*Biol. Jb. Dodonaea, 50, 1982, 182-201 (27/12/1982).*

# SHELL COLOUR AND BANDING POLYMORPHISM IN *CEPAEA NEMORALIS* (L.) (GASTROPODA), FROM THE BELGIAN COASTAL DUNE REGION

by

W. H. O. DE SMET

## 1. Introduction

*Cepaea nemoralis* (L.) is a highly polymorphic land snail, which displays shell colour varieties and banding patterns, determined by two closely linked multiple allelic series (a.o. LAMOTTE, 1954, 1959 ; CAIN and SHEPPARD, 1957 ; CAIN, KING and SHEPPARD, 1960 ; CAIN, SHEPPARD and KING, 1968 ; MURRAY, 1963). The shell colour varies from dull brown, red to pale pink, and dark to light yellow, with dark colours dominant to lighter ones. The completely banded snail has five (very rarely more) dark brown pigmented longitudinal bands. The bands may be reduced to 1, 2, 3 or 4, or completely absent. Absence of bands is dominant to presence and epistatic over all other loci that affect banding (CAIN, SHEPPARD and KING, 1968 ; CARTER, 1968).

*Cepaea nemoralis* lives in diverse habitats and is subject to many selective forces that cause and maintain the polymorphism. Amongst them are visual selection by predators (LAMOTTE, 1951 ; SHEPPARD, 1951 ; O'DONALD, 1968), climatic selection (LAMOTTE, 1959, 1966 ; RICHARDSON, 1974), frequency-dependent selection (ALLEN, 1976), etc. JONES *et al.* (1977) state that the genetic structure of each population usually requires a complex and perhaps unique explanation.

## 2. The sampling region

The collections were taken from the whole Belgian coastal dune region (about 65 km length), extending from the most southern part (Westhoek) to the most northern part (Zwin). The dunes form a stretch of 0.1-2 km along the North Sea, composed of calcareous moderate-sandy soil (150-200 μ). They are mostly very arid to arid and locally damp. The topography is relatively hilly, with heights varying from 5-30 m, and interspersed with somewhile humid depressions.

Our Belgian dunes have been severely damaged in the past by an inappropriate policy and no longer constitute a continuous entity. Moreover most of the remaining dunes are submitted to a strong recreation pressure, resulting in dune abrasion and disturbance of vegetation and fauna. This may partly explain the complete absence or rarity of *Cepaea nemoralis* at too many localities examined.

## 3. Habitat classification

The dune vegetation shows several plant communities reflecting the development of the dunes. For our study we distinguished four main habitats : mobile to semi-mobile dune (A), fixed dune (H), scrub (S) and bramble (R). The mobile and semi-mobile dune is characterized by a patchiness vegetation, mainly composed of *Ammophila arenaria* (L.) Link, and to a lesser extent *Euphorbia paralias* L., *Elymus arenarius* L. and *Calystegia soldanella* (L.) R. Brown. The fixed dune shows an increased plant cover composed of different vegetation units with most characteristic species : *Ammophila arenaria* (L.) Link, *Phleum arenarium* L., *Festuca rubra* L., *Catapodium rigidum* (L.) C. E. Hubbard, *Polygala vulgaris* L., *Asperula cynanchica* L., *Galium verum* var. *littorale* Bréb., *Corynephorus canescens* (L.) P. Beauv., *Viola tricolor maritima* (Schweigg.) Hyl., *Ononis spinosa* L., *Arabidopsis thaliana* (L.) Heynh., *Syntrichia ruralis* (L.) Brid., etc. The bramble (*Rubus* spec.) can grow over large surfaces in the fixed dune area, forming a closed habitat, the ground under the bramble being devoided of vegetation. The dominant plants of the shrub communities are *Hippophae rhamnoides* L. and *Salix repens* L., associated by *Sambucus nigra* L. and *Ligustrum vulgare* L. on more wet grounds. The herbaceous underlayer may consist of *Urtica dioica* L., *Galium verum* L., *Claytonia perfoliata* Donn ex Willd., *Senecio jacobaea* L., *Hypnum cupressiforme* L., etc.

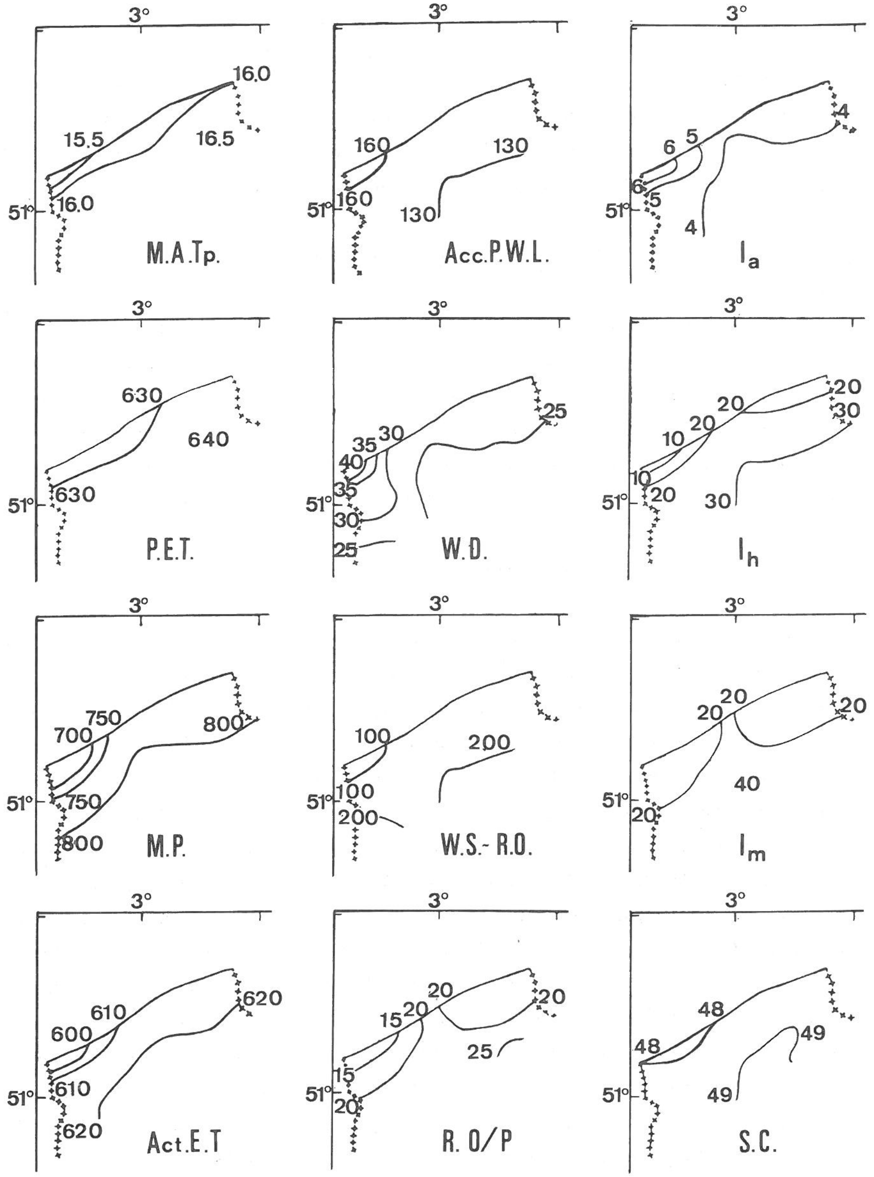


FIG. 1. – Climatic elements. M.A.Tp. : mean air temperature (°C) summer ; P.E.T. : annual potential evapotranspiration (mm) ; M.P. : annual mean precipitation (mm) ; Act.E.T. : annual actual evapotranspiration (mm) ; Acc.P.W.L. : annual accumulated potential water loss (mm) ; W.D. : water deficit (mm) ; W.S.-R.O. : annual water surplus (mm) and run off (mm) ; R.O./P. : yearly ratio run off/precipitation (%) ; $I_a$ : aridity index ; $I_h$ : humidity index ; $I_m$ : moisture index ; S.C. : summer concentration of thermal efficiency (modified after DINGENS & VERNEMMEN, 1963).

