THREE SPECIES OF *THEBA* (GASTROPODA: HELICIDAE) FROM A PLEISTOCENE DUNE IN SW MOROCCO

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Abstract *Marine and terrestrial molluscs are recorded from a coastal dune deposit in SW Morocco. The geological setting and the faunal content of the site suggest an Upper Pleistocene age. Most abundant were shells of the genus* Theba *which fell into three groups by means of qualitative, metric, and landmark analyses.* Theba subdentata*, a small form of* T. chudeaui*, and a new species* T. tantanenis *sp. nov. document the former co- existence of three species of* Theba *in a now desert-like part of the NW African coast.*

Key words *Helicidae, taxonomy, Morocco, Pleistocene*

INTRODUCTION

Raised beaches and ancient dunes are evidence of climatic changes in the past. In the eastern Atlantic, the analysis of such deposits has resulted in detailed knowledge of sea level changes and of the associated marine fauna (Hoang *et al*., 1978; Weisrock *et al*., 2002; Meco *et al*., 2006; Meco, 2008). Marine molluscs and other invertebrates play a major role in the palaeontological record of fossil beaches. On the other hand some terrestrial gastropods prefer coastal habitats and halophytic plants, and their shells are often found together with shells of marine molluscs on beaches and in dunes, like snails of the genus *Theba*. They occur along the coast of the Mediterranean as well as in West Africa and on many of the Atlantic islands (Sacchi, 1971; Gittenberger & Ripken, 1987; Hutterer & Groh, 1997). A number of extant and extinct species were recorded and described from Pleistocene and Holocene dune deposits on the Canary Islands (Gittenberger & Ripken, 1987; Hutterer, 1990; Yanes *et al*., 2007). No data on Quaternary *Theba* are available from the neighbouring mainland of West Africa (Biberson & Jodot, 1965; Jodot & Lecointre, 1965); other authors dealt with marine molluscs or referred terrestrial molluscs to "Helicidae" (Biberson & Lecointre, 1956; Ortlieb *et al*., 1974) or "gastéropodes pulmonés" (Brebion *et al*., 1986). Here, we report on a new fossil site in SW Morocco which yielded marine and terrestrial molluscs, including three interesting species of *Theba*.

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SITE, MATERIAL AND METHODS

The material described herein was collected from a fossil dune in SW Morocco in March 2008 (Fig. 1). The site is situated about 1 km north of Tan Tan Plage, a small coastal settlement west of the city of Tan Tan (Guelmim-Es Semara Region). The beach is composed of pebble stones at the shore line but merges into sand and rolling dunes after 10–20 m. Some dunes are covered with sparse halophytic vegetation (Fig. 1). In some dune valleys, consolidated, darker sediments are exposed and form a horizontal platform (Fig. 2). The soil is ochre to reddish-brown in colour and composed of small crystalline

Figure 1 View of Tan Tan Plage, showing white shifting sand on the left, and the darker (reddish brown) consolidated fossil dune on the right. Shells were picked from the wind-exposed surface of the fossil dune.

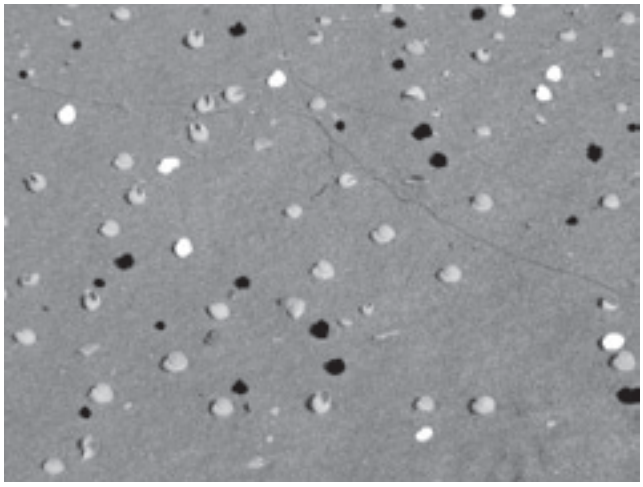

Figure 2 Surface of the fossil dune with numerous shells freshly exposed by wind. Shells of *Theba tantanensis* sp. nov. stained black, and shells of *T. subdentata*, white; other shells represent *T*. cf. *chudeaui* or unidentified.

granules and tiny shell fragments. Numerous shells of marine and terrestrial molluscs are dispersed all over the surface. Incessant strong winds destroy the shells on the surface and uncover new ones from below. We picked a sample of well preserved shells directly from the surface of the platform, shown in fig. 2. The site is about 4–8 m above sea level and gently slopes down towards the sea some 30 m away. The dark consolidated sediments are localized; further north and south they were not present or not exposed.

