Reassessment of the keeled subspecies of *Theba pisana* (Gastropoda: Helicidae) from the sand dunes of south-western Portugal

Reevaluación de las subespecies de *Theba pisana* (Gastropoda: Helicidae) con quilla en las dunas del suroeste de Portugal

David T. HOLYOAK and Geraldine A. HOLYOAK*

ABSTRACT

A form of *Theba pisana* with the shell keeled along the periphery and an open umbilicus has been known from sand dunes in south-western Portugal since 1989 when shells were reported from near Monte Clérigo, Algarve. It was initially identified as *T. p. arietina* (Rossmässler, 1846), a rare taxon otherwise reported only from Cádiz province in Spain, and this name has been adopted in all subsequent literature on the Portuguese populations. Comparisons of topotypical Spanish *T. p. arietina* with samples from Monte Clérigo show that these are indeed similar in having ± large keeled shells that are pale coloured and usually unbanded, but differ in several characters and do not represent the same taxon. However, there are much more extensive populations on sand dunes in south-western Portugal, very different in appearance, with smaller shells, a blunt keel, larger umbilicus and usually banded. These are likely to have originated independently from the Spanish *T. p. arietina*, and are therefore named as a new subspecies, *T. p. almogravensis*. Three extensive areas of coastal dune vegetation (each 2.5-4.8 km²) up to *ca* 82 km apart support large populations of it with almost constant shell characters. Descriptions of shells and genital anatomy are provided for both *T. p. arietina* and *T. p. almogravensis*. Shell samples from six smaller coastal areas (0.1-0.3 km²) of sand dune or transitional habitat in SW. Portugal, including Monte Clérigo resembling *T. p .arietina*, differ widely between populations and appear to show nearly stable combinations of characters of *T. p. almogravensis* and *T. p. pisana*. They are probably of hybrid origin, since similar forms arise among the much more variable "hybrid swarms" on some disturbed margins of habitats of typical *T. p. almogravensis*, where it meets *T. p. pisana*, and where mixed pairs were seen mating. Threats to *T. p. almogravensis* may therefore arise from introgression with *T. p. pisana*, but to ascertain this, further research is needed on changes in local populations and their habitats.

RESUMEN

Una forma de *Theba pisana* con una quilla periférica en la concha y el ombligo abierto se conoce en dunas de arena en el suroeste de Portugal desde 1989, con la cita de conchas recogidas cerca de Monte Clérigo, Algarve. Fue inicialmente identificada como *T. p. arietina* (Rossmässler, 1846), un taxon raro conocido por otra parte solamente de la provincia de Cádiz en España, y este nombre se adoptó posteriormente en toda la literatura tratando de poblaciones portuguesas.

* Quinta da Cachopa, Barcoila, 6100-014 Cabeçudo, Portugal;. E-mail: holyoak9187@gmail.com

Comparando ejemplares de *T. p. arietina* de la localidad tipo española con muestras de Monte Clérigo, se pone de manifiesto que son parecidos en tener conchas ± grandes y con quilla, con coloración pálida y generalmente sin bandas, pero difieren en varios caracteres y no representan el mismo taxón. Sin embargo, hay poblaciones más extensas en dunas de arena del suroeste de Portugal, que son muy diferentes en aspecto, con conchas más pequeñas, una quilla roma, un ombligo más grande y generalmente tienen bandas. Éstas probablemente se originaron independientemente de las poblaciones españolas de *T. p. arietina* y por lo tanto se nombran como nueva subespecie, *T. p. almogravensis*. Tres extensas áreas de vegetación dunar costera (cada una de 2.5-4.8 km^2) separadas por hasta unos 82 km sostienen grandes poblaciones de ella con caracteres casi constantes en la concha. Se proporcionan descripciones de las conchas y de la anatomía genital tanto para *T. p. arietina* como para *T. p. almogravensis*. Muestras de conchas de seis áreas costeras más pequeñas (0.1-0.3 km^2) de dunas arenosas o hábitat transicional en el suroeste de Portugal, incluyendo las de Monte Clérigo parecidas con *T. p. arietina*, difieren ampliamente entre poblaciones y muestran combinaciones casi estables de caracteres de *T. p. almogravensis* y *T. p. pisana*. Son probablemente de orígen híbrido, puesto que formas similares surgen entre los "enjambres híbridos" mucho más variables en bordes perturbados de hábitats de *T. p. almogravensis* típica, en donde se encuentra con *T. p. pisana* y se observaron parejas mixtas. Amenazas sobre *T. p. almogravensis* pueden por lo tanto derivarse de una introgresión por parte de *T. p. pisana*, pero para afirmarlo se necesita profundizar la investigación sobre cambios en poblaciones locales y sus hábitat.

INTRODUCTION

Theba pisana (O.F. Müller, 1774) was treated as a polytypic species with four subspecies in the review by GITTENBERGER AND RIPKEN (1987). In addition to *T. p. pisana* which is widespread in western and southern Europe and in Morocco, they recognised *T. p. arietina* (Rossmässler, 1846) as a localised Spanish endemic (in Sierra de San Cristobal in Cádiz province) and two endemic Moroccan subspecies. They commented that "The subspecies... are interconnected by broad zones with intermediate forms and, therefore, their morphological and geographical delimitation cannot be but rather subjectively indicated". SACCHI (1957: 81) had previously suggested that the two very localised subspecies characterized by strongly keeled shells, *T. p. arietina* and the Moroccan *T. p. cantinensis* (Sacchi, 1955), originated in small, isolated refuges near Atlantic coasts. It was suggested that subsequent dramatic range expansion of *T. p. pisana* led to secondary contacts as it surrounded the small refuges of both keeled taxa.

BANK AND DEKKER (1989) reported *T. p. arietina* from the coastal dunes at Monte Clérigo in the Algarve, Portugal, representing a range expansion of *ca* 250 km. GITTENBERGER, RIPKEN AND BUENO (1992: 151) did not discount the possibility of these shells having reached Portugal as a result of human transport, or that their keeled form might be a result of evolutionary convergence rather than of affinity with *T. p. arietina*. However, DE OLIVEIRA (2008, 2009) found that keeled shell types occur over a series of coastal localities in south-western Portugal from the western Algarve northwards to near Sines in Baixo Alentejo. He figured specimens from Monte Clérigo and Castelejo in the Algarve as *Theba pisana arietina* (*op. cit.*: 35, figs 1-4) and others attributed to *T. pisana arietina s. l.* (figs 5-12) from localities further north and also commented at length on evidence of hybridization between *T. p. pisana* and the keeled forms, which he therefore regarded as threatened ("em perigo") through introgression.

Our own comparisons of shell samples of topotypical *T. p. arietina* and Portuguese sand dune specimens nevertheless suggest they are mainly very different in appearance (Fig. 1A-C, cf. 1D-G). Because the large majority of the Por-

tuguese dune populations from the extensive areas of coastal dune vegetation (each 2.5-4.8 km^2) not only differ markedly in appearance from *T. p. arietina*, but are also likely to have had an independent origin, they are named here as a new subspecies, *T. p. almogravensis*. Use of different subspecies names should also serve to emphasise that the conservation of each of them should be regarded as a separate issue, with *T. p. arietina* especially being regarded as Endangered in Spain (RUIZ, CÁRCABA, PORRAS, AND ARRÉBOLA, 2006: 178).

Among Portuguese populations, only the shells from Monte Clérigo show a strong resemblance to those of *T. p. arietina* (Fig. 2A, B), but they differ from it in detail. As discussed later in this paper, they appear to be one of a number of localised populations intermediate between *T. p. pisana* and *T. p. almogravensis*: each of them having ± stable shell characters that differ between their populations, and small ranges confined to patches of sand-dune or transitional habitats (0.1-0.3 km^2). It is suggested that these localised intermediate populations are of hybrid origin because similar forms occur among the much more variable "hybrid swarms" present on some anthropogenically disturbed margins of habitats. In those places, typical populations of *T. p. almogravensis* meet *T. p. pisana* and mixed pairs were seen mating. Possible threats to *T. p. almogravensis* from introgression with *T. p. pisana* are discussed.

MATERIAL AND METHODS

Samples of shells and specimens preserved in alcohol were collected for topotypical *T. p. arietina* in December 2007, representing a characteristic population of that subspecies (site 51) and evident intermediates (perhaps hybrids) with *T. p. pisana* (site 52). Large samples of shells from sand dune areas of south-western Portugal were collected during visits in February 2011, March and October 2014 and April 2015, likewise involving locations with and without evidence of possible hybridization with *T. p. pisana*. The visit in October 2014 when the species was seen to be mating allowed mature specimens to be collected and preserved in alcohol for subsequent dissection; only immatures were found living on the other visits, implying that there is a clearly defined annual cycle with breeding occurring in the autumn. On the last two visits care was taken to collect representative samples of living snails or empty shells from small areas with well defined habitats that were described. Thus, specimens were not deliberately selected according to shell shape or coloration. A hand-held GPS was used to record locations in the field (accurate to within 10 m), as U.T.M. grid references.