## 4. Climatological information

The annual mean temperature of the dune region is 10°C ; the mean January temperature is 3.5°C and the mean July temperature is 16.5°C. There is a frost-free period of 220 days, and an annual precipitation of 800 mm (Tavernier and Marechal, 1959).

For a more detailed analysis of the distribution of *Cepaea nemoralis* and climatic selection we used the THORNTHWAITE classification of climate (Dingens and Vernemmen, 1963). The climatic elements considered are shown in Fig. 1. Except for a small humid stretch in the middle (type $B_1rB'_1b'_4$), the region studied is moist subhumid, with a megathermal temperature efficiency regime ($C_2rB'_1a'$) in the southern half and fourth mesothermal temperature efficiency regime ($C_2rB'_1b'_4$), in the northern half.

## 5. Sampling and scoring

Collections were taken from 50 different colonies in April and May 1981. Two colonies sampled in April 1975 (N° 25, Appendix I & II) and 1977 (N° 26, Appendix I & II), are included in this study as it was demonstrated (Lamotte, 1951 ; Goodhart, 1956, 1958, 1973 ; Gerdeaux, 1978) that phenotype composition of populations is not changing rapidly with time. Each station was searched carefully in order to sample as much snails as possible. Live snails were released after recording the shell colour and banding morph ; empty and predated shells were taken to the laboratory. The bands were numbered 1 to 5, the uppermost being 1 ; absence was indicated by 0 (cf. Von Martens, 1865). Fusions were recorded only if they occupied a large part of the largest whorl of the shell (Cain and Sheppard, 1950) and indicated by bracketing the band numbers of the fused bands. Doubled bands (e.g. 003300) were classified as single banded (Wolda, 1969) ; extra thin bands (:) were not recorded. For shell ground colour three main classes were distinguished : brown, pink and yellow. The shells were also examined for hyalozonate bands, white peristome lip, open umbilicus and sinistrality. Data on shell size will be published later.

## 6. Results

### 6.1. *General survey*

A total of 13,415 snails from 50 populations have been studied. The composition of the collections, classified by banding and by ground colour is to be found in Appendix I and II. Table 1 gives the banding morph frequencies by number and percentage. Table 2 shows the frequencies of the most important banding morphs for different shell colours.

Table 1

*Banding morph frequencies for* C. nemoralis *from the Belgian coastal dune region*

| Banding morph | Number of individuals | Percentage |
|---|---|---|
| 00000 | 2,707 | 20.1789 |
| 02000 | 3 | 0.0224 |
| 00300 | 5,213 | 38.8595 |
| 00040 | 1 | 0.0075 |
| 10300 | 13 | 0.0969 |
| 02300 | 13 | 0.0969 |
| 00340 | 9 | 0.0671 |
| 00305 | 8 | 0.0596 |
| 00045 | 11 | 0.0820 |
| 12300 | 5 | 0.0373 |
| 10305 | 4 | 0.0298 |
| 10045 | 9 | 0.0671 |
| 02340 | 2 | 0.0149 |
| 02045 | 1 | 0.0075 |
| 00345 | 278 | 2.0723 |
| 12305 | 2 | 0.0149 |
| 12045 | 34 | 0.2534 |
| 10345 | 797 | 5.9411 |
| 02345 | 133 | 0.9914 |
| 12345 | 4,172 | 31.0995 |
| *Total* | 13,415 | 100 |

Twenty banding morphs are found. Three of them are predominant and account for 90.14 % of all snails found : they are in decreasing order 00300, 12345, and 00000. Together with the less frequent morphs 10345 and 00345 they make 98.15 % of the total collection.

The frequency of yellow shells is 69.44 % ; the frequency of pink and brown shells is respectively 29.12 % and 1.44 %. Brown shells are almost exclusively unbanded. For yellow shells the frequency of formula 00000 (23.59 %) is clearly higher than for pink ones (8.14 %), whereas the frequency of morph 12345 is higher for pink shells (41.15 % versus 27.53 % for yellow). The remainder of the banding morphs has a similar frequency for yellow and pink.

Table 2

*Frequencies of the main banding morphs for different shell colours in* Cepaea nemoralis *from the Belgian coastal dune region*

| Banding morph | Yellow | | Pink | | Brown | |
|---|---|---|---|---|---|---|
| | Number | % | Number | % | Number | % |
| 00000 | 2,197 | 23.59 | 318 | 8.14 | 192 | 99.48 |
| 00300 | 3,517 | 37.76 | 1,695 | 43.38 | 1 | 0.52 |
| 00345 | 227 | 2.44 | 51 | 1.31 | – | – |
| 10345 | 652 | 7.00 | 145 | 3.71 | – | – |
| 12345 | 2,564 | 27.53 | 1,608 | 41.16 | – | – |
| Others | 158 | 1.68 | 90 | 2.30 | – | – |
| Total | 9,315 | 69.44 | 3,907 | 29.12 | 193 | 1.44 |

No shell displayed sinistrality or an open umbilicus. Only one shell with white peristome lip was found in the stations 7 (Y00000) and 40 (Y00300) respectively. Shells with hyalozonate bands were scarce : one individual was found in station 18 (P00300), 14 (B12300) and 7 (Y00300). There was no indication for high numbers of hyalozonates with or without white peristome lip as mentioned by COLBEAU (1863-65) for Lombardsijde (stations 22-23).

*Cepaea hortensis* (MÜLL.) which is known to be rare in the dune region (ADAM : 1947), was only found in station 9 (Koksijde) and 35 (Bredene) at low numbers.

## 6.2. *Geographical variation in polymorphism*

Fig. 2 shows the location of all samples collected and the frequencies of eight characters of the polymorphism.

