those from S. Tunisia, or be umbilicate, banded, or both).

*E. desertorum* (Forskål 1775)

*Helix desertorum* Forskål 1775, Descriptiones animalium avium ... itinere orientali observavit ..., pp. xxvii (name only), 127; TL “Inter Káhiram & Sués in arbufculis deferti” [= Egypt].

*Helix (Chilogymnus) Hemprichii* Ehrenberg 1831, Symbolae Physicae, Animalia Evertebrata exclusis insectis, Series prima cum tabularum decade prima, Berlin, vol. 2 [unpaginated]; TL Egypt, Libyan desert margin near Alexandria.

*Helix desertorum* [& vars]: Kobelt (1876), Iconogr., (1) 4 (2–4), pp. 13–16, pls 96–97.

*Helix desertorum* var.: Kobelt (1888), Iconogr., (2) 3 (5–6), p. 44, pl. 83 figs 464, 465; Nähe von Kairo [Egypt].

*Eremina desertorum tunetana* Hesse 1915, Iconogr., (2) 23, pp. 21–22, pl. 633 figs 9a–c (jaw), 10 (male genitalia); TL Fom Tahtaouine im südlichen Tunis, nahe der tripolitanischen Grenze (S. Tunisia); type at ANSP; the name was attributed to Pallary but the description was by Hesse.

*Eremina hemprichi* Ehrenberg Var. *tunetana*: Pallary 1926, J. Conchyl., 70 (1), p. 11, pl. 1, fig. 12; Fom Tahtaouine, dans l’extrême Sud tunisien.

*Eremina Hemprichi*: Pallary (1939), J. Conchyl., 83 (2), p. 106.

*Eremina Hemprichi*, Ehrenberg 1831, var. *tunetana* Pallary, 1926: Llabador (1969), J. Conchyl., 100, pp. 58, 60–61, 70.

See Biggs (1959) and Llabador (1969: 60) for additional synonymy from Egypt and Sinai; Heller (2009: 340) illustrated shells from Israel.

*E. dillwyniana* (L. Pfeiffer 1851) s.s. Figs 1A, B, 6

*Helix Dillwyniana* L. Pfeiffer 1851, Proc. zool. Soc., Lond., 19–20, pp. 254–255; TL unknown; NHMUK 20150074 (Fig. 1A) is labelled as a syntype, but since no other specimens seen by Pfeiffer are known to exist this may be the holotype.

*Helix Dillwyniana* Pfr.: L. Pfeiffer (1853), Monographia Heliceorum viventium ..., 3, no. 1409, pp. 240–241.



*Helix Dillwyniana* Pfr.: L. Pfeiffer (1854), Systematisches Conchylien-Cabinet ..., Bd. 1, Abt. 12, T. 2–3, No. 911, pp. 374–375, pl. 140, figs. 13, 14.

*Helix dillwyniana* Pfr: Tryon (1888), Man. Conch. (2) 4, p. 127, pl. 36, figs 29–30; Habitat unknown. *H.[elix] (Eremina) dillwyniana* Pfr.: Pilsbry (1894), Man. Conch. (2) 9, p. 335.

*Eremina dillwyniana* Pfeiffer, 1851: Steenberg (1949), Det Kgl. Danske Videns. Selsk., Biol. Medd., 20 (14), p. 23.

*Eremina dillwyniana* Pfeiffer: Biggs (1959), J. Conch., Lond., 24, p. 333. Shell labelled as type is in British Museum [NHMUK]; “in my opinion, a unique monstrosity of [*Eremina*] *ehrenbergi* Roth.” *Eremina linanprietoae* Cossignani & Ahuir, 2012, Malacologia (Cupra Marittima), 75, p. 28, figs; TL North Sidi Akhfennir, West Sahara, Morocco. Holotype MMM. This name is superfluous even at subspecies rank, since a syntype of *E. dillwyniana* (Fig. 1A) is a shell with open umbilicus and low spire.

*Eremina linanprietoae* Cossignani & Ahuir 2012: Cossignani (2014), African Landshells, p. 85; figs of four shells, from North Sidi Akhfennir (holotype, MMM); Tarfaya.

*Eremina dillwyniana* (Pfeiffer 1851), with syn. *E. linanprietoae* Cossignani & Galindo 2012: Ali *et al.* (2016), Zoologica Scripta, 45, p. 48.

*Eremina duroi* (Hidalgo 1886) Figs 1E, F, 2A–C, 4, 7, 9A, B, C, 10A–D

*Helix Duroi* Hidalgo 1886, J. Conchyl., 34, pp. 152–153, pl. 8, figs. 1, 1a, 2; TL Littoral Atlantique du désert de Sahara, dans le lieu nommé *Vina*. L'espèce vit sur l'*Euphorbia Beaumeriana*, Hooker [Maroc].

*Helix Duroi*: Hidalgo (1887), Revista de geographica commercial, no. 29, p. 94; dans le Guerguer (Rio de Oro) (leg. Quiroya). n.v.

*Helix Duroi* Hidalgo: Kobelt (1888), Iconogr., (2) 3 (5–6), pp. 43–44, pl. 83 figs 461; atlantischen Küste der Sahara.

*Helix Duroi* Hidalgo var. *minor* Kobelt 1888, Iconogr., (2) 3 (5–6), p. 44, pl. 83 figs 462, 463; TL neuen spanischen Colonie am Rio d'Oro.

*Helix duroi* Hidalgo: Tryon (1888), Man. Conch. (2) 4, p. 128, pl. 45, figs. 38–40. Morocco.

*H.[elix] duroi* var. *minor* Kobelt 1888: Tryon (1888), Man. Conch. (2) 4, p. 261, pl. 46, fig. 63. Rio d'Oro, Western border of the Sahara.

*H.[elix] [sect. Eremina] duroi* Var. *haploa* Westerlund 1889, Fauna der Pal. Region, 2, p. 152, no. 360; TL not given for Var., but range for species as a whole given as “atlantischen Küste der Sahara”; however, this was clearly intended as new name for var. *minor* Kobelt [Iconogr., N.F. figs 462–463] which was from “neuen spanischen Colonie am Rio d'Oro” (see above).

*H.[elix] (Eremina) duroi* Hid.: Pilsbry (1894), Man. Conch. (2) 9, p. 335.

*H.[elix] (Eremina) duroi* f. *minor* Kob.: Pilsbry (1894), Man. Conch. (2) 9, p. 335.

*Helix Duroi*, Hidalgo 1886: Pallary (1899), J. Conchyl., 46, pp. 72–73; Le littoral atlantique du Sahara; le Comte de Dalmas l'a aussi rapporté dernièrement du Cap Blanc [= Cabo Blanco, NW. Mauritania].

*Helix Duroi* Var. *haploa* W.: Pallary (1899), J. Conchyl., 46, p. 73; briefly described by Pallary, starting as “(var. *minor*)”, but apparently without any intention of introducing a new varietal name.

*Helix Duroi* var. *minor*: Font y Sagué (1903), Bol. Soc. esp. Hist. nat., 3 (5), p. 209; Rio de Oro. n.v.

*Helix (Eremina) Duroi* Hidalgo: Pallary (1904), J. Conchyl., 52 (1), p. 45; Rio de Bra (Sahara); Cap Blanc (leg. Cte de Delmas).

*Helix (Eremina) Duroi* Hidalgo var. *haploa* W.: Pallary (1904), J. Conchyl., 52 (1), p. 45.

*Helix (Eremina) Duroi* and var. *haploa*: Germain (1908), Bull. Mus. Natn. Hist. nat., 14, p. 290; environs de Port-Etienne, près du Cap Blanc [Mauritania].

*Helix Duroi*: Germain (1909), Arch. zool. experim. et gener., 5<sup>th</sup> ser., 1, p. 169; Mauritanie, depuis le cap Blanc jusqu'au sud Marocain.

*Helix Duroi*: Germain (1910), Actes Soc. Linn. Bordeaux, 64, pp. 27, 29–32, pl. 1 figs 19–23; dans la région d'El Aïoudj [Mauritania].

*Helix (Eremina) Duroi* sous-var. *minima* Germain, 1910, Actes Soc. Linn. Bordeaux, 64, p. 32.

*Helix (Eremina) Duroi* var. *alta* Germain, 1910, Actes Soc. Linn. Bordeaux, 64, pp. 29, 31.

*Helix (Eremina) Duroi* var. *depressa* Germain, 1910, Actes Soc. Linn. Bordeaux, 64, p. 29.

*Helix (Eremina) Duroi* var. *nivea* Germain, 1910, Act. Soc. Linn. Bordeaux, 64, p. 30; TL Port-Étienne [Mauritania].

*Otala duroi* Hid.: Boettger (1909), NachrBl. d. malak. Ges., 41 (1), p. 12.

*Eremina duroi*: Boettger (1915), Bol. Real Soc. Esp. Hist. Nat., 15 (5), pp. 235–243., fig. 4, pls 6, 7; mentioned but did not recognise f. *obtecte*

*umbilicata* Hidalgo, var. *minor* Kobelt, var. *haploa* Westerlund, f. *alta* Germain, f. *depressa* Germain, subvar. *minima* Germain.

*Eremina duroi* Hidalgo var. *haploa* Wstld.: Hesse (1915), Iconogr., (2) 23, pp. 23–25, pl. 634, figs 1, 2; spanischen Kolonie Rio de Oro.

*Eremina dillwyniana* Pfr. (*duroi* Hid., *haploa* Wstld.): Hesse (1920), Iconogr., (2) 23, p. 256; Atlant. Küste der Sahara.

*Eremina dillwyniana* Pfr. f. *nivea* Germain: Hesse (1920), Iconogr., (2) 23, p. 256.

*Eremina duroi* Hid.: Boettger (1921: 75–77); spanischen Kolonie Rio de Oro.

*Eremina Duroi* Hid.: Pallary (1923), Bull. Soc. Hist. nat. Afr. Nord 14 (7), p. 279.

*Eremina Duroi*: Pallary (1939), J. Conchyl., 83 (2), p. 106.

*Eremina dillwyniana*, var. *nounensis* [Pallary] Steenberg (1949), Det Kgl. Danske Videns. Selsk., Biol. Medd., 20 (14), pp. 13–19, pl. 6 fig. 3, pls 7, 8; TL près poste de l'oued Noun ... un peu au Sud de Tiznit, entre l'enclave espagnol d'Ifni et le Rio de Oro; Pallary provided the name for the var., but the description was written by Steenberg. This taxon is clearly based on hybrids between *E. dillwyniana* and *E. vermiculosa*.

*Eremina dillwyniana*, var. *minor* Kob.: Steenberg (1949), Det Kgl. Danske Videns. Selsk., Biol. Medd., 20 (14), pp. 19, 24.

*Eremina duroi* Hidalgo, 1886: Steenberg (1949), Det Kgl. Danske Videns. Selsk., Biol. Medd., 20 (14), p. 23.

[*Eremina*] *haploa* Westerlund, 1889: Steenberg (1949), Det Kgl. Danske Videns. Selsk., Biol. Medd., 20 (14), p. 24.

*Eremina dillwyniana* var. *nivea* Germain, 1910: Steenberg (1949), Det Kgl. Danske Videns. Selsk., Biol. Medd., 20 (14), p. 24.

*Eremina Duroi* Hidalgo: Vidal y Lopez (1950: 214); Sahara Español.

*Eremina Duroi*, Hidalgo 1886: Llabador (1969), J. Conchyl., 100, pp. 57–60, 65–67, 70, pl. 2 figs 8, 9; Cap Blanc (leg. Monod, 1922–1923, in MNHN); 35km de Asmara al Dium de la Saguia El Hamra (Sahara espagnol: the northernmost known locality) (leg. Rutllant); etc.

*Eremina Duroi*, Hidalgo 1886 Var. *minor* Kobelt 1888 (= var. *haploa* Westerlund 1889): Llabador (1969), J. Conchyl., 100, p. 66.

*Eremina Duroi*, Hidalgo 1886 Sous-var. *minima* Germain 1910: Llabador (1969), J. Conchyl., 100, p. 66.

*Eremina Duroi*, Hidalgo 1886 Var. *alta* Germain 1910: Llabador (1969), J. Conchyl., 100, p. 67.

*Eremina Duroi*, Hidalgo 1886 Var. *depressa* Germain 1910: Llabador (1969), J. Conchyl., 100, p. 67.

*Eremina Duroi*, Hidalgo 1886 Var. *nivea* Germain 1910: Llabador (1969), J. Conchyl., 100, p. 67.

*Eremina duroi* (Hidalgo, 1886): Rour *et al.* (2002: 194).

*Eremina dillwyniana* Pfeiffer 1851: Cossignani (2014), African Landshells, p. 83; figs of three shells, from Imlily; Tan Tan Plâge.

*Eremina dillwyniana minor* (Kobelt 1888): Cossignani (2014), African Landshells, pp. 83–84; figs of two shells, from Dakhla.

*Eremina dillwyniana nivea* (Pallary 1933): Cossignani (2014), African Landshells, p. 84; figs of two shells, from Boujdour [the reference to Pallary 1933 is apparently incorrect].

*Eremina dillwyniana nounensis* (Pallary): Cossignani (2014), African Landshells, p. 84; figs of two shells, from Sidi Ifni.

*Eremina dillwyniana* f. *umbilicata* (Pfeiffer 1851): Cossignani (2014), African Landshells, p. 84; figs of shell, from Tan Tan Plâge; “f. *umbilicata*” appears to be a *nomen nudum* introduced by this author.

*Helix duroi* Hidalgo 1886, as syn. of *Eremina dillwyniana* (Pfeiffer 1851), but excluding that species and *E. linanprietoae* Cossignani & Galindo 2012: Ali *et al.* (2016), Zoologica Scripta, 45, p. 48.

*E. inexpectata* Llabador 1969 Figs 1C, 2F, G, 6, 9F, 10I

*Eremina inexpectata* Llabador 1969, J. Conchyl., 100, pp. 55, 58, 67–70, pl. 2 figs 11–14; TL Tane-Tane (Zona sur Protectorado español) [= Tan-Tan, S. Morocco].

*Eremina ziheli* [sic] Pallary: Mouna (1997) n.v., cited by Rour *et al.* (2002: 194); Llabador (1969: 68–69, fig. 1) had clarified distinctions between the Moroccan *E. inexpectata* and *E. zitteli* Pallary 1909 from Libya when he named the former species.

*Eremina ziheli* [sic] Pallary: Rour *et al.* (2002: 194).

*Eremina inexpectata* [sic] (Llabador 1960 [sic]): Cossignani (2014), African Landshells, p. 84; figs of shell, from Tan Tan.

*Eremina inexpectata* [sic] (Llabador 1960[sic]) × *Eremina vermiculosa* (Morelet, 1874): Cossignani (2014), African Landshells, pp. 84–85; figs of three shells, from Oued Draa; El Krabi; apparently hybrids.

*Eremina vermiculosa inexpectata* [sic]: Kittel (2012).  
*Eremina vermiculosa inexpectata* [sic]: Ali et al. (2016), *Zoologica Scripta*, 45, p. 48.

*E. vermiculosa* (Morelet 1874) Figs 1H, 2D, E, 5, 7, 8, 9C–E, 10E–G

*Helix vermiculosa* Morelet 1874, *J. Conchyl.*, 22, p. 179; TL “circa Hir [sic,=Ilir, see under Pallary 1935b below] in prov. Sous, imperii Maroccani” (non *H. vermiculosa* A. Férussac 1821, *Tabl. syst.*, p. 42, no. 242, *nomen nudum*). A var. is described as “β albido-cretacea, fasciis evanidis”; since the descriptive phrase is polynomial it is unavailable for nomenclature, despite repeated later citation as var. *cretacea* Morelet [it was validated as var. *cretacea* Pallary, 1899, p. 120: see below].

[The basionym “*clathrata* Morelet 1874” appears never to have been published. The apparently erroneous combination *Eremina vermiculosa clathrata* Morelet 1874 was listed in WMSDB – Worldwide Mollusc Species Data Base, by Bagni Liggi, Genova, Italy, accessed 29 Dec. 2014]

*Helix vermiculosa* Morelet: L. Pfeiffer (1875), *Mon. Helic. viv.*, 7 (3), p. 323.

*Helix vermiculosa* Morelet: Kobelt (1879), *Iconogr.*, (1) 7 (1–3), pp. 7–8, pl. 182 fig. 1829; bei Hir in der marokkanischen Provinz Sus.

*Helix vermiculosa*, Morelet: Morelet (1880), *J. Conchyl.*, 28, pp. 18–19, pl. 2, figs 5; “sur les collines du Tézaroualt, aux environs de Hir, dans le Sous indépendant (Beaumier)”; Pallary (1935b, p. 259, see below) noted that two localities are involved here, the first should be spelled Ilir, and the second (which should be spelled Tazéroualt) was erroneous.