COWIE (1980) found that British *T. pisana* is capable of producing viable eggs and sperm even when approximately half-grown, although precocious breeding was not found in studies in Israel (HELLER, 1982, 2009: 68; AVIVI AND ARAD, 1993). Shell growth in the species also appears to be indeterminate, with the peristome edge remaining thin even on large shells. Even the presence of a thickened rib inside the peristome does not confirm maturity; a second rib is often present deeper inside the aperture. We therefore chose shells for measurement from the largest 25% in samples from each locality, from which we selected those which possessed a firm rather than membranous mouth edge. This approach does not allow population means and standard deviations to be used for anything more than general comparisons of the taxa (despite their apparent precision), since the proportion of immature snails among those selected for measuring will be unknown and probably vary between localities. Measurements of shell breadth and height and counts of whorls followed the methods illustrated by KERNEY AND CAMERON (1979: 13); umbilicus width was measured as the maximum width across the umbilicus inside the body-whorl. Measurements of whole shells were made with vernier callipers or an eyepiece graticule (both accurate to within ± 0.05 mm), those of the umbilicus only with the eyepiece graticule.

The literature contains conflicting interpretations of the banding patterns on *Theba* shells and how they should be categorised (HELLER, 1981: 86; CAIN, 1984; COWIE, 1984: 362; GITTENBERGER AND RIPKEN, 1987: 5). In Portuguese *T. p. pisana* and *T. p. almogravensis* we find the pattern corresponds well to that summarised by HELLER (2009: 120 fig. 87) with up to four yellow to pale brown (spiral) bands, the two uppermost on the suture side of the whorl, the two lowermost on the umbilicus side; "each of the four bands may be overlain with numerous narrow, dark-brown stripes". In our descriptions, we therefore follow his distinction between *bands* and *stripes*.

External coloration of the body was described from specimens preserved in alcohol for over seven years for *T. p. arietina*, for just over one year in alcohol and from living animals or photographs of them for the Portuguese sand-dune populations. Only the darkness of the skin was taken into account, this apparently being due to (insoluble) melanin pigmentation as in many other snails since it does not change even after many years of preservation in alcohol, although allowance may be needed for shrinkage of the specimen or extraneous staining. The genital anatomy was studied from the same material, dissection being carried out using Meiji RZ Series stereo-microscopes and drawings prepared with a Meiji drawing tube. The genital anatomy of *T. p. pisana* has been described in detail and figured many times in the literature, e.g. by HESSE (1915: 2-8, pl. 631), GIUSTI AND ANDREINI (1988: 333), PUENTE (1994: 844-846) and SCHILEYKO (2006: 1784). The descriptions given here are therefore limited to a few comparative notes on characters known to vary within *Theba*, especially on the length of the flagellum on the epiphallus (which is characteristically rudimentary or lacking in *T. p. pisana*: GITTENBERGER AND RIPKEN, 1987: 35), the size of the vaginal mucus glands, relative lengths of vagina and free oviduct, and relative lengths of the parts of the duct of the bursa copulatrix, (i.e. the stalk arising from the vagina, the diverticulum and the "free" duct). In descriptions of the genital anatomy the terms proximal and distal refer to lesser and greater distances from the gonad.

All specimens are in CGAH unless otherwise noted.

Abbreviations:
B: shell breadth,
bod: bodies kept separately from shells,
CGAH: Collection of G.A. and D.T. Holyoak,
Coll.: collected by,
DTH: D.T. Holyoak,
GAH: G.A. Holyoak,
H: shell height,
n: number (sample size),
s.d.: sample standard deviation,
sh: shells,
spm: specimens in alcohol (70-80% industrial methylated spirit),
U: maximum width of umbilicus.

RESULTS AND TAXONOMY

<div align="center">

Family HELICIDAE Rafinesque, 1815
Subfamily HELICINAE Rafinesque, 1815
Tribe THEBINI Wenz, 1923

</div>

Synonym Euparyphinae Perrot, 1939

Placed in Subfamily Helicinae Rafinesque, 1815, Tribe Euparyphini Perrot, 1939 by CLECOM (BANK, BOUCHET, FALKNER, GITTENBERGER, HAUSDORF, VON PROSCHWITZ & RIPKEN, 2001; FALKNER, BANK & VON PROSCHWITZ, 2001). HAUSDORF AND BOUCHET (2005) recognised the Tribe Thebini within the Helicidae. The recent molecular-phylogenetic study by RAZKIN, GÓMEZ-MOLINER, PRIETO, MARTÍNEZ-ORTÍ, ARRÉBOLA, MUÑOZ, CHUECA & MADEIRA (2015) tends to confirm that *Theba* is correctly placed in a separate tribe of the Helicinae.

Genus *Theba* Risso, 1826 (p. 73)

Type species: *Helix pisana* O.F. Müller, 1774 by subsequent designation of Gray (1847) (ICZN Opinion 431, 1956).

Theba pisana (O.F. Müller, 1774)

Basionym *Helix pisana* O.F. Müller, 1774 (pp. 60-61).

Theba pisana arietina (Rossmässler, 1846) Figs 1A-C, 3A-D

Helix arietina Rossmässler, 1846 (p. 172).
syn. *Helix planata*: Rossmässler (1854: 22 *partim*, pl. 67 fig. 825).
Euparypha pisana arietina: Sacchi (1956: 1-5, figs 1, 2; 1957: 77-84, figs 1, 2, 4).
Theba pisana arietina (Rossmässler, 1846): Gittenberger & Ripken (1987: 40, figs 33, 34, 47).
Theba pisana arietina (Rossmässler, 1846): Ruiz *et al.* (2006: 178-179).

Specimens studied: *T. p. arietina*, Spain, Prov. Cádiz, *ca* 2.5 km SW. of El Portal, 29S 07544/40575, herb-rich grassland on rocky slopes by road, 29 Dec. 2007, Coll. GAH site 51, CGAH (14 sh + bod, 26 sh live-collected; 76 sh dead); shells intermediate with *T. p. pisana*, near San Ignacio (*ca* 3 km NE. of El Puerto de Santa María), 29S 075079/405743, low herbs and grasses on roadside bank, 29 Dec. 2007, Coll. GAH site 52, CGAH (8 sh + bod live-collected, 39 sh dead).

Shell: of *T. p. arietina s. str.* discoid with low domed spire (occasionally almost flat above), more rounded below; B 16.0-21.9 (mean 17.98, s.d. 1.55) mm, H 9.2-12.8 (mean 10.76, s.d. 1.05) mm, H/B 0.54-0.65 (mean 0.60, s.d. 0.036), n = 30. Whorls 4.3-4.7, with breadth increasing rather rapidly, almost flat to slightly convex above, with sharp angular keel near upper edge (ending peripherally in rounded raised cord). Suture obvious around protoconch; other sutures between upper whorls usually slight, often nil except for borders of the raised cord, occasionally a prominent suture when shell slightly scalariform. Last part of body whorl often descending slightly, exposing keel on part of penultimate whorl, the body whorl slightly expanded near aperture. Aperture broadly ovate overall, its shape interrupted by penulti- mate whorl and extended outwards by the prominent keel (the line of which is marked internally by a small sinus). Peristome nearly straight on upper palatal margin, much more strongly curved below keel, thin, plane except where reflected over umbilicus and near it. Aperture commonly with low rounded internal rib slightly set back from edge, sometimes also with second rib deeper inside. Umbilicus small (U 0.68-1.22, mean 1.02, s.d. 0.161 mm; U/B 0.039-0.071, mean 0.057, s.d. 0.0087; n = 30), narrow, usually exposing inside of body whorl although partly overlapped by peristome for *ca* one half of its width (rarely completely covered by peristome edge). Shells strong, nearly opaque. Fresh shells with silky lustre, but glossy on protoconch and in aperture. Ground- colour whitish to cream or light buff, the majority not striped or banded, others mostly with narrow interrupted and rather inconspicuous stripes of light brown to brown (one shell with broader diffuse light brown bands, two above keel, two below it: Fig. 1B). Interior of aperture usually white or whitish, light pink on few shells. Protoconch (whorl 0- 1) smooth apically, developing weak radial riblets; teleoconch with fine rather irregular radial ribs and rather irregular spiral grooves, these intersecting to give radially elongate riblets or papillae. Underside of shell with radial sculpture lower, so spiral elements appear more prominent than on upperside.

