THE GENUS *THEBA* (MOLLUSCA: GASTROPODA: HELICIDAE), SYSTEMATICS AND DISTRIBUTION

by

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Our knowledge concerning taxonomy and zoogeography of the fossil and recent species of the helicid genus *Theba* is summarized and enlarged. The fossil *T. arinagae* spec. nov. is described from Gran Canaria. The recent *T. andalusica* spec. nov. and *T. sacchii* spec. nov. are described from the southernmost part of the Iberian peninsula and the southernmost part of Morocco, respectively. This implies that four fossil and ten recent *Theba* species are recognized. Two of the fossil species are very insufficiently known. Some recent species are polytypic, which results in 17 (sub)specific taxa in total. Neotypes are selected for *T. subdentata legionaria* and *T. solimae*. The nominate subspecies of *T. pisana* is shown to be aberrant because of its very wide range; the other *Theba* (sub)species have much smaller ranges, situated in W. Morocco, Western Sahara, the southernmost part of the Iberian peninsula and some Atlantic islands.

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INTRODUCTION

The genus *Theba* Risso, 1826 is known best by the nominate subspecies of its type species, i.e. by *T. pisana pisana* (Müller, 1774), which is widely distributed around the Mediterranean and along parts of the Atlantic coasts of western Europe. As a result of human actions this subspecies has become established in various other parts of the world (e.g. Australia, California and S. Africa), sometimes being considered a plague.

Most of the other *Theba* (sub)species are poorly known and hardly ever cited in the literature. They have small or very small ranges, found within a comparatively narrow centre of diversity, viz. W. Morocco, the southernmost part of the Iberian peninsula and the three eastern Canary Islands (fig. 1). At several localities two *Theba* species occur sympatrically: *T. impugnata* (Mousson, 1857) with *T. geminata* (Mousson, 1857), *T. pisana* with either *T. andalusica* spec. nov., *T. geminata* or *T. subdentata* (Férussac, 1821), and *T.*

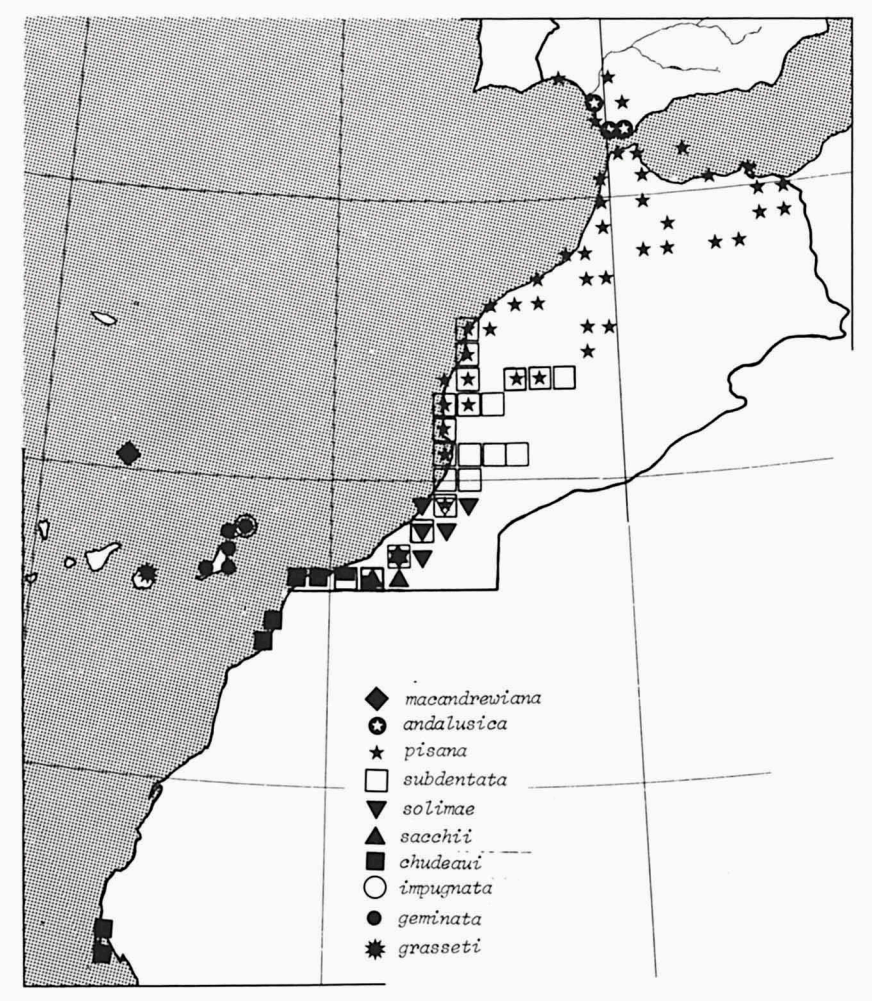


Fig. 1. UTM 50 km squares distribution map for *Theba* species. Records of *T. pisana* are indicated in Morocco and the Spanish provinces of Huelva, Sevilla and Cádiz only; on the Canary Islands and in the Madeiran archipelago *T. pisana* most probably is a very recent immigrant.

subdentata with either *T. pisana, T. solimae* (Sacchi, 1955), *T. sacchii* spec. nov., or *T. chudeaui* (Germain, 1908).

Only Sacchi (1955a, b, 1956, 1957) has published in the modern literature on more than only *T. pisana*. According to Prof. Dr. C. F. Sacchi (in litt., 29.XII.1982) the *Theba* material from Morocco he had published upon (1955b) should be in Naples, in the "Stazione Zoologica di Napoli"; some material could also be in the "Museo di Storia Naturale" in Milano. It turned out, however, that no *Theba* material is still present in Naples (only some Helicellinae, once studied by Prof. Dr. Sacchi, proved to be left), whereas nothing of importance could be traced in Milano as well. As a consequence, neotypes had to be designated for two problematical nominal taxa (pp. 31, 48).

Two *Theba* species are polytypic, viz. *T. pisana* and *T. subdentata*. The subspecies distinguished in the present paper are more or less subjectively defined; the borderlines separating them may be vague, even if the morphological differences involved are very conspicuous in "easy" populations. Clinal variation is evident in some species.

Conchological characters and geographical distribution constitute the basis for the present classification. *T. pisana* is a "bewilderingly variable snail" (Cain, 1984a: 163) only with regard to the colour pattern of the shell. This variation has been misleading to both predators, because a hunting image is not easily constructed and strengthened (Cain, 1984b: 410) and systematists, overlooking the less conspicuous shell characters, which can be used to classify the various (sub)species. In *Theba* not only the general shape of the shell, keeled or not, but also its microsculpture, the structure of the umbilical region and the shape of the aperture can be important.

The (sub)globose heliciform shell may be very glossy or more silky shining, which depends upon the prominence of the microsculpture. The shell is sculptured with numerous incised, interrupted, spiral lines, crossing the equally fine growth-lines. On a whitish or yellowish background there usually are darker spiral bands, which are frequently interrupted and vary greatly. In nearly all species shells of juvenile snails with only a few whorls are sharply keeled. *T. macandrewiana* (L. Pfeiffer, 1853) and *T. arinagae* spec. nov. are exceptional with regard to this character. In *T. pisana* there may be a denticle on the parietal wall of the aperture in juvenile shells (Girard, 1888); in full-grown specimens this denticle is lacking. It is unknown whether a parietal denticle can also be found in juvenile shells of other species; more material should be studied to answer this question. In *T. subdentata* adult shells have a prominent parietal denticle in two of the five subspecies.

There has been some dispute as to the basic number of bands discernible in *Theba* shells (Heller, 1981: 86; Cowie, 1984: 362). This problem earns our

attention because it is linked to the classification of the genus *Theba* itself. We cannot agree with Cowie (1984: 362), who refers to "the pentataeniate model used in the descriptions of most helicids so far studied", if "helicids" stands for Helicidae. In many Helicidae (sensu Zilch, 1960: 663) a basic pattern with five bands cannot be indicated; this number is never found in e.g. the speciose Ariantinae (= Helicigoninae, = Campylaeinae). Schmidt (1855: 22, 23) has discussed this problem already. Ahead of even the present time he did not classify "*H. pisana*" (= *Theba*) with his own "Gruppe Pentataenia" (1855: 11), suggesting instead an independant position for the taxon, comparable to that of the "Xerophilen" (= Helicellinae). He emphasized that *T. pisana* clearly differs from the Pentataenia in the structure of the mucous glands, an argument still valid; the glandulae mucosae resemble those of the Elonidae, at least in shape (Gittenberger, 1979). Above the periphery of the shell of *Theba*, Schmidt distinguished a peripheral band and a broad group of bands, extending as far as the suture, considering it "sehr zweifelhaft" [very doubtful] whether one should accept five bands for the basic pattern in *Theba*, viz. two lower and three, not two, upper bands. We can only add that without typical Pentataenia in mind, one would hardly be inclined to distinguish five main bands on a *Theba* shell.

It has not yet been possible to characterize the various *Theba* species anatomically. In *T. pisana* the relative measurements of various parts of the genitalia may vary conspicuously. This variation might be at least partly seasonal. The other *Theba* species are much less well known anatomically and there is only a very limited amount of alcohol material available for study, or nothing at all. This implies that speculations about specific differences are too premature in view of the variation observed in a few species and the (very) restricted number of specimens that could be studied in most of the other species. Therefore only figures of the genitalia are given if possible, or referred to in the literature, without detailed descriptions or discussions. For a general introduction to the anatomy of *Theba* and other Helicidae we refer to Hesse (1915).

The glandulae mucosae may differ conspicuously in relative size. In e.g. *T. macandrewiana* and *T. chudeaui* we found them much smaller than in e.g. *T. andalusica* and *T. pisana*. There might be specific differences in the relative lengths of the two parts of the spermatheca duct and the diverticulum, and in the ratio penis versus epiphallus length. The internal structure of the genitalia has not been studied systematically. Only in *T. andalusica* the penial papilla has been dissected (fig. 44a). The structure of the dart is unknown in most species (see Hesse, 1915). A conspicuous membrane has been found not far from the genital atrium (see fig. 17); its location in the various species is

Fig. 2. Empty shells of *Theba macandrewiana* occur in great abundance on Ilha Selvagem Grande. Photograph by J. C. den Hartog.

unknown. Summarizing we may say that a more detailed study of the anatomy of the *Theba* species will provide us with many more taxonomic characters than those available at present. Maybe these additional characters will enable the reconstruction of the phylogeny of these species.

A very extensive, well illustrated survey concerning a wide range of data on "*Helix pisana*" has been published by Taylor (1911: 368; 1912: 369-398, figs. 408-450, pls. 30, 31). Because Taylor's concept of this taxon encompasses the entire genus *Theba*, his work can serve as an introduction to the life history, morphology, variation etc. of *Theba* species. It would lead far beyond the scope of the present paper to discuss what illustrations and notes apply to the individual species. Most of Taylor's text clearly concerns *T. pisana pisana*.

Theba species may occur in great abundance, with large amounts of individuals clustering on e.g. food plants (Taylor, 1912: figs. 421, 450). The empty shells are sometimes found in very high concentrations (fig. 2). The animals manage to live in relatively dry and arid regions, in habitats hostile to (nearly) all other gastropod species (fig. 52).

We have not listed all the nominal taxa belonging to *Theba*. Most of them clearly apply to forms of *T. p. pisana* and have never been used in another sense. Only the cases in which the stability of the nomenclature might be involved are dealt with. An index of epithets is given on p. 57.

ABBREVIATIONS

The following abbreviations are used for collections: GD, K. Groh (Darmstadt); MCNM, Museo Nacional de Ciencias Naturales (Madrid); MK, H. P. M. G. Menkhorst (Krimpen aan de IJssel); MNHN, Muséum National d'Histoire Naturelle, Laboratoire de Biologie des Invertébrés Marins et de Malacologie (Paris); RD, Th. E. J. Ripken (Delft); RGM, Rijksmuseum van Geologie en Mineralogie (Leiden); RMNH, Rijksmuseum van Natuurlijke Historie (Leiden); SMF, Senckenberg Museum (Frankfurt am Main); SR, H. L. Strack (Rotterdam); UZM, Universitetes Zoologiske Museum (Copenhagen); ZMA, Instituut voor Taxonomische Zoölogie, Zoölogisch Museum (Amsterdam).

In the figures illustrating genitalia the following abbreviations are used: A, vas deferens; D, spermathecal duct; d, distal; E, epiphallus; F, flagellum; G, mucous gland; Ga, glandula albuminifera; I, diverticulum; O, oviduct; P, penis; p, proximal; R, penial retractor muscle; S, spermatheca; T, dart sac; V, vagina.

KEY TO THE RECENT *THEBA* (SUB)SPECIES

The key can be used for samples of full-grown fresh shells, provided with locality data.

1. Columellar lip clearly reflected and (nearly) completely closing the umbilicus 7
— Umbilicus open, not (nearly) completely closed 2
2. Shell surface silky because of a prominent microsculpture; colour pattern dull or lacking ..... *chudeaui*, p. 53
— Shell glossy, without a conspicuous microsculpture; colour pattern usually bright or lacking 3
3. Seen from below the margin of the apertural base is curved upward near the relatively wide umbilicus (see fig. 53) ..... *sacchii*, p. 51
— Margin of the apertural base nearly straight, umbilicus narrowed (see figs. 32, 34); subspecies of *pisana* 4
4. The entire body-whorl is keeled or prominently angular at least 5
— Not so 6
5. Aperture about as high as broad; carina situated somewhat above the middle of the shell ..... *pisana cantinensis*, p. 43
— Aperture more broad than high; carina situated higher because of a more depressed spire of the shell ..... *pisana arietina*, p. 40

6. Shell less than 15 mm broad and nearly equally high; not particularly fragile ..... *pisana ampullacea*, p. 39
— Shell usually larger and more depressed; relatively small specimens more fragile ..... *pisana pisana*, p. 34
7. Material from the Canary Islands or the Salvages Islands 8
— Material from NW. Africa or S. Spain 11
8. Shell high globular; often with many spiral lines *macandrewiana*, p. 12
— Shell depressed; never with many spiral lines 9
9. Body-whorl simple, neither angular nor keeled ..... *geminata*, p. 16
— Body-whorl angular, or partly or entirely keeled and provided with a crenulate periphery 10
10. With a crenulate periphery and (partly) keeled; apertural lip thickened ..... *impugnata*, p. 19
— With an angular periphery; apertural lip not thickened . *grasseti*, p. 15
11. Aperture clearly broader than high; apertural lip very prominent; with or without a parietal denticle; subspecies of *subdentata* 12
— Aperture about as high as broad; apertural lip more or less prominent; without a parietal denticle 16
12. Body-whorl entirely keeled ..... *subdentata helicella*, p. 23
— Body-whorl not or only partly keeled 13
13. Shell more or less depressed; aperture without a prominent parietal denticle 14
— Shell more globular; aperture usually with a prominent parietal denticle 15
14. Aperture regularly oval; shell width 12.3-17.8 mm ..... *subdentata legionaria*, p. 31
— Aperture with a more oblique base; shell width 16.0-19.3 mm ..... *subdentata dehnei*, p. 26
15. Shell globular; apertural lip and parietal denticle usually prominent ..... *subdentata subdentata*, p. 28
— Shell very globular; apertural lip and parietal denticle very prominent; sometimes with an additional angular denticle ..... *subdentata meridionalis*, p. 30
16. Apertural lip prominent, columellar margin with a notch (front view); spire dome-shaped ..... *andalusica*, p. 44
— Apertural lip slightly thickened, columellar margin regularly curved; spire conical ..... *solimae*, p. 48

SYSTEMATIC TREATMENT

The species will be treated in the following, rather subjective sequence, which is based on morphological and zoogeographical considerations:

1, *T. arinagae* and *T. macandrewiana* (juvenile shells not sharply keeled along the periphery; on Atlantic islands);

2, *T. orzolae* Gittenberger & Ripken, 1985, *T. grasseti* (Mousson, 1872), *T. geminata, T. impugnata* and *T. subdentata* (juvenile shells keeled and full-grown shells more or less depressed and often with an angular or keeled periphery, always with a closed umbilicus; on the Canary Islands and in SW. Morocco);

3, *T. pisana, T. andalusica, T. solimae, T. sacchii* and *T. chudeaui* (juvenile shells keeled and full-grown shells with a rounded periphery and, in three species, an open umbilicus; in S. Spain, W. Morocco and Western Sahara).

The fossil taxa *Helix cartaxensis* Roman, 1907 and *Helix quintanellensis* Roman, 1907, both from Portugal and listed with doubt under *"Euparypha"* by Wenz (1923: 558, 559), are very poorly known and cannot be dealt with satisfactory therefore.

Theba arinagae spec. nov.
(figs. 3, 4)

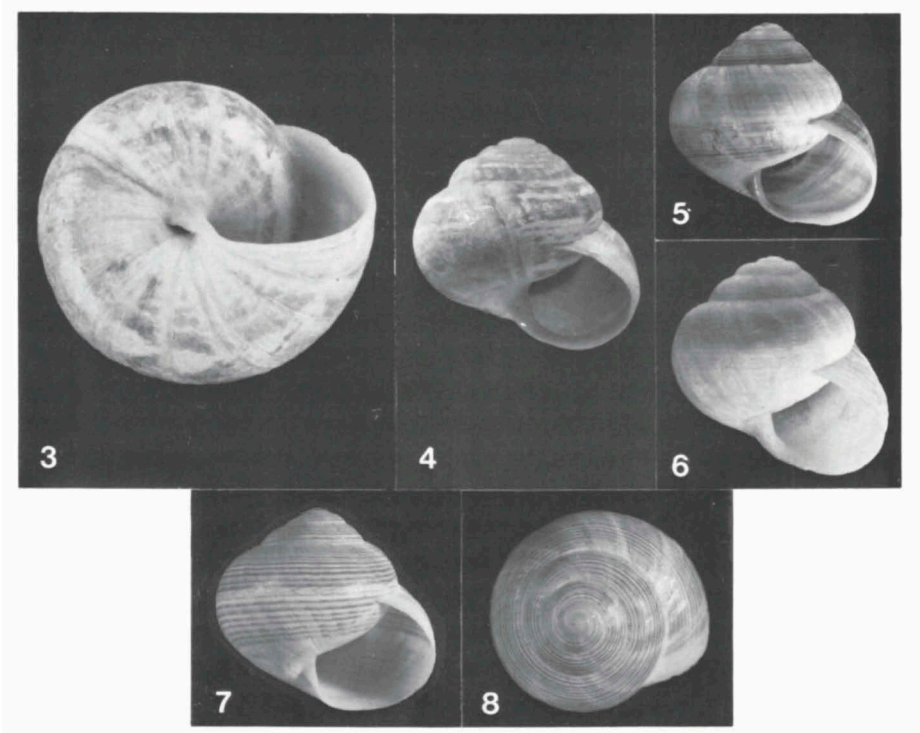
Euparypha pisana Var. *alboranensis*; Odhner, 1931: 103. Not *H. alboranensis* Beck, 1837 (see p. 38).
Theba pisana alboranensis; Backhuys, 1972: 122-124. Not Beck, 1837.

Material. — CANARY ISLANDS. Gran Canaria: Arinaga — lighthouse, semidesertous area (MK/10 paratypes; RD/62 paratypes; RMNH 55927/holotype, 55928/15 paratypes); Playa Ojo de Garza, N. of Aeropuerto de Gando (RMNH 55929/12 paratypes; SR/17 paratypes).

Shell (figs. 3, 4). — Shell globular, with 4¼ - 5¼ very convex whorls. In adult shells the periphery is evenly rounded; in a juvenile specimen with 3½ whorls (RMNH 55929) the periphery is slightly angular. Aperture circular, apart from a more or less prominent columellar angle below; outer lip only vaguely thickened inside. Umbilicus (nearly) completely closed by the reflected columellar lip.

In specimens showing remains of a colour pattern there are two broad bands above the periphery and two broad bands below it. The bands are irregularly delimitated, frequently interrupted, and more or less clearly subdivided into narrower irregular bands.

Width 9.7-14.3 mm; height 8.2-13.7 mm.



Figs. 3-8. *Theba* spec. from Atlantic islands. 3, 4, *T. arinagae* spec. nov., holotype, actual width 12.6 mm, Gran Canaria, fossil sands between Arinaga and the lighthouse (RMNH 55927, Th. E. J. Ripken leg.). 5-8, *T. macandrewiana*; 5, syntype of *ustulata* Lowe, actual width 17.0 mm, Ilha Selvagem Pequena (RMNH 51167, ex Lowe & Wollaston); 6, large specimen, actual width 18.0 mm, Ilha Selvagem Pequena (RMNH, W. Backhuys leg.); 7, 8, shell of a live collected specimen with the typical spiral lines, actual width 17.4 mm, Ilha Selvagem Grande (RMNH. Th. Monod leg.). Photographs by E. G.

T. arinagae is most similar to *T. macandrewiana* in general shape; the latter species differs from the former one by its larger dimensions and the colour pattern with many narrow spiral lines. Very small shells of *T. macandrewiana* have a relatively large aperture. *T. pisana ampullacea* (Pallary, 1915) from SW. Morocco (fig. 36) closely resembles *T. arinagae*, but its whorls are increasing more rapidly in width, which results in a relatively larger aperture and about a half whorl less in equally sized adult specimens.

The three recent, endemic *Theba* species of the Canary Islands differ conspicuously from *T. arinagae* by their larger, relatively much lower shells, which are clearly keeled or angulate along the periphery, at least when juvenile.

