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Survey of the distribution and shell polymorphism of *Cochlicella acuta* (MÜLLER, 1774) and *Theba pisana* (MÜLLER, 1774) (Pulmonata, Helicidae) along the Belgian coastal dune area

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Summary

A general survey is given of the distribution and polymorphism of *Cochlicella acuta* and *Theba pisana* (Pulmonata, Helicidae) along the Belgian coastal dunes.
Cochlicella acuta is to be found between the French-Belgian border and Zeebrugge (51°20'N). Its banding polymorphism is latitude-dependent.
Theba pisana is found throughout the whole coastal dune region. Shell ground colour, effectively bandedness and effectively unbandedness are latitude-dependent.
For both species the relationship between the frequencies of some of the morphs and latitude probably results from climatic selection.
Key-words: *Cochlicella acuta, Theba pisana*, distribution, polymorphism, Belgium.

Résumé

Les auteurs donnent un aperçu général de la distribution et du polymorphisme de *Cochlicella acuta* et de *Theba pisana* (Pulmonata, Helicidae), le long des dunes littorales de Belgique.
La distribution de *Cochlicella acuta* s'étend de la frontière franco-belge jusqu'à Zeebrugge (51°20'N). Le polymorphisme des bandes colorées de la coquille montre un rapport avec la latitude.
Theba pisana est répandu tout le long des dunes littorales. La couleur de base de la coquille, le caractère effectivement sans bandes et le caractère effectivement bandé dépend de la latitude.
Les corrélations entre la composition phénotypique des populations de ces deux espèces, et la latitude laissent apparaître des effets sélectifs en rapport avec le climat.
Mots-clefs: *Cochlicella acuta, Theba pisana*, distribution, polymorphisme, Belgique.

Introduction

Genetic polymorphism is the occurrence in the same locality, of two or more discontinuous forms of a species, in such proportions that the rarest morph is not being maintained by recurrent mutation. A great number of our terrestrial snails show an obvious polymorphism, concerning colour and banding pattern. During the last ten years we studied the distribution and shell polymorphism of some helicid snails from the Belgian coastal dune region. Results have been published for *Cepaea nemoralis* (LINNÉ, 1758) (DE SMET, 1982; DE SMET & VAN ROMPU, 1983, 1984a, b) and *Cochlicella acuta* (MÜLLER, 1774) (DE SMET, 1983, 1985; DE SMET & VAN ROMPU, 1987.) In the present contribution we give additional information on *C. acuta* and some preliminary results on *Theba pisana* (MÜLLER, 1774).

Results and discussion

I. Cochlicella acuta

I.1. Distribution

Cochlicella acuta is considered to be an element of the Mediterranean malacofauna, that dispersed along the coastal regions of west and nord-west Europe. For Belgium it was recorded first in 1910, at De Panne (BOULY DE LESDAIN, 1911). Later on the species is mentioned again from the same locality by DUPUIS (1924, in ADAM: 1947a), ADAM (1947a), VERHAEGHE (1947) and ANTEUNIS (1956). Empty shells were collected in 1930 at Nieuwpoort-Bad (ADAM, 1947a). In 1956 the species still did not extend north of Oostduinkerke (DE LEERSNYDER & HOESTLANDT, 1957), and in 1960 ADAM mentions it from De Panne, St. Idesbald, Koksijde and Oostduinkerke. MARQUET (1982), DE WILDE et al. (1986) and DE SMET (1983) confirm the earlier reports and add a number of new localities to the species' range. In 1981 the most northern colony (DE SMET, 1983) was at Raversijde-Bad (Oostende). In 1983 some colonies were found north of Oostende, the northernmost being situated at Wenduine (DE SMET, 1985). Since 1986 the most northern colony of the species' range along the east coast of the North Sea lies at Zeebrugge (51°20'02"N). It is a well established colony, located near a cross-road, 675 m from the sea (OH). This means an expansion of some 53 km north in about 78 years since the first record (Fig. 1).
The dispersal of *C. acuta* is doubtless largely due to human activity, as indicated by the many colonies near roadsides and parking-places. The expansion of the colony at Wenduine discovered on 26.10.83, and now extending over 600 m along the roadside was probably enhanced by wind action, as we saw specimens rolling over the asphalt-paving at high windspeads.