External coloration of body: Generally rather dark and dull-coloured; exposed foreparts of body, flanks, dorsum and tail light brownish; foot and foot-fringe dull

light brown; mantle-collar dark grey externally, usually orange-brown in band along inner edge; mantle surface inside body-whorl brown, often with variable grey to nearly black suffusion (sometimes covering more than half of surface), strongest towards front edge, or fine dark-grey reticulation; albumen gland light brown; digestive gland dull dark brown.

Genital anatomy: SACCHI (1956: fig. 2, 1957: fig. 2) published a schematic figure of the genitalia, showing no flagellum on the epiphallus. However, both of our dissections revealed a short flagellum, inconspicuous and appressed to proximal end of epiphallus in one snail, slightly longer, free and recurved in the other. Other characters varying in the genus were recorded as follows: vaginal mucus glands wide, moderately large (as long as penis plus epiphallus, or slightly longer); vagina about equal to free oviduct in one specimen, longer than rather short free oviduct in the other;

bursa copulatrix duct long, so reservoir when *in situ* was beside proximal end of spermoviduct (close to distal end of albumen gland); diverticulum seen in only one specimen, length of the stalk not established. These characters are generally similar to those of *T. p. pisana*.

Range and ecology: This subspecies is known only in SW. Spain, from a few locations in parts of the Sierra de San Cristóbal, Prov. Cádiz, with forms intermediate to *T. p. pisana* in other parts (GITTENBERGER AND RIPKEN, 1987: 41-42, 47; RUIZ *ET AL.*, 2006: 179). Our specimens of *T. p. arietina* were collected from herb-rich grassland on rocky (calcareous) slopes by a road, where they were plentiful. There were no obvious features of this habitat that differed from conditions at many sites overlying limestone in Portugal and Spain where *T. p. pisana* occurs. Specimens intermediate with *T. p. pisana* were from roadside banks, among low herbs and grasses or under rubbish.

Theba pisana almogravensis subsp. nov. (Figs. 1D-G, 3E-H, 4, 5A-F)

Holotype: MNCN reg. no. 15.05/60170, Shell breadth 10.8 mm, 26 Oct. 2014, Coll. G.A. & D.T. Holyoak site P411.

Paratypes: all in CGAH, 36 sh + bod from type locality, collected 26 Oct. 2014; 31sh + bod collected close to type locality on 26 Mar. 2014, at coast W. of Almograve, 29S 0517/4167, sand dunes on coastal slopes, 32 m alt., Coll. GAH & DTH site P370; 99 sh from Baixo Alentejo, just SE. of Praia de Morgavel, *ca* 4 km SE. of Porto de Sines, 29S 05177/41966, sand dunes, with patchy low bushes and some tall bushes, 34 m alt., 21 Mar. 2014, Coll. GAH & DTH site P361 (6 apparently hybrid shells from this material separated, not paratypes); 31 sh + bod from close to last locality at 29S 051740/419667, sand dunes on slope above coast, with patches of herbs and low shrubs, *ca* 25 m alt., 26 Oct. 2014, Coll. GAH & DTH site P412.

Other material that comprises only presumed hybrids (marked**, or includes them marked*) **intermediate with *T. p. pisana* (not paratypes; all in CGAH)**: *Baixo Alentejo, just SE. of Praia de Morgavel, *ca* 4 km SE. of Porto de Sines, 29S 051740/419667, edge of car park in dirty heavily trampled area bordering sand dunes on slope above coast, with patches of herbs and low shrubs, *ca* 20

(Right page) Figure 1. Shells of *Theba pisana* (Helicidae). A-C: *T. p. arietina*, topotypes, Spain, Prov. Cádiz, *ca* 2.5 km SW. of El Portal, 29 Dec. 2007, site 51; D-G: *T. p. almogravensis* subsp. nov., Portugal, D (holotype, MNCN) and E (paratype) from type-locality, Baixo Alentejo, just W. of Almograve, 26 Oct. 2014, site P411, F and G from Algarve, *ca* 0.5 km W. of Carrapateira, 7 Feb. 2011, site P123. See text for details of localities, etc.

(Página derecha) Figura 1. Conchas de Theba pisana *(Helicidae). A-C:* T. p. arietina, *topotipos, España, Prov. Cádiz, unos 2,5 km SO. de El Portal, 29 Dec. 2007, sitio 51; D-G:* T. p. almogravensis *subsp. nov., Portugal, D (holotipo, MNCN) y E (paratipo) de la localidad tipo, Baixo Alentejo, justo al O. de Almograve, 26 Oct. 2014, sitio P411, F y G del Algarve, unos 0,5 km O. de Carrapateira, 7 Feb. 2011, sitio P123. Véase el texto para detalles de localidades, etc.*

m alt., 26 Oct. 2014, Coll. GAH & DTH site P412, 49 sh + bod (mainly live-collected); *Baixo Alentejo, N. of Porto Covo, 29S 05177/41953, blown sand on shaly slope with patchy low scrub, *ca* 15 m alt., 21 Mar. 2014, Coll. GAH & DTH site P362, 18 sh; *N. of Porto Covo, 29S 051767/419559, low sand dunes with grasses and patchy herbs on slope between head of beach and car-parking at roadside, *ca* 12 m alt., 27 Oct. 2014, Coll. GAH & DTH site P413, 48 sh + bod (including pairs with mixed shell types collected *in copula* in early morning); **Baixo Alentejo, just W. of Vila Nova de Milfontes, 29S 0518/4174, sand dunes, 17 m alt., 26 Mar. 2014, Coll. GAH & DTH site P371, 41 sh; **Algarve, above Praia de Monte Clérigo (W. of Aljezur), 29S 051323/413289, blown sand with dune vegetation on open rocky (sandstone) slopes above beach and on sea-cliffs (mainly beneath *Carpobrotus edulis* forming large patches near garden), *ca* 52 m alt., 16 Apr. 2015, Coll. GAH & DTH site P420, 75 sh; *Algarve, NW. of Carrapateira (*ca* 1 km S. of Praia da Bordeira), 29S 050846/411637, sand dunes with natural vegetation on slopes S. of beach, 28 m alt., 15 Apr. 2015, Coll. GAH & DTH site P417, 148 sh; *Algarve, *ca* 0.5 km W. of Carrapateira, 29S 050845/411537, sand dunes with patchy vegetation of mainly low bushes, stony locally, 43 m alt., 7 Feb. 2011, Coll. GAH & DTH site P123, 61 sh (includes apparent hybrids; most shells with lower spire than topotypes: Fig. 1F, G); **Algarve, W. of Carrapateira (S. of Ponta do Arco do Pau), 29S 050804/411460, flat ground on top of limestone sea-cliffs, with blown sand at surface, patchy low scrub, 42 m alt., 15 Apr. 2015, Coll. DTH site P418, 48 sh; **Algarve, above Praia da Cordoama (NW. of Vila do Bispo), 29S 050568/410690, rocky (shaly) slopes of valley side on coast and small sand dunes, *ca* 14 m alt., 15 Apr. 2015, Coll. GAH & DTH site P416, 56 sh; **Algarve, above Praia do Castelejo (W. of Vila do Bispo), 29S 050495/410592, blown sand on slope above beach, with semi-natural dune vegetation, 27 m alt., 15 Apr. 2015, Coll. GAH & DTH site P415, 106 sh.

Type locality: Portugal, Baixo Alentejo, just W. of Almograve, 29S 051758/416737, sand dunes on open slope above coast, with patches of herbs, *ca* 34 m alt.

Etymology: The subspecies epiphet is an adjective based on the type locality near Almograve.

Description of shell: based on topotypes (sites P370 and P411) and paratypes from near Praia de Morgavel (P361 and P412), thus excluding apparent hybrids with *T. p. pisana*. Shape depressed-conical with ± flattened top to spire; rounded below; B 9.0-11.0 (mean 9.91, s.d. 0.651) mm; H 5.5-7.3 (mean 6.25, s.d. 0.560) mm; H/B 0.58-0.66 (mean 0.631, s.d. 0.023); n = 30. Whorls 3.7-4.2, with breadth increasing rather gradually; strongly convex above, with rounded-angular periphery (commonly forming blunt keel, but with raised peripheral cord absent or inconspicuous). Sutures deep to very deep. Last part of body whorl usually descending, widened near aperture. Aperture broadly oval, interrupted by penultimate whorl and with upper lip straighter than lower (outer lip lacking any keel or sinus). Peristome thin, plane except

(Right page) Figure 2. Shells of *Theba pisana* (Helicidae): A, B, D-G: Representative shells from populations intermediate between *T. p. pisana* and *T. p. almogravensis* subsp. nov., from Portugal, Algarve; C: Typical shell of *T. p. pisana*, from Portugal, Estremadura, between Setúbal and Outão, CGAH site 2007/12. A, B: from Monte Clérigo, Apr. 2015, site P420; D: from cliff top W. of Carrapateira, Apr. 2015, site P418; E: from sand dunes NW. of Carrapateira, Apr. 2015, site P417; F: from above Praia da Cordoama, Apr. 2015, site P416; G: from above Praia do Castelejo, Apr. 2015, site P415. See text for details of localities, etc., Table II for additional data on population characteristics.

