## PHYLOGENY, SPECIES-LIMITS AND TAXONOMIC REVISION OF OTALINI (HELICIDAE) FROM NORTH-WEST AFRICA

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Abstract The affinities and detailed phylogeny of the tribe Otalini of the Helicidae are elucidated from DNA sequence data, derived from all the recognised genera and most of the NW African species. The genus Theba (Thebini) emerges as the sister group of all Otalini. Eremina is placed here in a separate new tribe Ereminini; it forms a clade sister to the combined Thebini and Otalini. The nine genera recognised within the Otalini are placed in two subtribes, as follows: Cantareusina (new subtribe, for Cantareus, Cornu, Erctella, Rossmaessleria), and Otalina (Maurohelix, Massylaea, Eobania, Otala and Loxana). Other nominal genera based on type species from NW. Africa are synonymised. The first comprehensive modern revisions of species limits in Loxana and Maurohelix are presented, based on studies of genital anatomy and shells from extensive recent collections, mapping of distributions and DNA sequence data. Numerous conchologically distinctive allopatric populations within the expanded concept of Loxana appear to be more realistically regarded as forming far fewer biological species. Hence, this supports reduction of five polytypic genera previously recognised (including Alabastrina and Atlasica) to the single genus Loxana. The habitat preferences of these species are described, their ranges are mapped and evolution and differentiation of their shell characters are discussed. Data supplementary to those from other recent studies are also presented for Rossmaessleria, Massylaea, Eobania and Otala. Massylaea and Eobania are maintained as separate genera based on new molecular and morphological data. One new species is described within Otala, three other species are recognised as valid and additions to that genus (O. juilleti, O. orientalis, O. pallaryi) and the placement of O. hieroglyphicula therein is confirmed. Evolution of the distal genitalia in Helicidae is discussed, revealing several remarkable instances of convergent evolution that had not been reported previously.

*Key words* Otalini, Helicidae, Maghreb, DNA, phylogeny, evolution, species limits, genital anatomy, taxonomy, distribution

## INTRODUCTION

The Helicoidea of north-west Africa include many hundreds of beautiful and varied shell forms that have attracted the interest of collectors and malacologists alike for almost 200 years. Bourguignat (1863-1864, 1863-1870, 1868; Bourguignat in Péchaud, 1883; Letourneux & Bourguignat, 1887) was prominent among the early workers who set about giving species names to this rich diversity, essentially by giving a different name to most shells that look different. Paul Pallary continued this practice from about 1894 onwards, while successfully becoming a dealer selling shells to European collectors. Thus, hundreds of new species names and many more for varieties were established from Morocco, Algeria and Tunisia (the W. Maghreb).

Attempts to clarify what biological entities lay behind the many names provided by Bourguignat were begun in earnest by Kobelt (e.g. 1882: 27–29), informed by his own collecting

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trips to the region (Kobelt, 1881b, 1885) which provided sufficient shells to demonstrate variability within and between local populations. Hesse (1909–1911, 1915–1920) also made substantial contributions to taxonomic understanding by finding anatomical characters that could help to better arrange the systematics of families and genera. However, Hesse mainly just repeated the species names given by Pallary, while expressing gratitude for specimens received from him.

Pallary was able to report many new finds in the Moyen Atlas and other regions inland in Morocco resulting from the first detailed studies of the snail faunas as access to these regions became possible during and after the subjugation of local tribes by the French army. However, the later works by Pallary himself (1926, 1928, 1933, 1935, 1936, 1939b) reached an extreme in his use of narrow concepts of morphological species, adorned with many additional varieties for shells differing only slightly in form, coloration, or both. A later checklist reviewing the Moroccan

fauna by Rour, Chahlaoui & van Goethem (2002) mainly provided an uncritical catalogue from Pallary's publications. The old style of treatment naming finely split local shell forms as new species has been continued over the past decade by Ahuir Galindo (e.g. 2016, 2017b, 2018a, 2018b, 2020), with some of his novelties from Morocco being advertised for sale online (e.g. Shellauction. net, 2019).

The modern development of molecular methods has provided new insights into phylogeny of Helicoidea, with the first data on several genera and species from NW. Africa being included in the study by Razkin et al. (2015). Walther, Neiber & Hausdorf (2016) and Neiber (2017) provided a molecular and morphological study of the genus Rossmaessleria, reducing the 13 named (allopatric) species to a single polytypic species. On the basis of extensive new collections of shells and anatomical material, Holyoak & Holyoak (2017) reviewed Otala reducing 130 species names in five genera from the W. Maghreb to five species in a single genus, but few molecular data were available. Holyoak et al. (2018) reviewed the W. Maghreb Eremina, with fuller molecular data on them added to shell and anatomical information from new collections. Kneubühler et al. (2019) have recently presented data on anatomy and DNA sequences of Alabastrina (= Loxana), Otala species and Siretia (= Otala) species from NE. Morocco.

The present study complements recently published work by covering all recognised genera of tribe Otalini of the Helicidae, from Europe and NW. Africa. Recent field collecting in the W. Maghreb has added to material amassed in 1984 and 1986, so almost all distinctive Otalini species of the region could be studied by DNA sequencing, from the genital anatomy and from large shell samples. The new molecular data thus fill gaps in previous taxonomic coverage to allow the first detailed phylogeny to be presented for the Otalini. The genera Loxana (including Alabastrina, Atlasica, Beaumieriana, Guilea and Lechatelieria), Maurohelix and Massylaea are reviewed in detail; a key to the species is presented. The habitat preferences of their species are described, their ranges are mapped and evolution and differentiation of their shell characters are discussed. Data supplementary to those from other recent studies are also presented for Rossmaessleria, Eobania and Otala.

On the basis of our new phylogeny of genera within the Otalini based only on molecular data, the evolution of the distal genitalia is discussed. This reveals several remarkable instances of convergent evolution that had not been reported previously. Hence, contrary e.g. to the work of Schileyko (2006), it appears that only rather limited reliance can be placed on characters of the genital anatomy for phylogenetic reconstruction.

Our delimitation of taxa at tribal and genus levels relies on DNA sequence data that have vielded results which, even with the benefit of hindsight, could not be predicted from shells or genital morphology. Hence, the paper proceeds from a "Methods" heading to "Molecular Results" which present and justify a novel phylogeny. Following this, "Taxonomy, nomenclature and distribution" establishes the nomenclature and species-limits in accordance with that phylogeny, added to data on distribution, coexistence and variability of local populations. A Key for identification of species follows, because it is needed for identification of specimens, and at the same time, it provides a structured summary of differences between the genera and some species groups in shell characters, and where necessary, genital anatomy. The final three sections consider "Ecology of Loxana and other Otalini and Evolution of their Shell Characters", "Evolution of the Distal Genitalia in Otalini", and "Biogeographical Notes". By dealing with the latter topics in this way the features of shells and genitalia and patterns of species distribution can be considered in relation to a molecular phylogeny which they have not influenced.

#### Methods

During the summers of 1984 and 1986 extensive fieldwork was carried out in Morocco and Algeria to collect land snails. Samples of large Helicidae were obtained from more than 300 localities. This material is housed at NMW.Z and was available on loan for the present study. DTH and GAH extended the results of that fieldwork with five additional visits to Morocco concentrating on large Helicidae, in 2016 (Feb.–Mar., May, Oct.) and 2017 (May–June, Aug–Sept.). Details of the methodology are given by Holyoak & Holyoak (2017: 421) and Holyoak *et al.* (2018). Conventions used in study and descriptions of shells and genitalia and in the presentation of synonymies follow those set out in the papers cited. An Appendix to the present paper (available online) lists the specimens studied.

Specimens selected for DNA sequencing are listed in Table 1. Genomic DNA was extracted from a piece of foot using the DNeasy Tissue kit (QIAGEN, Valencia, CA, U.S.A.). Two mitochondrial gene fragments [the cytochrome c oxidase subunit I (*COI*) and the 16S rRNA] and one nuclear gene cluster (5.8S-ITS2-28S) were selected for this study. General PCR cycling conditions used for DNA amplification were 1 min at 96 °C, 35 cycles (30 s at 96 °C, 30 s at 55 °C, 1 min at 72 °C) and 72 °C for 10 min. The primer pairs used are listed in Table 2. PCR products were purified and sequenced at Macrogen Inc. using ABI3730XL or ABI3700 sequencers. Genbank accession numbers are provided in Table 1.

Sequences were aligned with MAFFT online version (Katoh et al., 2002) using the Q-INS-i algorithm for the 16S rRNA and 5.8S-ITS2-28S and the 'auto' strategy for COI data. Available Helicidae sequences from recent molecular phylogenetic works (Bouaziz-Yahiatene et al., 2017; Caro, Gómez-Moliner & Madeira, 2019; Chueca, Madeira & Gómez-Moliner, 2015; Colomba et al., 2011, 2015; Holyoak et al., 2018; Kneubühler et al., 2019; Neiber & Hausdorf, 2015; Razkin et al., 2015; Walther et al., 2016) were also included in the alignments. The evolutionary model for each gene partition was estimated prior to analysis with jModelTest2 v2.1.6 (Darriba et al., 2012), according to 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 dataset partitioned by genes, through CIPRES Science Gateway (Miller, Pfeiffer & Schwartz, 2010), allowing each one to evolve at different rates. The COI gene fragment was divided into three partitions according to codon position. Bayesian inference analyses were conducted with MrBayes v.3.2.6 (Ronquist et al., 2012). Two independent runs were continued for 60×10<sup>6</sup> generations saving trees each 1000 generations with the first 25% of trees being discarded as burn-in. Convergence between runs was assessed using Tracer v1.6 (Rambaut et al., 2007). Maximum likelihood analyses were carried out using RAxML v8.2.10 (Stamatakis, 2014) under the GTRGAMMA model, with 1000 nonparametric bootstrap replicates to assess node support. For the different topologies obtained, we interpreted values above 70% for bootstrapping procedures (BS) as meaningful support and Posterior Probabilities (BP) values from the BI analyses above 0.95 as significant statistical support.

## **Abbreviations**

ANSP Academy of Natural Sciences, Philadelphia, U.S.A.; BI Bayesian inference; BP Bayesian posterior probability; BS Maximum likelihood bootstrap support values; D Diameter of shell; EHUMC Euskal Herriko Unibertsitatea Malacological Collection, Vitoria-Gasteiz, Spain; H Height of shell; H&S Holyoak & Seddon Collection at NMW.Z; Icon. Iconographie (of Rossmässler, continued by Kobelt, Hesse, et al.); leg. Collected by; MHNG Muséum d'histoire naturelle de la ville de Genève, Switzerland; MMM Museu Malacologico Piceno, Cupra Marittima, Italy; MNHN Muséum national d'Histoire naturelle, Paris, France; MVHN Museu Valencià d'Història Natural, Valencia, Spain; NHMUK Natural History Museum, London, U.K.; NMBE Naturhistorisches Museum of the Burgergemeinde Bern, Bern, Switzerland; NMW.Z Dept. of BioSyB, National Museum of Wales, Cardiff, U.K.; syn. synonym; TL type locality; ZISP Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

#### MOLECULAR RESULTS

The phylogeny obtained by combining the mitochondrial and nuclear gene fragments is shown in Fig. 1. The topology of the phylogeny is based on Bayesian inference (BI) but both Bayesian posterior probabilities (BP) and ML bootstrap values (BS) are indicated at the nodes of the main clades. The Otalini and Thebini tribes sensu Razkin et al. (2015) formed a clade together (BP=1; BS=93). Within the Otalini, we identified two main groups which are well supported named here as Cantareusina (BP=1; BS=98) and Otalina (BP=1; BS=100). The Cantareusina clade grouped the genera Cantareus, Erctella, Cornu and Rossmaessleria with strong support for its internal relationships, whereas the Otalina group comprised the genera Eobania, Loxana, Massylaea, Maurohelix and Otala, but only the relationship

Table 1 Taxa and spe	cimens used in th	uis study for molecular phylog numbers for <i>COI</i> , 16S	genetic analyse rNRA and 5.8	ss: voucher nu 8S-ITS2-28S lo	mbers, sampl ci.	ing localities	and GenBan	k accession
						GenBar	rk accession 1	number
Species	Voucher	Locality	Latitude	Longitude	Country	COI	16S	ITS2
Allognathus graellsianus	EHUMC-1045	Finca Mortitx, Escorca, Mallorca	39.8683° N	2.9246° E	Spain	KM592535	KM592625	KM592710
Arianta arbustorum Cantareus apertus	MVHN-2159 MVHN-2013	Stockholm Djelfa	59.3476° N 3.4691° N	18.0773° E 3.1653° E	Sweden Algeria	KP727358 MN241258	KJ458486 KJ458491	KJ458584 KJ458589
Caucasotachea leucoranea	MN-207	Lankaran, Hirkan, near Dastatuk, 2km NW of the northern edge of	38.6800° N	48.7506° E	Azerbaijan	KR705045	KR705008	KR705085
Cepaea nemoralis	MN-026	Aanouan reservoir Saxony Anhalt, Volkmarskeller near	51.7958° N	10.8856° E	Germany	KR705033	KR704993	KR705070
Chilostoma desmoulinsii Cornu aspersum	MVHN-2165 CA3	blankenburg La Riba, Tarragona Cefalù, Mazzaforno,	41.3155° N 38.0267° N	1.1736° E 13.9669° E	Spain Italy	MN241259 KR921888	KJ458500 GQ402389	KJ458596 GQ402426
-		Palermo			2		!	!
Eobania constantinae Eohania constantinae	Ec-1984:275 NMBE-540543	9km W. of Bouhamama Makouda	35.2833° N 36.7909° N	6.6333° E 4.0659° E	Algeria Algeria	MN241260 MF564167	MN227731 MF564121	MN207585 MF564153
Eobania constantinae	NMBE-534211a	Draâ-Ben Khedda	36.7318° N	3.9654° E	Algeria	MF564164	MF564118	MF564150
Eobania constantinae	NMBE-534211b	Draâ-Ben Khedda	36.7318° N	3.9654° E	Algeria	MF564165	MF564119	MF564151
Eobania constantinae	NMBE -540542	Azaghar d'Ait Bouaddou	36.5214° N	3.9425° E	Algeria	MF564166	MF564120	MF564152
Eobania constantinae (?)	NMBE-519961	iguu bournu Aurès Mountains, Batna,	nd 2/04/00	a crou.4	Algeria Algeria	MF564169 MF564169	MF564123	4C140C11VI
		Kenchela			)			
Eobania vermiculata	NMBE-540544 NIMBE 540061	Makouda Viinadanii	36.7909° N 27 8600° M	4.0659° Е 27 2600° Е	Algeria	MF564159	MF564112	MF564144
Eobania vermiculata	NMBE-549959	Agia Napa	34.9728° N	24.0427° E	Cvprus	MF564160	MF564113	MF564145
Eobania vermiculata	EHUMC-2274	Hammamet	36.3988° N	10.6117° E	Tunisia	MN241261		
Eobania vermiculata	MVHN-1349	Ses Salines, Mallorca	39.3350° N	$3.0515^\circ E$	Spain	MN241262		
Eobania vermiculata	MVHN- 080709DR04	Girona	41.9769° N	2.8262° E	Spain	MN241263		
Eobania vermiculata	MVHN- 080709DR05	Castillo de Jumilla, Murcia	38.4789° N	1.3335° W	Spain	MN241264		
Eobania vermiculata	MVHN- 260410DB03_1	Staoueli, dunas, antes del	36.7805° N	2.8959° E	Algeria	MN241265	MN227732	MN207586
Eobania vermiculata	EHUMC-2275	Marsella – Toulon, Var	43.2649° N	5.7440° E	France	MN241266		
Eobania vermiculata	MVHN- 280610ZB16	Guardamar, Dunas Norte, Alicante	38.0922° N	0.6482° W	Spain	MN241267		

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Species	Voucher	Locality	Latitude	Longitude	Country	COI	16S	ITS2
Eobania vermiculata Erctella cephalaeditana	EHUMC-1011 CM4	Murchante, Navarra Cefalù, La Rocca, Palermo	42.0241° N 38.0400° N	1.6687° W 14.0272° E	Spain Italy	MN241269 KR921892	KJ458510 GQ402396	KJ458604 GQ402433
Erctella insolida	SV3	Trapani, San Vito lo Capo, Cala Mancina	38.1786° N	12.7186° E	Italy	KR921900	GQ402422	GQ402459
Erctella mazzullii	PEC3	Mt. Pecoraro, Cinisi, Palermo	38.1578° N	13.1283° E	Italy	KR921914	GQ402419	GQ402456
Eremina dillwyniana	M17	41.5km due SW. Of El Ouatia	28.2518° N	11.6585° W	Morocco	KY304090	KY197736	KY304103
Eremina duroi	MN-161	Souss-Massa-Draa, Sidi Ifni	29.3833° N	10.1667° W	Morocco	KR705036	KR704999	KR705076
Eremina duroi	M3	4.4km due NE. Of Mirleft	29.5994° N	10.0263° W	Morocco	KY304081	KY197727	KY304094
Eremina duroi	M4	7.3km due NE. of Sidi Ifni	29.4320° N	10.1162° W	Morocco	KY304082	KY197728	KY304095
Eremina duroi	M18	15km due SW. of El Ouatia	28.3832° N	11.4268° W	Morocco	KY304091	KY197737	KY304104
Eremina duroi	M19	13.5km due SW. of El Ouatia	28.3944° N	11.4150° W	Morocco	KY304092	KY197738	KY304105
Eremina duroi×E. vermiculosa	M20	38km due SW. of Tantan	28.1374° N	11.2903° W	Morocco	KY304093	KY197739	KY304106
Eremina vermiculosa	M7	22.7km due SW. Of Guelmim	28.8500° N	10.2300° W	Morocco	KY304083	KY197729	KY304096
Eremina vermiculosa	6M	21.5km due NE. from Oued Draa	28.7222° N	10.5139° W	Morocco	KY304084	KY197730	KY304097
Eremina vermiculosa	M10	1.75km due NNE. of Oued Draa	28.5425° N	10.9402° W	Morocco	KY304085	KY197731	KY304098
Eremina vermiculosa	M11	2.1km NNE. of Oued Draa	28.5460° N	10.9402° W	Morocco	KY304086	KY197732	KY304099
Eremina vermiculosa	M12	0.6km due SW. of Oued Draa	20.5245° N	10.9524° W	Morocco	KY304087	KY197733	KY304100
Eremina vermiculosa	M13	36km due SW. of Tantan	28.1467° N	11.2601° W	Morocco	KY304088	KY197734	KY304101
Eremina vermiculosa	M14	36.4km due SW. of Tantan	28.1411° N	10.2624° W	Morocco	КҮ304089	KY197735	KY304102
Helicigona lapicida	EHUMC-1013	El Serrat	42.6178° N	1.5367° E	Andorra	MN241270	KJ458523	MN207588
Helix pomatia	MN-012	Lower Saxony, Hannover Anderten, N side of the Mittelland Canal	52.3586° N	9.8681° E	Germany	KR705053	KR705016	KR705093
Hemicycla bidentalis	MVHN-2160	Anaya, Tenerife, Canary Islands	nd	nd	Spain	KM592619	KJ458528	KJ458615
Iberus gualtieranus	EHUMC-1014	Sierra Elvira, Granada	37.2405° N	3.7260° W	Spain	KM592620	KJ458530	KJ458617
Loxana alabastrites	MVHN-2169	Mzo. Taras	35.1756° N	1.6605° W	Algeria	MN241271	KJ458484	KJ458582
Loxana alabastrites	M114	1.1km due N. of Tafoughalt	34.8163° N	2.4122° W	Morocco	MN241272	MN227734	MN207589
Loxana alabastrites	NMBE-549812	Cave Ifri n'Ammar, 20km SW Berkane	34.7820° N	3.0940° W	Morocco	MK754456	MK585085	MK585109

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	Latitude	34.9550° N	32.1355° N	31.3129° N	31.5289° N	33.4423° N		33.9744° N	30.5519° N	29.4073° N	28.9608° N		21 21 21 20 00 NI	31 2156° N	1 0017:10	32.3259° N	33.5180° N		34.1435° N	33.4423° N	43.7000° N		44.4208° N		pu	35.2833° N	35.4667° N	35.1833° N	24 /0/ I V	
	Locality	Rif, Tiztoutine, village Bouaza	6.6km due WSW. of Bin-el- Ouidane	Gorges du Moulay Brahim	Oued Zate valley at 2.9km due SE. of Talbanine	13.8km due NW. of	Boulemane	1.6km due S. of Debdou	7.1km due WNW. of Taliouine	1.5km SW. of Mirght	3.9km due E. along road		Takin are NE. Of Mirrlett	Surges du Moutay Dratini	Oukaimeden	8.5km due NNW. of Rich	0.6km ESE. of centre of	Skoura	Jbel Tazzeka, 7.6km due S. of Tazza	13.8km due NW. of Boulemane	Provence-Alnes-Cote	d'Azur, Nice	Provence-Alpes-Cote	d'Azur, Jausiers	(165): Castle, Fiumedinisi, Sicily; (COI; 5.8-ITS2-28S): Pomneva Nánoles Italv	9km W. of Bouhamama	2km W. of Bouhamama	Bou-Saad	Monts de Llemcen NVV	
	Voucher	NMBE-555174	M140	M160	171M	M128.2		M119	M035	M088	M091			M165	COTIN	M043	M046		M051	M128	MN-218		ZMH-DNA-	2842	MVHN-1276	Mp-1984:275	Mp-1984:274	Mr-1984.306.14	()P-14X4 1/2 12	
	Species	Loxana alabastrites "tistutensis"	Loxana beaumieri	Loxana beaumieri	oxana beaumieri	Loxana lechatelieri		Loxana massesylica	oxana rerayana	Loxana rerayana	Loxana rerayana		охана гегауана	охана тегацина - охана теганана	JOANTH TOTAGATHA	Loxana rufa	Loxana rufa		oxana rufa	Loxana rufa	Macularia niciensis		Macularia sylvatica	:	Vlarmorana muralis	Massylaea punica	Massylaea punica	Maurohelix raymondi	)tala hieroolubhicula	Jumma was a free was

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Species	Voucher	Locality	Latitude	Longitude	Country	COI	16S	ITS2
Otala lactea lactea	M039 Ol_2014.0413	Ruins of Lixus M of Dorto Corro	35.2018° N 37 0085° N	6.1130° W 8 7090° W	Morocco	MN241294 MND41295	MN227751	MN207606
Otala lactea lactea	NMBE-554174	Finca de la Concepción, N Málaga	36.7600° N	4.4280° W	Spain	MK754463	MK585093	MK585117
Otala lactea murcica	EHUMC-2278	GR-92 Tentegorra a Collado de Roldán, Murcia	37.5966° N	1.0382° W	Spain	MN241296	MN227753	MN207608
Otala lactea murcica	EHUMC-2083	Bardenas, Navarra	42.2285° N	1.4825° W	Spain	MG585403	MG585436	MG585479
Otala lactea murcica	NMBE-554176	Punta Entinas, W Almería	36.6900° N	2.6940° W	Spain	MK754465	MK585095	MK585119
Otala occulta	Oc-1986:377	15km NE along road from Imouzzer-des-Marmoucha	33.5833° N	4.1833° W	Morocco	MN241297	MN227754	MN207609
Otala orientalis	MVHN- 080709DR03	Berkane	34.9091° N	2.3304° W	Morocco	MN241298	KJ458563	KJ458641
Otala pallaryi	M114.2	1.1km due N. of	34.8163° N	2.4122° W	Morocco	MN241299	MN227755	MN207610
Otala nallarui	NIMBF 549815	Tafoughalt Montes de Kehdana	35 0270° N	2 6140° W	Monoco	MK754461	MK585090	MK585114
O were present of		Kebdana Mountain, Rif						
Otala punctata	EHUMC-2277	Murchante, Navarra	42.0203° N	1.6700° W	Spain	MN241300	MN227756	MN207611
Otala punctata	M062	54.6km due W. of Aïn- Benimathar	34.0325° N	2.6191° W	Morocco	MN241301	MN227757	MN207612
Otala punctata	CGAH-2016.01	Castell de Bairèn, Gandia, Valencia	38.995° N	0.186° W	Spain	MN241302	MN227758	MN207613
Otala punctata	NMBE-534228a	Makouda	36.7909° N	4.0659° E	Algeria	MF564170	MF564124	MF564155
Otala punctata	NMBE-534228b	Makouda	36.7909° N	4.0659° E	Algeria	MF564171	MF564125	MF564156
Otala tingitana	M046.2	0.6km ESE. of centre of Skoura	33.5180° N	4.5385° W	Morocco	MN241303	MN227759	MN207614
Otala tingitana	M115	near entrance to Grotte	34.8381° N	2.3563° W	Morocco	MN241304	MN227760	MN207615
Otala xanthodon	NMBE-549840	Montes de Kebdana	35.0297° N	2.6134° W	Morocco	MF564173	MF564127	MF564158
Otala xanthodon	MVHN-2171	Orán-Tlemcén	pu	pu	Algeria	MN241305	KJ458507	KJ458603
Otala xanthodon	M048	10.5km due NE. of Outat- Oulad-El-Haj	33.4071° N	3.6445° W	Morocco	MN241306	MN227761	MN207616
Otala xanthodon	M050	14.3km due WSW. of Guercif	34.2054° N	3.4999° W	Morocco	MN241307	MN227762	MN207617
Otala xanthodon	M057	11.3km due NW. of Taourirt	34.4688° N	2.9898° W	Morocco	MN241308	MN227763	MN207618
Otalini sp.	MVHN- 010211FR03	Essaouira and Agadir	nd	nd	Morocco	MN241309	KJ458490	KJ458588
Rossmaessleria scherzeri olcesei	M068	above Chefchaouèn	35.1732° N	5.2569° W	Morocco	MN241310	MN227764	MN207619

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umber	ITS2	MN207621	MN207622	KR705080	MN207623	KJ458638	KJ458639	KR705081	KJ458640
k accession r	16S	MN227766	MN227767	KR705003	MN227768	KJ458559	KJ458560	KR705004	KJ458562
GenBar	COI	MN241312	MN241313	KR705040	MN241314	MN241315	MN241316	KR705041	MN241317
	Country	Gibraltar	Gibraltar	Morocco	Morocco	Spain	Spain	Spain	Spain
	Longitude	5.3422° W	5.3422° W	5.3750° W	5.4586° W	13.5563° W	13.5563° W	16.8056° W	2.3497° W
	Latitude	36.1285° N	36.1285° N	35.5417° N	35.8122° N	29.0585° N	29.0585° N	28.3292° N	36.8524° N
	Locality	Mediterranean Steps, Gibraltar	Mediterranean Steps, Gibraltar	Tangier-Tetouan, Yebel Beni Hozmar	2.8km due NNE. of Taghramt	Teguise, Lanzarote	Teguise, Lanzarote	Canary Islands, Tenerife, Teno Mountains, Erjos, gardens in the village	El Alquián, Almería
	Voucher	CGAH- 2016.02.1	CGAH- 2016.02.2	MN-153	M105	MVHN- 241109AZ01	MVHN- 241109AZ02	MN-001	MVHN-1269
	Species	Rossmaessleria scherzeri scherzeri	Rossmaessleria scherzeri scherzeri	Rossmaessleria scherzeri sicanoides	Rossmaessleria scherzeri subscabriuscula	Theba geminata	Theba impugnata	Theba pisana	Theba subdentata

Gene	Primer	Sequence	Reference
COI	LCO1490	5′-GGTCAACAAATCATAAAGATATTGG-3′	Folmer <i>et al.,</i> 1994
	HCO2198	5′-TAAACTTCAGGGTGACCAAAAAATCA-3′	Folmer <i>et al.,</i> 1994
16S rRNA	16Scs1	5′-AAACATACCTTTTGCATAATGG-3′	Chiba, 1999
	16Scs2	5′-AGAAACTGACCTGGCTTACG-3′	Chiba, 1999
5.8S-ITS2-28S	LSU-1	5'-CTAGCTGC GAGAATTAATGTGA-3'	Wade <i>et al.,</i> 2006
	LSU-3	5'-ACTTTCCCTCACGG TACTTG-3'	Wade <i>et al.,</i> 2006

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

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

			-			
		COI		16S rRNA	5.8S-ITS2	28S
	1 <sup>st</sup>	2 <sup>nd</sup>	$3^{\rm rd}$			
Evolutionary model selected	TrN+I+G	F81+I	TPM1uf+I+G	HKY+I+G	TPM3uf+G	K80+I

between *Otala, Loxana* and Otalini sp. was recovered with statistical support.