A comparison of the new material with shells of extant and fossil species was mainly based on material from our working collections, currently housed at ZFMK, and from museum material in the collections of Frankfurt (SMF), Leiden (RMNH), Zürich (ZMZ) and Paris (MNHN). This included type material of most species of *Theba* described to date. Poppe & Goto (1991) and Fischer (2005) were consulted for the identification of the marine molluscs.

The terminology of shell characters and the method for whorl counts follow Seddon (2008). Measurements were taken with a digital calliper under a binocular. Photographs were made with a digital camera and a Hitachi S-2460N Natural Scanning Electron Microscope (SEM), respectively. Morphometric analyses were conducted in the framework of geometric morphometrics based on 10 landmarks, placed on shells photographed in standardized position (Fig. 3). The repeatability of the entire procedure was demonstrated in a foregoing analysis (Haase & Misof, 2009). Geometric morphometrics allow analysing shape independent of size, which is not possible with traditional measurements (Bookstein, 1991; Zelditch *et al*., 2004). In particular, we conducted a canonical variates analysis including assignment tests, using CVAGen6n, after Procrustes superimposition with CoordGen6h, both programmes of the imp suite developed by David Sheets and co-workers (available at http://www2.canisius.edu/~sheets/morphsoft.html). Landmark coordinates were generated using tpsUtil and tpsDig2 from the tps prgramme suite written by F. James Rohlf (available at http://life.bio.sunysb.edu/morph/).

Abbreviations used in the text

CHB	R. Hutterer private collection, Bonn, Germany;
MNHN	Museum National d'Histoire Naturelles, Paris, France;
RMNH	National Museum of Natural History (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands;
SMF	Forschungsinstitut Senckenberg, Frankfurt/Main, Germany;
TFMC	Museo de Ciencias Naturales de Tenerife, Canary Islands, Spain;
ZMZ	Zoologisches Museum der Universität Zürich, Switzerland;
ZFMK	working collection of the authors at Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

Results

The fossil dune yielded remains of marine and terrestrial molluscs. The marine fauna was represented by few shells or fragments of *Phalium saburon* (Bruguière 1792), *Cabestana cutacea* (Linnaeus 1767), *Cabestana dolaria* (Linnaeus 1758), *Nassarius mutabilis* (Linnaeus 1758), *Thais haemastoma* (Linnaeus 1758) (abundant, not collected), and by unidentified fragments of bivalves. Terrestrial gastropods included *Rumina saharica* Pallary 1901, *Xeroleuca* sp., *Eremina duroi* (Hidalgo 1866), and, most abundant, *Theba* spp. (Fig. 2).