(Página derecha) Figura 2. Conchas de Theba pisana *(Helicidae): A, B, D-G: Conchas representativas de poblaciones intermedias entre* T. p. pisana *y* T. p. almogravensis *subsp. nov., de Portugal, Algarve; C: Concha típica de* T. p. pisana, *de Portugal, Estremadura, entre Setúbal y Outão, CGAH sitio 2007/12. A, B: de Monte Clérigo, Abr. 2015, sitio P420; D del alto del acantilado, O. de Carrapateira, Abr. 2015, sitio P418; E: de dunas de arena NO. de Carrapateira, Abr. 2015, site P417; F; de arriba de Praia da Cordoama, Abr. 2015, sitio P416; G: de arriba de Praia do Castelejo, Abr. 2015, sitio P415. Véase el texto para detalles de localidades, etc. y Tabla II para datos adicionales sobre las características de las poblaciones.*
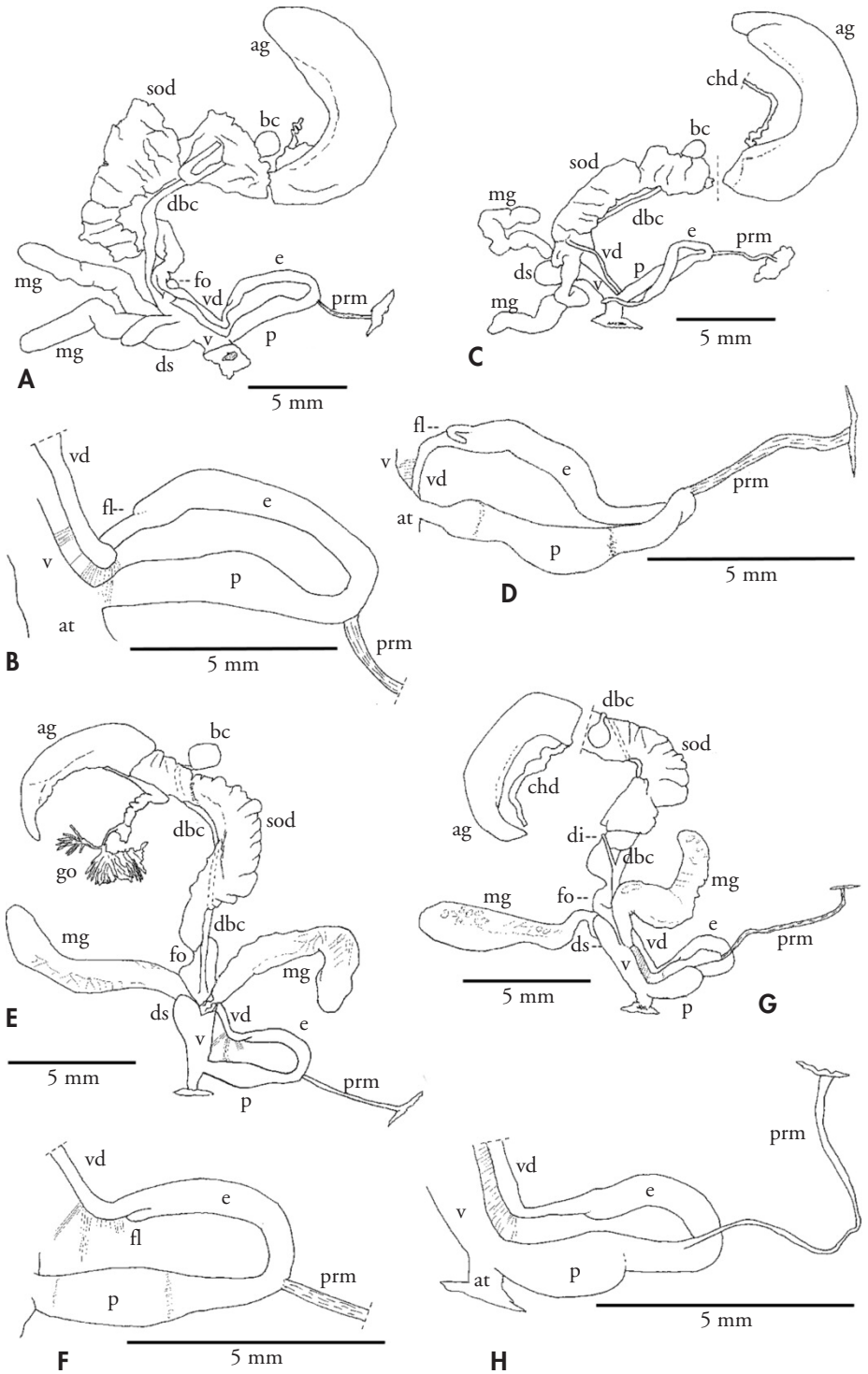
where reflected over and close to umbilicus. Aperture usually lacking thickened internal rib, with single thin rib close behind peristome in a few shells. Umbilicus small, narrow (U 0.6-1.1, mean 0.815, s.d. 0.158 mm; U/B 0.066-0.113, mean 0.082, s.d. 0.014; n = 30), exposing inside of body whorl and often also of most of spire, usually overlapped by peristome for less than one-half of its width. Shells rather thin and fragile, somewhat translucent. Fresh shells with glossy surface, especially below. Ground-colour pale buff or buff, less often whitish; a large majority marked with bands of deeper buff or light brown, with up to two such bands above periphery and two below it. As in *T. p. pisana*, each band often with one to several narrow dark brown spiral stripes, which may be interrupted or represented only as spots, in varied pattern combinations. Interior of aperture generally much like exterior in colour, although thickened rib whitish when present. Protoconch (whorl 0-1) smooth apically, with fine low radial riblets developing. Teleoconch with pattern of radial riblets intersecting spiral grooves, resulting in somewhat irregular low radially elongated papillae of variable shapes. Underside of shell with weaker sculpture.

External coloration of body: (based on samples from sites P411 and P412 and live animals): Generally very pale, mainly whitish; exposed body mainly white, somewhat translucent, with only eyes and ommatophore retractor muscles blackish (visible through translucent skin); front of head above mouth grey in some snails; exterior of mantle-collar grey, sometimes light grey, occasionally white except for narrow grey area around outer edge; interior edge of mantle-collar with yellowish to light brown band of variable extent, sometimes faint; mantle inside body-whorl usually white, with weak greyish marks on a few snails; spire white or whitish, with intestine often dull grey or blackish; digestive gland light brown to brown.

Genital anatomy: Two studied in detail (Fig. 3E-H) and several incomplete dissections reveal a close general similarity to the anatomy of *T. p. pisana* and *T. p. arietina*: penial flagellum very short and appressed to proximal end of epiphallus (hardly discernible in one specimen); mucus glands wide and very long (about twice length of penis plus epiphallus); vagina and free oviduct roughly similar in length; diverticulum on bursa copulatrix duct arising proxi-

(Right page) Figure 3. Genital anatomy of *Theba* (Helicidae). A-D: *T. p. arietina*, topotypes from Spain, Prov. Cádiz, *ca* 2.5 km SW. of El Portal, CGAH site 51; E-H: *T. p. almogravensis* subsp. nov., paratypes from type-locality, Portugal, Baixo Alentejo, just W. of Almograve, CGAH site P411; A, C, E and G show all or almost all of the genitalia from four different specimens; B, D, F and H show the penis-complex in greater detail for the same specimens. Abbreviations: ag: albumen gland; at: genital atrium; bc: bursa copulatrix; chd: common hermaphrodite duct; dbc: duct of bursa copulatrix; di: diverticulum on duct of bursa; ds: dart sac; e: epiphallus; fl: flagellum; fo: free oviduct; go: gonad; mg: mucus gland; p: penis; prm: penis retractor muscle (inserted on epiphallus); sod: spermoviduct; v: vagina; vd: vas deferens. See text for details of localities, etc.