Some NE-SW trends in morph frequencies are apparent, however without all being continuous throughout. Brown shells are almost confined to the SW (present in 9 colonies) and lacking, except for one colony, at the NE part of the dune region. For yellow and pink shell colour there is no clear trend. Pinks (and browns) show a higher percentage in the middle of the SW dune area. Of the banding morphs, phenotype 12345 is abundant at most stations and shows no specific distribution. Morph 00000 reaches remarkable frequencies in the SW corner and shows a decreasing tendency towards the N.E. (Spearman's

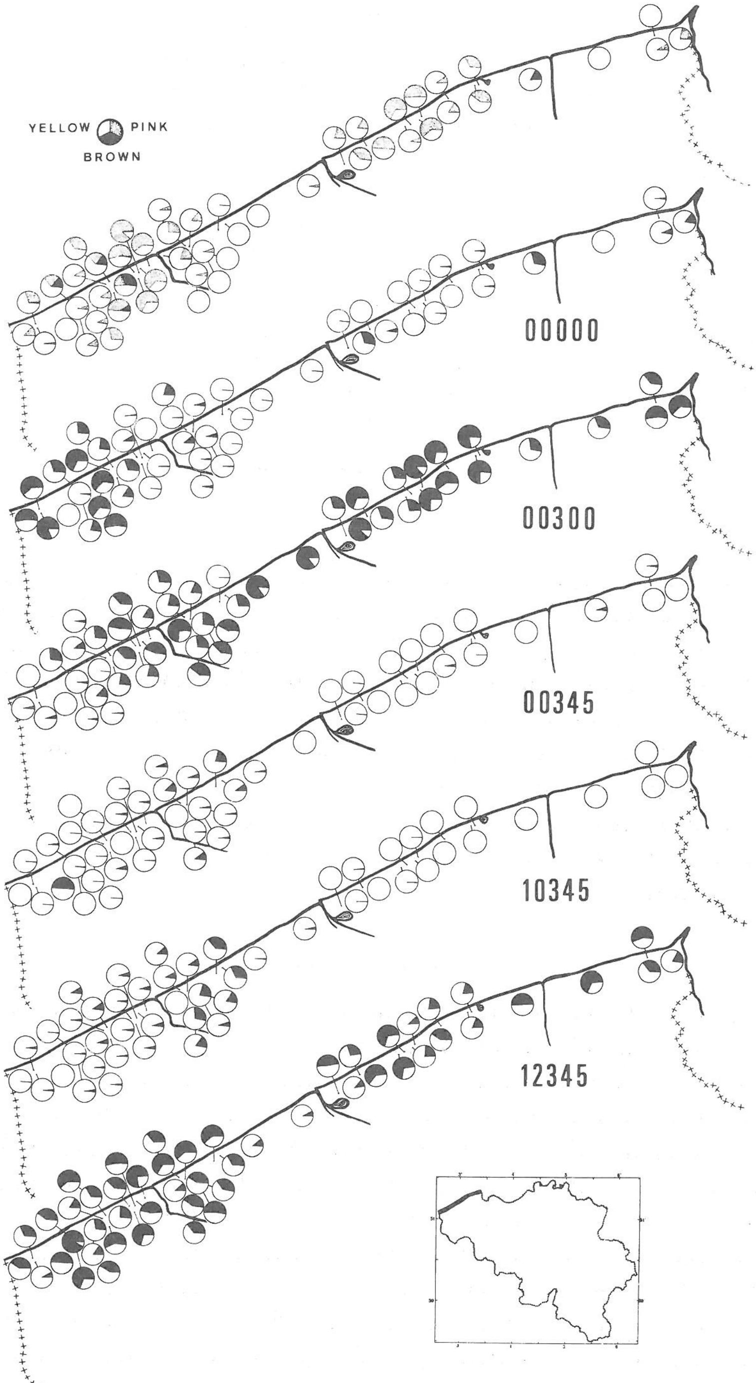


FIG. 2. – Distribution of colonies and frequencies of shell colour and main banding morphs for *Cepaea nemoralis* from the Belgian coastal dune region.

rank correlation coefficient $r_s = -0.449$, $z = 3.145$, $p < 0.0016$). The distribution of phenotype 00300 is inverse to that of morph 00000 : low frequencies in the SW and increasing to the NE ($r_s = 0.714$, $z = 4.997$, $p < 0.0001$). The morph frequencies for 10345 and 00345 are higher in the SW part of the dune region ; besides there is a more or less increasing trend from SW to NE in that area, which is most pronounced for morph 10345.

### 6.3. *Variation in polymorphism with climate*

The areas delimited by the isoplets for ten of the climatic elements given in Fig. 1, were analysed for differences in colour, main banding morphs and fusion of the colonies by a single classification analysis of variance (Table 3). It must be remarked that most elements are interdependent.

#### 6.3.1. The yellow phenotype

There is a significant added variance component among the areas delimited by eight climatic elements for yellow. The mean frequency for yellow shells is significantly lower (66-68 % v. 71-93 %) in the areas with the lowest mean summer air temperature, mean precipitation, actual evapotranspiration, accumulated potential water loss, water surplus-run off, and humidity index. The lowest percentages (33 % v. 71-83 %) are found in the area with a water deficit of 30 mm.

#### 6.3.2. The pink phenotype

Pink shells are less frequent (7 % v. 23-30 %) in the areas with a respective mean precipitation of 750 mm, an actual evapotranspiration of 610 mm and a humidity index of 20. The highest mean frequency is found in the area with a water deficit of 30 mm (67 % v. 14-21 %).

#### 6.3.3. The brown phenotype

The areas with the highest water deficit (35-40 mm) and aridity index (6) show the highest numbers of brown shells (2-8 % v. 0.4-0.9 %).

#### 6.3.4. The phenotype 00000

The unbanded phenotype displays significant differences for all climatic elements, the potential evapotranspiration excepted. The areas with the lowest mean summer air temperature, mean precipitation, actual evapotranspiration, water surplus-run off, humidity index, and summer concentration of thermal efficiency on the one side, and the highest accumulated potential water loss, water deficit and aridity index on the

Table 3

*Variance ratios ($F_S$) for climatological elements : shell colour, banding morph and fusions*

| | d.f. | Yellow | Pink | Brown | 00000 | 00300 | 00345 | 10345 | 12345 | E.U.B. | Fusions |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean air temperature : summer | 1,48 | 5.94* | 3.73 | 3.91 | 24.25** | 25.67** | 0.08 | 0.92 | 0.34 | 0.97 | 0.11 |
| Potential evapotranspiration | 1,48 | 1.33 | 1.35 | 0.01 | 1.69 | 6.73* | 0.71 | 5.51* | 0.29 | 1.80 | 12.16** |
| Mean precipitation | 2,47 | 5.31** | 3.99* | 1.95 | 11.87** | 22.21** | 2.45 | 35.52** | 0.72 | 3.38* | 5.82** |
| Actual evapotranspiration | 2,47 | 5.31** | 3.99* | 1.95 | 11.87** | 22.21** | 2.45 | 35.52** | 0.72 | 3.38* | 5.82** |
| Accumulated potential water loss | 1,48 | 5.10* | 3.25 | 3.26 | 17.93** | 22.75** | 0.41 | 0.62 | 0.66 | 1.11 | 0.54 |
| Water deficit | 3,46 | 10.80** | 12.08** | 3.79* | 19.55** | 11.06** | 0.78 | 0.51 | 1.34 | 1.15 | 0.56 |
| Water surplus-run off | 1,48 | 5.94* | 3.73 | 3.91 | 24.25** | 25.67** | 0.08 | 0.92 | 0.34 | 0.97 | 0.11 |
| Aridity index | 2,47 | 0.09 | 0.55 | 3.29* | 29.48** | 27.78** | 1.87 | 19.70** | 1.73 | 4.43* | 3.83* |
| Humidity index | 3,46 | 3.98* | 3.07* | 1.34 | 7.75** | 11.87** | 1.48 | 17.79** | 0.34 | 1.45 | 5.73** |
| Summer concentration of thermal efficiency | 1,48 | 0.08 | 0.29 | 0.90 | 6.81* | 25.86** | 3.40 | 14.76** | 0.63 | 3.25 | 10.23** |

* $p < 0.05$ ; ** $p < 0.01$

other side show the highest frequencies varying from 18-43% depending on the variable. The percentages for unbanded at the remainder of the areas average 3-7%. The aridity index shows the highest variance ratio. It follows from the overall results that phenotype 00000 preponderates in the most arid stretch of the dune region.

