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 Plage] to Tafraoute) 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. Intergenders 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 sympathy, 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 (Saquiat 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.

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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 nomenclatorially 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% im 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 epiphetes 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 96ºC, [30 s at 94ºC, 30 s at 50ºC, 1 min at 72ºC] (repeated for 35 cycles) and 10 min at 72ºC for COI and nuclear fragment, and (2) 20 s at 94ºC, [20 s at 94ºC, 30 s at 55ºC, 30 s at 72ºC] (repeated for 40 cycles) and 30 s at 72ºC 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 (Katoh & 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
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
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 gualteranus 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 Museu 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

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

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Site field number</th>
<th>COI</th>
<th>16S</th>
<th>ITS-2</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. duroi</em></td>
<td>M3</td>
<td>KY304081</td>
<td>KY197727</td>
<td>KY304094</td>
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<td><em>E. duroi</em></td>
<td>M4</td>
<td>KY304082</td>
<td>KY197728</td>
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<td>KY304083</td>
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<td>KY304096</td>
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<tr>
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<td>KY304084</td>
<td>KY197730</td>
<td>KY304097</td>
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<tr>
<td><em>E. vermiculosa</em></td>
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<td>KY304085</td>
<td>KY197731</td>
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<td><em>E. exspectata</em></td>
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<tr>
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<td>KY197733</td>
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<td>KY304101</td>
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<td>KY304092</td>
<td>KY197738</td>
<td>KY304105</td>
</tr>
<tr>
<td><em>E. duroi × E. vermiculosa</em></td>
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<td>KY304093</td>
<td>KY197739</td>
<td>KY304106</td>
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### Table 2  List of primers used for DNA amplification and sequencing.

<table>
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<tr>
<th>Gene</th>
<th>Primer</th>
<th>Sequence</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>COI</td>
<td>LCO1490 (5')</td>
<td>5' GGTCACAAATCATAAAGATATTGG 3'</td>
<td>Folmer et al. (1994)</td>
</tr>
<tr>
<td></td>
<td>HCO2198 (3')</td>
<td>5' TAAACTTCAGGGTGACCAAAAAATCA 3'</td>
<td>Folmer et al. (1994)</td>
</tr>
<tr>
<td>16S rRNA</td>
<td>16sar (5')</td>
<td>5' CGCCTGTATCAAAAACAT 3'</td>
<td>Palumbi et al. (1991)</td>
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<tr>
<td></td>
<td>16sbr (3')</td>
<td>5' CCGGTCTGAACCTCAGTACGT 3'</td>
<td>Palumbi et al. (1991)</td>
</tr>
<tr>
<td>ITS2</td>
<td>LSU-1 (5')</td>
<td>5' CTAGCTGGAGAAATTAATGTGA 3'</td>
<td>Wade et al. (2006)</td>
</tr>
<tr>
<td></td>
<td>LSU-3 (3')</td>
<td>5' ACTTCCCCACGGTACCTG 3'</td>
<td>Wade et al. (2006)</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
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<th>Evolutionary model selected</th>
<th>1st</th>
<th>2nd</th>
<th>3rd</th>
</tr>
</thead>
<tbody>
<tr>
<td>16S rRNA</td>
<td>HKY</td>
<td>HKY+G</td>
<td>JC</td>
</tr>
<tr>
<td>5.8S-ITS2-28S</td>
<td>HKY</td>
<td>HKY+G</td>
<td>JC</td>
</tr>
</tbody>
</table>

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 gualteranus* and *Otala lactea* were used as outgroups. Uncorrected pairwise p-distances were calculated with PAUP v. 4.0b10.

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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)


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 vermicultata* (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


*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* Plyr 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 semidiaural 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. inexspectata (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 genitalic 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. vermicolosa] 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. hasselequisti 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. inexspectata; 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. inexspectata

.- 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. 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. 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; 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 arabfculis deferti” [= Egypt].