(Página derecha) Figura 3. Anatomía genital de Theba *(Helicidae). A-D:* T. p. arietina, *topotipos de España, Prov. Cádiz, unos 2,5 km SO. de El Portal, CGAH sitio 51; E-H:* T. p. almogravensis *subsp. nov., paratipos de la localidad tipo, Portugal, Baixo Alentejo, justo al O. de Almograve, 26 Oct. 2014, sitio P411; A, C, E y G muestran la totalidad o casi-totalidad de los genitalia de cuatro ejemplares diferentes; B, D, F y H muestran el complejo penial con más detalle en los mismos ejemplares. Abreviaciones: ag: glándula del albúmen; at: átrio genital; bc: bursa copulatrix; chd: conducto hermafrodito compartido; dbc: conducto de la bursa copulatrix; di: divertículo en el conducto de la bursa; ds: saco del dardo; e: epifalo; fl: flagelo; fo: oviducto libre; go: gónada; mg: glándula mucosa; p: pene; prm: músculo retractor del pene (insertado en el epifalo); sod: espermoviducto; v: vagina; vd: vas deferens. Véase el texto para detalles de localidades.*
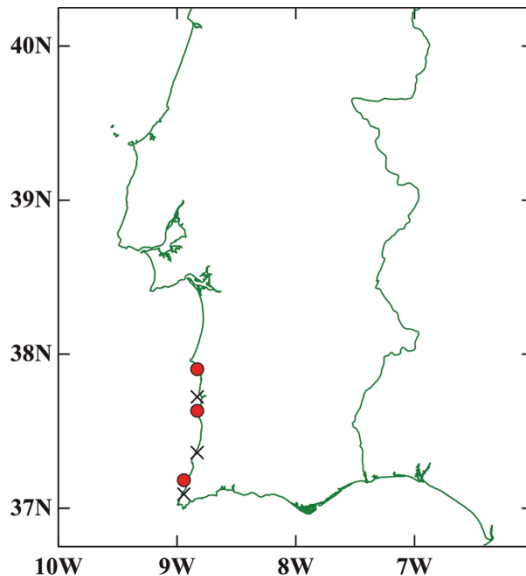
Figure 4. Map of distribution of *Theba pisana almogravensis* subsp. nov. and of forms intermediate with *T. p. pisana* in southern Portugal represented in 10-kilometre squares of the U.T.M. grid: ● authors' records of extensive well characterised populations, 2011-2015; × authors' records of populations intermediate between *T. p. almogravensis* and *T. p. pisana*, 2011-2015.
Figura 4. Mapa de distribución de Theba pisana almogravensis *subsp. nov. y de formas intermedias con* T. p. pisana *en el sur de Portugal representato sobre cuadrículas UTM de 10 kilómetros: ● registros de los autores de poblaciones extensas y bien caracterizadas, 2011-2015; × registros de los autores de poblaciones intermedias entre* T. p. almogravensis *y* T. p. pisana, *2011-2015.*

mal to a rather short stalk; "free" bursa duct long, so bursa copulatrix reservoir when *in situ* was beside proximal end of spermoviduct (close to distal end of albumen gland). The vaginal mucus glands were extraordinarily large with a pattern of elongate internal cavities partly visible by translucence; SCHI-LEYKO (2006: 1785) mentions that in *T. p. pisana* they "look like alveolar in structure". They were proportionately larger than in *T. p. arietina*, but more study would be necessary to check whether this is a consistent difference or due to the stage in the breeding cycle.

Comparative diagnosis: The very short penial flagellum in *T. p. almogravensis* is significant in confirming that this taxon resembles *T. pisana* anatomically rather than *T. subdentata helicella* (Wood, 1828). The latter is known from W. Morocco and from sand dunes in SE. Spain (Prov.

Almería) and typically has a keeled shell, but its flagellum is longer than the penis and epiphallus combined (MORE-NO & RAMOS, 2007: 98, 100).

T. p. almogravensis differs from *T. p. arietina* in: smaller shell size (B 9-11 mm, cf. (13)16-22 mm); spire almost always with deep sutures, giving pronounced scalariform appearance, whereas only a few shells of *T. p. arietina* appear scalariform; peripheral keel weaker, blunter and lacking prominent spiral cord; keel not reaching shell aperture, so no sinus in outer peristome; proportionately larger umbilicus (U/B 6.6-11.3%, cf. 3.9-7.1%); much higher frequency of bands and other dark markings on shell; much paler body coloration (mainly white); habitat on coastal sand dunes not open calcareous slopes inland.

It is only among those Portuguese samples from locations with direct or in-

Table I. Distribution of *Theba pisana almogravensis* and of specimens intermediate with *T. p. pisana* in relation to extent of sand-dune habitats in SW. Portugal.
Tabla I. Distribución de Theba pisana almogravensis *y de ejemplares intermedios con* T. p. pisana, *en relación con la extensión de hábitats de dunas de arena en el suroeste de Portugal.*

Locality (listed from N. to S.)	Minimum total area of sand dune vegetation (km²) (1)	Largest patch of dune vegetation (km²) (2)	Typical *T. p. almogravensis* (3)	Intermediate with *T. p. pisana*
Praia de Morgavel southwards	2.6	0.58	abundant	present locally at edges
Vila Nova de Milfontes	0.25		-	plentiful
W. of Almograve (& southwards)	4.8	2.73	abundant	present locally at edges
Monte Clérigo	0.3		-	present locally
W. and NW. of Carrapateira	2.5	1.5	abundant	present locally
above Praia da Cordoama	0.1		-	plentiful
above Praia do Castelejo	0.2		-	plentiful

(1) Areas were estimated from Google Earth imagery dated October 2013. Sand dune vegetation was defined as partly open terrestrial vegetation on blown sands, with the sandy substratum visible in many places, the vegetation comprised of herbs, grasses, subshrubs or bushes < 2 m tall.
(2) as (1), but the largest contiguous patch of vegetation.
(3) - absent.

Association of presence of typical *T. p. almogravensis* with larger areas of sand-dune vegetation, likely but not statistically significant: χ^2 (applying Yates's Correction) = 3.512, with 1 d.f.; p <0.10, >0.05.

ferential evidence of introgression with *T. p. pisana* that larger shells showing more characters resembling those of *T. p. arietina* are apparent. Among such samples, we can match the shells figured as Portuguese "*T. p. arietina*" from Monte Clérigo by DE OLIVEIRA (2008: 35 figs 1-4) and by MATOS (2014: 221, fig. 181) (our Fig. 2A, B). Nevertheless, even those "exemplars" are an inexact match for Spanish topotypes of *T. p. arietina*, lacking its usually flatter shell (with height lower relative to breadth), the shell aperture descending less, the keel not reaching the aperture and not forming an obvious sinus in the outer lip, and especially, lacking the much more prominent raised cord-like rib at the periphery of the body whorl (cf. ROSSMÄSSLER, 1854: pl. 66 fig. 825; GITTENBERGER & RIPKEN, 1987: figs 33, 34; RUIZ *ET AL.*, 2006: 179). Living snails from Monte Clérigo photographed by Rui Mendes (*in litt*.) in December 2011 also showed the predominantly whitish body coloration of *T. p. almogravensis*, not the dark body of *T. p. ari-*

etina (body coloration in Portuguese *T. p. pisana* varies from dark to light in different populations).

Range and ecology: SW. Portugal, on western coasts of Algarve and Baixo Alentejo (Fig. 4). Large populations of *T. p. almogravensis* showing little variation in shell characters are apparently restricted to three extensive areas of sand dunes (Table I), two in Baixo Alentejo (centred on areas SE. of Praia de Morgavel, 29S 051/419 and W. of Almograve, 29S 051/416) and one in the Algarve (centred W. of Carrapateira, 29S 050/411), although shells from the last locality mainly have a lower spire. This range extends over a total distance of *ca* 82 km from north to south, but has wide gaps in areas where there are no dunes.

This entire stretch of coast has a wide coastal and submarine plain, extending *ca* 100 km from Sines to Cabo de São Vicente, with the 100 m submarine contour consistently at least 5 km offshore and the 20 m submarine contour remaining at least 1 km offshore

(Carta Militar de Portugal, 1:250 000, Continente, Folha No. 7, Lagos, Série M586, Edição 5, I.G.E. 2008). It is generally accepted that eustatic sea-levels rose >90 m from the Last Glacial Maximum (LGM; *ca* 21,000 years B.P.) to attain modern levels around the mid-Holocene (*ca* 5000 years B.P.) (e.g. PELTIER, 2002). There may be some uncertainty regarding differences of sea-level history from the prevailing global pattern in south-western Portugal which might result from neo-tectonics affecting local land levels (e.g. PEREIRA, 2005). However, ALLEN & FLETCHER (2010) summarise detailed studies that revealed thicknesses of 15 m of Holocene estuarine sedimentation from the Arade and Boina rivers and 40 m from the Guadiana, implying the regional post-LGM rise was at least as large as its eustatic contribution. Lower sea-levels of the latest Pleistocene and early Holocene could therefore have provided more continuous sandy terrestrial habitats along this coast, at least intermittently, prior to sea-level rising to reoccupy the older cliffed coastline. It is reasonable to speculate therefore that range limits of *Theba* here may be of some antiquity, with the modern isolated populations relict from a more continuous former distribution.