### 6.3.5. The phenotype 00300

The mean frequencies of the mid-banded phenotype are found to be significantly different for all climatic elements considered. It has its maximal development in the areas with on the one hand the highest mean summer air temperature, potential evapotranspiration, mean precipitation, actual evapotranspiration, water surplus-run off, humidity index, and summer concentration of thermal efficiency and on the other hand the lowest accumulated potential water loss, water deficit and aridity index : mean frequencies 49-61% versus 6-32% for the other areas. The overall results show that phenotype 00300 prefers a humid environment with higher temperatures.

### 6.3.6. The phenotype 00345

The sample variances for the phenotype 00345 are not significantly different. Banding morph 00345 is however more abundant (Mann-Whitney U test, $z = 3.294$, $p < 0.0014$) in the southern half of the dune region which has a megathermal efficiency regime (summer concentration of thermal efficiency 48).

### 6.3.7. The phenotype 10345

As for the preceding phenotype, the banding morph 10345 is mainly restricted to the region with a megathermal efficiency regime. Six climatic elements seem determinative for its distribution : potential evapotranspiration, mean precipitation, actual evapotranspiration, aridity index, humidity index, and summer concentration of thermal efficiency. The highest frequencies (14-18%) are found in the areas with moderate precipitation (750 mm), actual evaporation (280 mm), aridity index (5) and humidity index (20).

### 6.3.8. The phenotype 12345

Phenotype 12345 shows no correlation with any of the climatic elements considered.

### 6.3.9. The effectively unbanded phenotype

The effectively unbanded phenotype (shells with bands 1 and 2 both absent) averages the highest frequencies (65%) in the areas with the highest precipitation (800 mm) and actual evapotranspiration (620 mm), and the lowest aridity index (4).

### 6.3.10. The phenotype with band-fusions

The phenotype with two or more bands fused shows a preference for the areas with the highest potential evapotranspiration, mean precipitation, actual evapotranspiration, humidity index, summer concentration of temperature efficiency, and the lowest aridity index. The highest numbers of the phenotype with all bands fused (12345) are found in the most northern colony (Appendix I). It is clear that the phenotype with band fusions has its maximum development (35-46%) in the region with fourth mesothermal temperature efficiency regime of the dune area.

## 6.4. *Variation in polymorphism with habitat*

Mean frequencies per colony of the colour morphs in the habitat classes are shown in Table 4. *Ammophila*, herbage and scrub have high frequencies (72-87%) of yellow shells, whereas pink shells are predominant in *Rubus* (68%). The herbage samples tend to have higher frequencies for pink than the *Ammophila* and scrub samples. Brown shells are most frequent in scrub and to a lesser extent in *Ammophila*.

Table 4

*Shell colour frequencies (%) in* Cepaea nemoralis *from different habitats*

| Habitat | Brown | Pink | Yellow | Total |
|---|---|---|---|---|
| *Ammophila* | 1.18 | 11.95 | 86.87 | 4,429 |
| Herbage | 0.10 | 27.56 | 72.34 | 2,415 |
| Scrub | 3.86 | 19.57 | 76.57 | 4,930 |
| *Rubus* | 0.39 | 68.47 | 31.14 | 1,641 |

Fig. 3a is a scatter diagram in accordance with the method of Cain and Sheppard (1954), showing the distribution of two classes of phenotypes in the colonies sampled, and the nature of the habitat. The position of a colony is determined by the percentage of yellow shells and the frequency of effectively unbanded shells regardless of colour. The samples form a more or less homogeneous group, without clear-cut clustering with habitat of the colour morph frequencies. The application of the extention of the median test for yellow shells gives a $\chi^2$ of 11.976, which is a significant departure from expectation $p < 0.005$ : *Rubus*-samples have higher frequencies of the dark colour morphs, and the *Ammophila*-samples tend to contain a higher proportion of yellow shells. For herbage and scrub there is no trend. Any significant evidence of variation ($\chi^2 = 3.642$, n.s. $\alpha = 0.05$), with habitat of effectively unbanded shells, could not be demonstrated.

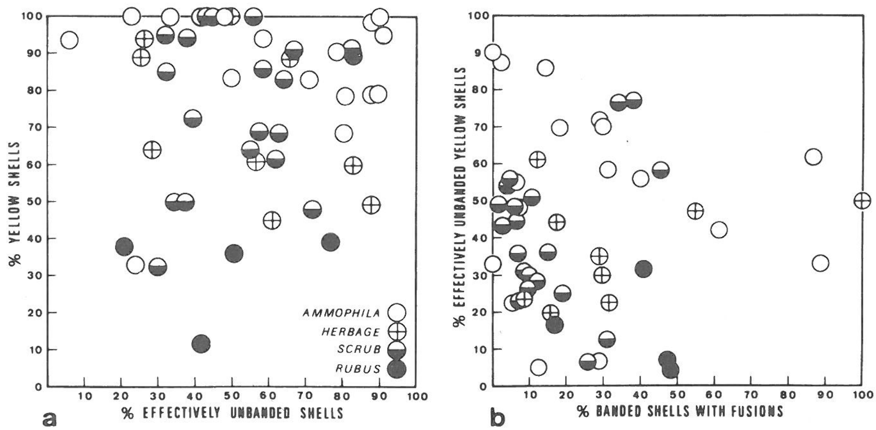


FIG. 3. – Scatter-diagram showing :

a) the relation between the percentage of yellow shells, the percentage of effectively unbanded shells, and the nature of the habitat,

b) the relation between the percentage of yellow effectively unbanded shells, the percentage of banded shells showing fusions of two or more bands, and the nature of the habitat.

Mean frequencies per colony of the major banding morphs in the habitat classes are shown in Table 5. The odd banding patterns 12300, 10300, 00340, etc. were classified as 00300 ; 00045 was classified as 00345 and 10045 as 10345 (WOLDA : 1969). *Ammophila* and herbage exhibit similar frequencies for the different banding morphs : the mid banded morph takes the highest frequency (53 %) ; 12345 (26-28 %) and 00000 (13-15 %) are less important. The scrub is characterized by high frequencies for 00000 (35 %) and 12345 (32 %) and to a lesser extent

00300 (22%). In the *Rubus* habitat morphs 12345 (47%) and 00300 (40%) predominate. The frequency of the effectively unbanded shells, including 00300, 00345 and 00000 is highest in *Ammophila*, herbage and scrub (65-71%).