Eremina desertorum tunetana Hesse 1915, Iconogr., (2) 23, pp. 21–22, pl. 633 figs 9a–c (jaw), 10 (male genitalia); TL Foum Tahtaoui 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; Foum Tahtaoui, dans l’extrême Sud tunisien.


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: Tryon (1888), Man. Conch. (2) 4, p. 127, pl. 36, figs 29–30; Habitat unknown. 

Helix duroi Hidalgo: Tryon (1888), Man. Conch. (2) 9, p. 335.


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] ehrenbergii Roth.”

Eremina linanprietoae Cossignani & Ahuir, 2012, Malacologia (Cupra Marittima), 75, p. 28, figs; TL North Sidi Akhfennir, West Sahara, Marocco. 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 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 géographica commercial, no. 29, p. 94; dans le Guerguer (Rio de Oro) (leg. Quiroya). n.v.

Helix Duroi: 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.


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).


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


Helix Duroi: Germain (1909), Arch. zool. experim. et gener., 5th ser., 1, p. 169; Mauritania, depuis le cap Blanc jusqu’au sud Marocain.


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

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


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


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. verniculosa.


Eremina Duroï 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. Rutlant); etc.


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


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.


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

Eremina inexspectata 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. inexspectata and E. zitteli Pallary 1909 from Libya when he named the former species.


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

Eremina inexspectata [sic] (Llabador 1960[sic]) × Eremina verniculosa (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). 

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, nonem 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 Liggia, Genova, Italy, accessed 29 Dec. 2014]


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


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


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 Bgnt., 1898 [= 1899] is unwarranted.


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 (fide 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).


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. major

Eremina vermiculosa Morelet 1874 var. minor

Eremina vermiculosa Morelet 1874 var. inflata

Eremina vermiculosa Morelet 1874 var. depressa


Eremina vermiculosa var. cretacea Morelet 1874:

Eremina vermiculosa var. candida Llabador 1969, J. Conchyl., 100, p. 63; environs de Goulimine; El Dioum du Draâ (Zona sur Protectorado español).


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


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


**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
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. inexspectata* 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

![Figure 3](image-url)
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 as 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 Plage] 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.

### Table 4

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

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<th>L3</th>
<th>L4</th>
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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 anteuphorbi*um (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
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. inexspectata on rock were concealed).

At the two sites where living populations of E. inexspectata 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. inexspectata 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. inexspectata (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.
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 16th 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 dasyurus*) 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

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**Figure 6** Map to show distributions of *Eremina dillwyniana* s.s. and *E. inexspectata* 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. inexspectata.*
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 snail shells have been reported at sites where bones of the song thrush were also present (op. cit., p. 501).

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.
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 273mm²), 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. inexspectata* 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. inexspectata* is

![Figure 8](image-url) Map to show distribution of the hybrid between *Eremina inexspectata* and *E. vermiculosa* in relation to the ranges of both parent species, based on specimens studied by the authors (see Appendix for list).
Figure 9  Habitats of species of Eremina in SW. Morocco: A, Coastal slope overlying sandstone with open scrub rich in succulents (Euphorbia officinarum, Kleinia anteflouribium), 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. inexspectata. See Appendix for additional details of localities.
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. inexspectata* 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 228mm²; 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. dillwyniana nounensis* 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.
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. inexspectata*, 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. inexspectata*. The molecular data (Fig. 3) show genetic differences between the northern and southernmost
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 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 mm²; 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 Area = 0.8 × (mean AB + mean AH)/4 × π². 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  | *dillwyniana*                                           | *duroi* | *inexpectata* | *vermiculosa* |
| 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 | small-medium | small-large |
| Mean body size | larger                                                    | larger   | smaller  | smaller |
| N adult bodies examined | 5                                                    | 60      | 14      | 25      |
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 interspecific hybrids, or both. The figures give counts of shells collected. * = old shells only; † = subfossil. Detailed data on each site are in the Appendix.