Within Otalina, the most diverse genera were Otala and Loxana. The genus Otala was recovered as monophyletic with full support (BP=1; BS=100), comprising at least nine species: O. hieroglyphicula, O. juilleti, O. lactea, O. occulta, O. orientalis, O. pallaryi, O. punctata, O. tingitana and O. xanthodon. Although the taxon O. hieroglyphicula could not be included in the combined molecular phylogeny, it was recovered within the genus Otala for the COI analysis as an independent lineage (Fig. S1 in Supplementary material). Loxana was also recovered as monophyletic (BP=1; BS=87), forming the sister group of the genus Otala. According to the molecular phylogeny, Loxana grouped at least 6 species: L. alabastrites, L. beaumieri, L. lechatelieri, L. massesylica, L. rerayana and L. rufa. Although most Loxana species included in the analyses were recovered as monophyletic, one specimen conchologically similar to Loxana beaumieri ("Otalini sp." MVHN-010211FR03, from W. Morocco between Essaouira and Agadir) was recovered as an independent lineage within the Otalina. The anatomical study of those two specimens only allowed them to be placed within the tribe Otalini, their tiny genitalia being too immature to provide detailed information.

Two species were recovered within the genus *Eobania, E. vermiculata* and *E. constantinae*. Populations from the whole Mediterranean

basin that had been identified as *E. vermiculata* were grouped together with full support (Fig. 1, Fig. S1 in Supplementary material, Table 1). However, the specimens classified as *E. constantinae* were not recovered as a monophyletic group. We found a clade joining several specimens from Tizi Ouzou province (north Algeria) and two lineages from Bouhamama region, one of them an immature named as *Massylaea massylaea* by Bouaziz-Yahiatene *et al.* (2017), which we place as "*E. constantinae* 519961".

## TAXONOMY, NOMENCLATURE AND DISTRIBUTION

The majority of Otalini show geographical differentiation of populations in shell form and coloration and this is so striking in many of the species that it led historically to description of numerous species. On the basis of anatomical and molecular data most of these species are now regarded as synonyms, so that intraspecific geographical variation becomes conspicuous and might be regarded as worthy of description by recognising subspecies. Nevertheless, we use formal nomenclature of subspecies sparingly and for only a few of the species. In reviewing the genus Otala, Holyoak & Holyoak (2017: 479) did not recognise subspecies despite the existence of large numbers of distinctive local populations. This was "because many of the populations show intergrading characters, the characters often vary independently, and some



**Figure 1** Phylogenetic relationships of Otalini taxa based on Bayesian inference from a combined dataset of two mitochondrial loci (*COI* and 16S rRNA) and one nuclear gene cluster (5.8S rRNA – ITS2 – 28S rRNA). Numbers at nodes correspond to Bayesian posterior probability (BP) and maximum likelihood bootstrap (BS) support values. Asterisks (\*) at nodes indicate full support for both analyses (BP=1; BS=100). Number sign (#) indicates that the name has been modified from the original publication to match the taxonomic classification proposed here.

'forms' reappear at widely separated localities". Also, "At least some local populations have shell coloration that appears to match that of the rocks and soils among which they live (pers. obs.), so selection for camouflaging coloration and patterns may account for convergence in appearance of geographically separated populations. Furthermore, the existence of complex colour and shell-banding polymorphisms in most populations makes interpretation difficult." A similar situation exists within the species treated here in the genus Loxana, where many geographically separated populations of L. beaumieri (Mousson) and L. rerayana (Mousson) could be diagnosed and named as identifiable subspecies (e.g. using the classical 75% rule of distinctness), but as in Otala their patterns of variation tend to be repetitive in different areas with shell coloration matching that of local substrata, and the limited molecular data provide no evidence that the differences reflect phylogenetic affinities. Similarly, in Moroccan Theba it was found by Greve et al. (2010, 2017) that intraspecific molecular variation mainly did not support the morphological subspecies provided in the detailed study by Gittenberger & Ripken (1987) and sometimes contradicted them.

The present study and other recent work has found that striking local populations of Otalini with keeled shells mainly lack differentiation from forms with rounded shells in the molecular markers studied (in Otala tingitana (Paladilhe), (Anton), Loxana alabastrites О. xanthodon (Michaud), L. beaumieri), as in Moroccan Theba pisana (O.F. Müller) (Greve et al., 2010, 2017) and other Helicidae species (Elejalde et al., 2008; Fiorentino et al., 2013). In contrast, some keeled forms in Rossmaessleria were distinguishable at subspecies rank from populations with rounded shells using molecular data (Walther et al., 2016) and the keeled Eremina inexspectata Llabador was afforded species rank (Holyoak et al., 2018).

## EREMININI new tribe

Type genus: *Eremina* L. Pfeiffer 1855, Malak. Bl., 2, p. 139; type species *Helix desertorum* Forskål 1775, by monotypy.

Description Helicidae with mainly rather large, dextral, subglobular to discoid shells. Spire usually raised, so height exceeds breadth or not, sometimes planorboid. Whorl profile usually rounded, less often with keeled periphery. Shell whorls expand rapidly to relatively large aperture. Peristome simple to widely expanded outwards and reflected. Shell surface nearly smooth to roughly malleate. Shell unmarked whitish or darker, often with multiple dark spiral bands that may show complicated and highly variable patterns. Male part of distal genitalia with penial flagellum absent or very short and a welldeveloped epiphallus. Interior of penis with single large verge located in distal part of middle portion of penis, lacking any second verge or lateral papilla in proximal part of penis. Female part of distal genitalia having proximal part of vagina bearing single rather small dart sac and two large branched mucous glands. Free oviduct of similar length to vagina or slightly longer. Duct of vas deferens lacking diverticulum. Distinction from other tribes of Helicidae nevertheless relies mainly on molecular evidence of phylogeny (Fig. 1).

This tribe contains only the genus *Eremina*. It is not considered further in this paper because the Moroccan and Tunisian populations were reviewed by Holyoak *et al.* (2018). Ali *et al.* (2016) also made combined molecular and morphological studies of Egyptian populations. Modern studies remain desirable for populations further east, extending from Israel through Arabia to Somalia, and also for possible representatives of the genus in the Cape Verde Islands.

## TRIBE THEBINI Wenz 1923

Subfamily Thebinae Wenz 1923, Fossilium Catalogus (1923–1930), 1, p. 381; Thebini placed on Official List by I.C.Z.N. (2006, Opinion 2135). Syn. Euparyphinae Perrot 1939 (p. 35).

## Theba Risso 1826

Hist. nat. Eur. merid., 4, p. 73, type species *Helix pisana* O.F. Müller 1774, by subsequent designation of Gray, 1847 (cf. ICZN Opinion 431, 1956).

Syn. *Xerophila* Held 1838 (invalid name, ICZN Opinion 431, 1956), *Euparypha* Hartmann 1843 (p. 204).

This complex genus native in S. Europe, N. Macaronesia and NW. Africa is not treated in detail here. Gittenberger & Ripken (1987) reviewed the genus based on shell and genital characters and distribution patterns. They recognised several Moroccan subspecies within both *T. pisana* and *T. subdentata* (A. Férussac 1821) based mainly on shell characters, but none of these subspecific taxa is supported by molecular data (cf. Greve *et al.*, 2010; Böckers *et al.*, 2016; Greve *et al.*, 2017).

Currently, classification of Moroccan taxa into species and subspecies appears rather arbitrary, since some molecular differences seem independent of the shell characters. Our dissections show that T. pisana differs markedly from all other Moroccan taxa in having the penial flagellum very short or absent, whereas it is long in all the rest. T. pisana is widely sympatric (and often syntopic) with T. subdentata. T. subdentata is at least locally sympatric with T. solimae Sacchi 1955 and T. sacchii Gittenberger & Ripken 1987. Shell data imply that *T. chudeaui* (Germain 1908) is also a distinct species. In addition, published molecular-phylogenetic and distributional data imply that T. chudeaui consists of at least two species, and a rather cryptic taxon (Theba sp. 3 of Greve et al., 2016: 2) occupies an extensive range between those of T. sacchii and T. cf. chudeaui.

## TRIBE OTALINI Pfeffer 1930 (as Otalae)

## Cantareusina new subtribe

Type genus: *Cantareus* Risso 1826.

Description Helicidae with medium-sized to large dextral shells varying from (mainly) subglobular to (less commonly) discoid. Whorl profile rounded to sharply keeled at periphery. Whorls expanding more or less rapidly to relatively large aperture. Peristome simple or reflected. Shell surface smooth to ribbed or malleate. Shell colour whitish or pale to dark, with or without up to five darker spiral bands. Male part of distal genitalia with long to very long penial flagellum and well-developed epiphallus. Interior of penis with distal verge, often also a proximal verge terminating epiphallus, sometimes also with lateral papilla (false verge) on inner wall of proximal part of penis. Female part of distal genitalia with proximal part of vagina

bearing single dart sac and pair of mucous glands each with 4–25 branches (branches being most numerous in large-bodied taxa). Duct of vas deferens with long diverticulum. However, distinction from subtribe Otalina relies mainly on molecular evidence of phylogeny (Fig. 1).

## Cantareus Risso 1826

Hist. nat. Eur. merid., 4, p. 64, type species *Helix naticoides* Draparnaud 1802 (= *Helix aperta* Born 1778), by monotypy.

Syn. *Tapada* [Gray in] Turton 1840: 127 (not Studer 1820), *Canthareus* Agassiz 1847, *Cantarelus* Pallary 1924 (p. 210, unnecessary nom. nov. pro *Cantareus* Risso "puisque l'étymologie de ce nom est Cantarel"), *Cantarus* auctt. (spelling error).

Until recently this was regarded as a monotypic genus for *Cantareus apertus* (Born 1778), from Mediterranean regions of S. Europe and Algeria. However, a review by Bouaziz-Yahiatene *et al.* (2019) using DNA sequence data and genital morphology in addition to shell characters separated the european *C. aperta* from two Algerian species, *C. subapertus* (Ancey 1893) and *C. korae-gaelius* Bourguignat in Locard 1882.

## Cornu Born 1778

Index Mus. Caes. Vindobon., 1, p. 371, type species *Cornu copiae* Born 1778. Syn. *Cryptomphalus* Charpentier 1837, *Coenatoria* 

Held 1837.

Numerous authors (including e.g. Schileyko, 2006: 1817) adopt the generic name Cryptomphalus Charpentier, 1837, regarding Cornu Born 1778 as a "nomen oblitum" or unavailable because based on a monstrous (scalariform) shell. However, an application to the ICZN to place the genus-group name Cornu Born 1778 on the Official List was granted. ICZN (2015, Opinion 2354) thus stated: "(1) ... that the name copiae Born, 1778, as published in the binomen Cornu copiae, is not unavailable by reason of being based on a teratological specimen, as it was not explicitly described as such. (2) The name Cornu Born, 1778 (gender: neuter), type species by monotypy Cornu copiae Born, 1778, is hereby placed on the Official List of Generic Names in Zoology, with the endorsement that it is based on an available type species, as ruled in (1) above. (3) The entry on the Official

List of Specific Names in Zoology for the name *aspersa* Müller, 1774, as published in the binomen *Helix aspersa*, is hereby amended to record that this is the valid name of the type species of *Cornu* Born, 1778 (a senior subjective synonym of *copiae* Born, 1778, as published in the binomen *Cornu copiae*)."

See Nordsieck (2013) for a clear and useful summary of the reasons for treating this species in a monotypic genus apart from *Helix, contra* the treatment on AnimalBase (Welter-Schultes, 2012: 610). Razkin *et al.* (2015) have subsequently provided molecular-phylogenetic data demonstrating it belongs in tribe Otalini, as sister to *Cantareus* Risso 1826, not in tribe Helicini (cf. Fig. 1).

#### Erctella Monterosato 1894

Naturalista Siciliano, 13(9), p. 168 (as *Helix* subgenus), type species *Helix mazzullii* De Cristofori & Jan 1832; genus originally contained *Helix mazzullii* and *H. costae*; type fixed by Schileyko (2006: 1800) who assumed monotypy, type fixed on this occasion under ICZN Art. 69.1.1. Colomba *et al.* (2011: 16) regarded *Helix mazzullii* as type designated by Pilsbry (1895: 316), but (*fide* AnimalBase) Pilsbry "1894" [2 Feb. 1895]: 316 gave a statement that *Erctella* was established "for *H. mazzullii*" but this was not a type designation (because term "type" was not used and the statement was incorrect because *H. costae* had also been included).

A review by Colomba *et al.* (2011) treated *Erctella* as a genus, containing three species, all of them endemic to Sicily.

On the basis only of shell characters, Schileyko (2006: 1800) tentatively listed *Erctella* as a synonym of the genus *Tyrrhenaria* Hesse 1918, Nachrichtsbl. d. malakozool. Ges., 50, p. 38. If that was correct, *Tyrrhenaria* would in fact become a synonym of *Erctella*, not *vice versa*, since the type species of *Tyrrhenaria* is *Helix tristis* L. Pfeiffer 1845, by monotypy, this nominal species being a synonym of *Helix ceratina* Shuttleworth 1843 (p. 16). However, *Tyrrhenaria* has subsequently been shown to fall within the genus *Helix* by the molecular investigations of Fiorentino *et al.* (2016). Together with the anatomical data presented by Hesse (1919, Iconogr., N. F. 23) its placement in *Helix* thus appears to be secured.

#### Rossmaessleria P. Hesse 1907

Icon., (2) 14, p. 8, type species *Helix sultana* Morelet 1880 by monotypy (see discussion by Walther *et al.*, 2016).

Syn. Rossmassleria [sic] Pallary 1939.

A detailed molecular and morphological study was presented by Walther *et al.* (2016), reducing the 13 named (allopatric) species to a single polytypic species which must be treated as *R. scherzeri* (Zelebor 1867). Torres Alba *et al.* (2016) provided morphological and other data on the nominotypical subspecies of *R. scherzeri* known only from Gibraltar and Neiber (2017) added molecular data for that population.

Ahuir Galindo (2017a) named four new taxa from NW. Morocco as *Rossmaessleria marocana*, *R. keltiensis*, *R. kucerai*, and *R. weberi paulae*; Ahuir Galindo (2018a: 24–25) named two more subspecies from the same region as *R. sultana septentrionalis* and *R. galindoae taghramtensis*; all of these seem best regarded as additional subspecies of *R. scherzeri*. Our fieldwork has also revealed additional populations resembling *R. scherzeri olcesei* (Pallary 1899) from around Chefchaouèn that could be named as several more new subspecies because they deviate consistently in shell characters (collected in 1984 from three localities: Torres Alba *et al.*, 2016: 8–11; in 2017 from five other localities).

Treatment of the whole genus as a single species by Walther et al. (2016) was well argued based on results of rather complex species-delimitation analyses of their molecular data. It is also clear that several of those named populations are connected by others with intermediate shell morphology, supporting allocation to subspecies rank. Nonetheless, although there are no localities with two distinct forms coexisting, there are regions where allopatric representatives have ranges that approach each other closely (within one kilometre) without evidence of intergradation. This is particularly striking near Tétouan which is the type-locality for four distinctive forms named by Kobelt (1881a) as Helix sicanoides, H. platycheloides (= H. weberi Kobelt 1887), H. tetuanensis and H. boettgeri (his type locality of "Beni Hosemar" for all of them corresponds to the old Beni Hozmar tribal area, not a single mountain). Experiments to test potential inter-breeding capability of these would be worthwhile.

## Subtribe Otalina Pfeffer 1830

## Maurohelix P. Hesse 1917

Nachrichtsbl. d. malakozool. Ges., 49, p. 122 (nom. nov. pro *Wiegmannia* Hesse 1916), type species *Helix raymondi* Moquin-Tandon 1848, by monotypy.

Syn. *Gaetulia* Kobelt 1898 (not Stål 1864 [Hemiptera]), *Wiegmannia* P. Hesse 1916 (not Collinge 1901 [Ariophantidae]).

## M. raymondi (Saint-Simon 1848)

Helix Raymondi Saint-Simon 1848, Misc. Malac., 1<sup>er</sup> décade, pp. 9–10, TL les crêtes rocailleuses des environs de Tuquin, le Djebel-el-Amoun [authorship is often atributed to Moquin-Tandon, e.g. Bourguignat, 1863, t.1: 104 gave Moquin-Tandon, mss., in Saint-Simon; however, the publication itself gives no evidence of this since Moquin-Tandon is mentioned only in the dedication at the front of the work]; Saint-Simon (1852: 21), observations on live animal, external features of body and anatomy; Morelet (1852: 240), as Raymondii [sic]; Morelet (1853b: 287); Saint-Simon (1856: 18); Bourguignat (1863, t. 1: 104–108, pl. 9 figs 1–4) (Algeria: les crêtes rocailleuses des environs de Tuquin; le Djebel-el-Amoun; alentours de Djelfa; d'Aumale; sur les hauts plateaux, au sud de Boghar); Bourguignat (1864, t. 2: 305) (Environs de Bousaada; Djebel-Meketsit, à l'éxtremité est du Zahres-el-Chergui); Kobelt (1878, Icon., (1) 6 (1-3), p. 2, pl. 151 figs 1531), "in felsigen Gebieten der Provinz Oran"; Bourguignat in Servain (1880: 50); Bourguignat in Péchaud (1883: 110), environs de Boghari; près de Boghar; alentours de Djelfa; Ancey (1893); Kobelt (1898: 208, 357), Gaetulia gen. nov. (preoccupied), type species by monotypy H. raymondi (see Schileyko, 2006: 1791); [Helix] Raymondi – Bourguignat (1899), J. Conchyl., 46, pp. 168, 169; Hesse (1916: 124), Wiegmannia nom. nov. (preoccupied) pro Gaetulia Kobelt 1898, type species by monotypy H. raymondi (see Schileyko, 2006: 1791); Maurohelix raymondi (Moq.-Tand.) St. Simon - Hesse (1920, Icon., (2) 23 (5–6), p. 243); Pallary (1939a: 66; 1939b: 107); Schileyko (2006: 1791, fig. 2292), figs of shell and genital anatomy, latter based on NMW.Z 1993.051.1314; Razkin et al. (2015: 103, 108), DNA sequence data from NMW.Z specimen).

*Helix Desfontanea* Morelet 1851, J. Conchyl., 2, p. 355, pl. 9, figs. 7–8, TL "les plateaux au sud de Boghar, dans la province d'Oran" (Algeria); Breure, Audibert & Ablett (2018: 270, fig. 33); *Desfontainea* [*sic*] Petit de la Saussaye 1852.

*Helix Miloni* Bourguignat in Péchaud 1883, Excurs. malac., pp. 110–112, TL Djebel Sahari, près de Djelfa; Ancey (1893); *Helix Miloni*, Bourguignat (1899), J. Conchyl., 46, pp. 168, 169, Djebel Sahari, près Djelfa; *Maurohelix miloni* (Bgt.) Péchaud – Hesse (1920, Icon., (2) 23 (5–6), p. 243), as one of two species dubiae in this genus.

Helix Sollieri Bourguignat in Péchaud 1883, Excurs. malac., p. 112, TL Djebel Sahari, près de Djelfa; Helix (Iberus) sollieri Bourguignat - Kobelt (1893, Icon., (2) 6 (3-4), pp. 79-80, pl. 170, figs 1096-1097), bei Boghari am Rande des Hochplateaus südlich von Algier ("ausschliesslich am steil abfallenden Südrand des Plateaus, welches den Ksor Boukhari trägt"); Westerlund (1889, Fauna palaearct. Binnenconch., 2, p. 407); Ancey (1893), (near Boghar, in that region not extending beyond mountain d'Ain Seba situated 9km to the south; similar forms from hills of Ain Boucif at 57km E. of Boghar and to SE. on denuded crests of Barine, on the route to Bou Saada, and at ca 80km from Boghar; further south it is numerous in the chain of diebel Sahari not far from Guelt-es-Stel and near Djelfa, also (type) in the djebel Amour near Taguine); Bourguignat (1899: 166, 168, 170), (environs de Djelfa; environs de Boghar); Gaetulia sollieri Pechaud - Hesse (1911, Icon., (2) 16 (5-6), pp. 113-116, pl. 450 figs 1-10), (bei Boghar, Prov. Algier), figs of radula, jaw and genitalia; Maurohelix sollieri (Bgt.) Péchaud – Hesse (1920, Icon., (2) 23 (5-6), p. 243); Pallary (1939a: 66; 1939b: 107).

[*Helix*] *Tachypopta* "Bourg." Bourguignat in Servain (1880: 50), *nomen nudum; Helix tachypopta* Bourguignat 1899, J. Conchyl., 46, pp. 167 (description), 168, 170, TL environs de Djelfa, dans le dj-Sahari (leg. Bourguignat); vieux tumulus de Mader Romana, près Bou Saàda; dans le Djdar, près du Hodna, dans la province de Constantine; *Maurohelix tachypopta* (Bgt.) Péchaud – Hesse (1920, Icon., (2) 23 (5–6), p. 243), as one of two species dubiae in this genus.

*Maurohelix Selimani* Pallary 1933, Bull. Soc. Hist. nat. Afr. Nord, 24(7), p. 246, TL Beni Seliman (Maroc oriental); Rour *et al.* (2002: 195). *Shell* Figures: Bourguignat (1863, Malac. Algérie, 1, pl. 9), Kobelt (1879, Icon., (1) 6, pl. 151), Tryon (1888, Man. Conch., (2) 4, pl. 44), Kobelt (1893, Icon., (2) 6, pl. 170), Schileyko (2006: 1791, fig. 2292A); Fig. 3B.

*Genital anatomy* Figures: Saint-Simon in Bourguignat (1863, *op. cit.*, p. 108), Hesse (1911: pl. 450, *sollieri*), Schileyko (2006: 1791, fig. 2292B); Fig. 5A, F.

*Range* E. Morocco (reported only from "Beni Seliman"); N. Algeria (restricted to rather arid regions of Hauts Plateaux); Fig. 8. Not sympatric with any other species of Otalini.

*Ecology* Ancey (1893) described the *H. raymondi* species group as strictly limited to the Hauts Plateaux of Algeria, reporting his observations (of *H. sollieri*, see above) from localities on stony hills, on denuded massifs and denuded crests of hills, one locality being on beds of calcareous sandstone. He described it as rupestral, living in fissures in the rocks. When it was resting in dry periods he found that the shells adhered so strongly to rock surfaces that they broke when attempts were made to remove them.

Notes (1) Identification of *Helix gyrostoma* A. Férussac 1821 and *H. pseudogyrostoma* by Bourguignat (1899: 170) as forms allied to *Maurohelix raymondi* was not accepted by Hesse (1911, Icon., (2) 16 (5–6), p. 113), who stated that these belong in *Levantina* Kobelt 1871. Hesse (1920, Icon., (2) 23 (5–6), p. 246) later listed two species from Tripolitania in *Levantina* (Subgenus *Gyrostomella* P. Hesse 1911), *L. gyrostoma* and *L. leachii* (A. Férussac 1821). (2) Two nominal species of *Maurohelix* are known only as fossils: *Helix altavensis* Pallary 1901, Mem. Soc. Geol. Fr., Palaeont., 9 (22), p. 137, and *H. boulei* Pallary 1901, *ibid.*, p. 121.

#### Massylaea Möllendorff 1898

Nachrbl. d. malak. Ges., 30, p. 120, Type species *Helix massylaea* Morelet 1851, by absolute tautonymy.

Westerlund (1902, Methodus disp. Conch. extram. reg. pal. ..., p. 16) has been regarded as author of this generic name (e.g. by Schileyko, 2006: 1806), presumably because *Massylaea*  Möllendorff 1898 was dismissed as a *nomen nudum*. However, Möllendorff (1898) wrote "..., denen sich die angeblichen *Macularia massylaea* und *punica* anschliessen (Sect. *Massylaea* m.)." Hence Möllendorff (1898) clearly included *massylaea* and *punica* under the new name *Massylaea* which is therefore available under ICZN Art. 12.2.5 by indication.

Syn. *Punica* Pallary 1936, J. Conchyl., Paris, 80 (1), p. 31, as "groupe" within *Massylaea*, type species *Helix punica* Morelet 1851, by tautonymy.

Bouaziz-Yahiatene et al. (2017) studied the Algerian M. massylaea (type of genus Massylaea) and M. punica and made comparisons with Eobania constantinae and E. vermiculata. They claim to have examined a single live-collected Massylaea specimen (given, op. cit.: 113 as NMBE 519961, from Aurès Mountains, Batna/Kenchela (which are towns 89km apart), with no altitude or habitat data; described and figured, op. cit .: 119 fig. 3 genital anatomy, 120 fig. 8 shell); this was assigned by them to M. massylaea and provided both immature genital anatomy (possessing false verge in the proximal part of the penis as in Eobania) and DNA sequence data placing it in the same clade as *Eobania*. On that basis alone, they proposed that the genus Eobania should be merged with Massylaea.