Fig. 3b is a scatter diagram showing the relationship between the percentage yellow effectively unbanded shells and the percentage of five-banded shells with two or more bands fused. A tendency of the colonies from each habitat class to be grouped together is less distinct again. Testing the median separation on the yellow effectively unbanded axis proved not significant ($\chi^2 = 4.916$, n.s. $\alpha = 0.05$). As regards fusion of two or more bands, the proportion of fused bands is dependent of habitat ($\chi^2 = 11.941$, $p < 0.005$). The scrub samples show less fusions ; for *Rubus* there is some tendency for a higher frequency of fusions, whereas for *Ammophila* and herbage there is no difference in frequency of either of the fusion classes. There is a positive regression of lower band fusions on upper band fusions ($y = -0.407 + 1.943x$ ; $F_{(1,46)}$, $p < 0.001$).

Table 5

*Banding morph frequencies (%) in* Cepaea nemoralis *from different habitats*

| | 00000 | 00300 | 00345 | 10345 | 12345 |
|---|---|---|---|---|---|
| *Ammophila* | 13.39 | 53.01 | 5.28 | 2.30 | 26.01 |
| Herbage | 15.37 | 53.14 | 2.87 | 0.76 | 27.86 |
| Scrub | 34.85 | 22.33 | 7.95 | 2.70 | 32.17 |
| *Rubus* | 2.01 | 40.04 | 8.96 | 2.13 | 46.86 |

## 6.5. *The phenotypic diversity*

The phenotypic diversity of each colony was calculated using the Shannon-Wiener function : $H = -\sum_{i=1}^{S} (p_i)(\log_2 p_i)$, where H = information content of the sample, S = number of morphs, and $p_i$ = proportion of total sample belonging to the $i^{th}$ morph. The variants of the polymorphism considered are : shell colour, presence or absence of bands, number of bands and band fusions. For the colonies studied the number of morphs varies from 2 to 37 ; the diversity varies from 0.823 to 3.510, monomorphic samples being absent. The phenotypic diversity is not related to the relative population density (Spearman's rank correlation coefficient,

$r_s = 0.015$, n.s.), neither to the increasing distance northeast across the study area ($r_s = 0.045$, n.s.). A plot of S against H for all colonies (Fig. 4) shows a positive relationship ($y = 1.805 + 5.474\,x$ ; $p < 0.001$, $F_{(1,48)}$). It is further evident that the populations of *C. nemoralis* are more polymorphic in scrub and *Rubus* than in *Ammophila* habitat (Mann-Whitney U test, $z = 3.02$, $p < 0.0026$) ; the diversity of the herbage samples is about intermediate to the former habitats.

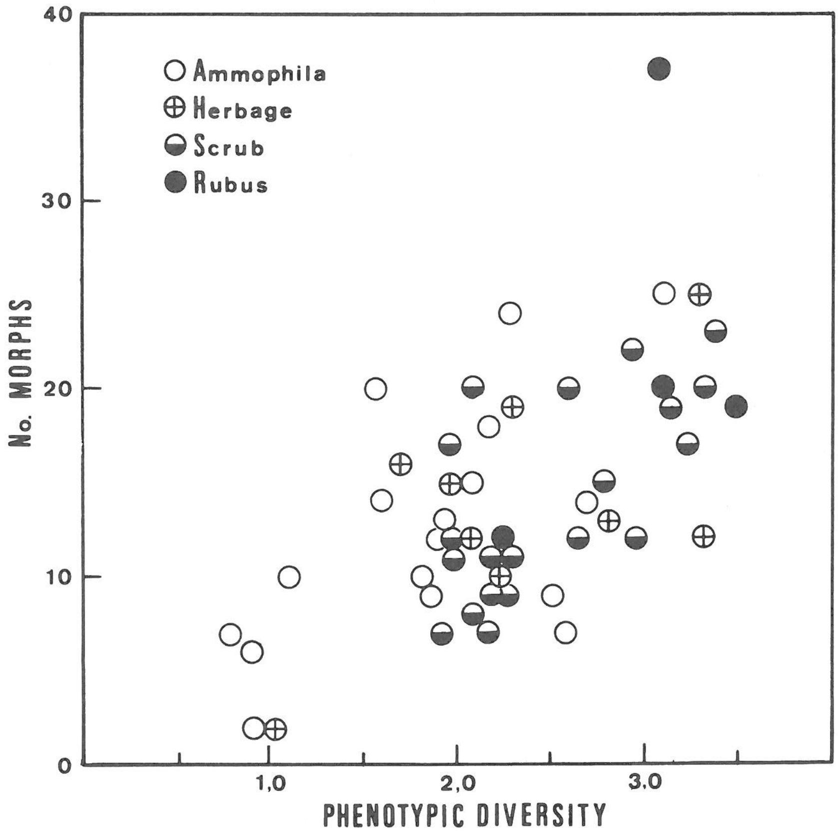


FIG. 4. – Relationship between the number of morphs (S) and the phenotypic diversity (H).

## 6.6. *Association between loci for banding and shell colour*

It follows from Table 2 that considerable disturbances occur in the joint distribution of the colour and banding classes. The associations between the colour loci for yellow ($C^Y$) and pink ($C^P$) with the loci for midbanded ($U^3$) and completely banded ($U^-$), and respectively the loci for bandless ($B^o$) and banded ($B^B$) shells, were tested for linkage disequilibrium (SPIESS, 1979). Only samples totalling at least 50 individuals and with 5 individuals for each pair of these loci were considered. Among 23 of such samples, only 4 (station 7, 39, 44 and 50) showed a significant departure from expectation for the C and U loci, which agrees with the theoretical assumption that the U locus is not linked to the B or C locus (e.g. LAMOTTE, 1954 ; CAIN & SHEPPARD, 1957 ; CAIN *et al.*, 1968). As for the B and C loci which are known to be very closely linked, out of the 15 colonies that came into consideration, there were 11 that showed a strong linkage disequilibrium with an excess unbanded within yellow and banded within pink. There is an almost absolute disequilibrium (Table 2) between the allele for brown shell colour ($C^B$) and that for the absence of shell bands ($B^o$).

## 7. DISCUSSION

The shell colour and banding polymorphism of *Cepaea nemoralis* is affected by at least eight evolutionary forces (JONES *et al.*, 1977), the spatial environmental heterogeneity, especially climatic factors (e.g. CAIN and CURREY, 1963 ; RICHARDSON, 1974, 1979) and differential predation (e.g. CAIN, 1953 ; CAIN and SHEPPARD, 1950, 1952, 1954 ; CARTER, 1968 ; SHEPPARD, 1951), being the main causative agent. Comparison of our data for the distribution of *C. nemoralis* with the types of water balance (THORNTHWAITE classification of climate) shows that climatic selection is operating and explains in part the observed distribution of the colour and banding morphs.

The yellow shell colour is favoured in the more humid stretch ; pink is more frequent in the intermediate areas, and brown is almost confined to the most arid stretch of the dune area. As in the British Isles (CAIN, 1954), brown shells were associated with enclosed hollows of complex dunes that accumulate cold air during the night. Snails with brown shells ought to be favoured in these places since they absorb more solar energy. The presence of brown shells at station 46 (Zeebrugge) near a large pond, and the effectively unbanded brown shells at station 50 (Zwin) near the mud flat and Zwin river, could also originate from the colder and wetter microclimate.