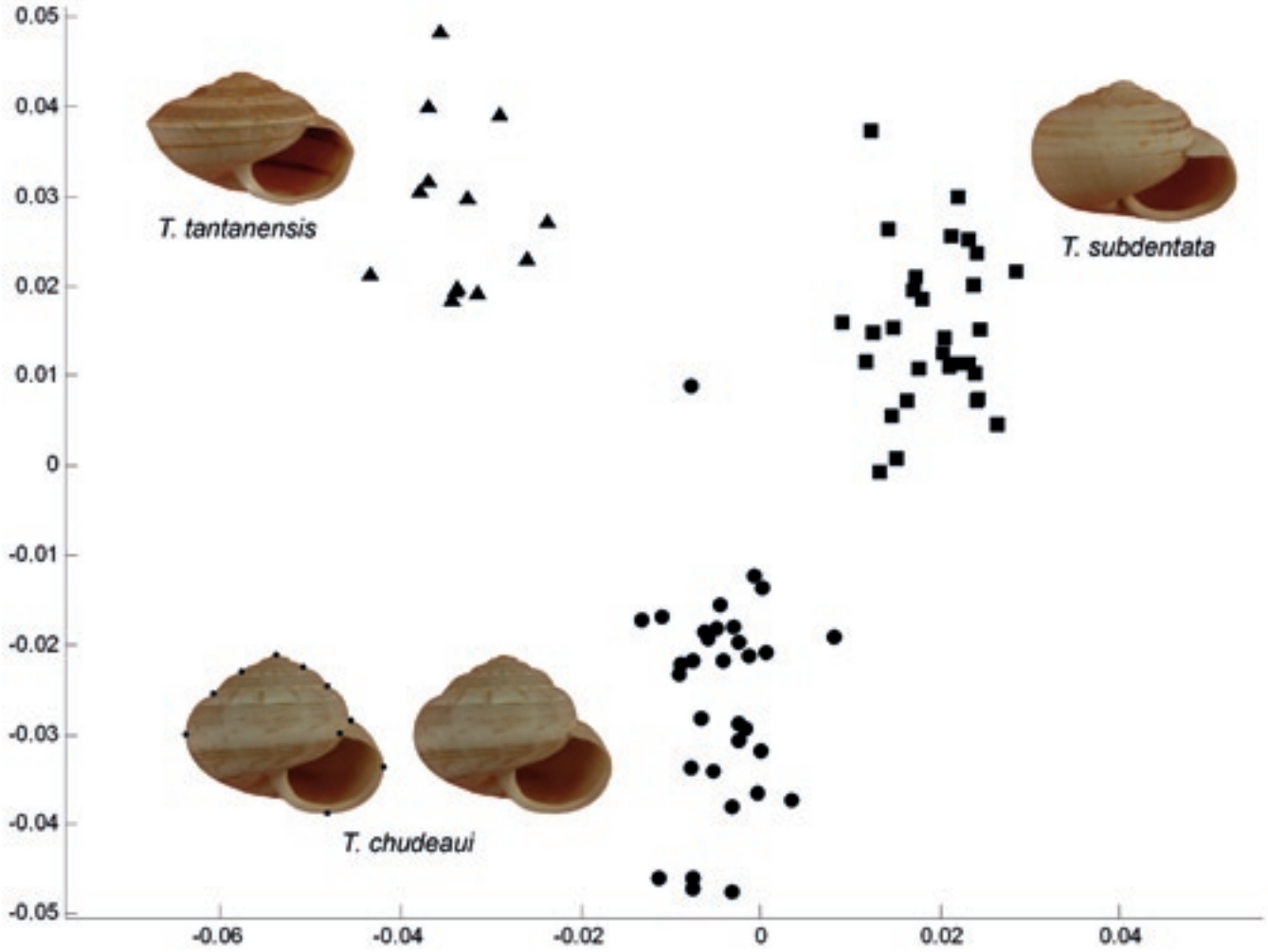

Figure 3 Canonical variates analysis (CV 1 and CV 2) based on 10 landmarks of a subsample of shells from the Tan Tan Plage deposit. The position of landmarks is shown on a shell of *Theba chudeaui.*

Some 300 fairly complete shells of *Theba*, of which 295 were saved after screen-washing and cleaning, were extracted from the surface and sediment of the consolidated reddish-brown dune. According to size, shape, condition of the umbilicus and surface structure, they fell into three groups, represented in the sample by 48%, 29%, and 23%, respectively (n=295). These figures coincide roughly with the relative abundance of three morphotypes observed on the surface of the dune, as shown in a photograph taken before collecting (Fig. 2). They were identified on the enlarged photograph (species stained in fig. 2 for better recognition) and allocated to morphotypes at about 57%, 14%, and 29%, respectively (n=72). We are confident that these figures more or less reflect the abundance of the three species in the fossil dune deposit.

A canonical variates analysis, performed on a subset of our sample and based on 10 landmarks, supported the existence of three distinct groups (Fig. 3). All individuals were assigned to their respective *a priori* identified taxon. For only three shells, this allocation was statistically not significant. Two of the groups could be assigned to known species; the third form represents a new species which is named and described below.

Family Helicidae Rafinesque 1815
Genus *Theba* Risso 1826
Type species *Helix pisana* Müller 1774

Theba cf. *chudeaui* (Germain 1908)

Material 140 sh, leg. R. Hutterer and C. Greve, 5–03-2008, ZFMK.