Unfortunately these authors do not consider the more obvious but less exciting possibility that their single subadult snail was in fact a misidentified Eobania "constantinae", not M. massylaea. Both species are known from the Aurès Mountains and the published shell figure cannot be reliably identified with either species. Despite citing Hesse (1915) they appear not to have noticed that his figures of the genital anatomy of M. massylaea and M. punica differ markedly from those of Eobania, especially in having a much shorter diverticulum on the duct of the bursa copulatrix which is not tightly coiled in situ and fewer branches on the vaginal mucous glands. Hesse's figures also show close similarity of M. massylaea and M. punica; he did not figure or describe the internal structure of the penis. M. punica was regarded as a synonym of M. massylaea by Bouaziz-Yahiatene et al. (2017: 117–119). Our studies of bodies from seven M. punica collected from two locations in 1984 show an exact match for Hesse's figures: our dissections also show that all seven lack a false verge

of *Eobania* type. Hence, we can indeed conclude that the anatomy and sequence data presented by Bouaziz-Yahiatene *et al.* (2017) for *Massylaea massylaea* derive from a misidentified specimen of *Eobania "constantinae"*, negating their suggestions for revision of the generic classification. Furthermore, their sequence data appear to be closest to those of *Eobania constantinae*, in a different clade to *Massylaea punica* (see our Fig. 1), although inexplicably their *COI* data alone match those of *Otala* closely (see Supplementary Fig. S1).

The absence of reliable molecular data for the type species of *Massylaea*, *M. massylaea*, results in the taxonomic position of the genus being based mainly on its close anatomical similarity to *M. punica* (based on Hesse, 1915: pl. 636 figs 23–28), for which we provide new molecular data here. The two species are also very similar in shell characters and have parapatric ranges, such that Bouaziz-Yahiatene *et al.* (2017: 117–121) regarded them as conspecific.

## M. massylaea (Morelet 1851)

*Helix Massylaea* Morelet 1851, J. Conchyl., 2, pp. 354–355, pl. 9, figs 1, 2, TL "la province de Constantine, mais nous ne pouvons préciser la localité" [Algeria].

Helix Massylæa Morlt. - Morelet (1853b: 286), with var.  $\beta$  grisea absque fasciis (descriptive phrase, not valid as name), "In prov. Cirtensi" (i.e. in Prov. Constantine, Algeria); Pfeiffer (1853, Mon. Helic. viv., 3: 198); Morelet (1857: 371), "Sur le territoire des Ouled-Sassi, non loin de Constantine"; Bourguignat (1863, t. 1: 108–110, pl. 9 figs 5-9), with new vars concolor ("trèscommune") and conoidea (Rare, Ouled-Sultan), species also "au sud de Constantine, dans une localité nommée Zenatias" and "sur le territoire des Oulad-Sassy (province de Constantine)"; Kobelt (1875, Icon., (1) 4 (1), pp. 3-4, pl. 92 figs 977), Süden der Provinz Constantine; Pfeiffer (1878–1881, Nomenclator, p. 155); Bourguignat in Péchaud (1883: 95, 100), erroneous spelling of massyloea on p. 100 [twice, with oe as diphthong], with locality data; Kobelt (1888, Icon., (2) 3 (1-2), pp. 2–4, pl. 62 figs 312–315), additional localities (Umgebung der Quelle des Bu Merzug; gegen die Bahnstation el Guerrah; in den Dolmen am Wed Zenati; Höhen der Aurès in ca. 5000' Meereshöhe

kronenden Kalkklippen hinter Lambessa; in ca. 7000' Meereshöhe in der durch die Einsenkung von den Aurès geschiedenen Bergmasse des Dschebel Tuggur; Dolmen bei Bu Nuar), also described variability of shells, including banding morphs, with description of var. zenatia (p. 3); Tryon (1888, Man. Conch., (2) 4, pl. 38); Pallary (1917: 135); Breure et al. (2018: 342, fig. 649); Massylaea massylaea Morelet - Hesse (1915, Icon., (2) 23 (1-2), pp. 41-43, pl. 636 figs 21-28) (from Sigus, Prov. Constantine), figs of jaw, radula and genitalia; Hesse (1920, Icon., (2) 23 (5-6), p. 234), with var. zenatia Kob.; Pallary (1936: 31; 1939b: 107); Rour et al. (2002: 194), incorrectly included in list of Moroccan species; Schileyko (2006: 1806–1807 fig. 2315).

*Helix Moquiniana* L. Raymond mss. – Bourguignat (1863: 108), *nomen nudum* listed as synonym (non *Helix Moquiniana* Raymond, 1853).

Shell Figures: Bourguignat (1863 t. 1: pl. 9 figs 5–9); Kobelt (1875, Icon., (1) 4 (1), pl. 92 figs 977; 1888, ibid., (2) 3 (1–2), pl. 62 figs 312–315); Tryon (1888, Man. Conch., (2) 4, pl. 38), Schileyko (2006: 180 fig. 2315), Bouaziz-Yahiatene *et al.* (2017: 120, fig. 4); their fig. 8 purporting to be *M. massylaea* represents misidentified *Eobania* sp. (see above); Breure *et al.* (2018: 342, fig. 649); Fig. 2A.

*Genital anatomy* Figures: Hesse (1915: pl. 636 figs 23–28). Figs and descriptions in Bouaziz-Yahiatene *et al.* (2017: 119) purporting to be *M. massylaea* represent misidentified *Eobania* sp.

*Range* Endemic in E. Algerian mountains of region S. of Constantine, where recorded at 1524–2306m elevation (Kobelt 1888 gave sites at 5000 and 7000 feet, i.e. 1524 and 2134m); Fig. 8. Not recorded as sympatric with any other species of Otalini, but may coexist locally with *Eobania constantinae*.

*Notes* (1) The close resemblance of shells of this species to those of *Helix* (*Codringtonia*) *codring-toni* Gray 1834 from Greece has been discussed in detail in the literature (cf. Morelet, 1851: 354; Kobelt, 1888: 3–4) and is attributed to convergent evolution. (2) *M. massylaea* appears close to *M. punica* (differing most obviously in having the interior of the aperture white not brown, stronger radial sculpture on shell giving weakly ribbed



**Figure 2** Representative shells of *Massylaea* and *Loxana rerayana* (Otalini: Helicidae): A *Massylaea massylaea* (Algeria, 35°35'N 6°04'E, NMW.Z.1993.051.857); B *Massylaea punica* (Algeria, 35°28'N 6°42'E, NMW.Z 1993.051.4532); C–F *Loxana rerayana*, all from Morocco, in CGAH, C (N31.3129° W7.9578°, M160), D (N28.9608° W10.5551°, M91), E (N30.7812° W8.3940°, M162), F (N31.2156° W7.8394°, M165). See Appendix for additional data on specimens figured.

appearance) and it might be conspecific with it, occupying higher altitudes in the same region. Furthermore, Kobelt (1888, Icon., (2) 3 (1-2), p. 5) noted from his own field observations in his account of *H. punica*, "Es scheint dem Gebiete der Helix massylaea ziemlichparallel zu laufen und hier und da in es hineinzugreifen, aber ich habe beide Arten nie zusammen gefunden." [ranges of the two taxa appear to lie parallel and here and there approach each other closely, but they were never found together]. Bouaziz-Yahiatene et al. (2017) regarded them as conspecific, but without any detailed discussion or comparisons of them. These authors acted as the first revisers who considered the taxa conspecific, therefore establishing that the name *massylaea* should be given priority at species rank over the name punica if they are treated as conspecific.

## M. punica (Morelet 1851)

Helix Punica Morelet 1851, J. Conchyl., 2, pp. 352–353, pl. 9 figs 3, 4, TL "la grande plaine de Temlouk, au sud-est de Constantine" [Algeria]; Morelet (1853b: 287), "Ad orientem prov. Cirtensis in agro Temloukanco"; Reeve (1854, Conch. Icon., 7, p. CXCIII, species 1352); Bourguignat (1863, t. 1: 110–111, pl. 9 figs 10–14) (plaine de Temlouk; Environs de l'Ouled-Sultan; Zuchthauses von Lambessa; etc.); Kobelt (1875, Icon., (1) 4 (1), p. 3, pl. 91 figs 976), östlichen Algerien in der Provinz Constantine; Pfeiffer (1878-1881, Nomenclator, p. 155); Bourguignat in Péchaud (1883: 99), with locality data; Kobelt (1888, Icon., (2) 3 (1-2), pp. 4-6, pl. 63 figs 316-322), distributional data ("Characterschnecke für einen grossen Distrikt in der Provinz Constantine, südlich von der gleichnamigen Stadt"; Gebiete des Wed Rummel; Wed Bu Merzug; subfossil ... vor dem Hôtel du Kantara (el Kantara) am "Munde der Wüste"), discussion of variation in shell characters, with description of var. speculatorum, a subfossil dwarf form from near El Kantara (op. cit., p. 6, fig. 322); Tryon (1888, Man. Conch., (2) 4, pl. 40); Pallary (1917: 135; 1936: 31); Breure et al. (2018: 400, figs 907, 908); Massylaea punica Morelet - Hesse (1915: pp. 43-45, pl. 636 figs 29-30, pl. 637 figs 31–34) (von Tebessa in Algerien; von Redyef im südlichen Tunis), with figs of jaw and genitalia; Hesse (1920, Icon., (2) 23 (5-6), p. 235), with var. speculatorum Kob.; Punica punica, Pallary (1939b: 107).

*Helix nitefacta* Bourguignat in Péchaud 1883, Excursions malac., pp. 99–100 (description), TL l'Aurès oriental à Ain-Tamagra, au sud de Khenchala (cited *Helix nitefacta*, Bourguignat, spec. noviss., no. 121, 1878, but this was a fictional publication: Connolly 1934, Dance 1970); *Massylaea nitefacta* (Bgt.) Péch. – Hesse (1920, Icon., (2) 23 (5–6), p. 234), östl. Algerien, Tunis; Pallary (1936: 31), unique specimen at MHNG has been repaired at least seven times.

*Massylaea massylaea* pars – Bouaziz-Yahiatene *et al.* (2017: 117–121).

*Shell* Figures: Morelet (1851: pl. 9 figs 3, 4), Bourguignat (1863 t. 1: pl. 9 figs 10–14); Kobelt (1876, Icon., (1) 4, pl. 91; 1888, *ibid.*, (2) 3, pl. 63); Tryon (1888, Man. Conch., (2) 4, pl. 40); Bouaziz-Yahiatene *et al.* (2017: 120 figs 5–7); Breure *et al.* (2018: 400, fig. 907); Fig. 2B.

*Genital anatomy* Figures: Hesse (1915: pl. 636 fig. 30, pl. 637 figs 31–34); Fig. 5B, G.

*Range* E. Algeria in region S. of Constantine; also reported just across border in W. Tunisia (Redyef: Hesse 1915: 43); recorded at 530–1500m elevation (Fig. 8). Sympatric with *Eobania constantinae*.

*Notes* (1) Pallary (1936: 31–32) commented on characters and behaviour of this species which he thought might distinguish it from (other) *Massylaea* spp. (2) See comments under *M. massylaea* regarding tentative separation of this taxon at species rank.

## Eobania P. Hesse 1913

Nachrbl. d. malakozool. Ges., 45, p. 13; type species *Helix vermiculata* O.F. Müller 1774, by monotypy.

Syn. *Macularia* sensu Martens in Albers & Martens 1860: 132 (non Albers 1850; *Helix* subg.; type species *Helix vermiculata* O.F. Müller 1774, invalid designation because this species not originally included).

The genus is not treated in detail here because it was reviewed by Holyoak & Holyoak (2017: 467– 473) who treated all forms as a single species and Bouaziz-Yahiatene *et al.* (2017) who recognised two species. Thus, the latter authors provided molecular evidence that *E. constantinae* may after all be a valid species, which usually also differs



**Figure 3** Representative shells of *Loxana rerayana*, *L. beaumieri*, *Maurohelix raymondi*, *Otala occulta* and *O. pallaryi* (Otalini: Helicidae): A *Loxana rerayana* (Morocco, N29.4073° W9.7176°, CGAH M88); B *Maurohelix raymondi* (Algeria, 35°11'N 4°09'E, NMW.Z.1993.051.1314); C–F *Loxana beaumieri*, all from Morocco, in CGAH, C (N31.2822° W7.9683°, M166); D (N31.5289° W7.5690°, M171); E (N31.2190° W8.1105°, M170); F (N32.1355° W6.5237°, M140); G *Otala occulta* (holotype, Morocco N33°35' W4°11', NMW.Z 1993.051.04050a); H *O. pallaryi* (Morocco, N34.8171° W2.3910°, CGAH M116). See Appendix for additional data on specimens figured.

in having the shell surface smooth rather than finely malleate as in *E. vermiculata*. Our analysis of the molecular data (Fig. 1) nevertheless gives a puzzling result with all *Eobania* in a single clade, within which all six exemplars of *E. vermiculata* cluster together, whereas *E. constantinae* forms three separate basal sub-clades which may imply three separate cryptic species are involved. There is no evidence of *E. constantinae* and *E. vermiculata* ever occurring sympatrically or any reason to infer that they are reproductively isolated, but the deep molecular-phylogenetic divisions apparently imply that they are widely separated.

## Otala Schumacher 1817

Essai d'une nouv. syst. habitations Vers test., Copenhagen, pp. 58, 191; type species *Helix lactea* O.F. Müller, 1774, by subsequent designation of Pilsbry (1895, Man. Conch., (2) 9, p. 323).

The genus is not treated in detail here because it was reviewed by Holyoak & Holyoak (2017), who gave a detailed generic synonymy (*op. cit.*: 423). The following nominal genus should be added: *Siretia* Pallary 1926, J. Conchyl., 70 (1), p. 19, as sect. of *Helix*; type species *Helix pallaryi* A. Koch, by original designation.

The following changes to treatment of species in that study also need to be made:

## Otala pallaryi (A. Koch 1909)

Archelix pallaryi A. Koch in Kobelt 1909, Nachrbl. d. malakozool. Ges., 41, pp. 134–135, TL Taforalt im Gebiet der Beni Snassen; Kobelt made it clear that the description ("Koch mss.") and an illustration were sent to him by Pallary, and Pallary (see below) was subsequently consistent in attributing authorship of the name to Koch (cf. Kneubühler et al., 2019: 15, who gave Kobelt as author despite noting that Kobelt explicitly mentions "Koch mss."); Archelix pallaryi (A. Koch) Kob. - Hesse (1911, Icon., (2) 16 (5-6) pp. 68-70, pl. 442 figs 14-19), (bei Taforalt im Gebiete der Beni Znassen im östlichen Marokko), figs of jaw and genitalia; Archelix pallaryi Koch - Pallary (1914: 20, pl. 1 fig. 5), "Die Art ist in Form und Färbung sehr wenig variabel"; Archelix pallaryi (Koch mss.) Kobelt [p. 21], H.[elix] pallaryi Koch [legend to pl. 547] - Kobelt (1914, Icon., (2) 20 (1-2), p. 21, pl. 547 fig. 2790); Archelix (Archelix) pallaryi (A. Koch) Kob. – Hesse (1920, Icon., (2) 23

(5–6), p. 239); H.[elix] Pallaryi A. Koch – Pallary (1923b: 277), groupe des Beni Znassen; Siretia Pallaryi A. Koch - Pallary (1926: 19, pl. 3 figs 5, 6, 8), with new var. discula (pl. 3 fig. 7, TL Les Kiffans); vars major and minor named, "Avec le type à Berkane" but both were nomina nuda; Siretia Pallaryi – Pallary (1939a: 64; 1939b: 107); Siretia pallaryi (Kobelt, 1914) – Cossignani (2014: 96), figs of shell, from Berkane; Siretia pallaryi minor (Kobelt 1914) – Cossignani (2014: 96), figs of two shells, from Ras el Ma (authorship erroneous; not valid as species-group name); Siretia pallaryi (A. Koch) Kobelt - Llabador (1952: 106-107, pl. 5 figs 4-6), Tatsfachts (Oulad Settout), with new var. settoutensis (p. 107, pl. 5 figs 7-9, TL Tatsfachts (Oulad Settout)); Siretia pallaryi settuatensis [sic] Llabador 1952 - Cossignani (2014: 96), figs of shell, from Ouled Settout (not valid as species-group name); Alabastrina (Siretia) pallaryi (Kobelt 1914) - Schileyko (2006: 1795-1796, fig. 2300), figured shell from Locux Mexera, Morocco (from "SPb", now ZISP collection).

*Shell* Figures: Pallary (1926), Llabador (1952), Schileyko (2006: 1796), Kneubühler *et al.* (2019: 16); Fig. 3H.

*Genital anatomy* Figures: Hesse (1911, Icon., (2) 16 (5–6), pl. 442 figs 15–19); Fig. 5E, H.

*Range* Endemic in NE. Morocco (Fig. 8): published reports mainly in and near Beni Snassen Mts. (Berkane; "Les Kiffans"; Taforalt), further west at Tatsfachts (Oulad Settout). Sympatric and syntopic with *O. xanthodon*; its range also overlaps that of *O. lactea*, *O. orientalis*, *O. punctata* and *O. tingitana* although they have not been found to coexist.

*Notes* (1) Kobelt (1909), Hesse (1911) and Pallary (1914) were clearly correct in regarding this as a species of *Otala*. Although Holyoak & Holyoak (2017) excluded it from that genus, our subsequent anatomical study of specimens collected in 2017 confirms the account by Hesse (1911), based on presence of the two large vaginal mucous glands typical for *Otala*, each having a stout stalk and lower branches and numerous terminal branches (see Fig. 5E). Kneubühler *et al.* (2019: 14) retained it as a genus on the basis of their phylogenetic analyses (but mention doubts: *op cit.*, p. 31). Our phylogenetic analyses place it within *Otala* as sister to *O. juilleti* (Fig. 1). (2) *Michaudia aenigmatica* 



**Figure 4** Representative shells of *Loxana rufa*, *L. lechatelieri*, *L. alabastrites*, *L. massesylica* and *L. bailloni* (Otalini: Helicidae) from Morocco, all in CGAH unless otherwise noted: A–C, *L. rufa*, A (N33.5642° W4.2059°, M123); B, C (N33.4423° W4.8446°, M128); D *L. lechatelieri* (N33.2094° W4.5267°, M121); E *L. bailloni* (N33.9744° W3.0397°, NMW.Z 1993.051.2077); F, G *L. alabastrites* (N34.8163° W2.4122°, M114); H *L. massesylica* (N33.9744° W3.0397°, M119). See Appendix for additional data on specimens figured.

(Pallary 1918) (based on *Archelix* (?) *aenigmatica* Pallary 1918, Bull. Soc. Hist. nat. Afr. Nord, 9(7), pp. 147–148, TL ravin de Noiseux (Oran); syn. *Michaudia enigmatica* Pallary 1929 (p. 129) is of uncertain identity. Pallary (1926: 16–17, pl. 3 fig. 9; 1929 (p. 129) knew of three shells. He thought it was probably based on a hybrid between [*Otala*] *hieroglyphicula* and [*Loxana*] *soluta*, but this seems unlikely in view of anatomical differences between these species (cf. Figs 5, 6).

## Otala juilleti (Terver 1839)

Notes Holyoak & Holyoak (2017: 435-437, 444) treated Helix juilleti Terver 1839 as a synonym of O. lactea (O.F. Müller 1774) commenting (p. 444) that it nevertheless looks very distinctive in samples from eastern parts of its Algerian range (e.g. NMW.Z 1993.051.621, -635, -666), with up to 4.7 slowly expanding whorls, a low spire and rather flat base to the shell, peristome with white upper and outer edges, prevalence of morphs with four and five well defined narrow bands, and weak spiral microsculpture on the periostracum. Holyoak & Holyoak (2017: 434, fig. 2C) figured a representative shell alongside those of O. lactea. It was treated as a form of O. lactea in that publication because these distinctive characters are less marked in samples from the Monts de Tlemcen in NW. Algeria (1993.051.603, -590; fig. 2D).

In our phylogenetic tree incorporating many additional samples, the sequence data for MVHN 2186 from NW. Algeria identified as "Otala (Otala) punctata?" in Razkin et al. (2012: 103 table 1, 108 fig. 2) were found to form a clade sister to O. pallaryi, and far from those of five exemplars of O. punctata and indeed of any other Otala species (Fig. 1). Prof. Martínez-Ortí has confirmed that the collection locality of MVHN 2186 was by the N22 road ca 7km SW. of the centre of Tlemcen (i.e. ca 34°50.16'N 1°22.32'W, at around 1176m alt.). Our study of MVHN 2186 (two specimens, one adult that was used for the DNA sample and one subadult) reveals that they match the shell figured from the Monts de Tlemcen by Holyoak & Holyoak (2017: fig. 2D, showing NMW.Z 1993.051.603 from 34°48'N, 1°05'W) as O. lactea, which was noted (op. cit., p. 444, and see comments above) as showing less marked distinctive characters of Helix juilleti than specimens from further east in Algeria. Nonetheless, MVHN 2186 can be regarded as conspecific with *H. juilleti*.

Hence, Otala juilleti (Terver 1839) should be regarded as a valid species. Synonyms of it are listed in detail by Holyoak & Holyoak (2017: 435-443), those which have been used at species rank being Helix wagneri Rossmässler 1839, H. chottica Ancey 1882, H. margueritii Bourguignat [in Péchaud] 1883, H. beguirana Kobelt 1887, and H. saidana Debeaux in Kobelt 1887. Its range is apparently restricted to NW. Algeria (Fig. 8; see Appendix for details of records of O. juilleti from our field collections, revising the Supplementary Appendix from Holyoak & Holyoak, 2017). Within Algeria it is distinct from O. punctata in the body whorl not being disproportionately wider than the penultimate whorl, and from the local forms of O. lactea in the same character and also the brown coloration inside the aperture tending to be paler and extending less far outside the aperture, the mainly white peristome edge and the often slightly larger number of shell whorls (up to 4.7). Hesse (1911, Icon., (2) 16: pl. 443) described and figured the genital anatomy of Archelix juilleti and its synonym Archelix chottica (Ancey 1882) (op. cit., pl. 444) and we have studied the similar genital anatomy of MVHN 2186. These specimens all show *juilleti* has the penial flagellum distinctly longer than the epiphallus as in O. lactea and thus differing from that of O. punctata; no other differences were apparent in the external features of the genital organs.

The Key below summarises characters distinguishing *juilleti* from all other *Otala*.

## Otala occulta sp. nov.

*Holotype* NMW.Z 1993.051.04050a, shell (Fig. 3G), part of collection made on 16 Aug. 1986 by DTH, M. Holyoak & M.B. Seddon., H&S field number 1986.421.11 (site 377).

*Type locality* By road 4656 at 15km NE. along road from Immouzer-des-Marmoucha, Moyen Atlas, Morocco, 33°35'N 4°11'W; from crags and rocky slopes (sandstone), with patchy cover of evergreen oaks (*Quercus*), shrubs., etc., water running locally. The site was probably at *ca* 1569–1590m alt. judged on a return visit in 2017.

*Paratypes* Nine shells with bodies in spirit (1993.051.04051) and three dry shells (1993.051.04050b), all from type locality, collected with the holotype during same visit.



**Figure 5** Anatomy of distal genitalia of Otalini 1 (Figs F–I give partly diagrammatic longitudinal sections of the penis): A, F *Maurohelix raymondi* (Algeria, 35°11'N 4°09'E, NMW.Z.1993.051.1314); B, G *Massylaea punica* (Algeria, 35°17'N 6°38'E, NMW.Z.1993.051.1236); C *Loxana lechatelieri* (Morocco, 33.4423°N 4.8446°W, CGAH M128); D *Otala hieroglyphicula* (Algeria, 34°43'N 1°33'W, NMW.Z 1993.051.560); E, H *Otala pallaryi* (Morocco, 34.8171°N 2.3910°W, CGAH M116); I *Otala orientalis* (Morocco, Berkane, MVHN 080709DR3). All scale bars represent 3.0mm.

Abbreviations (for Figs 5–7): a genital atrium, ag albumen gland, bc bursa copulatrix, bcd duct of bursa copulatrix, div diverticulum on bcd, dp distal penis, ds dart sac, dv distal verge, e epiphallus, ee extension of epiphallus into lumen of pp, f free oviduct, fl flagellum, fv false verge (papilla), hd hermaphrodite duct, m mucous gland(s), m1 & m2 details of mucous glands, p penis, pe papilla on exterior of ee, pi pilaster, pp proximal penis, prm penis retractor muscle, ps penis sheath, pv proximal verge, ts transverse section, so spermoviduct, va vagina, vd vas deferens. See Appendix for additional data on specimens used.

*Diagnosis* (based on holotype, but 12 paratypes generally similar). Shell conical-subglobular, flattened beneath, D 26.0, H 16.4mm, of 4.5 whorls, the whorls increasing gradually in width in the spire but with body whorl enlarging more rapidly. Whorls round, convex above with moderately deep suture. Body whorl descending more abruptly near aperture, which relatively large and facing obliquely downwards. Aperture rounded-oval with straighter bottom edge, the outline interrupted by penultimate whorl; peristome whitish, rather thin, not or hardly reflected, the lower lip without a tooth. Shell colour with complex pattern: buff to pale greyish background colour, marked on body-whorl with three rather indistinctly demarcated bands of dull dark brown: the uppermost band thin and interrupted and located just below suture, the middle band largest and wide located above periphery, the lowest band of medium width and located high on underside of shell. All the dark bands marked with spots, small streaks or small blotches of the lighter background colour, all areas of pale ground colour between bands with similarly small markings of the same dark colour as the bands. Underside of shell mainly lighter than upperside and predominantly unmarked close to aperture; upper whorls of spire lacking distinct spiral bands but having mainly oblique irregular pattern of light and dark markings. Inside of aperture chestnut-brown, this colour fading gradually to pale buff in zone close to edge of aperture. Protoconch unmarked browngrey. Shell sculpture of fine, irregular, radial riblets (weak on underside of shell), with fine, indistinct, spiral striae ±throughout; protoconch nearly smooth.

*Genital anatomy* Two bodies of paratypes both had genital anatomy typical for *Otala* (see e.g. Holyoak & Holyoak, 2017: 466 fig. 7D), with long epiphallus, long to very long flagellum, single large dart sac, long free oviduct; diverticulum on duct of bursa copulatrix with single loop when *in situ*; two vaginal mucous glands, each of them with basal stalk thick and lower branches thick, dividing above into "palmate" finger-like apical branches. No differences from *O. tingitana* anatomy were apparent in external features of the organs.