Range. — *T. arinagae* is only known from sandy deposits of unknown age at two localities along the eastern coast of Gran Canaria.

Notes. — Judging from Mousson's (1872: 31) short description only, *Helix geminata* var. *parvula* might be this species. The form is compared to *alboranensis* because of its globular shape and the dimensions (8-12 mm in width), but considered different because of the closed umbilicus. It is unlikely, however, that Mousson would have classified our *T. arinagae* with his *T. geminata*. Whatever the results of future research may be, there will be no consequences in nomenclature, *Helix parvula* Rang, 1831 being a senior homonym.

T. arinagae is not sympatric with any other fossil *Theba* species.

Etymology. — The epithet *arinagae* is formed after the name of the type locality Arinaga.

Theba macandrewiana (L. Pfeiffer, 1853)
(figs. 1, 2, 5-9)

Helix ustulata Lowe, 1852: 114 ("in Insulis 'Salvages'"). Not *H. ustulata* Férussac, 1823: cover of the "livraison 20" (see the text below).
Helix Mac-Andrewiana L. Pfeiffer, 1853: 53 ("Great Salvages Island").
Theba pisana ustulata; Backhuys, 1972: 117-130, figs. 1-12.

Material. — ILHAS SELVAGENS. Ilha Selvagem Grande (= Gran Salvage, = Great Salvages Island) (RD; RMNH); id., Ponta de Leste (RMNH); id., Altiplano (SMF); Ilha Selvagem Pequena (= Gran Piton = Great Piton) (RD; RMNH, RMNH 51167 ex Lowe & Wollaston/2 syntypes of *ustulata*; SMF, SMF ex Preston/syntype of *ustulata*); Ilheu de Fora (= La Salvajita, = Little Piton) (RD; RMNH).

Shell (figs. 5-8). — Shell globular, with 4 - 5 very convex whorls. The periphery is evenly rounded, in adult as well as in juvenile shells (the smallest specimens studied had c. three whorls). Aperture circular, with or without a columellar angle below; outer lip not or only vaguely thickened inside. Umbilicus (nearly) completely closed by the reflected columellar lip.

The shells are rather dull. There may be up to c. fifteen (dark) brown spiral lines, varying in width and more or less clearly fused, above the periphery on the body-whorl; below the periphery the spiral lines are usually somewhat less conspicuous, whereas they are lacking around the umbilicus. The spiral colour pattern is more or less vaguely interrupted along certain growth-lines. In comparison with other *Theba* species the pattern is rather simple. The aperture is whitish or pinkish inside; the outside pattern is shining through.

Width 12.7-19.5 mm; height 11.2-19.7 mm.

T. macandrewiana is characterized by (1) its globular general shape, even in juvenile specimens, which are neither keeled nor angular at the periphery, and

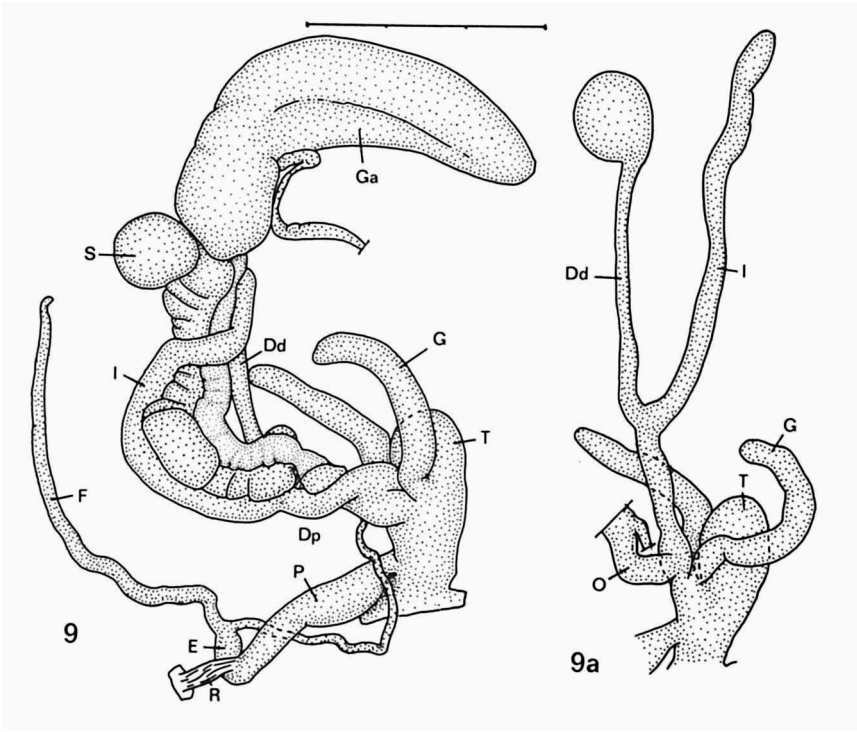


Fig. 9, 9a. *Theba macandrewiana*, genitalia, two views of the same specimen, Ilha Selvagem Grande (RMNH, Th. Monod leg.); Scale line: 3 mm. For abbreviations see p. 8.

(2) the relatively simple colour pattern, often consisting of many brown, narrow, spiral lines on a light background.

T. arinagae is smaller than *T. macandrewiana*, its colour pattern is different and the umbilicus is more frequently not completely closed.

Genitalia (fig. 9). — The genitalia of this species have been figured by Backhuys (1972: fig. 10), after a juvenile animal. We can give an additional figure of a full-grown specimen.

The flagellum is more than one and a half times as long as penis and epiphallus together and about twice as long as the glandulae mucosae, which are relatively small as compared to e.g. those of *T. pisana* or *T. subdentata*. The proximal part of the spermatheca duct is about half as long as the distal part; the diverticulum reaches clearly beyond the spermatheca. The oviduct is about as long as the vagina.

According to Germain (1934: 324) there is no flagellum in this species; this statement appears to be incorrect.

Backhuys (1972) compared his *"T. pisana ustulata"* with *"T. pisana"* from

Orzola, Lanzarote, Canary Islands. From his fig. 11 it becomes obvious that he confused *T. pisana* with *T. impugnata*; the latter species is characterized by a long flagellum, which is (nearly) completely lacking in the former one.

Range (fig. 1). — *T. macandrewiana* occurs on the three Salvages Islands, where living animals have been found together with many empty shells (fig. 2).

Notes. — *Helix ustulata* Férussac, 1823 is not a nomen nudum; the nominal taxon is based on two figures (pl. 125 figs. 1, 2), published in combination with the name on the cover of the 20th part of Férussac's well-known "Histoire" (Kennard, 1942a: 15). According to ICZN Art. 12 (b)(7) the name is available, although the text on "Achatina ustulata, Lamarck" was published much later, i.e. by Deshayes (1851: 164). As a consequence *Helix ustulata* Lowe, 1852 is a junior homonym and not available. It has been misleading that Deshayes & Milne Edwards (1838: 297) described *Achatina ustulata* without referring to Férussac's earlier use of the name *Helix ustulata* for the same species. Thus *T. macandrewiana* is the correct name for the endemic *Theba* species of the Salvages Islands; its original description leaves no doubt.

In RMNH there are two syntypes (shells) of *Helix ustulata* Lowe (RMNH 51167/2) from "Little Salvage" (= Ilha Selvagem Pequena, = Gran Piton). In addition there are large series of shells from the three main Salvages Islands, collected by W. Backhuys, and a few specimens in alcohol, mainly juvenile animals, also from the three main islands. The living snails have been collected by W. Backhuys (Oegstgeest), J. C. den Hartog (Leiden) and Th. Monod (Paris).

Bravo & Coello (1978: 21, fig. 12) and Baez & Sánchez-Pinto (1983: 99, fig.) have mentioned the abundance of terrestrial gastropod shells on Ilha Selvagem Grande, apparently referring to *T. macandrewiana*. According to the latter authors, this occurrence of subfossil shells of terrestrial snails indicates a more humid climate in the past. This conclusion cannot be supported because only a single, extant, gastropod species is involved.

T. macandrewiana is the only non-marine gastropod species known from the Salvages Islands. Taylor (1912: 376) reported the finding of "seven shells of this species in the crop of a Kestrel shot on the Salvages". We noticed specimens of two species of beetles, belonging to the Tenebrionidae, conserved together with the soft parts of the snails in their shells in samples in alcohol.

Theba orzolae Gittenberger & Ripken, 1985
(figs. 15, 16)

Theba orzolae Gittenberger & Ripken, 1985: 402 ("Late Miocene deposit at Orzola"). Holotype & 39 paratypes: RGM 229363, 229364.

Notes. — We refer to Gittenberger & Ripken (1985: 402) for a description of this Late Miocene species, characterized by a very small shell (width 9.6-13.1 mm; height 6.9-8.8 mm), with an inflated body-whorl and a low spire. The general shape of the shell reminds that of the recent endemic *Theba* species of the Canary Islands. However, juvenile shells of about two whorls have an angular periphery, which is not keeled. *T. arinagae* has a much more globular shell. Because of the state of preservation of the specimens it remains uncertain whether the umbilicus is really open (as in fig. 16); in the umbilical region the apertural lip may be fragile and can easily be damaged, e.g. without noticing during preparation.

T. orzolae is known from the deposits at Orzola on Lanzarote only.

Theba grasseti (Mousson, 1872)
(figs. 1, 14)

Helix grasseti Mousson, 1872: 31, pl. 2 figs. 33, 34 ("près de Las Palmas").
Helix pisana var. *grasseti*; Wollaston, 1878: 371. Taylor, 1912: 381, pl. 30 fig. 9.

Material. — CANARY ISLANDS. Gran Canaria: La Isleta, 50-100 m alt. (RMNH); id., La Luz (SMF); id., Las Coloradas (RD; RMNH); Las Palmas (RMNH; SMF); id., Santa Catalina (RMNH); Las Palmas — Angostura, c. 300 m alt. (RD; RMNH).

Shell (fig. 14). — Shell depressed, somewhat lens-shaped, with 4 - 4½ flattened whorls; periphery strongly angular and sometimes slightly carinate near the beginning of the body-whorl, more rounded near the aperture. Umbilicus (nearly) completely closed by the reflected columellar lip. Aperture more or less elliptical; the columellar angle below may be rather prominent, i.e. more distinct than in the specimen figured. Usually the outher lip is not or only slightly thickened inside.

The shells are dull. All specimens studied have a varied pattern of (dark) brown (interrupted) spiral lines and spirally arranged blotches on a whitish background. The aperture is light brownish inside, with the outside pattern shining through.

Juvenile shells of c. three whorls have a more triangular aperture (apart from the incision by the penultimate whorl), with a prominent angle below and

at the periphery; the outer lip is more strongly developed than in full-grown specimens.

Width 13.7-16.2 mm; height 8.4-11.4 mm.

T. grasseti differs from *T. impugnata* by (1) the periphery of the shell, which is angular with an obsolete keel at most, not crenulate, (2) the usually more simple peristome, without a thickened internal lip, (3) a slightly less prominent microsculpture, and (4) more fragile shell walls. The other *Theba* species can be distinguished from *T. grasseti* more easily.

Genitalia. — Only a few badly preserved subadult specimens were available for anatomical study. They made clear that *T. grasseti* belongs to the majority of the *Theba* species with a relatively long flagellum on the epiphallus.

Range (fig. 1). — *T. grasseti* is only known from Gran Canaria. Taylor (1912: 381) published interesting information on this species and its relation to *T. pisana*: "It . . . always lives apart from the typical *pisana*, being practically confined to the highlands and to the topmost ridges of the barrancos, and is never found naturally below an altitude of 400 feet, except on the Isleta, where the typical *pisana* does not exist. The var. *grasseti* is always found feeding on the *Euphorbia balsamifera*, while the typical *pisana*, which is exceedingly variable, swarms in the gardens, etc., feeding mostly on the Aloe (*Agave americana*) and the Prickly Pear (*Opuntia dillenii*) near the sea level, and is never found more than 100 feet above it . . .".

Ripken found live specimens in 1982, on the peninsula La Isleta, N. of Las Palmas; he could not reconfirm the occurrence on the mainland of Gran Canaria, especially not near La Angostura, where *T. grasseti* had been collected 13.viii.1938 by H. J. Lam and A. D. J. Meeuse. The species might be confined to La Isleta and the adjacent extreme northeastern part of Gran Canaria near Las Palmas.

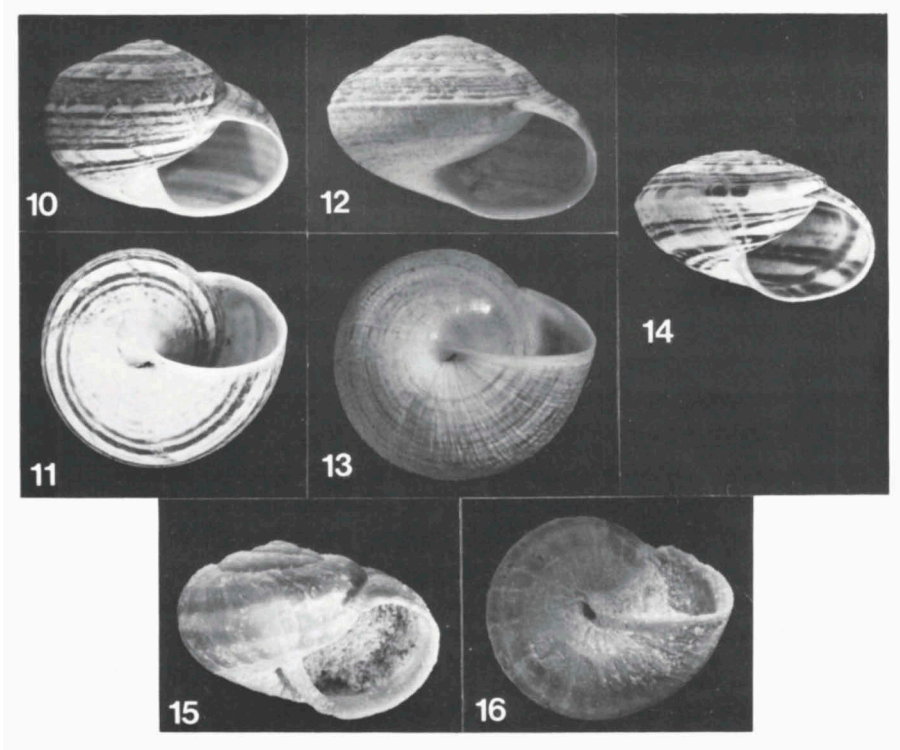
Notes. — The original description, the clear figure accompanying it, and the type locality, leave no doubt as to the identity of *Helix grasseti*.

T. grasseti is not known to occur sympatric with any other *Theba* species. (See also the preceding remarks under the heading "Range").

Theba geminata (Mousson, 1857)
(figs. 10, 11, 18-20)

Helix pisana var. *geminata* Mousson, 1857: 132 ("Lanzarote und Fuerta Ventura"); 1859: 84. Wollaston, 1878: 371.
Helix pisana var. *clauso-inflata* Mousson, 1857: 132 ("Fuerta Ventura"); 1859: 83.
Helix geminata; Mousson, 1872: 29.
Helix geminata var. *clauso-inflata*; Mousson, 1872: 30.
Helix geminata var. *parvula* Mousson, 1872: 31 ("Fuerteventura"). Not *Helix parvula* Rang, 1831.

Material. — CANARY ISLANDS. Isla Graciosa: (Wollaston, 1878: 372, "pisana"). Lanzarote: El Risco (RD; RMNH); Orzola (GD); Malpais de la Corona (RMNH); Jameos del Agua (RMNH); Haría (RMNH; ZMA); Haría — los Valles (SMF; ZMA); la Caleta — Bajamar (ZMA); Playa de Famara (RMNH; ZMA); El Mojón (ZMA); Montaña de las Nuevas (RMNH); Castillo de Guanapay (RMNH); Tinajo — Tiagua (ZMA); Teguise — Mozaga (GD); Mozaga (RMNH); Yaiza (RMNH); Playa de Janubio — Playa Blanca (GD; ZMA); Playa Blanca (GD); Punta del Papagayo (RD; RMNH; ZMA). Isla de Lobos (SMF). Fuerteventura: Corallejo (RMNH); La Oliva (RMNH); Montaña Muda (RMNH); Playa del Matorral (RMNH); Los Molinos (RMNH); Betancuria (GD; RMNH); Vega del Río de Palmas (RMNH); Barranco Morra Fénduca (RD; RMNH); Toto (RMNH); Cortijo de Chilegua (RMNH); Playa de Ugán (RMNH); Gran Tarajal (RMNH); Istmo de la Pared (RMNH); Morro Jable (RMNH); Cofete (RD; RMNH); Punta de Gandia (GD). Gran Canaria (Mousson, 1872: 30). Tenerife: Bajamar (RD; RMNH); Buenavista — Los Silos (GD; RD; RMNH). La Palma (SMF). Gomera (RMNH ex Lowe & Wollaston). Hierro: Sabinosa (RMNH).



Figs. 10-16. Endemic recent [10-14] and fossil [15, 16] *Theba* spec. from the Canary Islands. 10, 11, *T. geminata*, actual width 18.8 mm, Fuerteventura, barranco Morro Fenduca, N. of Pájara (RMNH, W. Backhuys leg.). 12, 13, *T. impugnata*, actual width 14.3 mm, Lanzarote, N. of Haría (RMNH, W. Backhuys leg.). 14, *T. grasseti*, actual width 16.2 mm, Gran Canaria, along the road from Las Palmas to Angostura, 300 m alt. (RMNH, H. J. Lam & A. D. J. Meeuse leg.). 15, 16, *T. orzolae*, holotype, actual width 11.5 mm, Lanzarote, Late Miocene deposits at Orzola (RGM 229363, G. J. Boekschoten leg.). Photographs by G. J. van Zonneveld.

Shell (figs. 10, 11). — Shell more or less depressed globular, with 4¼ - 5 moderately convex whorls. At the beginning of the body-whorl the periphery is regularly rounded in most specimens. The aperture is irregularly elliptical, with an oblique, nearly straight columellar edge; the outer lip is clearly thickened inside. Umbilicus (nearly) completely closed by the reflected columellar lip.

The shells are dull or somewhat silky. There is a colour pattern with (dark) brown spiral bands, varying in width, sometimes fused and sometimes interrupted, and usually a few rows of spirally arranged blotches, on a whitish background. The aperture is whitish inside, with the outside colour pattern shining through. In bleached specimens the brown colouration may have turned to bluish.

The most juvenile specimen studied, with c. 3½ whorls, is angular at the periphery, but not as strongly as are comparable specimens of *T. impugnata*.

Width 14.6-20.2 mm; height 10.7-16.8 mm.

T. geminata differs from the sympatric *T. impugnata* most clearly by its more inflated body-whorl, which has a regularly rounded or slightly angular periphery, without a crenulate band. The species cannot be confused with *T. pisana* because of its (nearly) closed umbilicus.

Genitalia (fig. 18). — We dissected a specimen of *T. geminata* and found the flagellum about twice as long as penis and epiphallus together and about one and a half times as long as the slender glandulae mucosae. The proximal part of the spermatheca duct is clearly shorter than the distal part, which is shorter than the diverticulum. The oviduct is somewhat shorter than the vagina. In absolute size the genitalia of *T.geminata* are about twice as large as those of *T. impugnata*.

Range (figs. 1, 19, 20). — *T. geminata* is a common species on the two eastern Canary Islands, Lanzarote and Fuerteventura, with adjacent islets. On the other islands of the archipelago the species is known from only a very limited number of localities; some of these records are vague, e.g. mentioning only the island as such, and need to be confirmed. Therefore, *T. geminata* might be indigenous only on Lanzarote and Fuerteventura and not so on the other Canary Islands.

Notes. — There can be no doubt concerning the identity of the form described as var. *geminata* of *T. pisana* by Mousson (1857: 132), which was given specific status by the same author later on (1872: 29). The original description, the localities mentioned with it and the fact that Mousson himself described the partly sympatric *T. impugnata* as well, enable an easy judgement. The interpretation of the "var. *clauso-inflata*", introduced as a variety of *T. pisana* by Mousson (1857: 132) and listed with *T. geminata* by the same

author afterwards (1872: 30), is more problematical. We follow Mousson (1872), considering his variety a form of *T. geminata*, because of the original description of the variety and the fact that Mousson can be considered a specialist in *Theba* species, who had noticed the importance of the shape of the umbilicus as a diagnostic character.

Despite the abilities of Mousson, mentioned in the preceding paragraph, it remains quite obscure what is meant with "*Helix geminata* var. *parvula*". Judging from the short description (Mousson, 1872: 31) only, this fossil form might be similar to, or even identical with *T. arinagae*. However, whatever the status of this form may be, the name chosen for it cannot be used because of *Helix parvula* Rang, 1831 having priority.

Shells of *T. geminata* and maybe of *T. impugnata* as well occur in great abundance locally on the islet Graciosa, as may be concluded from figures published by Baez & Sánchez-Pinto (1983: 109) and Baez & Bacallado (1984: 344). These authors consider this an indication for a more humid climate in the past. We cannot accept this view because the species involved are still flourishing in the area. Local abundance is seen in various *Theba* species (fig. 2).