Remarks The shells of this form resemble those of *Theba chudeaui*, a rare extant species described from northern Mauritania (Germain, 1908) and

Table 1 Measurements of shells (in mm) of *Theba tantanensis* sp. nov. and some other species with an open umbilicus. Mean, SD, and range is given.

Character	*T. tantanensis* Tan Tan Plage Pleistocene (ZFMK)	*T.* cf. *chudeaui* Tan Tan Plage Pleistocene (ZFMK)	*T. sacchii* S Tan Tan extant (ZFMK)	*T. costillae* Fuerteventura Pleistocene (CHB)
Sample size	25–30	30	25–30	30
Whorls	4.20 ± 0.18 (3.75–4.4)	4.29 ± 0.05 (4.25–4.4)	4.65 ± 0.22 (4.15–4.9)	4.27 ± 0.05 (4.2–4.4)
Shell width	14.74 ± 1.20 (13.11–17.34)	15.38 ± 0.77 (14.17–16.94)	17.07 ± 1.30 (15.31–21.38)	13.51 ± 1.10 (11.39–16.02)
Shell height	9.45 ± 0.83 (8.13–11.26)	12.09 ± 0.81 (10.63–13.64)	10.14 ± 0.77 (8.83–11.79)	8.29 ± 0.74 (6.86–10.31)
Aperture width	8.62 ± 0.70 (7.64–10.40)	8.42 ± 0.51 (7.43–9.47)	9.03 ± 0.67 (8.02–11.06)	7.28 ± 0.62 (6.22–8.44)
Aperture height	6.86 ± 0.52 (5.74–8.33)	7.46 ± 0.42 (6.66–0.09)	6.82 ± 0.54 (5.95–7.77)	5.86 ± 0.57 (4.89–6.97)
Umbilicus width	1.75 ± 0.29 (1.10–2.22)	1.37 ± 0.24 (0.56–1.72)	2.05 ± 0.21 (1.8–2.56)	1.63 ± 0.26) (1.03–2.23)
Spirals/penultimate whorl	13.8 ± 1.9 (10–17)	8.3 ± 1.6 (6–11)	15.1 ± 2.3 (11–19)	16.6 ± 1.5 (15–19)

known to occur along the coast in West Sahara and southern Morocco (Gittenberger & Ripken, 1987). However, the Tan Tan fossils are smaller (Table 1) and have a higher spire, as compared to the type series of *Theba chudeaui* in the MNHN (Haase *et al*., unpublished data). At present Tan Tan Plage is the northernmost known locality of the species in West Africa. We tentatively assign the fossils to the extant species until a more comprehensive study of extant and fossil populations has been carried out.

Theba subdentata (Férussac 1821)

Material 55 sh, leg. R. Hutterer and C. Greve, 5–03-2008, ZFMK.

Remarks This is the fourth record of the species south of the Oued Draa, a deep river valley that functions as a physical barrier for the distribution of animals. Gittenberger & Ripken (1987, fig. 30) recognised two subspecies from there, T. *s. legionaria* (Sacchi 1955), described from a fossil-bearing soil near Aoreora (NW of Oued Draa), and T. *s. meridionalis* (Sacchi 1955), described from live-collected animals further north (Sacchi, 1955). Whether the recognition of the two subspecies is justified or not, can only be decided after an analysis of the entire group, which is in progress. Neither Gittenberger & Ripken (1987) in 1975 nor we (in 2008) were able to find living animals south of the Oued Draa; the southernmost populations of *Theba subdentata* are presumably extinct.

Theba tantanensis new species

Holotype 1 sh, leg. R. Hutterer & C. Greve, 5–03-2008, SMF 332463 (Fig. 4).

Paratypes 67 sh (30 ad, 37 juv), same data as holotype, SMF 332464/5, RMNH/5, MNHN/5, CHB/5, ZFMK/27.

Type locality Morocco, Guelmim-Es Semara Region, Province of Tan Tan, Tan Tan Plage (28°30′31.87′′N, 11°19′34.99′′W), Quaternary dune deposit, c. 30 m from shore, 4–8 m a.s.l. (Fig. 1).

Measurements Holotype, shell width 17.34 mm, shell height 11.26 mm, aperture width 9.2 mm, aperture height 7.15 mm, umbilicus width 2.22 mm; number of whorls 4.25. For other measurements, see Table 1.