*Etymology* The species name *occulta* is derived from the latin *occultus* (part. A9 meaning hidden,

with suffix *-a* to agree with *Otala* which is a feminine noun. The name reflects the views of DTH and GAH reached during a long hot day attempting unsuccessfully to refind it at (or very near) the original locality on 5 June 2017.

*Range* Known only from the type locality, where not sympatric with other Otalini species.

Notes A medium-sized species of Otala, with shell form and coloration recalling that of some populations of Loxana rerayana, but with affinity to Otala clearly evident from the brown coloration inside the aperture. This sample was exluded from the publication by Holyoak & Holyoak (2017) because we could not place it securely with any Otala species and there were lingering doubts whether it really belonged in Loxana instead. DNA sequence data (Fig. 1) later revealed it as closest to O. tingitana (Paladilhe 1875), but well separated from the other two exemplars of that species (with strong statistical support). It is therefore named here. The shell differs from that of other O. tingitana in shape, the spire having a rather deep suture much like that of O. lactea; from O. lactea it differs in the paler brown coloration inside the shell aperture which hardly extends beyond the aperture, and the complete lack of any tooth on the lower lip. The key below characterises O. occulta in more detail in relation to other Otalini.

## Otala orientalis (Pallary 1918)

*Notes Tingitana orientalis* was named by Pallary (1918: 145–146, 1926: 31–33, pl. 5 figs 10–12) from "Berkane, dans la partie supérieure des Beni Snassen, localisée dans le vallon de Zegzel" (NE. Morocco) and it has not been reported elsewhere. Holyoak & Holyoak (2017: 460) did not hesitate in placing it as one of the numerous synonyms of the highly polytypic *O. tingitana*, since it shows the very shallow suture on the spire characteristic of that species and the typical light brown coloration inside the shell aperture that does not extend far outwards from it. Cossignani (2014: 109–110) also figured shells of this taxon.

It was therefore a surprise to find that the sequence data for *T. orientalis* based on MVHN-080709DR03 (labelled as from Berkane, Marruecos, 29 Dec. 2006, leg. A. Martínez-Ortí) used by Razkin *et al.* (2015: 103, 108) formed a

clade widely separated from that comprised of two exemplars of O. tingitana newly sequenced for the present study (M046 from near Skoura in N. Moyen Atlas; M115 from 0.5km SW. of Zegzel in the Beni Snassen mountains). Thus, M115 is not only from the same mountain range as the typelocality of Tingitana orientalis, it was collected in the same valley and near the same village. The shells nevertheless differ markedly in appearance, with the MVHN specimens subglobular, dull brown, with indistinct darker markings and a notably rough shell surface, which matches Pallary's descriptions of T. orientalis; Cossignani, 2014: 109-110 also illustrated similar shells). In contrast, our M115 shells have a pale cream to whitish ground-colour and bold interrupted bands formed of large blackish-brown blotches. The apertural tooth is also strong in some T. orientalis whereas it is weak in M115. Hence, it appears that our M115 represents O. tingitana with similar sequence data to material from the Moyen Atlas, whereas T. orientalis is a different species, with different DNA sequence data, known only from the Beni Snassen mountains (Fig. 8). The two species are evidently sympatric in parts of the Beni Snassen, including the valley near Zegzel. At our site M115 O. tingitana was collected from crevices of a crag of clean nearly white limestone above a stream. Pallary (1926: 32) noted that with T. orientalis "Cette coquille, par sa coloration sombre et son teste chagriné, se distingue difficilement des rochers sur lesquel elle est fixée", which probably implies it was not on white limestone, instead it was most likely on sandstone matching the dull brown shell coloration.

*Tingitana rutllanti* Ahuir Galindo (2017b: 25–26) was named as a new species with TL"Taforalt, in the Beni-Snassen Mts., N.E Morocco" and holotype at MMM. It was described as differing from T. orientalis in having a smooth rather than granulated shell surface and the first whorls of the shell rounded rather than keeled. The taxon was named after Dr Juan Rutllant Bassets who provided at least some of the specimens and used a provisional name Tingitana elenae for them. Ahuir Galindo did not mention that Cossignani (2014: 106) had figured similar shells under the name *elenae*, or that it was regarded as a nomen nudum by Holyoak & Holyoak (2017: 461). Since the holotype of T. rutllanti figured by Ahuir Galindo (2017b: 25) resembles our M115 shells (see above), the name is apparently a synonym of *O. tingitana*.

*Genital anatomy* Anatomical study of the most mature individual of the two in MVHN-080709DR03 allows a comparison of the distal genitalia of *O. orientalis* with those of a single fully mature *O. tingitana* described by Holyoak & Holyoak (2017: 425–426, 462, table 1, fig. 7D). Externally, those of *O. orientalis* are noteworthy in having the diverticulum on the duct of the bursa copulatrix proportionately longer (1.2×length of bursa duct rather than subequal) with more folds when *in situ* and conspicuously thicker (3× that of duct in the mature snail). Also, the two vaginal mucous glands are conspicuously large in *O. orientalis*, those of the mature snail having respectively 18 and 19 terminal branches.

Internally, the structure of the genital atrium is generally similar in the two species, O. orientalis having a lingulate flap comparable in size (2.3mm long) to that of O. tingitana (2.0mm), and similar in structure and orientation. However, significant differences are evident inside the penis, where O. orientalis (Fig. 5I) has the lumen (chamber) of the proximal penis larger and straight, not narrow and meandering as in O. tingitana. Also, O. orientalis alone has a raised muscular pilaster running longitudinally along almost the entire length of the inner wall of the proximal penis; the pilaster forms a long broad ridge with a semicircular cross-section, with its distal end only narrowly separated from the distal verge; this distal end of the pilaster is concave with a blind central hollow extending proximally for a short distance.

It is tempting to suggest a functional significance for the anatomical differences, based on suggestions in Holyoak & Holyoak (2017: 426). Thus, the proximal penis of O. orientalis is presumably eversible during mating as likely also in O. lactea, whereas the complex convolutions of the chamber of the proximal penis should preclude eversion in O. tingitana. If so, a longer spermatophore (containing more sperm) could be delivered with the total penis length being longer when both proximal and distal parts of the penis are everted compared to the length achieved with eversion of only the distal part. Consequently, the diverticulum on the duct of the bursa copulatrix needs to be longer to receive a longer spermatophore. The duct is indeed proportionately longer in O. orientalis than in O.

*tingitana*; the former taxon also appears to be more closely related to *O. lactea* (Fig. 1) which has a similarly open and straight lumen of its proximal penis. Nevertheless, more individuals of both species need to be studied to confirm the constancy of the anatomical differences involved and observations on mating are also desirable to critically assess functions of the structures involved.

## Otala xanthodon with keeled shells

Synonymy and range data: Tingitana minetti [sic] decussata (Pallary 1936) – Cossignani (2014: 109), from Ras el Ma on coast of NE. Morocco, nomen nudum; non Tingitana minettei var. decussata Pallary 1936 (p. 39, nomen nudum, for shells from Peineta (chez les Kebdana), rive gauche de la Moulouïa, in Moyen Atlas.

*Tingitana minettei decussata* (Pallary, 1936: 39, *nomen nudum*) – Holyoak & Holyoak (2017: 459 fig. 5G, 462–463), for a keeled shell from drift-line at Sabkhat Bou Arg, non *Tingitana minettei* var. *decussata* Pallary 1936.

*"Tingitana minettei decussata"* – Kneubühler, Hutterer, Pfarrer & Neubert (2019: 5, 24–27, 30), non *Tingitana minettei* var. *decussata* Pallary 1936.

*Notes* Holyoak & Holyoak (2017: 459, fig. 5F, G) figured drifted shells (NMW.Z 1993.051.4178) collected on 19 Aug. 1986 from the strand-line on coastal saltmarsh on shore of Sabkhat Bou Arg, NE. Morocco (35°06'N 2°45'W) as *Otala tingitana*. One shell had a sharp peripheral keel and rough upper surface (see below for detailed description), two others had shells intermediate between that specimen and a taxon with a globular whitish shell, implying interbreeding had occurred with a globular-shelled taxon.

Kneubühler *et al.* (2019: 5, 24–27, 30) described and illustrated live-collected material of the same keeled form and reported observations by R. Hutterer that it occurs "on top of one mountain in the Kebdana range" (Montes de Kebdana, Djebel Sebaa Reyal, Rif, Morocco; N35.030° W2.613°; shell D 32.45, H 16.12mm; NMBE 549840). Molecular data obtained by Kneubühler *et al.* (2019) demonstrated that the form with a keeled shell was surely *O. xanthodon*, not *O. tingitana*, despite its strong resemblance in shell characters to "*Tingitana minettei decussata*" (see Holyoak & Holyoak 2017: 459 fig. 5A, B, 462 for illustrations and description of keeled shell forms of *O. tingitana* from the Moyen Atlas). The markers studied show the keeled form from the eastern Rif is part of a single clade formed by *O. xanthodon* that is separated from other *Otala* species including *O. tingitana* with strong support (Fig. 1). The apparent lack of genetic differentation of the keeled *O. xanthodon* from the round-shelled populations, and occurrence of intermediates that are likely to be of hybrid origin, imply there is little value in taxonomic recognition of the keeled form even as a subspecies.

The following description is based on the keeled shell from Sabkhat Bou Arg, (NMW.Z 1993.051.4178): Depressed-conical (almost discoid), D 28.0, H 14.4mm, of 3.2 whorls increasing regularly in width. Whorls slightly convex above and below, separated by shallow suture on spire. Body whorl descending strongly near aperture, which faces downwards. Aperture oval/ suboblong, except where interrupted by penultimate whorl; peristome white, broadly reflected; ridge just inside lower lip with single tooth arising near mid-point, the tooth strong, broad, whitish. Shell colour whitish, with brownish periostracum persisting in places on top and base of shell; interior of aperture faded dull brown, the dark coloration hardly extending out of the aperture. Periphery of body whorl with prominent raised spiral chord. Sculpture of whorls above and beneath rough, decussate, with rather irregular spiral ridges intersected by radial ridges, giving a coarsely malleate effect; fine spiral sculpture also visible in places on upper surface; protoconch smooth.

See Kneubühler *et al.* (2019: 25–26, 30) for description and figures of the genital anatomy of the keeled form and comment that there are almost no differences in inner and outer morphology of the genital organs from those of *O. xanthodon* specimens with rounded shells.

## Otala hieroglyphicula (Michaud 1833)

*Genital anatomy* Holyoak & Holyoak (2017: 465) were unable to study the genital anatomy of a specimen dissected by DTH in 1987 (NMW.Z 1993.051.560), which could not be refound. Subsequently, the specimen has been found and

the genitalia described and figured (Fig. 5D). From this it is clear that the descriptions and figures by Hesse (1910: pl. 440, 1911: pl. 441) are generally accurate, with penial flagellum longer than the epiphallus, a pair of large dart sacs with multiple branches arising from a stout basal stalk, and moderately long free oviduct. Schileyko (2006: 1793-1794, fig. 2297) dissected a different specimen (Vienna no. 56.175) and also provided good illustrations, although he showed the penial flagellum as clearly shorter than the epiphallus. Pallary (1926: 15) introduced the generic name Michaudia with this species as its type, as a section of Helix. As discussed by Holyoak & Holyoak (2017: 465), Hesse's (1910, 1911) treatment of the species in Archelix (i.e. Otala) was well justified by anatomical characters and the brown interior of the shell mouth, whereas moving it to Alabastrina as Alalabastrina (Michaudia) hieroglyphicula by Schileyko (op. cit.) was unwarranted.

The new study of NMW.Z 1993.051.560 allows description of several internal features of the distal genital organs not hitherto reported (cf. Holyoak & Holyoak, 2017: 425, table 1): The genital atrium has a lingulate muscular flap 1.2mm in length, with shallow central hollow in its inner surface; the flap arises distally to the exit from the distal end of the penis with its base also entering distal end of vagina as a thickened band; it crosses the lumen of the atrium and nearly closes the exit from the distal end of the vagina (much as in the larger O. tingitana). The inner wall of the distal half of the penis has five raised longitudinal ridges, which appear flat-topped. The distal verge is moderately short, with rounded-conical tip. The proximal penis is thick-walled, its inner chamber having strong transverse ribs so that the course of the lumen is meandering. This specimen also has mucous glands with respectively 14 and 12 terminal branches, so despite the small body size their complexity matches those of larger Otala species.

*Notes* Our attempts to obtain DNA sequence data from NMW.Z 1993.051.560 which was collected in 1984 had only limited success. However, the sequence for *COI* was recovered and a phylogenetic tree based on this marker alone (see Supplementary Material Fig. S1) reveals the position of *hieroglyphicula* as a well separated taxon, but within the radiation of *Otala* s.l.

#### Loxana Bourguignat in Pallary 1899

J. Conchyl., Paris, 46, p. 168; type species *Helix beaumieri* Mousson 1873, by subsequent designation of Pallary (1928b: 7–8; see Pallary 1922: 150–151 for clarification of that author's interpretation of the application of this species name; despite the apparent tautonymy, *Helix loxana* Rossmässler 1854 was not among the species originally included in the genus by Bourguignat, 1899); *Loxona* (in Pallary, 1922: 150, follows *Loxana* on the previous line and was clearly a spelling error).

Syn. *Alabastrina* Kobelt 1904, pp. 132, 194; type species *Helix alabastrites* Michaud 1833, by mono-typy; *Alabastra* Kobelt 1904 (p. 100) seems to be an error for this name (*fide* Schileyko, 2006: 1792; Kneubühler *et al.*, 2019: 10).

*Atlasica* Pallary 1917, J. Conchyl., 63 (2), p. 135, as *Helix* subsect.; type species *Helix atlasica* Mousson 1873, by original designation and tautonymy.

Beaumieriana ["Bourguignat"] Pallary 1926, J. Conchyl., 70 (1), p. 21; type species Helix beaumieri var. rostrata Pallary 1926, by monotypy. Loxana Bourguignat 1899 is not preoccupied, so it is unclear from Pallary's (1926) text why he proposed Beaumieriana, and similarly unclear why Pallary (1939b: 106) adopted it as "Beaumieriana (Bgt) Plry 1898" for the species Beaumieri and anatisana (the true date of first publication appears to be 1926 as cited here, whereas Loxana Bourguignat in Pallary 1899 was published in J. Conchyl. volume 46 (for 1898) as cited above, with its type species subsequently being fixed as H. beaumieri by Pallary (1928). In the meantime, Pallary himself had referred to "le groupe Loxana ou Beaumieriana" (Pallary, 1917: 135), as if unsure which name to use. He was apparently not intending at that point to establish Beaumieriana as new (infra)generic nomenclature since the first part of the same sentence reads "que je propose sous le nom d'Atlasica nov. subsect. ....", which differs in explicitly introducing that new name. Pallary (1922: 150) also referred to Section Loxana Bourguignat (of Helix) containing Loxona (sic) Beaumieri, implying that he thought Loxana was the valid name for a genus that included *L*. beaumieri, albeit that he appears to have either changed his mind or overlooked this four years later.

*Guilia* Pallary 1926, J. Conchyl., 70 (1), p. 17, as sect. of *Helix*; type species *Helix bailloni* Debeaux in Kobelt 1887, by original designation.

*LeChatelieria* Pallary 1926, J. Conchyl., 70 (1), p. 20, as "Groupe *Le Chatelieria*"; type species *Helix Le Chatelieri* Pallary 1917, by original designation.

This large *Loxana* assemblage has remained something of a taxonomic muddle. Their shell characters are rather diverse, but with many linking forms between extreme types (which include keeled taxa, shiny globular taxa, etc.). Genital anatomy is now known for most of the species and it is hardly distinct from that of *Rossmaessleria* (Table 4; Key below, couplet 14). Some of the species have thus been placed in varied genera, including *Iberellus* P. Hesse 1908 (for *beaumieri* and *atlasica* by Hesse, 1920, 1931) and *Iberus* Montfort 1810 subgenus *Massylaea* (by Zilch, 1960). Schileyko (2006: 1792–1795) placed most of the W. Maghreb species in *Alabastrina*, recognising four subgenera, none of which was known to him anatomically, including *Atlasica* and *Loxana*. He evidently overlooked the nomenclatural priority of the generic name *Loxana* over *Alabastrina* and apparently also overlooked information available from the work of P. Hesse on their genital anatomy.

Razkin *et al.* (2015) obtained the first molecular data on several species. They showed that *Alabastrina alabastrites* and "*A. atlasica*" are in the same clade which is sister to *Otala s.l.*, nested within the Otalini. However, *Rossmaessleria* [*olcesei*] was the most basal clade of Otalini.

**Table 4** Characters of the distal genital anatomy varying between species in the genus Loxana (Otalini:Helicidae), based on authors' observations. Abbreviations: L. ala., Loxana alabastrites; L. bea., L. beaumieri; L. lec.,<br/>L. lechatelieri; L. mas., L. massesylica; L. rer., L. rerayana; L. ruf., L. rufa.

	L. ala.	L. bea.	L. lec.	L. mas.	L. rer.	L. ruf.
Total N dissected from (n) localities	10 (3)	9 (5)	10 (3)	4 (1)	16 (7)	14
		(0)	(0)	(1)		(0)
PF	M–L	(M)L	L-VL	M–L	M-L(VL)	M
EP	M–L	Μ	S-M	Μ	М	Μ
EE	2	0	1	2	$0(1^{1})$	2
PE	y	n	n	y	n	y
PP	Ő	0	L	Ő	$0^{1}$	0
VA	L	VS–S	S	L	$VS-L^1$	$(VS)L(VL)^2$
MB	8-16	4–9	9–13	7-10	6–13	4–9
FO	S–L	L	L-VL	S	$L-VL^1$	VS

Characters and codes: PF Length of penial flagellum (M, medium, i.e.  $0.2-1.0\times$ length of epiphallus; L, long, i.e.  $1.0-2.0\times$  length of epiphallus; VL, very long, i.e.  $>2.0\times$  length of epiphallus); EP Length of epiphallus (S, short, i.e.  $<0.5\times$ length of penis; M, i.e.  $0.5-1.0\times$ length of penis; L, i.e.  $>1.0\times$ length of penis); EE Extension of epiphallus distally through lumen of proximal part of penis (0, no extension or distal end of epiphallus forms only small proximal verge; 1, epiphallus ends distally as long proximal verge inside lumen of proximal penis; 2, epiphallus passes through lumen of proximal penis to end as distal verge); PE Development of large papilla on external wall of the extension of epiphallus inside lumen of proximal part of penis (0, lacking; Y, large papilla); VA Total length of vagina (from insertion of duct of bursa copulatrix to proximal end of genital atrium; VS,  $<0.5\times$ length of penis; S,  $0.5-1.0\times$  length of penis; L, longer than penis); MB Total number of terminal branches on both vaginal mucous glands (count of number of branch tips, combining totals from both of the pair of mucous glands); FO Length of free oviduct (VS, very short, i.e.  $<0.5\times$ length of vagina; S, short, i.e.  $0.5-1.0\times$  length of vagina; L, long, i.e.  $>1.0\times$  length of vagina).

Other notes: <sup>1</sup>As discussed under the species heading in the text, the single adult specimen from sample M165 shows marked differences from 15 other specimens studied from 6 different populations: it has a longer penial flagellum, the epiphallus extends distally into the proximal penis lumen, a tiny (0.4mm) false verge is present, the free oviduct is VL and convoluted, and the diverticulum on the duct of its bursa copulatrix is atypically long and convoluted *in situ*, in a manner suggestive of *Eobania*. <sup>2</sup>Most *L. rufa* from six populations studied have the vagina slightly shorter than the penis, but a few individuals have it much shorter, especially the section proximal to insertion of the mucous glands.



**Figure 6** Anatomy of distal genitalia of Otalini 2, genus *Loxana*, all specimens from Morocco, in CGAH: A *L. alabastrites* (N34.8163° W2.4122°, M114); B *L. beaumieri* (N31.5289° W7.5690°, M171); C *L. rufa* (N33.5642° W4.2059°; D *L. massesylica* (N33.9744° W3.0397°, M119); E, F *L. rerayana*, E (N28.9608° W10.5551°, M91), F (N31.2156° W7.8394°, M165). All scale bars represent 5mm. For abbreviations see Fig. 5. See Appendix for additional data on specimens used.

Holyoak & Holyoak (2017: 424) commented on the occurence of Hesse's Gland as a peculiarity of the genus *Otala*, occurring on the left side of the body adjacent to the front outer edge of the mantle and resembling a whitish bean sliced in half. Further studies have revealed that this structure also occurs in some populations of *Loxana rerayana*, being large in some populations (e.g. M91:  $15 \times 2.0$ ,  $11.5 \times 1.5$ mm; M97:  $13.5 \times 2.0$ ,  $11 \times 2.5$ mm; M35) but smaller and less obvious in others (e.g. M88: forming arcuate rim up to 1.0mm wide). We have not seen it in other genera of Otalini but have not made comprehensive searches for it.

#### L. beaumieri (Mousson 1873)

Helix (Macularia) Beaumieri Mousson 1873, Malakozool. Bl., (1) 21, p. 153, TL "Von Urica am Ausgang des Dermatthals, 1000 Meter hoch"; Mousson 1874, Jb. d. malakozool. Ges., 1, pp 89–91, pl. 4, fig. 5) ("Von Urika, am Ausgang des Dermatthals, 1000 Meter hoch"; slightly different form from "Plateau von Mtuga"); Helix Beaumieri Mousson - Kobelt (1876, Icon., (1) 4 (5-6), pp. 54-55, pl. 113 figs 1124 [not "1125" as given on text p. 54]), "im maroccanischen Atlas, bei Urica am Ausgang des Dermatthales in einer Meereshöhe von 1000 Meter, sowie auf dem Plateau von Mtuga"; [Bourguignat's later claims that Kobelt misidentified Mousson's taxa and figured the wrong ones (e.g. see comments under Pallary, 1899 for H. atlasica), do not appear to have been well founded]; Pfeiffer (1875, Mon. Helic. viv., 7, pp. 341, 583); Bourguignat in Servain (1880: 50); Morelet (1880: 24); Bourguignat in Péchaud (1883: 95–99), mainly a detailed and sarcastic critique of treatment by Kobelt in Icon.; Pallary (1917: 134, 135); Helix Beaumieri Mousson 1874 var. major Morelet 1880, J. Conchyl., 28, p. 24, TL Tézaroualt, dans la partie montagneuse du Sous; Helix (Marmorana) Beaumieri - Pallary (1904: 49), Demnata, Derma, Ourika, Sernana, with vars demnatensis B. (see below), minor Morel., major Morel.; [Helix groupe Loxana] Beaumieri – Bourguignat (1899: 168); Iberellus beaumieri Mss. [= Mousson] - Hesse (1915, Icon., (2) 23 (1-2), pp. 66-69, pl. 640 figs 26-30), figs of jaw, radula and genitalia; Atlasica beaumieri Mss. [= Mousson] - Hesse (1920, Icon., (2) 23 (5-6), p. 235), with syn. graëllsopsis Bgt. and var. demnatensis Bgt.; Loxona [sic] Beaumieri -Pallary (1922: 150-152), localisée dans la partie basse de la chaîne atlasique, with vars demnatensis (Demnate; Tanant), minor (Serarna; Pont des Alamna), major (Tazeroualt; Dar Anflous; Dar M'tougui; Bezzou), striata Pallary (newly described, p. 150, TL Touggana) [on p. 152 Pallary claimed that Kobelt, 1876, Icon., fig. 1125 was an error of identification, representing *Helix* atlasica not H. Beaumieri; this is incorrect, fig. 1125 on pl. 114 shows *Helix Constantinae*, as captioned; Pallary was probably confused by the error on text p. 54 of Icon., (1) 4 (5-6), where H. Beaumieri is attributed to fig. 1125 instead of 1124; Pallary (1899: 102) had previously claimed fig. 1124 represented H. atlasica not H. beaumieri but this may also be incorrect]; Beaumieriana Beaumieri Mousson Var. rostrata Pallary 1926, J. Conchyl., 70 (1), p. 21, pl. 3 fig. 19, TL sources de l'Oum er Rebia; Beumieriana Beaumieri [sic] – Pallary (1939a: 63); Beaumieriana Beaumieri – Pallary (1939b: 106); Rour et al. (2002: 194).

(Macularia) atlasica Helix Mousson 1873, Malakozool. Bl., (1) 21, p. 153, TL "Vom Rerayathal im hohen Atlas"; Mousson (1874: 91-92, pl. 4, fig. 7 [labelled as fig. 6; note that Mousson's figs 6 (labelled atlasica) and 7 (labelled praedisposita) were transposed; this mistake was copied in Tryon, 1888, Man. Conch., (2) 4, pl. 39] ("Rerayathal im hohen Atlas, 12-1500 Meter"; "Etwas grösser, sonst übereinstimmend auf dem Plateau von Mtuga"); Helix atlasica Mousson -Kobelt (1876, Icon., (1) 4 (5-6), pp. 53-54, pl. 113 figs 1120-1123 [not "1121-1124" given on text p. 53], "im westlichen maroccanischen Atlas, im Rerayathal 12-1500 M. über dem Meere, und auf dem Plateau von Mtuga"; Pfeiffer (1876, Mon. Helic. viv., 7: 342, 583); Morelet (1880: 24-25); Bourguignat in Servain (1880: 50); Bourguignat in Péchaud (1883: 95-99, 108-109), Haute vallée de Reraya dans les montagnes du Maroc (pointed out that Mousson (1874: fig. 4) transposed figs of H. atlasica and H. praedisposita; otherwise mainly a critique of treatment by Kobelt in Icon.); Tryon (1888, Man. Conch., (2) 4, pl. 39: copying erroneously transposed figures from Mousson, 1874); Pallary (1899: 102–103), on p. 102 cited Icon. fig. 1124 as H. atlasica (non Beaumieri) but incorrectly [fig. 1124 is in fact a good match for beaumieri as figured in Mousson 1874: pl. 4 figs 5, showing the widened peristome; n.b. numbering of figs on Icon. text pages 53–54 is incorrect]; Pallary (1904: 25); Pallary (1917: 127, 134, 135), Taourirt (as



**Figure 7** Details of anatomy of distal genitalia of Otalini 3, genus *Loxana*, all specimens from Morocco, in CGAH, continued from Figs 5 and 6. (Figs A–H give partly diagrammatic longitudinal sections of the penis; Figs I–N give partly diagrammatic longitudinal sections of genital atrium). All scale bars represent 2mm. A, I *L. alabastrites* (N34.8171° W2.3910°, M116); B, J *L. beaumieri* (N31.5289° W7.5690°, M171); C, D, K *L. lechatelieri* (N33.4423° W4.8446°, M128); E *L. massesylica* (N33.9744° W3.0397°, M119); F, L *L. rufa* (N33.5642° W4.2059°, M123); G, H, M, N *L. rerayana*, G, M (N28.9608° W10.5551°, M91), H, N (N31.2156° W7.8394°, M165). For abbreviations see Fig. 5. See Appendix for additional data on specimens used.

new northernmost locality); Helix (Marmorana) atlasica – Pallary (1904: 49), Dj. Reraya; Atlasica atlasica Mss. [= Mousson] – Hesse (1920, Icon., (2) 23 (5-6), p. 235), with vars agagourensis Pallary, dilatata Pallary, serarnaensis Pallary; Pallary (1922: 152–153), with vars serarnaensis (Serarna), aguergourensis (Azilal; Aït Attab; Gorges de l'oued Amersid; Aguergour n'Kik; Aïn Redassi; Imi n'Tella; Au pied de l'Atlas, versant sud, sous Tizi n'test; Aoullouz), major (Aguergour. Dar Goundafi; a nomen nudum), minor (Amismiz; Imi nT'anout; a nomen nudum); Pallary (1939b: 106); Rour et al. (2002: 194); Cossignani (2014: 77), figs of two shells (from Ozoud; Asni); Alabastrina (Atlasica) atlasica (Mousson 1873) - Razkin et al. (2015: 102, 108), Between Agadir and Essauira [= Essaouira], Morocco, with DNA sequence data.