The presence of populations intermediate between *T. p. almogravensis* and *T. p. pisana* at other smaller sand dune areas in this region (Fig. 4, Table I) is discussed in the following section of this paper.

Well characterised forms of *T. p. almogravensis* were found by us only on dunes of calcareous sand on open slopes near the coast (Fig. 5), especially in areas with patchy low vegetation of native subshrubs and perennial herbs. It was abundant on 26th October 2014 W. of Almograve, resting during the day above the ground on low plants, especially *Artemisia campestris* L. subsp. *maritima* Arcang. and the introduced *Carpobrotus edulis* (L.) N.E. Br. The *Theba* were commonly found resting in clusters of 10-15 individuals, although some large plants had hundreds of individuals, occurring in several clusters in addition to small groups and single snails. *Cochlicella conoidea* (Draparnaud) were resting with them on the same plants, but occurring singly and in generally lower numbers. The only other snails present nearby were a few *Cornu aspersum* (O.F. Müller) and shells of *Rumina decollata* (Linnaeus). Also on 26th Oct. 2014, just SE. of Praia de Morgavel, *T. p. almogravensis* was similarly abundant, resting 5-20 (-60) cm above the ground in clusters typically of 5-15 snails together on most kinds of vegetation that were present, but they were especially numerous on *Carpobrotus edulis* and *Ononis ramosissima* Desf., with fewer aggregations on *Armeria pungens* (Link) Hoffmanns. & Link, grasses and old dead plants. *Cochlicella conoidea* and *C. acuta* (O.F. Müller) were living there in smaller numbers, along with a few *Cornu aspersum* and rare *Otala lactea* (O.F. Müller). No *T. p. pisana* were present in the semi-natural vegetation, but they occurred *ca* 150 m away at the edge of a large car park, in dirty, heavily trampled areas with rubbish lying and patches of bushes, along with *T. p. almogravensis* and apparent hybrids. The associated snails there were similar, except that *Otala lactea* and *Cornu aspersum* were much more plentiful.

HYBRIDIZATION AND POSSIBLE THREATS FROM GENETIC INTROGRESSION

A molecular phylogenetic study of *Theba* by GREVE, HUTTERER, GROH, HAASE & MISOF (2010) included almost all known taxa of the genus, except unfortunately *T. p. arietina* and Portuguese keeled specimens. However, their results are relevant here because they found that different named populations with keeled shells varied widely in the amount of differentiation from globular-

Figure 5. Habitats and living animals of *Theba pisana almogravensis* subsp. nov. in Baixo Alentejo, SW. Portugal, 26-27 Oct. 2014. A-C: at type-locality, just W. of Almograve (site P411); D, F: just SE. of Praia de Morgavel (site P412); E: N. of Porto Covo (site P413). A and D show semi-natural sand dune vegetation, although A has invading *Carpobrotus edulis*; E shows disturbed habitat at edge of roadside parking, where hybrid *Theba* recorded. B, C and F show typical aggregations of *T. p. almogravensis* resting on plants (B on *Artemisia campestris* subsp. *maritima*; C on *Carpobrotus edulis*; F on *Armeria pungens*).

Figure 5. Habitats y animales vivos de Theba pisana almogravensis *subsp. nov. en el Baixo Alentejo, SO. de Portugal, 26-27 Oct. 2014. A-C: en la localidad tipo, justo al O. de Almograve (sitio P411); D, F: justo al SE. de Praia de Morgavel (sitio P412); E: N. de Porto Covo (sitio P413). A y D muestran vegetación semi-natural de dunas de arena, aunque A tiene la invasora* Carpobrotus edulis*; E muestra un hábitat perturbado bordeando un aparcamiento al lado de la carretera, en donde se registraron* Theba *híbridos. B, C y F muestran agregaciones típicas de* T. p. almogravensis *sobre plantas (B sobre* Artemisia campestris *subsp.* maritima*; C sobre* Carpobrotus edulis*; F sobre* Armeria pungens*).*

shelled conspecifics in the mitochondrial COI marker. Thus the keeled *T. p. cantinensis* (Sacchi, 1955) from W. Morocco formed a clade sister to several taxa lacking keels (*T. andalusica* Gittenberger & Ripken, 1987 – a local endemic in the Spanish Provinces Cádiz and Sevilla –, *T. p. ampullacea* (Pallary, 1915) from W. Morocco and *T. p.* subsp. from NW. Morocco, and the widespread *T. p. pisana*), whereas the three subspecies of *T. subdentata* studied were placed in only two clades, among which the keeled *T. s. helicella* were not distinguished from the two subspecies with globular shell shapes. *T. p. cantinensis* thus appears to be phylogenetically distinct from the COI data; nevertheless, GITTENBERGER AND RIPKEN (1987: 43) noted that "Apparently *T. p. cantinensis* is connected with *T. p. pisana* by a broad zone of intermediate forms", for which details are provided by the latter authors. These possible discrepancies between molecular and conchological data revealed by GREVE ET AL. (2010) were not adequately resolved. Hence, taxonomic changes seem unwarranted because mitochondrial markers such as COI are known to show extreme intraspecific divergence among pulmonates, including Helicidae (cf. THOMAZ, GUILLER AND CLARKE, 1996; DAVISON, 2002; PINCEEL, JORDAENS AND BACKELJAU, 2005). GREVE ET AL. (2010: 577 table 4) found much more differentiation in COI than in the nuclear ITS1 marker within *T. pisana*, so the latter provided little information on phylogeny. Additional information is therefore needed to test whether phylogeny of the whole organisms was congruent with evolution of the COI part of their mitochondrial genome.

At any event, a future molecular phylogenetic study involving *T. p. arietina* and various different populations of *T. p. almogravensis* is desirable to increase the amount of information available to interpret their affinities. In relation to those, the taxonomic status of the weakly keeled *"Theba gittenbergeri"* might also be clarified by molecular studies: In the unpublished doctoral thesis by PUENTE (1994: 847-854, Lamina CXCII) it was described in detail and figured as a new species from a single locality in Almería province; RUIZ ET AL. (2006: 176-177) gave a brief description and a clear figure, but did not validate the name.

Populations of *Theba* with shells intermediate between *T. p. almogravensis* and *T. p. pisana* occur at most if not all of the smaller sand dune areas from Praia de São Torpes (SE. of Sines, Baixo Alentejo) southwards to Praia do Castelejo (W. of Vila do Bispo, Algarve) and on various sandy habitats with vegetation transitional to that of dunes, such as on blown sand deposits on slopes of siliceous and calcareous sea-cliffs and slopes (for details see Tables I and II, Figs 2 and 4, and list of localities given above). In principle, these intermediate populations might indicate that *T. p. almogravensis* had a more extensive range in the past, which has been reduced by hybridization (i.e. by introgression following secondary contact of ranges), or merely that those populations have never diverged fully in shell characters (i.e. primary divergence has not yet led to full development of the subspecific characters).

Hybridization between *T. p. pisana* and *T. p. almogravensis* seems almost certain to occur because mixed pairs have been collected while they were mating. Thus, at our site P413 (Beira Baixa, N. of Porto Covo, 29S 051767/419559) on 27th October 2014, pairs with mixed shell types were collected *in copula* in the early morning at 08:30-09:00 hours. These were from low sand dunes with grasses and patchy herbs on a disturbed slope between the head of a beach and car-parking at the roadside (Fig. 5E). The vegetation here was trampled, with patches of the alien *Carpobrotus edulis* among native plants as well as litter discarded by tourists. Typical snails of both *T. p. pisana* and *T. p. almogravensis* were present and mating on low vegetation wet from dew, along with mixed pairs. Associated snails were *Cochlicella acuta, C. conoidea, Cornu aspersum* and *Otala lactea,* all of which were plentiful.

Table II. Shell characters of populations intermediate between *Theba pisana almogravensis* and *T. p. pisana* at different localities with sand-dune habitats in SW. Portugal. All samples differ from typical Portuguese *T. p. pisana* in having the spire ± depressed and the umbilicus partly open (± overlapped by reflected edge of peristome). Characters of small minority of shells are listed in square brackets [ ].