Diagnosis A species of *Theba* of medium size with a prominent keel, a slightly trochiform spire,

Figure 4 Holotype of *Theba tantanensis* sp. nov. in dorsal, lateral, and ventral view.

and a wide umbilicus. Surface of shell strongly wrinkled.

Description The shell is ovate-discoidal to almost trochiform with 4.2 (3.75–4.4) keeled, slightly shouldered and slowly increasing whorls (Figs 3, 4). The periphery is keeled, both in juveniles and adults. Aperture elliptical; parietal thin but columella thickened. Columella reflected and covering less than ¼ of the umbilicus. Umbilicus deep and wide, its width about 11% of total shell width. Shell of medium size, mean width 14.75 ± 1.20 mm, mean height 9.45 ± 0.84 mm (n = 30). Protoconch small, evenly merging into the first whorl (Fig. 4). Shell surface with a prominent microsculpture: deeply engraved radials crossed by 10–17 spirals per whorl, giving the surface of shell and keel a wrinkled, cushion-like appearance (Fig. 5). Several shells bear traces of the former colour pattern. The protoconch is partly reddish-brown, and the dorsal surface of the whorls bears irregular radial blotches of the same colour; a group of 4–5 parallel fine dark

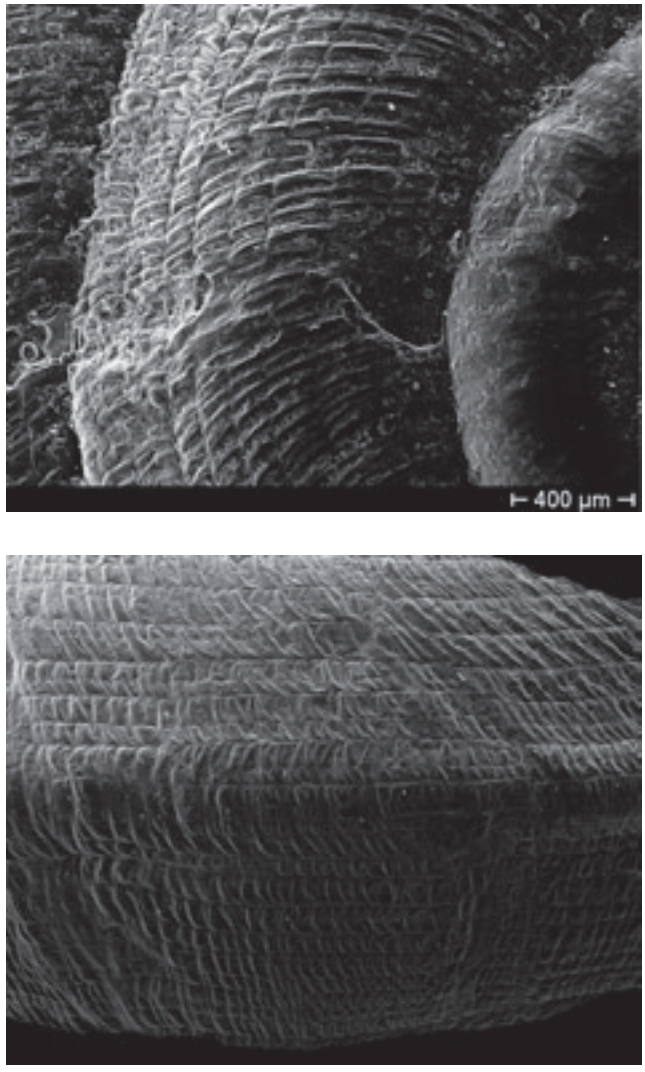

Figure 5 Shell surface of *Theba tantanensis* sp. nov.; above, dorsal view of protoconch and first whorl, below, lateral view of the keel (SEM views).

spirals runs from the first to the ultimate whorl (Fig. 4).

Derivation of name The species epithet was derived from the name of the type locality, Tan Tan Plage.

Geographical and temporal range Currently known only from the type locality; not found on several fossil beaches that we studied further north and south. The age of the dune deposit was estimated as Upper Pleistocene (see discussion below).

Comparisons An open umbilicus is only found in *Theba sacchii* Gittenberger & Ripken 1987, *Theba chudeaui,* and *Theba costillae* Hutterer 1990. Therefore, we restrict comparisons to the three species.