I.2. Shell polymorphism

An account of the shell polymorphism in *C. acuta,*

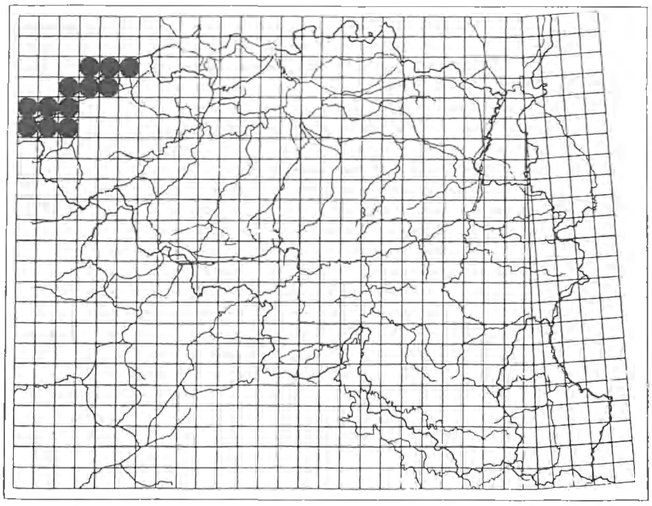

Fig. 1. Actual distribution of Cochlicella acuta.

Table 1 Frequencies of the banding morphs and shell opacity in *Cochlicella acuta* from the Belgian coastal dune region.

Banding	Discontinuously opaque		Continuously opaque		Total	
morph	N	%	N	%	N	%
00000	5,866	46,8	2,333	18,6	8,199	65,4
00040	2,118	16,9	1,339	10,7	3,457	27,6
00340	232	1,8	374	3,0	606	4,8
00300	67	0,5	150	1,2	217	1,7
12340	28	0,2	1	0,01	29	0,2
02340	23	0,2	9	0,1	32	0,3
02300	2	0,02	-	-	2	0,02
12345	-	-	1	0,01	1	0,01
02345	-	-	1	0,01	1	0,01
00045	-	-	1	0,01	1	0,01
Total	8,336	66,4	4,209	33,6	12,545	100

based on breeding experiments is given by LEWIS (1975). The principal variation (Fig. 2) involves the banding pattern (a system of five dark pigmented bands), the opacity of the extra-band areas (continuous ostracum: opaque, usually white shell; discontinuous ostracum: opaque shell interrupted by transverse and transparent areas), and the shell gound colour (amber, pale amber, white). Combined with our former collections (DE SMET, 1983), altogether 12,545 snails from 61 colonies have now been examined. The frequencies of the banding morphs and the shell opacity are summarized in Table 1. There are as twice discontinuously opaque shells as continuously ones. The unbanded type 00000 (65%) and the one-banded morph 00040 (28%) together account for 93% of all morphs found. In addition to the morphs 00000, 00300, 00340 and 00040, collected earlier, a series of other morphs (12345, 12340, 02345, 02340, 02300, 00045) showing different degrees of band-fusion were discovered in a colony north of Oostende. In our search for *C. acuta,* extending from Etaples, north of France (latitude 50°30'N) till Zeebrugge, the latter banding morphs were only found in a restricted area near Dunkerque and their occurrence at Oostende is probably the result of import from that area.

Only one colony near Klemskerke is monomorphic (DO 00000), all other colonies segregate simultaneously for up to 5 loci, controlling shell polymorphism. The monomorphic colony probably results from a founder effect, rather than being the result of selective forces.

Opacity neither banding show a significant association with habitat. Visual selection for crypsis by predators is therefore assumed to play an unimportant role in population differentiation.