[*Helix*] *Plæsia*, Bourg. – Bourguignat in Servain (1880: 50), *nomen nudum*; [*Helix* groupe *Loxana*] *Plaesia* Bourguignat 1899, J. Conchyl., 46, p. 168, *nomen nudum*; *H*[*elix*] *plaesia* "Bgt" – Pallary (1922: 152), from Dj. Aoghri, specimen seen in Bourguignat's Collection at MHNG, cited Bourguignat, Sp. nov. Moll., No. 128 (a work never published and evidently fictitious: see Connolly 1934, Dance 1970), no description was presented, so it remained a *nomen nudum*; *Beaumieriana plaesia* (Bourguignat 1880) – Rour *et al.* (2002: 194).

Helix Schousboei, Bourguignat 1899, J. Conchyl., 46, p. 168 (spelling Schousboëi also used), nomen nudum; H[elix] Schousboei "Bgt., 1880" Pallary, 1922, J. Conchyl., 66 (2), p. 151, TL djebel Aoghri, près de Demnate (with a description minimally adequate to validate the name: "plus grand, plus déprimé que Beaumieri"; Pallary commented that he had been unable to locate dj. Aoghri); Beaumieriana schousbei (Bourguignat, 1880) [sic] – Rour et al. (2002: 194).

[Helix] Demnatensis, Bourg. – Bourguignat in Servain (1880: 50), nomen nudum; [Helix groupe Loxana] Demnatensis Bourguignat 1899, J. Conchyl., 46, p. 168, nomen nudum; Helix (Marmorana) Beaumieri var. demnatensis "B. sp." Pallary 1904, J. Conchyl., 52 (1), pp. 26 (with brief description), 49, pl. 1 fig. 19, TL not stated, but presumably based on specimen from Demnate; H[elix] demnatensis Bgt. – Pallary (1922: 151), Dj. Aghbalo, entre Mogador et Marrakech; Dj. Takreda et dj. Aoghri; *Loxana beaumieri demnatensis* (Mousson, 1874) [sic] – Cossignani (2014: 88), figs of shell, from Demnate; *Beaumieriana demnatensis* (Bourguignat 1880) – Rour *et al.* (2002: 194).

[*Helix*] *Etæra*, Bourg. – Bourguignat in Servain 1880: 50, *nomen nudum*; [*Helix* groupe *Loxana*] *Etaera* Bourguignat 1899, J. Conchyl., 46, p. 168, *nomen nudum*; *H*[*elix*] *etaera* "Bgt." – Pallary, 1922, J. Conchyl., 66(2), p. 151,TL dj. Toug el Kheïr, described only as "ne diffère en rien, à premiere vue, du *L. Beaumieri*" so it remains a *nomen nudum*; *Beaumieriana etaera* (Bourguignat 1880) – Rour *et al.* (2002: 194).

[*Helix*] *Epagoga*, Bourg. – Bourguignat in Servain (1880: 50), *nomen nudum*; [*Helix* groupe *Loxana*] *Epagoga* Bourguignat 1899, J. Conchyl., 46, p. 168, *nomen nudum*; *H*[*elix*] *epagoga* "Bgt." – Pallary 1922, J. Conchyl., 66(2), p. 151, TL Environs de Demnate; Dj. Takreda, name validated by very brief description ("plus petit et plus déprimé que *L. Beaumieri"*); *Beaumieriana epagoga* (Bourguignat 1880) – Rour *et al.* (2002: 194).

[*Helix*] *Euclasta*, Bourg. – Bourguignat in Servain (1880: 50), *nomen nudum*; [*Helix* groupe *Loxana*] *Euclasta*–Bourguignat, 1899, J. Conchyl., 46, p. 168, *nomen nudum*; *H*[*elix*] *euclasta* "Bgt." Pallary 1922, J. Conchyl., 66(2), p. 151, TL Dj Aoghri, described only as "à spire à peine distincte du *Beaumieri*" so it remained a *nomen nudum*; *Beaumieriana euclasta* (Bourguignat 1880) – Rour *et al.* (2002: 194).

[*Helix*] *Raymondopsis*, Bourg. – Bourguignat in Servain (1880: 50), *nomen nudum*; [*Helix* groupe *Loxana*] *Raymondopsis* – Bourguignat, 1899, J. Conchyl., 46, p. 168, *nomen nudum*; [*Helix*] *Raymondopsis* – Bourguignat in Servain (1880: 50), *nomen nudum*; *H*[*elix*] *raymondopsis* "Bgt." – Pallary (1922: 151), type from "Aït Mella, au S. O. de Demnate; Egalement dans le Dj. Touq el Kheïr", no description, so it remained a *nomen nudum*; *Beaumieriana raymondopsis* (Bourguignat 1878) – Rour *et al.* (2002: 194).

[*Helix*] *Graellsopsis*, Bourg. – Bourguignat in Servain (1880: 50), nomen nudum; [*Helix* groupe *Loxana*] *Graellopsis* [sic] – Bourguignat 1899, J. Conchyl., 46, p. 168, nomen nudum; Helix (*Marmorana*) *Beaumieri* var. *Graellsopsis* "B. sp." – Pallary, 1904, J. Conchyl., 52 (1), p. 27 (nomen *nudum*), a footnote cited Bourguignat (1878, Spec. nov. mollusc., 2<sup>nd</sup> cent., no. 129, a work never published and evidently fictitious: see Connolly 1934, Dance 1970); *H*[*elix*] graellsopsis "Bgt." – Pallary (1922: 151), Dj Tougel Khaïr, Dj. Takreda et dj. Aoghri, described only as "à peine différent du *L. Beaumieri*" so it remained a *nomen nudum; Beaumieriana graellopsis* [sic] (Bourguignat 1880) – Rour *et al.* (2002: 194); *Loxana graellopsis* [sic] (Bourguignat) – Cossignani (2014: 88), figs of shell, from Bzou.

Helix (Marmorana) Atlasica var. serarnaensis Pallary 1904, J. Conchyl., 52 (1), p. 25, pl. 2 fig. 6, TL Serarna; Helix (Marmorana) atlasica var. sernanica Pallary, 1904, J. Conchyl., 52(1), p. 49, Sernana (apparently errors, or corrections, for var. serarnaensis); Atlasica atlasica serarnaensis Pallary 1904 – Cossignani (2014: 78), figs of two shells, from Sraghna (invalid as species-group name).

*Helix* (*Marmorana*) *Atlasica* var. *agagourensis* Pallary 1904, J. Conchyl., 52 (1), pp. 26, 49, pl. 2 fig. 7, TL Agagour; *Atlasica atlasica* var. *aguergourensis* [*sic*] Pallary (1922: 152–153), apparently a deliberate emendation of the name; *Atlasica aguergourensis* (Pallary 1904) – Rour *et al.* (2002: 194) (invalid as species-group name); *Atlasica atlasica aguergourensis* (Pallary 1904) – Cossignani (2014), African Landshells, p. 78, figs of shell, from Aguergour (invalid as species-group name).

*Gætulia* (?) *atlasica* Mousson var. *dilatata* Pallary 1913, Bull. Mus. natn. Hist. nat., Paris, 19 (6), pp. 363–364, TL Mechera-ben-Abbou ... fentes d'une falaise de calcaire dur, sur la rive droite de l'Oum er-Rebia, non loin du poste de télégraphie sans fil; Pallary (1917: 135); *Atlasica atlasica dilatata* (Pallary 1913) – Cossignani (2014: 78), figs of shell, from Mechra Benabbou (invalid as speciesgroup name).

*Atlasica tildiana* Pallary 1922, J. Conchyl., 66 (2), pp. 153–154, pl. 4 figs 16, 17, TL "Aïn Tildi, à 6 kilom. S.-E. d'Agadir"; with new var. *minor*, TL not stated but doubtless also Aïn Tildi; Pallary (1939a: 62); Rour *et al.* (2002: 194); *Atlasica tildiana* (Pallary 1921 [error]) – Cossignani (2014: 79), figs of two shells, from Ain Tildi.

*Atlasica zimana* Pallary 1926, J. Conchyl., 70(1), p. 24, pl. 4 figs 7, 8, TL Oued Zima et Oued Mentaga, dans la région du Sous (rather ambiguously described as "Cette espèce du groupe *Beaumieriana*" but named as an *Atlasica*); Pallary (1939a: 61); Rour *et al.* (2002: 194).

Rossmæssleria Vondeli Pallary 1928, J. Conchyl., 72(1), p. 5, pl. 1 figs 5, 6, TL le massif de calcaire dur jurassique du Tizi R'nim, depuis Timoulit jusque sur le versant d'Ouaouizert au sud du Moyen Atlas occidental; Rossmæssleria Vondeli var. major Pallary 1928, J. Conchyl., 72, p. 5, TL not stated, but the var. was "dominent" at Timoulit; Rossmæssleria Vondeli var. minor Pallary 1928, J. Conchyl., 72, p. 5, pl. 1 fig. 7, TL not stated (see above for species as a whole); Rossmæssleria Vondeli var. conica Pallary 1928, J. Conchyl., 72, p. 5, nomen nudum; Rossmæssleria Vondeli var. subplana Pallary 1928, J. Conchyl., 72, p. 5, almost a nomen nudum, TL not stated (see above for species as a whole); Rossmaessleria (?) vondeli -Hesse (1934: 48, pl. 9 figs 73a-d), figs of genital anatomy and jaw (legend to plate on p. 57 uses the erroneous spelling *condeli*); *Rossmassleria* [*sic*] Vondeli – Pallary (1939a: 63; 1939b: 106); Loxana vondeli conica (Pallary 1928) - Cossignani (2014, African Landshells, p. 88), figs of shell from Beni-Mellal (invalid as species-group name); Loxana vondeli subplana (Pallary 1928) – Cossignani (2014, African Landshells, p. 88), figs of shell from Beni-Mellal (invalid as species-group name); Loxana vondeli vondeli (Pallary 1928) - Cossignani (2014, African Landshells, p. 88), figs of shell from Beni-Mellal.

*Loxana anatisana* (?) Pallary 1928, J. Conchyl., 72 (1), pp. 6–7, pl. 1 fig. 3, TL Beni Mellal, Foum el Ançeur, dans les fentes de calcaire jurassique et sur toute la bordure occidento-méridionale du Moyen Atlas (the ? in the original description referred to doubt over its allocation to the genus *Loxana; Beaumieriana anatisana* – Pallary (1939b: 106); Rour *et al.* (2002: 194); *Loxana anatisana* Pallary 1928 – Cossignani (2014: 88), figs of shell, from Foum el Ancer (topotype).

*Loxana pedroi* Cossignani & Ahuir Galindo 2013, Malacologia Mostra Mondiale, 80, pp. 20–21, TL Beni-Mellal, sud di Ras-El-Ait, Marocco, in fessure di rocce calcaree; Cossignani (2014: 88), shell figs.

*Loxana ksibaensis* Ahuir Galindo 2013a, Malacologia Mostra Mondiale, 80, p. 4, TL Sud di Ksiba, Marocco, in fessure di rocce calcaree;

Cossignani (2014: 88), figs of shell, from Sud Ksiba (holotype, MMM).

Atlasica rutllanti Ahuir Galindo 2015, Malacologia Mostra Mondiale, 86, pp. 23–24, TL Tilougguite, High Atlas [Morocco] ("at the northeast of Tilougguite ... between 1600 and 1800 meters over the sea level ... inside deep calcareous rock cracks").

*Atlasica anflousiana* Ahuir Galindo 2016, Malacologia Mostra Mondiale, 92, p. 5, TL West of Bouabout, north side of the Western Great Atlas [Morocco].

*Atlasica azemmourensis* Ahuir Galindo 2017b, Malacologia Mostra Mondiale, 97, pp. 26–27, TL Azemmour, Southeast of the town, Morocco.

*Loxana nuriae* Ahuir Galindo 2018b, Malacologia Mostra Mondiale, 100, pp. 20–21, TL Between Souk Hebdomadaire and Ait Jabri, west of Ait Attab, at the confluence of Middle and Great Atlas [Morocco].

*Shell* Figures: Kobelt (1876, Icon., (1) 4, no. 1120– 1123 [as *atlasica*] and 1124), Pallary (1926, 1928: pl. 1 figs 5–7), Schileyko (2006: 1795), Cossignani & Ahuir Galindo (2013c: 20), Cossignani (2014: 88); Fig. 3C–F.

*Genital anatomy* Figures: Hesse (1915: pl. 640 figs 28–30), see also Hesse (1931: 93); Hesse (1934: pl. 9 figs 73a–d, *vondeli*); Figs 6B, 7B, J, Table 4.

*Range* Endemic in Morocco: in NC. and W. Haut Atlas (including coastal foothills) and SW. Moyen Atlas (Fig. 9). Sympatric with *L. rerayana* in parts of its range, sometimes syntopic.

*Notes* (1) The names *H. beaumieri* and *H. atlasica* were published at the same time, by Mousson (1873). Apparently no previous author has regarded them as conspecific, so we act as First Revisers (see ICZN Code Art. 24.2) in giving nomenclatoral precedence to the name *H. beaumieri*. This name is preferred because the original description (Mousson, 1873) and the same author's subsequent more detailed account with figures (Mousson, 1874) provide clearer information on the identity of its type specimen(s) compared to those of *H. atlasica*, and its type locality is more precise. Furthermore, previous authors have been clearer about the identity of

*H. beaumieri* than of *H. atlasica*. Pallary (1922: 151) for example, noted it is clearly distinct from L. atlasica by its globular shape, more dilated aperture with external border thin and well reflected, and by its darker coloration. Pallary (1928) also designated H. beaumieri as the type species of Loxana. (2) Mousson (1873: 153) made it clear in his descriptions that both *H. beaumieri* and *H.* atlasica were based on small shells with a very shallow suture (both having "sutura lineari, plana"), whereas H. praedisposita had a deeper suture (op. cit., p. 154: "sutura impressula"), and larger shell. Pallary (1899: 102) suggested that the figures in Mousson (1874) of H. atlasica and H. beaumieri had been interchanged (presumably in addition to the transposition of those of H. praedisposita and H. atlasica previously pointed out by Bourguignat in Péchaud 1883, as noted above). Whether correct or not, this now seems unimportant because we regard the two nominal taxa as conspecific. (3) We follow the text descriptions by Mousson (1873, 1874) in regarding H. atlasica as having a small shell with a consistently very shallow suture. Therefore, various nominal taxa that have been regarded as its junior synonyms despite a deeper suture (and larger shell size) have been transferred here to the synonymy of L. rerayana (q.v.). (4) Cossignani (2014: 88) figured Loxana pedroi alongside three forms of Loxana vondeli, as cited above, all from Beni-Mellal. His L. pedroi has a slight peripheral keel and rather strong shell ribs but is otherwise much like L. beaumieri, L. v. vondeli has a very sharp keel with prominent spiral cord on its crest, L. v. subplana is similar but less sharply keeled. All four taxa have the upper surface of the shell with oblique (radial-tangential) ribs that have pale crests, and the general pattern of their colour banding is similar. Hence it would appear that these represent more or less strongly keeled forms of the same species, clearly derived from the L. beaum*ieri* present nearby in the SW. Moyen Atlas.

#### L. rerayana (Mousson 1873)

*Helix* (*Macularia*) *Rerayana* Mousson 1873, Malakozool. Bl., (1) 21, p. 152, TL "Aus einem Olivenhain am Eingang des Rerayathals, 900– 1200 Meter"; Mousson (1874: 87, pl. 4, fig. 4), Eingang des Rerayathals, 900–1200 Meter; *Helix Rerayana*, Mousson 1874 – Morelet (1880: 21), province de Demnate, à deux ou trois journés

	PF	PP	DI	DA	MS	MB	FL	FO
Cantareus	L-VL	VL	L-VL	+	L	17–35	0 <sup>2</sup>	$S^1$
Cornu	VL	L	L	+	S	30-47	$0^{2}$	$S^1$
Erctella	L	Ра	L-VL	?	L	$25-33^3$	$0^{2}$	$S^1$
Rossmaessleria	L-VL	0	L	$T^4$	S–L	8-18	0	S
Theba	$0-VL^5$	0	S	Т	0	2	0	L
Maurohelix	S	Pa	$0^{6}$	+	L	5-8	?	S
Massylaea	L	$0^{7}$	L	+	S–L	15-25	S	S
Eobania	L	VL	VL	Т	L	41-48	0	S
Otala	$(M)L^8$	0/Pi	L	Т	L	12–36	S–L	L
Loxana	L(VL)	$0/L^{9}$	L(VL)	+	S–L	4–18	2	S-L

Table 5 Characters of the distal genital anatomy varying between genera in the tribe Otalini (Helicidae).

Characters and codes: PF Length of penial flagellum (0, lacking; S, very short, i.e.  $<0.2 \times$  length of epiphallus; M, medium, i.e.  $0.2-1.0 \times$  length of epiphallus; L, long, i.e.  $1.0-2.0 \times$  length of epiphallus; VL, very long, i.e.  $>2.0 \times$  length of epiphallus); PP Development of papilla (false verge) on inner wall of proximal part of penis (0, lacking; Pa, small papilla; L, large papilla; VL, very long cylindrical papilla; Pi, thickened pilaster); DI Length of diverticulum on duct of bursa copulatrix (S, short, i.e.  $<0.5 \times$  length of duct of bursa; L, long, i.e.  $0.5-2.0 \times$  length of duct of bursa; VL, very long, i.e.  $>2.0 \times$  length of gland; L, long but slender, i.e.  $>0.25 \times$  total length of gland; L, long and stout, i.e.  $>0.25 \times$  total length of gland); MB Total number of terminal branches on both vaginal mucous glands (count of number of branch tips, combining totals from both of the pair of mucous glands); FL Development of flap in genital atrium (0, absent; S, single and small, i.e. not reac

Other notes: <sup>1</sup>Both free oviduct and vagina short; <sup>2</sup>it is uncertain whether the «penial lobe» described by Chase *et* al. (2010) in Cornu corresponds to the «comb-like structure» of Cornu and Erctella figured by Colomba et al. (2011) and the «atrial stimulator» of Bouaziz-Yahiatene et al. (2019: 9, table 3); some or all of these may have a similar function to the flap we describe, but the locations of some of the structures differ and further study is needed to establish homologies; <sup>3</sup>illustrations in Colomba *et al.* (2011: 25–27) do not allow accurate counts, so the figures given are doubtless too low; <sup>4</sup>most populations of *Rossmaessleria* have the cross-section of the dart with all four lamellae T-shaped apically, but some have two opposite lamellae with simple apices and the other two merely thickened at their apices; <sup>5</sup>the epiphallus is very short in *Theba*, so when flagellum is developed it is always VL (it can thus be >10× length of epiphallus, e.g. in *T. chudeaui* (Germain 1908) figured by Gittenberger & Ripken, 1987: 155); <sup>6</sup>Hesse (1911: pl. 450 fig. 3) figured a short diverticulum but there was no trace of this in the specimen dissected by DTH and Schileyko (2006: 1791) noted «diverticle rudimentary or absent» and did not show it on his figure 2292B; <sup>7</sup>data for *M. punica* only; <sup>8</sup>M applies only to most *O. punctata*, other species are L; <sup>9</sup>a (large) papilla is present only in *L lechatelieri*; Kneubühler *et al.* (2019: 10–16) erroneously reported a papilla in *L. alabastrites*, but the structure in that species, L. massesylica and L. rufa is developed on the exterior of the continuation of the epiphallus into the proximal penis, not on the interior wall of the lumen of the proximal penis (see our Fig. 7 and Table 5). Sources additional to authors' observations: Bouaziz-Yahiatene et al. (2019), Colomba et al. (2011), Gittenberger & Ripken (1987), Giusti et al. (1995), Hesse (1910, 1911, 1915, 1920, 1931, 1934), Hesse in Pallary (1936: 26), Schileyko (2006), Kneubühler et al. (2019).

de la ville de Maroc (Beaumier), etc., Var.  $\beta$ minor, castanea, 5-fasciata, ... is also described but as a polynomial that cannot enter nomenclature; Kobelt (1875, Icon., (1) 4 (1), p. 4, pl. 92 figs 978), «im Rerayathal im westlichen maroccanischen Atlas in einer Höhe von 9 bis 1200 M»; Morelet (1880: 21), with var. *minor* (nov.); Bourguignat in Péchaud (1883: 97–98, 100–101), vallée de Reraya; montagnes de Demnate; *Helix rerayana* var. *sparsa* Westerlund 1889, Fauna pal., p. 429; *Helix rereyana* [sic] Mss. – Pilsbry (1894); *Helix rerayana*, Mousson 1874 – Pallary (1899: 109), (vallée de Reraya; montagnes de Demnate); *Helix rerayana* Mousson 1874 Var. *major* Pallary 1899(a), J. Conchyl., 46, p. 109, TL dj. Reraya; *Helix rerayana*, Pallary (1900: 734; 1917: 134, 135);

Helix (Marmorana) rerayana, Pallary (1904: 29, 50), (Agagour; O. Reraya; Demnate; with vars sparsa W., major P.); Massylaea Rerayana Mousson Var. alta Pallary 1915, Bull. Mus. natn. Hist. nat., Paris, 21 (1), p. 27, TL Haute vallée de l'oued Nfis et de ses affluents; Massylaea rerayana Mss. [= Mousson] - Hesse (1920, Icon., (2) 23 (5-6), p. 235); Pallary (1922: 146–147), abonde ... haute vallée du Reraya; plus rare ... Telouet (Glaoua) et à Demnate; with vars alta, major, minor, sparsa; Hesse (1931: 92-93, pl. 13, fig. 109); Massylaea rerayana – Pallary (1936: 31; 1939a: 63; 1939b: 107); Rour et al. (2002: 194); Massylaea rerayana sparsa Westerlund 1889 - Cossignani (2014: 89), figs of shell, from High Reraia (invalid as species-group name).

Helix (Macularia) praedisposita Mousson 1873, Malak. Bl., (1) 21, p. 154, TL "Subfossil, aus dem Travertin des Rerayathals"; Mousson (1874: 92-93, pl. 4, fig. 6 (labelled as fig. 7 due to his figs 6 and 7 being transposed), single somewhat damaged shell found "Subfossil, aus dem Travertin des Rerayathals"; Helix prædisposita -Pfeiffer (1876, Mon. Helic. viv., 7: 352 no. 2445, 584); Morelet (1880: 25); Bourguignat in Péchaud (1883: 95-99, 102-103), apparently common in vallée de Reraya (also corrected transposition of Mousson's figures (see above); gave detailed and sarcastic critique of treatment by Kobelt (1876, Icon., (1) 4 (5-6), pl. 113 figs 1120-1124) claiming specimens were misidentified, but without giving convincing reasons); Tryon (1888, Man. Conch., (2) 4, p. 145 [his pl. 39 figs 4, 5 depicted H. atlasica not H. praedisposita resulting from copying transposed figures from Mousson 1874: pl. 4]; Pallary (1899: 109), vallée du Reraya; Helix (Marmorana) prædisposita – Pallary (1904: 29: 50), (Oued Aouerne; O. Reraya); Massylaea praedisposita Mss. [= Mousson] – Hesse (1920, Icon., (2) 23 (5-6), p. 234); Pallary (1922: 148) (travertins de l'oued Reraya (TL); dar Goundafi (vivant); oued Aouarne); Pallary (1936: 31; 1939a: 63); Rour et al. (2002: 194); Cossignani (2014: 89), figs of shell, from Imin N'Tezt.

*?Helix alcyone* Kobelt 1882(b), Nachr.-Bl. d. malakozool. Ges., 14, p. 122, TL parte meridionali imperii Maroccani; Kobelt (1883, Icon., (2) 1 (3–4), pp. 35–36, pl. 14, figs 103), in Südmarocco; Bourguignat in Péchaud (1883: 102), chaine du Takreda [noted as excessivement abondante dans tous les montagnes du sud du Maroc; also as much misidentified in collections as *H. atlasica*, due to errors made in publications by Kobelt]; Pallary (1899: 110–111), extrêment commune dans toutes les montagnes du sud du Maroc; Pallary (1900: 734; 1917: 135); *Helix (Marmorana) alcyone* Kobelt – Pallary (1904: 50), Sud Maroc; *Massylaea alcyone* – Pallary (1922: 149), Djebel Takreda; Pallary (1936: 31; 1939a: 63; 1939b: 107); Rour *et al.* (2002: 194).

Helix lamprimathia "Bourguignat, 1878" Bourguignat in Péchaud 1883, Excursions malacologiques, p. 101 (with description), TL la chaine du Diebel-Takreda, entre Mogador et la ville de Maroc (cited Helix lamprimathia Bourguignat, 1878, Spec. noviss., no. 123, but that publication was fictitious: Connolly 1934, Dance 1970); Pallary (1899: 110); Kobelt (1914, Icon., (2) 20 (3–4), pp. 47–48, pl. 560 figs 2843); Helix (Marmorana) lamprimattria [sic], B. – Pallary (1904: 50), Dj. Takreda; Massylaea lamprimathia -Pallary (1922: 148, pl. 4 fig. 15), Telouet; Pallary (1936: 31); Rour et al. (2002: 194).