*Helix Percallosa*, Bourg.[uignat] in Servain 1880, *Étude Moll. D’Esp. et de Portugal*, p. 50 (new name for *H. vermiculosa* Morelet, 1880 [sic, i.e. 1874], non *H. vermiculosa* A. Férussac, 1821, *Tabl. syst.*, p. 42, no. 242, but unwarranted because latter name is a *nomen nudum*). Although G. Servain is given as sole author of this publication, there is clear evidence that Servain worked closely with Bourguignat (cf. Holyoak & Holyoak, 2012: 32), and a note on p. 49 states that the tableau (p. 50) was “d’après notre ami Bourguignat”.

*Helix percallosa*, Bourguignat: Pallary (1899), *J. Conchyl.*, 46, p. 120.

*Helix percallosa*, Bourguignat Var. *cretacea*, M.[orelet] Pallary, 1899, *J. Conchyl.*, 46, p. 120; Pallary provided a short description, thus

validating this varietal name which was based on the unavailable descriptive phrase provided by Morelet (1874: 179).

*Helix Percallosa*: Bourguignat (1899), *J. Conchyl.*, 46, pp. 168–169.

*Helix (Pomatia) percallosa* B: Pallary (1904), *J. Conchyl.*, 52 (1), p. 45.

*Helix (Pomatia) percallosa* B var. *cretacea*, M.: Pallary (1904), *J. Conchyl.*, 52 (1), p. 45.

*Hessea* gen. nov., C.R. Boettger, with type species *Hessea vermiculosa* Mor.: Boettger (1911), *NachrBl. d. malak. Ges.*, 43 (3), p. 128.

*Helix (Hessea) vermiculosa* Morel.: Hesse (1920), *Iconogr.*, (2) 23, p. 247; Marokko (Prov. Sus).

*H.[elix] vermiculosa* Morelet: Pallary (1923), *Bull. Soc. Hist. nat. Afr. Nord*, 14 (7), p. 277.

*Helix vermiculosa* Morelet 1874: Hesse (1932: 3), pointed out correctly that the name *Helix vermiculosa* Férussac (*Tabl. Syst.*, 1821, p. 42, no. 242) was unavailable because it was not accompanied by a description; thus replacement of *Helix vermiculosa* Morelet 1874 by *Helix percallosa* Bgt., 1898 [= 1899] is unwarranted.

*H.[elix] vermiculosa*: Pallary (1935a), *C. r. Assoc. Franç. p. Avanc. des Sciences, Nantes*, p. 354; Goulimine.

*Helix vermiculosa* Morelet: Pallary (1935b), *J. Conchyl.*, 79, pp. 258–260; Goulimine, localité en ruines à la lisière d’Ifni, au Sud-Ouest de Tiznit (leg. Pallary); also reinterpretation of localities given by Morelet (1974, 1880), as noted above; allocation to *Eremina* confirmed by ecology and anatomy (*vide* P. Hesse); claimed that name *percallosa* need not be substituted [as it was by Pallary 1899: 120] because Férussac’s earlier usage of *H. vermiculosa* was for an unrelated species, but the reason given for this was incorrect: it was in fact an unavailable *nomen nudum* (cf. Hesse, 1932).

*Helix vermiculosa* Morelet var. *cretacea*: Pallary (1935b), *J. Conchyl.*, 79, p. 260.

*Helix vermiculosa* Morelet var. *minor* Pallary 1935(b), *J. Conchyl.*, 79, p. 260 (*nomen nudum*).

*Helix vermiculosa* Morelet var. *major* Pallary 1935(b), *J. Conchyl.*, 79, p. 260 (*nomen nudum*).

*Helix vermiculosa* Morelet var. *inflata* Pallary 1935(b), *J. Conchyl.*, 79, p. 260 (*nomen nudum*).

*Eremina vermiculosa* Morelet 1874: Pallary (1936), *J. Conchyl.*, 80 (1), pp. 17–18, Fig. 4 (fig. of genital anatomy by P. Hesse).

*Eremina vermiculosa* Morelet 1874 var. *cretacea* Morelet: Pallary (1936), *J. Conchyl.*, 80 (1), p. 17.



*Eremina vermiculosa* Morelet 1874 var. *major* Pallary: Pallary (1936), J. Conchyl., 80 (1), p. 17; *nomen nudum*.

*Eremina vermiculosa* Morelet 1874 var. *minor* Pallary: Pallary (1936), J. Conchyl., 80 (1), p. 17; *nomen nudum*.

*Eremina vermiculosa* Morelet 1874 var. *inflata* Pallary: Pallary (1936), J. Conchyl., 80 (1), p. 17, pl. 1 fig. 4; although this var. is figured, no description in words is given other than that all four varieties named “se définissent elles-même, comme disait feu Bourguignat”; this does not satisfy the Requirements of the ICZN Code (art. 13.1.1, regarding Names published after 1930) so it is also a *nomen nudum*.

*Eremina vermiculosa* Morelet 1874 var. *depressa* Pallary 1936, J. Conchyl., 80 (1), p. 17; *nomen nudum*.

*Eremina vermiculosa*: Pallary (1939), J. Conchyl., 83 (2), p. 106.

*Eremina vermiculosa* var. *cretacea* Morelet 1874: Steenberg (1949), Det Kgl. Danske Videns. Selsk., Biol. Medd., 20 (14), p. 23.

*Eremina vermiculosa* var. *depressa* Pallary 1936: Steenberg (1949), Det Kgl. Danske Videns. Selsk., Biol. Medd., 20 (14), p. 23.

*Eremina vermiculosa* var. *inflata* Pallary 1936: Steenberg (1949), Det Kgl. Danske Videns. Selsk., Biol. Medd., 20 (14), p. 24.

*Eremina vermiculosa* var. *major* Pallary 1935: Steenberg (1949), Det Kgl. Danske Videns. Selsk., Biol. Medd., 20 (14), p. 24.

*Eremina vermiculosa* var. *minor* Pallary 1935: Steenberg (1949), Det Kgl. Danske Videns. Selsk., Biol. Medd., 20 (14), p. 24.

*Eremina vermiculosa*, Morelet 1874 (= *H. percallosa* Bgt 1880): Llabador (1969), J. Conchyl., 100, pp. 57, 58–59, 61–64, 70, pl. 2 figs 2–5; El Dioum du Draâ (Zona sur Protectorado español); etc.

*Eremina vermiculosa*, Morelet 1874 Var. *cretacea* Morelet 1874: Llabador (1969), J. Conchyl., 100, p. 63; environs de Goulimine; El Dioum du Draâ (Zona sur Protectorado español).

*Eremina vermiculosa*, Morelet 1874 Var. *candida* Llabador 1969, J. Conchyl., 100, p. 63, pl. 2 fig. 4; TL El Dioum du Draâ (Zona sur Protectorado español).

*Eremina vermiculosa*, Morelet 1874 Var. *minor* Pallary 1935: Llabador (1969), J. Conchyl., 100, p. 63.

*Eremina vermiculosa*, Morelet 1874 Var. *major* Pallary 1935: Llabador (1969), J. Conchyl., 100, p. 63.

*Eremina vermiculosa*, Morelet 1874 Var. *inflata* Pallary 1935: Llabador (1969), J. Conchyl., 100, p. 64.

*Eremina vermiculosa*, Morelet 1874 Var. *depressa* Pallary 1936: Llabador (1969), J. Conchyl., 100, p. 64.

*Eremina vermiculosa* (Morelet, 1874): Rour *et al.* (2002: 194).

*Hessea vermiculosa* (Morelet 1874): Schileyko (2006), Treatise Rec. terr. Pulmonate Moll, Ruthenica, Suppl. 2, pp. 1791–1792, fig. 2293 (shell); Marokko, Prov. Sorno.

*Eremina vermiculosa* (Morelet 1874): Cossignani (2014), African Landshells, p. 85; figs of shell, from El Labiar.

*Eremina vermiculosa cretacea* (Morelet 1874): Cossignani (2014), African Landshells, pp. 85–86; figs of three shells, from El Labiar.

*Eremina vermiculosa minor* (Pallary 1935): Cossignani (2014), African Landshells, p. 86; figs of shell, from El Labiar.

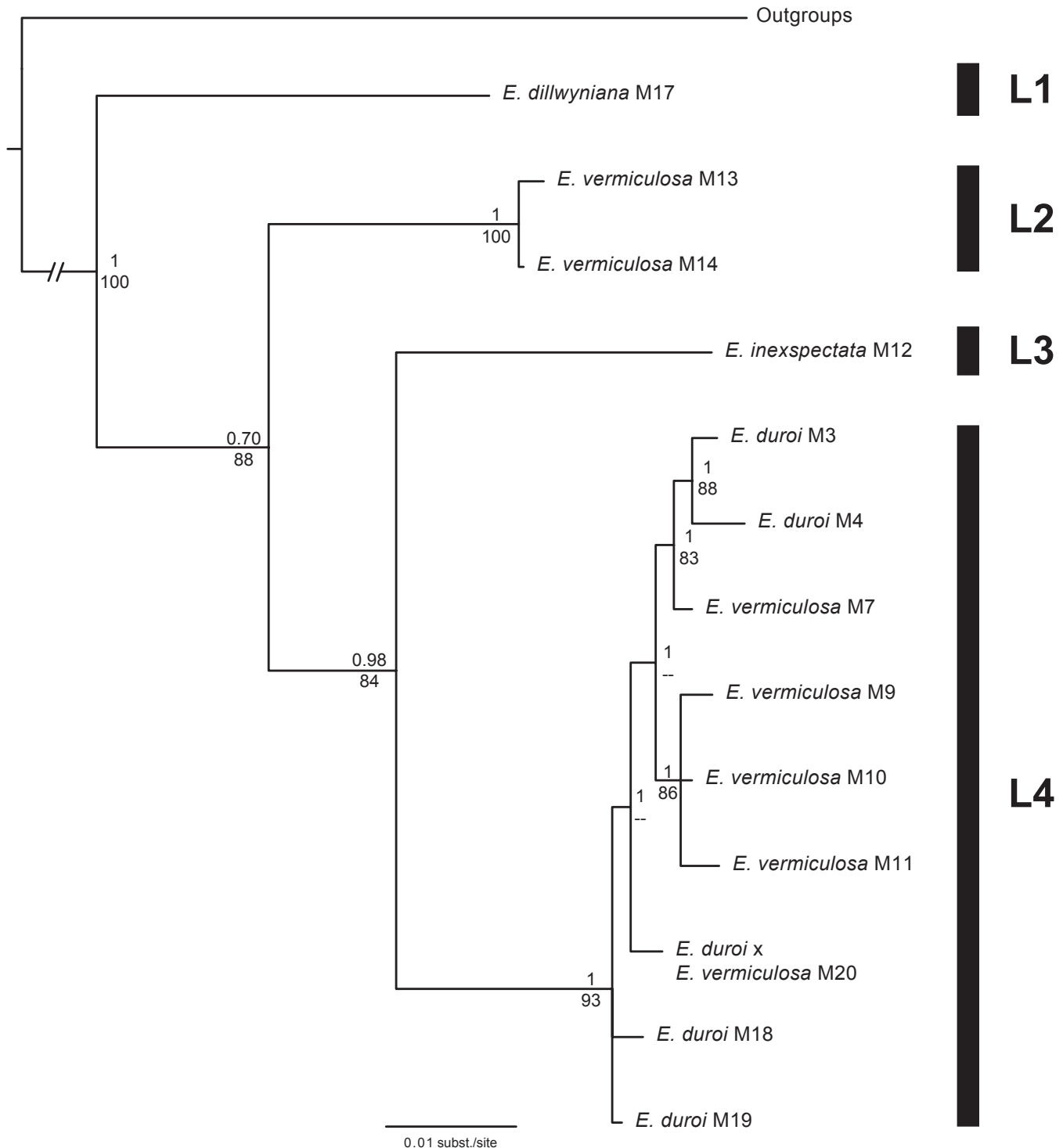
*Eremina smaraensis* Ahuir 2015, Malacologia (Cupra Marittima), 86; TL South-east of As-Saka, Morocco.

*Eremina vermiculosa vermiculosa*: Ali *et al.* (2016), Zoologica Scripta, 45, p. 48.

## MOLECULAR RESULTS

The data-set used for the phylogenetic reconstruction corresponded to 13 representatives of the genus, with 1973 aligned characters. A total of 168 sites without alignment gaps were polymorphic, 85 of them being parsimony informative (63 sites for COI, 20 for 16S rRNA and 2 for ITS-2). The phylogeny obtained by concatenating the mitochondrial and nuclear genes is shown in Fig. 3. The topology of the phylogeny is based on BI but both BI posterior probabilities and ML bootstrap values are indicated at the nodes of the main clades.

Using both procedures, the populations of Moroccan *Eremina* included in our study constituted four lineages. Lineage 1 (L1) corresponded to *E. dillwyniana* s.s., which was recovered with full support as the sister clade of all the remaining lineages (PP=1.0; BS=100%). Populations with subglobular (*E. vermiculosa*) and with flatter (*E. duroi*) shells, did not constitute monophyletic entities. Conversely, northern populations of *E. vermiculosa* from north of the Oued Draa were recovered in a polytomy with northern



**Figure 3** Phylogeny obtained for Moroccan taxa of *Eremina* by concatenating data from mitochondrial and nuclear genes. Topology of the phylogeny is based on Bayesian Inference but both BI posterior probabilities (above) and ML bootstrap values (below) are indicated at the nodes of the main clades.

and southern populations of *E. duroi* within lineage L4, with the southernmost populations of *E. vermiculosa* living south of Tan-Tan grouped in a distinct lineage (L2). *E. inexpectata* constituted the last lineage (L3), recovered as the

sister group of L2 with strong support (PP=0.98; ML=84%). Sister relationship of L2 with L3+L4 was supported only by ML phylogenetic analysis (PP=0.70; BS=88%), indicating that *E. vermiculosa* is probably polyphyletic. Ali *et al.* (2016) found

**Table 4** Uncorrected average p-distances for COI (below) and 16S rRNA (top) among the four main lineages (L1-L4).

	L1	L2	L3	L4
L1		0.055	0.062	0.062
L2	0.100		0.048	0.043
L3	0.121	0.090		0.038
L4	0.099	0.088	0.082	

lack of reciprocal monophyly of the mitochondrial haplotypes of *E. desertorum desertorum* and *E. d. irregularis* in N. Egypt. Similarly, we were unable to find reciprocal monophyly of *E. vermiculosa* and *E. duroi*. Uncorrected p-distances between groups for COI and 16S rRNA gene fragments are shown in Table 4.

As noted above under the genus heading and in our key, *E. desertorum* does not show any clear differences from the Moroccan *Eremina* taxa in genital anatomy or shell morphology. We therefore investigated the possibility that *E. desertorum* might be conspecific with a Moroccan form, by means of a phylogenetic reconstruction using our 16S rRNA sequences from Moroccan taxa and some of those published by Ali *et al.* (2016) for 16S of *E. desertorum* (data not shown). It was found that they constitute two well-differentiated clades, that are respectively monophyletic. In addition, mean genetic distance between *E. desertorum* and the Moroccan taxa for the 16S gene fragment is quite high (8%), providing an additional indication that *E. desertorum* may be considered a different species.