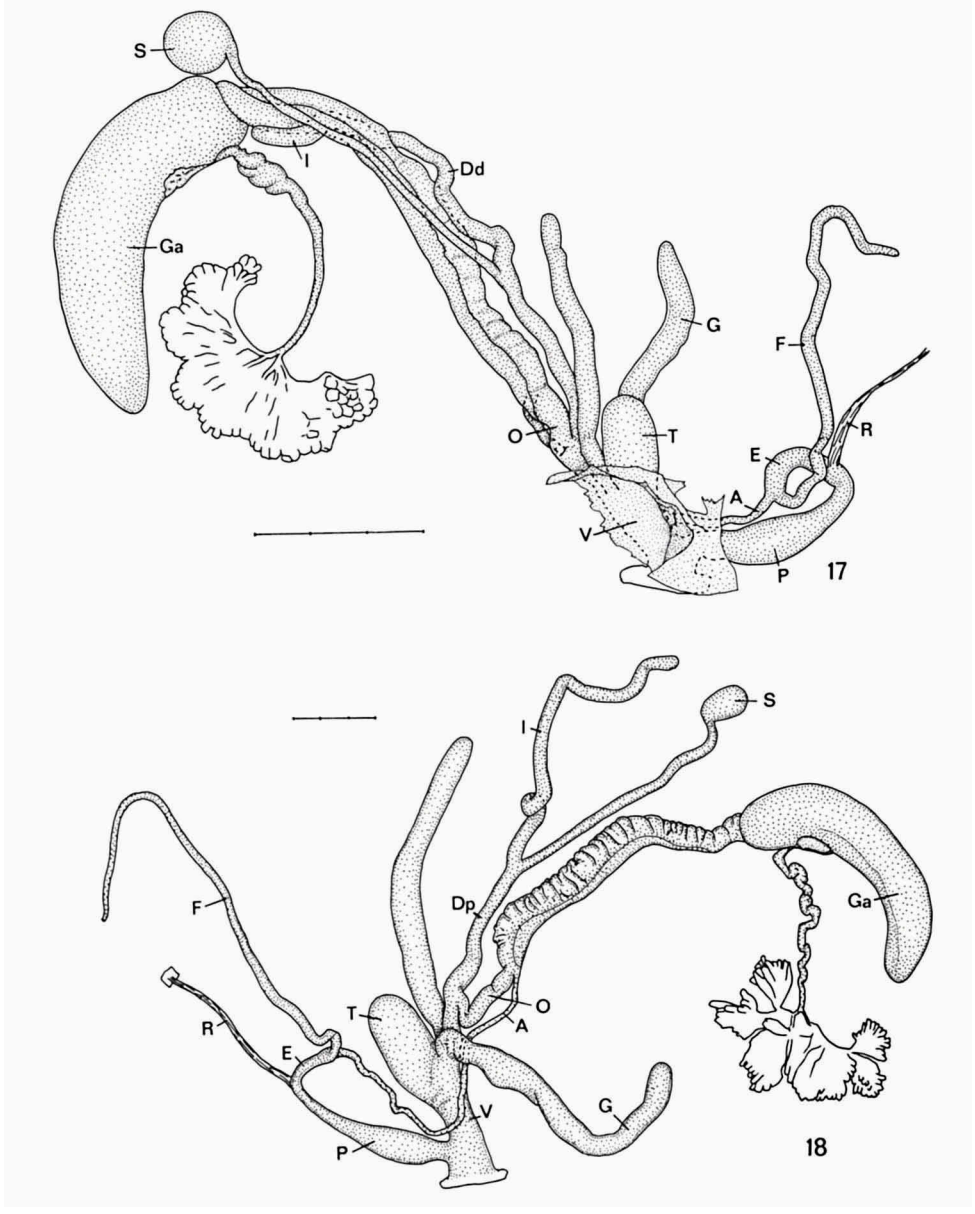
T. geminata and *T. impugnata* are sympatric on northern Lanzarote and on Graciosa. Where the two species are found together they are about equally common. According to Mousson (1872: 30) *T. geminata* is found with *T. p. pisana* on both Tenerife and Gran Canaria. A mixed population has been found indeed by the second author of the present paper on Tenerife.

Theba impugnata (Mousson, 1857)
(figs. 1, 12, 13, 17, 19)

Helix impugnata Mousson, 1857: 133 ("Lanzarote" [not on Fuerta Ventura, as becomes obvious from Mousson, 1872: 32, 33]); 1859: 84; 1872: 32, pl. 2 figs. 35, 36.
Helix impugnata var. *subgeminata* Mousson, 1872: 32 ("Lanzarote").

Material. — CANARY ISLANDS. Isla Graciosa: (Wollaston, 1878: 373). Lanzarote: El Risco (RD; RMNH); Orzola (RMNH); Malpais de la Corona (RMNH); Cueva de los Verdes (RD; RMNH); Jameos del Agua (RMNH); Haría (GD; RMNH); Haría — los Valles (SMF; ZMA); Teneguime (RMNH); Playa de Famara (RMNH); Montaña Corona (RMNH); Montaña de las Nuevas (RMNH).

Shell (figs. 12, 13). — Shell depressed, with 4 - 4½ whorls; initial whorls strongly flattened and body-whorl slightly shouldered. Near the beginning of the body-whorl the periphery is angular to more regularly rounded and more or less clearly carinate; there is always a narrow crenulate band around the periphery, discernible as far as the peristome. Often the suture is partly



Figs. 17, 18. Genitalia of *Theba impugnata* [17] and *T. geminata* [18] from Lanzarote, Haría — los Valles (ZMA, R. G. Moolenbeek leg.); scale lines: 3 mm. For abbreviations see p. 8.

situated slightly below the keel, which may be followed along the upper whorls then; otherwise the suture is not indented at all or it is situated in a slightly concave zone. Aperture more or less elliptical, sometimes with a rather prominent columellar angle below; the outer lip is clearly thickened inside. Umbilicus (nearly) completely closed by the reflected columellar lip.

The shells are dull. The colour pattern is extremely variable, with (dark) brown (interrupted) spiral lines and spirally arranged blotches on a whitish background. The aperture is whitish inside, sometimes with a pinkish hue at the parietal side; the outside pattern is shining through.

In juvenile shells the keel is (much) more prominent than in full-grown specimens.

Width 12.6-17.7 mm; height 7.7-12.0 mm.

T. impugnata can be distinguished from both *T. geminata* and *T. grasseti* by (1) the crenulate band marking the periphery of the body-whorl, which usually is sharply angular and (2) the dull aspect of the shell surface.

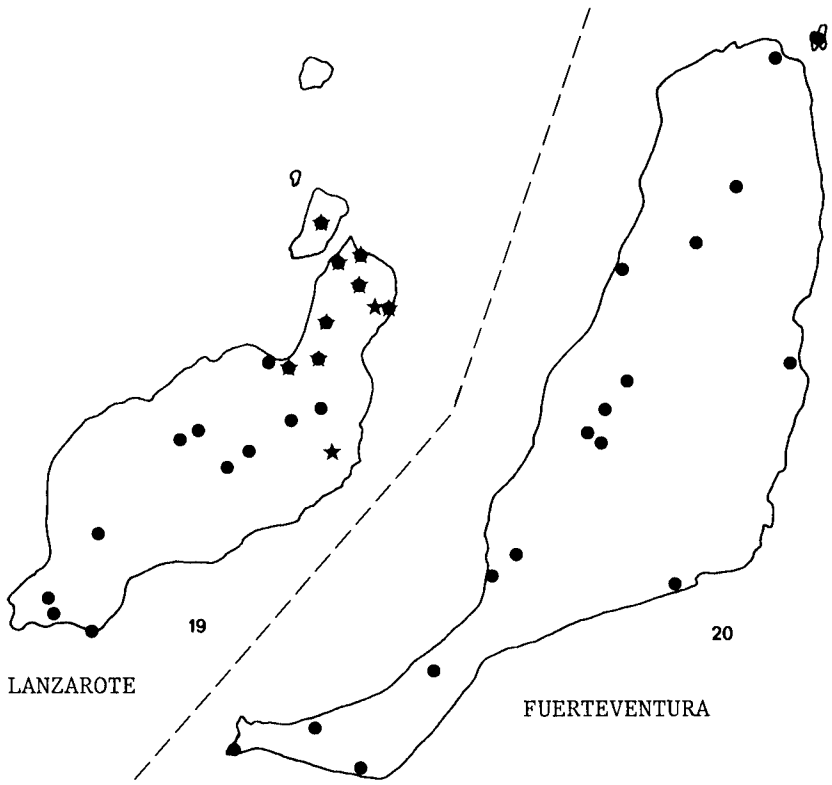
The other *Theba* species differ by these and additional characters from *T. impugnata*.

Genitalia (fig. 17). — We dissected a specimen of *T. impugnata* and found the flagellum less than one and a half times as long as the slender glandulae mucosae, which are about as long as penis and epiphallus together. The proximal part of the spermatheca duct is half as long as the distal part, which is slightly shorter than the diverticulum. The oviduct is somewhat shorter than the vagina. In absolute size the genitalia of *T. impugnata* are about half the size of those of *T. geminata*.

Range (fig. 19). — The species is restricted to the northeastern part of Lanzarote and the adjacent islet of Graciosa.

Notes. — *T. impugnata* has been described and figured quite satisfactory by Mousson (1857: 133; 1872: 32, pl. 2 figs. 35, 36). The "var. *subgeminata*" has clearly been introduced for extreme forms of *T. impugnata* with a weekly developed peripheral keel, which becomes obsolete on the body-whorl. Such forms do not necessarily indicate hybridization with *T. geminata*. They are as frequent as are very sharply keeled shells, which mark the other end of the range of variation concerning this character. The sculpture of the periphery of the shells is independent of the prominence of the angularity.

We could study eleven samples of *T. impugnata* from Lanzarote and found this species sympatric with *T. geminata* in eight of these. Where the two species occur together they are about equally common.



Figs. 19, 20. Records of *Theba impugnata* (stars) and *T. geminata* (dots) on Lanzarote [19] and Fuerteventura [20], illustrating the occurrence of *T. impugnata* on Isla Graciosa and N. Lanzarote only (nearly always sympatric with *T. geminata*).

Theba subdentata (Férussac, 1821)

This polytypic species is found in western Morocco (figs. 1, 30). It can be subdivided, somewhat arbitrarily, into five subspecies. North of the Oued Sous there is a form with a very characteristic, sharply keeled shell, viz. *T. subdentata helicella* (Wood, 1828). This subspecies is represented in sand-dunes along the coast. At several places where sand-dunes and rocky areas come together there are forms intermediate between *T. s. helicella* and *T. s. dehnei* (Rossmässler, 1846). The latter subspecies, which is found in a more rocky habitat, also north of the Oued Sous, has a shell which is hardly or not angular at the periphery. It is the northernmost member of an indistinctly stepped cline, constituted by *T. s. dehnei*, *T. s. subdentata*, and *T. s. meridionalis* (Sacchi, 1955). From north to south the shells get a more

prominent apertural lip, more strongly developed parietal denticle(s), and a relatively higher body-whorl. However, in the southwestern subspecies *T. s. legionaria* (Sacchi, 1955) characters of *T. s. meridionalis* and *T. s. dehnei* are combined.

Theba subdentata helicella (Wood, 1828)
(figs. 21, 22, 30, 50)

Helix planata Chemnitz, 1795: 281, pl. 209 figs. 2067-2069. Invalidated publication. Off. index rej. inv. works zool. nomencl., 1958: 5.

[*Helix*] *Helicella* (*Heliomanes*) *planata* Férussac, 6.iv.1821: xij (explanation to pl. 30 fig. 2 [published 26.ii.1820]; no locality mentioned, but see next reference). Not *Helix planata* Maton & Rackett, 1807 (= *Planorbis* spec.).

Helix (*Helicella*) *planata*; Férussac, 26.v.1821: 49 [45] ("royaume de Maroc").

Carocolla planata; Lamarck, 1822: 99. Deshayes & Milne Edwards, 1838: 148.

Helix helicella Wood, 1828: 21, pl. 7 fig. 7 (= Férussac, 1820: pl. 30 fig. 2). Replacement name for *Helix planata* (see notes).

Helix (*Theba*) *erythrostoma* Beck, 1837: 15. Replacement name for *Helix planata* Férussac, 1821.

Helix (*Theba*) *planata*; Beck, 1837: 15.

Helix planata; L. Pfeiffer, 1846: 22; 1848: 158, pl. 21 figs. 10-12 [pl. 21 was published in 1843]; 1854: 397, pl. 144 figs. 5, 6 [pl. 144 was published in 1852]. Kobelt, 1876: 58, pl. 115 figs. 1135-1137. Morelet, 1880: 30 (part.).

Helix calliostoma Adams & Reeve, 1848: 59, pl. 14 fig. 7a, b (no locality mentioned). Reeve, 1852: pl. 105 fig. 585a, b (no locality mentioned).

Helix erythrostoma L. Pfeiffer, 1850: 84 (no locality mentioned) [An independent description, not Beck, 1837]; 1853: pl. 132 figs. 23, 24.

Helix planata a. *acutangula* Lowe, 1861: 196 ("Mogador").

Helix planata b. *obtusangula* Lowe, 1861: 197 ("Mogador").

Helix dehnei var. *thlipsa* Westerlund, 1889: 155 (no locality mentioned).

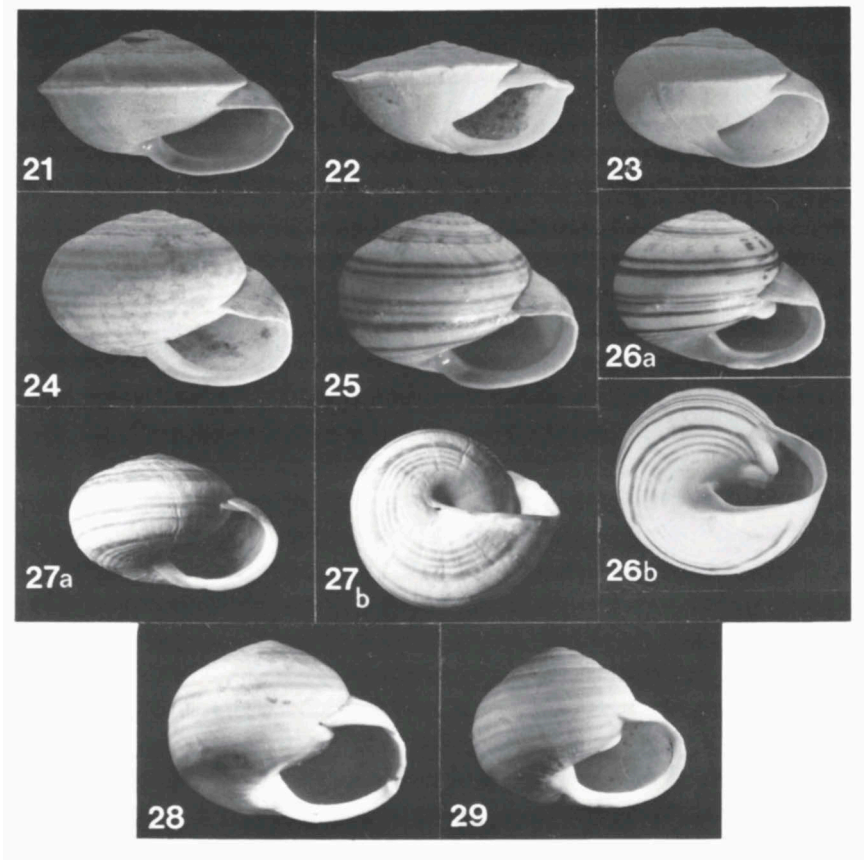
Euparypha planata var.; Pallary, 1921: 111, pl. 3 figs. 13-15.

Material. — SPAIN. Almería: El Alquián, WF57 (see notes) (RMNH).

MOROCCO. Safi: Mouth of the Oued Tensift, MR64 (Sacchi, 1955b: fig. 1); 14 km NE. of Essaouira (= Mogador), MQ39 (SMF); 9 km E. of Essaouira, MQ38 (SMF); Essaouira, MQ28 (RD; RMNH, RMNH 51166 ex Lowe & Wollaston/2 syntypes of *acutangula*, 51165 [[1]→*dehnei*] ex Lowe & Wollaston/2 syntypes of *obtusangula*; SMF); 3 km S. of Essaouira, MQ28 ((SMF); 8 km S. of Essaouira, MQ28 (RD; RMNH; SMF); Cap Sim, MQ27 (Pallary, 1904: 45); 5 km E. of Sidi-Kaouki, MQ27 (SMF); 2 km S. of Sidi-Kaouki, MQ27 (SMF); 7 km N. of Tamri, MQ20 [→*dehnei*; recent and fossil] (SMF); 3 km N. of Tamri, MP19 (SMF); Tamri, MP29 (SMF); 6 km W. of Tamri, MP19 [→*dehnei*; fossil] (RD; RMNH); 5 km N. of Cap Rhir, MP19 (RD; RMNH).

Shell (figs. 21, 22). — Shell depressed, more or less lens-shaped, with 4¼ - 5 flattened whorls, which are all sharply keeled at the periphery. Sometimes the carina can be (partly) followed along the whorls of the spire; if not, the sutures are not incised at all. Aperture broad elliptical, with a slight angle at the right

1) →, with characters of . . .



Figs. 21-29. *Theba subdentata* from Morocco. 21, *T. s. helicella*, actual width 19.4 mm, province of Safi, Essaouira (= Mogador) (RMNH, ex Altimira). 22-24, three shells, actual widths 19.6, 17.8 and 20.2 mm, illustrating the range of variation between *T. s. helicella* and *T. s. dehnei* in a fossil population, province of Safi, Essaouira — Agadir, 6 km SW. of Tamri (RMNH, Th. E. J. Ripken leg.). 25, *T. s. dehnei*, relatively high specimen, actual width 18.2 mm, province of Safi, Tamri (RMNH, ex Altimira). 26a, b, *T. s. meridionalis*, actual width 16.2 mm, province of Agadir, Bu Talán (hill), S. of Sidi-Ifni (RMNH, ex Altimira). 27a, b, *T. s. legionaria*, neotype, actual width 17.6 mm, province of Tarfaya, along the coastal road 11.5 km W. of the Oued Chebeica (RMNH 55952, Th. E. J. Ripken leg.). 28, *T. s. subdentata*, lectotype, actual width 18.0 mm, unknown locality (MNHN, ex Férussac). 29, *T. s. subdentata*, actual width 16.8 mm, province of Agadir, 3 km E. of Âït-Melloul (RMNH, Th. E. J. Ripken leg.). Photographs by E. G.

side (in front view), corresponding with the carina, and without a columellar angle below; the outer lip is clearly thickened inside. Only exceptionally there is an obsolete angular denticle. The umbilicus is completely closed by the reflected columellar lip.

The shells are rather glossy if fresh. The colour pattern is not very variable.

Usually the shell is light brown, with a vague spiral pattern and a few radial lighter streaks below the periphery and whitish above it. Above the periphery there may be a light spiral band adjacent to the carina. Additional bands are rarely seen. The aperture is purple to pinkish inside.

Juvenile specimens could not be studied. Most probably they are quite similar to the adult shells in general shape.

Width 16.8-21.3 mm; height 8.6-11.9 mm.

Genitalia. — Various data concerning the anatomy of *T. s. helicella* ("*Euparypha planata*") have been published by Hesse (1915: 9-11, pl. 632 figs. 1-7), who dissected five adult animals. The flagellum is more than twice as long as penis and epiphallus together and one and a half to nearly twice as long as the relatively thick glandulae mucosae. The proximal part of the spermatheca duct is shorter than the distal part, which measures about two thirds of the length of the diverticulum, which thus reaches far beyond the spermatheca. The ratios of these parts vary between 7 : 9.5 : 14 and 9 : 16 : 27. The oviduct is about as long as the vagina or clearly shorter, measuring only slightly more than one fourth of it in the most extreme specimen.

Range (fig. 30). — *T. s. helicella* is known from W. Morocco, where it is found in sand-dunes in the coastal area. The subspecies is known from the mouth of the Oued Tensift, c. 30 km S. of Safi, southward to the surroundings of Cap Rhir, c. 35 km NW. of Agadir. There is a sample in the former Altimira collection (RMNH), indicating that the subspecies has once been found in southern Spain, in the province of Almería, at El Alquián. The second author tried in vain to confirm this record. Most probably *T. s. helicella* has once been introduced in Spain and eventually became extinct again.

Notes. — There is a sample with six juvenile shells from the Férussac collection in MNHN, labelled *Helix planata*. We cannot consider these specimens syntypes, however, because they do clearly not agree with the figure published by Férussac (1820: pl. 30 fig. 2), which shows a full-grown shell. Nevertheless there can be no doubt about the identity of Férussac's species from the "royaume de Maroc", because the main diagnostic characters are obvious from the original figure. *H. calliostoma* Adams & Reeve can hardly be misinterpreted, even if judging from only the first description and figures, as we did; we agree with L. Pfeiffer (1854: 397), who synonymized this nominal taxon with *H. planata*.

H. erythrostoma L. Pfeiffer, clearly illustrated by the author (1853: pl. 132 figs. 23, 24), *H. planata obtusangula* Lowe, two syntypes of which are in RMNH (no. 51165), and, after its description; *H. dehnei* var. *thlipsa* Westerlund, represent forms intermediate between *T. s. helicella* and *T. s. dehnei*. The shells are sharply keeled at the beginning of the body-whorl, but much less

so near the aperture. A similar intermediate form has been figured as *H. planata* by Morelet (1880: pl. 3 fig. 7 left). With Kobelt (1876: 58) we consider *H. erythrostoma* L. Pfeiffer a junior synonym of *H. planata*; *H. planata obtusangula* is equally subjectively listed in the synonymy of *T. s. helicella*. The original description, the type locality and two syntypes (RMNH 51166) of *H. planata acutangula* Lowe lead to the conclusion that Morelet (1880: 30) correctly considered this nominal taxon a junior synonym of *H. planata*.