Helix takredica "Bourguignat, 1878" Bourguignat in Péchaud 1883, Excursions malacologiques, pp. 101-102 (with description), TL "la chaine du Takreda, près de la ville de Maroc" (cited Helix takredica Bourguignat, 1878, Spec. noviss., no. 122, but that publication was fictitious: Connolly 1934, Dance 1970); Pallary (1899: 110; 1900: 734); Kobelt (1914, Icon., (2) 20 (3-4), p. 48, pl. 560 figs 2844); Massylaea takredica – Pallary (1922: 148), noted that "Takreda" given as TL by Bourguignat apparently does not exist (possibly Taguetrant 18km E. of Taroudant was intended, but the specimens were perhaps more likely to have been collected by Rabbi Mardochée in the Sous Valley, especially in the Anti Atlas); Pallary (1936: 31; 1939a: 63); Rour et al. (2002: 194); Cossignani (2014: 89), figs of shell, from Demnate (but likely to be misidentified, since this locality is to the E. of Bourguignat's TL and far to the NE. of the correction to it suggested by Pallary, noted above).

*Helix sticta* "Bourguignat, 1878" Bourguignat in Péchaud 1883, Excursions malacologiques, p. 103 (with description), TL "parait assez abondante dans les chaînes de montagnes au sud du Maroc" (cited *Helix sticta* Bourguignat, 1878, Spec. noviss., no. 124, but that publication was fictitious: Connolly 1934, Dance 1970); Pallary (1899: 109; 1904: 50), Sud Maroc; Kobelt (1914, Icon., (2) 20 (3–4), pp. 49–50, pl. 560 figs 2846); *Massylaea sticta* – Pallary (1922: 149; 1936: 31; 1939a: 63); Rour *et al.* (2002: 194).

*Helix azorella* "Bourguignat, 1878" Bourguignat in Péchaud 1883, Excursions malacologiques, pp. 103–104 (with description), TL "des mêmes régions méridionales du Maroc" [i.e. at least chaine du Takreda] (cited *Helix azorella* Bourguignat, 1878, Spec. noviss., no. 125, but that publication was fictitious: Connolly 1934, Dance 1970); Pallary (1899: 109; 1904: 50); Sud Maroc; Kobelt (1914, Icon., (2) 20 (3–4), pp. 48–49, pl. 560 figs 2845); *Massylaea azorella* – Pallary (1922: 149; 1936: 31; 1939a: 63); Rour *et al.* (2002: 194).

Atlasica interica Pallary 1923(a), Bull. Soc. Hist. nat. Afr. Nord, 14 (3), pp. 112–113, TL le dj. Inter, dans l'anti Atlas, à 25 kil. au sud de Tiznit, with new var. *major* (TL not stated, but presumably same as for the species); Pallary (1923b: 277; 1926: 23–24, pl. 4 figs 1, 2); Pallary (1935: 354), Goulimine ... espèce de la zone des Euphorbes; Pallary (1936: 24), s'étend jusqu'à l'oued Massa au N. E. de Tiznit, sur les rives de cet oued, au pont de Toubouzer, sur la route d'Agadir et à quelques kilomètres au sud, sur la route de Goulimine; with var. *major* and new var. *minor* (TL not stated); Pallary (1939a: 61); Rour *et al.* (2002: 194); Cossignani (2014: 78–79), figs of two shells, from Tiznit, Anti-Atlas, ..., Crevice rocks.

*Atlasica* (?) *aguellizensis* Pallary 1926, J. Conchyl., 70 (1), pp. 24–25, pl. 4, figs 5, 6, TL Oued Aguelliz, dans le Sous; *Atlasica aguellizensis* – Pallary (1939a: 61); Rour *et al.* (2002: 194).

*Atlasica Tamanarensis* Pallary 1933, Bull. Soc. Hist. nat. Afr. Nord, 24 (7), pp. 243–244, TL Tamanar, au bas du poste d'Ighil Akachen, territoire du Tadla [not place of same name on route from Mogador to Agadir]; Pallary (1936: 22–23, pl. 2 fig. 3; 1939a: 62; 1939b: 106); Rour *et al.* (2002: 194).

*Massylaea Derbesi* Pallary 1933, Bull. Soc. Hist. nat. Afr. Nord, 24 (7), p. 245, TL Zaouia Ahançal; Pallary (1936: 28–29, pl. 2 fig. 1), with new vars (p. 29) *minor* and *depressa*, the first of them figured (*op. cit.*, pl. 2 fig. 2) but not otherwise described; Pallary (1939a: 63; 1939b: 107); Rour *et al.* (2002: 194). *Massylaea bisseyana* Pallary 1933, Bull. Soc. Hist. nat. Afr. Nord, 24 (7), p. 245, TL Tamda (cercle d'Azilal, à 45 kil. S. E. d'Azilal); Pallary (1936: 29–30, pl. 1 fig. 2), with new vars *minor* (TL D'Agherbou n'Masko) and *depressa* (same TL); *Massylaea Bissayana* [sic] – Pallary (1939a: 63); *Massylaea Bisseyana*, Pallary (1939b: 107); Rour *et al.* (2002: 194); Cossignani (2014: 89), figs of shell, from Tamda.

Atlasica illirensis Pallary (1935: 354), Goulimine, nomen nudum; Atlasica illirensis Pallary 1936, J. Conchyl., 80 (1), pp. 23–24, pl. 1 fig. 3, TL fentes de calcaire dur du djebel Sidi Gadir, à Illir, dans le Tazéroualt, à 50 kilomètres S. E. de Tiznit; ... atteint le dj. Taïert, près de Goulimine; Pallary (1939a: 61); Rour *et al.* (2002: 194); Cossignani (2014: 78), figs of shell from Illigh.

*Atlasica ahuiri* Cossignani 2012, Malacologia Mostra Mondiale, 74, pp. 12–13, TL Notfia (Nord Est di Tan-Tan), Marocco; Cossignani (2014: 77), shell figs.

*Atlasica cossignanii* Ahuir Galindo 2013b, Malacologia Mostra Mondiale, 80, p. 5, TL El-Abiar, ovest Guelmin [Morocco]; Cossignani (2014: 78), figs of two shells, from El-Abiar (holotype, MMM), S. Sidi Ifni.

*Atlasica aitbahaensis* Ahuir Galindo 2016, Malacologia Mostra Mondiale, 90, TL Ait Baha (Anti Atlas).

*Shell* Figures: Mousson (1874: pl. 4 fig. 4), Kobelt (1876, Icon., (1) 4, pl. 92); Figs 2C–F, 3A.

Genital anatomy Figures: see Hesse (1931: 92–93, pl. 13, fig. 109); Figs 6E, F, 7G, H, M, N, 7, Table 4. Our only mature specimen from one locality at high altitude in the Haut Atlas (sample M165 from sandstone crags at 2494m alt., NE. of Oukaimeden) differs markedly in characters of the genital anatomy from several other populations (e.g. sample M91). M165 differs in its longer diverticulum on the duct of the bursa copulatrix which is more coiled in situ (cf. Fig. 6E and F), the smaller flaps in the genital atrium (cf. Fig. 7M and N), and especially, the internal structure of the proximal part of the penis (with epiphallus continuing into penis lumen, coiling at its proximal end, then ending as a proximal verge: Fig. 7H; cf. epiphallus ending as very short proximal verge

at proximal end of penis: Fig. 7G). Shells from sample M165 are not distinctive compared to those of *L. rerayana* which varies widely between populations (Figs 2C–F, 3A). Although the differences in its genital anatomy might imply that a different species is involved, the only DNA sequence data we were able to obtain from M165 (from *COI*) places it within the clade formed by *L. rerayana* and close to sample M091 (Fig. S1 in Supplementary Material).

*Range* Endemic in Morocco: West-central Haut-Atlas, much of Anti Atlas, and coastal regions W. of Guelmim (subfossil near coast further south) (Fig. 9). Sympatric with *L. beaumieri* in parts of the C. Haut Atlas, occasionally syntopic with it.

*Notes* (1) Mousson (1873) published the names *H. rerayana* and *H. praedisposita* at the same time. No previous author appears to have regarded them as conspecific, so we act as First Revisers (cf. ICZN Code Art. 24.2) in giving nomenclatoral precedence to the name *H. rerayana*. The latter is preferred because Mousson's (1873, 1874) description and figures of it are much more clearly identifiable than those of *H. praedisposita*, and also because the type of the latter was subfossil. (2) *H. praedisposita* appears to have been based on a small high-altitude form or geographical subspecies of *M. rerayana*. Intermediate forms are known elsewhere that bridge the difference in size between *praedisposita* and *rerayana*.

## L. lechatelieri (Pallary 1917)

Archelix Le Chatelieri Pallary 1917, J. Conchyl., 63 (2), p. 133, pl. 5, fig. 1, TL Tarzout-du-Guigou; Archelix (Archelix) lechatelieri Pallary – Hesse (1920, Icon., (2) 23 (5–6), p. 239); Le Chatelieria Le Châtelieri Plry [sic] – Pallary (1923b: 279); Le Chatelieria Le Chatelieri Plry – Pallary (1926: pl. 2 figs 4–6), localisée dans les bassins supérieurs de la Moulouïa et du Sebou, with new vars minor and major, both nomina nuda; Le Chatelieria Le Châtelieri [sic] – Pallary (1939a: 63; 1939b: 107); Lechatelieria lechatelieri – Rour et al. (2002: 194).

*Lechatelieria Leprevieri* Pallary 1926, J. Conchyl., 70 (1), pp. 20–21, pl. 2 figs 1–3, TL Timdighas (région de Khénifra, Maroc Oriental); Rour *et al.* (2002: 194).

*Le Chatelieria Mikaelae* Pallary 1933, Bull. Soc. Hist. nat. Afr. Nord, 24 (7), pp. 245–246, TL Tighremt

ou Dedi (see Pallary 1936: 25–27 for detailed description of location); *Le Châtelieria Mikaelae* – Pallary (1936: 25–27, pl. 2 fig. 4), fig. of genital anatomy (p. 26 fig. 5), with new var. *minor* (p. 25; TL not stated, but presumably same as for species); *Le Châtelieria Mikalelae* [sic] – Pallary (1939a: 63); *Le Châtelieria Mikaelae* – Pallary (1939b: 107); *Lechatelieria mikaelae* – Rour *et al.* (2002: 194).

*Massylaea Bournazeliana* Pallary 1933, Bull. Soc. Hist. nat. Afr. Nord, 24 (7), p. 244, TL Amougueur et Talrist (Maroc méridional); Pallary (1936: 27–28, pl. 2 fig. 6; 1939a: 63); Rour *et al.* (2002: 194).

*Shell* Figures: Pallary (1917, 1926, 1936, cited above), Schileyko (2006: 1793, fig. 2295); Fig. 4D.

*Genital anatomy* Figures: P. Hesse in Pallary (1936: 26, of *mikaelae*); Figs 5C, 7C, D, K, Table 4; our study shows important differences from Hesse's figure.

*Range* Endemic in C. and E. Morocco in Moyen Atlas and W. Haut Atlas (Fig. 9). See synonymy above for old records and Appendix (in Supplementary material) for list of our localities. Subfossil shells from regions south of the modern range that are now very arid appear to be small representatives of *L. lechatelieri* (mapped with ? symbol in Fig. 9) but distinctions of these from shells of *L. rufa* are often unclear through loss of all shell coloration. Sympatric with *L. rufa* over a large part of its range, sometimes syntopic.

*Note* Local populations differ in shell size among our samples of living material; some subfossil shells are apparently smaller as noted above.

## L. rufa Pallary 1918

Atlasica (?) soluta Michaud, variété *rufa* Pallary 1918, Bull. Soc. Hist. nat. Afr. Nord, 9 (7), p. 148, TL Bessabis, Scourra, Tazouta; Foum Zadel, col entre Rich et Ksar es Souq, Tizi n' Firest, col au sud du Tiallatin; *Alabastrina soluta* Michaud Var. *Dilatata* Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), p. 19, TL Bessabis ("mode ex col. *rufa"*); *Alabastrina soluta* Var. *rufa* Plry – Pallary (1920b: 24–25), Tazouta, Scoura et Bessabis (dans la partie inférieure de la boncle du haut Sebou); "Foum Zadel, col entre Rich et Ksar es Souq et de Tizi n'Firest, col au sud de Tiallalin"; *Alabastrina*  soluta rufa – Pallary (1923b: 279); Alabastrina soluta var. dilatata - Pallary (1926: 12), Bessabis ("mode ex col. rufa"); Alabastrina rufa – Pallary (1936: 21-22), with new var. gracilis (p. 22; TL entre Aïn Guettara et Rorgia, dans le bassin moyen de la Moulouïa et aussi à Rich, plus au sud); Pallary (1939a: 62), Rich; Foum Zabel; Pallary (1939b: 106); Rour et al. (2002: 194); Alabastrina rufa (Pallary, 1926) – Cossignani (2014: 74), figs of shell from Rich; ?Alabastrina soluta var. rufa -Llabador (1952: 105), Cala Trifa (Beni Sicar), var. rufa treated as form of the polymorphic A. soluta, with note that at Cala Trifa vars alabastrites, bifasciata and rufa coexist [the note suggests to us that Llabador may have either mistaken a form of what we regard below as L. alabastrites for L. rufa, or used the name "rufa" merely for a variety of L. alabastrites as a nomen nudum].

*Alabastrina Marmouchana* Pallary 1933, Bull. Soc. Hist. nat. Afr. Nord, 24 (7), p. 244, TL Immouzer des Marmoucha, dans la tache de Taza; Pallary (1936: 17–19, pl. 2 fig. 7; 1939b: 106); Rour *et al.* (2002: 194).

*Alabastrina Tilmiratensis* Pallary 1933, Bull. Soc. Hist. nat. Afr. Nord, 24 (7), pp. 244–245, TL Tilmirat, dans la tache de Taza; Pallary (1936: 19–20, pl. 2 fig. 9); Rour *et al.* (2002: 194); Cossignani (2014: 76), figs of two shells from Tilmirat, Middle Atlas.

Alabastrina skouraensis Pallary 1936, J. Conchyl., 80 (1), pp. 20–21, pl. 2 fig. 5, TL Skoura, à 86 kil. S. E. de Sefrou, with new vars (p. 21) *Major, Minor, Quadrifasciata, Alba, Trifasciata* (the last of them a *nomen nudum*); Rour *et al.* (2002: 194); *Alabastrina skouraensis* Pallary 1933 [sic] – Cossignani (2014: 74), figs of two shells, from Skoura.

*Shell* Figures: Cossignani (2014: 74 as *rufa* and *skouraensis*, 76 as *tilmiratensis*); Fig. 4A–C.

Genital anatomy Figs 6C, 7F, L, Table 4.

*Range* Endemic in Morocco in Moyen Atlas (including Jbel Tazzeka) and neighbouring areas of NE. Haut Atlas (Fig. 9). Sympatric with *L. lechatelieri* over much of its range, sometimes syntopic.

*Note* Pallary (1918) introduced the name *rufa* for what he tentatively regarded as the form of *Atlasica soluta* (= *Loxana alabastrites*) occurring in

the Moyen Atlas. He regarded it as a var. or subsp. in several subsequent papers, but later (Pallary, 1936: 21–22) treated it as a distinct species. Hesse (1920, Icon., (2) 23 (5-6), p. 235), relegated it to f. rufa Pallary. As noted above, Llabador (1952: 104-106) treated var. rufa as a form of the polymorphic species Alabastrina soluta (= Loxana alabastrites) with a rather puzzling note (p. 105) that at Cala Trifa vars *alabastrites*, *bifasciata* and *rufa* all coexist. However, rufa differs markedly and consistently from L. alabastrites in having a deeper suture, fewer branches on vaginal mucous glands and a discrete geographical range, so it is regarded as a distinct species here. This treatment is supported by our molecular data (Fig. 1). L. massesylica has an older name, but is treated here as a species distinct from L. rufa.

## L. massesylica Pallary 1917

Atlasica massesylica Pallary 1917, J. Conchyl., 63 (2), pp. 133–134, pl. 5 fig. 4, TL la gada de Debdou, dans les fentes de rochers, with var. *minor* (p. 134);

Pallary (1923b: 278), gada de Debdou; Pallary (1926: 22–23), with new vars *Guyoni* (p. 22; TL Beni Fachette, à 25 kilometres S.-E. de Debdou) and *albina* (p. 23; TL Debdou, almost a *nomen nudum*, but it was noted as "des exemples d'albinisme"); Hesse (1929, Icon., (2) 23 (5–6), p. 235); *Atlasica massesylica* [sic], Pallary (1939b: 106); *Atlasica massesylica* – Rour *et al.* (2002: 194); Cossignani (2014: 79), figs of shell from Dedbou [*sic*=Debdou].

*Atlasica ainensis* Ahuir Galindo 2020, Malacologia Mostra Mondiale, 106, figs. TL Guefait, small town in north-east Morocco. (Accessed 30 March 2020 from malacologia.org./rivista.htm).

*Shell* Figures: Cossignani (2014: 79 as *Atlasica massesylica*); Fig. 4H.

*Genital anatomy* Figs 6D, 7E, Table 4; hitherto undescribed.

*Range* Endemic in Debdou hills (NE. Morocco) (Fig. 9). *Atlasica ainensis* Ahuir Galindo 2020 from Guefait (N34.240° W2.408°) appears to be a synonym representing an extension of range along the hills running north-eastwards from Debdou. Not sympatric with any congener.

Note Pallary (1917: 134) regarded the Debdou form as the north-easternmost representative of H. atlasica, which it resembles in shell coloration but not in shell form. The unreflected peristome and moderately deep suture on the spire provide a greater resemblance in form to *rufa* which Pallary named as a var. of *H. soluta* in 1918. The geographical range of the latter centred on the Moyen Atlas is much closer to Debdou than the ranges of L. beaumieri (reaching only the SW. Moyen Atlas) or atlasica (in the Haut Atlas). Furthermore, the subsequent discovery of forms of massesylica with all-white shells (albina) in the Debdou region strengthen its resemblance to rufa, since they are unknown in atlasica or beaumieri. The shell coloration of *massesylica s.s.* with light buff ground colour and interrupted dark brown bands is apparently procryptic against the reddish soils and rocks of the Debdou region, which differ markedly from the limestones in the range of rufa in the Moyen Atlas. The validity at species rank of this taxon has now also gained support as different from L. rufa from our molecular data (Fig. 1); some anatomical differences also exist between them (Table 4, Figs 6C and D, 7E and F).

## L. alabastrites (Michaud 1833)

Helix alabastrites Michaud 1833, Catalogue Testaces vivans envoyés d'Alger par M. Rozet, ..., p. 4, no. 8, pl. 1 figs. 6–8, TL not given [= Alger, i.e. Algeria], (See Note below for precedence of this name over H. soluta Michaud 1833); Terver (1839: 18, pl. 4 figs 1–3); Rossmässler (1839, Icon., (1) 2 (3-4), pp. 4-5, 43, pl. 42 figs 557-559) bei Oran; Algier; zwischen St. Gregoire und Mers-el-Kebir; bei Arzew; Rossmässler (in Wagner, 1841, Reisen, t. 2 pp. 249, 259; Atlas, pl. 12 fig. 4); Wagner (1841, Reisen, t. 2, p. 266); Erdl (1841, in Wagner, Reisen, t. 2, p. 271; Atlas, pl. 13); Morelet (1853b: 281); Gassies (1856, Desc. coq. univ. Mayran, in Act. Soc. Linn. Bordeaux, 21, p. 106); Hidalgo (1909: 211), Chafarinas, Melilla, Restinga, Cabo del Agua, Beni-Bu-Fruor; Helix soluta, Michaud var. alabastrites Mich. - Pallary (1899: 103), as with typical var., from O. de l'Algérie; falaises de l'O. Kiss, près d'Adjeroud; rochers entre Marnia et Ouchda; Helix (Marmorana) soluta var. alabastrites, Pallary (1904: 49); *Helix soluta, alabastrites*, Pallary (1917: 135); Macularia alabastrites Michaud varr. -Kobelt (1904, Icon., (2) 10 (5-6), p. 66, pl. 297 figs 1905–1911), described and figured variation in

shells, including var. subvanvincquiae Pallary (figs 1910, 1911), from marokkanischen Rif; Alabastrina alabastrites Michaud Var. complanata Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), p. 19, TL Cap Falcon, Tlemcen; Alabastrina alabastrites Michaud Var. Globosa Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), p. 19, TL Oran, Tléta (invalid junior homonym); Alabastrina alabastrites Michaud Var. Major Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), p. 19, TL Oran (invalid junior homonym); Alabastrina alabastrites Michaud Var. Sphaeroidea Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), pp. 19-20, TL Marnia; Alabastrina alabastrites, Pallary (1920b: 23), Kebibibicha; Pallary (1939b: 106); Alabastrina alabastrites, Llabador (1936: 200), Massif des M'Sirdas au Sud-Ouest de Nemours; Rour et al. (2002: 194); Kneubühler et al. (2019: 10-14); Alabastrina (Alabastrina) alabastrites (Michaud, 1833) - Razkin et al. (2015: 102, 108), Honaine, Traras Massif, Algeria, with DNA sequence data.

Helix soluta Michaud 1833, Catalogue Testaces vivans envoyés d'Alger par M. Rozet, ..., Strasbourg, p. 3, no. 5, pl. 1 figs 9, 10, TL not given [= Alger, i.e. Algeria]; Bourguignat (1863 t. 1: 134-137, pl. 13 figs 12-21), with vars conoidea, microstoma (Environs d'Arzew; ile de Rachgoun; embouchure de la Tafna), subcarinata (Environs d'Alger), zonulis interruptis ornata ("Rare"), late fasciata, bifasciata, alabastrites (last based on H. alabastrites Michaud), also (p. 137) with description of body of snail, notes on habitat and additional Algerian localities (environs d'Oran; entre Saint-Grégoire et Mers-el-Kébir; cap Lindeles; au-dessous des ruines de Touent, près de Djemma-Gazaouat; Lalla-Maghrnia; Mostaghanem); Helix soluta, Michaud – Pallary (1899: 103), O. de l'Algérie; falaises de l'O. Kiss, près d'Adjeroud; rochers entre Marnia et Ouchda; Helix (Marmorana) soluta, Pallary (1904: 26, 49), îles Zaffarines; commune sur la frontière algérienne ... devient plus rare vers l'ouest; Mélilla; Adjéroud; Massylaea soluta Mich. - Hesse (1915, Icon., (2) 23 (1-2), pp. 46-48, pl. 637 figs 35-39), Umgebung von Oran, figs of jaw and genitalia; Hesse (1920, Icon., (2) 23 (5–6), p. 235), with syn. alabastrites Mich., also, vars. hemisphaerica Kob., pycnochilia Bgt., subvanvincquiae Pallary [his f. rufa Pallary was presumably L. rufa]; Alabastrina soluta Michaud Var. globulosa Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), p. 19, TL

Oran, Berkane; Alabastrina soluta Michaud Var. Sphaerula Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), p. 19, TL Beni-Saf, Marnia, le Kef et Tléta; Alabastrina soluta Michaud Var. Minor Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), p. 19, TL Zaffarines, Nemours, Beni-Saf, Marnia; Alabastrina soluta Michaud Var. Major Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), p. 19, TL Oran; Alabastrina soluta Michaud Var. Depressa Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), p. 19, TL Cap Falcon; Alabastrina soluta Michaud Var. articulata Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), p. 19, TL Le Kef, près Marnia; Alabastrina soluta Michaud Var. Plumbea Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), p. 19, TL Berkane; Alabastrina soluta Michaud Var. Albina Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), p. 19, TL Oran, nomen nudum; Alabastrina soluta, Pallary (1920b: 23-24), Kebibicha, entre Safsafat et Bou Yacoubat; dans les Beni Znassen; Cheràa; Taforalt; Aïn Sfa; Berkane; with "variétés ex colore plumbea et brunnea" [brunnea is a nomen nudum, but regarded here as infrasubspecific] in "modes" quinquefasciata, quadrifasciata Ancey, bifasciata Bgt., and "variétés ex forma" globulosa, minor [also subvanvincquiae and rufa treated separately here because they were later regarded as species-group names, "rufa" being our L. rufa]; Alabastrina soluta, Pallary (1926: 12–13), with vars globulosa, sphaerula, minor, major, depressa (from Aïn-el-Turk), articulata; new var. chottini (p. 12, pl. 1 figs 7, 8, TL "rochers au sommet de la montagne située au S.-S.-E. d'El Aïoun, qui porte le nom de Rich el Ammam" ([Alabastrina soluta] Chottini, Pallary (1923b: 279), was a nomen nudum); new var. albina (p. 13; TL not stated, but given as Oran by Pallary 1920a: 19, where nomen nudum); Alabastrina Chottini, Pallary (1939b: 106); Rour et al. (2002: 194); Cossignani (2014: 73), figs of two shells from El Aioun; Alabastrina soluta, Pallary (1939b: 106); Llabador (1936: 200), Massif des M'Sirdas au Sud-Ouest de Nemours; Rour et al. (2002: 194); Alabastrina soluta, Llabador (1952: 104-106), new locality data (Cala Trifa (Beni Sicar); Iles Zaffarines; Tatsfachts (O. Settout); Tizi-Karuat (Beni bou Yahi)), with vars alabastrites, bifasciata (pl. 5 fig. 1), chafarinensis (pl. 5 figs 2, 3), Chottini, subvanvincquiae; [var. rufa also treated as form of this polymorphic species with note (p. 105) that at Cala Trifa vars alabastrites, bifasciata and rufa coexist, but see our notes above under L. rufa]; Alabastrina soluta (Michaud

1833) – Hutterer, Mikdad & Ripken (2011: 62); Cossignani (2014: 74–75), figs of six shells, from Hassi-Berkane; Zaio; Tistoutine; *Alabastrina soluta bifasciata* Bourguignat 1864 – Cossignani (2014: 75), figs of two shells, from Charrana; *Alabastrina soluta globulosa* Pallary 1926 – Cossignani (2014: 75), figs of two shells, from Ain Zorah.

Helix (Marmorana) soluta var. subvanvincquiae Pallary 1904, J. Conchyl., 52 (1), pp. 26, 49, pl. 2 figs 10, 11, TL Rare à Mélilla ... parait plus commune dans l'intérieur ... trouvés sur les plâges de l'Algérie; Alabastrina soluta Var. subvanvincquiae Plry – Pallary (1920b: 24), rare à Berkane; entre Safsafat et Bou Yacoubat; [Alabastrina soluta] subvanvincquiae, Pallary (1923b: 279); Alabastrina subvanvincquiae albina<sup>+</sup> (Pallary, 1926) – Cossignani (2014: 75), figs of shell, from Berkane; Alabastrina subvanvincquiae bifasciata† (Pallary, 1904) -Cossignani (2014: 75), figs of shell, from Berkane; Alabastrina subvanvincquiae chafarinensis<sup>+</sup> (Pallary, 1904) - Cossignani (2014: 75-76), figs of two shells, from Chafarinas I.; Alabastrina subvanvincquiae lineata<sup>+</sup> (Pallary 1903) – Cossignani (2014: 76), figs of shell, from Ras el Ma; Alabastrina subvanvincquiae muscata<sup>+</sup> (Pallary 1903) – Cossignani (2014: 76), figs of shell, from Ras el Ma; Alabastrina subvanvincquiae zonata<sup>+</sup> (Pallary 1903) – Cossignani (2014: 76), figs of shell, from Ras el Ma [† none of the preceding six subspecific names formed by Cossignani 2014 from an earlier varietal name is valid as a species-group name].