#### DISTRIBUTION, HABITATS AND ECOLOGY

Populations of *Eremina* occur near the Atlantic coast of southern Morocco from around Mirleft (SW. of Tiznit at 29°36'N.) southwards into Mauritania (21°N.) and apparently also to the Cape Verde Is. (15°N.) (Groh, 2005, 2012, seemingly revising treatment of *Leptaxis* from Groh, 1983). Ozenda (1983: 82, 563) commented on the peculiar conditions in this coastal strip of semi-desert *ca* 50km wide of “Sahara océanique bien individualisé”: it is the only part of the N. or W. Sahara with large succulent plants (e.g. Fig. 9A) and its only region with foliose lichens, which grow on branches and even on the soil, sustained by the dew condensing from regular coastal

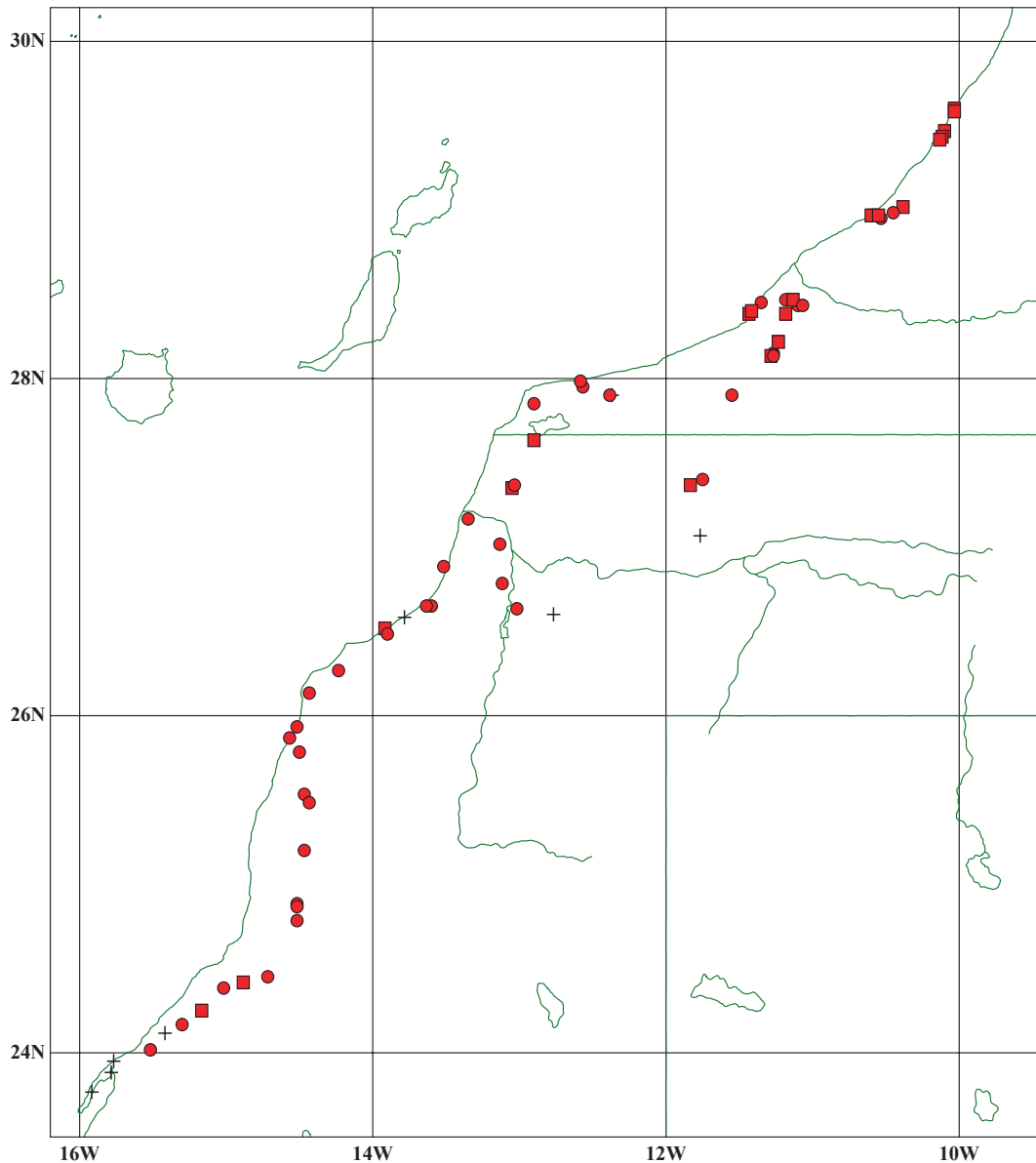
mists. In their Moroccan range the *Eremina* now live mainly in a coastal region up to a maximum of *ca* 75km wide that has at least patches of semi-desert vegetation. Quaternary fossils of the genus also occur over a wider region 75–150km inland from the coast.

Figs 4–6 give distribution maps of each of the four Moroccan species of *Eremina*. Figs 7 and 8 show occurrences of the two intergrades we regard as interspecific hybrids, mapped in relation to ranges of the parent species. *E. dillwyniana s.s.* and *E. duroi* live in the most humid zone on and inland of the Atlantic coast (e.g. Fig. 9A, B), the former in a small region between S. of El Ouatia [= Tan-Tan Plâge] and Tarfaya (Fig. 6), the latter over an extensive range in mainly coastal regions from near Sidi Ifni southwards to N. Mauritania (Fig. 4 shows the Moroccan part of the range); *E. vermiculosa* (Fig. 5) occurs somewhat further inland into drier country east of the range of *E. dillwyniana s.s.* and the northern part of that of *E. duroi* (from near Guelmim to region SW. of Tan-Tan; cf. Fig. 7); *E. inexpectata* (Fig. 6) has a small range in rocky sandstone and quartzite hills (e.g. Fig. 9F) from the Oued Draa southwards to near Tan-Tan.

Subfossil (Quaternary) shells show that the overall ranges of both *E. duroi* and *E. vermiculosa* formerly extended further inland (Figs 4, 5), into what are now desert regions where a hot dry climate prevails so that the landscape is too arid and sparsely vegetated to support either species.

Care is needed to base habitat studies of *Eremina* on living populations because shells from the accumulations of old or subfossil material may relate to different climatic and vegetation conditions, resulting both from Pleistocene and Holocene climatic changes, or to relatively modern over-grazing by domestic animals. There do not appear to be any clear-cut differences between *E. duroi* and *E. vermiculosa* in the habitats they occupy, although the northern part of the range of the former includes much more succulent vegetation (but not the southern part, beyond the range limits of *E. vermiculosa*). Either species seems able to live on silty plains (e.g. Fig. 9B), sandy plains and slopes (e.g. Fig. 9A), or gravelly, stony or rocky slopes (e.g. Fig. 9C) composed of sandstones or limestones, with more or less vegetation. Where their ranges meet (e.g. south of Tan-Tan) they live together locally on limestone slopes with rather sparse low shrubs





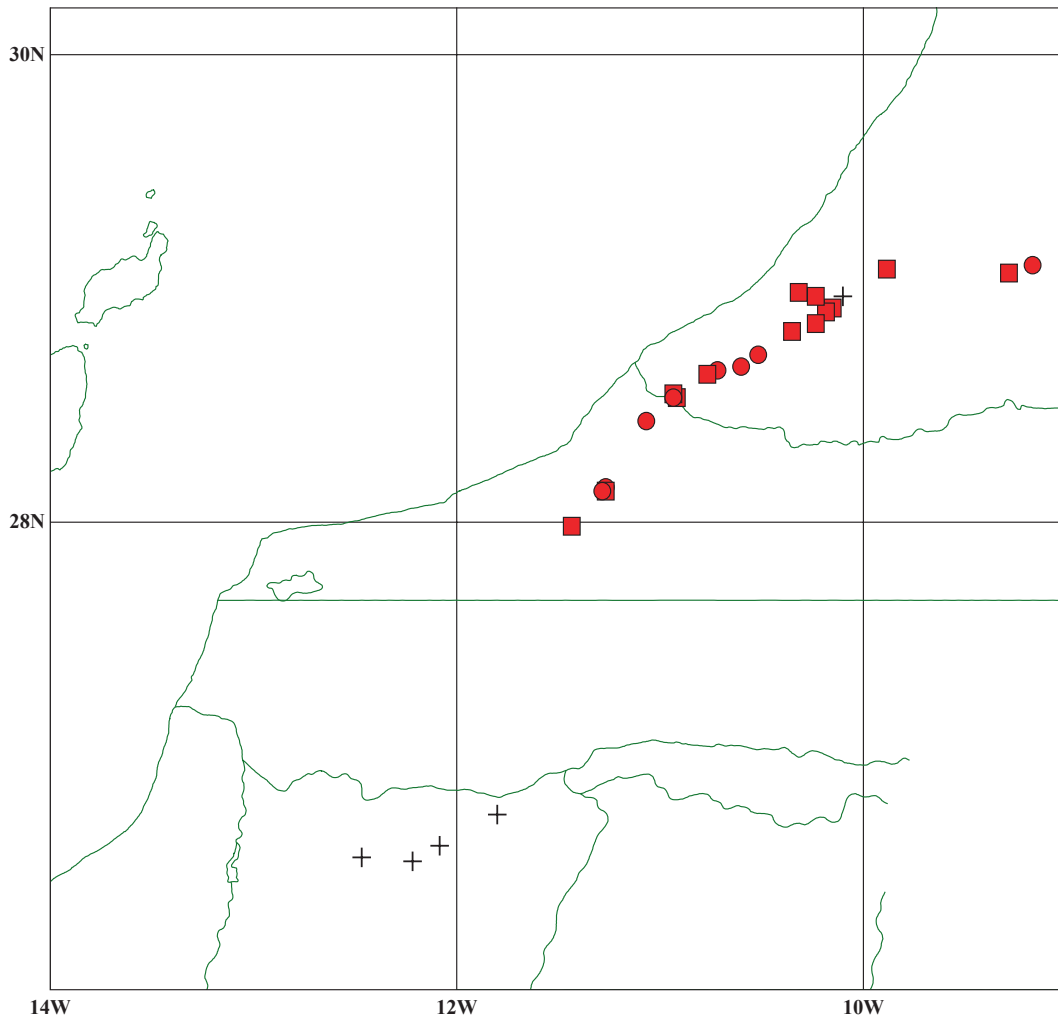
**Figure 4** Map to show distribution of *Eremina duroi* in Morocco, based on specimens studied by the authors (see Appendix for list). This taxon also occurs in N. Mauritania. Key: squares, living or fresh shells; circles, old shells; +, subfossil.

and few succulents (Fig. 9C). *E. dillwyniana* s.s. at least sometimes lives in places with calcareous sandstone exposures (site #155), but elsewhere on open sandy or gravelly plains (sites #153, #154, #156, M17).

Table 5 records counts of daytime resting places of living snails of these two species recorded in March and October 2016, demonstrating much overlap between the types of sites used. Both of them occurred repeatedly in the open on tops or sides of rocks (e.g. Fig. 10E, H), on thorny bushes (e.g. *Launaea arborescens* (Batt.) Murb.), low halophytic shrubs (e.g. Amaranthaceae

such as *Salsola*, Fig. 10F) and on “cactiforme” succulent plants including the spiny *Euphorbia officinarum* L. which has densely packed stems (e.g. Fig. 10C) but also the unarmed more open succulent-stemmed bushes of *Kleinia anteuphorbium* (L.) Haw. (e.g. Fig. 10B) and *Euphorbia regis-jubae* J.Gay.

*E. duroi* was recorded proportionately more often resting on succulents than *E. vermiculosa* but this may be coincidental because such plants are absent or scarce at many of the sites where the latter species occurs. *E. dillwyniana* s.s. is known living from sites with patchy cover of



**Figure 5** Map to show distribution of *Eremina vermiculosa* in SW. Morocco, based on specimens studied by the authors (see Appendix for list). Key: squares, living or fresh shells; circles, old shells; +, subfossil.

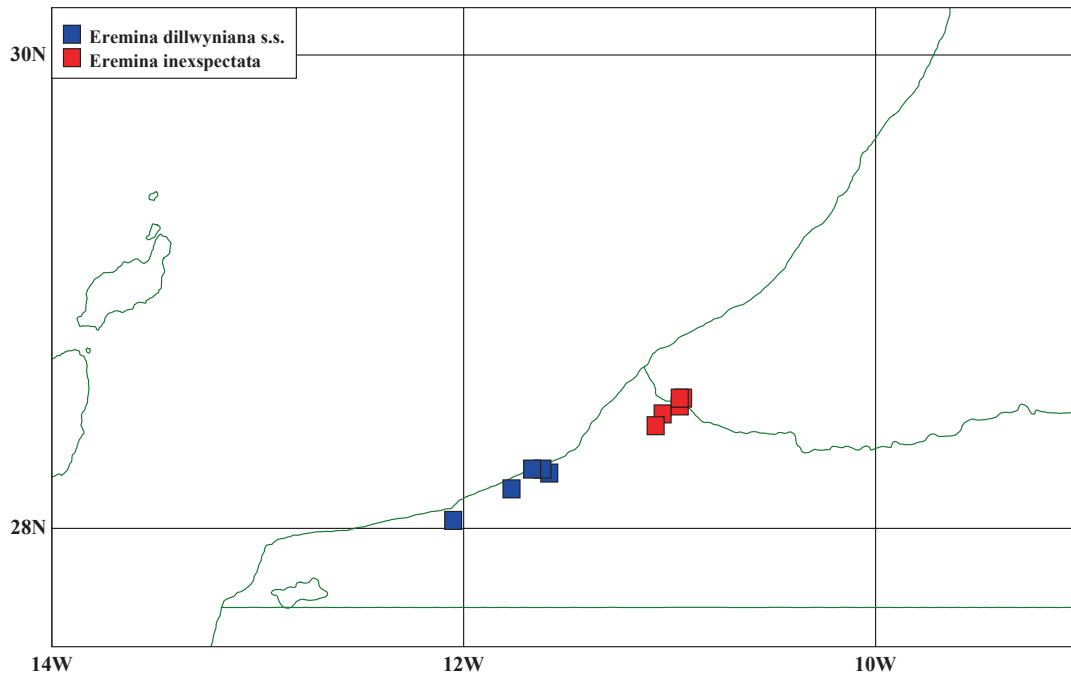
large succulents (e.g. #153), or none (M17); the few data we have on its resting places are only from M17 (on bushes or open soil).

All of ten *E. duroi* snails resting on rocks were in exposed positions on the tops or sides, whereas four out of seven *E. vermiculosa* on rock were concealed beneath the cobbles or boulders involved (five out of fifteen *E. inexpectata* on rock were concealed).

At the two sites where living populations of *E. inexpectata* were studied in 2016, only a single snail was found above ground on vegetation (on twigs of small shrub). This is easily explained since site M12 had little vegetation on the quartzitic slopes (Fig. 9F) and at site M27 *E. inexpectata* was living only on rather bare stony upper slopes, with none a few hundreds of metres away on lower sandy slopes with low shrubs; neither site had many succulent plants. However, at site

M27 the bases of decayed *Euphorbia officinarum* plants had accumulations of mainly undamaged shells of *E. inexpectata* (Fig. 10I), which appear to have remained from populations that formerly used the living plants.

Zeev Arad (in Heller, 2009: 76) described *E. desertorum* in Israel as “a bush-dwelling species of Saharan origin limited to bushes on sandy soil in the Negev Desert”, which apparently resembles the habitat and behaviour of at least some Moroccan populations of *E. dillwyniana* s.s., *E. duroi* and *E. vermiculosa*. Arad (1993) also demonstrated that *E. desertorum* shows a high degree of resistance to water loss in standardised laboratory studies, comparable to that in the desert-dwelling *Sphincterochila zonata* (Bourguignat 1853). Earlier authors had reported *E. desertorum* living in captivity for almost four years without any food or water (Woodward, 1870) or six years



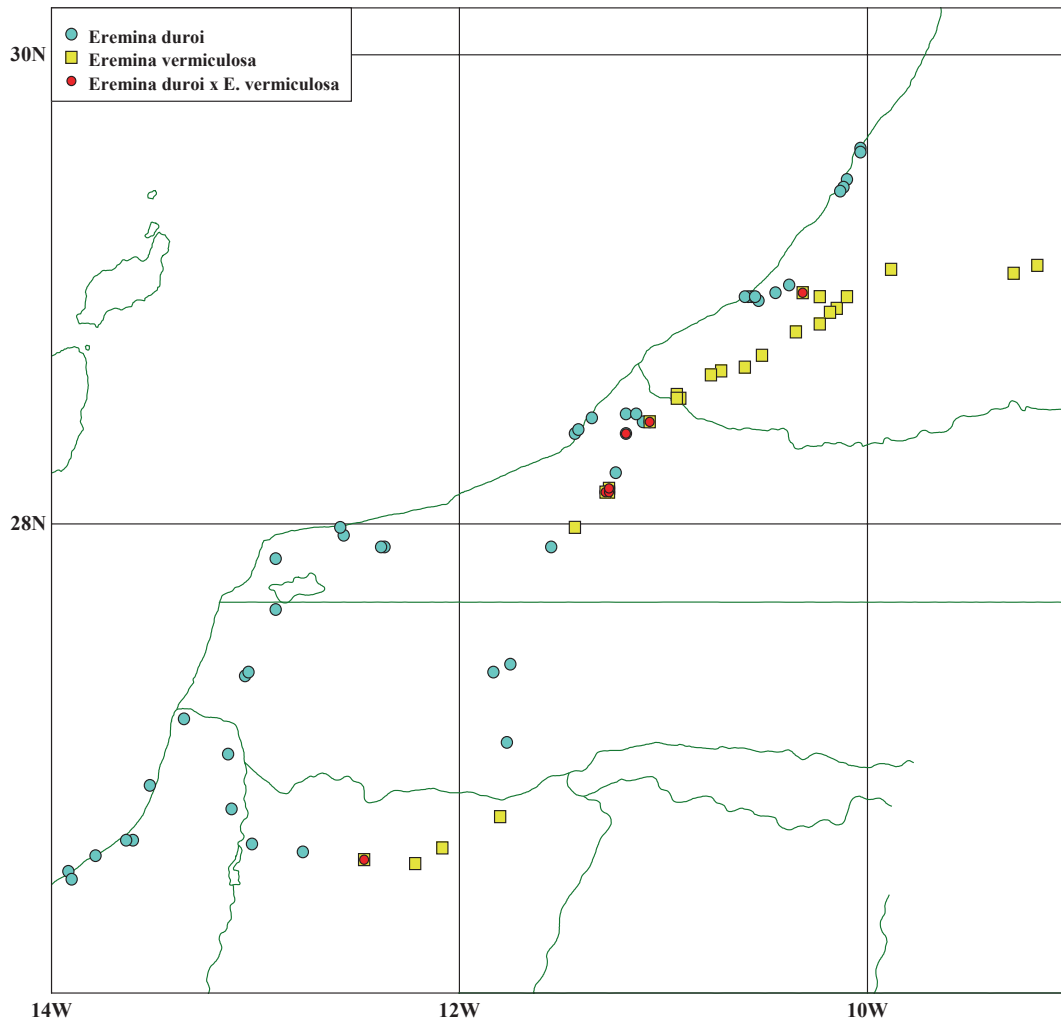
**Figure 6** Map to show distributions of *Eremina dillwyniana* s.s. and *E. inexpectata* in southern Morocco, based on living or fresh shells studied by the authors (see Appendix for list). Key: blue symbols (in south-west) *E. dillwyniana*; red symbols (in north-east), *E. inexpectata*.

without food (Pallary, 1924). Biggs (1959: 336) published notes on breeding of *E. desertorum* in Egypt, with egg laying in late autumn, when each of five snails studied excavated a hole (39–57mm deep) in sand which was damp just below the surface, digging with its head and forepart of the foot, before laying in the hole. Hegazi (1981: 500) reported that reproductive activity of the species in the Egyptian western desert during 1974–1979 involved egg-laying from January to the end of April or May, when the snails are active during the day; during summer they fed only early in the day and at night; at the end of summer (when temperatures are high and relative humidity is low) the snails remained inactive and aestivated, attached firmly to stems or branches of low-growing plants. There is little comparable information on the biology of Moroccan taxa, with which we did not see any really small immature snails, evidence of mating, or egg-laying in March 2016. However, on 16<sup>th</sup> October 2016 at 09:30 hours a mating pair of *E. duroi* was found at site M92, in copula on open soil in the usual head-to-head position for Helicidae.