In contrast however, latitude-related selection, probably due to climate, determines the banding-morph frequencies. The over-all frequency of the one-banded 4, and all banding types taken together, shows a significant increase towards the north (Fig. 3), where it is more humid (DINGENS & VERNEMMEN, 1963). The frequency of the bandless morphs increases significantly southwards, where it is more arid. The clinal structure of the

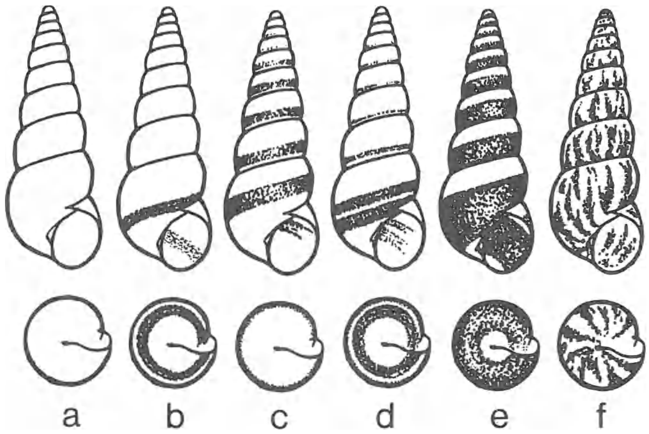

Fig. 2. Opacity and banding morphs of Cochlicella acuta *(umbilical aspects shown beneath). a: continuously opaque (CO) 00000; b: CO 00300; c: CO 00040; d: CO 00340; e: CO 00(345) ; f : discontinuously opaque (DO) 00000.*

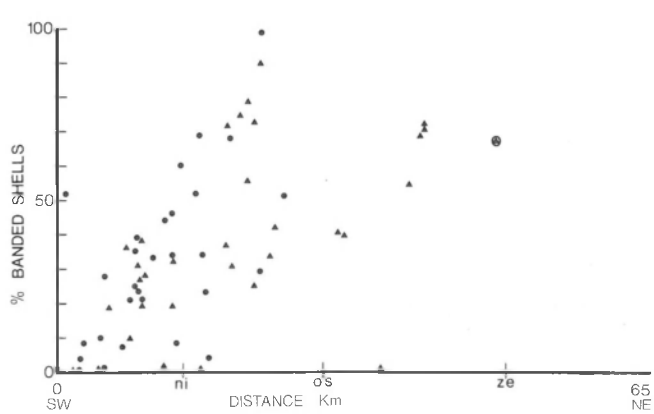

Fig. 3. Relationship between colonial frequency of banded shells and latitude for Cochlicella acuta. *samples of 1981; ● samples of 1982-83; ▲ 1986. ni = Nieuwpoort; os = Oostende; ze = Zeebrugge.*

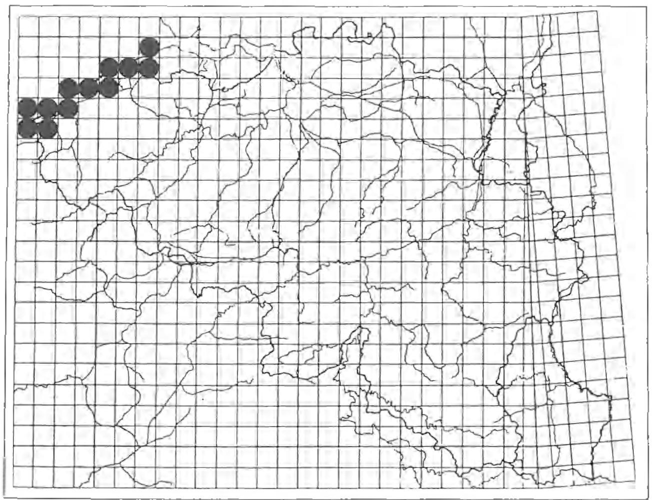

Fig. 4. Actual distribution of Theba pisana.

shell-banding was explained physiologically (DE SMET, 1983). A shell with dark pigmented bands will heat up the snail more rapidly to his activity temperature, and will be advantageous by speeding up temperature-dependent processes such as growth and gametogenesis.