T. sacchii differs from *T. tantanensis* sp. nov. in larger size (Table 1), by a more depressed shell with rounded whorls, and by the lack of a keel (Gittenberger & Ripken, 1987, figs 53–54). The colour pattern of *T. sacchii*, however, is rather similar to that of *T. tantanensis* sp. nov., e.g. a group of thin parallel spirals in combination with star-like radial blotches (Hutterer, 1990, plate fig. 2).

Theba chudeaui, known to occur from Mauritania to SW Morocco (Germain, 1908; Gittenberger & Ripken, 1987), differs by larger size, a higher spire (Fig. 4), and a smaller umbilicus which is partly covered by the columellar lip (Gittenberger & Ripken, 1987, figs 56–61; Hutterer, 1990, plate fig. 1).

Theba costillae, known from the Pleistocene of Fuerteventura, Canary Islands, resembles *T. tantanensis* sp. nov. in its wide umbilicus and in its flattened and keeled whorls (Hutterer, 1990, plate fig. 3); however, it is much smaller (Table 1), and the microsculpture of the shell surface is different (15–19 faint spirals per whorl versus 10–17 deeply engraved spirals in the new species).

Discussion

The age of the dune deposit was estimated as Upper Pleistocene, based on the geological setting (consolidated dune of ochre to reddish colour at low altitude, 4–8 m, buried by recent white dunes) and the faunal composition (*Thais haemastoma* and *Cabestana dolaria* as marine gastropods, plus extinct helicids). Gigout (1949, 1957) described such coastal deposits from NW Morocco as consolidated dunes above 2 m and actually buried by sediment, often red in colour, and frequently found at 5–8 m above sea level. At Temara (northern Morocco) he found these sediments "rich in helicids and bones." In 1949, he coined the term "Ouljien" for this period and allocated it to the last interpluvial. The term Ouljien has been frequently used by subsequent researchers (Ortlieb *et al*, 1974; Hoang *et al*., 1978; Brebion *et al*., 1986; Saaidi, 1988; Weisrock *et al*., 1999), who also considered *Thais haemastoma, Cabestana dolaria*, and the limpet *Patella safiana* Lamarck 1819 as characteristic marine species for this period. Age estimations for the Ouljien of the Maroccan littoral vary from 43 kyr to 148 kyr (Hoang *et al*., 1978; Brebion *et al*., 1986; Choukri *et al*., 1995; Azougagh *et al*., 2001).

Similar consolidated dunes were described from the Canary Islands (Petit-Maire *et al*., 1986; Rognon & Coudé-Gaussen, 1987; Meco *et al*., 1997; Meco *et al*., 2006). AMS dating of the lowest levels of such dunes, based on shells of *Theba* and other terrestrial gastropods, ranged around 40 kyr (Ortiz *et al*., 2006; Yanes *et al*., 2007). Meco (2006, 2008), however, raised doubt on these age determinations, as Th/U dating (Meco *et al*., 1997) of some of the same sites resulted in much higher ages (95 – 235 kyr). These Th/U ages, however, would coincide with the Ouljien in Morocco. Age determinations of shells must be taken with caution. Choukri *et al*. (1999) warned that Th/U dating of mollusc shells may yield much younger ages than corals or other organisms, because re-crystallization and aragonite contamination may disturb the dating.

For the Tan Tan Plage site, we can not provide a chemical or physical age determination. Based on the arguments provided above, an Ouljien age seems probable. Therefore, we consider the age of the site as "Upper Pleistocene" without any further precision.

If we accept *Theba* cf. *chudeaui* as different from the extant forms, then two of the three taxa of *Theba* from Tan Tan Plage must be considered as extinct. *T*. cf. *chudeaui* was once linked to extant populations further south, and *T. subdentata* to extant populations further north. *Theba tantanensis* sp. nov., however, has no close relatives in Morocco. Conchologically, it resembles the extinct

Theba costillae from northern Fuerteventura. It has been suggested before (Hutterer, 1990) that *T. costillae* derived from an African founder population. However, we can not exclude a parallel evolution of the two extinct species.

The high abundance of shells and their stochastic distribution in the sediment suggest that the three species of *Theba* occurred in the surroundings of the dune sympatrically, if not syntopically, in the past. Today no species of *Theba*, nor any other terrestrial snail, live in the vicinity of the beach or further inland.