Only occasional evidence of vertebrate predation on Moroccan *Eremina* was seen by us, in the form of dead shells with damage to the

spire. It is nevertheless tempting to speculate that Moroccan *Eremina* resting by day deep among the spines on *Euphorbia officinarum* (Fig. 10C) may be gaining protection from potential vertebrate predators. Elsewhere, *E. desertorum* is reported to sometimes be a preferred food of the Cairo Spiny Mouse *Acomys cahirinus* (Kingdon *et al.*, 2013: 221), for which the snail diet compensates for high evaporative water-loss (Shkolnik & Borut, 1969; Heller, 2009: 112). Empty shells of *E. desertorum* have been found piled near the entrance holes to burrows of the Fat-tailed Gerbil *Pachyuromys duprasi* in Egypt, suggesting they form part of its diet (in *Bulletin Zoological Society of Egypt* 27: 174, 1977, n.v.) and Setzer (1957: 60) suggested this rodent eats terrestrial snails, although Kingdon *et al.* (2013: 342) regarded that as unconfirmed. Other gerbil species (e.g. *Gerbillus dasyrurus*) are well known to eat large numbers of snails in Israel (Heller, 2009: 112). The Moroccan ranges of *Eremina* species overlap those of *Acomys cahirinus*, *Pachyuromys duprasi* and *Gerbillus* spp. (Aulagnier *et al.*, 2009) and further study of their possible significance there as snail predators is needed. The diurnal Fat Sand Rat *Psammomys obesus* was conspicuous at some localities where we found living *Eremina* in March 2016 (M7, M10, M17, M18, M32) and



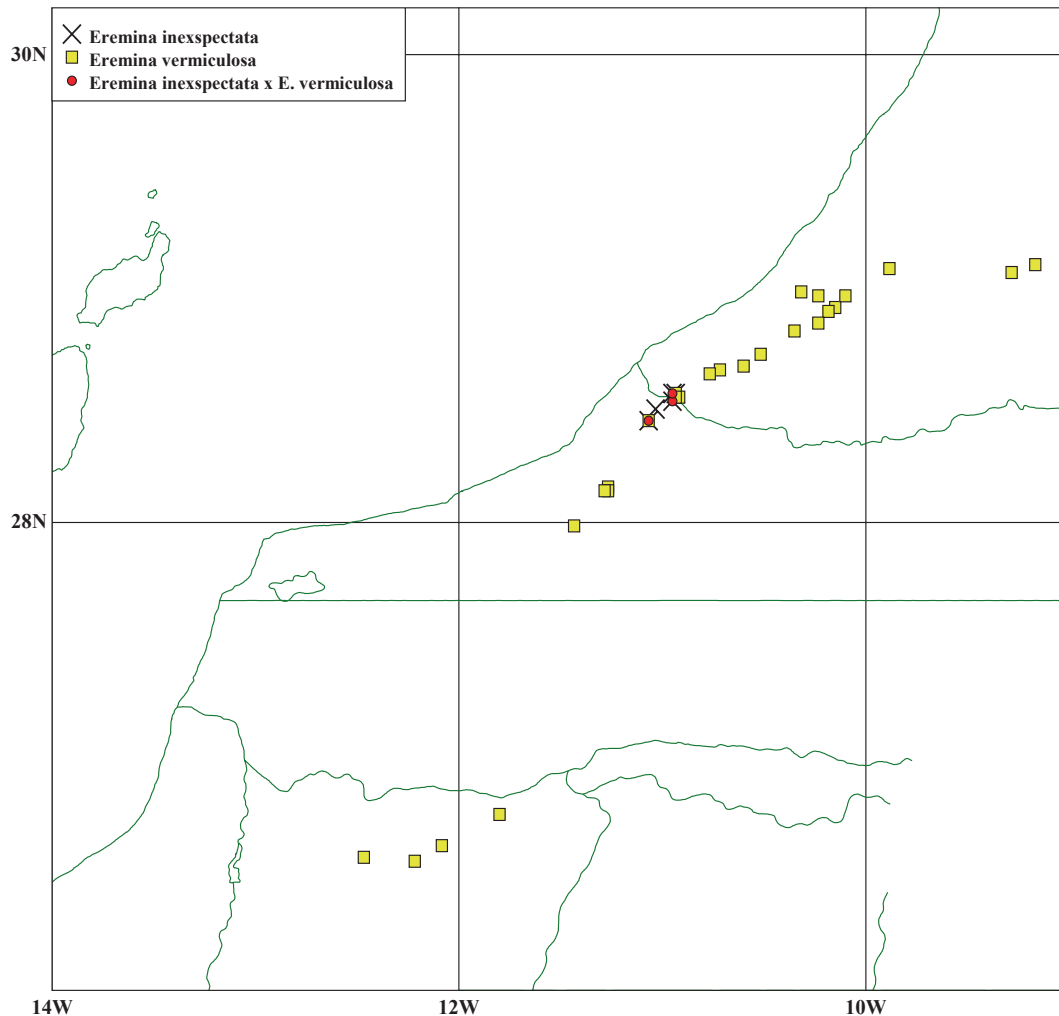


**Figure 7** Map to show distribution of the hybrid between *Eremina duroi* and *E. vermiculosa* in relation to the ranges of both parent species, based on specimens studied by the authors (see Appendix for list). The southernmost record of the hybrid and the four southernmost records of *E. vermiculosa* are based on subfossil shells.

seen eating leaves as it climbed into low *Salsola* bushes, but no evidence could be found of it eating snails.

The Hoopoe Lark *Alaemon alaudipes* was reported to have *Eremina desertorum* forming a large part of its diet in desert near El Hammam in Egypt. Here, the snails were abundant: from February to late June 1979, ca 6–11 birds removed 1090 snails (6.5 kg of flesh) from an area of 2.4 ha (Hegazi, 1981). The lark was reported to deal with each of the snails by flying with it to a height of 6–23m, then dropping it onto a stone; if this did not break the shell, they would beat it directly against the nearest stone. Although this remarkable account has been cited repeatedly in the standard ornithological literature (D.J. Brooks in Cramp *et al.*, 1988: 76; E. de Juana, F. Suárez & P.G. Ryan in del Hoyo, Elliott & Christie, 2004:

524, 567) there is no independent confirmation of any details, and it is unclear how much of what was reported was directly observed, or how often, and how much was surmised by the two students acknowledged for “conducting this research” (*op. cit.*, p. 501). Song Thrushes *Turdus philomelos* were noted as being present at the locality, so these might also have accounted for some of the snail shells accumulated at anvil stones. Hoopoe Larks are widespread in the Moroccan Sahara, mainly in sandy desert, extending far inland of the range of *Eremina*, and conspicuous in spring because of their loud songs. However, there is apparently not much overlap of their habitat with that of living *Eremina*: in March 2016 we found them at only two of the sites where any *Eremina* were found (M15, M33), both of which had only old shells. Accumulations of broken



**Figure 8** Map to show distribution of the hybrid between *Eremina inexpectata* and *E. vermiculosa* in relation to the ranges of both parent species, based on specimens studied by the authors (see Appendix for list).

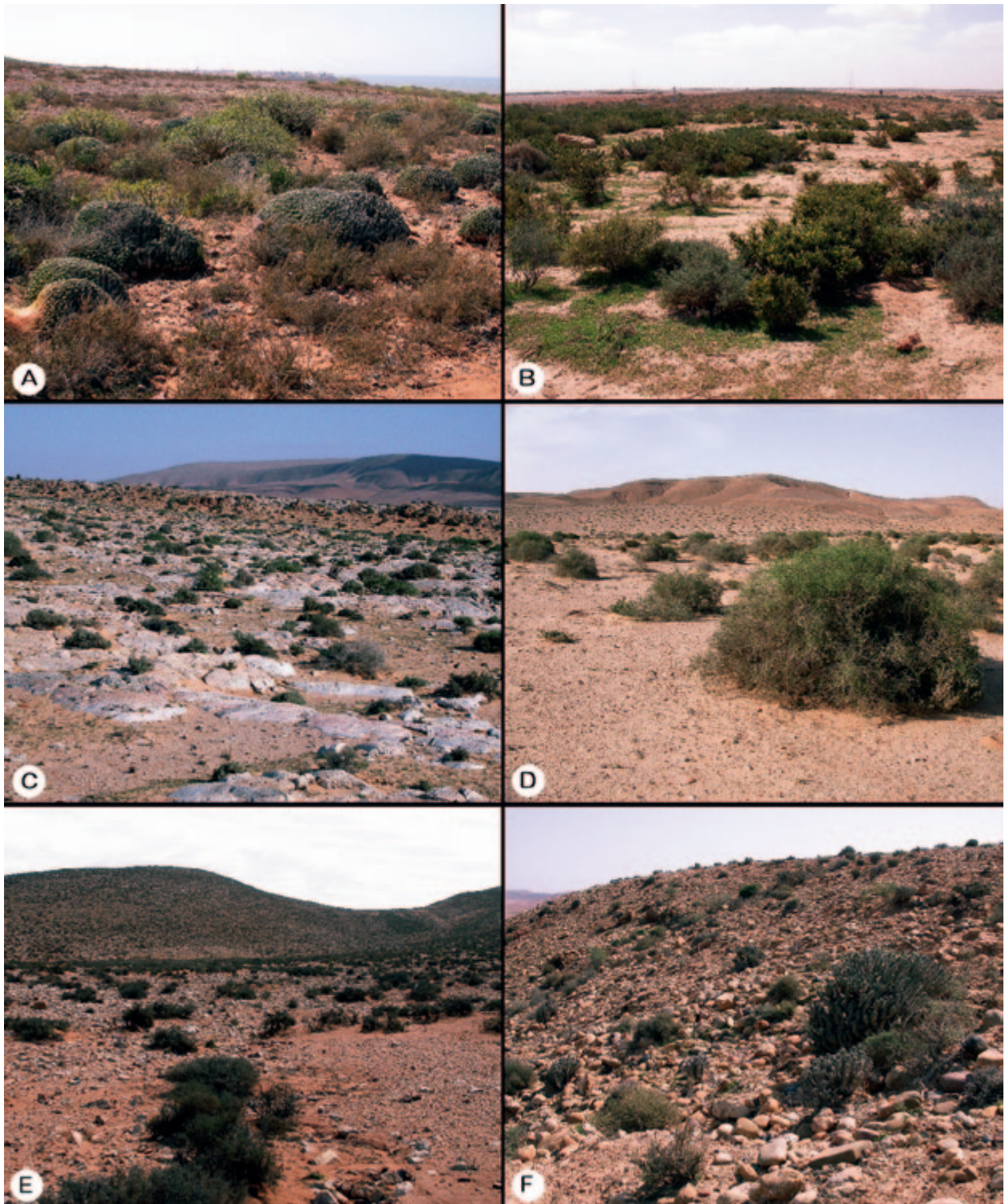
snail shells around anvil stones were not seen at any of our sites.

#### NOTES ON EVOLUTION OF SHELL FORM IN MOROCCAN *EREMINA*

This section describes the main differences in shell form between Moroccan *Eremina* taxa, then discusses how at least some of the differences between them are likely to correspond to different segments of the wide variety of habitats occupied by the genus. The possibility is considered that different shell forms might be selected for by differing threats from rodents and other predators where different microhabitats are used by resting (inactive) snails. Table 6 summarises measurements from representative populations of the four Moroccan species of *Eremina* that we recognise.

*E. vermiculosa* has a globular shell (H 0.7–0.9×B), shallow sutures between whorls of the spire, rounded aperture (mean AH 1.07×AB) that is rather large (mean *ca* 273mm<sup>2</sup>), and rough surface sculpture. The large rounded shell mouth is also associated with a large foot but unlike with some *Helix* spp. the foot is not important in enabling the snail to regularly bury itself in loose sandy substrata. Nevertheless, it is possible that the large foot facilitates excavation of holes for egg-laying, which has been recorded for *E. desertorum* (see above) although egg-laying in *E. vermiculosa* has not been described.

Shells of *E. inexpectata* are unique among the Moroccan forms of *Eremina* in having a sharp peripheral keel and even rougher shell surface sculpture, but it also has a high spire (H 0.70–0.80×B) like *E. vermiculosa*. *E. h. zitteli* from Libya has a similar but larger shell. *E. inexpectata* is



**Figure 9** Habitats of species of *Eremina* in SW. Morocco: A, Coastal slope overlying sandstone with open scrub rich in succulents (*Euphorbia officinarum*, *Kleinia anteuphorbium*), Site M3, with living *E. duroi*; B, Silty hollow on stony plain inland, shrubs up to 1.5m high (mainly *Launaea arborescens*, *Ononis* sp. and *Salsola*), Site M25, with living *E. duroi*; C, Limestone hillslope inland, with blown sand, sparse low shrubs (no succulents), Site M20, with living or fresh shells of *E. duroi*, *E. vermiculosa* and intermediates; D, Sandy ground inland above wadi floodplain with patchy bushes (mainly *Launaea arborescens*) and sandstone slopes behind with few low bushes, Site M10, both habitats with living *E. vermiculosa*; E, Quartzite slope inland with sandy surface and sparse low shrubs (succulents rare), Site M9, with living *E. vermiculosa*; F, Rocky slopes (mainly quartzite) with few low shrubs and sparse succulents locally, Site M12, with living *E. inexpectata*. See Appendix for additional details of localities.



**Table 5** Daytime resting places of *Eremina* species recorded in SW. Morocco in March and October 2016. The numbers given are counts of living adult snails, excluding those actively moving or mating.