II. Theba pisana

II.1. Distribution

Theba pisana probably has a Maghrebian origin and actually shows an Atlantic-Mediterranean distribution (SACCHI, 1971). The earliest record for the species in Belgium was by HOSTIE (1935) in 1934 at Mariakerke (Oostende). The presence at Mariakerke was confirmed by ADAM & LELOUP (1937) in 1936. From 1947 till 1960 *T. pisana* is established between Mariakerke and Raversijde (ADAM, 1947b, 1960), and between De Panne and the French-Belgian border (VERHAEGHE, 1947; ADAM, 1947b, 1960; ANTEUNIS 1956). In 1946

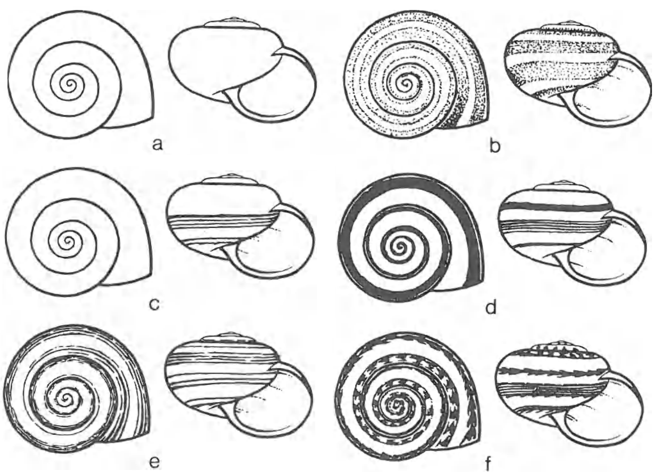

Fig. 5. Some banding morphs of Theba pisana. *Top views of the shells are shown with the corresponding side views. a: 0000, b: 1234 yellow banded; c: 0034; d: 0234; e-f: 1234 with variations in bandlets from stripes (e) to arrowheads (f).*

three specimens were collected between Oostende and Bredene, but the species could not be found back afterwards (ADAM, 1947b). DEBLOCK & HOESTLANDT (1967) recorded *T. pisana* without interruption from Boulogne (France) till Koksijde, and from Westende till Oostende. During our survey of the dune region in 1981-83, we found *T. pisana* distributed throughout the whole area (Fig. 4). The northernmost colony at the Zwin area (51°22'01"N, 450 m from OH) was already established in 1981. It must be remarked that specimens of *T. pisana,* originating from Algeria, were artificially introduced at Oostende around 1869 (ADAM, 1947a). DEBLOCK & HOESTLANDT (1967) considered the colonies found between Westende and Oostende, being the result of the latter artificial introductions. As the species is known from the region of Boulogne since 1921 (DEBLOCK & HOESTLANDT, 1967) it is likely that the south-western populations at least originate from individuals from the littoral of the Channel.

The rapid expansion of the species during the 50 years since its first record (or during the 120 years since its introduction at Oostende) cannot be explained solely by the snail's own locomotion. The linear expansion of the species is estimated to vary between 4,7 metres.year-1 (HICKSON, 1972) and 21 metres.year^{-1} (JOHNSON & BLACK, 1979). Man obviously is the most important dispersal agent, transporting the species over long distances and barriers such as rivers, unsuitable habitats, etc. The snail's own locomotion probably plays a major role by filling-in its area of distribution. The colonising ability of *T. pisana* is also enhanced by its high productivity. COWIE (1984a) observed the mean egg production per pair of snails to be 368 eggs, with one pair producing up to 1303 eggs over the course of the breeding season.

II.2. Polymorphism

Theba pisana is an extremely variable species, especially with regard to shell pattern. The genetic basis of the polymorphism is now becoming elucidated (COWIE, 1984b; CAIN, 1984). The shell ground colour ranges from white through cream and buff. Depending on the author (for a discussion see CAIN, 1988) the banding (Fig. 5) consists of 4 (SACCHI, 1952; HELLER, 1981) or 5 (COWIE, 1984b; CAIN, 1984) yellow-buff to dark-brown bands. The bands may be reduced in number or completely absent. Each of these bands may be overlaid with up to six delicate bandlets, that show great variation in their intensity of pigmentation and continuity. The bandlets may be feathered, broken into dashes or dots, or take the aspect of chevrons, arrowheads, etc. Scoring of the morphs is often difficult as there can be considerable variation in their expression, caused in part by genetic modifiers so that variation appears to be continuous (CAIN, 1984).