Syntopic occurrence of two or more species of *Theba* is a rare phenomenon. During our fieldwork, we observed only two such cases: *Theba geminata* (Mousson 1857) and *T. impugnata* (Mousson 1857) on Lanzarote, and *Theba subdentata* and *T. pisana ampullacea* (Pallary 1915) in Morocco. In all other cases, species were separated by at least some distance, or by altitude. However, in fossil assemblages one can find more than two species together. This could either be explained by a chronological occurrence of the species, now mixed up in the sediment, or by more favourable conditions that supported more than one species at a time. In order to better understand the fossil assemblages, we still have to learn more about the ecology of the extant species of *Theba*.

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REFERENCES

AZOUGAGH M, CHOUKRI A, LFERDE M, CHERKAOUI EL MOURSLI R, CHOUAK A & ABRKAN M 2001 Mollusc shell dating by uranium series method on quaternary material at Moroccan sea level. *Radiation Physics and Chemistry* **61**: 713–715.

BIBERSON P & JODOT P 1965 Faunes mollusques continentaux du Pléistocène de Casablanca (Maroc) Essai de conclusions paléoclimatiques. *Notes du Service Géologique du Maroc* **25**: 115–170.

BIBERSON P & LECOINTRE G 1956 Progrès dans la conaissance du Quaternaire de Casablanca (Maroc). *Bulletin de la Société géologique de France 6e ser.* **6**: 855–860.

BOOKSTEIN FL 1991 *Morphometric tools for landmark data: geometry and biology.* Cambridge University Press, New York. 435 pp.

BREBION P, RAYNAL JP, TEXIER JP & ALOUANE M 1986 Nouvelles données sur le Quaternaire littoral du Maroc atlantique à Casablanca et Cap Achakar. *Comptes Rendus de l'Académie des Sciences Paris série 2* **302**: 901–904.

CHOUKRI A, REYSS JL, PLAZIAT JC, ORSZAG-SPERBER F & BERRADA M 1995 Reliability of sea level dating using Th/U method for mollusks from the west coast of the Red Sea and from the Atlantic coast of the Moroccan High Atlas. *Applied Radiation and Isotopes* **46**: 653–654.

CHOUKRI A, REYSS JL, JAHIOUH EK, SEMGHOULI S & PLAZIAT JC 1999 Discussion de la fiabilité de datation de quelques matériaux par la méthode $^{230}Th/^{234}U$. Application à l'étude de la variation du niveau marin dans le passé. *Recontre Franco-Marocaine de Physique Nucléaire, El Jadida 10–13 mars 1999*: 81–85.

FISCHER W 2005 *Cabestana cutacea* (Linné 1767) (Gastropoda: Ranellidae), eine neue Art für die griechische marine Molluskenfauna. *Club Conchylia Informationen* **37**: 59–61.

GERMAIN L 1908 Contributions à la faune malacologique de l'Afrique équatoriale. *Bulletin du Muséum nationale d'Histoire naturelle* **14**: 290–291.

GIGOUT M 1949 Définition d'une étape Ouljien. *Comptes Rendus de l'Académie des Sciences Paris* **229**: 551.

GIGOUT M 1957 L'Ouljien dans le cadre du Tyrrhénien. *Bulletin de la Société géologique de France 6e ser.* **7**: 485–400.

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

HAASE M & MISOF B 2009 Dynamic gastropods: stable shell polymorphism despite gene flow in the land snail *Arianta arbustorum. Journal of Zoological Systematics and Evolutionary Research* **47**: 105–114.

HOANG C, ORTLIEB L & WEISROCK A 1978 Nouvelle datations $^{230}Th/^{234}U$ de terrasses marines « ouljiennes » du sud-ouest du Maroc et leurs significations stratigraphique et tectonique. *Comptes Rendus de l'Académie des Sciences Paris série D* **286**: 1759–1762.

HUTTERER R 1990 A new Canarian *Theba* (Gastropoda: Helicidae) with African affinities. *Schriften zur Malakozoologie* **3**: 1–6.

HUTTERER R & GROH K 1997 The eastern Canary Islands: Centre of diversity of the genus *Theba. Heldia* **4**: S72.

Jodot P & Lecointre G 1965 Malacologie continentale de quelques gisements quaternaires du littoral atlantique marocain. *Notes du Service géologique du Maroc* 25 : 101–108.