The forms intermediate between *T. s. helicella* and *T. s. dehnei* may occur in quite variable populations, in which both extremes are found as well, or in much less variable populations in which all shells are intermediate in character. A sample of 49 fossil shells of *T. subdentata* s.l. collected 6 km W. of Tamri by the second author of the present paper contains c. 35 specimens of typical *T. s. helicella*, whereas the remaining shells vary between this form and *T. s. dehnei* (see figs. 22-24); it is unknown whether these forms actually lived together at the same time. Maybe this sample documents a former shift in ranges. Nearby, at 9 km SSW. of Tamri, 25 living *T. subdentata* were collected which are all intermediate in character.

T. s. helicella is largely sympatric with *T. pisana ampullacea*.

Theba subdentata dehnei (Rossmässler, 1846)
(figs. 23-25, 30)

Helix dehnei Rossmässler, 1846: 173 ("Afrika"). L. Pfeiffer, 1848: 153; 1849: 250, pl. 36 figs. 22-24. Reeve, 1854: pl. 175 fig. 1186. Kobelt, 1876: 59, pl. 115 figs. 1138-1140 ("Djebel Hadid nördlich von Mogador und am Gilishügel nahe der Stadt Marocco"). Morelet, 1880: 28, pl. 2 fig. 1 (3 figs.).
Helix erythronixia Kobelt, 1876: 59 (no locality mentioned).
Helix planata; Morelet, 1880: 30 (part.), pl. 3 figs. 7 left and right. Not *H. planata* Férussac, 1821.
Helix pisana var. *semifulva* Taylor, 1912: 390, pl. 30 fig. 6 ("Mogador").
Euparypha dehnei var. *depressa* Pallary, 1921: 114, pl. 3 fig. 16 ("Mogador").

Material. — MOROCCO. Safi: Cap Beddouza (= Cap Cantin), MS 70 (SMF); 6 km N. of Safi, MR78 (SMF): 3 km N. of Safi, MR77 (SMF); Safi, MR77 (SMF); 5 km S. of Safi, MR77 (RMNH); 10 km S. of Safi, MR76 (SMF); 12 km S. of Safi, MR76 (SMF); Djebel Hadid, 35 km NE. of Essaouira (= Mogador), MR51 (Morelet, 1880: 28); 3 km E. of Ounara, MQ59 (SMF); Essaouira, MQ28 (RMNH; SMF; ZMA); 10 km S. of Essaouira, MQ38 (RD); 23 km S. of Essaouira, MQ36 (SMF); 3 km S. of Smimou, MQ35 (SMF); Cap Tafelney, MQ24 (SMF); 3 km E. of Cap Tafelney, MQ24 (RD); 10 km E. of Cap Tafelney, MQ34 (SMF); 25 km S. of Smimou, MQ33 (SMF); 4 km N. of Pointe Imessouane, MQ21 (SMF); Pointe Imessouane, MQ21 (SMF); 12 km N. of Tamri, MQ20 (SMF); 10 km N. of Tamri, MQ20 (RD; RMNH; SMF); 7 km N. of Tamri, MQ20 [→ *helicella*; recent and fossil] (SMF); Tamri, MP29 [fossil] (SMF); 6 km W. of Tamri, MP19 [→ *helicella*; fossil] (RD; RMNH); Cap Rhir, MP19 [→ *helicella*] (Sacchi, 1955b: fig. 1); 2.5 km E. of Cap Rhir, MP 18 [→ *helicella*] (RD; RMNH).

Shell (figs. 23-25). — Shell with an inflated body-whorl and a rather low spire; with 4¾ - 5 flattened to moderately convex whorls. Near the beginning of the body-whorl the periphery is angular to regularly rounded. Aperture broad elliptical, sometimes with an indistinct columellar angle below; the outer lip is clearly thickened inside. There may be an obsolete angular denticle close to the upper end of the parietal wall. The umbilicus is completely closed by the reflected columellar lip.

The shells are rather glossy when fresh. A minority of the specimens is uniformly whitish. The colour pattern is more variable than in *T. s. helicella*. Usually there is a variable number of (rather) narrow, brown, spiral bands; spirally arranged blotches are far less common. The aperture is purple to pinkish inside.

Juvenile specimens could not be studied. In certain adult specimens, however, the structure of the spire indicates that juvenile shells are sharply keeled.

Width 16.0-19.3 mm; height 10.9-12.8 mm.

See also the descriptions of *T. s. subdentata* and *T. s. legionaria*.

Genitalia. — Various data concerning the anatomy of *T. s. dehnei* have been published by Hesse (1915: 11-13, pl. 632 figs. 8-11), who dissected five adult animals. The genitalia are said to be very similar to those of *T. s. helicella* (*"Euparypha planata"*). The flagellum is twice as long as penis and epiphallus together and somewhat longer than the relatively thick glandulae mucosae. The proximal part of the spermatheca duct is clearly shorter than the relatively thin distal part, which is only half as long as the diverticulum, which thus reaches far beyond the spermatheca. The oviduct is nearly as long as the vagina or clearly shorter. The ratios of these parts vary between 10 : 12 : 22 and 10 : 14 : 31.

Range (fig. 30). — *T. s. dehnei* is known from the coastal area in W. Morocco, from Cap Beddouza, c. 25 km N. of Safi, southward to the surroundings of Cap Rhir, c. 35 km NW. of Agadir.

Notes. — The exact type locality of this subspecies is unknown, because the single specimen on which Rossmässler (1846: 173) based his description had been found by Dr. Dehne under gum arabic. Therefore it was considered an African species. L. Pfeiffer (1849: 251) noticed the similarity with *H. subdentata*. The localities mentioned by Kobelt (1876: 59) are based on new material. Obviously Kobelt did not distinguish between *T. s. dehnei* and *T. s. subdentata*, because only the locality north of "Mogador" (= Essaouira) applies to *T. s. dehnei*; near "Stadt Marocco" (= Marrakech) *T. s. subdentata* is found.

Helix erythronixia has been described as simply a form of *H. dehnei* by its author already (Kobelt, 1876: 59). In fact the authorship is only a consequence

of the present rules of nomenclature: Kobelt cited a supposed Bourguignat name in combination with a short description.

The diagnosis and illustration of Pallary's (1921) "var. *depressa*" apply to *T. s. dehnei* tending to *T. s. helicella*. Intermediate forms between the two subspecies are not uncommon near Essaouira (= Mogador). The shell figured by Morelet (1880: pl. 3 fig. 7 left) as *H. planata* and our fig. 23 belong to this form. *H. erythrostoma* L. Pfeiffer and *H. planata obtusangula* Lowe are considered *T. s. helicella* tending to *T. s. dehnei* in the present paper. Because it is absolutely impossible to distinguish sharply between the two subspecies, the distribution over two synonymy lists of nominal taxa applying to intermediate forms remains a quite subjective procedure.

It is unclear what form Servain (1880: 113) had in mind while dealing with material from near Sevilla, Spain, as similar to *dehnei*: ". . . de la forme *Pisana* type, on passe à la forme *Dehnei*, dont nous avons retrouvé, près de Séville, quelques échantillons difficiles à distinguer de ceux du Maroc."

Because of its large size, the depressed shape and its provenance ("Mogador") we consider Taylor's *H. pisana* var. *semifulva* a colour form of *T. s. dehnei*.

See also the notes with *T. s. legionaria*.

T. s. dehnei occurs sympatric with three subspecies of *T. pisana*, viz. *T. p. cantinensis* (Sacchi, 1955), *T. p. pisana* and *T. p. ampullacea*.

Theba subdentata subdentata (Férussac, 1821)
(figs. 28-30)

[*Helix*] *Helicella* (*Heliomanes*) *subdentata* Férussac, 6.iv.1821: xj (explanation to pl. 27 figs. 1, 2, of Férussac's "Histoire naturelle générale et particulière des mollusques terrestres et fluviatiles, published 26.ii.1820; no locality mentioned); lectotype, design. nov.: MNHN (fig. 28, the specimen figured by Férussac, pl. 27 figs. 1, 2).

Helix (*Helicella*) *subdentata*; Férussac, 26.v.1821: 49 [45] ("La Perse?").

Helix (*Theba*) *subdentata*; Beck, 1837: 15.

Helix subdentata; L. Pfeiffer, 1843: 83, pl. 10 figs. 13, 14; 1848: 154. Morelet, 1880: 31, pl. 1 fig. 3 (8 figs.). Kobelt, 1881: 39, pl. 197 fig. 1979, a, b.

Euparypha dehnei var. *turgida* Pallary, 1915: 22 ("Agadir"); 1921: 115, pl. 3 fig. 17.

Material. — MOROCCO. Marrakech: 14 km S. of El-Kelâa-des-Srarhna, PR53 (SMF); 27 km SW. of Tamelelt, PR20 (SMF); Marrakech, NR90 (SMF); Imi-n-Tanoute, 820 m alt., NQ15 (RD). Ouarzazate: 11 km NW. of Taliouine, 1020 m alt., NP98 (RD). Agadir: 11 km NW. of Aoulouz, NP79 (RD); 2 km E. of Taroudannt, NP17 (SMF); 3 km NE. of Oulad-Teima, MP86 (RD; RMNH); 11 km NW. of Tarhazoute, MP 28 (RD); 1 km NW. of Tarhazoute, MP 38 (RD); Tarhazoute — Tamrhakht, MP37 (ZMA); 4 km E. of Tamrhakht, MP37 (SMF); 9 km NW. of Agadir, MP 37 (RD; SMF); Agadir, MP46 (RD; RMNH; SMF); 3 km E. of Âït-Melloul, MP55 (RD; RMNH); dunes W. of Âït-Melloul, MP45 (RMNH); 8 km SE. of Biougra, MP64 (RMNH); 11 km S. of Tiferhal, MP41 (RD; RMNH); Oued Massa, 25 km NE. of Tiznit, MP40 (RD; SMF);

3.5 km E. of Tiznit, MN38 (RD; RMNH); Tiznit, MN38 (SMF); 11 km W. of Tiznit, MN28 (RD); 4 km S. of Tiznit, MN38 (SMF); 11 km S. of Tiznit, MN37 (RD); 16 km S. of Tiznit, MN36 (SMF); 18 km S. of Tiznit, MN36 (SMF); 31 km S. of Tiznit, MN35 (SMF); 12 km NW. of Tirhmi, MN58 (RD).

Shell (figs. 28, 29). — Shell similar to that of *T. s. dehnei*, but usually with a more or less prominent parietal denticle in the aperture. There are some additional slight differences, which are not clearly developed in every single specimen, however. In general *T. s. subdentata* is somewhat more compressed laterally and, consequently, its body-whorl is relatively higher and its aperture slightly less broadly elliptical. The apertural lip may be somewhat more prominent than it usually is in *T. s. dehnei*.

Width 14.0-20.1 mm; height 10.3-14.9 mm.

Genitalia. — It is unclear whether Hesse's (1915: 13) notes concerning the anatomy of a specimen of "*Euparypha subdentata*" apply to the nominate subspecies or to *T. s. meridionalis*. According to Hesse the proximal part of the spermatheca duct is slightly less than half as long as the distal part; the diverticulum reaches beyond the spermatheca, but not as far as in the specimens of *T. s. dehnei*. The ratios are 4 : 9 : 14.

Range (fig. 30). — *T. s. subdentata* is known from W. Morocco, from the surroundings of El-Kelâa-des-Srarhna, c. 70 km NE. of Marrakech, southwestward to the surroundings of Tiznit, c. 110 km S. of Agadir.

Notes. — There are two shells in the Férussac collection (MNHN), which are labelled *subdentata*, one of which is clearly the specimen figured by Férussac (1820: pl. 27 figs. 1, 2). This figured shell (fig. 28) is designated as the lectotype. The specimen has the shape described above for *T. s. subdentata*, i.e. a relatively high body-whorl, which is somewhat flattened laterally. A parietal denticle is lacking, which is unusual for this form. The epithet *subdentata* probably refers to an obsolete angular denticle. The second type specimen (?) has a prominent parietal denticle; this shell is most similar to *T. s. meridionalis*. Most probably the two shells are from different localities; it is very unlikely that they are from "Mogador" (this locality is indicated on the label).

Pallary's (1915) "var. *turgida*" cannot be distinguished from *T. s. subdentata*. *T. s. subdentata* is partly sympatric with *T. p. ampullacea* and probably also (near Marrakech) with *T. p. pisana*.

Theba subdentata meridionalis (Sacchi, 1955)
(figs. 26, 30)

Euparypha subdentata meridionalis Sacchi, 1955b: 46, fig. 6, pl. 1 fig. 7 (left specimen) ("foce del Nun").

Material. — MOROCCO. Agadir: 6.5 km NE. of Mirhleft, MN07 (RD/25); 5 km NE. of Mirhleft, MN07 (RD/3); 10.5 km NE. of Sidi-Ifni, LN95 (RD/74); Bu Talán hill, S. of Sidi-Ifni, LN84 (RMNH/7); 8 km S. of Sidi-Ifni, LN94 (RMNH/13); 10 km SW. of Sidi-Ifni, LN83 (RMNH/8); Oued Noun, LN62 (SMF); 3.5 km N. of Goulimime, LN91 (RD/2); Goulimime, LN90 (RMNH/2; SMF); 1.5 km SW. of Goulimime, LN90 (RD/32; RMNH/9). Tarfaya: 0.5 km NW. of Tan-Tan, KM94 (RD/68; RMNH/11); 5 km NW. of Tan-Tan, KM94 (RD/10; RMNH/24); Hassi Oued Amma Fatma, 40 km SW. of Tan-Tan-Plage, KM42 (RMNH/11).

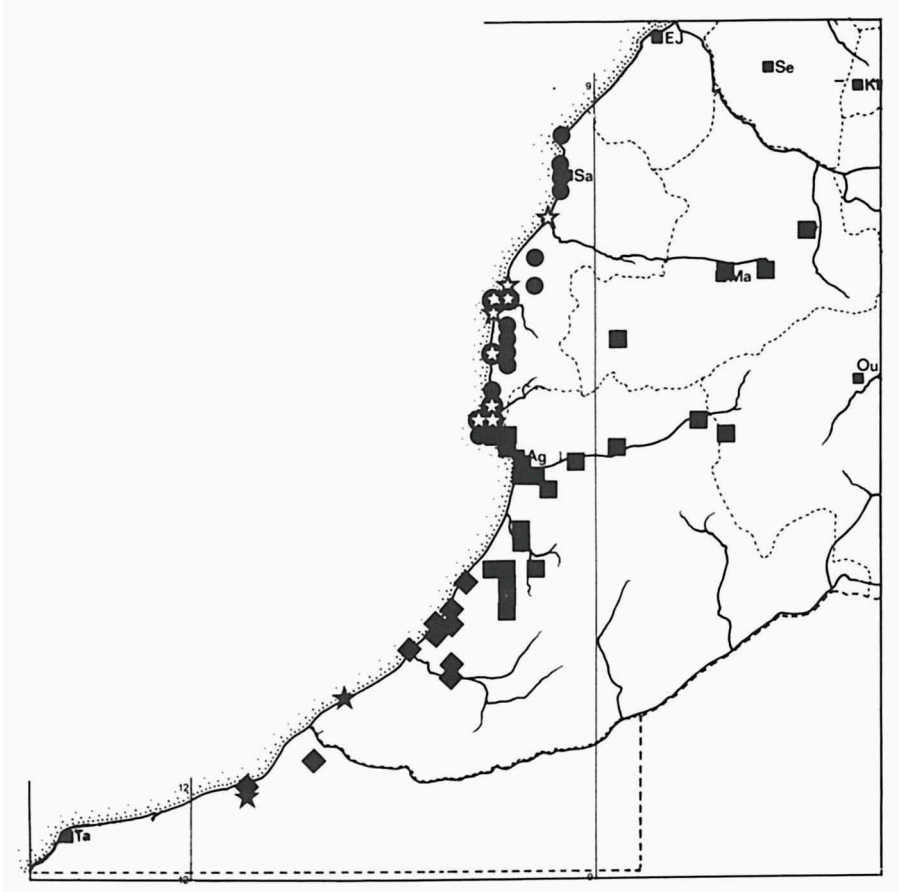


Fig. 30. UTM 10 km squares distribution map for *Theba subdentata dehnei* (dots), *T. s. helicella* (open stars), *T. s. legionaria* (solid stars), *T. s. meridionalis* (oblique squares), and *T. s. subdentata* (squares).

Shell (fig. 26). — Shell similar to that of *T. s. subdentata*, but which (1) a more prominent apertural lip, (2) a (much) more prominent parietal denticle, (3) a more globular general shape. There may be a conspicuous angular denticle, which may be more prominent than the parietal denticle and connected with it (fig. 26b).

Width 11.5-17.1 mm; height 8.7-14.4 mm.

Genitalia. — A schematic figure of the genitalia has been published by Sacchi (1955b: fig. 6). The flagellum measures one and a half times the length of penis and epiphallus together and is about as long as the relatively thick glandulae mucosae. The proximal part of the spermatheca duct measures nearly one third of the length of the distal part, which is slightly shorter than the diverticulum.

Range (fig. 30). — *T. s. meridionalis* is known from a limited number of localities in the coastal area of the extreme southwest of Morocco, from the surroundings of Sidi-Ifni, c. 40 km N. of Goulimime, southwestward to Hassi Oued Amma Fatma, c. 40 km SW. of Tan-Tan-Plage.

Notes. — *T. s. meridionalis* has been described and figured unequivocally by Sacchi (1955b).

The subspecies occurs sympatric with both *T. solimae* and *T. sacchii*.

Theba subdentata legionaria (Sacchi, 1955)
(figs. 27, 30)

Euparypha subdentata legionaria Sacchi, 1955b: 44, 46 ("Razza fossile a livello del suolo ad Aereora"), pl. 1 figs. 8 (left shell), 9 (except the left shell). Neotype (design. nov.): RMNH 55952.

Material. — MOROCCO. Tarfaya: Aoreora (not "Aereora"), c. 80 km SW. of Goulimime, LM19 (Sacchi, 1955b: 46); along the coastal road, 11.5 km W. of the Oued Chebeica, KM42 (RD/20; RMNH 55952/neotype, 55958/17).

Shell (fig. 27). — Shell clearly different from that of *T. s. meridionalis*, the geographically closest relative, by (1) a more depressed general shape, (2) obsolete or (usually) lacking parietal denticles and, (3) a moderately prominent apertural lip. *T. s. legionaria* is very similar to *T. s. dehnei*, differing only vaguely by (1) a more regularly shaped, broad oval aperture, (2) smaller dimensions, and (3) a more regular general shape, with an evenly rounded body-whorl. *T. sacchii*, which differs clearly by its widely open umbilicus, is very similar to *T. s. legionaria* in front view.

Width 12.3-17.8 mm; height 9.9-12.4 mm.

Genitalia. — Unknown.

Range (fig. 30). — *T. s. legionaria* is known from only two localities in the extreme southwest of Morocco, viz. 80 km and 170 km SW. of Goulimime. Because these localities are situated far apart its real range might be still largely unknown.

Notes. — Most unfortunately there are no syntypes of *T. s. legionaria* available anymore. The original figures accompanying the incomplete description of the subspecies are insufficient to recognize the taxon with certainty; no data are given concerning the structure of the umbilical region. To bring the doubtful identity of *T. s. legionaria* to an end, a neotype has been designated. Because material from the original type locality is not available (see p. 5), we had to select the neotype from a sample collected as close as possible to that locality. See also the notes with *T. sacchii*.

It is not known with certainty whether or not *T. s. legionaria* is an extant subspecies. Some shells belonging to it look rather fresh, however.

T. s. legionaria is aberrant in *T. subdentata* because it disturbs the cline into which the other four subspecies can be arranged (p. 22). We classify the taxon as a subspecies of *T. subdentata* because of the existence of a few shells tending to *T. s. meridionalis*, especially by the presence of two parietal denticles situated as in the specimen figured in fig. 26b. In *T. s. dehnei* specimens with two such denticles have not been observed. Also Sacchi (1955b: 47) mentions forms intermediate between *legionaria* and *meridionalis*.

Apparently the range of *T. s. legionaria* is still insufficiently known. Additional distributional data might better illustrate the relation between this subspecies and *T. s. meridionalis*.

At first sight *T. sacchii* resembles this subspecies. The former occurs sympatric with a subspecies of *T. subdentata*, however. As a consequence *T. sacchii* should be considered a separate species.

T. s. legionaria occurs partly sympatric with *T. chudeaui*.

Theba pisana (Müller, 1774)
(figs. 1, 31-40, 43)

Shell (figs. 31-40). — The polytypic *T. pisana* is characterized conchologically by glossy, not silky, light yellowish to whitish shells, mostly provided with an additional (dark) brownish, spirally arranged colour pattern, which may be extremely variable. There is always a narrow, open umbilicus. Juvenile shells have a sharp keel along (part of) the periphery.

The subspecies of *T. pisana* are interconnected by broad zones with intermediate forms and, therefore, their morphological and geographical delimita-

tions cannot be but rather subjectively indicated.

The various subspecies differ from each other mainly in general shape, being provided with a keeled body-whorl, in full-grown specimens, or a regularly rounded one. There are additional differences in the amount of variation in the colour pattern.

Genitalia. — There is no or only a rudimentary flagellum on the epiphallus.

Range. — The range of *T. pisana* is in fact determined by the range of its nominate subspecies, which is found in the Mediterranean area and along the Atlantic coasts as far north as the southernmost part of the Netherlands, SW. England, S. Wales and E. Ireland (Kerney & Cameron, 1979: 203; Sacchi, 1971: fig. 1 [except the extreme southwestern area; the Madeira archipelago should be added]).