A total of 30,066 snails from 176 populations distributed over the whole dune area have been studied. The

Table 2 Frequencies of the banding morphs and ground colour in *Theba pisana* from the Belgian coastal dune region.

Banding morph	N	%	Shell ground colour	N	%
0000	10,021	33,3	White	19,267	64,1
0234	3,779	12,6	Creamish	10,799	35,9
0034	2,784	9,3			
0004	259	0,9			
1234 yellow	7,421	24,7			
1234 striated	1,155	15,4			
Minor variat.	1,187	3,9			
Total	30,066	100			

detailed results will be published elsewhere.

Shells showing a white ground colour (64%) are more frequently found than those with a creamisch (36%) one.

The banding morphs (Tab. 2) observed could be grouped into 10 main classes, the five most important accounting for 95% of all banding morphs collected are:

- 0000: the shell shows neither bands or bandlets (Fig. 5a)

- 1234 yellow: shell with 4 coloured bands, but without bandlets (Fig.5b)

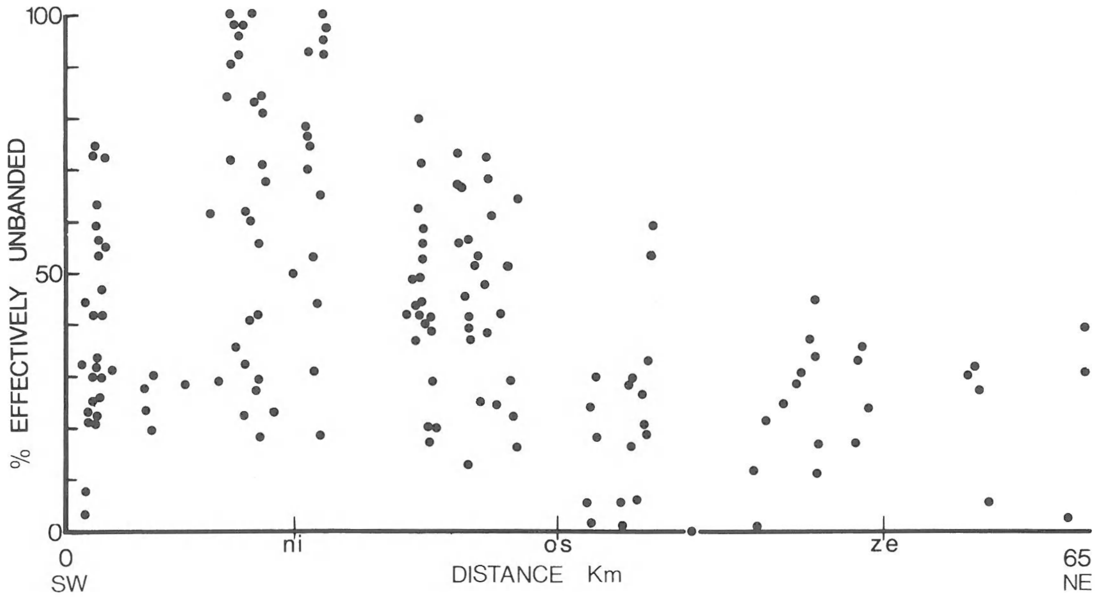

Fig. 6. Relationship between colonial frequency of bandedness and latitude. 100% effectively unbanded = 0% effectively banded and vice versa. ni = Nieuwpoort; os = Oostende; ze = Zeebrugge.