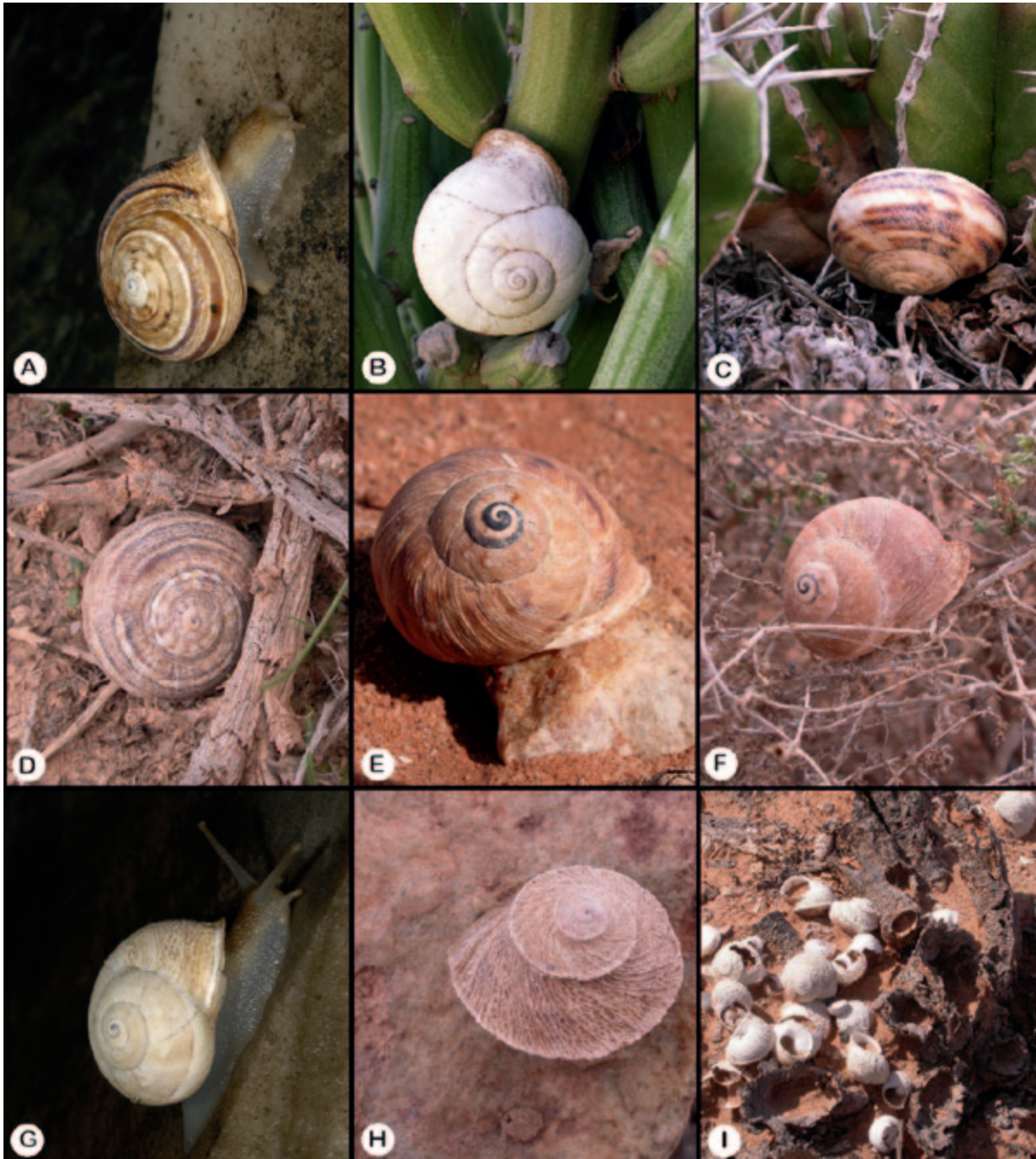
Resting place	<i>Eremina</i> species:			
	<i>dillwyniana</i>	<i>duroi</i>	<i>inexpectata</i>	<i>vermiculosa</i>
On soil ~ in open	3	14	-	1
On low rocks, in open or on sides	-	10	10	3
Concealed beneath cobbles or boulders of rock	-	-	5	4
On low herbs	-	2	-	-
On shrubs or low bushes	2	16	1	3
On <i>Euphorbia officinarum</i> , – on top (spiny succulent with dense stems) – at base or inside	-	4	-	-
On <i>Euphorbia regis-jubae</i> (succulent stems, open growth)	-	17	-	7
On <i>Kleinia anteuophorbium</i> (open bush with succulent stems)	-	7	-	-
On <i>Kleinia anteuophorbium</i> (open bush with succulent stems)	-	16	-	2
Total snails	5	86	16	20

known only from a small region north of Tan-Tan where it lives on slopes among hard sandstone and quartzite rocks. In other genera of Helicacea containing some forms with keeled shells and others with globular shells, the keeled forms are sometimes associated with concealment in narrow rock crevices (e.g. De Bartolomé, 1982; Alonso *et al.*, 1985; Goodfriend, 1986; Fiorentino *et al.*, 2012), but this is untrue e.g. of *Theba*. Since, as noted above, *E. inexpectata* lives only in rocky places, this may indicate the adaptive significance of its keeled shell form. However, although the adult snails sometimes rest concealed within rock crevices or under boulders, more often they lie on the surfaces of open ground (Fig. 10H). Unfortunately there is no information on the resting places of juvenile snails of this species. Being thinner shelled than adults, they might be more vulnerable to predation than adults and therefore derive greater benefit from concealment in rock crevices.

Shells of *E. duroi* mainly have a moderate to low spire (mean H 0.59×B, maximum H < 0.7×B), moderately deep sutures between whorls of the spire, closed umbilicus, rather smooth surface and relatively rather small oval aperture (mean area 260mm<sup>2</sup>; mean AH 0.76×AB), with the peristome lip strongly reflected outwards. The live snails typically rest on soil surfaces in the open (Fig. 10D), or on or under loose rocks or on or among plants, often firmly attached to their surfaces (Fig. 10B, C), for which the wide peristome may be important.

*E. dillwyniana* s.s. has planorboid shells with a flat spire (but with moderately deep sutures between its whorls), rather small oval aperture (mean area 228mm<sup>2</sup>; mean AH 0.85×AB) and exposed umbilicus. The syntype of *Helix dillwyniana* resembles shells from the region south of El Ouatia, but its provenance is unknown. Likewise, the exact provenance in the former Spanish colony of “Rio de Oro” of possibly similar umbilicate shells figured by Boettger (1915) is unknown. Similar planorboid forms with a flat or even slightly depressed spire are also known further south near Tarfaya (named as *E. linanprietoae* Cossignani & Ahuir 2012), this area being separated geographically from our sites, with intervening areas occupied by populations of *E. duroi* having a closed umbilicus. Further research is needed to check whether intermediate populations connect *E. dillwyniana* s.s. with *E. duroi* (cf. Boettger, 1915: pl. 6), since their ranges approach each other closely (within ca 25km at sites M17 and #153).

The tall globular shell shape of *E. vermiculosa* is approached but not attained by that of “*E. dillwyniana nounensis*” and other local populations, but these intergrades are evidently hybrids of *E. duroi* with *E. vermiculosa*, occurring where the ranges of the two species meet (Fig. 7). Elsewhere, *E. vermiculosa* populations vary from lacking a reflected peristome lip to having it rather widely reflected as in most *E. duroi* and especially in *E. dillwyniana* s.s.; shell colouration also varies widely, without apparent correlation with shell form.



**Figure 10** Moroccan species of *Eremina*: A, *E. duroi*, from site M24, showing typical body colouration; B, *E. duroi*, resting on stem of *Kleinia anteuphorbium*, Site M3; C, *E. duroi*, resting among stems of *Euphorbia officinarum*, Site M3; D, *E. duroi*, resting on soil among debris of low bush (Amaranthaceae), Site M18; E, *E. vermiculosa*, resting on quartzite pebble, site M9; F, *E. vermiculosa*, resting on twigs of shrub (*Salsola*, Amaranthaceae), site M9; G, *E. vermiculosa*, from Site M31, showing typical body colouration; H, *E. inexpectata*, resting on quartzite boulder, Site M12; I, *E. inexpectata*, accumulation of old shells at base of decayed plant of *Euphorbia officinarum*, Site M27. See Appendix for additional details of localities.

The southernmost populations of *E. vermiculosa* (south of Tan-Tan) form a distinct clade from those occurring disjunctly from the Oued Draa northwards. The intervening area is now occupied by living *E. inexpectata*, although the southernmost

locality of the latter (M27) also had subfossil *E. vermiculosa*, and at least 12 fresher shells were assigned to the hybrid *E. vermiculosa* × *E. inexpectata*. The molecular data (Fig. 3) show genetic differences between the northern and southernmost

**Table 6** Measurements of *Eremina* species from Morocco. Linear measurements of representative samples of shells are in mm; the estimate derived for area of aperture is in mm<sup>2</sup>; s.d.=one standard deviation. Mean area of aperture was estimated on the basis of it being circular, except that 20% of total area was lost to penultimate whorl; thus it was calculated from data tabulated below as  $\text{Area}=0.8 \times [(\text{mean AB} + \text{mean AH})/4 \times \pi]^2$ . Adult body size (relative volume) is based on direct comparisons of whole bodies extracted from shells and preserved in imms, from all collections made in March 2016. All material used is in CGAH (see Appendix for data).

Species		<i>dillwyniana</i>	<i>duroi</i>	<i>inexpectata</i>	<i>vermiculosa</i>
Shell breadth	mean	31.98	31.26	26.05	24.70
	sample s.d.	1.740	1.504	1.318	1.110
Shell height	mean	14.56	18.41	19.68	20.03
	sample s.d.	0.540	0.996	1.254	1.565
Aperture breadth	mean	11.64	13.06	12.06	11.34
	sample s.d.	0.607	0.790	0.480	0.548
Aperture height	mean	9.85	9.88	12.23	12.17
	sample s.d.	0.695	0.520	0.595	1.095
Estimated mean area of aperture		228	260	291	273
Whorls	range	3.8–4.3	4.1–4.3	3.3–3.9	3.5–4.1
N shells measured		16	20	22	24
Localities		M17	M3, M19	M12, M27	M7, M10, M13
Body size		medium-very large	small-very large	small-medium	small-large
	Mean body size	larger	larger	smaller	smaller
N adult bodies examined		5	60	14	25

populations of *E. vermiculosa* implying the taxon is polyphyletic. However, despite prolonged and repeated direct comparisons studying ample material, we have been unable to find any differences in shell characters (or genitalia) between these southern and northern clades within the *E. vermiculosa* shell phenotype.

As discussed above in our Molecular Results, based on *16SrRNA* data the possibility was discounted that the *Eremina* living near the Moroccan Atlantic coast are conspecific with *E. desertorum*. The latter species is currently accepted as having a very extensive range from S. Tunisia through N. Libya and Egypt to Israel, albeit with numerous large range gaps. The extent of geographical variation of shell characters in *E. desertorum* provides close parallels with the Moroccan taxa, since it also has umbilicate forms with low spires, globular forms, keeled forms, and even similar evidence that these local forms hybridize (Biggs, 1959; Ali *et al.*, 2016). As discussed above, the genital anatomy of *E. desertorum* is also closely similar to that of the Atlantic coastal taxa. Thus, when material from throughout their ranges is considered, there do not appear to be any clear morphological differences between *E. desertorum* and *E. dillwyniana*.

Ali *et al.* (2016) demonstrated that *Eremina desertorum desertorum* occupies drier regions than *E. d. irregularis* (A. Férussac 1821) in N. Egypt and that it has a relatively smaller shell aperture, leading to the conclusion that there has been selection for reduced aperture size in the drier regions to reduce water loss. Nevertheless, the same authors pointed out that shell shape might be affected by the different behaviour and the preferred habitats of the two subspecies, since *E. d. desertorum* occurs mainly in sandy deserts and feeds at and rests in shrubs, under stones or in rock crevices, whereas *E. d. irregularis* prefers stone deserts, feeding mainly on lichens and resting attached to sunny sides of stones. The flatter shells of *E. d. desertorum* were therefore seen as a possible adaptation to moving in dense shrubs and resting in narrow spaces under stones or in rocks, but no detailed data on resting places were provided.

The Moroccan *Eremina* appear to provide somewhat different insights into selection for shell shape. As detailed above, *E. duroi* has a flatter shell with an actually and relatively smaller aperture than the globular-shelled *E. vermiculosa* (Fig. 1, Table 7). Here though, unlike the situation with Egyptian *E. desertorum*, the correlation



**Table 7** Localities of Moroccan *Eremina* with more than one species, with interspecific hybrids, or both. The figures give counts of shells collected. \*=old shells only; †=subfossil. Detailed data on each site are in the Appendix.

Locality	<i>Eremina duroi</i>	<i>Eremina duroi</i> × <i>vermiculosa</i>	<i>Eremina inexpectata</i>	<i>Eremina inexpectata</i> × <i>vermiculosa</i>	<i>Eremina vermiculosa</i>	<i>Eremina</i> sp. unidentified (juv., broken)
#210 (wadi bed)	30*	0	0	0	13†	
#209 living	3	0	0	0	0	
dead	48	8	0	0	0	
#208 live	0	0	0	0	29	
subfossil	0	6†	0	0	0	
#199 subfossil	0	10	0	0	94	
M14i living	0	0	0	0	3	
dead	7	6	0	0	10	
M14ii dead	62	15	0	0	8	(7)
M14iii	5	4	0	0	10	(5)
M20 live	0	4	0	0	0	
dead	20	25	0	0	4	(1)
M21 live	8	17	0	0	0	
M22 live	1	0	0	0	0	
dead	5	24	0	0	4	(2)
M23 live	0	3	0	0	4	
dead	4	84	0	0	59	(5)
M25 live	1	0	0	0	0	
dead	22	1?	0	0	0	
M31 live	0	0	0	0	1	
dead	0	20	0	0	137	
M27 live	0	0	9	0	0	
dead	2*	8*	100	12	61*	
#148 live	0	0	12	0	0	
dead	0	0	105	5	0	
M12 live	0	0	6	0	0	
dead	0	0	89	15	0	
M10 live	0	0	0	0	2	
(by wadi) dead	0	0	1	0	30	

of aperture size with drier habitats is reversed: the larger aperture of *E. vermiculosa* occurring in the form consistently occupying drier regions (cf. Figs 4 and 5). From this, it can only be concluded that selection acting directly to reduce water loss is not of paramount importance in determining aperture size. Instead, as discussed above, the species differ to some extent in the amounts and types of vegetation in the habitats they occupy and perhaps in their preferred resting places, and these factors are more likely to be important. Future work probably needs to consider the role of predators in selection for shell size and shape, alongside possible behavioural differences in habitat use by the snails, albeit without ignoring adaptations to physiological factors such as

water loss and inter-related effects of high and low temperatures.

#### INTERSPECIFIC HYBRIDIZATION AND SPECIES-LIMITS

Table 7 summarises data on localities of Moroccan *Eremina* with more than one species, with intergrades (interpreted as interspecific hybrids), or both. Before drawing conclusions from the information presented there, it is necessary to discount samples of shells collected from in or beside wadi beds, which are likely to have lived in different locations upstream (sites #210, M10, M14ii, M14iii). Samples where one species is only known fossil must also be treated with caution

since past replacement of one species by another may have occurred without them ever coexisting, e.g. at site M27 where living *E. inexpectata* was found alongside shells of *E. vermiculosa* that may be subfossil which were eroding from colluvium, with old shells of *E. duroi* and *E. duroi* × *E. vermiculosa* also present on the ground surface nearby.

The remaining data nevertheless give a clear demonstration that hybrid populations occur in a narrow zone at or near where the ranges of living *E. duroi* and *E. vermiculosa* meet (Figs 1G, 7; sites M14i, M20, M21, M22, M23, M31). Despite this local hybridization, shells of the neighbouring populations of both species appear to have maintained their distinctive species characters, with no evidence of wider introgression. The narrow zone in which these intergrades (hybrids) occur implies that the shell characters of these two taxa have a genetic basis, rather than being developmental responses to environmental conditions. There is no evidence that those conditions change abruptly at the locations involved and this would seem highly unlikely in view of the varied physiographic contexts. Despite the lack of support from the phylogenetic reconstructions presented above, recognition of *E. duroi* and *E. vermiculosa* as “morphological species” is also justified since every normally developed adult shell from outside the hybrid zones is easily separated.

Subfossil shells of the hybrid of *E. duroi* with *E. vermiculosa* show that hybridization also occurred when they met in the past, far outside the modern range of either species (Fig. 7; sites #199, #208; perhaps also #209, M27). It is noteworthy therefore that *E. duroi* and *E. vermiculosa* show narrow modern zones of hybridization without introgression into neighbouring populations of either parental species, coupled with evidence that their hybridization elsewhere during the Quaternary did not lead to widespread introgression. This may suggest that intermediate shells are at a disadvantage. Ali *et al.* (2016) found a comparable abrupt transition between *E. desertorum desertorum* and *E. d. irregularis* in N. Egypt and argued that “selection is probably involved in the differentiation in shell shape and size”.