It is unknown to what extent the range of *T. pisana* has been enlarged in historic times. See also following notes.

Notes. — According to Wenz (1923: 559) *T. pisana* has been reported from young Pliocene ("Astien") deposits in Algeria. Unfortunately the material on which this record is based could not be restudied. The authors to which Wenz referred simply mention the species, without giving a clear description or a good figure. Therefore and because the epithet *pisana* has been used for nearly every *Theba* (sub)species in the past, it remains uncertain what (sub)species is actually involved.

Sacchi (1956: 81) emphasized that *T. p. pisana* ("populations d'euparyphes normales") is a very recent immigrant in most of its present circum-Mediterranean and coastal Atlantic range. This is confirmed by e.g. Heller & Tchernov (1978: 1), stating that *T. p. pisana* must have reached Israel during historic times because it is not found in fossil deposits, being the most abundant landsnail in the coastal plain of Israel today. *T. p. pisana* invaded the southernmost part of the Netherlands quite recently (Gittenberger, Backhuys & Ripken, 1984: 146). It is unknown to what extent the subspecies could enlarge its range because of human action. *T. p. pisana* has also become established, by human introductions, in the U.S.A. (California), S. Africa and Australia, demonstrating its success as an invader.

In striking contrast with the large range of the well-known *T. p. pisana*, are the very restricted ranges of both *T. p. arietina* (Rossmässler, 1846) and *T. p. cantinensis*. Sacchi (1957: 81) has suggested the interesting view that these two subspecies, characterized by strongly keeled shells, originated in isolated, small, Atlantic refuges, prior to the dramatic expansion in range of *T. p. pisana*, which might still be going on. This could have led to the present situation in which *T. p. pisana* surrounds *T. p. arietina* and *T. p. cantinensis*: "Les populations d'euparyphes "normales" auraient entouré, comme une

marée montante, les îles aux caractères carénées, les effacant peu-à-peu, les réabsorbant dans le pool génique". There are no obvious ecological differences between the subspecies of *T. pisana*. The great evolutionary success of only *T. p. pisana*, i.e. its expansion, which apparently started during the Holocene, remains unexplained. (See also the notes with the various subspecies).

Theba pisana pisana (Müller, 1774)
(figs. 31, 32, 35, 39, 40, 43)

Helix albella Linnaeus, 1758: 768 ("in Europae rupibus"). Lectotype (design. Forcart, 1965: 255): Gualtieri, 1742: pl. 3 fig. Q. See the notes below.
Helix pisana Müller, 1774: 60 ("Italia"). Lectotype (design. Pallary, 1921: 107, left figure): UZM.
Helix alboranensis Beck, 1837: 15 ("I. Madera").
Helix (Euparypha) pisana var. *donnelli* Pallary, 1904: 11, pl. 2 fig. 12 ("Tétouan"). Lectotype (design. nov.): MNHN (fig. 40).
Euparypha pisana var. *donnelli*; Pallary, 1921: 107, pl. 3 figs. 5-7.

Material (S = Sacchi, 1955b). — SPAIN. Huelva: Huelva, PB82 (ZMA); Coto de Doñana, Matalascañas, QA19 (RMNH). Sevilla: Sevilla, TG34 (MK; SMF). Cádiz: 4 km E. of Villamartín, TF68 (RMNH); 1 km W. of Bornos, TF 57 (RD); Jerez de la Frontera, QA56 (RMNH); El Portal, QA55 (RD); 3 km NE. of Sanlúcar de Barrameda, QA37 (RMNH); 1.4 km W. of Rota, QA35 (RD); El Puerto de Santa María, QA45 (RMNH); Cádiz, QA44 (RMNH; SMF); 1 km S. of Medina Sidonia, TF33 (MK); 10 km W. of Vejer de la Frontera, QA62 (MK); 1 km E. of Vejer de la Frontera, TF31 (RD); 3 km SE. of Vejer de la Frontera, TF31 (MK); Vejer de la Frontera — Barbate, TF31 (RMNH); Río Jara, 5 km NW. of Tarifa, TE69 (MK); mouth of the Río Jara, 5 km NW. of Tarifa, TE69 [→ *arietina*] (RMNH); Tarifa, TE68 (SMF); Playa de Getares — lighthouse, S. of Algeciras, TE89 (MK); Algeciras, TF70 (SMF; ZMA); 8 km NW. of Los Barrios, TF71 (RD). Gibraltar, TF80 (SMF; ZMA). Alborán Isla, VE97 (ZMA). Melilla, WEOO (RMNH; ZMA).

MOROCCO. Oujda: Taourirt, WD11 (S); 25 km S. of Oujda, WD91 (SMF); Oujda, WD94 (S); Saïdia, WD78 (SMF); 1 kmW. of Saïdia, WD78 (RD). Nador: Ras-el-Ma, WD59 (RD); Kariet-Arkmane (= La Restinga), WD18 (Llabador, 1952: 102). Taza: Guercif, VC68 (S); Taza, VC08 (S). Al Hoceima: 10 km SE. of Al Hoceima, VD19 (SMF). Fès: Djebel Messaoud, S. of Ourtzarh. UD22 (Pallary, 1929: 52); Oued Sebou, E. of Fès, UC27 (SMF); Fès, UC17 (S). Meknes: Moulay-Idriss, TC67 (SMF); Meknes, TC65 (RMNH; SMF). Tanger: Chechaouèn, TD99 (Pallary, 1904: 11); Tétouan, TE84 (MNHN/lectotype & 5 paralectotypes of *donnelli*; SMF); Ceuta — Fnideq, TE87 (RMNH); Tanger, TE46 (RMNH; SMF); Cap Spartel, TE36 (SMF); 3 km N. of Larache, QV50 (SMF). Rabat: 13 km N. of Ouezzane, TD66 (ZMA); Ouezzane, TD65 (S); Souk-el-Arba-du-Rharb, QU74 (S); 12 km SW. of Souk-el-Arba-du-Rharb, QU63 (RMNH); Moulay-Bousselham, QU46 (SMF); Rabat, PT96 (RMNH; SMF); Khemisset, QT74 (S); Rabat — Mehdiya QT08 (SMF); 4 km W. of Rommani (= Marchand), QT21 (SMF). Casablanca: Mohammedia (= Fedala), PT43 (RMNH); 16 km E. of Casablanca, PT42 (SMF); Casablanca, PT22 (S); 25 km S. of Casablanca, PS29 (SMF); 13 km S. of Oued-Zem, QS22 (SMF). Beni-Mellal: Oued Dirma, NW. of Kasba-Tadla, QS51 (SMF); 6 km W. of Beni-Mellal, QR48 (SMF). Marrakech: "Oued Tessaout", 35 km NE. of Marrakech, PR22 (S); 11 km W. of Marrakech, NR80 (S); 8 km W. of Sidi-Moktar, MQ99 (SMF). El-Jadida: 37 km NE. of Azemmour, NT80 (SMF); Azemmour, NS68 (RMNH); El-Jadida (= Mazagan), NS48 (SMF); Cap

Blanc, NS37 (S); 22 km SW. of El-Jadida, NS36 (RMNH); 30 km S. of El-Jadida, NS45 (S); Sidi-Smaïl, NS43 (S); 5 km NE. of Oualidia, NS02 [→*cantinensis*] (RD); Oualidia, MS92 (SMF). Safi: 6 km N. of Safi, MR78 (SMF); 4 km N. of Safi, MR77 (SMF); Safi, MR77 (RMNH; SMF); mouth of the Oued Tensift, MR64 (SMF); "Karmuda", 45 km NE. of Essaouira, MR52 (S); "Sidi Moulay Doran", 20 km NE. of Essaouira, MR30 (S); 9 km E. of Essaouira (= Mogador), MQ38 [→ *ampullacea*] (SMF).

CANARY ISLANDS. Gran Canaria: Barranco de Guayedra, S. of Agaete (RMNH); 2.5 km SW. of Galdar (RD); Moya-Guía (RMNH); Montaña de Arucas (RMNH); Las Palmas (RMNH; SMF; ZMA); Tamaraceite (RD); Las Goteras, E. of Santa Brígida (RD); Montaña de las Palmas, W. of Telde (RMNH); Maspalomas (RMNH). Tenerife: Tacoronte (SMF); Bajamar (RD; RMNH); Barranco Andura or Andola, S. of Realejo Alto (RMNH).

Shell (figs. 31, 32, 35, 39, 40). — *T. p. pisana* is characterized by the slightly depressed, globular shell; the beginning of the body-whorl may be somewhat angular or (in single specimens) keeled. See Cain (1984a, b) for an analysis of the variation in colour pattern.

The number of whorls varies between 4 and 5⅛.

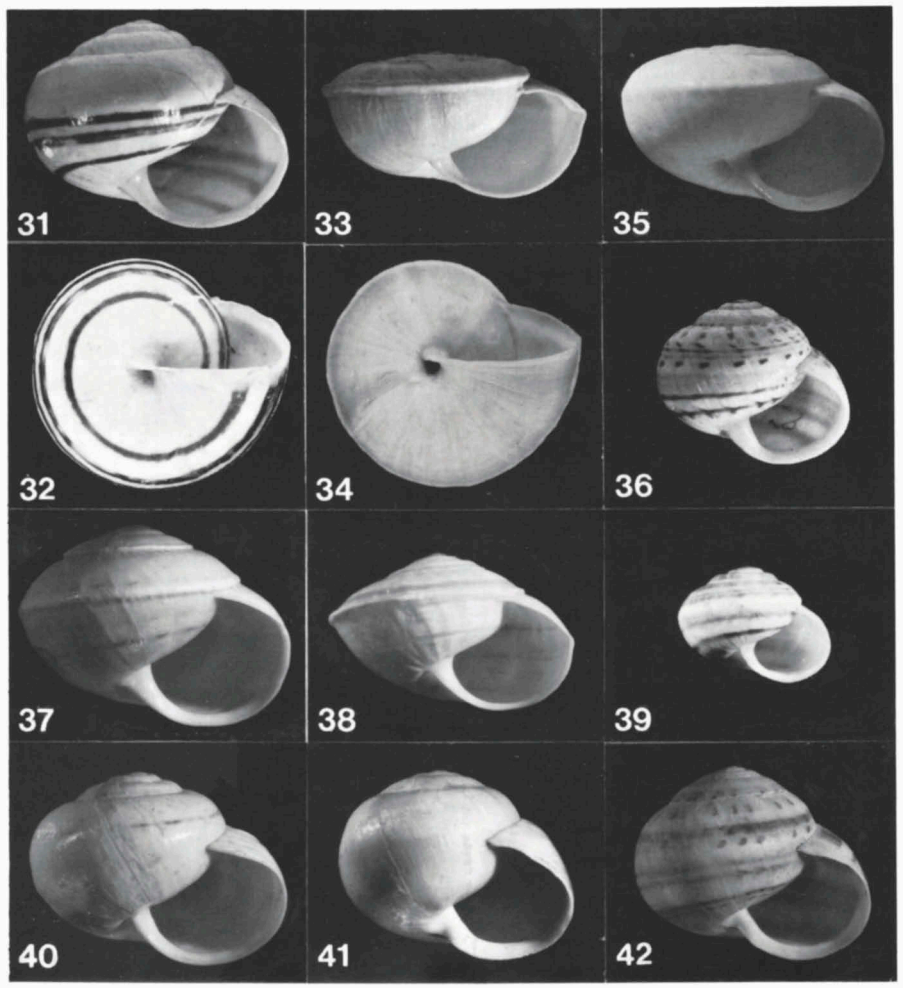
Over large distances *T. p. pisana* is not very variable in size. Occasionally populations with (very) small shells are found; such populations are not restricted to a particular area. See further the following notes.

Width 10.3-21.5 mm; height 7.5-17.0 mm.

Genitalia. — A thorough description of the anatomy of *T. pisana* has been published by Hesse (1915: 2-8, pl. 631), who considered the "var. *donnelli*" from Tetuan, sent to him for dissection by its author, a separate entity. Conchologically this variety cannot be clearly distinguished from *T. p. pisana*, however (see the following notes). Fuchs & Käufel (1936: 654) suggested that it might be possible to distinguish several local forms in *T. pisana*, characterized by features of the genitalia; the authors had noted that there may be conspicuous differences in various characters of the genitalia when animals from different populations are compared. According to Fuchs & Käufel the var. *donnelli* is only one of several forms of *T. pisana*.

Apparently the relative lengths of different parts of the genitalia may vary considerably. This applies especially to the segments of the spermatheca duct and the diverticulum and the relation between oviduct and vagina. Most characteristic for *T. p. pisana* is the rudimentary, often hardly or not discernible, flagellum of the epiphallus; if present at all, the flagellum remains always much shorter than the epiphallus. The glandulae mucosae are relatively thick and about twice as long as penis and epiphallus together.

Range (fig. 43). — We have only studied the range of *T. p. pisana* in Morocco in some detail. The subspecies is not restricted to the coastal area in this country. It occurs north of the Haut and the Moyen Atlas. The south-westernmost locality known is situated 20 km NE. of Essaouira.



Figs. 31-42. *Theba pisana* [31-40] and *T. andalusica* [41, 42]. 31, 32, *T. p. pisana*, actual width 19.5 mm, Morocco, province of Safi, Safi (RMNH, F. van der Plas leg.). 33, 34, *T. p. arietina*, actual width 20.1 mm, Spain, province of Cádiz, Sierra de San Cristóbal between Puerto de Santa María and Jerez de la Frontera (RMNH, ex Altimira). 35, *T. p. pisana*, with a prominently angular periphery and a low spire (see the text), actual width 14.2 mm, Spain, province of Cádiz, near the mouth of the Rio Jara, 5 km NW. of Tarifa along the road N340 (RMNH, L. B. Holthuis leg.). 36, *T. p. ampullacea*, actual width 13.2 mm, Morocco, province of Agadir, Âït-Melloul (RMNH, W. Backhuys leg.). 37, 38, *T. p. cantinensis*, actual widths 19.9 and 18.1 mm, Morocco, province of Safi, Cap Beddouza (SMF 20939, H. Kaltenbach leg.). 39, *T. p. pisana*, dwarf form, actual width 11.5 mm, Spain, province of La Coruña, Peninsula El Grove (RMNH, Ria de Arosa Exp.). 40, *T. p. pisana*, lectotype var. *donnelli* Pallary, Morocco, province of Tanger, Tétouan (MNHN, ex Pallary). 41, 42, *T. andalusica* spec. nov., holotype and paratype, actual widths 18.0 and 17.6 mm, Spain, province of Cádiz, 5 km NW. of Tarifa along the Rio Jara (RMNH 55905, 55906, H. P. M. G. Menkhorst leg.). Photographs by E. G. (37-42) and G. J. van Zonneveld (31-36).

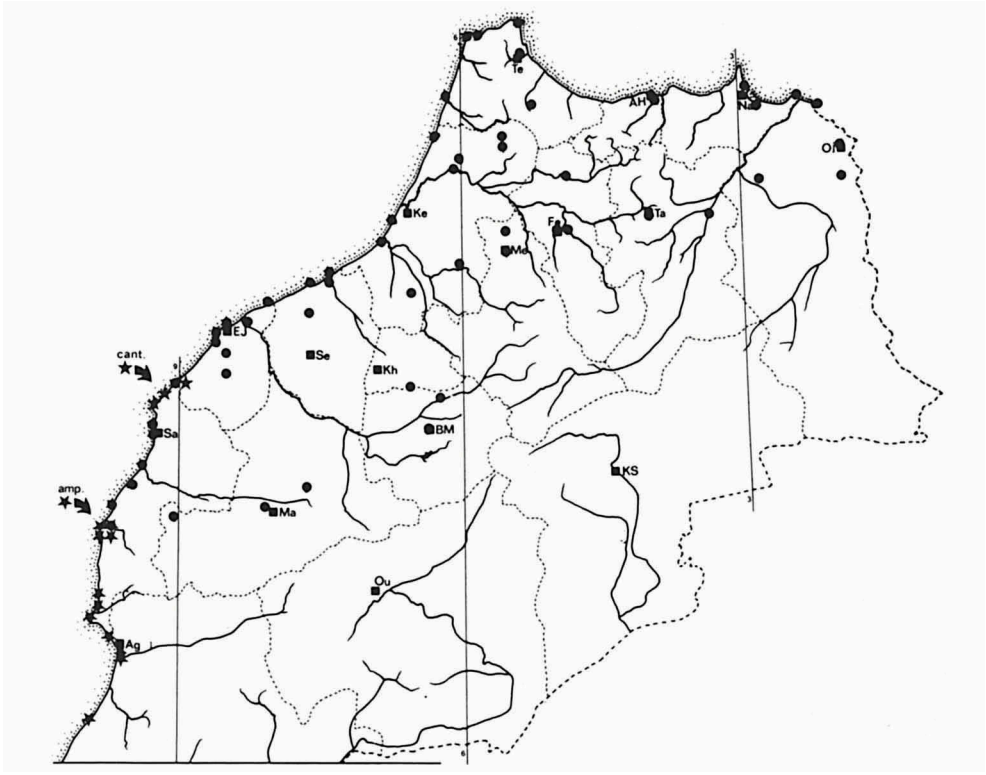


Fig. 43. UTM 10 km squares distribution map for *Theba pisana* in Morocco; *T. p. pisana* (dots), *T. p. cantinensis* (stars pointing upwards), and *T. p. ampullacea* (stars pointing downwards).

Notes. — *Helix albella*, based on two species, is the oldest name for the well-known *T. pisana*. This is a consequence of the selection of a lectotype by Forcart (1965: 255). Because the name *T. pisana* has been used by a great variety of authors in many systematical and non-systematical papers during the preceding fifty years, whereas the senior name has not been used as a valid name during even much longer than the same period, we will propose to the Commission to reject the name *Helix albella*.

Pallary (1921: 107) has selected a lectotype of *Helix pisana* from the Müller collection in UZM. This selection was in agreement with the usual interpretation of the nominal taxon.

We have not tried to compile a full list of synonyms for *T. p. pisana*. Many junior nominal taxa have been introduced for colour forms of this subspecies and have never been used in another sense.

The nominal taxon *Helix alboranensis*, often incorrectly ascribed to Webb

& Berthelot, has been introduced by Beck (1837: 15) for a form "d" of "*Helix (Theba) pisana*", characterized as "minor, subdepressa, umbilico subclauso". The name is available, i.e. given to a subspecific category and, in contrast to what is stated by Kennard & Woodward (1926: 263), not simply cited "in synom.". Because Beck mentions only "I. Madera" for *H. alboranensis*, the Atlantic island Madeira and not the Mediterranean islet Alborán should be considered the type locality of this taxon (German, 1934: 317).

T. pisana (var.) *alboranensis* is a name used by many others for various small forms of *Theba* spec. (e.g. *T. arinagae* and *T. pisana ampullacea*). Therefore the form of *T. pisana* occurring on the islet Alborán deserves our attention. In ZMA (ex J. Rutllant) there are two samples of *T. pisana* from Alborán, with four (three adult) and six (all adult) shells, respectively. The nine adult specimens have 4 tot 4⅝ whorls; they vary in width from 11.0 tot 14.9 mm and in height from 8.1 to 12.0 mm. In most shells the dark pattern covers relatively much of the shell surface. A very similar shell from Alborán has been figured in colour by Taylor (1912: pl. 31 fig. 12). There is no obvious reason to consider this form more than a small, relatively dark-shelled *T. p. pisana*. Occasionally, although rarely, still smaller shells are found in this subspecies. In a sample in RMNH, from the Peninsula del Grove, province of Pontevedra, western Galicia, Spain, the two smallest adult shells have the following dimensions and number of whorls: 10.7 × 7.5 mm, 4 whorls; 10.3 × 8.1 mm, 4¼ whorls. From the same area along the Ria de Arosa populations with more normally sized shells are also known.

We could study six syntypes of Pallary's (1904) "var. *donnelli*", considered a separate entity ("eine gute Varietät") by Hesse (1915: 8), who studied specimens from the type locality, sent to him by Pallary. Conchologically this form could be characterized simply as a rather globular, relatively large *T. p. pisana*. The shells have an open umbilicus, which is not clearly narrower than usual in the species and thus we cannot confirm Pallary's (1904: 11) remark "à ombilic recouvert". This implies that *T. andalusica* is different from the form *donnelli*, although the original description of the latter taxon suggests that there might be no differences at all. In *T. andalusica* the shell is somewhat less depressed than in *T. p. pisana* forma *donnelli* (see figs. 40, 41, 42).

T. p. ampullacea is hardly more than a relatively small form of *T. p. pisana*, with a slightly more globular, relatively higher shell.

T. p. pisana may occur sympatric with *T. andalusica, T. s. subdentata* (near Marrakech ?), *T. s. dehnei* and *T. geminata*.

Theba pisana ampullacea (Pallary, 1915)
(figs. 36, 43)

Helix pisana var. *alboranensis*; Lowe, 1861: 196. Not Beck, 1837.
?*Helix pisana* var. *dentata* Taylor, 1912: 384, pl. 30 fig. 5 ("Mogador"). Not *Helix dentata* Wood, 1828.
Euparypha pisana var. *ampullacea* Pallary, 1915: 22 ("Mogador"); 1921: 108, pl. 3 figs. 8, 9).
Euparypha pisana var. *gracilis* Pallary, 1915: 22 ("Mogador"); 1921: 109, pl. 3 fig. 12.