The unbanded phenotype in general and the yellow unbanded in particular, is at an advantage in the most arid stretch of the study area.

Laboratory experiments (BOETTGER, 1954 ; GARCIA, 1977 ; LAMOTTE, 1959) and field observations (RICHARDSON, 1979) have shown that snails with yellow and unbanded shells have a higher temperature tolerance than the darker and banded ones because of their low albedo. We suppose that differences in shell reflecticity for solar energy, not only will cause selective heat death, but also differential deshydration, thus favouring lighter and unbanded shells in arid environments. The frequency of the mid-banded phenotype increases from SW to NE and seems associated with a more humid climate. ARNOLD (1971), CAMERON and COOK (1971), BANTOCK and PRICE (1975) found that mid-banded is favoured in harsh climate. The effectively unbanded phenotype which is mainly determined by the mid-banded morph shows, in accordance with this morph, the highest mean frequencies in the area with the highest precipitation. The five-banded phenotype is well represented throughout the area and shows no cline. The frequency of the band-fusion morph is higher in the region with fourth mesothermal temperature efficiency regime. Banding morphs 00345 and 10345 are almost confined to the region with a megathermal efficiency regime, and tend to increase from SW to NE within that region. The clines for the characters 00000, 00300, 00345 and 10345 do not coincide, demonstrating that the climatic gradients act differently on the different loci. CLARKE (1966) however has shown that epistatic modifying genes could produce and maintain changes in gene frequency without correspondence with environmental gradients.

Evidence of predation by thrushes was found at all sites, and blackbird and song-thrush were observed feeding on *C. nemoralis* on several occasions. It is accepted that the data on shell colour and banding with respect to habitat, could give and indication on the influence by visual predators. The closed habitats (scrub and *Rubus*) are more polymorphic and display a higher diversity than the open *Ammophila* habitat ; the herbage occupies an intermediate position. This suggests some visual selection for diversity (apostatic selection). On the basis of visual selection for cryptic morphs by thrushes, closed habitat samples should be less yellow and less five-banded than those from open habitats (e.g. CAIN and SHEPPARD, 1954). In the dune area studied, the *Rubus* samples only have a higher frequency for dark colour, five-banded and band-fusion morphs, pointing towards visual selection against yellow shells on the dark background of *Rubus*. The impact of predation on *C. nemoralis* in the other habitats seems to have less selective value : shell colour but not banding are related to the *Ammophila* and herbage habitat, whereas banding and not shell colour frequencies are related to scrub.

## Abstract

The colour and banding polymorphism of *Cepaea nemoralis* (L.) (Gastropoda, Helicidae) from the Belgian coastal dune region was investigated. The frequency of yellow shells is 69 %. Three banding patterns are predominant and account for 90% of all snails found: 00300, 12345 and 00000. The distribution of morph frequencies can be related to climatic factors and habitat. Unbanded shells are to be found in arid areas and mid-banded in more wet areas. The five-banded morph is not correlated with the factors studied.

## References

Adam, W. (1947). Revision des mollusques de la Belgique. I. Mollusques terrestres et dulcicoles. *Verhandl. Kon. Nat. Mus. Belg.* **106** : 298 pp.

Allen, J. A. (1976). Further evidence for apostatic selection by wild passerine birds – 9 : 1 experiments. *Heredity* **36** : 173-180.

Arnold, R. (1971). *Cepaea nemoralis* on the east Sussex Downs, and the nature of Area Effects. *Heredity* **26** : 277-298.

Bantock, C. R., Price, D. J. (1975). Marginal populations of *Cepaea nemoralis* (L.) on the Brendon Hills, England. I. Ecology and ecogenetics. *Evolution* **29** : 267-277.

Boettger, C. R. (1954). Zur Frage der Verteilung bestimmter Varianten bei der Landschneckengattung *Cepaea* Held. *Biol. Zentralbl.* **73** : 318-333.

Cain, A. J., Sheppard, P. M. (1950). Selection in the polymorphic land snail *Cepaea nemoralis*. *Heredity* **4** : 275-294.

Cain, A. J., Sheppard, P. M. (1952). The effects of natural selection on body colour in the land snail *Cepaea nemoralis*. *Heredity* **6** : 217-231.

Cain, A. J. (1953). Visual selection by tone of *Cepaea nemoralis* (L.). *J. Conchol.* **23** : 333-336.

Cain, A. J., Sheppard, P. M. (1954). Natural selection in *Cepaea*. *Genetics* **39** : 89-116.

Cain, A. J., Sheppard, P. M. (1957). Some breeding experiments with *Cepaea nemoralis* (L.). *J. Genet.* **55** : 195-199.

Cain, A. J., King, J. M. B., Sheppard, P. M. (1960). New data on the genetics of polymorphism in the snail *Cepaea nemoralis* (L.). *Genetics* **45** : 393-411.

Cain, A. J., Currey, J. D. (1963). Area effects in *Cepaea*. *Philos. Trans. Roy. Soc., Ser. B, Lond.* **246** : 1-81.

Cain, A. J. (1968). Studies on *Cepaea*. V. Sand dune populations of *Cepaea nemoralis* (L.). *Philos. Trans. Roy. Soc., Ser. B, Lond.* **253** : 499-517.

Cain, A. J., Sheppard, P. M., King, J. M. B. (1968). Studies on *Cepaea* I. The genetics of some morphs and varieties of *Cepaea nemoralis* (L.). *Philos. Trans. Roy. Soc., Ser. B, Lond.* **253** : 383-396.

CAMERON, R. A. D., COOK, L. M. (1971). *Cepaea nemoralis* on Whitbarrow Scar, Lancashire. *Proc. Malacol. Soc. London* **39** : 399-408.

CARTER, M. A. (1968). Studies on *Cepaea*. II. Area effects and visual selection in *Cepaea nemoralis* (L.) and *Cepaea hortensis*. *Phil. Trans. Roy. Soc., Ser. B, Lond.* **253** : 397-446.

CLARKE, B. C. (1966). The evolution of morph-ratio clines. *Amer. Natur.* **100** : 389-402.

COLBEAU, J. (1863-65). Excursions et découvertes malacologiques. *Ann. Soc. malacol. Belg.* **1** : p. 66.

DINGENS, P., VERNEMMEN, C. (1963). De klimaatklassifikatie van C. W. Thornthwaite toegepast op België en het Groot-Hertogdom Luxemburg. *Natuurwet. Tijdschr.* **45** : 145-198.

GARCIA, M.C. L. R. (1977). Écophysiologie de l'escargot *Cepaea nemoralis* (L.) (Helicidae) : quelques conséquences de l'échauffement par l'énergie rayonnée. *Arch. Zool. exp. gén.* **118** : 495-514.

GERDEAUX, D. (1978). Le polymorphisme de *Cepaea nemoralis* en Provence ; ses relations avec le milieu. *Arch. Zool. exp. gén.* **119** : 565-584.

GOODHART, C. B. (1956). Genetic stability in populations of the polymorphic snail, *Cepaea nemoralis* (L.). *Proc. Linn. Soc., Lond.* **167** : 50-67.