Meco J 2008 (ed.) *Historia geológica del clima en Canarias.* Edition J Meco, Las Palmas de Gran Canaria. 296 pp.

Meco J, Ballester J, Betancort JF, Cilleros A, Scaillet S, Guillou H, Carracedo JC, Lomoschitz A, Petit-Maire N, Ramos AJG, Perera N & Meco JM 2006 *Paleoclimatología del Neógeno en las Islas Canarias. Geliense, Pleistoceno y Holoceno.* Ministerio de Medio Ambiente & Universidad de Las Palmas de Gran Canaria, Las Palmas de Gran Canaria. 204 pp.

Meco J, Petit-Maire N, Fontugne M, Shimmield G & Ramos AJ 1997 The Quaternary deposits in Lanzarote and Fuerteventura (eastern Canary Islands, Spain): an overview. *In:* Meco J & Petit-Maire N (eds) *Climates of the Past:* 123–126. International Union of Geological Sciences, Unesco and Universidad de Las Palmas de Gran Canaria, Las Palmas de Gran Canaria.

Ortiz JE, Torres T, Yanes Y, Castillo C, de la Nuez, J, Ibanez M & Alonso MR 2006 Climatic cycle inferred from the aminostratigraphy and aminichronology of Quaternary dunes and palaeosols from the eastern islands of the Canary Archipelago. *Journal of Quaternary Science* **21**: 287–306.

Ortlieb L, Metir-Maire M & Berge C 1974 Rapport succinct sur la mission effectuée dans le sud marocain (Province de Tarfaya). *ORSTOM Fonds Documentaire no* **29160**: 1–12, 5 pls.

Petit-Maire N, Delibrias G, Meco J, Pomel S & Rosso J–C 1986 Paléoclimatologie des Canaries orientales (Fuerteventura). *Comptes Rendus de la Academie des Sciences Paris série 2* **303**: 1241–1246.

Poppe GT & Goto Y 1991 *European seashells Vol I*. Christa Hemmen, Wiesbaden. 352 pp.

Rognon P & Coude-Gaussen G 1987 Reconstitution paléoclimatologique à partir des sédiments du Pleistocène supérieur et de l'Holocène du nord de Fuerteventura (Canaries). *Zeitschrift für Geomorphologie Neue Folge* **31**: 1–19.

Saaidi E 1988 *Geologie du Quaternaire Marocaine* Société Marocaine des Editeurs Réunis, Rabat, 440 pp.

Sacchi CF 1955 Fattori ecologici e storici nel polimorfismo delle « *Euparypha* » (« Helicidae Helicinae ») del Maroc occidentale. *Studia Ghisleriana* **(3) 2**: 43–66, pl 1.

Sacchi CF 1971 Écologie comparée des gastéropodes pulmonés des dunes Méditerranéenes et Atlantiques. *Natura Milano* 62: 277–358.

Seddon MB 2008 *The landsnails of Madeira An illustrated compendium of the landsnails and slugs of the Madeiran archipelago.* Studies in Biodiversity and Systematics of Terrestrial Organisms from the National Museum of Wales, Biotir Reports **2**: viii + 196 pp.

Weisrock A, Occhietti S, Hoang CT, Lauriat-Rage A, Brebion P & Pichet P 1999 Les séquences littorales pléistocènes de l'Atlas entre Cap Rhir et Agadir, Maroc. *Quaternaire* **10**: 227–244.

Weisrock A, Adele B, Charif S & Tannouch-Bennani S 2002 Dunes littorales et dunes continentales au Maroc atlantique semi-aride (29°–30° N) du Pleistocène supérieur a l'actual. *Revista Cuarternario y Geomorfología* **16**: 43–56.

Yanes Y, Kowalewski M, Ortiz JE, Castillo C, de Torres T & de la Nuez J 2007 Scale and structure of time averaging (age mixing) in terrestrial gastropod assemblages from Quaternary eolian deposits of the eastern Canary Islands. *Palaeogeography Palaeoclimatology Palaeoecology* **251**: 283–299.

Zelditch ML, Swiderski DL, Sheets HD &. Fink WL 2004 *Geometric Morphometrics for biologists: a primer.* Elsevier Academic Press, London. 443 pp.