Material. — MOROCCO. Safi: 9 km E. of Essaouira (= Mogador), MQ38 [→ *pisana*] (SMF); Essaouira, MQ28 (RD; RMNH; SMF); 3 km S. of Essaouira, MQ28 (SMF); 8 km S. of Essaouira, MQ28 (RD; SMF); Cap Sim, MQ27 (MNHN); 5 km E. of Sidi-Kaouki, MQ27 (SMF); 2 km S. of Sidi-Kaouki, MQ27 (SMF); 15 km S. of Essaouira, MQ37 (SMF); Pointe Imessouane, MQ21 (SMF); 7 km N. of Tamri, MQ20 (SMF); 3 km N. of Tamri, MP19 (SMF); 1 km N. of Tamri, MP19 (RD; RMNH); 6 km W. of Tamri, MP19 [fossil] (RD; RMNH); 5 km N. of Cap Rhir, MP19 (RD); 14 km NW. of Agadir, MP37 (RMNH). Agadir: Agadir, MP46 (RD); dunes W. of Âït-Melloul, MP45 (RMNH); Sidi-Moussa-d'Aglou, MN19 (Sacchi, 1955b: fig. 1).

Shell (fig. 36). — *T. p. ampullacea* is smaller than *T. p. pisana* usually is and the shell is relatively higher, which results in a very globular general shape. See also *T. arinagae*.

The measurements (in mm), the values for (height/width) × 100, and the number of whorls are given for the shells belonging to two small samples, from 1 km N. of Tamri (left) and the dunes W. of Âït-Melloul (right):

height	width	$\frac{h}{w} \times 100$	whorls	height	width	$\frac{h}{w} \times 100$	whorls
14.3	15.8	90.5	5	12.3	13.0	94.6	5
14.3	15.9	89.9	5¼	11.8	14.1	83.6	4¾
12.5	15.6	80.1	5	11.4	12.7	89.7	5
13.4	14.3	93.7	5¼	10.4	11.8	88.1	4½
12.6	13.9	90.6	4¾	10.1	11.8	85.5	4½
12.0	12.7	94.4	4¾	9.8	11.8	83.0	4½

Genitalia. — Unknown.

Range (fig. 43). — *T. p. ampullacea* is known from W. Morocco along the coast, from the surroundings of Essaouira southward to Sidi-Moussa-d'Aglou, c. 15 km NW. of Tiznit.

Notes. — With much doubt we list *E. pisana* var. *gracilis* with *T. p. ampullacea*, because its description and subsequent illustration (Pallary, 1915: 22; 1921: pl. 3 fig. 12) do not make very clear what taxon is meant. The "var. *ampullacea*" has been described and figured unequivocally (Pallary, 1915: 22; pl. 3 figs. 8, 9).

At its southernmost localities in Morocco *T. pisana* is found with populations containing specimens which can be characterized conchologically as

globular dwarfs. These shells differ conspicuously from those of *T. pisana pisana* known from northern Morocco. However, the change from one form into the other is a very gradual one and we would not have paid much attention to the southern form if it had not been mentioned in the literature several times. Morelet (1880: 27, pl. 1 fig. 2a) mentioned it as "Une autre variété également curieuse ou plutôt une race, car elle est constante", providing also an excellent figure. He indicated that the form resembles that of the islet Alborán.

We hesitated with giving this form subspecific status, because it can be only vaguely delimitated. We did so, because in general populations of *T. pisana* with small shells are relatively rare and not concentrated in a certain area. These small shells are usually not clearly different in general shape from larger ones, apart from a more prominently angular beginning of the body-whorl (fig. 39). In *T. p. ampullacea* from W. Morocco the shells are not only relatively small but also very globular. The fact that there exists already a name for this form in the literature has also influenced our decision.

Most probably *Helix pisana* var. *dentata* was based by Taylor (1912: 384, pl. 30 fig. 5) on an aberrant specimen of *T. p. ampullacea*. The locality Essaouira (= Mogador), the shape and the dimensions of the shell leave no other conclusion.

T. p. ampullacea has been found sympatric with *T. s. subdentata, T. s. helicella* and *T. s. dehnei*.

Theba pisana arietina (Rossmässler, 1846)
(figs. 33, 34, 47)

Helix arietina Rossmässler, 1846: 172 ("Sierra de S. Cristoval zwischen Puerto de Sta. Maria und Jerez").
Helix planata; Rossmässler, 1854: 22 [part.], pl. 67 fig. 825 (not 826).
Euparypha pisana arietina; Sacchi, 1956: 1-5, figs. 1, 2; 1957: 77-84, figs. 1, 2, 4.

Material. — SPAIN. Cádiz: Sierra de San Cristóbal, S. of Jerez de la Frontera, QA55 (RMNH; SMF, SMF 7522/holotype, 7523/2 paratypes); 2.0 km SW. of El Portal, QA55 [→ *pisana*] (RD); 2.3 km SW. of El Portal, QA55 (MK; RD); Jerez de la Frontera — El Puerto de Santa María 1.5 km N. of the crossroad to El Portal, QA55 (RD); Jerez de la Frontera — El Puerto de Santa María near the crossroad to El Portal, QA55 (MK); 1.4 km W. of Rota, QA35 [→ *pisana*] (RD).

Shell (figs. 33, 34). — The shell is provided with a very prominent keel along the periphery, running all along the body-whorl, i.e. reaching the apertural lip, where it is still easily discernible in front view. The shell is more strongly depressed than it is in *T. p. pisana*. There is an open umbilicus; the columellar

lip is not clearly reflected over it. The colour pattern is less variable than it is in the nominate subspecies; in a relatively high percentage of the specimens there are no dark bands or dots at all.

We could study only one population in which all the shells (133 specimens: MK/124; RMNH/9) are very typical *T. p. arietina*. This sample contains 113 shells (= 85%) without dark (remains of) spiral bands, 10 shells with a vague pattern, four shells with two bands below the periphery, two shells with one band just above and two below the periphery and four shells with two bands above and two below the periphery. There are 4 - 4½ whorls.

Width 13.1-20.9 mm; height 7.3-12.7 mm. See also the notes.

In *T. p. cantinensis* the carina is situated relatively lower along the body-whorl, which results in a more equal upper and lower part of the shell; in front view the outer lip of the aperture is less clearly interrupted by the carina and the aperture itself is relatively higher. *T. subdentata helicella* differs from *T. p. arietina* most clearly by its closed umbilicus.

Genitalia. — A schematic figure of the genitalia has been published by Sacchi (1956: fig. 2; 1957: fig. 2). There is no flagellum on the epiphallus.

Range (fig. 47). — See the following notes.

Notes. — Sacchi (1956, 1957) has clearly demonstrated that the taxon described by Rossmässler (1846) as *Helix arietina* should be considered a subspecies of *T. pisana* with a very small range in the Spanish province of Cádiz, viz. the elongate, c. 8 km long Sierra de San Cristóbal, which reaches only 112 m altitude. The Sierra is enclosed by two roads, viz. the main road from Jerez de la Frontera in SW. direction to El Puerto de Sta. María, and a secondary road from the same city southward to El Portal and from there westward to the main road just mentioned. North of El Portal *T. p. pisana* is found. Along the road 2 km SW. from El Portal 21 depressed shells have been collected; they have a more of less prominent keel only at the beginning of the body-whorl and 4¾ - 5⅛ whorls, measuring 15.0-19.6 mm in width and 10.1-13.8 mm in height. Nearly 0.5 km further southwestward from El Portal, i.e. less than 2.5 km SW. from this place, the most characteristic population of *T. p. arietina* known to us has been located. The general description applies to this population. North of El Puerto de Sta. María, where the two roads mentioned before come together, 125 shells (MK/114; RMNH/11) of a relatively small form have been collected, measuring 9.1-13.3 mm in width and 6.0-9.3 mm in height. Nearly all specimens have a sharp keel at the beginning of the body-whorl; near the aperture the periphery of the shell is evenly rounded or somewhat angular. The shells have 4⅛ - 4⅝ whorls. This sample contains 63 shells (= 54%) without dark (remains of) spiral bands, 18 shells (= 14%) with a vague pattern, 25 shells (= 20%) with all bands, 11 shells with two

bands below the periphery, seven shells with one band just above and two below the periphery, and one shell with only a band encircling the umbilicus. About 1.5 km north of the site at which the relatively small individuals have been collected, 35 shells (RD/33; RMNH/2) were found, with 4¼ - 4¾ whorls, measuring 12.5-18.2 mm in width and 8.3-13.2 mm in height. In this population the keel is variable in prominence, especially near the aperture, where the periphery may be nearly evenly rounded.

We have described our material of *T. p. arietina* and closely related forms in length to illustrate the striking variation in *T. pisana* around the Sierra de San Cristóbal. Much more material should be collected systematically in the area, in order to get a more detailed picture of the actual ranges of the various (intermediate) forms. Only by doing so we will be able to decide once in the future whether Sacchi (1957: 81) is right in considering the present situation not a balanced one, assuming that *T. p. pisana* is absorbing *T. p. arietina* after a recent secondary contact. 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.

We might speculate that the range of *T. p. arietina* has been larger than only the Sierra de San Cristóbal in the past. If so, traces of the once more substantial gene pool might be found at sites not too far from the Sierra. With this in mind we mention an interesting small sample of *Theba* spec. collected 1.4 km W. of Rota, which is about 20 km W. of the Sierra. Next to ten shells of *T. andalusica* there are three shells of typical *T. p. pisana* and six shells with a clearly angulate or even partly keeled periphery of the body-whorl, which are intermediate between the nominate subspecies and *T. p. arietina*. Three other intermediate shells (see fig. 35) have been collected c. 50 km SW. of the Sierra. Further research on *Theba* in the province of Cádiz might reveal interesting data.

Apparently there are conspicuous differences between the various samples, in prominence of the keel, width and height of the shells, and colour pattern. Although within a population the largest specimens have more whorls than the smallest ones have, there is no such correlation when populations with relatively small shells are compared to populations with larger shells; in the latter group there may be even less whorls than in the former one.

Theba pisana cantinensis (Sacchi, 1955)
(figs. 37, 38, 43)

Euparypha pisana var. *arietina*; Pallary, 1921: 109, pl. 3 figs. 10, 11. Not *Helix arietina* Rossmässler, 1846.

E[*uparypha*] *pisana cantinensis* Sacchi, 1955a: 88 ("capo Cantin"); 1955b: 58, fig. 4, pl. 1 figs. 5 (two shells), 6 (right shell).

Material. — MOROCCO. El-Jadida: 4 km NE. of Oualidia, NS02 [→ *pisana*] (RMNH/10 of 14). Safi: 14 km SW. of Oualidia, MS81 (SMF 174161/32); 20 km NE. of Cap Beddouza (= Cap Cantin), MS81 (RD/30; RMNH/30); 15 km NE. of Cap Beddouza, MS81 (Sacchi, 1955b: 59); Cap Beddouza, MS70 (RD/53; RMNH/5 & 53; SMF 20939/98).

Shell (figs. 37, 38). — *T. p. cantinensis* differs from *T. p. pisana* by the presence of a prominent keel along the periphery, not only in juvenile but also in full-grown shells. Only (very) shortly before the apertural lip is reached the keel becomes somewhat less sharp; as a consequence the outer lip is not clearly indented (in front view). The aperture is roundish to slightly oval; there is no columellar angle below. The shells are whitish or provided with one or more, sometimes interrupted, spiral lines; the lines may be combined to bands. In full-grown shells there are 4¼-5 whorls.

In *T. p. arietina* the keel is still prominent where the apertural lip is reached and the upper part of the shell is more clearly smaller than the lower part because the keel is situated relatively higher; the aperture is relatively higher in *T. p. cantinensis*.

Width 15.4-22.5 mm; height 9.8-14.8 mm.

In the specimens collected 14 km SW. of Oualidia the keel is somewhat less prominent than in shells from the type locality. The material from 4 km NE. of Oualidia is intermediate between *T. p. cantinensis* and *T. p. pisana*; in c. ten specimens there is a prominent keel along nearly the entire body-whorl, whereas it is more obsolete in c. four shells. There is a gradual change from one subspecies into another, which has also been observed by Sacchi (1955 a, b).

Range (fig. 43). — The most extreme forms of *T. p. cantinensis* are found at Beddouza and between this cape and Oualidia. According to Pallary (1921: 109) this subspecies occurs between Safi and Essaouira; this record needs confirmation. See also the following notes.

Notes. — Although there is no type material available anymore, there can be no doubt about the identity of this conspicuous subspecies of *T. pisana* from the former Cap Cantin. Therefore a neotype is not designated.

Apparently *T. p. cantinensis* is connected with *T. p. pisana* by a broad zone of intermediate forms. Sacchi (1955b: 54, figs. 3, 59) has noted that in a sample collected 20 km S. of the cape only 15% of the shells are keeled, whereas at 15

km NE. of the cape all specimens are provided with a keel. At Oualidia, 30 km NE. of the cape, Sacchi found only 5% of the shells with "tracce evidenti di carenatura". It is rather surprising therefore that 4 km NE. of Oualidia, i.e. still further away from Beddouza, we found a prominent keel at least along the first half of the body-whorl in about ten of fourteen adult specimens. Apparently there is no simple clinal variation with gradually less prominent development of keels in NE. direction. According to Sacchi the general shape of the shell also changes from Beddouza on, in both NE. and S. direction. The most strongly depressed shells are found near Beddouza; in both directions they become gradually less depressed. These changes in the relation between height and width cannot be easily correlated with the changes in the prominence of the keel. See Sacchi (1955b) for a more detailed description of the two independent morphoclines.

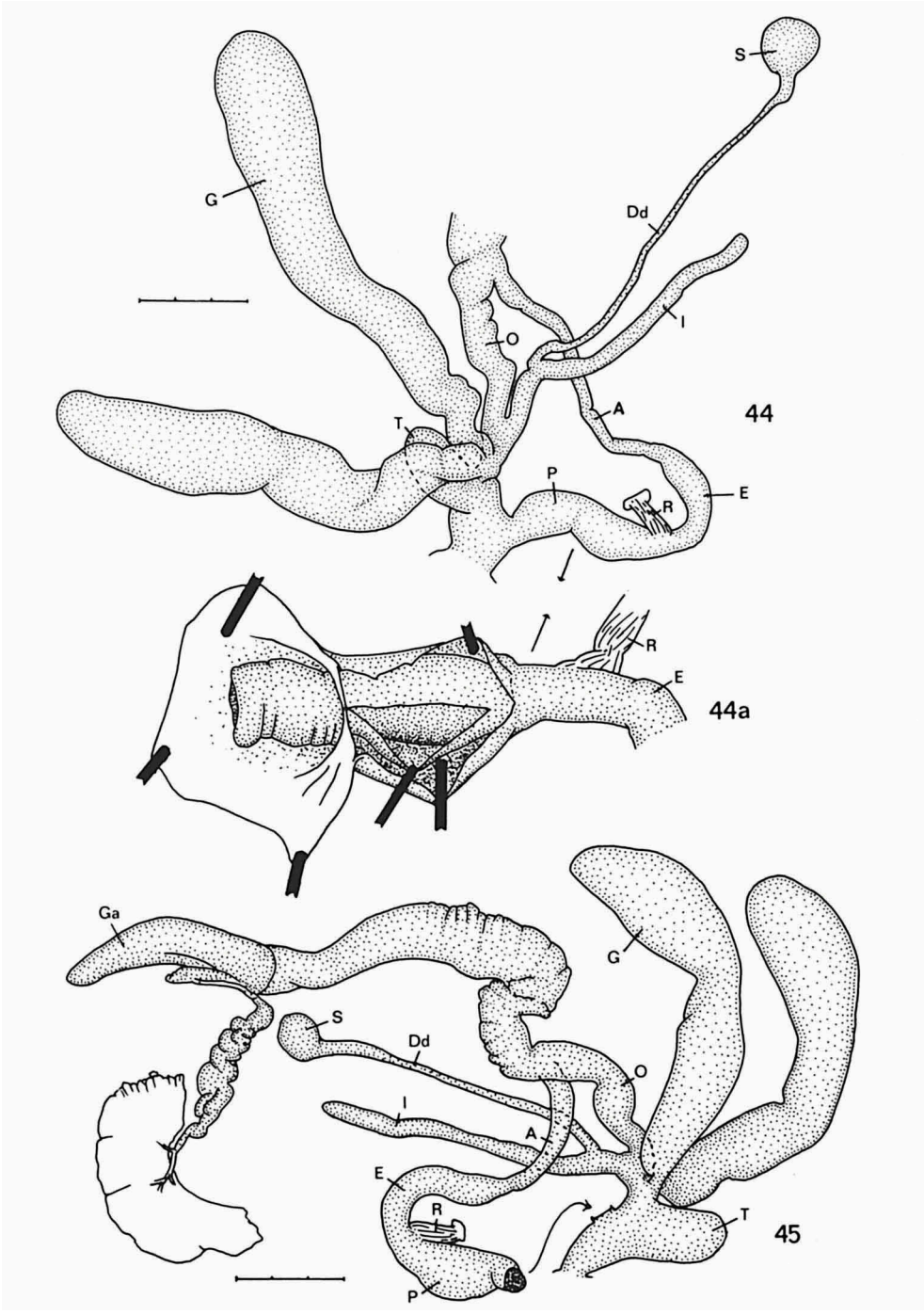
T. p. cantinensis occurs partly sympatric with *T. subdentata dehnei.*

Theba andalusica spec. nov.
(figs. 41, 42, 44, 47)

Material. — SPAIN. Sevilla: Lebrija, QA58 (RMNH 55910/12 paratypes). Cádiz: Chipiona, QA37 (RMNH 55908/paratype); 1.4 km W. of Rota, QA35 (RD/8 paratypes; RMNH 55909/2 paratypes); 3 km SE. of Vejer de la Frontera, TF31 (MK/3 paratypes); Rio Jara, 5 km NW. of Tarifa, TE69 (MCNM/5 paratypes; MK/202 & 22 paratypes; RD/10 paratypes; RMNH 55905/ holotype, 55906/12 paratypes, 55907/2 paratypes; ZMA/3 paratypes); Tarifa, TE68 (RMNH 55911/3 paratypes; ZMA/37 paratypes).

Shell (figs. 41, 42). — Shell globular, with 4¾ - 5¾ (usually c. 5) flattened to moderately convex whorls. The periphery is evenly rounded or (exceptionally) very vaguely angular at the beginning of the body-whorl. In several specimens the whorls are narrowly shouldered. Juvenile shells of less than four whorls are sharply angular at the periphery. Aperture circular, without a columellar angle below; outer lip clearly thickened inside. Umbilicus nearly completely closed by the abruptly reflected columellar lip, which has a characteristic notch (front view: figs. 41, 42).

The shells are glossy, with only a microsculpture of spirally arranged, short, incised line fragments. A high percentage in most populations is uniformly cream-white or yellowish. In the largest sample available, from the type locality, 155 of the 233 shells (67%) do not have a colour pattern; in 40 shells (17%) there is a row of (very) small brownish dots or short lines just above the periphery, 30 shells (13%) have two bands above and two below the periphery, two shells have one band just above and one just below the periphery, two



Figs. 44, 44a, 45. *Theba andalusica* spec. nov., paratypes, genitalia, Spain, province of Cádiz, Tarifa; fig. 44a shows the inner structure of the penis of 44 (H. W. E. Croockewit leg.). Material in RMNH (45) and ZMA (44). Scale lines: 3 mm. For abbreviations see p. 8.

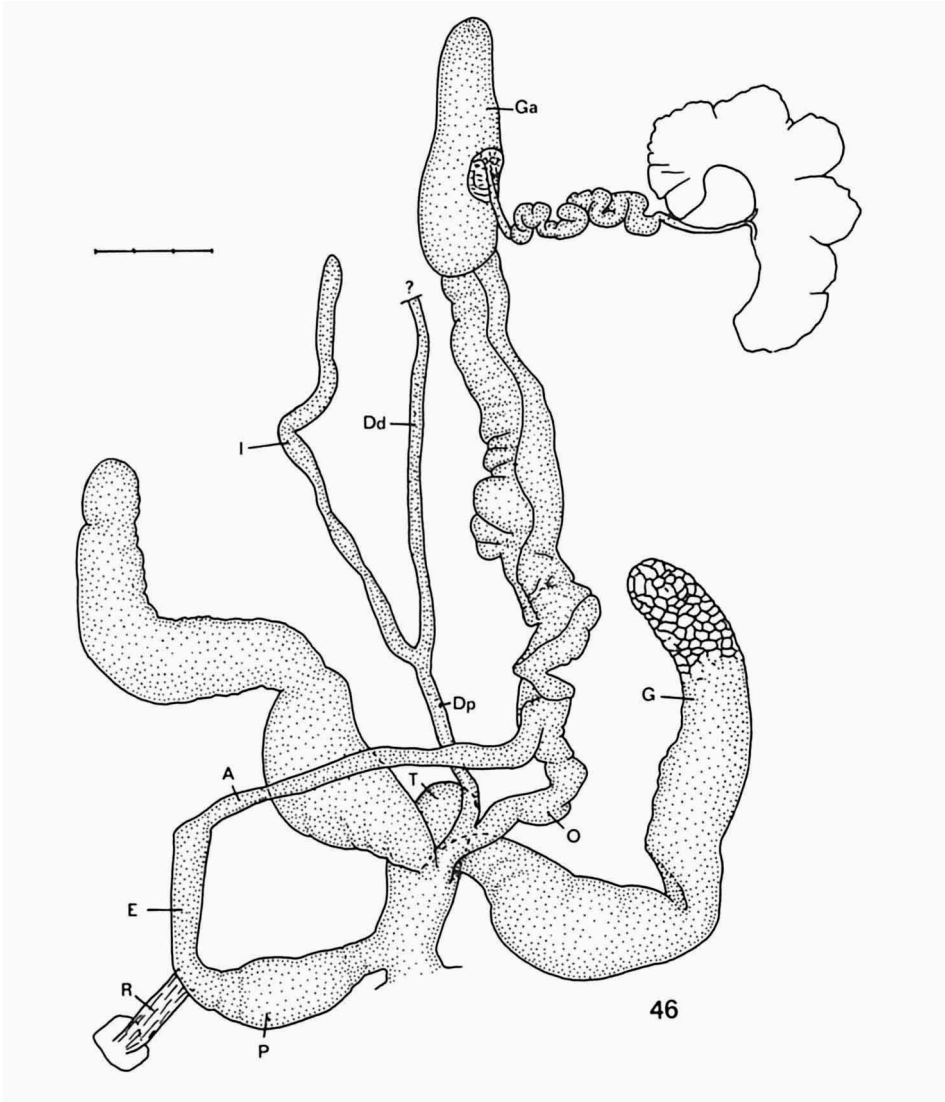


Fig. 46. *Theba andalusica* spec. nov., paratype, genitalia, Spain, province of Cádiz, Tarifa (RMNH, H. W. E. Croockewit leg.). Scale line: 3 mm. For abbreviations see p. 8.

shells have one band just above and two below the periphery, and in four shells the colour pattern is unclear. The apertural lip is whitish in nearly all specimens; in only a few shells it is light pinkish.