Tabla II. Caracteres de la concha en poblaciones intermedias entre Theba pisana almogravensis *y* T. p. pisana *en distinctas localidades con hábitats de dunas de arena en el SO. de Portugal. Todas las muestras difieren de* T. p. pisana *típica de Portugal por tener la espira ± deprimida y el ombligo parcialmente abierto (± solapado por la parte reflexionada del peristoma). Caracteres de una minoría pequeña de conchas están listados detre corchetes [ ].*

Locality (sample number; sample size)	Shell breadth (mm)*	Keel**	suture depth	unbanded %†	% pink on peristome††	Figures
Vila Nova de Milfontes (P371; 20)	11-15	nil [slight]	moderate	55%	25%	-
Monte Clérigo (P420; 75)	13-18	sharp	shallow	95%	0%	2A, B
NW. of Carrapateira (P417; 148)	10-14	± blunt	deep	33%	0%	2E
W. of Carrapateira (P418; 48)	13-17	nil [slight]	moderate	0%	8%	2D
above Praia da Cordoama (P416; 56)	12-17	± sharp to slight	shallow [moderate]	9%	14%	2F
above Praia do Castelejo (P415; 106)	11-15	sharp	shallow	23%	0%	2G

*Measurements based on adult or near adult shells, avoiding obviously immature shells with thin peristome.

**Assessed at start of body whorl.

†The percentages are for shells with no trace of bands above or beneath; a single faint or interrupted band would exclude a shell from this category.

††Percentages are minimal because the pink coloration soon fades on old shells and it does not develop on some subadults until the peristome margin thickens.

The shell characters of the intermediate populations (Fig. 2) can be matched very closely among those of some of the obvious hybrids from the variable "hybrid swarms" occurring locally at margins of large populations (such as that at site P413), where *T. p. almogravensis* and *T. p. pisana* undoubtedly meet and mate. Thus, hybridization following secondary contact could account for the intermediate populations, assuming recombination and perhaps selection have led to reduced ranges of variability in their offspring. Nevertheless, other explanations for the origin of the intermediate populations remain possible and untested, including the possibility that the different shell forms arose parapatrically (cf. ENDLER, 1977). It is also uncertain whether they are now stable populations, e.g. maintained in a balanced equilibrium by the combination of strong selection pressure for shell shape and very limited mobility of the snails, or whether they are still evolving towards one or other parental shell type.

Each of the intermediate populations associated with small dune areas or transitional habitat (Table I) differs

somewhat from the others, by combinations of shell breadth, development of a peripheral keel, depth of suture on the spire and the frequencies of dark banding and of pink coloration on the peristome (Fig. 2, Table II). It would certainly be possible to correctly define up to six additional subspecies among them, e.g. using the widely adopted "75% Rule" (MAYR, 1969: 190), but there seems little purpose in doing this as each population appears to display a stable or partly stable array of phenotypes that most likely arose following past hybridization events. Nonetheless, future molecular studies are desirable, to seek direct evidence of the ancestry of each of the six populations. More fieldwork is also likely to reveal more of these definable populations with very small ranges. The Monte Clérigo population is one of the most distinctive among them (Fig. 2A, B), with comparatively large shells, low spire, sharp keel and an unusually low proportion of banded or striped shells (only 4 of 75 shells banded, none with distinct stripes). However, all of these characters are intermediate between those of typical *T. p. pisana* and *T. p. almogravensis*, except that the low frequency of banding occurs in only a minority of Portuguese populations of *T. p. pisana*.

If it can be assumed that intermediate shell types are (often) of hybrid origin, then both of the keeled subspecies of *T. pisana* discussed in this paper appear to hybridize regularly with the round-shelled *T. p. pisana* when their ranges meet. *T. p. pisana* is very common and widespread along roadsides and in other open, disturbed habitats over much of central and southern Portugal and southern Spain. Its use as human food certainly dates back to the Roman occupation of Portugal; it was traditionally, and still is, collected for human food over much of the region. A recent estimate is that the people of Portugal consume about 4000 tonnes of snails annually (*Wikipedia*), much of which may consist of *T. pisana*. Annual "Festa do Caracol" (snail festivals) are held in some rural towns, those at Cernache do

Bonjardim and Sertã (Castelo Branco District) featuring mainly *T. pisana*. This species and several larger species of Helicidae have undoubtedly been widely disseminated by local people to maximise the free food resource. Furthermore, some of the massive consumption of snails in both Spain and Portugal is based on imports of living *Theba* from Morocco, so more widespread mixing of widespread populations has also become possible. SACCHI (1957: 81) stressed that *T. p. pisana* is a very recent immigrant in most of its range around the Mediterranean and along the Atlantic coasts of western Europe and there can be little doubt that deliberate human introductions have contributed to its colonisation. Because it habitually seeks resting places above the ground the species often attaches itself to vehicles, and it is also prone to being carried with horticultural plants, so the opportunities for further spread are probably now greater than they may have been historically. Whether deliberate or accidental, human introductions have allowed it to colonise the U.S.A. (California), Bermuda, S. Africa and Australia, where it has sometimes become a pest.

As noted above, well characterised populations of abundant *T. p. almogravensis* were recorded in the absence of *T. p. pisana* from semi-natural vegetation on dunes near Almograve (Fig. 5A) and Praia de Morgavel (Fig. 5D), the only alien plant present in quantity at those sites being *Carpobotus edulis*. However, areas with much anthropogenic disturbance (trampling, deposition of rubbish, eutrophication resulting from use of scrub patches as toilets near busy public beaches) at the dune edges at Praia de Morgavel (and nearby at Porto Covo: Fig. 5E) also had *T. p. pisana* and apparent hybrids. The *Theba* found by us at several sand dune areas further south (e.g. near Vila Nova de Milfontes) and in sandy habitats on slopes above sea-cliffs (e.g. at Monte Clérigo and above Praia do Castelejo) were all intermediate between *T. p. pisana* and *T. p. almogravensis*, even in areas of semi-natural vegetation, the populations

having shell forms closer to *T. p. pisana* than to *T. p. almogravensis*. However, most of two large samples from semi-natural vegetation on dunes in between the last two localities mentioned, near Carrapateira, were assigned to *T. p. almogravensis* (although the spire was lower than in topotypes and some apparent hybrids were found).

T. p. arietina in its most distinctive form has a very small range, while shells intermediate to those of *T. p. pisana* occur over a larger area surrounding this range (GITTENBERGER AND RIPKEN, 1987: 41-42). SACCHI (1957: 81) and RUIZ ET AL. (2006: 178) speculated that occurrence of inter-mediate shells over a larger area than that occupied by "the most characteristic population" may give evidence that subsp. *arietina* had a wider range in the past. Nevertheless, there is no direct evi-dence to confirm this, or indeed to confirm that a secondary contact of former isolates is involved.

Widespread occurrence of intermedi-ate shell types around the ranges of both *T. p. almogravensis* and *T. p. arietina* has been taken as evidence of hybridization with *T. p. pisana*, leading to the assump-tion that *T. p. pisana* may be gradually replacing the localised keeled forms (e.g. by SACCHI, 1957: 81; RUIZ, ET AL., 2006: 179; DE OLIVEIRA, 2008: 33). As noted above, we have found mixed pairs mating at one locality where *T. p. almo-gravensis*, *T. p. pisana* and intermediates were all living together, so it can hardly be doubted that hybrids occur. Our evi-dence that well characterised *T. p. almo-gravensis* alone occupies some areas of semi-natural dune vegetation, whereas *T. p. pisana* and hybrids occur only in the marginal, anthropogenically disturbed areas bordering them might therefore imply vulnerability of *T. p. almogravensis*

if further loss of natural vegetation occurs. We also argue above that stable populations of hybrid origin may have replaced typical *T. p. almogravensis* in several areas where the sand-dune vege-tation is of small extent (up to 0.3 km^2). Nevertheless, it may be incorrect to infer that the future survival of either *T. p. almogravensis* or *T. p. arietina* as a geneti-cally and morphologically distinct taxon may be threatened by introgression from *T. p. pisana*, provided that the habitat types in which they evolved persist. For-tunately, many of the sand dune areas occupied by *T. p. almogravensis* are pro-tected as parts of the Parque Natural do Sudoeste Alentejano e Costa Vicentina, although habitat changes such as the seemingly inexorable spread of the alien *Carpobrotus edulis* are difficult to prevent even on land that should be managed for conservation purposes.

In discussing *T. p. arietina*, GITTEN-BERGER AND RIPKEN (1987: 42) pointed out that "If the zone between the two subspecies is (slowly) moving in a certain direction, this process could be demonstrated after some time only by locating this zone as exactly as possible now and later on." This remains true with both subspecies, so that future work should consider monitoring the location of the snail populations and possible habitat changes, over a suffi-cient time interval to establish whether changes are occurring.

ACKNOWLEDGEMENTS

BIBLIOGRAPHY

ALLEN H. & FLETCHER W. (2010). Holocene en-vironmental change in southern Portugal. http://www.geog.cam.ac.uk/research/pro-jects/holocenechangeportugal/ (accessed 30 October 2010).