*Atlasica Zâtica* Pallary 1920(a), Bull. Soc. Hist. nat. Afr. Nord, 11 (2), pp. 18–19, TL Taourirt, sur les pentes septentrionales du djorf; Pallary (1923b: 279); *Atlasica zatica*, Pallary (1926: 14, 21–22, pl. 3 figs 13–17), Taourirt, sur les pentes septentrionales du djorf; Aïn Guettara; with new var. *minor* (p. 22; TL not stated); Rour *et al.* (2002: 194); *Atlasica zatica*, Pallary (1939b: 106) – Cossignani (2014: 79), figs of three shells, from Ain Guettera, ..., Crevice rock.

*Alabastrina cherrierei* Pallary 1923(a), Bull. Soc. Hist. nat. Afr. Nord, 14 (3), p. 113, TL Région des Kiffans, à la lisière sud du Riff, with new var. *minor* (TL not stated, but presumably same as for the species); [*Alabastrina soluta*] *Cherrierei*, Pallary (1923b: 279).

*Alabastrina kiffansensis* Pallary 1926, J. Conchyl., 70 (1), pp. 13–14, pl. 1 figs 16, 17, as unnecessary

new name for *Alabastrina cherrierei* Pallary 1923(a), based on its supposed homonymy with *Helix (Camaena) Cherrieri* Bavay, 1908; *Alabastrina kiffansensis* Pallary 1926 – Rour *et al.* (2002: 194).

*Alabastrina carminis* Cossignani & Ahuir Galindo 2012, Malacologia Mostra Mondiale, 75, p. 26, TL Nord-ovest di Hassi-Berkane, Marocco; Cossignani (2014: 73), shell figs.

Alabastrina homadensis (Rutllant) – Cossignani (2014: 73), figs of shell, from Hassi-Berkane (nomen nudum; Rutllant was apparently the collector not an author); Alabastrina homadensis intermedia (Ahuir 1990) – Cossignani (2014: 73), figs of shell, from Hassi-Berkane (nomen nudum); Alabastrina homadensis Ahuir Galindo 2018a, Malacologia Mostra Mondiale, 99, pp. 22–23, TL Mechra Homadi, small town about 50km south of Nador [Morocco]. The same publication (p. 23 fig. 1) showed shells of "Hybrid series between Alabastrina homadensis n. sp. and Alabastrina cf. soluta"; we interpret occurrence of these intermediate shells as evidence that the taxa involved are conspecific.

Alabastrina tistutensis (Rutllant 1974) – Cossignani (2014), African Landshells, pp. 76–77, figs of three sharply keeled shells, from Tistoutine (nomen nudum; Dr J. Rutllant of Melilla formed a large collection of molluscs that he made available to Llabador [see Llabador 1952: 97] but he apparently never authored any published name for a snail); Alabastrina tistutensis Ahuir Galindo 2018a, Malacologia Mostra Mondiale, 99, pp. 23-24, TL "Tistoutine, located about 30km to the SO. of Nador [Rif, Morocco; although the article is written in English, "SO." from a Spanish author in an Italian magazine can only mean south-west]; Alabastrina tistutensis Galindo, 2018 [sic=Ahuir Galindo] - Kneubühler et al. (2019: 11-13), on p. 31 these authors also mentioned that "this extreme local form should probably be considered a local subspecies rather than a species in its own rights".

Alabastrina tistutensis  $\times$  A. subvanvincquiae – Cossignani (2014), African Landshells, p. 77; figs of two shells, from Guerruau; we note that these intermediate shells suggest the taxa involved are conspecific.

*Shell* Figures: Rossmässler (1839, Icon., (1) 2 (3–4), pl. 42 figs 557–559), Bourguignat (1863 t. 1:

pl. 13 figs 12–21), Pallary (1926), Llabador (1952), Schileyko (2006: 1793, fig. 2296), Kneubühler (2019: 11–16); Fig. 4F, G.

*Genital anatomy* Figures: Hesse (1915: pl. 637 figs 36–39), Kneubühler (2019: 12–16, but see below under "Evolution of the distal genitalia" heading for a correction); Figs 6A, 7A, I, Table 4.

*Range* Reported in the literature from NE. Morocco (extending westwards to S. slopes of Rif in "region des Kiffans" and north and east to near Melilla, Berkane, Oujda, etc.) and NW. Algeria (near Oran; Beni Saf; Tlemcen) (Fig. 9 shows our own records). Not sympatric with any congener, but coexists locally with *Otala pallaryi*.

Note The names H. alabastrites and H. soluta were published in the same work by Michaud (1833). It was noted by many subsequent authors (e.g. Rossmässler, 1839, Icon., (1) 2 (3-4), p. 5; Terver, 1839: 18, pl. 4 figs 1–3; Bourguignat, 1863, t. 1: 136) that they should be treated as the same species since they often occur together and differ only in coloration, the former having an all-white shell, the latter dark bands. Several early authors rejected the name soluta because "soluta Ziegler" which Michaud listed as a synonym refers to a Sicilian species. Indeed, Rossmässler (1838, Icon., (1) 2 (1–2), pp. 8–9, pl. 32, figs 446) adopted H. soluta Z.[iegler] for the Sicilian species. However, Ziegler did not publish this name until 1836 (in Philippi), so it is a junior homonym of H. soluta Michaud 1833.

When Rossmässler (1839, Icon., (1) 2 (3–4), p. 5) regarded *H. alabastrites* Michaud and *H. soluta* Michaud as the same species he adopted the name *H. alabastrites* in preference to *H. soluta* Michaud. Likewise, Terver (1839: 18) also treated both as conspecific under *H. alabastrites*, as noted by Rossmässler (1839, Icon (1) 2, p. 43). Either of them may thus have acted as first reviser in giving precedence to the name *H. alabastrites* Michaud, although at least Rossmässler was explicit in regarding *H. soluta* Michaud (incorrectly) as a junior homonym of *H. soluta* Ziegler.

Bourguignat (1863, t.1: 134) agreed that *H. alabastrites* Michaud and *H. soluta* Michaud are the same species, but he gave precedence to the name *H. soluta* Michaud, since the latter was evidently not a junior homonym of *H. soluta* Ziegler. Subsequently, Pallary (1899: 103; 1904: 49; 1917: 135) also gave precedence to *H. soluta* in

regarding *alabastrites* as a variety, as did Llabador (1952: 104–106).

The ICZN Code (Art. 24.2.2) on Determination of precedence of names or acts by the First Reviser, states "If two or more names, different or identical, and based on the same or different types, ..., are published on the same date in the same or different works, the precedence of the names ... is fixed by the First Reviser unless Article 24.1 [names at different ranks] applies."; Article 24.2.5, on Unnecessary action by a First Reviser states "If it is shown subsequently that the precedence of names, ..., can be objectively determined, the action of the First Reviser is nullified." There is nothing in the Code to disqualify determination of precedence for any other erroneous reason, such as mistaken belief that one name is unavailable as a junior homonym. Thus, H. alabastrites Michaud 1833 takes precedence over H. soluta Michaud 1833 on the basis of the choice by the first reviser being either Rossmässler (1839) or Terver (1839).

## L. bailloni (Kobelt 1887)

Helix (Macularia) Bailloni ["Debeaux in litt."] Kobelt 1887, Nachrichtsbl. d. malakozool. Ges., 19, pp. 123–124, TL in deserto meridionali prov. Oranensis [Algeria]; Helix Bailloni ["Debeaux"] Kobelt 1888, Icon., (2) 3 (5-6), pp. 48-49, pl. 85 figs 474, in der oranesischen Sahara, das abgebildete Exemplar [holotype] in einem sandigen Ravin zwischen Tiût und Mograr im Gebiet der Ulad Sidi Scheikh nahe der marokkanischen Gränze"; Westerlund (1889, Fauna pal., Helix, pp. 425-426), placed close to Helix Wagneri; Helix (Macularia) Bailloni – Pallary (1900: 733), suggested it is a small form related to Helix punica, adds locality of Aïn-el-Bey (département de Constantine); Massylaea bailloni (Deb.) Kob. - Hesse (1920, Icon., (2) 23 (5-6), p. 234); H.[elix] Bailloni Debeaux - Pallary (1923b: 278), montagnes de Figuig; A.[rchelix] (Massylaea) Bailloni Debeaux - Pallary (1924: 112); Helix (sect. Guilia) Bailloni (Deb.) Kobelt – Pallary (1926: 17), entre Moghrar et Figuig (cercle des Beni Guil); Guilia Bailloni, Pallary (1939b: 107); Guilia bailloni (Debeaux, 1882) – Rour et al. (2002: 194).

*Shell* Figures: Kobelt (1888, Icon., (2) 3 (5–6), pl. 85 figs 474), Schileyko (2006: 1792 fig. 2294); Fig. 4E.

*Genital anatomy* At present undescribed, but Kneubühler *et al.* (2019: 31) mentioned that a publication giving anatomical and genetic data is in preparation.

*Range* Reported in the literature as endemic to E. Morocco (near Figuig) and W. Algeria (between Tiut and Mograr in region of Uled Sidi Scheikh near Moroccan border; Aïn-el-Bey) (Fig. 9 shows our own records). Not sympatric with any congener.

Notes (1) Kobelt headed the original description with "Helix Bailloni Debeaux" and also noted it as "Debeaux in litteris" and "gesammelt und mir von Debeaux mitgetheilt". However, the style of the written descriptions (Latin and German) matches others in the Icon., leaving little doubt that they were written by Kobelt, or at least rewritten by him, although Debeaux supplied the type specimen and probably the name. (2) For notes on characters of this species see Pallary (1926: 17–18). The generic allocation is tentative because the genital anatomy is unknown. (3) Richardson (1980) listed it as a fossil species but the original description makes no reference to it being fossil; shells in NHMUK (pers. obs.) look recent as does one shell collected in 1984 (H&S in NMW.Z 1993.051.2077) although others in the latter collection are subfossil. However, as mentioned above, Kneubühler et al. (2019: 31) mentioned that a publication giving anatomical and genetic data on this species is in preparation.

## L. severinae (Pallary 1918)

*Massylaea* (?) *Severinae* Pallary 1918, Bull. Soc. Hist. nat. Afr. Nord, 9 (7), p. 148, TL Aïn el Bey (Constantine); *Massylaea severinae* Pallary – Hesse (1920, Icon., (2) 23 (5–6), p. 235); *Guilia Severinæ* – Pallary (1926: 18, pl. 3 fig. 10; 1939b: 107).

Shell Figure: Pallary (1926: pl. 3 fig. 10).

Genital anatomy unknown.

*Range* Endemic in NE. Algeria, where known only from TL at "Ain-el-Bey (Constantine)". Not sympatric with any congener.

*Note* A poorly known taxon, for which affinity to *L. bailloni* has been suggested; see Pallary (1926: 18) for notes on its characters. The TL is close to the southern edge of the city of Constantine, hence in a region much less arid than that inhabited by

*L. bailloni*. The description and figure suggest a shell rather similar to that of *L. lechatelieri*, but the TL is even more distant from the range of that species than from that of *L. bailloni*. However, it

endemic to Djurdjura Mountains of Algeria

is close to the range of *Massylaea punica*, so the taxon possibly represents small shell(s) of that species with the inside of the aperture white rather than the usual light brown colour.

10.

### Artificial Key to all Genera of Helicidae in the W. Maghreb and all species of Loxana, Massylaea and Otala

Besides Otalini, the key covers all genera of Helicidae occurring in the W. Maghreb. Some Geomitridae from this region have shells as large as Helicidae, but they mainly have the umbilicus open; in W. Maghreb Helicidae it is open in adult shells only in *Theba sacchii* Gittenberger & Ripken 1987 from SW. Morocco, and narrow in that species which otherwise has the shell coloration and general appearance typical of *Theba. Loxana severinae* is excluded from the key because no specimens and only scanty information were available; it was named from near Constantine in Algeria and described as resembling *L. bailloni*.

1.	-Two vaginal mucous glands each with more than two branches3Two unbranched vaginal mucous glands2.
2.	-Free oviduct long, convoluted; penial flagellum nil to long; vaginal mucous glands wide and cylindrical at maturity; peristome not much reflected Theba -Free oviduct short; penial flagellum long; vaginal mucous glands slender at maturity; peristome reflected on mature shells; in W. Maghreb only in N. Tunisia Murella muralis (O.F. Müller 1774)
3.	-Penial flagellum well developed; diverticulum on duct of bursa copulatrix well developed5Penial flagellum very short; diverticulum on duct of bursa copulatrix absent (possibly4.sometimes rudimentary)4.
4.	-Vaginal mucous glands lacking stout basal stalk, with total of <10 terminal branches;
5.	-Inner wall of proximal part of penis with single small or large papilla (longer than wide), arising laterally (not terminating epiphallus as a proximal verge)6Inner wall of proximal part of penis lacking a papilla longer than wide12.
6.	<ul> <li>Papilla in proximal penis long and cylindrical, nearly filling lumen of proximal part of penis;</li> <li>diverticulum much longer than duct of bursa copulatrix, strongly convoluted <i>in situ</i></li> <li>Papilla in proximal penis smaller and shorter, &lt; half length of lumen of proximal part of penis; diverticulum rarely much longer than duct of bursa copulatrix, usually with few loops or folds when <i>in situ</i></li> </ul>
7.	-Papilla in proximal penis small; penial flagellum usually 1–2× length of epiphallus; shells often thick and solid; 3 rupestral species all endemic in N. SicilyErctella-This combination of characters lacking; wide ranges, including Sicily8.
8.	-Vaginal mucous glands with total of <20 branches; shells with white ground colour, unmarked or with dark bands ( <i>Loxana</i> spp.)17Vaginal mucous glands with total of >20 branches; shells with buff, greenish or brown ground (not clean white), unmarked or with dark bands9.
9.	-Penial flagellum clearly more than twice length of epiphallus; peristome usually reflected in adult shells; shell surface often malleate; shell often with weak or interrupted dark bands; wide geographical range in Europe and north Africa <i>Cornu aspersum</i> -Penial flagellum approximately twice length of epiphallus; peristome not or slightly reflected; shell surface rather smooth, or ribbed, but not malleate; shell unbanded except in a species

10.	-Southern Europe eastwards to Turkey; shell lacking dark bands; distal verge inside penis very short -Algerian species; distal verge inside penis large and triangular; shell unbanded except in a	tus
	species endemic to Djurdjura Mountains of Algeria	11.
11.	-Shell lacking dark bands; epiphallus as long as penis; north Algeria (perhaps also Tunisia) <i>Cantareus koraegael</i> -Shell with conspicuous dark bands, ribbed; epiphallus at least three times length of penis; species apparently endemic to upper levels of Djurdjura Mountains, Kabylie, north-east Algeria <i>Cantareus subaper</i>	ius tus
12.	-Shell distinctly higher than wide, large, solid; aperture very large (obviously > half shell breadth); exterior of shell typically whitish and almost unmarked, aperture dark brown inside N. Algeria & Tunisia <i>Helix melanostoma</i> Draparnaud 18 -This combination of characters lacking	; 301 13.
13.	-Free oviduct longer than vagina; interior of aperture brown to blackish (except in some forms with whole shell usually white); mucous glands with total of 12–36 branches and stout basal stalk Otala 2 -Free oviduct shorter than vagina; interior of aperture white (brown only in Massylaea punica from NE. Algeria); mucous glands with total of 4–25 branches and lacking stout	28.
	basal stalk	14.
14.	-Large whitish shells (B 25–38mm), inside of aperture white or brown; mucous glands with total of 15–25 branches; NE. Algeria only <i>Massylaea</i> -Shells mainly smaller; inside of aperture white; mucous glands with 4–18 branches; Morocco and NW. Algeria (absent from NE. Algeria)	22. 15.
15.	-Mucous gland branches (12–16 in total) very long, extending proximally beyond middle of spermoviduct; diverticulum of bursa copulatrix duct conspicuously stout; penis internally with distinct cylindrical proximal verge and long cylindrical distal verge (length >3× breadth); shell with rather thin peristome, not much reflected except towards umbilicus; in Maghreb only in NW. Morocco <i>Pseudotachea litturata</i> (L. Pfeiffer 188] -Mucous gland branches (4–18 in total) not very long, not extending proximally to middle of spermoviduct; diverticulum of bursa copulatrix duct not conspicuously stout; penis internally with small or indistinct proximal verge and distal verge often shorter or somewhat conical; peristome reflected or not	; 51) 16.
16.	-Atrium with two variously small to large flaps arising around exit from distal penis; epiphallus extending into lumen of proximal penis, not extending into it, or passing right through it; inner wall of proximal penis with papilla (1 species); wings of dart forming simple + shape in cross-section; absent from NW. Rif (Morocco) Loxana -Atrium lacking a flap; epiphallus ending at proximal end of proximal penis as small proximal verge; inner wall of proximal penis without papilla; wings of dart T-shaped in cross-section or forming simple +; restricted to NW. Rif Rossmaessleria scherz	17. l zeri
17.	-Immature shell with sharp peripheral keel, so spire of adult shell has flat whorls with very shallow sutures	18.
	whorls and depressed sutures	21.
18.	-Adult shell with body whorl sharply keeled	19.
	-Adult shell with body whorl rounded	20.
19.	-Epiphallus continues through proximal penis to form distal verge; local forms in E. Rif L. alabastri	ites

(localised populations respectively near Tistoutine, *L. a. "tistutensis"* and *L. a. "carminis"*, and Hassi-Berkane, *L. a. "homadensis"*, connected to typical forms by intermediate shells)

-Epiphallus ends at proximal end of penis, not continuing through it; local forms in SW. Moyen Atlas near Beni Mellal *L. beaumieri* 

(L. b. "vondeli", connected to typical forms by intermediate shells)

-Shell predominantly white or very pale, with or without dark bands that are usually 20. sharply defined when present; lower lip of aperture often with small tooth near outer end; epiphallus extending through interior of proximal penis; only in NE. Morocco and L. alabastrites NW. Algeria -Shell predominantly buff or brown, often with dark bands that are ill-defined and interrupted with paler flecks; lower lip of aperture without tooth; epiphallus not extending into interior of proximal penis; only in SW. and WC. Morocco in WC. and W. Haut Atlas and SW. Moyen Atlas L. beaumieri 22. 21. -Species endemic in NE. Algeria, having large whitish shells with brown bands 23. -Species endemic in Morocco or extending only into western edge of Algeria 22. -Interior of aperture of adult shell brown; spiral sculpture on body whorl weak; altitudinal M. punica range up to 1500m -Interior of aperture of adult shell white; spiral sculpture on body whorl strong; altitudinal M. massylaea range above 1500m 23. -Restricted to Figuig region of extreme SE. Morocco and W. Algeria; first two whorls of shell relatively large; shells small (B <24.5mm, H <13mm) L. bailloni -Not in Figuig region or W. Algeria; first two whorls of shell smaller in proportion to adult shell size; shells small to much larger 24. -Background colour of shell usually predominantly buff or brown, with dark bands that are 24. usually ill-defined; aperture relatively large; Haut-Atlas, Anti-Atlas, Guelmim region; further north only in Debdou hills (NE. Morocco) 25. -Background colour of shell white or pale; dark bands normally present and well defined; aperture relatively small (except in region of SW. Morocco around and S. of Sidi Ifni) 26. -Shell aperture relatively small; epiphallus continues distally through interior of proximal 25. penis to end in distal verge; in Debdou Hills (NE. Morocco) only L. massesylica -Shell aperture relatively large; epiphallus does not continue distally right through interior of proximal penis (epiphallus usually ends as short proximal verge, rarely forming long proximal verge); in Haut-Atlas and Anti-Atlas L. rerayana (part) -Forms endemic to region around and S. of Sidi Ifni in SW. Morocco; with relatively large 26. L. rerayana "ahuiri" rounded aperture; epiphallus ends at proximal end of penis -Range in Moyen Atlas or eastern to central Haut Atlas; aperture relatively small, oval; epiphallus enters proximal penis to form large proximal verge or passes right through it to 27. form distal verge 27. -Shells usually with 5 broad dark bands, with dark bands on top of body-whorl broader than pale zones between bands (Fig. 4A–C); shells often smaller (B19.9–27.2mm); body-whorl often forms smaller proportion of shell breadth, so aperture relatively narrow; epiphallus continuous through proximal penis, ending as distal verge; papilla arising from outside wall of continuation of epiphallus within proximal part of proximal penis L. rufa -Shells usually with 4 narrow dark bands, with dark bands on top of body-whorl narrower than pale zones between bands (Fig. 4D); shells often larger (B 22.8–29.9mm); body-whorl often forms larger proportion of shell breadth, so aperture relatively wide; epiphallus extends into lumen of proximal penis to end forming large proximal verge; large papilla (false verge) on inner wall of lumen of proximal penis not attached to extension of epiphallus L. lechatelieri (small-shelled individuals can be difficult to distinguish, although larger shells are often present

in the same population; best shell characters are those of the banding pattern)

28.	-Immature shell with sharply keeled periphery, resulting in very shallow suture on upper spire of adult shell 29
	-Immature shell with rounded periphery, resulting in deeper suture on upper spire of adult shell 32
29.	-Shell breadth <25mm; adult shell very glossy, subglobular (H/B 0.58–0.68) with rounded periphery; peristome only slightly reflected; tooth on lower lip ~ strong; almost endemic in NW. Algeria, just reaching NE. Morocco O. hieroglyphicula -Shell breadth 21–42mm; adult shell not very glossy, subglobular to almost discoid, with periphery rounded to keeled; peristome slightly to strongly reflected; tooth on lower lip weak or lacking (especially in subglobular shells) to strong; endemic in C., NW. and NE. Morocco 30
30.	-Combination of whitish depressed-conical shell with rough decussate surface, blunt peripheral keel with raised spiral cord, reflected peristome and large tooth in middle of lower lip; known living only in Kebdana Mountains in NE. Morocco <i>O. xanthodon</i> keeled form (shells intermediate with
	-This combination of characters lacking those of typical <i>O. xanthodon</i> also occur 31
31.	-Shell coloration and sculpture varying widely between different populations; lumen of proximal penis narrow and meandering, lacking longitudinal pilaster on inner wall; diverticulum on duct of bursa copulatrix shorter ( <i>ca</i> 1.0× bursa duct); widespread, including Beni Snassen Mountains
	-Shell dull brown with indistinct darker markings and rough surface; lumen of proximal penis large and straight, with raised pilaster running longitudinally for most of length of inner wall; diverticulum on duct of bursa copulatrix longer ( <i>ca</i> 1.2× bursa duct); known only from NE. Morocco in Beni Snassen Mountains O. orientalis
32.	-Shells always small (B 19.0–22.4mm) with low spire, flattened base and narrow aperture pale brown inside, the peristome not reflected and without a tooth; shell coloration distinctive and almost constant within populations, with whitish to buff ground-colour and four bold bands of brown to blackish-brown; endemic in small area of NE. Morocco O. pallary -This combination of characters lacking 33
33.	-Shell aperture often with second tooth on outer palatal area, inside peristome; tooth on lower lip often high, commonly located close to outer edge of aperture; interior of aperture brown, partly brown or white; shells typically smaller or medium-sized with raised spire (B 19–35mm); all-white shells (except inside aperture) present in many populations, others usually with 4 (less often 3) well defined dark bands; restricted to NE. Morocco and NW. Algeria O. xanthodor -Shell aperture always lacking a second outer palatal tooth; with single tooth on lower lip, variable in size, usually located nearer middle of lip than to outer edge of aperture; interior of aperture brown to blackish; shells small to large (B 22–46mm), spire raised to low; populations
	very varied; includes more widespread taxa 34
34.	-Parietal area of aperture with brown to blackish coloration of interior most often sharply distinct at its edge from pale coloration of exterior; shells small or large; with or without well-defined dark bands, very often lacking a pattern of pale spots; flagellum usually much longer than epiphallus; SW. Europe & widespread in W. Maghreb (over most of W. and N. Morocco and NW. and NC. Algeria) O. lacted -Parietal area of aperture with brown coloration of interior blending gradually with pale coloration of exterior; shells small or large; with or without well-defined dark bands, often with a pattern of pale spots; flagellum shorter than epiphallus or up to 1.5× its length; less widespread taxa 35

35. -Shells typically large (B 28–46mm), body-whorl disproportionately larger than penultimate whorl; shell most often with weakly defined dark bands and obvious pattern of pale spots; flagellum often shorter than epiphallus or ~ equal to its length; in W. Maghreb only in NE. Morocco (absent from Moyen Atlas) and NW. Algeria; also SW. Europe O. punctata -Shells usually smaller (B <35mm, often <28mm), body whorl disproportionately larger than penultimate whorl or not; shell variable in colour and pattern; flagellum longer than epiphallus (local forms known from Moyen Atlas, NW. Algeria and possibly also NE. Morocco) 36.</li>

36. -Body-whorl not disproportionately wider than penultimate whorl; up to 4.7 shell whorls; shell surface rather glossy with strong fine spiral sculpture; endemic in mountains of NW. Algeria

-Body-whorl usually disproportionately wider than penultimate whorl; 4.3–4.5 shell whorls; shell surface less glossy; not known in Algeria 37.

37. -Shells small (26.0mm); suture of spire moderately deep; shell coloration rather drab with intricate pattern, recalling that of some forms of *Loxana rerayana* (buff with complex darker pattern of three indistinct dark bands and smaller dark and light marks); lower lip without tooth; known only from *ca* 1580m alt. near Immouzer-des-Marmoucha in Moyen Atlas of *O. occulta* 

-Shells larger, up to 35mm; depth of suture in spire often shallower; shell coloration variable; lower lip often with low tooth O. tingitana

(local forms known from few sites in Moyen Atlas and possibly also NE. Morocco).

#### ECOLOGY OF LOXANA AND OTHER OTALINI AND EVOLUTION OF THEIR SHELL CHARACTERS

Holyoak & Holyoak (2017: 476–477) provided data and an analysis of the habitats and ecology of most *Otala* and *Eobania* species in the W. Maghreb. The present section presents a similar analysis for *Loxana*, *Massylaea*, *Maurohelix* and a few *Otala* species that were not covered previously. Tables 6 and 7 summarise the data on these from our own field studies and allow a comparative approach which would be difficult to achieve by reporting this mainly new information separately under each species heading.