Table 7

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<th><em>Eremina duroi</em> × <em>vermiculosa</em></th>
<th><em>Eremina inexspectata</em></th>
<th><em>Eremina inexspectata</em> × <em>vermiculosa</em></th>
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<td>0</td>
<td></td>
</tr>
<tr>
<td>M10 live</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>2</td>
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<tr>
<td>(by wadi) dead</td>
<td>0</td>
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<td>1</td>
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<td>30</td>
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</table>
since past replacement of one species by another may have occurred without them ever coexisting, e.g. at site M27 where living E. inexpsectata 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 geographic 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. inexpsectata 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. inexpsectata 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 Rossmaessleria (Walther et al., 2016). An argument for subspecies rank for E. inexpsectata 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 inexpsectata. Unfortunately, it is difficult to study the closest neighbouring populations of Eremina: The southern range limit known for E. inexpsectata 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. inexspectata* (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. inexspectata*) 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 sympathy, 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 interspecific 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.


M17, ca 1 km S. of N1 at 41.5km due SW. along road from Tan-Tan-Plâge, 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.


**Eremina duroi**

#331, Coast by road 7064 [now R104] 2km NE. of Mirleft [Mihrlt], 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.


#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.

#332, By road 7064 [now R104] 17.5km SW. along road from Mirleft [Mihrlt], 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 antaeuphorbium*), 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 low herbs, old shells, 195m, living seen in field, 4 sh & bod, 9 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°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.

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 anteuphorbium), 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), 28º57'N 10º32'W, rocky (slaty) crags and slopes in small gorge, open vegetation of low shrubs (including succulent Kleinia anteuphorbium 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 seaciffs 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 Tan-Tan (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 Tan-Tan (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 Ouattia (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 Ouattia (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.
from bed of small wadi (prone to occasional flooding).

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

M16, ca 0.5 km S. of N1 at 34.4 km 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, 34 m, old shells, 20 sh dead, CGAH.


#157, By P41 [now N1] ca 66 km 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.

#163, 0.5 km W of P41 [now N1] at 10 km 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. 1993.051.17.

#164, By P41 [now N1] ca 15 km 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.


#195, By P44 [now N5] ca 19 km 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 21 km 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.


#167, By P41 [now N1] ca 56 km 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 52 km SSW. along road from Laayoune-Plâge, 26°39'N 13°36'W, open sandy plain with patches of low shrubs

#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.


#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.


#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.


#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.


#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°31'W, sandy/gravelly plain with patchy low shrub 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 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.


#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

#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, 24°07'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.


#181, By road ca 7km NE. of Ad-Dakhla, 23°54'N 15°45'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, 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°09'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, 15 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
 Eremina inexspectata
M10, ca 1 km N. of N1 at 1.75 km 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, 22 m, old shells, 1 sh, CGAH.

M12, ca 0.3 km SW. of N1 at 0.6 km 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, 57 m, living, 6 sh & bod, 2 juv spm, 89 sh dead, CGAH, DNA sample kept.


#149, By P41 [now N1] ca 8 km NE. of Tantan, 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.

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

Eremina vermiculosa
M33, ca 1 km N. of N1 at 2 km due ENE. of Taghjijt (centre), 29°06'N 09°10'W, shallow sandy depression in rocky (quartzite) plain, with open cover of shrubs and few taller bushes, 709 m, old shells, 23 sh dead, CGAH, eroding from sand (no fresh shells here).


#337, By P30 [now N12] ca 16 km 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 24.3 km 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, 195 m, living, 1 sh & bod, 137 sh dead, CGAH.

#143, By P41 [now N1] 5 km 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 16.4 km due W. of Guelmim (centre), 28°58'N 10°14'W, stony hillslope (slaty rock) with open vegetation of low shrubs and succulents, 184 m, living, 1 sh & bod, 43 sh dead, CGAH.
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.

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 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°21’W, sandstone hillslope 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.

M11, ca 1km N. of N1 at 2.1km due NE. of Oued Draa at N1 road bridge, 28°33’N 10°21’W, 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.

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.


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°17’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°17’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.


#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.