Width 15.4-21.0 mm; height 11.9-17.4 mm.

T. andalusica differs from the largely sympatric *T. p. pisana* by (1) the

abruptly reflected columellar lip, which covers most of the umbilicus, (2) a very globular, comparatively higher shell, with often somewhat shouldered whorls, and probably (3) a higher percentage of uniformly coloured shells. See also the notes.

The other *Theba* species with a (nearly) closed umbilicus differ from *T. andalusica* most clearly in general shape.

Genitalia (fig. 44-46). — Three specimens of *T. andalusica* could be dissected; in one of these the spermatheca got lost during dissection. There is no trace of even a rudimentary flagellum on the epiphallus. The glandulae mucosae are very large and thick, they measure about one and a half times the length of penis and epiphallus together. The proximal part of the spermatheca duct measures about one sixth of the length of the distal part, which is slightly or more conspicuously longer than the diverticulum (see figs. 44 and 45); in the specimen without spermatheca (fig. 46) the proximal part of the spermatheca duct is relatively longer. The oviduct is about one and a half times as long as the vagina.

Range (fig. 47). — *T. andalusica* is known from a limited number of localities in the Atlantic coastal area of the extreme south of Spain, from the valley of the Río Guadalquivir southward to the Strait of Gibraltar.

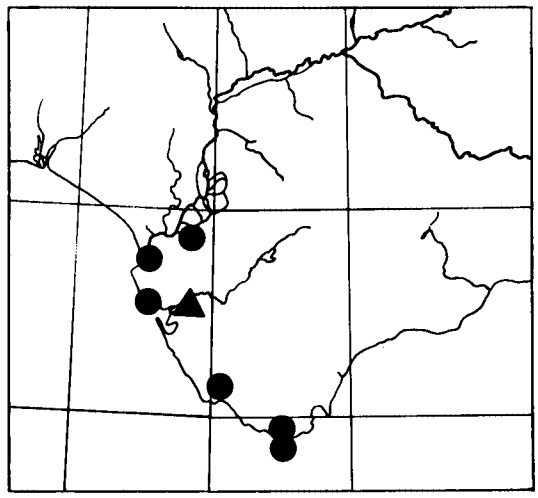


Fig. 47. UTM 10 km squares distribution map for *Theba andalusica* spec. nov. (dots) and *T. pisana arietina* (triangle).

Notes. — In the southernmost part of the Iberian peninsula, in the Spanish province of Cádiz, the genus *Theba* exhibits a remarkable variation in shell shape. *T. pisana* is represented here by the nominate subspecies, which is

widely distributed, and the very local *T. pisana arietina*, known from the small Sierra de San Cristóbal only (see p. 40). In addition we found a third form, usually clearly different from *T. pisana* by the characters mentioned above. This third form is considered a separate species, *T. andalusica*, because it may occur together with *T. p. pisana* without anything suggesting hybridization. At e.g. the type locality of *T. andalusica* a few specimens of a depressed form of *T. p. pisana* have also been found. Near Rota and SE. of Vejer de la Frontera, however, typical *T. andalusica* has been collected together with very similar *T. p. pisana* (relatively high globular shells, with an uncovered but very narrow umbilicus). Therefore we cannot exclude the possibility that occasionally hybridization between *T. p. pisana* and *T. andalusica* occurs. At three localities, viz. Lebrija, Chipiona and Tarifa, *T. andalusica* is the only *Theba* species represented, according to our samples. From much more localities in the area *T. p. pisana* is known without an accompanying *Theba* species. It is worth mentioning here that only at its type locality *T. andalusica* has been collected (by H. P. M. G. Menkhorst), while being aware of its special taxonomic status. While studying museum material from the southern part of the Iberian peninsula additional material was discovered by the authors of the present paper. (See also the notes with *T. pisana arietina*).

T. andalusica is known sympatric with *T. p. pisana*.

Etymology. — The epithet *andalusica* is formed after the name of the Spanish region Andalucía (Andalusia).

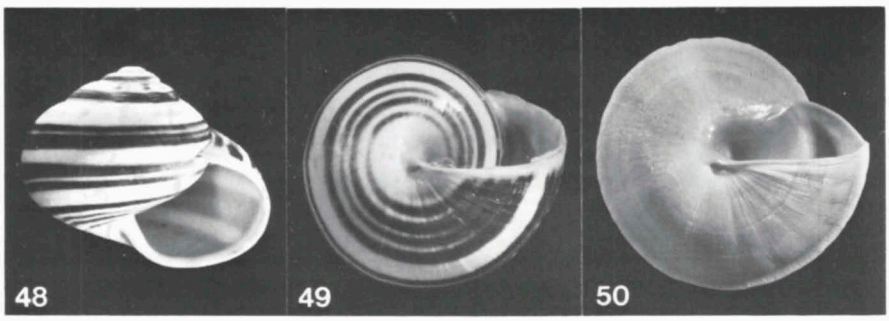
Theba solimae (Sacchi, 1955)
(figs. 1, 48, 49, 51)

Euparypha subdentata solimae Sacchi, 1955b: 44 ("Medio corso del Nun"), 47, 57, fig. 7, pl. 1 fig. 2 (two left shells). Neotype (design. nov.): RMNH 55741.

Material. — MOROCCO. Agadir: 4.5 km NW. of Tirhmi, MN57 (RD/10; RMNH/10); 6.5 km NE. of Mirhleft, MN07 (RD/1); 5 km NE. of Mirhleft, MN07 (RD/1); 10.5 km NE. of Sidi-Ifni, LN95 (RD/8); middle course of the Oued Noun, LN71 (Sacchi, 1955b: fig. 1); 11 km SW. of Bou-Izakarn, MN22 (SMF); 26 km NE. of Goulimime, MN11 (RD/29; RMNH 55741/neotype & 10); 20 km NE. of Goulimime, MN01 (SMF); 19 km N. of Goulimime, LN92 (RD/5); 3.5 km N. of Goulimime, LN91 (RD/7; RMNH/7); Goulimime, LN90 (SMF); 1.5 km SW. of Goulimime, LN90 (RD/1); 10.5 km SW. of Goulimime, LN80 (RD/1); 29.5 km SW. of Goulimime, LM79 (RD/1); Goulimime — Tan-Tan, 23 km NE. of the Oued Drâa, LM 26 (RD/4).

Shell (figs. 48, 49). — Shell rather constant in general shape, globular with a low conical spire and 4 - 4½ moderately convex whorls. At the beginning of the body-whorl the periphery is regularly rounded or (more rarely) slightly angular. Juvenile specimens were not available for study. Aperture nearly as

high as broad, usually with a prominent columellar angle below; outer lip only slightly thickened inside. The umbilicus is closed by the reflected columellar lip.



Figs. 48-50. *Theba* spec. from Morocco, 48, 49, *T. solimae*, neotype, actual width 18.6 mm, Morocco, province of Agadir, 26 km NE. of Goulimime (RMNH 55741, Th. E. J. Ripken leg.). 50, *T. subdentata helicella*, actual width 19.4 mm, Morocco, province of Safi, Essaouira (= Mogador) (RMNH, ex Altimara). Photographs by G. J. van Zonneveld.

The shells are dull. There is a colour pattern of mainly brown to blackish spiral bands, sharply contrasting with the whitish background over most of their length. On the body-whorl, above the periphery, there may be an upper row with irregular blotches and a zone with two or three spiral lines; there are two zones with one or a few spiral lines below the periphery. The aperture may have a pinkish hue inside.

Width 15.2-19.5 mm; height 10.6-14.8 mm.

T. solimae differs from the partly sympatric *T. subdentata meridionalis* by (1) the lack of a parietal denticle, (2) the thin outer lip of the aperture, and (3) the more clearly incised suture. *T. solimae* differs from both *T. pisana* and *T. sacchii* by the closed umbilicus.

Genitalia. — A schematic figure of the genitalia has been figured by Sacchi (1955b: 57, fig. 7). The flagellum measures slightly less than penis and epiphallus together and is nearly as long as the relatively thick glandulae mucosae. The proximal part of the spermatheca duct measures half the length of the distal part, which is clearly shorter than the diverticulum.

Range (figs. 1, 51). — *T. solimae* is known from a limited number of localities in the extreme SW. of Morocco, from the surroundings of Tirhmi, c. 25 km SE. of Tiznit, southwestward to the Oued Drâa.

Notes. — Most unfortunately there are no syntypes of *T. solimae* available anymore (see p. 5). The original figures accompanying the incomplete description of the species are insufficient to recognize the taxon with certainty. To

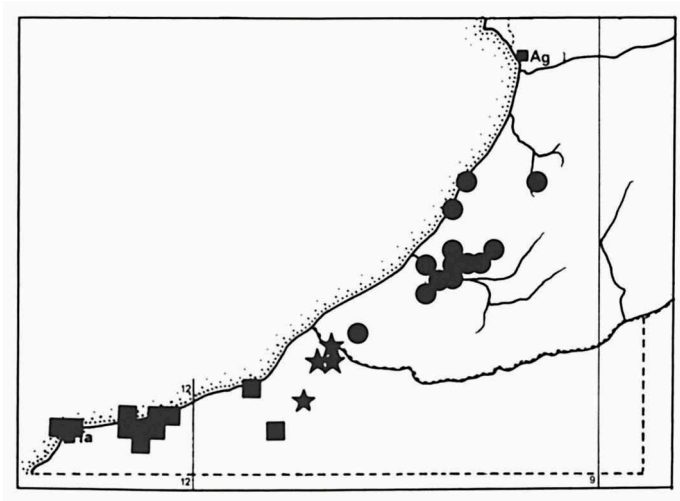


Fig. 51. UTM 10 km squares distribution map for *Theba solimae* (dots), *T. sacchii* spec. nov. (stars) and *T. chudeaui* (squares). For *T. chudeaui* only the northernmost localities are indicated.

bring the somewhat doubtful identity of *T. solimae* to an end a neotype has been designated from a sample collected as close as possible to the original type locality.

We cannot consider *T. solimae* a subspecies of *T. subdentata* because we have not seen any intermediate forms. At several localities the two taxa have been observed being sympatric.

Four specimens collected along the road from Goulimime to Tan-Tan, 23 km NE. of the Oued Drâa, are considered to belong to *T. solimae* with some doubt. The shells in question have a more regularly rounded aperture, without a columellar angle below; the brown spiral lines are somewhat more numerous, narrower and partly interrupted. Maybe this is the form figured by Sacchi (1955b: pl. 1 fig. 10) from "Fum Dra" (= Foum-el-Oued-Drâa). It should be emphasized that this form is quite different from the geographically adjacent *T. sacchii*.

T. solimae is partly sympatric with *T. subdentata meridionalis*.

Theba sacchii spec. nov.
(figs. 1, 51, 53, 54)

Material. — MOROCCO. Tarfaya: Goulimime — Tan-Tan, 1.5 km SW. of the Oued Drâa, LM05 (RD/4 paratypes; RMNH 55740/holotype, 55953/2 paratypes); Goulimime — Tan-Tan, 7 km SW. of the Oued Drâa, LM05 (RD/11 paratypes; RMNH 55954/10 paratypes); Goulimime — Tan-Tan, 12.5 km SW. of the Oued Drâa, LM04 (RD/3 paratypes); 0.5 km NW. of Tan-Tan, KM94 (RD/8 paratypes; RMNH 55955/3 paratypes); 5 km NW. of Tan-Tan, KM94 (RMNH 55956/2 paratypes); road to Smara, 36 km S. of the road Tan-Tan — Tan-Tan-Plage, KM81 (RD/2 paratypes; RMNH 55957/2 paratypes).

Shell (figs. 53, 54). — Shell quite variable in general shape, more or less depressed globular, with 4¼ - 4¾ moderately convex whorls. The periphery is regularly rounded, at least in adult shells. Juvenile specimens were not available for study. Aperture elliptical, with an indistinct to prominent (in the smallest specimens) columellar angle below; outer lip clearly thickened inside. The umbilicus is narrow but in general broader than in any other *Theba* species and not or hardly obscured by a reflected columellar lip.

The shells are dull, with a brown to bluish colour pattern on a whitish background. The pattern is not very variable. On the body-whorl, above the periphery, there are an upper row with radially elongated blotches and a zone with three to five spiral lines; there are two zones with a few spiral lines below the periphery. The aperture may have a pinkish hue inside.

Width 10.4-19.1 mm; height 8.6-12.9 mm.

T. sacchii differs from *T. subdentata meridionalis* and *T. s. legionaria* by (1) the total lack of a parietal denticle, (2) the widely open umbilicus, and (3) a slightly less shallow suture. Especially the latter subspecies can be very similar to *T. sacchii* in general shape (front view). See also *T. chudeaui*.

Genitalia. — Unknown.

Range (figs. 1, 51). — *T. sacchii* is known from the surroundings of Tan-Tan in the extreme SW. of Morocco.

Notes. — In the original description of *T. subdentata legionaria* nothing is said about the shape of the umbilical region; the description might even apply to *T. sacchii*. However, Sacchi (1955b: 47) mentions forms intermediate between *legionaria* and *meridionalis*. This and the provenance of the material in question strongly suggest that we have designated a neotype for "*Euparypha s. legionaria*" in agreement with the intention of the author.

It is not known with certainty whether or not *T. sacchii* is an extant species. Some shells belonging to it look very fresh, however. The extreme habitat of the species is figured (fig. 52).

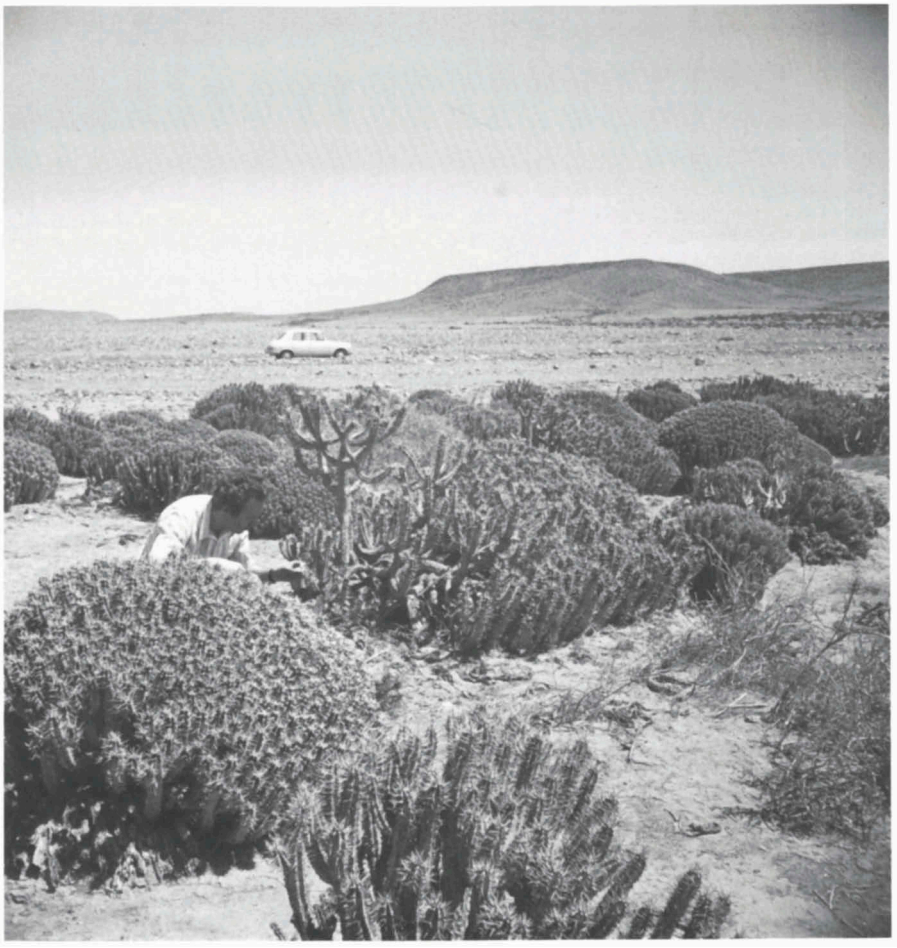


Fig. 52. Type locality of *Theba sacchii* spec. nov.: between Goulimime and Tan-Tan, 1.5 km SW. of the Oued Drâa. Photograph by H. J. Ripken-Schlieker.

T. sacchii is known sympatric with *T. subdentata meridionalis*.

Etymology. — This species is named in honour of Dr. C. F. Sacchi, who has contributed substantially to our knowledge of the systematics and ecology of the *Theba* species occurring in Morocco and elsewhere.

Theba chudeaui (Germain, 1908)
(figs. 1, 51, 56-62)

Helix (*Euparypha*) *chudeaui* Germain, 1908: 290 ("Port-Étienne"); 1910: 33, pl. 1 figs. 8-10, 28. Lectotype (design. nov.) & 8 paralectotypes: MNHN.

Material. — MOROCCO. Tarfaya: 2 km N. of Abttih, KL69 (RD/6); coastal road, 11.5 km W. of the Oued Chebeica, KM42 (RD/5; RMNH/5); coastal road, 76 km E. of Tarfaya, GS70 (RD/10); coastal road, 66 km E. of Tarfaya, GR69 (RD/33; RMNH/25); Sidi Lemsid, 67 km E. of Tarfaya, GS70 (RD/5; RMNH/30); Lagune de Khnifiss, 64 km E. of Tarfaya, GS60 (MNHN/4; RMNH/52); northern border of Sebkha Tazra, S.of the Lagune de Khnifiss, 66 km E. of Tarfaya, GS60 (RMNH/13); coastal road, 56 km E. of Tarfaya, GR59 (RD/1); coastal road, 46 km E. of Tarfaya, GR49 (RD/1); Sebkha Tazra — Sebkha Houiselgua, 57 km E. of Tarfaya, GR58 (RMNH/5); 2 km from the coast, 40 km E. of Tarfaya, GS40 (RMNH/24); coastal road, 5 km E. of Tarfaya, GR09 (RD/75); dunes W. of Tarfaya, FR99 (RD/5; RMNH/38).

WESTERN SAHARA. La 'Youne: 82 km N. of Smara, KL24 (RD/3); 57 km N. of Smara, KL22 (RD/7); 14 km N. of La 'Youne, FR70 (RD/3; RMNH/10); "Cobeza Playa" near La 'Youne, FQ49 (RMNH/4); 50 km N. of Nouadhibou, CJ78 (Germain, 1910: 35).

MAURITANIA. Nouadhibou (= Port Étienne), Cap Blanc, CJ73 (MNHN/lectotype & 8 paralectotypes).