AVIVI T. & ARAD Z. 1993. Population dynam-ics of the snail *Theba pisana* in the sand dunes of northern Israel. *Israel Journal of Zoology*, 39: 245-254.

BANK R.A., BOUCHET P., FALKNER G., GITTEN-BERGER E., HAUSDORF B., VON PROSCHWITZ T. & RIPKEN T.E.J. 2001. Supraspecific classification of European non-marine Mollusca (CLECOM Sections I + II). *Heldia*, München, 4 (1/2): 77-128.

BANK R.A. & DEKKER H. 1989. On *Theba pisana arietina* (Rossmässler, 1846), a land snail new for Portugal (Gastropoda Pulmonata: Helicidae). *Basteria*, 53 (1-3): 28.

CAIN A.J. 1984. Genetics of some morphs in the land snail *Theba pisana*. *Malacologia*, 25 (2): 381-411.

COWIE R.H. 1980. Precocious breeding of *Theba pisana* (Müller) (Pulmonata: Helicidae). *Journal of Conchology*, 30 (4): 238.

COWIE R.H. 1984. Ecogenetics of *Theba pisana* (Pulmonata: Helicidae) at the northern edge of its range. *Malacologia*, 25 (2): 361-380.

DAVISON A. 2002. Land snails as a model to understand the role of history and selection in the origins of biodiversity. *Population Ecology*, 44: 129-136.

ENDLER J.A. 1977. *Geographic variation, speciation, and clines*. Princeton University Press (Monographs in Population Biology 10), Princeton, New Jersey, ix + 246 pp.

FALKNER G., BANK R.A. & VON PROSCHWITZ T. 2001. Check-list of the non-marine molluscan species-group taxa of the states of northern, Atlantic and central Europe (CLECOM I). *Heldia*, München, 4: 1-76.

GITTENBERGER E. & RIPKEN T.E.J. 1987. The genus *Theba* (Mollusca: Gastropoda: Helicidae), systematics and distribution. *Zoologische Verhandelingen*, Leiden, 241: 1-59.

GITTENBERGER E., RIPKEN T.E.J. & BUENO M.L. 1992. The forgotten *Theba* species (Gastropoda, Pulmonata, Helicidae). In Gittenberger, E. & Goud, J. (Eds.): *Proceedings of the Ninth International Malacological Congress, Edinburgh, 1986.* Unitas Malacologica, Leiden, pp. 145-151.

GIUSTI F. & ANDREINI S. 1988. Morphological and ethological aspects of mating in two species of the family Helicidae (Gastropoda Pulmonata): *Theba pisana* (Müller) and *Helix aperta* Born. *Monitore Zoologico Italiano*, (N.S.) 22: 331- 363.

GRAY J.E. 1847. A list of the genera of recent mollusca, their synonyms and types. *Proceedings of the Zoological Society of London*, 15: 129-219.

GREVE C., HUTTERER R., GROH K., HAASE M. & MISOF B. 2010. Evolutionary diversification of the genus *Theba* (Gastropoda: Helicidae) in space and time: a land snail conquering islands and continents. *Molecular Phylogenetics and Evolution*, 57: 572-584.

HAUSDORF B. & BOUCHET P. 2005. Pulmonata, pp. 263-270. In Bouchet P. and Rocroi J.P. (Eds): Classification and nomenclature of gastropod families. *Malacologia*, 47 (1-2): 1-397.

HELLER J. 1981. Visual versus climatic selection of shell banding in the land snail *Theba pisana* in Israel. *Journal of Zoology*, 194 (1): 85-101.

HELLER J. 1982. Natural history of *Theba pisana* in Israel. *Journal of Zoology*, 196: 475-487.

HELLER J. 2009. *Land snails of the land of Israel. Natural history and a field guide.* Pensoft, Sofia & Moscow, 360 pp.

HESSE P. 1915. *Iconographie der Land- & Süsswasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten*. C.W. Kreidel's Verlag, Wiesbaden, Neue Folge, Band 23, Heft 1-2, pp. 1-72, pls 631-640.

KERNEY M.P. & CAMERON R.A.D. 1979. *Land snails of Britain and north-west Europe*. Collins (Collins Field Guide), London, 288 pp., 24 pls.

MATOS R.M. ALBUQUERQUE DE, 2014. *Atlas dos Caracóis terrestres e de águas doces e salobras Portugal continental.* Published by the author, Portugal, iv + 258 pp.

MAYR E. 1969. *Principles of systematic zoology*. Tata McGraw-Hill Publishing Co. Reprint, New Delhi, xi + 428 pp.

MORENO D. & RAMOS M.A. 2007. New data on *Theba subdentata helicella* (Wood, 1828) (Gastropoda, Helicidae) in Almería (SE Spain). *Iberus*, 25 (1): 89-113.

MÜLLER O.F. 1774. *Vermivm terrestrium et fluviatilium, seu animalium infusoriorum, Helminthicorum et Testaceorum, non marinorum, succincta historia*. 2. Heineck & Faber, Havniae & Lipsiae, xxxvi + 214 [10] pp.

OLIVEIRA Á. DE 2008. *Theba pisana arietina* (Rossmässler, 1846) (Pulmonata, Helicidae) nas províncias de Baixo Alentejo e Algarves. Materiais para o estudo da malacofauna não-marinha de Portugal. 3. *Noticiario S.E.M.*, 50: 31- 35 (& correction, *ibid.*, 51: 48, 2009).

PELTIER W.R. 2002. On eustatic sea level history: Last Glacial Maximum to Holocene. *Quaternary Science Reviews*, 21 (1-3): 377-396.

PEREIRA A.R. 2005. Sea level changes and neotectonics: some examples in Portugal (Arrábida and Southwest). In: Seminário, Porto, 19 Setembro 2005, *Mudanças globais, variações do nível do mar e dinâmica costeira*, pp. 47-55. http://www.web.letras.up.pt/asaraujo/Trabalhos/Sea%20level%20changes.pdf (accessed 10 October 2015).

PINCEEL J., JORDAENS K. & BACKELJAU T. 2005. Extreme mtDNA divergences in a terrestrial slug (Gastropoda, Pulmonata, Arionidae): accelerated evolution, allopatric divergence, and secondary contact. *Journal of Evolutionary Biology*, 18: 1264-1280.

Puente A.I. 1994. *Estudio taxonómico y biogeográfico de la Superfamilia Helicoidea Rafinesque, 1815 (Gastropoda: Pulmonata: Stylommatophora) de la Península Ibérica e Islas Baleares*. Unpublished Doctoral Thesis, Universidad del País Vasco, Facultad de Ciencias, Departamento de Biología Animal y Genética.

Razkin O., Gómez-Moliner B.J., Prieto C.E., Martínez-Ortí A., Arrébola J.R., Muñoz B., Chueca L.J. & Madeira M.J. 2015. Molecular phylogeny of the western Palaearctic Helicoidea (Gastropoda, Stylommatophora). *Molecular Phylogenetics and Evolution*, 83: 99-117.

Risso A. 1826. *Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes*. 4. Levrault, Paris, vii + 439 pp., 12 pls.

Rossmässler E.A. 1846. Diagnosen einiger neuen Binnen-Mollusken. *Zeitschrift für-Malakozoologie*, 3: 172-173.

Rossmässler E.A. 1854. *Iconographie der Land- und Süsswasser-Mollusken Europa's, mit vorzüglicher Berücksichtigung kritischer und noch nicht abgebildeten Arten.* Hermann Constenoble, Leipzig, Band 3, Heft 1-2 [13-14], viii, 139 pp., pls 61-70.

Ruiz A., Cárcaba Á., Porras A.I. & Arrébola J.R. 2006. *Guía y manual de identificación. Caracoles Terrestres de Andalucía.* Consejería de Medio Ambiente, Junta de Andalucía & Fundación Gypaetus, Sevilla, 303 pp.

Sacchi C.F. 1956. Ricerche su *Euparypha arietina* (Rossmaessler). I. –Posizione sistematica. *Annuario R. Museo Zoologico della R. Università di Napoli*, 8 (8): 1-6.

Sacchi C.F. 1957. Une bonne race géographique d'*Euparypha pisana* (Müll.) (Helicidae) dans la région de Cadix. *Publicaciones del Instituto de Biologia Aplicada*, Barcelona, 26: 77-84.

Schileyko A.A. 2006. Treatise on recent terrestrial pulmonate molluscs. Part 13. Helicidae, Pleurodontidae, Polygyridae, Ammonitellidae, Oreohelicidae, Thysanophoridae. *Ruthenica*, Suppl., Moscow 2: 1764-1906.

Thomaz J.L., Guiller A. & Clarke B. 1996. Extreme divergence of mitochondrial DNA within species of pulmonate land snails. *Proceedings of the Royal Society of London*, B 263: 363-368.