GOODHART, C. B. (1958). Genetic stability in the snail *Cepaea nemoralis* (L.) : a further example. *Proc. Linn. Soc., Lond.* **169** : 163-167.

GOODHART, C. B. (1973). A 16-year survey of *Cepaea* on the hundred foot bank. *Malacologia* **14** : 327-331.

JONES, J. S., LEITH, B. H., RAWLINGS, P. (1977). Polymorphism in *Cepaea* : a problem with too many solutions ? *Ann. Rev. Ecol. Syst.* **8** : 109-143.

LAMOTTE, M. (1951). Recherches sur la structure génétique des populations naturelles de *Cepaea nemoralis* (L.). *Bull. biol. Fr. Belg.* **35** : 1-239.

LAMOTTE, M. (1954). Sur le déterminisme génétique du polymorphisme, chez *Cepaea nemoralis* L. *Compt. Rend. Acad. Sci.* **239** : 365-367.

LAMOTTE, M. (1959). Polymorphism of natural populations of *Cepaea nemoralis*. *Cold. Spring. Harbor Symp. Quant. Biol.* **24** : 65-86.

LAMOTTE, M. (1966). Les facteurs de la diversité du polymorphisme dans les populations naturelles de *Cepaea nemoralis* (L.). *Lav. Soc. Malacol. Ital.* **3** : 33-73.

MURRAY, J. (1963). The inheritance of some characters in *Cepaea hortensis* and *Cepaea nemoralis* (Gastropoda). *Genetics* **48** : 605-615.

O'DONALD, P. (1968). Natural selection by glow-worms in a population of *Cepaea nemoralis*. *Nature* **217** : 194.

RICHARDSON, A. M. M. (1974). Differential climatic selection in natural populations of land snail *Cepaea nemoralis*. *Nature* **247** : 572-573.

RICHARDSON, A. M. M. (1979). Morph frequencies of empty intact shells from *Cepaea nemoralis* (L.) colonies on sand dunes in South West England. *J. moll. Stud.* **45** : 98-107.

Sheppard, P. M. (1951). Fluctuations in the selective value of certain phenotypes of the polymorphic land snail *Cepaea nemoralis* (L.) *Heredity* **5** : 125-134.
Spiess, E. B. (1977). Genes in populations. John Wiley & Sons. New York, London.
Tavernier, R., Marechal, R. (1959). De bodemassociatiekaart van België. *Natuurwet. Tijdschr.* **41** : 161-204.
Von Martens, G. (1865). Die Bänder der Hain- und Gartenschnecke. *Jahresb. Ver. Vaterl. Naturk. Würtemberg* **21** : 218-226.
Wolda, H. (1969). Genetics of polymorphism in the land snail, *Cepaea nemoralis*. *Genetica* **40** : 475-502.

Rijksuniversitair Centrum Antwerpen
Laboratorium voor Algemene Biologie en Dierkunde
Groenenborgerlaan 171,
B-2020 Antwerpen.

Sheppard, P. M. (1951). Fluctuations in the selective value of certain phenotypes of the polymorphic land snail *Cepaea nemoralis* (L.) *Heredity* **5** : 125-134.

Spiess, E. B. (1977). Genes in populations. John Wiley & Sons. New York, London.

Tavernier, R., Marechal, R. (1959). De bodemassociatiekaart van België. *Natuurwet. Tijdschr.* **41** : 161-204.

Von Martens, G. (1865). Die Bänder der Hain- und Gartenschnecke. *Jahresb. Ver. Vaterl. Naturk. Würtemberg* **21** : 218-226.

Wolda, H. (1969). Genetics of polymorphism in the land snail, *Cepaea nemoralis*. *Genetica* **40** : 475-502.

Rijksuniversitair Centrum Antwerpen
Laboratorium voor Algemene Biologie en Dierkunde
Groenenborgerlaan 171,
B-2020 Antwerpen.