Hybrids of *E. inexpectata* with *E. vermiculosa* occur within populations of the former species (Figs 1D, 8; sites #148, M12, M27), but none were detected among neighbouring populations of *E. vermiculosa*. Occurrence of similar keeled

shell forms to that of *E. inexpectata* in some other genera of Helicidae has been shown to be of only infraspecific genetic significance, e.g. in *Iberus* (Elejalde *et al.*, 2008a, 2008b), *Murella* (Fiorentino *et al.*, 2012), *Theba* (Greve *et al.*, 2012) and *Rossmassleria* (Walther *et al.*, 2016). An argument for subspecies rank for *E. inexpectata* might also be supported by evidence of its hybridization with *E. vermiculosa* (Table 7), but the apparent lack of introgression affecting neighbouring populations of the latter species may suggest hybrids are at some disadvantage implying instead that species rank is warranted for *inexpectata*. Unfortunately, it is difficult to study the closest neighbouring populations of *Eremina*: The southern range limit known for *E. inexpectata* abuts the city of Tan-Tan where there is probably no suitable habitat remaining for the genus; the northern limit is a “sensitive” area with a police checkpoint at the bridge over the Oued Draa and a communications installation on the neighbouring hilltop close above our site M12, so only rapid and superficial searches close to roads are currently possible.

The narrow zones of hybridization described in this paper for *Eremina duroi* and *E. vermiculosa* and by Ali *et al.* (2016) for *Eremina d. desertorum* and *E. d. irregularis* appear to represent steep clines in gene frequencies for shell characters, although the genes involved were clearly not among those sequenced since neither study resolved any genetic differences diagnostic of the taxa involved. Endler (1977: 152–175) discussed the problems of interpreting whether steep clines are results of secondary intergradation following secondary contact of populations that diverged in allopatry, or products of primary intergradation resulting from parapatric speciation. His general conclusion (*op. cit.*: 178) was that primary and secondary intergradation produce the same kinds of geographical phenomena, and can evolve in the same order of magnitude of time, so it will be impossible to distinguish them by interpreting a given geographic pattern without knowing the palaeontological history of the region.

With *E. duroi* and *E. vermiculosa* evidence is presented above of at least two geographically separated hybridization zones involving living populations (Fig. 7, Table 7), respectively W. of Guelmim and SW. of Tan-Tan. It can be argued that both of these result from recent secondary contacts of populations, as might the Egyptian

contact zone between *E. desertorum desertorum* and *E. d. irregularis* described by Ali *et al.* (2016). If so, their relevance to judging species limits may be uncertain because of insufficient time (too few generations) having elapsed for the eventual outcomes of hybridization to become apparent, e.g. whether widespread introgression will result, or reduction of hybrid frequency due to development of isolating mechanisms.

However, with *E. duroi* and *E. vermiculosa* there is also a third southernmost hybrid zone (Fig. 7; site #199 at 26°34'N.) known from Quaternary subfossil shells in a region that also has subfossils of both parent species but which is now dry desert without living populations of either of them. Subfossil hybrid shells of the same parentage are also known further north (site #208) close to living populations of both parent species. From these subfossil hybrids it seems clear that in the past widespread introgression did not lead to merging of the parental shell types, since to the present day they remain distinctive on either side of a long border where their ranges sometimes meet (Fig. 7). This appears to provide a strong argument for regarding *E. duroi* and *E. vermiculosa* as distinct biological species that have met and hybridized in the past, yet maintained their distinctive shell characters.

Both *E. duroi* (at least the northern populations) and *E. vermiculosa* are also very commonly found as old shells of varying ages where their populations live now, including at the sites with hybrids. This implies that neither of them has recently colonised the more northerly regions where hybrids currently occur, so it seems unlikely that they have very recently come into secondary contact coincidentally in both of the present-day hybrid zones. Instead, it seems more likely that hybrids are at some selective disadvantage so that narrow hybrid zones may have been long persistent and therefore they still occur in places that are widely separated geographically (cf. Fig. 7).

Hybrid zones involving *E. dillwyniana* s.s. have not been found, although detailed searches have not been carried out. The phylogenetic interpretation of our DNA sequence data (Fig. 3) shows the lineage containing all *E. duroi* and the northern populations of *E. vermiculosa* (L4) without resolution of those two species, whereas there is strong support for *E. inexpectata* (L3) having diverged earlier and full support for *E. dillwyniana* (L1) as diverging earlier than any of the other

populations sampled. It therefore seems reasonable to expect that the lineages diverged earlier (*E. dillwyniana*, *E. inexpectata*) are at least as likely to have attained the status of independent species as are the more recently diverging *E. duroi* and northern *E. vermiculosa*.

The genetic distances (p-distances) between the four Moroccan lineages of *Eremina* range from 8.2% to 12.1% for COI and from 3.8% to 6.2% for 16S (Table 4), whereas those obtained by Ali *et al.* (2016) for the 16S gene fragment in Egyptian *E. desertorum* populations averaged much lower at 0.9% (from 0.2% to 1.7%). Genetic distances alone are regarded as insufficient to decide specific or subspecific rank of taxa. Nevertheless, these distances are much higher between our four Moroccan lineages than those found within Egyptian *E. desertorum*, despite all the taxa concerned belonging to the same genus and living in similar semi-desert conditions. Furthermore, the different Moroccan lineages are well supported in our tree (Fig. 3), although we could analyze only a few sequences or only one for each of those lineages. Hence, whereas Ali *et al.* (2016) gave subspecific rank to the two different Egyptian taxa, the four Moroccan taxa show much greater p-distances, which may imply species rank would be more appropriate for them. The differences in shell morphology are also greater between each of the Moroccan forms treated here as species than they are between the two Egyptian *Eremina desertorum* subspecies.

Treatment of all four Moroccan forms at species rank is thus based mainly on the very narrow modern hybrid zones between *E. duroi* and *E. vermiculosa* along with evidence that their hybridization elsewhere during the Quaternary did not lead to widespread introgression. Nevertheless, lack of sympatry, evidence of repeated hybridization where forms meet, the rather small differences in habitats, lack of differences in genital morphology and sometimes unresolved DNA sequences may imply that the speciation process in these taxa may still be at an early stage or incomplete, with no evidence of species isolating mechanisms having developed.

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## APPENDIX

List of specimens studied. Species and inter-specific hybrids are listed in alphabetical order (with unidentified *Eremina* at the end); records within each species are listed from north to south. For each record, data are listed in the following sequence: Site field number (prefaced with # for records from 1986, with M for records from 2016), Locality name, Coordinates, Habitat, Altitude (for 2016 samples, in metres), Condition of the freshest specimens (live/old shells/subfossil), Number of specimens, Type of specimens (sh/bod/spm), H&S Number, NMW.Z Accession Number, Other notes. Moroccan place names often differ from one map to another, partly because of different approaches to transcription of Arabic; we have mainly kept to the original forms as used in contemporary notes and on specimen labels. Revision of road numbers has also mainly been avoided, most of those used in 1986 having been changed by 2016.

*Eremina dillwyniana* s.s.

#154, By P41 [now N1] 43km SW. along road from Tan-Tan-Plâge, 28°15'N 11°37'W, open sandy/gravelly plain with scattered low (succulent) bushes, old shells, 31 sh, 1986.198.3, NMW.Z. 1993.051.2738.

M17, ca 1km S. of N1 at 41.5km due SW. of El Ouatia (centre), 28°15'N 11°40'W, sandy and gravelly plain near coast, with up to 50% cover of low shrubs, 28m, living, 5 sh & bod, 3 spm juv, 44 sh dead, CGAH, DNA sample kept.

#153, 1km SE. of P41 [now N1] at ca 40km SW. along road from Tan-Tan-Plâge, 28°14'N 11°35'W, open sandy plain with patchy cover of succulent *Euphorbia* and low thorn bushes, living (umbilicate), 3 spm, 1986.197.3, NMW.Z. 1993.051.2733; ditto, 45 sh, 1986.197.2, NMW.Z. 1993.051.6.

#155, By P41 [now N1] ca 60km SW. along road from Tan-Tan-Plâge, 28°10'N 11°46'W, open sandy/rocky (calcareous sandstone) plain with patchy low herbs, old shells, 13 sh, 1986.199.1, NMW.Z. 1993.051.2740.

#156, By P41 [now N1] 93km SW. along road from Tan-Tan-Plâge, 28°02'N 12°03'W, plain behind beach with surface of cobbles (sandstone) and gravelly sand with patches of herbs, old shells, 35 sh, 1986.200.2, NMW.Z. 1993.051.2744.

*Eremina duroi*

#331, Coast by road 7064 [now R104] 2km NE. of Mirleft [Mihrlleft], 29°36'N 10°02'W, rocky slopes above sea cliffs (sandstone) with patchy cover of succulent *Euphorbia* and other herbs, living, 2 spm, 1986.375.08, NMW.Z. 1993.051.3800; ditto, 28 sh, 1986.375.07, NMW.Z. 1993.051.4539.

M3, by coast N. of R104 at 4.4km due NE. of Mirleft (centre), 29°36'N 10°02'W, stony slopes (sandstone) above top of sea-cliff, with incomplete cover of low shrubs, mainly succulents, 48m, living, 23 sh & bod, 1 juv. spm, CGAH, DNA sample kept.

M95, near coast at 3.0km due NE. of Mirleft (centre), 29°35'N 10°2'W, rocky slopes (conglomerate and head) with patchy bushes (including succulents), 3–12m, living seen in field, 2 sh dead, CGAH.

#332, By road 7064 [now R104] ca 17.5km SW. along road from Mirleft [Mihrlleft], 29°28'N 10°06'W, rocky slopes (sandstone) above coast, with patchy cover of succulent *Euphorbia* and bushes, living, 11 spm, 1986.376.18, NMW.Z.

1993.051.125; ditto, 24 sh, 1986.376.14, NMW.Z. 1993.051.3.

M4, by R104 at 7.3km due NE. of Sidi Ifni (centre), 29°26'N 10°07'W, open stony (sandstone) slopes above coast with low bushes including succulent *Euphorbia*, 86m, living, 4 sh & bod, 11 sh dead, CGAH, DNA sample kept.

M30, by road 31km due W. of Guelmim (centre), 29°01'N 10°23'W, stony slope (hard sandstone) with gravelly and sandy surface, rather sparse vegetation of low shrubs including succulents, 195m, living, 1 sh & bod, 23 sh dead, CGAH.

M94, by R104 at 5.1km due NE. of Sidi Ifni (centre), 29°25'N 10°8'W, rocky slopes (calcareous sandstone) with open scrub (including much *Euphorbia officinarum*, some *E. regis-jubae* and *Kleinia anteuophorbium*), 70–74m, living seen in field, 2 sh dead, CGAH.

M93, 13.6km due E. of Echatea El Abied (38.0km due W. of Guelmim, centre), 28°59'N 10°27'W, stony (sandstone) slopes with sandy patches, locally with open cover of low shrubs (including succulent *Kleinia anteuophorbium* and *Euphorbia officinarum*), 145m, old shells, 4 sh dead, CGAH.

M29, by road at 51km due W. of Guelmim (centre), 28°58'N 10°35'W, stony (quartzite) plain with loose cobbles and much blown sand, vegetation of sparse low shrubs including succulents, 45m, living, 4 sh & bod, 9 sh dead, CGAH.

M28, by road at 49.7km due W. of Guelmim (centre), 28°58'N 10°34'W, gravelly and stony plain (quartzite pebbles) with very sparse low vegetation of shrubs including succulents, 45m, old shells, 64 sh dead, CGAH.

M89, Echatea El Abied (51.7km due W. of Guelmim, centre), 28°58'N 10°36'W, sandy plain near coast, scattered stones, sparse cover of low shrubs (mainly succulent chenopods, few *Euphorbia officinarum*), 33m, living seen in field, 1 sh dead, CGAH.

M90, ca 1km inland along road from Echatea El Abied (50.8km due W. of Guelmim, centre), 28°58'N 10°35'W, sandy plain with scattered rocks (calcareous sandstone), patches of low scrub (succulent chenopods, *Euphorbia officinarum*, etc.), 48m, living seen in field, 1 sh dead, CGAH.

M91, ca 3.9km due E. along road from Echatea El Abied (47.5km due W. of Guelmim), 28°58'N 10°33'W, lower parts of rocky (hard sandstone) slope with much loose rock, some blown sand, locally with cover of shrubs (mainly succulent

*Euphorbia officinarum* and *Kleinia anteupehorbium*), 80–86m, living immature seen in field, 3 sh dead, CGAH.

M29B, by road at 47km due W. of Guelmim (centre), 28°57'N 10°32'W, rocky (slaty) crags and slopes in small gorge, open vegetation of low shrubs including succulents, 117m, 1 living, 1 live adult and ca 15 sh dead, not kept.

M92, S. of road 6.8km due ESE. of Echatea El Abied (45.4km due W. of Guelmim), 28°57'N 10°32'W, base of sandstone/slaty slope with much blown sand, open cover of low shrubs (including succulent *Kleinia anteupehorbium* and *Euphorbia officinarum*), 146–150m, living, 2 sh & bod, 4 sh dead, CGAH.

#151, By P41 [now N1] ca 10km WNW. along road from Tan-Tan, 28°28'N 11°11'W, crags and rocky slopes (limestone; calcareous sandstone) with patchy low bushes and herbs, old shells, 26 sh, 1986.195.7, NMW.Z. 1993.051.2727.

#152, By P41 [now N1] ca 5km SW. along road from Tan-Tan-Plâge, 28°27'N 11°21'W, flat rocky area (sandstone) on top of seacliffs with patchy low succulents and herbs, old shells, 14 sh, 1986.196.2, NMW.Z. 1993.051.2730.

#150, By P41 [now N1] 2km NW. of Tan-Tan, 28°26'N 11°06'W, sandy plain with scattered low bushes, old shells (some subfossil), 40 sh, 1986.194.5, NMW.Z. 1993.051.2718.

M26, just S. of N1 at 4.2km due NW. of Tantan (centre), 28°28'N 11°08'W, gentle slope with sand (some gravel locally) and open vegetation of shrubs including succulents, 116m, living, 13 sh & bod, 32 sh dead, CGAH.

M27, ca 1km S. of N1 at 3.6km due E. of Tantan (centre), 28°26'N 11°04'W, NW. to W.-facing rocky slopes (hard sandstone) with sparse vegetation of low shrubs; gravelly and sandy lower slopes with patchy low shrubs, 72m, old shells, 2 sh dead, CGAH.

M19, just S. of N1 at 13.5km due SW. of El Ouatia (centre), 28°24'N 11°25'W, stony (calcareous sandstone) plain with temporary pool in shallow depression, with low shrubs fringing water, 40m, living, 7 sh & bod, CGAH, DNA sample kept.

M18, ca 0.5km S. of N1 at 15km due SW. of El Ouatia (centre), 28°23'N 11°26'W, silty hollows in stony plain (calcareous sandstone) with ca 50% cover of succulent *Euphorbia* and spiny shrubs, 27m, living, 4 sh & bod, 66 sh dead, CGAH, DNA sample kept.

M25, by R101 at 9.3km due SW. of Tantan (centre), 28°23'N 11°11'W, stony plain (sandstone) with very sparse low bushes, depressions with silty soil and incomplete cover of low shrubs up to 1.5m high, 211m, living, 1 sh & bod, 22 sh dead, CGAH.

M24, by R101 at 27.4km due SW. of Tantan (centre), 28°13'N 11°14'W, gravelly and sandy plain (calcareous sandstone) with patchy low shrubs in hollows prone to flooding, 201m, living, 2 sh & bod, 20 sh dead, CGAH.

#210, By P44 ca 47km SW. along road from Tantan, 28°09'N 11°16'W, sandy alluvium along bed of wadi, old shells, 30 sh, 1986.254.6, NMW.Z. 1993.051.2904.

M23, just W. of R101 at 36.3km due SW. of Tantan (centre), 28°09'N 11°16'W, rocky S.-facing limestone hillslope, rather sparse low shrubs with succulents locally, 134m, old shells, 4 sh dead, CGAH.

M22, just W. of R101 at 36.5km due SW. of Tantan (centre), 28°09'N 11°16'W, rocky S.-facing limestone hillslope, rather sparse low shrubs with succulents locally, 124m, living, 1 sh & bod, 5 sh dead, CGAH.

#209, By P44 ca 48km SW. along road from Tan-Tan, 28°08'N 11°17'W, rocky hillslope (calcareous sandstone and limestone), with patchy low shrubs and herbs, living, 3 spm, 1986.253.4, NMW.Z. 1993.051.2897; ditto, 48 sh, 1986.253.3, NMW.Z. 1993.051.2896.

M20, ca 1km W. of R101 at 38km due SW. of Tantan (centre), 28°08'N 11°17'W, rocky hillslope (hard limestone) with much blown sand, vegetation of rather sparse low shrubs, 102m, old shells, 20 sh dead, CGAH.