Information of this kind tends to show the habitat preferences of the collectors as well as those of the snails, with a bias likely towards searching in calcareous and stable sites which support rich faunas of Helicidae, and also favouring places similar to those found to be productive elsewhere. Nevertheless, comparisons of species within these genera can reasonably be made using our data so long as some allowance is made for under-representation of disturbed and species-poor habitat types.

New data on habitats are available for six of the eight species we recognise in the genus *Loxana* (Table 6). All sites where we found these were more or less rocky and the majority of populations were of snails found in crevices of crags, aestivating, or resting during the day. Indeed,

we have never found living Loxana or their fresh shells in areas with no rocks nearby, whether on open plains, in grasslands, scrub, or woodlands, despite much time spent searching these habitats for other snails. However, in the vicinity of rocky crags the Loxana species do not appear to be strictly confined to rupestral habitat and resting places. L. rerayana and L. beaumieri were mainly found in rock crevices and exclusively so at most sites, but both sometimes rest in secure niches on flat ground adjacent to rocks or tens of metres from them, where they are protected by robust plants. Examples for L. rerayana in the far south-west of Morocco are finds amongst bases of the spiny succulent Euphorbia officinarum L. (sites M088, M097) as well as amongst rocks, while nearby at M091 a majority of living adults of this species were found amongst E. officinarum and another succulent Kleinia anteuphorbium (L.) Haw. on an open rocky slope. Similarly with L. beaumieri in the SW. Moyen Atlas, at sites M151 and M156 dense patches of the spiny succulent Euphorbia resinifera O.Berg. on flat ground produced more fresh dead shells than rocks nearby, although it was only practicable for us to search the dead plants, after decay has caused loss of most of their spines and the caustic latex, so they can be kicked aside with boots.

In the Beni Snassen mountains, *L. alabastrites* occurred widely in rocky sites and was found

	L. ala.	L. bea.	L. lec.	L. mas.	L. rer.	L. ruf.
Altitudinal range (m above sea-level)	340–751	30-1450	1201–2030	1145	45-2494	450–1663
Rock type:						
no rock exposed	-	-	-	-	-	-
limestone	4	22	4	-	7	15
clay	-	-	-	-	-	-
shale	-	-	-	-	1	-
sandstone/conglomerate <sup>1</sup>	1	-	-	-	12	5
calcareous sandstone <sup>2</sup>	7	5	6	1	7	2
quartzite	-	-	-	-	1	-
granitic	-	-	-	-	1	-
metamorphic (hard)	-	-	-	-	2	-
schist	-	-	-	-	1	-
Topography:						
plains/nearly flat ground	-	-	-	-	1	-
slopes/banks	2	9	1	-	14	2
crags & slopes	10	18	9	1	17	20
Vegetation cover:						
scanty, on crag	1	-	-	1	1	-
mainly herbs or grasses	2	5	6	-	8	5
patchy shrubs or scrub	4	12	3	-	9	10
succulents & scrub	-	3	-	-	9	-
trees & bushes	5	7	1	-	5	7
woodland	-	-	-	-	-	-
Total N sites	12	27	10	1	32	22

Table 6 Habitats of *Loxana* species in Morocco and Algeria, based on specimens collected by the authors 1984–2017. Figs give numbers of sites with living snails or fresh shells of each species. Abbreviations: *L. ala., Loxana alabastrites; L. bea., L. beaumieri; L. lec., L. lechatelieri; L. mas., L. masseylica; L. rer., L. rerayana; L. ruf., L. rufa.*

Notes: <sup>1</sup>found once on conglomerate consisting of sandstone; <sup>2</sup>includes few sites with conglomerate of calcareous sandstone.

resting in numbers in rock crevices, but many also rested high on shrubs, or even several metres above the ground on tree saplings. Similarly, L. lechatelieri in the Moyen Atlas was often found only amongst rocks at sites which had rather few bushes (e.g. M121), but nearby at M131 a slope with much open scrub of Buxus balearica Lam. had numerous individuals resting by day among the branches and twigs of this and other shrubs. The apparent restriction of most Loxana populations to rock habitats where they can rest in crevices may therefore result at least partly from lack of plants providing alternative sites, as a clear result of the drastic over-grazing of vegetation by domestic animals that has become almost ubiquitous in semi-arid regions of Morocco in recent decades. The general restriction of the genus to the vicinity of rocky places may nevertheless

involve other factors, perhaps associated with low dispersal abilities, predation pressure, or competition from other Helicoidea that survive better in areas with fewer or insecure resting places.

Within *Loxana*, all species occur in calcareous habitats with limestone rocks or calcareous sandstones. Only *L. rerayana* occurs also on various metamorphic rocks (including quartzite and granitic lithologies) which are clearly poor in calcium, where it often lives at low densities. *L. lechatelieri* is restricted to the mountains (1201– 2030m in our records), *L. rufa* ranges from lower foothills (450m) to middle levels (up to 1663m) in some of the same regions in the Moyen Atlas as *L. lechatelieri*. Both *L. beaumieri* (recorded at 30–1450m) and *L. rerayana* (at 45–2494m) have populations ranging from relatively humid

Table 7 Habitats of species of *Massylaea*, *Maurohelix* and *Otala* in Morocco and Algeria, based on specimens collected by authors 1984–2017. Figs give numbers of sites with living snails or fresh shells of each species.
 Abbreviations: *M. mas., Massylaea massylaea*<sup>1</sup>; *M. pun., Massylaea punica; M. ray., Maurohelix raymondi; O. jui, Otala juilleti; O. occ., Otala occulta; O. pal., Otala pallaryi.*

	M. mas.	M. pun.	M. ray	O. jui.	O. occ.	O. pal.
Altitudinal range (m above sea-level)	1570	530–1500	670–920	770–1180	1580	658–783
Rock type:						
no rock exposed	-	1	-	-	-	-
limestone	-	3	-	7	-	-
sandstone	1	1	1	2	1	-
calcareous sandstone	-	1	1	-	-	4
Topography:						
plains/nearly flat ground	-	1	-	-	-	-
slopes/banks	-	2	1	3	-	1
crags & slopes	1	3	1	6	1	3
Vegetation cover:						
mainly herbs or grasses	-	2	1	5	-	1
patchy shrubs or scrub	-	3	1	2	-	1
trees & bushes	1	1	-	2	1	2
woodland	-	-	-	-	-	-
Total N sites	1	6	2	9	1	4

Note: <sup>1</sup>single shell found was neither fresh nor obviously old.

low levels near Atlantic coasts to moderately high (*beaumieri*) or high (*rerayana*) in the Haut Atlas. From our data, *L. alabastrites* (340–751m) was recorded only in hills and low mountains, but there is not much higher ground within its overall range, and it doubtless occurs close to sea-level in the Islas Chafarinas. All the species shun habitats with vegetation that remains very sparse throughout the year, although some of them sometimes rest among unvegetated rocks adjacent to areas with low seasonal herbs and grasses. They also appear to avoid shady closed woodlands even where there are plenty of rocks.

Fewer data are available on habitats of the other genera considered in this paper (Table 7), all of which prefer rocky calcareous habitats, often on crags or rocky slopes. We found *Otala pallaryi* only at the same sites as *Loxana alabastrites*, in very similar resting places, both in rock crevices and on the twigs and branches of bushes in well-developed low scrub, they were often intermixed. *Otala juilleti* seems from our data on living snails and fresh shells to be a montane species (770–1180m in Table 7), tolerating open grassy and herbaceous vegetation as well as scrub cover with patchy trees; a single

old shell found at 10m alt. in coastal dunes (Fig. 8) was possibly subfossil. As noted above under their species headings citing relevant literature, the two *Massylaea* species appear to replace each other altitudinally in the Aures Mountains of NE. Algeria, our only find of *M. massylaea* being at 1570m, whereas *M. punica* was found repeatedly, at 530–1500m. Our two finds of *Maurohelix raymondi* also match literature reports noted above, being restricted to the steppe-like Hauts Plateaux inland in N. Algeria, where they were found living in rocky (sandstone or calcareous sandstone) open habitats with sparse low vegetation at 670–920m.

Evolution of shell form in Otalini, Ereminini and Thebini has attracted much interest because of the occurrence of local populations with shells ranging from discoid with a sharp peripheral keel to subglobular with smoothly rounded whorls. Similar patterns of variability have also been well documented in several different families of Helicoidea, including Canariellidae, Geomitridae, Sphincterochilidae and Trissexodontidae, and other subfamilies within the Helicidae (e.g. Ariantinae, Murellinae), so they have clearly had multiple and entirely independent origins. An



**Figure 8** Distribution of species of *Massylaea, Maurohelix* and *Otala* (Helicidae: Otalini) in NE. Morocco and N. Algeria based on specimens collected by the authors (see Appendix for details).

association of sharply keeled shell forms with rupestral habitats and resting places in narrow crevices has often been suggested and sometimes confirmed, but it cannot explain all examples (e.g. with *Theba pisana* (O.F. Müller): Holyoak & Holyoak, 2016).

De Bartolomé (1982 and pers. comm.) carried out early experiments with *Rossmaessleria* demonstrating that representatives of keeled and globular forms interbred freely in captivity over two generations. Walther *et al.* (2016) argued from molecular data that the remarkably varied range of shell forms in *Rossmaessleria* occurs within a single species. Within Moroccan *Theba pisana* it is also apparent that keeled and globular forms are conspecific, with molecular data offering no support for separating them even at subspecies rank (Greve *et al.*, 2010).

The present study provides additional examples of keeled populations of Otalini and of these being conspecific with round-shelled forms. Thus, in *Otala*, the keeled form of *O. xanthodon* discussed above is connected to round-shelled forms by intermediates. Holyoak & Holyoak (2017: 462) showed that the keeled form "*minet*-*tei*" of *O. tingitana* has intermediate populations connecting it to globular forms, and the late J.F.M. de Bartolomé (pers. comm.) created similar intermediates with captive-bred hybrids. Thus, within *Otala* both *O. xanthodon* and *O. tingitana* have local populations with keeled adult shells that are clearly conspecific with their more

common round-shelled populations, but only O. tingitana is normally keeled in all populations as a juvenile. In contrast, O. hieroglyphicula is keeled only as a juvenile. In Loxana striking localised keeled forms are known in two species, L. beaumieri (around Beni Mellal in SW. Moyen Atlas as "vondeli", connected to globular forms by intermediates named "subplana", "conica" and "pedroi") and L. alabastrites (in E. Rif, near Tistoutine as "tistutensis", with intermediates; near Hassi-Berkane as "homadensis", with intermediates "carminis" and "intermedia": see species accounts above for nomenclatural details). Only the keeled form of Otala xanthodon and Loxana "tistutensis" have molecular data allowing comparison with related globular-shelled forms and in both cases it does not support even subspecific distinction (cf. Kneubühler et al., 2019; Fig. 1).

Holyoak & Holyoak (2017: 422, 481) commented on the basic five-banded pattern of shell coloration in Otalini. This is obvious in *Otala* and *Eobania*, and a similar pattern occurs in other tribes of Helicidae, but *Eremina* shows a complicated pattern of banding that is not obviously pentataeniate, whereas the complicated banding polymorphisms in *Theba* appear to be based on a four-banded pattern as pointed out by Heller (2009: 120 fig. 87). Among other Otalini, the genera *Cornu*, *Erctella*, *Loxana*, *Massylaea*, *Maurohelix* and *Rossmaessleria* show pentataeniate patterns on the more obviously banded shells, except that *Loxana lechatelieri* normally has four bands (occasionally three); *Cantareus* lacks dark bands except in *C. subapertus* which has up to five bands (Bouaziz-Yahiatene *et al.*, 2019: 14–15); insufficient banded shells of *Maurohelix* have been studied to ascertain their pattern.

The following comments are based on the recognition of two main types of shell coloration in Otalini (Figs 2-4), one banded with a whitish or pale background colour and up to five conspicuous dark bands, the other *plain* with a darker background colour and more or less indistinct darker bands; this distinction often seems somewhat arbitrary since weakly banded intermediates also occur within some species. All-white shells form a third type which is the only form in many populations of Otala xanthodon and a few of O. lactea, and occurs in a substantial proportion of shells in populations of the polymorphic Loxana alabastrites in which the other shells are all banded; those Otalini with strongly keeled shells also most often have them all-white, usually in association with rough sculpture; rare all-white shells reported in other species appear to be abnormal "albinos".

All or almost all shells are banded in Loxana lechatelieri, L. rufa, Massylaea massylaea, M. punica, Otala pallaryi and most Rossmaessleria (except the strongly keeled forms and the globular R. scherzeri boettgeri (Kobelt) and R. s. weberi (Kobelt)). At least some of these species are amongst those most often found resting among vegetation rather than in rock crevices. All shells are plain in Cantareus apertus, C. koraegaeilus and Loxana massesylica, and almost all are plain in Erctella, Loxana beaumieri and Maurohelix. Loxana rerayana is remarkable in having predominantly plain shells showing a remarkably varied range of colour tones and patterns in many different populations, but with one striking exception: in the far south-west of its range (M091, Fig. 2F). There they are whitish and conspicuously dark-banded at the only site where it was found resting predominantly on vegetation rather than among rocks (see above); DNA sequence data nevertheless show this population is part of the same clade as others (e.g. M002) with plain shells (Figs 2C–E, 3A). In contrast, each of the other Otala species and Eobania have different populations with either plain or banded shells, or variously intermediate between these types, and commonly polymorphic; they are very often found resting on vegetation as well as on rocks or soil (Holyoak & Holyoak,

2017). *Cornu* also shows wide variation in coloration between populations, with most *plain*, some obviously *banded*, many others intermediate, and it too often rests on vegetation as well as on soil or rocks.

Much as with *Otala*, the wide range of variation in *plain* shells between different populations of many other Otalini species is clearly related to procryptic matching of background colours of rocks and soils, with reddish shell hues associated with red-brown sandstones, pale buff hues with paler sandstones and whitish background colours and flecking associated with limestones. Similarly, background-matching is often clearly evident with *banded* shells, for example with *Loxana rufa* on sandstone having broad chestnut bands on a pale buff background colour, whereas its other populations on limestone have narrow blackish bands on a whitish ground-colour.

# Evolution of the Distal Genitalia in Otalini and Thebini

Table 4 gives a detailed presentation of features of the distal genitalia for the individual species of Loxana. Table 5 provides a wider comparison of characters for all genera of Otalini. At generic level it is clear that there is a remarkable amount of incongruence between the distribution of characters of the genitalia and the arrangement of genera dictated by the phylogenetic data from Fig. 1. The molecular phylogeny is based on many more characters than any phylogeny that might be deduced from the genital anatomy. Although those molecular characters used may include some that are directly adaptive, their functional correlates are doubtless independent of those causing variations in genital anatomy. Hence, the incongruence demands a critical reassessment of the significance of the genital characters that have been used for a century or more (following detailed studies by Hesse, 1910, 1911, etc.) on the assumption that they provide the best available phylogenetic indicators for classification at family and genus levels.

In particular, it is noteworthy that a large papilla (or false verge) on the inner wall of the lumen of the proximal penis appears to have evolved independently in subtribes Otalina (in *Eobania* and again in *Loxana lechatelieri*) and Cantareusina (in genera *Cantareus* + *Cornu*). For *Eobania* with its large cylindrical "false verge", the presence of a smaller papilla in the allied Otalina genera *Maurohelix* and *Loxana* (*L. lechatelieri;* with tiny structure also in *L. rerayana* from M165) appear also to represent independent origins (see next paragraph) rather than pointing to possible precursors of the structure in *Eobania*. Among allies of *Cornu*, the related Cantareusina genus *Erctella* has a smaller papilla.

Three different types of structure of the proximal penis occur within the genus Loxana (Fig. 7). (1) L. alabastrites, L. massesylica and L. rufa have the cylindrical strong-walled epiphallus continuing through the proximal penis to form the distal verge; all three have a bend in the wall of the epiphallus continuation from which a blind papilla arises. This anatomical arrangement does not occur in other Otalini, although it is approached in Theba (Schileyko, 2006: 1784 fig. 2285C). (2) In L. beaumieri and most populations of L. rerayana the epiphallus wall ends at the proximal end of the proximal penis without formation of any evident proximal verge; a distal verge extends beyond the distal end of the proximal penis; there is no papilla within the lumen of the proximal penis. This anatomical arrangement resembles that of many other Otalini, e.g. Massylaea punica and several Otala species. (3) The sixth Loxana species, L. lechatelieri, shows an intermediate condition, with the cylindrical strong-walled epiphallus continuing distally into the proximal penis, where it ends forming a long proximal verge; a separate distal verge (or similar-looking second false-verge) extends beyond the distal end of its proximal penis; a large papilla (false verge) is attached to the inner wall of the lumen of the middle part of the proximal penis. L. rerayana from sample M165 alone also has the epiphallus continuing into the proximal penis and forming a long proximal verge; it also has a false verge, but it is tiny (the free part 0.4mm long) and appears to be merely a small loose flap arising from a longer pilaster (Fig. 7H).

These structural features within the proximal penis of *Loxana* were previously unknown, except for description for *L. alabastrites* alone in Kneubühler *et al.* (2019: 10–16), which is inaccurate in suggesting the papilla is separate from the epiphallus, illustrated by photographs that are difficult to interpret. A traditional approach might have led to the anatomical differences between these *Loxana* species and comparable large differences among *Otala* species being used to justify recognition of additional genera, but the molecular-phylogenetic data contradict that approach and instead indicate major anatomical changes have occurred among these closely related species. Indeed, the molecular data (Fig. 1) demonstrate the same three groupings of the species as occur with the proximal penis anatomy, with our type (2) forming the most basal clade (for *L. beaumieri*) and our type (1) derived latest (with *L. alabastrites*, *L. massesylica* and *L. rufa* in the same well supported clade). As discussed above, within *L. rerayana* it appears that there is intraspecific differentiation of penis internal structure.

Very similar changes in internal structure of the penis have also occurred independently within other families of Helicoidea, affording clear examples of convergent evolution. For example, Schileyko (2005) figured species of different genera forming part of the endemic radiation of the Geomitridae of the Madeiran Islands with: (1) epiphallus continuing through penis to form distal verge (Pseudocampylaea portosanctana (G.B. Sowerby I 1824) - his fig. 2545C, D and Discula polymorpha (R.T. Lowe 1831) – fig. 2547C), (2) epiphallus forming short proximal verge (Plebecula nitidiuscula (G.B. Sowerby I 1824) - fig. 2556C), and (3) epiphallus ending at proximal end of penis without forming a proximal verge (Steenbergia paupercula (R.T. Lowe 1831) - fig. 2559C).

Structure of the dart also appears to show convergent evolution in different Otalini lineages, with repetitive changes from the simple + cross-section to that with T-shaped lamella, or vice-versa. Indeed, there is variation in its form between local populations within the single polytypic species *Rossmaessleria scherzeri*.

Development or reduction of a penial flagellum and of the length of the diverticulum on the duct of the bursa copulatrix appear to be merely species-specific differences. They are anyway likely to be characters with a causal link, since the flagellum creates the tail of the spermatophore and the diverticulum receives it from the partner during mating. Within *Theba*, *T. pisana* usually has no flagellum, whereas other species have it well developed, a difference likely to provide a reproductive isolating mechanism.

The large differences between species and genera in development of the pair of vaginal mucous glands is obvious when dissecting

Otalini taxa and comparing them. The single thick unbranched glands of Theba provide a decisive character for recognising tribe Thebini. The simple structures with fewer than 10 terminal branches of Maurohelix or some small Loxana are also very different to the massive structures with 30 or more branches in Cantareus and Cornu of subtribe Cantareusina, or Eobania and Otala of subtribe Otalina. Both of those subtribes have surely developed large and elaborate mucous glands independently from forms with simpler glands, such as Theba which lie near the stem for the whole tribe and Rossmaessleria which has a basal position within the subtribe Cantareusina that contains Cornu and its close allies. Instead, increase of body size appears to correlate well with increased size and complexity of the mucous glands, suggesting a causal explanation.

#### **B**IOGEOGEOGRAPHICAL NOTES

A large proportion of all species of Otalini are endemic in the W. Maghreb and three of its nine genera (Loxana, Massylaea, Maurohelix) are endemic there. In fact, among Otalini only the small genus Erctella, comprising three species endemic in small ranges in N. Sicily (Colomba et al., 2011) does not occur in the W. Maghreb. A single species of the fifth genus, Rossmaessleria, extends only marginally to Europe on Gibraltar, with the remainder of its numerous subspecies all localised as endemics in the NW. Rif of Morocco. Although Cornu aspersum is now widespread in Europe, Madec, Bellido & Guiller (2003: 225) and Guiller & Madec (2010) accepted that the European populations are a recent introduction from the W. Maghreb by man, with consequent loss of genetic variation. For Otala, Holyoak & Holyoak (2017: 480) recognised five species, all of which are present in the W. Maghreb with three of them being endemic there. The present paper (see above under Otala genus heading) increases the totals for Otala to nine recognised species, all present in the W. Maghreb, with seven of them endemic there. Of the remaining three genera: Eobania probably has two species in Algeria judging from molecular data (Bouaziz-Yahiatene et al., 2017, cf. Holyoak & Holyoak, 2017) only one of which extends to southern Europe. Theba (Thebini) also has most of its species endemic in Morocco, two of them extending to southern Europe of which one is very localised and

probably introduced, with a third species of uncertain validity that is apparently endemic in S. Spain, and several more endemic species in the Canary Islands (Gittenberger & Ripken, 1987; with modifications from Greve *et al.*, 2010, 2017). Finally, *Cantareus* has recently been reinterpreted as showing a single species in the Mediterranean zone from S. Europe to Turkey and two endemic species in the W. Maghreb, confirmed only from Algeria (Bouaziz-Yahiatene *et al.*, 2019).

Thus the overwhelming majority of Otalini and Thebini taxa are restricted to the W. Maghreb, and hence the few endemic taxa elsewhere in S. Europe and the Canary Islands are likely to have originated from NW. Africa. The evidence that most diversification of Otalini has occurred in the W. Maghreb may point to the tribe having its earliest origins there. However, molecularphylogenetic data (Fig. 1) show the Otalini as a whole forming a sister group to a clade consisting of *Eremina* plus *Macularia*; *Eremina* has a wide range from W. Morocco to NE. Africa and Israel, while *Macularia* are endemic in S. Europe.

Within the W. Maghreb a majority of congeneric Otalini species have allopatric ranges (e.g. Fig. 9), pointing clearly to geographical isolation as a major factor leading to their speciation. The geography of the region with several mountain ranges separated by extensive plains presumably contributed to this process, since a number of species appear to still be restricted to single ranges (Loxana massesylica, L. rufa, Otala juilleti, O. occulta, O. orientalis, Massylaea massylaea, Cantareus subapertus) while others extend to two or three adjacent ranges, onto adjoining low ground, or both (e.g. Eobania constantinae, Loxana alabastrina, L. bailloni, L. beaumieri, L. lechatelieri, L. rerayana, Massylaea punica, Otala hieroglyphicula, O. pallaryi, O. tingitana, Rossmaessleria scherzeri). Two species appear to be mainly restricted to arid plains with steppe-like vegetation: Maurohelix raymondi and Otala xanthodon. Only a few species have achieved really wide ranges, notably Cornu aspersum, Eobania vermiculata, Otala lactea and O. punctata, and some if not all of these are likely to have been spread by human activity because of their long history of exploitation for food, as discussed at length by Holyoak & Holyoak (2017: 477-478).

Mapping of the distribution of Otalini species in the W. Maghreb points to several geographical features beside mountains that may have served



**Figure 9** Distribution of *Loxana* species (Helicidae: Otalini) in Morocco and NW. Algeria based on specimens collected by the authors (see Appendix for details).

as intermittent barriers leading to isolation and speciation of populations. In particular, the Otalini fauna on each side of the Oued Moulouya in NE. Morocco has a different composition, with three species (*Otala hieroglyphicula*, *O. juilleti*, *O. orientalis*) occurring only east of the river, while others including *Loxana alabastrina*, *Otala pallaryi*, *O. punctata*, *O. tingitana* and *O. xanthodon* are on both sides. The open plains of this river valley may have formed a barrier to the dispersal of rupestral snails, while the river itself might have served to disperse others from around its headwaters in the Moyen Atlas towards the coast.

Climatic changes in the W. Maghreb during the Pleistocene, especially rainfall variations, are known to have led to widespread movements of the vegetation zones (e.g. Hooghiemstra et al., 1992; Rognon, 1993). However, detailed palaeontological studies to give direct evidence of past ranges of Otalini and other land-snails in the region are rare, although Limondin-Lozouet et al. (2013) have demonstrated their value by confirming the persistent presence of Otala lactea in the Middle Moulouya basin of NE. Morocco throughout much of the Holocene. Similarly, research at a well stratified and dated early Holocene archaeological site in NE. Morocco by Hutterer, Mikdad & Ripken (2011) provided valuable proof of the presence there of Loxana alabastrina (as Alabastrina soluta), Otala punctata and O. xanthodon (as O. tigri), as well as evidence that its early Neolithic inhabitants exploited the

last of these. Comparable information from other regions of the Maghreb and from older deposits is needed to give more direct evidence to elucidate the faunal history.

#### ACKNOWLEDGEMENTS

Field collecting in 1984 and 1986 involved Marcel Holyoak and Dr Mary B. Seddon, who are thanked for much good humour and hard work. During the 1980s, facilities at the Department of Geography, University of Nottingham and Department of Geography at the College of St Paul and St Mary, Cheltenham were used in initial study of the collections, for which a grant from the Nuffield Foundation to DTH provided a microscope. The Department of BioSyB at National Museum & Galleries of Wales, Cardiff allowed large loans of the specimens from 2015–2018 without which the completion of the study would not have been possible; thanks are due to Jennifer Gallichan and Harriet Wood for arranging these loans. Rui da Costa Mendes, Dr Marco Neiber, J. Sebas Torres Alba and Harriet Wood helped with obtaining copies of literature. Thanks are due to Prof. Alberto Martínez-Ortí for the loan of material from collections he made in NW. Algeria and Morocco housed in MVHN. LJC was supported by a Post-doctoral Fellowship awarded by the Department of Education, Universities and Research of the Basque Government (Ref.: POS\_2018\_1\_0012). The Basque Government through the Research group on "Sistemática, Biogeografía, Ecología del comportamiento y Evolución" (IT1163-19) partly funded this work. We are also grateful to a referee for helpful comments that improved the paper.

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