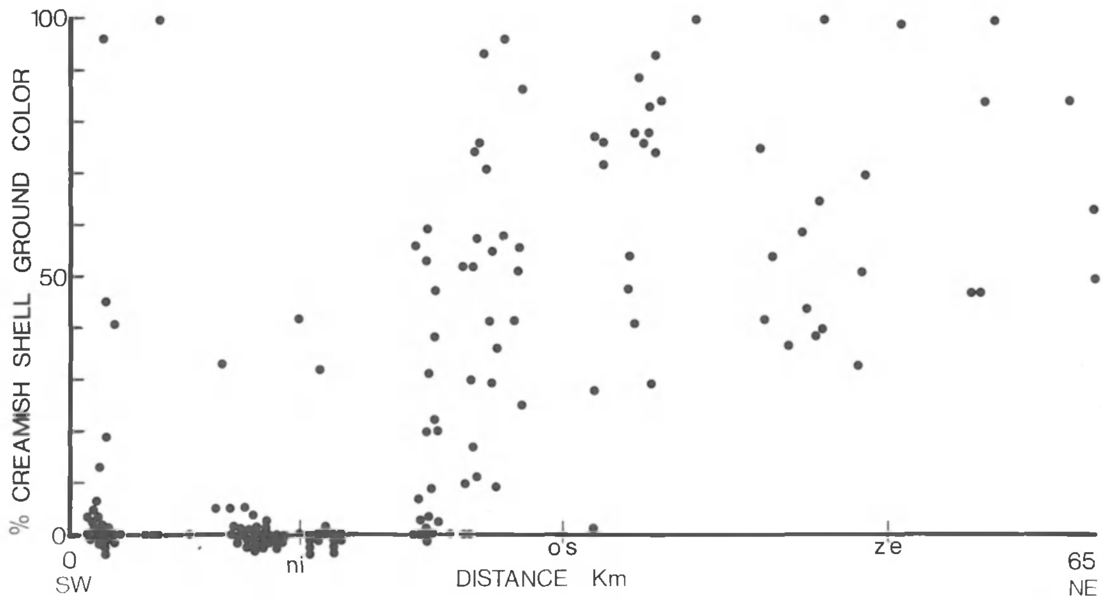

Fig. 7. Relationship between colonial frequency of shell ground colour and latitude. 100% creamish shell ground colour = 0% white ground colour and vice versa. ni = Nieuwpoort; os = Oostende; ze = Zeebrugge.

- 1234 striated: bandlets present; bands present or absent (Fig. 5e-f)
- 0234: the first band and his bandlets absent (Fig. 5d)
- 0034: bands 1 and 2, and their bandlets missing (Fig. 5c).

The distribution of the different morphs along the study area shows that the gene frequencies are probably determined by climate. The influence of habitat and predation on the morph composition of the colonies is less clear. The real geographical difference in climate (DINGENS & VERNEMMEN, 1963) between the SW and NE of the littoral is a.o. reflected in the frequency of the shell ground colour, the character "absence of banding" (0000) and the character "banding and bandlets 1 and 2 absent" (0034).

The frequency of the effectively unbanded shells (0000, 0034) and all other minor variations lacking bands 1 and 2, and/or the bandlets 1 and 2 decreases (or in other words effectively banded shells, with a banded appearance when seen from above, increase) from the SW to the NE (Fig. 6). Effectively unbanded shells will be at a selective advantage in the SW, due to their greater reflection of solar energy, whereas the shells with bands and bandlets at their upper side that will show up more dark and thus absorb more solar energy, are favoured in the more humid and northern localities. Shell ground colour shows an analogous evolution (Fig. 7). Animals with white shells, which reflect as much as 90% and more of visible light and of the near infrared radiation, predominate in the most arid area (mean annual precipitation 700 mm): about 91% of the colonies (86) out of that region have 90% or more white shells each. In the more humid stretch (mean annual precipitation 800 mm) shells with creamish ground colour are dominant: only 18% of the 90 colonies have less than 10% creamish shells each. An increased reflectance both by effectively unbandedness and white shell ground colour is undoubtedly of critical importance in reducing the temperature of the snails' tissue and minimizing desiccation during summer in the more arid stretch. Dark effectively banded shells and shells with a creamish ground colour are advantageous by the enhanced absorption of solar energy, by which temperature- dependent processes as locomotion, growth and gametogenesis are favoured in the more harsh stretch.

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