M21, just W. of R101 at 37.4km due SW. of Tantan (centre), 28°08'N 11°17'W, rocky S.-facing limestone hillslope with rather sparse low shrubs (including succulents locally), 119m, old shells, 8 sh dead, CGAH.

M14i, ca 0.5km E. of R101 at 36.4km due SW. of Tantan (centre), 28°08'N 11°16'W, rocky slopes (mainly quartzite cobbles), sparse low vegetation of shrubs and some succulents, 109m, old shells, 7 sh dead, CGAH, sample i from higher levels above wadi (never flooded).

M14ii, ca 0.5km E. of R101 at 36.4km due SW. of Tantan (centre), 28°08'N 11°16'W, rocky slopes (mainly quartzite cobbles), sparse low vegetation of shrubs and some succulents, 109m, old shells, 62 sh dead, CGAH, sample ii mainly or partly



from bed of small wadi (prone to occasional flooding).

M14iii, ca 0.5km E. of R101 at 36.4km due SW. of Tantan (centre), 28°08'N 11°16'W, rocky slopes (mainly quartzite cobbles), sparse low vegetation of shrubs and some succulents, 109m, old shells, 5 sh dead, CGAH, sample iii from same areas as both sample i and sample ii.

M16, ca 0.5km S. of N1 at 34.4km due E. of Tarfaya (centre), 27°59'N 12°35'W, plain near coast with sandy surface and patches of exposed limestone, rather sparse vegetation of low shrubs, 34m, old shells, 20 sh dead, CGAH.

#158, By P41 [now N1] ca 35km E. of Tarfaya, 27°57'N 12°34'W, sandy and rocky (sandstone) plain with patchy herbs and low shrubs, shells subfossil, from sands, 50 sh, 1986.202.4, NMW.Z. 1993.051.4540.

#157, By P41 [now N1] ca 66km E. of Tarfaya, 27°54'N 12°22'W, shells eroding from sand deposits on sandstone cliffs, subfossil, 6 sh, 1986.201.2, NMW.Z. 1993.051.2747.

#207, By road to Smara [= P44] ca 92km SW. along road from Tan-Tan, 27°54'N 11°33'W, low sandstone crags and rocky/sandy slopes with patches of succulent *Euphorbia*, low bushes and herbs, old shells, 4 sh, 1986.251.2, NMW.Z. 1993.051.2885.

M15, ca 1.5km S. of N1 at 53km due E. of Tarfaya (centre), 27°54'N 12°23'W, sandy plain with patches of stony ground, sparse vegetation of low shrubs, 32m, old shells, 24 sh dead, CGAH.

#160, By P41 [now N1] 10km S. along road from Tarfaya, 27°51'N 12°54'W, rocky (calcareous sandstone) plain with patchy herbs, low shrubs and succulent *Euphorbia*, old shells, 34 sh, 1986.204.4, NMW.Z. 1993.051.2757.

#161, By P41 [now N1] 24km NNE. along road from Daoura, 27°38'N 12°54'W, sand and rocky (calcareous sandstone) plain with patchy herbs, low shrubs and succulent *Euphorbia*, living, 3 spm, 1986.205.4, NMW.Z. 1993.051.2761; ditto, some living, 43 sh, 1986.205.3, NMW.Z. 1993.051.2760.

#lacking site no., By road ca 105km N. along road [= P44] from Smara, 27°24'N 11°45'W, sandy/gravelly plain with patches of succulent *Euphorbia*, sparse herbs and low shrubs, old shells, 27 sh, 1986.250.2, NMW.Z. 1993.051.2880.

#162, ca 1km E of P41 [now N1] at ca 8km S. of Daoura, 27°22'N 13°02'W, open sandy/

gravelly plain with scattered bushes, patches low shrubs and succulent *Euphorbia*, old shells, 17 sh, 1986.206.3, NMW.Z. 1993.051.2764.

#204, By road [= P44] 74km along road N. of Smara, 27°22'N 11°50'W, sandy/gravelly plain with sparse low bushes and herbs, some living, 53 sh, 1986.248.2, NMW.Z. 1993.051.2875; ditto, living, 6 spm, 1986.248.3, NMW.Z. 1993.051.2876.

#205, By road [= P44] 74km along road N. of Smara, 27°22'N 11°50'W, sandy/gravelly plain, subfossil shells eroding from surface of sand, 6 sh, 1986.249.1, NMW.Z. 1993.051.2878.

#163, 0.5km W of P41 [now N1] at 10km S. of Daoura, 27°21'N 13°03'W, rocky hillslope (calcareous sandstone) with sparse herbs and few low shrubs, some living, 28 sh, 1986.207.4, NMW.Z. 1993.051.2771; ditto, old shells, 8 sh or spm, 1986.207.5, NMW.Z. 1993.051.7.

#164, By P41 [now N1] ca 15km W. along road from Laayoune [Al-'Ayun], 27°10'N 13°21'W, open sandy plain with gravel patches with patchy low shrubs and herbs, old shells, 12 sh, 1986.208.2, NMW.Z. 1993.051.2774.

#203, By road [= P44] 42km N. along road from Smara, 27°04'N 11°46'W, open gravelly and sandy plain with very sparse herbs and low bushes, shells fossil eroding from sands, 40 sh, 1986.247.4, NMW.Z. 1993.051.2869; ditto, Subfossil shells, 24 sh, 1986.247.06, NMW.Z. 1993.051.4538.

#195, By P44 [now N5] ca 19km SE. along road from Laayoune, 27°01'N 13°08'W, open sandy and gravelly plain with patches of bushes and herbs, old shells, 14 sh, 1986.239.2, NMW.Z. 1993.051.2846.

#165, By P41 [now N1] ca 21km SSW. along road from Laayoune-Plâge, 26°53'N 13°31'W, open sandy and rocky (sandstone) plain with sparse low shrubs, old shells, 9 sh, 1986.209.1, NMW.Z. 1993.051.4542.

#196, By P44 [now N5] ca 51km along road SSE. from Laayoune, 26°47'N 13°07'W, sandy plain with patchy thorn bushes, succulent *Euphorbia* and other herbs, old shells, 29 sh, 1986.240.2, NMW.Z. 1993.051.2849.

#167, By P41 [now N1] ca 56km SSW. along road from Laayoune-Plâge, 26°39'N 13°38'W, sandy/gravelly plain with patches of bushes and herbs, old shells, 12 sh, 1986.211.1, NMW.Z. 1993.051.2780.

#166, By P41 [now N1] ca 52km SSW. along road from Laayoune-Plâge, 26°39'N 13°36'W, open sandy plain with patches of low shrubs

and herbs, old shells, 31 sh, 1986.210.1, NMW.Z. 1993.051.2778.

#197, By P44 [now N5 or N14] 82km SSE. along road from Laayoune, 26°38'N 13°01'W, sandy and gravelly plain with scattered low bushes and herbs, old shells (some subfossil, from surface of sands), 62 sh, 1986.241.3, NMW.Z. 1993.051.2853.

#198, By P44 [now N14?] ca 108km SE. along road from Laayoune, 26°36'N 12°46'W, open sandy/gravelly plain with sparse herbs and low bushes, shells subfossil, eroding from sands, 68 sh, 1986.242.2, NMW.Z. 1993.051.4537.

#168, By P41 [now N1] ca 74km SW. along road from Laayoune-Plâge, 26°35'N 13°47'W, low sandstone crags and sandy slopes with bushes locally, shells subfossil from sands, 19 sh, 1986.212.4, NMW.Z. 1993.051.2785.

#194, By P41 [now N1] ca 70km NE. along road from Boujdour, 26°31'N 13°55'W, sandy and gravelly plain with patches of bushes and herbs, few shells fresh, 33 sh, 1986.238.2, NMW.Z. 1993.051.2842.

#170, By P41 [now N1] ca 63km NE. along road from Boujdour, 26°29'N 13°54'W, sandy plain with patchy bushes and herbs, old shells, 20 sh, 1986.214.1, NMW.Z. 1993.051.2788.

#171, By P41 [now N1] ca 29km NE. along road from Boujdour, 26°16'N 14°14'W, sandy and rocky (calcareous sandstone) plain with patchy herbs and few shrubs, old shells, 18 sh, 1986.215.3, NMW.Z. 1993.051.2791.

#172, By P41 [now N1] ca 5km NE. along road from Boujdour, 26°08'N 14°26'W, rocky (calcareous sandstone) and sandy plain with scattered bushes and low herbs, old shells, 14 sh, 1986.216.2, NMW.Z. 1993.051.2794.

#173, ca 1km E. of P41 at 21km S. of Boujdour, 25°56'N 14°31'W, rocky slopes (calcareous sandstone) with patchy herbs and low shrubs, old shells, 26 sh, 1986.217.4, NMW.Z. 1993.051.2798.

#174, By P421 [now N1] ca 31km S. along road from Boujdour, 25°52'N 14°34'W, rocky (calcareous sandstone) slopes with patchy herbs, old shells, 9 sh, 1986.218.2, NMW.Z. 1993.051.2801.

#175, By track [now N1] ca 46km SW. of Boujdour, 25°47'N 14°30'W, rocky (calcareous sandstone) and sandy plain with patchy herbs and low shrubs, old shell (maybe subfossil), 1 sh, 1986.219.1, NMW.Z. 1993.051.2803.

#176, By track [now N1] ca 75km SW. of Boujdour, 25°32'N 14°28'W, sandy and gravelly

plain with sparse herbs and low shrubs, old shells, 23 sh, 1986.220.1, NMW.Z. 1993.051.2805.

#192, By track [now N1] ca 288km NE. along track from Ad-Dakhla (ca 82km SW. along track from Boujdour), 25°29'N 14°26'W, sandy/gravelly plain with patchy low bushes and herbs, old shells, 20 sh, 1986.236.2, NMW.Z. 1993.051.2839.

#191, By track ca 256km NE. along track from Ad-Dakhla (ca 114km SW. along track from Boujdour), 25°12'N 14°28'W, sandy/gravelly plain with patchy thorn bushes and low *Acacia* trees, old or subfossil shells, 34 sh, 1986.235.2, NMW.Z. 1993.051.2836.

#190, By track [now N1] ca 218km NE. of Ad-Dakhla (ca 152km SW. along track from Boujdour), 24°53'N 14°31'W, sandy/gravelly plain with sparse low thorn bushes, old shells, 13 sh, 1986.234.1, NMW.Z. 1993.051.2834.

#177, By track [now N1] ca 155km SW. of Boujdour (ca 219km NE. along track from Ad-Dakhla), 24°52'N 14°31'W, gravelly/sandy plain with very sparse herbs, old shells (possibly all subfossil), 27 sh, 1986.221.1, NMW.Z. 1993.051.2806.

#178, By track [now N1] ca 164km SW. of Boujdour (ca 210km NE. along track from Ad-Dakhla), 24°47'N 14°31'W, gravelly/sandy plain with very sparse herbs, old shells (possibly all subfossil), 18 sh, 1986.222.1, NMW.Z. 1993.051.2808.

#179, By track [now N1] ca 213km SW. of Boujdour (ca 161km NE. along track from Ad-Dakhla), 24°27'N 14°43'W, gravelly/sandy plain with very sparse herbs, old shells (possibly all subfossil), 17 sh, 1986.223.1, NMW.Z. 1993.051.2809.

#189, By track [now N1] ca 144km NE. along track from Ad-Dakhla, 24°25'N 14°53'W, rocky (calcareous sandstone) and sandy slopes with patchy low bushes and few herbs, some living, 18 sh, 1986.233.2, NMW.Z. 1993.051.2831; ditto, dead shells, 13 sh, 1986.233.5, NMW.Z. 1993.051.9.

#188, By track [now N1] ca 131km NE. of Ad-Dakhla along track, 24°23'N 15°01'W, crag and rocky slopes of calcareous sandstone, with sand banked on rocks and with sparse herbs and low shrubs, old shells (some subfossil, from sand/sandstone), 31 sh, 1986.232.2, NMW.Z. 1993.051.2827.

#186, By track [now N1] ca 107km NE. along track from Ad-Dakhla, 24°15'N 15°10'W, rocky

slopes (calcareous sandstone) with very sparse herbs and low shrubs, living, 8 spm, 1986.230.3, NMW.Z. 1993.051.2823; ditto, 12 sh, 1986.230.2, NMW.Z. 1993.051.2822; ditto, subfossil, 4 sh, 1986.230.4, NMW.Z. 1993.051.2824.

#180, By track [now N1] *ca* 278.5km SW. of Boujdour (*ca* 95.5km NE. along track from Ad-Dakhla), 24°10'N 15°18'W, sandy/gravelly plain with sparse herbs, old shells, 30 sh, 1986.224.1, NMW.Z. 1993.051.2811.

#185, By track [now N1] *ca* 78km NE. along track from Ad-Dakhla, 24°07'N 15°25'W, low crag of shelly calcareous sandstone and sandy slopes nearby with sparse low bushes, shells subfossil from fissure fills, colluvium and blown sand, 29 sh, 1986.229.2, NMW.Z. 1993.051.2820.

#184, On track [now N1] 63km NE. along track from Ad-Dakhla, 24°01'N 15°31'W, open plain with surface of sandstone rock and gravelly sand (no vegetation), old shells, 23 sh, 1986.228.1, NMW.Z. 1993.051.2818.

#183, 2km NW. of road at 37km NE. along road from Ad-Dakhla, 23°57'N 15°46'W, low sandstone crags and slope with banked-up blown sand, subfossil shells from slopes, 23 sh, 1986.227.1, NMW.Z. 1993.051.2816.

#182, By road 32km NE. along road from Ad-Dakhla, 23°53'N 15°47'W, sandy slopes with very sparse herbs, subfossil shells eroding from sands, 67 sh, 1986.226.2, NMW.Z. 1993.051.2814.

#181, By road *ca* 7km NE. of Ad-Dakhla, 23°46'N 15°55'W, sandy/gravelly plain, subfossil shells eroding from sands, 51 sh, 1986.225.1, NMW.Z. 1993.051.2812.

*Eremina duroi* × *E. vermiculosa*

M31, by road at 24.3km due W. of Guelmim (centre), 28°59'N 10°19'W, gravelly (hard sandstone) hillslope with sandy patches, sparse cover of low shrubs including many succulents, 195m, old shells, 20 sh dead, CGAH.

M27, *ca* 1km S. of N1 at 3.6km due E. of Tantan (centre), 28°26'N 11°04'W, NW. to W.-facing rocky slopes (hard sandstone) with sparse vegetation of low shrubs; gravelly and sandy lower slopes with patchy low shrubs, 72m, old shells, 8 sh dead, CGAH.

M25, by R101 at 9.3km due SW. of Tantan (centre), 28°23'N 11°11'W, stony plain (sandstone) with very sparse low bushes, depressions with silty soil and incomplete cover of low shrubs up to 1.5m high, 211m, old shell, 1 sh dead, CGAH.

M23, just W. of R101 at 36.3km due SW. of Tantan (centre), 28°09'N 11°16'W, rocky S.-facing limestone hillslope, rather sparse low shrubs with succulents locally, 134m, living, 3 sh & bod, 84 sh dead, CGAH.

M22, just W. of R101 at 36.5km due SW. of Tantan (centre), 28°09'N 11°16'W, rocky S.-facing limestone hillslope, rather sparse low shrubs with succulents locally, 124m, old shells, 24 sh dead, CGAH.

#209, By P44 *ca* 48km SW. along road from Tan-Tan, 28°08'N 11°17'W, rocky hillslope (calcareous sandstone and limestone), with patchy low shrubs and herbs, old shells, 8 sh, 1986.253.3, NMW.Z. 1993.051.2896.

M20, *ca* 1km W. of R101 at 38km due SW. of Tantan (centre), 28°08'N 11°17'W, rocky hillslope (hard limestone) with much blown sand, vegetation of rather sparse low shrubs, 102m, living, 4 sh & bod, CGAH, DNA sample kept.

M21, just W. of R101 at 37.4km due SW. of Tantan (centre), 28°08'N 11°17'W, rocky S.-facing limestone hillslope with rather sparse low shrubs (including succulents locally), 119m, living, 2 sh & bod, 17 sh dead, CGAH.

M14i, *ca* 0.5km E. of R101 at 36.4km due SW. of Tantan (centre), 28°08'N 11°16'W, rocky slopes (mainly quartzite cobbles), sparse low vegetation of shrubs and some succulents, 109m, old shells, 6 sh dead, CGAH, sample i from higher levels above wadi (never flooded).

M14ii, *ca* 0.5km E. of R101 at 36.4km due SW. of Tantan (centre), 28°08'N 11°16'W, rocky slopes (mainly quartzite cobbles), sparse low vegetation of shrubs and some succulents, 109m, old shells, 15 sh dead, CGAH, sample ii mainly or partly from bed of small wadi (prone to occasional flooding).