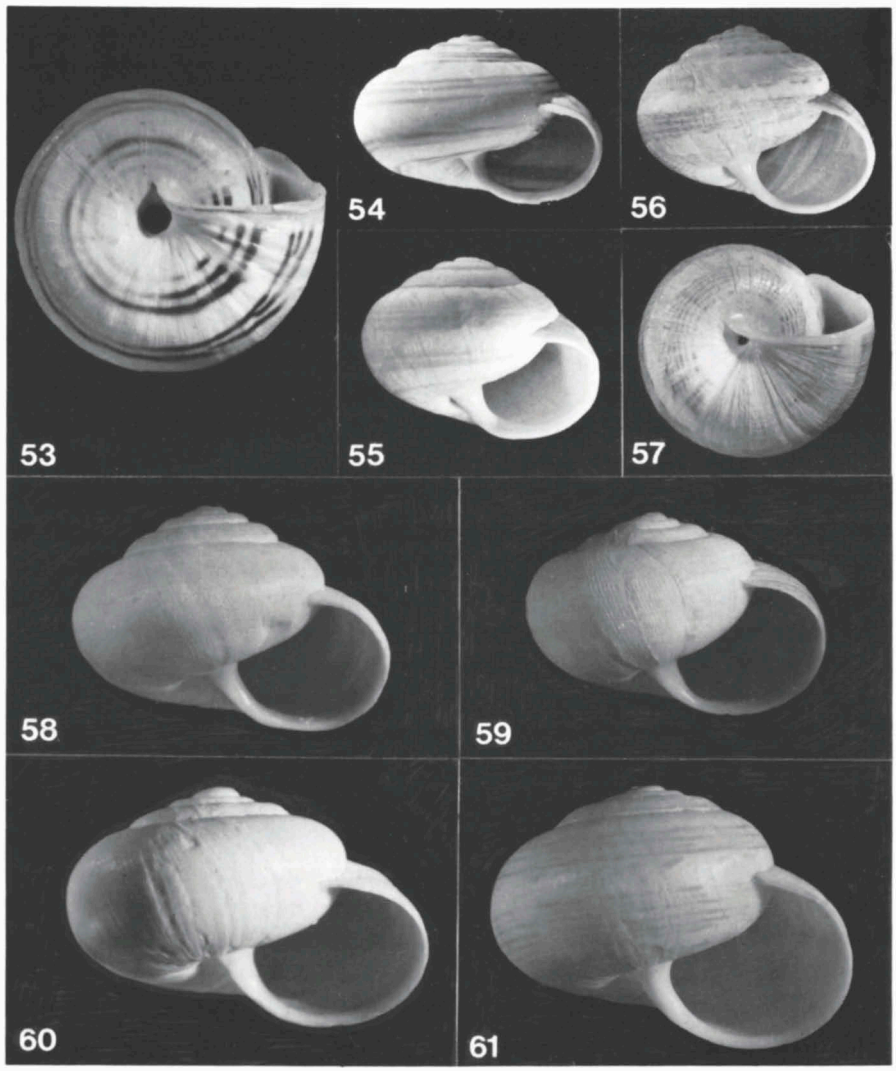
Shell (figs. 56-61). — Shell depressed globular, with 4¼ - 5¼ (moderately) convex whorls. At the beginning of the body-whorl the periphery is regularly rounded or (rarely) slightly angular; only juvenile shells of less than four whorls have a prominent keel. The aperture is rounded or (somewhat) elliptical, without or with an indistinct columellar angle below; the outer lip is not clearly thickened inside. The umbilicus is narrow but relatively broader than in *T. pisana* and not obscured by a reflected columellar lip. At the type locality the shells are much less fragile than they are in the Moroccan populations, where very thin, somewhat transparent specimens may occur.

The shells are silky because of the (very) prominent microsculpture. Usually the light brown spiral lines and spirally arranged dots are not strongly contrasting with the whitish to creamy white background colour of the shell. The aperture may be vivid pink or purple inside, with the outside pattern (vaguely) shining through.

Width 15.0-26.7 mm; height 10.7-18.6 mm.

T. chudeaui differs from *T. sacchii* by (1) the prominent microsculpture, giving the shell a silky gloss, (2) the relatively larger, more circular aperture, less descending in front, and (3) the peristome, which is hardly or not thickened inside. The character (2) is most conspicuous in the Moroccan populations, which come nearest to the range of *T. sacchii*.

T. chudeaui can be distinguished conchologically from *T. p. pisana* by (1) the microsculpture, (2) the slightly less narrow umbilicus, and (3) the much less brightly contrasting colours.



Figs. 53-61. The two southwesternmost *Theba* species along the NW. African coast. 53-55, *T. sacchii* spec. nov.; 53, 54, holotype, actual width 17.5 mm, Morocco, province of Tarfaya, 1.5 km SW. of the Oued Drâa between Goulimime and Tan-Tan (RMNH 55740, Th. E. J. Ripken leg.); 55, actual width 11.1 mm, idem, Tan-Tan (RMNH, W. Backhuys leg.). 56-61, *T. chudeaui*; 56, 57, actual width 15.1 mm, Western Sahara, "Cobeza Playa" near La 'Youne (RMNH, ex Altimira); 58, 60, lectotype and paralectotype, actual widths 20.0 and 22.4 mm, Mauritania, Nouadhibou (= Port Étienne), Cap Blanc (MNHN, ex Germain); 59, actual width 19.0 mm, Morocco, province of Tarfaya, 2 km from the coast, 40 km E. of Tarfaya (RMNH, J. R. Schouten leg.); 61, actual width 22.7 mm, Morocco, province of Tarfaya, Sidi Lemsid, 67 km E. of Tarfaya (RMNH, J. R. Schouten leg.). Photographs by E. G.

Genitalia (fig. 62). — Only one specimen, looking conchologically full-grown, could be dissected. The genitalia look quite different from those of the other *Theba* species. Maybe this is partly due to the fact that they are not completely full-grown; the ontogeny of the genitalia in *Theba* species is unknown. The glandula albuminifera and the spermoviduct are relatively large as compared to the more proximal parts of the genitalia.

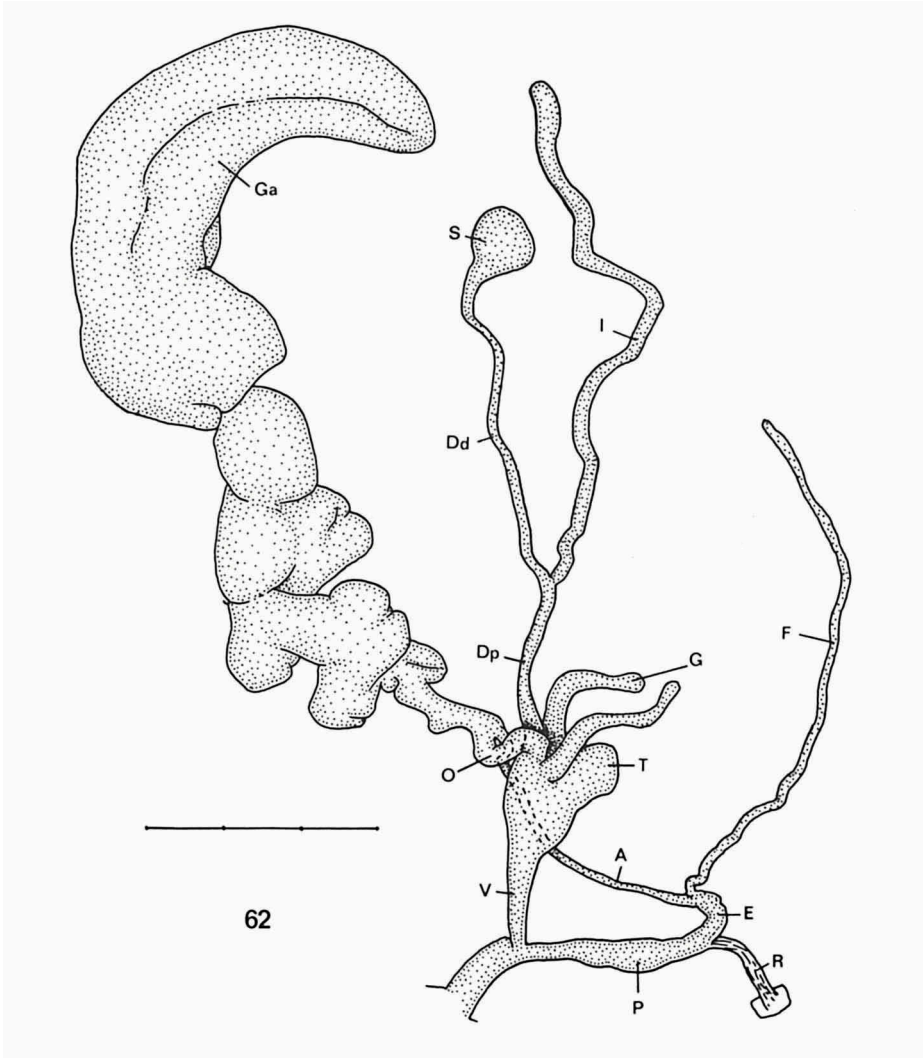


Fig. 62. *Theba chudeaui*, genitalia, Western Sahara, province of La 'Youne, 14 km N. of La 'Youne (RMNH, J. R. Schouten leg.); scale line: 3 mm. For abbreviations see p. 8.

The flagellum is about twice as long as penis and epiphallus together and more than three times longer than the small and slender glandulae mucosae. The proximal part of the spermatheca duct is twice as long as the distal part, which measures slightly more than half the length of the diverticulum. The vagina is twice as long as the oviduct, which is equal in length to the conspicuous genital atrium.

Range (fig. 1, 51). — *T. chudeaui* is known from along the coastal road, 11.5 km W. of the Oued Chebeica, in the extreme southwest of Morocco, southwestward in the coastal area to Nouadhibou in W. Mauritania, at the southern border of Western Sahara.

Notes. — After its description by Germain (1908, 1910) this species remained poorly known. New records have not been published until now. We selected a lectotype (fig. 58) from among the syntypes in MNHN.

Our knowledge concerning *T. chudeaui* could be enlarged because J. R. Schouten and the second author collected interesting new material in a not easily accessible area at the western border of the Sahara.

We classified the northeastern populations with the largely disjunct southwestern ones in a single species, without subspecies, although the two groups are slightly different from each other. Without additional material from the geographically intermediate area a well founded interpretation of the differences is impossible. Shells belonging to the former group (figs. 56, 57, 59, 61) have a relatively higher and, as a consequence, less elliptical aperture and slightly less inflated whorls as compared to those of the latter group (figs. 58, 60).

Most probably the large gap between the two groups of records (fig. 1) is at least partly due to inactivity of malacologists interested in terrestrial gastropods along the NW. African coast.

T. chudeaui occurs partly sympatric with *T. subdentata legionaria.*

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INDEX OF EPITHETS MENTIONED IN THE TEXT

Valid names in italics

REFERENCES

Adams, A. & L. A. Reeve, 1848. The zoology of the voyage of H.M.S. Samarang. Mollusca: i-x, 1-87, pls. 1-24.

Backhuys, W., 1972. Notes on Theba pisana ustulata (Lowe, 1852), the land-snail of the Salvages Islands. – Basteria 36 (2-5): 117-130.

Baez, M. & J. J. Bacallado, 1984. Los fosiles de Canarias. In: J. J. Bacallado Aránega (ed.), Fauna (marina y terrestre) del Archipielago Canario: 343-347. Las Palmas de Gran Canaria.

Baez, M. & L. Sánchez-Pinto, 1983. Islas de fuego y agua. Canarias, Azores, Madeira, Salvajes, Cabo Verde. Macaronesia: 1-184. Las Palmas de Gran Canaria.

Beck, H., 1837. Index molluscorum . . .: 1-124. Hafniae.

Bravo, T. & J. Coello, 1978. Aportacion a la geologia y petrologia de las Islas Salvajes. In: Contribucion al estudio de la historia natural de las Islas Salvajes: 15-35. Santa Cruz de Tenerife.

Cain, A. J., 1984a. Heterosematism in snails. — Malacologia 25 (1): 161-172.

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

Chemnitz, J. H., 1795. Neues systematisches Conchylien-Cabinet 11: 24 pp., 1-310. Nürnberg.

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

Deshayes, G. P., 1851. In: J. B. L. d'Audebard de Férussac & G. P. Deshayes, Histoire naturelle, générale et particulière des mollusques 2 (2): 1-260. Paris.

Deshayes, G. P. & H. Milne Edwards, 1838. In Lamarck, Histoire naturelle des animaux sans vertèbres (2nd ed.) 8: 1-660. Paris.

Férussac, J. B. L. d'Audebard de, 1820, 1821, 1823. In: J. B. L. d'Audebard de Férussac & G. P. Deshayes, Histoire naturelle, générale et particulière des mollusques. Pls. 27, 30 [26.ii.1820, see Kennard, 1942b: 109]. Explication des planches du premier volume: i-xvj [6.iv.1821, see Kennard, 1942b: 106]. Cover of "livraison" 20, with pl. 125 [1823, see Kennard, 1942a: 15].

Férussac, J. B. L. d'Audebard de, 26.v.1821. Tableau systématique de la famille des limaçons (part.): 33-56 [folio ed.] /25-48 [quarto ed.]. See Kennard, 1942b: 107.
Forcart, L., 1965. Leucochroa Beck, 1837. Eine nomenklatorische Studie. — Arch. Moll. 94 (5-6): 255-257.
Fuchs, A. & F. Käufel, 1936. Anatomische und systematische Untersuchungen an Land- und Süsswasserschnecken aus Griechenland und von den Inseln des Ägäischen Meeres. — Arch. Naturgesch. (n. F.) 5: 541-662.
Germain, L., 1908. Contributions à la faune malacologique de l'Afrique équatoriale. — Bull. Mus. nat. Hist. nat. 14 (6): 290-291.
Germain, L., 1910. Mollusques. Mollusques terrestres et fluviatiles. — Actes Soc. Linn. Bordeaux 64: 26-46, pl. 1.
Germain, L., 1934. L'Euparypha pisana Müller des archipels de l'océan Atlantique central et sa variété ustulata des îles Salvages. — Bull. Soc. Zool. France 59: 316-326.
Girard, A. A., 1888. Note sur les Helix catocyphia, Bourg. hyperplatae, Servain et pisana du Portugal. — Jorn. Sci. Math. Phys. Nat. 47: 160-166.
Gittenberger, E., 1979. On Elona (Pulmonata, Elonidae fam. nov.). — Malacologia 18: 139-145.
Gittenberger, E., W. Backhuys & Th. E. J. Ripken, 1984. De landslakken van Nederland (2nd ed.). — Bibl. Kon. Ned. Natuurhist. Ver. 37: 1-184.
Gittenberger, E. & Th. E. J. Ripken, 1985. Seven Late Miocene species of terrestrial gastropods (Mollusca: Gastropoda: Pulmonata) from the island of Lanzarote, Canary Islands. — Proc. kon. Ned. Akad. Wetensch. (B) 88 (4): 397-406.
Gualtieri, N., 1742. Index testarum conchyliorum . . .: i-xxiv, pls. 1-110. Florentiae.
Heller, J., 1981. Visual versus climatic selection of shell banding in the landsnail Theba pisana in Israel. — Journ. Zool., London 194 (1): 85-101.
Heller, J. & E. Tchernov, 1978. Pleistocene landsnails from the coastal plain of Israel. — Israel Journ. Zool. 27: 1-10.
Hesse, P., 1915. In E. A. Rossmässler, Icon. (n. F.) 23 (1-2): 1-72, pls. 631-640.
Kennard, A. S., 1942a. The Histoire and Prodrome of Férussac. Part I. — Proc. Malacol. Soc. 25 (1): 12-17.
Kennard, A. S., 1942b. The Histoire and Prodrome of Férussac. Part II. — Proc. Malacol. Soc. 25 (3): 105-110.
Kennard, A. S. & B. B. Woodward, 1926. Synonymy of the British non-marine Mollusca (recent and post-tertiary): i-xxiv, 1-447. London.
Kerney, M. P. & R. A. D. Cameron, 1979. A field guide to the land snails of Britain and North-West Europe: 1-288. London.
Kobelt, W., 1876. In: E. A. Rossmässler, Icon. 4 (5-6): 49-74, pls. 111-120.
Kobelt, W., 1881. In: E. A. Rossmässler, Icon. 7 (4-6): 25-94, pls. 194-208.
Lamarck, J. B. P. A. de, 1822. Histoire naturelle des animaux sans vertèbres 6 (2): 1-232. Paris.
Lowe, R. T., 1852. Brief diagnostic notices of new Maderan land shells. — Ann. Mag. Nat. Hist. (2) 9: 112-120.
Lowe, R. T., 1861. A list of the shells observed or collected at Mogador and its immediate environs during a few days' visit to the place in April 1859; with notes and observations. — Journ. Proc. Linnean Soc. London 5: 169-204.
Morelet, A., 1880. La faune malacologique du Maroc en 1880. — Journ. Conchyl. 28: 5-83.
Mousson, A., 1857. Verzeichniss der aufgefundenen Thiere und Pflanzen. 1. Landmollusken, mit Bemerkungen über die Molluskenfauna der canarischen Inseln überhaupt. Appendix 8 of G. Hartung, Die geologischen Verhältnisse der Inseln Lanzarote und Fuerte Ventura. — Denkschr. allg. schweiz. Ges. Naturwiss. 15: 130-139. According to Ruhoff (1980: 81) this publication dates from 1856; because no arguments are given, indicating why 1857 should be considered incorrect, we follow Mousson (1859, 1872) in citing 1857.
Mousson, A., 1859. On the land shells of Lanzarote and Fuerta Ventura; with observations on the molluscan fauna of the Canary Islands in general. — Ann. Mag. Nat. Hist. (3) 3: 81-91. Translated from Mousson (1857: 130-139) by R. T. Lowe, who added notes and observations.

Mousson, A., 1872. Révision de la faune malacologique des Canaries: i-vi, 1-176, pls. 1-6. Zürich.
Müller, O. F., 1774. Vermium terrestrium et fluviatilium 2: i-xxxvi, 1-214.
Odhner, N. H., 1931. Beiträge zur Malakozoologie der Kanarischen Inseln. Lamellibranchien, Cephalopoden, Gastropoden. — Arkiv Zool. 23A (14): 1-116.
Pallary, P., 1904. Quatrième contribution à l'étude de la faune malacologique du nord-ouest de l'Afrique. — Journ. Conchyl. 52 (1): 5-58.
Pallary, P., 1915. Description de quelques mollusques nouveaux du Grand Atlas. — Bull. Mus. nat. Hist. Nat. 21 (1): 21-28.
Pallary, P., 1921. Faune malacologique du Grand Atlas. — Journ. Conchyl. 66 (2): 89-154.
Pfeiffer, L., 1843-1849. Zweite Abtheilung der Heliceen. Eigentliche Schnirkelschnecken [part.]. In: Martini & Chemnitz, Systematisches Conchylien-Cabinet 1 (12-68): 73-96 [1843]; (12-77): 153-176 [1848]; (12-83): 241-272 [1849]. See Smith & England (1937: 91, 92) for additional bibliographical data concerning the dates of publication of the plates.
Pfeiffer, L., 1846. Symbolae ad historiam heliceorum 3: 1-100. Cassellis.
Pfeiffer, L., 1850. Beschreibungen neuer Landschnecken. — Zeitschr. Malakozool. 7 (6): 81-89.
Pfeiffer, L., 1853. Diagnosen neuer Heliceen. — Zeitsch. Malakozool. 10 (4): 51-58.
Pfeiffer, L., 1854. Die Schnirkelschnecken (Gattung Helix.). In Abbildungen nach der Natur. III. Teil [part.]. In: Martini & Chemnitz, Systematisches Conchylien-Cabinet 1 (12-130): 363-410, pls. 137, 138, 157-161. Nürnberg. Pl. 144 was published in (12-116), 1852. See Smith & England (1937: 92).
Reeve, L. A., 1852. Monograph of the genus Helix [part.]. — Conchologia Iconica 7: pls. 103-110 "June, 1852".
Reeve, L. A., 1854. Idem. — Ibidem: pls. 175-176 "April 1854".
Rossmässler, E. A., 1846. Diagnosen einiger neuen Binnen-Mollusken. — Zeitschr. Malakozool. 3: 172-173.
Rossmässler, E. A., 1854. Icon. 3 (1-2): 1-40, pls. 61-70.
Ruhoff, F. A., 1980. Index to the species of Mollusca introduced from 1850 to 1870. — Smithsonian Contr. Zool. 294: 1-640.
Sacchi, C. F., 1955a. Biogeografia e polimorfismo nelle Euparypha (Helicidae) del Marocco occidentale. — Atti Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano 94 (1): 85-95.
Sacchi, C. F., 1955b. Fattori ecologici e storici nel polimorfismo delle "Euparypha" ("Helicidae Helicinae") del Maroc occidentale. — Studia Ghisleriana (3) 2: 43-66, pl. 1.
Sacchi, C. F., 1956. Ricerche su Euparypha arietina (Rossmaessler). I — Posizione sistematica. — Annuario Ist. Mus. Zool. Univ. Napoli 8 (8): 1-6.
Sacchi, C. F., 1957. Une bonne race géographique d'Euparypha pisana (Müll.) (Helicidae) dans la région de Cadix. — Publ. Inst. Biol. aplic. 26: 77-84.
Sacchi, C. F., 1971. Écologie comparée des gastéropodes pulmonés des dunes Méditerranéenes et Atlantiques. — Natura, Riv. Soc. Ital. Sci. Nat., Milano 62 (3): 277-358.
Schmidt, A., 1855. Der Geschlechtsapparat der Stylommatophoren in taxonomischer Hinsicht gewürdigt. — Abh. naturwiss. Ver. Sachsen Thüringen in Halle 1: 1-52, pls. 1-14.
Servain, G., 1880. Étude sur les mollusques recueillis en Espagne et en Portugal: 1-172. Saint-Germain.
Smith, E. A. & H. W. England, 1937. Martini and Chemnitz (Kuester's edition) Systematisches Conchylien-Cabinet, 1837-1918. — Journ. Soc. Bibl. Nat. Hist. 1 (4): 89-99.
Taylor, J. W., 1911, 1912. Monograph of the land & freshwater Mollusca of the British Isles. Zonitidae. Endodontidae. Helicidae. 18, 19: 305-368, pls. 23-25, 27, 29 [18: 1911], 369-416, pls. 15, 30-32 [19: 1912]. Leeds.
Wenz, W., 1923. Gastropoda extramarina tertiaria. — Fossilium Catalogus 1 (18): 353-736.
Westerlund, C. A., 1889. Fauna pal. Reg. Binnenconchylien 2. Genus Helix: 1-473, 1-31 (Register). Berlin.
Wollaston, T. V., 1878. Testacea Atlantica or . . .: i-xiii, 1-588. London.
Wood, W., 1828. Supplement to the Index Testaceologicus; or a catalogue of shells, British and foreign: i-v, 1-59. London.
Zilch, A., 1960. Gastropoda 2. Euthyneura [part.]. — Handb. Paläozool. 6 (2, 4): 601-834.