M14iii, *ca* 0.5km E. of R101 at 36.4km due SW. of Tantan (centre), 28°08'N 11°16'W, rocky slopes (mainly quartzite cobbles), sparse low vegetation of shrubs and some succulents, 109m, old shells, 4 sh dead, CGAH, sample iii from same areas as both sample i and sample ii.

#208, By P44 *ca* 70km SW. along road from Tan-Tan, 27°59'N 11°26'W, rocky sandstone slopes, with patchy succulent *Euphorbia*, other herbs and low bushes, shells subfossil from colluvium and fissure fills, 6 sh, 1986.252.4, NMW.Z. 1993.051.4.

#199, 1.5km N. of P44 [now N14?] at 141km SE. along road from Laayoune, 26°34'N 12°28'W, open sandy/gravelly plain with sparse herbs



and low bushes, shells subfossil, from sands, 10 sh, 1986.243.3, NMW.Z. 1993.051.2859.

*Eremina inexpectata*

M10, ca 1km N. of N1 at 1.75km due NNE. of Oued Draa at N1 road bridge, 28°33'N 10°56'W, sandy ground above wadi floodplain and stony (sandstone) slopes nearby, with patchy bushes or low bushes, 22m, old shells, 1 sh, CGAH.

M12, ca 0.3km SW. of N1 at 0.6km due SW. of Oued Draa at N1 road bridge, 28°33'N 10°57'W, rocky and stony slopes (mainly quartzite cobbles and boulders) with sparse vegetation of succulents and few low shrubs, 57m, living, 6 sh & bod, 2 juv spm, 89 sh dead, CGAH, DNA sample kept.

#148, By P41 ca 19km NE. along road from Tan-Tan, 28°31'N 10°57'W, rocky sandstone hillslopes with sparse herbs and low bushes, surface with small boulders, living, 12 spm, 1986.192.8, NMW.Z. 1993.051.2704; ditto, 105 sh, 1986.192.7, NMW.Z. 1993.051.14.

#149, By P41 [now N1] ca 8km NE. of Tan-Tan, 28°29'N 11°02'W, rocky (sandstone) and sandy hillslopes with sparse herbs and low bushes, fresh shells, 65 sh, 1986.193.3, NMW.Z. 1993.051.2709.

#lacking site number, "also found by P41 [now N1] ca 4km NE. of Tan-Tan (numerous shells of unknown age)" 28°27'N 11°04'W, no habitat data, apparently no specimens collected.

M27, ca 1km S. of N1 at 3.6km due E. of Tantan (centre), 28°26'N 11°04'W, NW. to W.-facing rocky slopes (hard sandstone) with sparse vegetation of low shrubs; gravelly and sandy lower slopes with patchy low shrubs, 72m, living, 9 sh & 8 bod, 2 juv spm, 100 sh dead, CGAH.

*Eremina inexpectata* × *E. vermiculosa*

M12, ca 0.3km SW. of N1 at 0.6km due SW. of Oued Draa at N1 road bridge, 28°33'N 10°57'W, rocky and stony slopes (mainly quartzite cobbles and boulders) with sparse vegetation of succulents and few low shrubs, 57m, old shells, 15 sh, CGAH.

#148, By P41 ca 19km NE. along road from Tan-Tan, 28°31'N 10°57'W, rocky sandstone hillslopes with sparse herbs and low bushes, surface with small boulders, old shells, 5 sh, 1986.192.7, NMW.Z. 1993.051.14.

M27, ca 1km S. of N1 at 3.6km due E. of Tantan (centre), 28°26'N 11°04'W, NW. to W.-facing rocky slopes (hard sandstone) with sparse vegetation

of low shrubs, gravelly and sandy lower slopes with patchy low shrubs, 72m, old shells, 12 sh dead, CGAH.

*Eremina vermiculosa*

M33, ca 1km N. of N12 at 26km due ENE. of Taghijit (centre), 29°06'N 09°10'W, shallow sandy depression in rocky (quartzite) plain, with open cover of shrubs and few taller bushes, 709m, old shells, 23 sh dead, CGAH, eroding from sand (no fresh shells here).

#335, By P41 [now N1] ca 21km NE. along road from Goulimine, 29°05'N 9°53'W, sandy and rocky (calcareous sandstone) plain, with patchy cover of succulent *Euphorbia*, other herbs and low shrubs, living, 3 spm, 1986.379.11, NMW.Z. 1993.051.3831; ditto, 51 sh, 1986.379.10, NMW.Z. 1993.051.3830.

#337, By P30 [now N12] 16km E. along road from Tagmoute, 29°04'N 9°17'W, rocky hillslopes (sandstone), with sparse cover of low bushes and herbs, few succulent *Euphorbia*, living, 1 spm, 1986.381.09, NMW.Z. 1993.051.3844; ditto, 67 sh, 1986.381.08, NMW.Z. 1993.051.3843.

M31, by road at 24.3km due W. of Guelmim (centre), 28°59'N 10°19'W, gravelly (hard sandstone) hillslope with sandy patches, sparse cover of low shrubs including many succulents, 195m, living, 1 sh & bod, 137 sh dead, CGAH.

#143, By P41 [now N1] 5km WSW. of Goulimine [Guelmin], 28°58'N 10°06'W, open sandy plain with barley fields, subfossil shells eroding from sand deposits, 7 sh, 1986.187.6, NMW.Z. 1993.051.2.

M32, W. bank of Oued Noun at 16.4km due W. of Guelmim (centre), 28°58'N 10°14'W, stony hillside (slaty rock) with open vegetation of low shrubs and succulents, 184m, living, 1 sh & bod, 43 sh dead, CGAH.

#144, By P41 [now N1] 11km WSW. along road from Goulimine, 28°55'N 10°09'W, rocky slopes (sandstone) by wadi, with patchy cover of low bushes, succulents and other herbs, living, 3 spm, 1986.188.8, NMW.Z. 1993.051.2668; ditto, some living, 20 sh, 1986.188.7, NMW.Z. 1993.051.2667.

#145, By P41 [now N1] ca 14km SW. along road from Goulimine, 28°54'N 10°11'W, rocky sandstone hillslopes with patchy cover of low bushes, succulent *Euphorbia* and grasses, living, 2 spm, 1986.189.7, NMW.Z. 1993.051.2676; ditto, some living, 126 sh, 1986.189.6, NMW.Z. 1993.051.2675.

M7, ca 1km N. of N1 at 22.7km due SW. of Guelmim (centre), 28°51'N 10°14'W, sandy and stony plain with patchy low shrubs (mainly sparse) including few succulent *Euphorbia*, 235m, living, 1 sh & bod, 17 sh dead, CGAH, DNA sample kept.

#146, By P41 [now N1] 37km SW. along road from Goulimine, 28°49'N 10°21'W, sandstone crags and rocky hillside with patchy cover of low bushes and succulents, some living, 22 sh, 1986.190.11, NMW.Z. 1993.051.4541; ditto, living, 1 spm, 1986.190.12, NMW.Z. 1993.051.2681.

M8, by N1 at 53km due SW. of Guelmim (centre), 28°43'N 10°31'W, base of low-angled hillslope with rocky (quartzite) surface and sandy patches, sparse cover of low shrubs, 234m, old shells, 42 sh, CGAH.

#147, By P41 [now N1] 67km SW. along road from Goulimine, 28°40'N 10°36'W, rocky sandstone hillslope with patchy cover of low bushes, succulents, other herbs and grasses, old shells, 29 sh, 1986.191.5, NMW.Z. 1993.051.2697.

#213, By P41 [now N1] 53km NE. along road from Tan-Tan, 28°39'N 10°43'W, sandy and rocky (calcareous sandstone) slopes with sparse cover of low bushes and herbs, old shells, 52 sh, 1986.257.4, NMW.Z. 1993.051.2917.

M9, just S. of N1 at 21.5km due NE. from Oued Draa at N1 road bridge, 28°38'N 10°46'W, gentle W.-facing hillslope with sandy surface and many quartzite stones, sparse low cover of shrubs, 246m, living, 4 sh & bod, 2 juv spm, 29 sh dead, CGAH, DNA sample kept.

M10, ca 1km N. of N1 at 1.75km due NNE. of Oued Draa at N1 road bridge, 28°33'N 10°56'W, sandy ground above wadi floodplain and stony (sandstone) slopes nearby, with patchy bushes or low bushes, 22m, living, 2 sh & bod, 1 juv. spm, 30 sh dead, CGAH, DNA sample kept.

M11, ca 1km N. of N1 at 2.1km NNE. of Oued Draa at N1 road bridge, 28°33'N 10°56'W, slopes and top of low hill with boulders of sandstone and quartzite, sparse low cover of bushes, 33m, living, 2 sh & bod, 58 sh dead, CGAH, DNA sample kept.

#212, By P41 [now N1] ca 21km NE. along road from Tan-Tan, 28°32'N 10°55'W, rocky slopes (sandstone) with sparse succulent *Euphorbia*, other herbs and low shrubs, living, 3 spm, 1986.256.5, NMW.Z. 1993.051.2912; ditto, 45 sh, 1986.256.4, NMW.Z. 1993.051.2911.

M12B, by N1 ca 1.0km N. along road from Oued Draa at N1 bridge, 28°32'N 10°56'W, rocky (quartzite) slopes with loose cobbles, 40m, old shells, (6 sh observed), not kept, brief roadside stop in "sensitive area"(shells absolutely typical of *E. vermiculosa*: not keeled, not especially rough).

M27, ca 1km S. of N1 at 3.6km due E. of Tantan (centre), 28°26'N 11°04'W, NW. to W.-facing rocky slopes (hard sandstone) with sparse vegetation of low shrubs; gravelly and sandy lower slopes with patchy low shrubs, 72m, old shells, 61 sh dead, CGAH.

#210, By P44 ca 47km SW. along road from Tan-Tan, 28°09'N 11°16'W, sandy alluvium along bed of wadi, subfossil shells, 13 sh, 1986.254.7, NMW.Z. 1993.051.2905.

M13, by R101 at 36km due SW. of Tantan (centre), 28°09'N 11°16'W, open limestone hillslope with exposed rock, rather sparse open vegetation of low shrubs and succulents, 133m, living, 7 sh & bod, 11 juv spm, 89 sh dead, CGAH, DNA sample kept.

M23, just W. of R101 at 36.3km due SW. of Tantan (centre), 28°09'N 11°16'W, rocky S.-facing limestone hillslope, rather sparse low shrubs with succulents locally, 134m, living, 4 sh & bod, 59 sh dead, CGAH.

M22, just W. of R101 at 36.5km due SW. of Tantan (centre), 28°09'N 11°16'W, rocky S.-facing limestone hillslope, rather sparse low shrubs with succulents locally, 124m, old shells, 4 sh dead, CGAH.

M20, ca 1km W. of R101 at 38km due SW. of Tantan (centre), 28°08'N 11°17'W, rocky hillslope (hard limestone) with much blown sand, vegetation of rather sparse low shrubs, 102m, old shells, 4 sh dead, CGAH.

M14i, ca 0.5km E. of R101 at 36.4km due SW. of Tantan (centre), 28°08'N 11°16'W, rocky slopes (mainly quartzite cobbles), sparse low vegetation of shrubs and some succulents, 109m, living, 3 sh & bod, 10 sh dead, CGAH, DNA sample kept, sample i from higher levels above wadi (never flooded).

M14ii, ca 0.5km E. of R101 at 36.4km due SW. of Tantan (centre), 28°08'N 11°16'W, rocky slopes (mainly quartzite cobbles), sparse low vegetation of shrubs and some succulents, 109m, old shells, 8 sh dead, CGAH, sample ii mainly or partly from bed of small wadi (prone to occasional flooding).

M14iii, ca 0.5km E. of R101 at 36.4km due SW. of Tantan (centre), 28°08'N 11°16'W, rocky slopes (mainly quartzite cobbles), sparse low vegetation of shrubs and some succulents, 109m, old shells, 10 sh dead, CGAH, sample iii from same areas as both sample i and sample ii.

#208, By P44 ca 70km SW. along road from Tantan, 27°59'N 11°26'W, rocky sandstone slopes, with patchy succulent *Euphorbia*, other herbs and low bushes, some living, 29 sh or spm, 1986.252.1, NMW.Z. 1993.051.2887.

#202, By P44 [now N14] ca 13km W. along road from Smara, 26°45'N 11°48'W, rocky (sandstone) ridge on gravelly/sandy plain with no vegetation, subfossil shells, 2 sh, 1986.246.1, NMW.Z. 1993.051.2868.

#201, By P44 [now N14] ca 43km SW. along road from Smara, 26°37'N 12°05'W, low crag of calcareous sandstone and rocky/sandy slopes with sparse bushes and herbs, subfossil shells, 42 sh, 1986.245.4, NMW.Z. 1993.051.2867.

#199, 1.5km N. of P44 [now N14?] at 141km SE. along road from Laayoune, 26°34'N 12°28'W, open sandy/gravelly plain with sparse herbs and low bushes, shells subfossil, from sands, 94 sh, 1986.243.3, NMW.Z. 1993.051.2859.

#200, By P44 [now N14] ca 60km SW. along road from Smara, 26°33'N 12°13'W, open gravelly/sandy plain with scattered low bushes and herbs, subfossil shells, 45 sh, 1986.244.2, NMW.Z. 1993.051.2863.

#### *Unidentified Eremina species*

M23, just W. of R101 at 36.3km due SW. of Tantan (centre), 28°09'N 11°16'W, rocky S.-facing limestone hillslope, rather sparse low shrubs with succulents locally, 134m, old shells, 5 sh dead (broken or immature), CGAH.

M22, just W. of R101 at 36.5km due SW. of Tantan (centre), 28°09'N 11°16'W, rocky S.-facing limestone hillslope, rather sparse low shrubs with succulents locally, 124m, old shells, 2 sh (broken), CGAH.

M20, ca 1km W. of R101 at 38km due SW. of Tantan (centre), 28°08'N 11°17'W, rocky hillslope (hard limestone) with much blown sand, vegetation of rather sparse low shrubs, 102m, old shells, 1 sh dead (immature), CGAH.

M14ii, ca 0.5km E. of R101 at 36.4km due SW. of Tantan (centre), 28°08'N 11°16'W, rocky slopes (mainly quartzite cobbles), sparse low vegetation

of shrubs and some succulents, 109m, old shells, 7 sh dead (immature or broken), CGAH, sample ii mainly or partly from bed of small wadi (prone to occasional flooding).

M14iii, ca 0.5km E. of R101 at 36.4km due SW. of Tantan (centre), 28°08'N 11°16'W, rocky slopes (mainly quartzite cobbles), sparse low vegetation of shrubs and some succulents, 109m, old shells, 5 sh dead (immature or broken), CGAH, sample iii from same areas as both sample i and sample ii.

#159, By P41 [now N1] ca 5km E. along road from Tarfaya, 27°57'N 12°51'W, sandy and rocky (sandstone) slopes above shore, with patches of herbs, subfossil shells from sand, 11 sh, 1986.203.2, NMW.Z. 1993.051.2753.

#188, By track [now N1] ca 131km NE. of Ad-Dakhla along track, 24°23'N 15°01'W, crag and rocky slopes of calcareous sandstone, with sand banked on rocks and with sparse herbs and low shrubs, shells subfossil (from sand/sandstone), 5 internal casts of shells, 1986.232.4, NMW.Z. 1993.051.2829.

#187, By track [now N1] ca 197km NE. along track from Ad-Dakhla, 24°15'N 15°10'W, fossils from massive calcareous sandstone rock, 28 fossils and some impressions, 1986.231.1, NMW.Z. 1993.051.2825.

#### *Unidentified, probably Eremina species*

#329, By P30 [now N1] 7km S. of Ait-Bella, 29°59'N 9°36'W, rocky (limestone) slopes with patchy cover of succulent *Euphorbia*, grasses and herbs, living, 1 immature spm, 1986.373.08, NMW.Z. 1993.051.3786 [single spm possibly e.g. *Otala* sp.].

#### *Unidentified, Helicoidea sp. undet., possibly Eremina species*

#193, by track [now N1] ca 288km NE. along track from Ad-Dakhla (ca 82km SW. along track from Boudjour), 25°29'N 14°26'W, open sandy/gravelly plain, Quaternary fossil from calcareous sandstone exposed at surface, 1 internal cast, 1986.237.1, NMW.Z. 1993.051.8.

#189, By track [now N1] ca 144km NE. along track from Ad-Dakhla, 24°25'N 14°53'W, rocky (calcareous sandstone) and sandy slopes with patchy low bushes and few herbs, fossil shells (casts) from calcareous sandstone of cemented dune ca 4m thick, 3 casts, 1986.233.3, NMW.Z. 1993.051.2832.