# Appendix I

*Collections of* C. nemoralis *classified by banding*

| | Locality | Habitat | 12345 | 123(45) | 12(345) | 1(2345) | (12345) | 1(23)45 | 1(23)(45) | (123)45 | (123)(45) | (12)345 | (12)3(45) | 02345 | 023(45) | 0(23)(45) | 10345 | 103(45) | 12045 | 120(45) | (12)0(45) | 12305 | 00345 | 003(45) | 02045 | 02340 | 10045 | 10305 | 12300 | 00045 | 00305 | 00340 | 02300 | 10300 | 00040 | 00300 | 02000 | 00000 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Westhoek | A | 41 | – | – | – | – | 1 | – | – | – | – | – | 3 | – | – | 15 | – | – | – | – | – | 2 | – | – | – | – | – | – | – | – | – | – | – | – | 30 | – | 413 | 505 |
| 2 | Westhoek | S | 91 | 3 | – | – | – | – | – | – | – | – | 1 | – | – | – | 3 | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 13 | – | 127 | 239 |
| 3 | De Panne | S | 60 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | 10 | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 119 | 191 |
| 4 | Koksijde | H | – | 5 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 5 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 10 |
| 5 | Koksijde | H | 97 | 4 | – | – | – | – | – | – | – | 2 | 3 | – | – | – | 8 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 6 | – | 33 | 153 |
| 6 | Koksijde | S | 45 | 1 | – | – | – | – | – | – | – | – | 2 | – | – | – | 3 | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | 2 | – | 66 | 120 |
| 7 | Koksijde | S | 73 | 7 | – | – | – | 1 | 1 | – | 1 | – | 3 | 4 | – | – | 2 | – | – | – | 1 | – | 9 | – | – | – | – | – | 1 | – | – | – | – | – | – | 65 | – | 81 | 249 |
| 8 | Koksijde | A | 112 | 3 | – | – | – | 1 | – | – | 3 | – | 9 | 2 | – | – | 3 | – | – | – | – | – | 2 | – | – | – | – | – | – | – | – | – | – | – | – | 3 | – | 3 | 141 |
| 9 | Koksijde | S | 51 | 15 | – | – | – | – | – | 2 | 2 | 1 | 11 | 1 | – | – | 20 | – | 1 | – | – | – | 5 | – | – | – | – | – | – | – | – | – | – | – | – | 92 | – | 398 | 599 |
| 10 | Koksijde | S | 96 | 19 | – | – | – | – | – | – | 4 | – | 26 | 1 | – | – | 25 | 1 | – | – | – | – | 7 | – | – | – | – | – | – | – | – | – | – | – | – | 126 | – | 676 | 981 |
| 11 | Oostduinkerke | H | 71 | 7 | – | – | – | – | 1 | – | – | – | 2 | 1 | 1 | – | 22 | – | 2 | – | – | – | 2 | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | 202 | 312 |
| 12 | Oostduinkerke | H | 124 | 18 | – | – | – | – | – | – | – | – | 5 | 2 | – | – | 24 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 6 | – | 63 | 242 |
| 13 | Oostduinkerke | S | 158 | 9 | – | – | – | – | – | – | – | – | 11 | 10 | – | – | 10 | 1 | 1 | – | – | – | 20 | – | – | – | – | – | – | – | – | – | – | 1 | – | 86 | – | 63 | 370 |
| 14 | Oostduinkerke | S | 92 | 3 | – | – | 1 | – | – | – | 1 | – | 7 | – | – | – | 40 | – | – | – | – | – | 3 | – | – | – | – | – | 1 | – | 1 | – | – | 1 | – | 92 | – | 77 | 319 |
| 15 | Nieuwpoort | S | 17 | 1 | – | – | – | – | – | – | – | – | 3 | 2 | 1 | – | 3 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 37 | – | 32 | 96 |
| 16 | Nieuwpoort | A | 248 | 66 | – | – | – | – | 2 | – | 2 | – | 32 | 7 | 2 | – | 28 | 2 | 5 | – | – | – | 5 | – | – | – | – | – | – | – | – | – | 1 | – | – | 116 | – | 2 | 518 |
| 17 | Nieuwpoort | R | 301 | 157 | 1 | 1 | 1 | 5 | 2 | – | 2 | – | 113 | 8 | 4 | – | 86 | 7 | 1 | 2 | 2 | – | 21 | 2 | – | – | 2 | – | – | – | 3 | – | 3 | 5 | – | 455 | – | 28 | 1,212 |
| 18 | Nieuwpoort | H | 78 | 22 | – | – | – | 1 | – | – | 1 | – | 9 | 7 | 1 | – | 10 | 2 | 1 | 2 | – | – | 9 | – | – | – | – | – | – | – | – | 1 | – | – | – | 164 | – | 35 | 343 |
| 19 | Nieuwpoort | R | 53 | 8 | – | – | – | – | – | – | – | – | 3 | 6 | 1 | – | 12 | – | – | – | – | – | 6 | 1 | – | – | 1 | – | – | – | 1 | – | – | – | – | 77 | – | 3 | 172 |
| 20 | Nieuwpoort | R | 50 | 22 | 1 | – | – | 1 | – | – | 1 | – | 20 | 7 | 2 | – | 4 | – | – | – | – | – | 4 | 1 | – | – | – | – | – | – | – | – | – | – | – | 26 | – | – | 139 |
| 21 | Nieuwpoort | A | 9 | 1 | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 67 | – | 11 | 89 |
| 22 | Lombardsijde | S | 113 | 1 | – | – | – | – | – | – | 1 | 1 | 11 | 2 | 1 | – | 30 | – | 3 | – | – | – | 14 | 1 | – | – | 1 | – | 1 | – | – | – | – | – | – | 49 | – | 15 | 244 |
| 23 | Lombardsijde | S | 37 | 1 | – | – | 1 | – | – | – | – | – | 2 | 2 | 3 | – | 9 | – | – | – | – | – | 13 | – | – | – | – | – | – | 1 | – | – | – | – | – | 20 | – | 2 | 91 |
| 24 | Westende | A | 29 | 1 | – | – | – | – | – | – | – | – | 1 | – | – | – | 15 | – | 1 | – | – | – | 6 | 1 | – | – | – | – | – | 2 | – | – | – | – | – | 34 | – | 23 | 113 |
| 25 | Westende | S | 20 | – | – | – | – | – | – | – | – | 1 | – | – | 1 | – | 14 | – | – | – | – | – | 9 | – | – | – | – | – | – | – | – | – | – | – | – | 33 | – | 4 | 82 |
| 26 | Westende | S | 56 | 3 | – | – | – | – | – | – | – | – | 3 | – | – | – | 40 | – | – | – | – | – | 2 | – | – | – | – | – | – | – | – | – | – | – | – | 41 | – | 5 | 150 |
| 27 | Westende | S | 177 | 8 | – | – | – | – | – | – | – | – | 5 | 1 | – | – | 112 | – | 1 | – | – | – | 19 | 1 | – | – | 1 | 1 | – | – | – | – | 1 | 1 | – | 128 | – | 38 | 494 |
| 28 | Westende | S | 90 | 2 | – | – | – | – | – | – | – | 3 | 1 | 3 | – | – | 14 | – | – | – | – | – | 6 | – | – | – | 1 | – | – | – | 1 | – | – | 2 | – | 82 | – | 4 | 209 |
| 29 | Westende | A | 101 | 3 | – | – | – | – | – | – | 1 | – | 3 | 1 | – | – | 61 | – | 2 | – | – | – | 9 | – | – | – | – | – | – | 1 | – | – | – | – | – | 149 | 1 | 1 | 333 |
| 30 | Middelkerke | A | 89 | – | – | – | – | – | – | – | 1 | – | 4 | 1 | – | – | 92 | – | – | – | – | – | 51 | – | 1 | – | 3 | – | – | 4 | – | – | – | – | – | 1 | – | 1 | 248 |
| 31 | Middelkerke | S | 33 | – | – | – | – | – | – | – | – | 1 | – | – | – | – | 52 | – | 1 | – | – | – | 17 | – | – | – | – | 2 | – | 2 | – | – | – | – | – | 47 | – | 2 | 157 |
| 32 | Raversijde | A | 27 | – | – | – | – | – | – | – | – | – | – | – | – | – | 6 | – | 1 | – | – | 1 | 8 | – | – | – | – | – | – | – | – | – | – | – | – | 297 | – | 4 | 344 |
| 33 | Oostende | A | 6 | – | – | – | – | – | – | – | 1 | – | – | – | – | – | 2 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 69 | – | 1 | 79 |
| 34 | Oostende | A | 34 | 5 | – | – | 1 | – | – | – | 1 | 1 | 6 | 4 | – | – | 2 | – | 1 | – | – | – | 7 | – | – | 1 | – | – | 1 | – | – | – | 1 | – | – | 492 | – | 4 | 561 |
| 35 | Bredene | H | 5 | – | – | – | – | – | – | – | 2 | – | 1 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | 1 | – | – | – | 7 | – | 5 | 23 |
| 36 | Bredene | A | 57 | 10 | 1 | – | – | – | – | – | 3 | – | 12 | 10 | 2 | – | 5 | – | – | – | – | – | 2 | – | – | – | – | – | – | 1 | – | – | – | – | – | 241 | – | – | 344 |
| 37 | Bredene | S | 31 | 3 | – | – | – | – | 1 | – | 6 | – | 4 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 22 | – | 5 | 72 |
| 38 | De Haan | H | 32 | 14 | – | – | – | – | 1 | – | – | – | – | 2 | – | – | 1 | – | 1 | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | 19 | – | – | 71 |
| 39 | De Haan | S | 90 | 16 | – | – | – | – | 3 | – | 5 | – | 7 | 3 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | 55 | – | – | 181 |
| 40 | De Haan | R | 16 | 2 | – | – | 1 | – | – | – | 3 | – | 5 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | 88 | – | 2 | 118 |
| 41 | De Haan | H | 75 | 7 | – | – | – | – | – | – | 1 | – | 8 | 1 | – | – | 1 | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 1 | – | 707 | – | 6 | 809 |
| 42 | Wenduine | S | 17 | 1 | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 2 | – | – | – | – | – | – | – | – | – | – | – | – | 32 | – | – | 53 |
| 43 | Wenduine | A | 12 | 3 | – | – | – | – | – | – | 2 | – | – | 2 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | 1 | 68 | – | 3 | 92 |
| 44 | Blankenberge | H | 29 | 9 | – | – | 2 | – | – | – | 4 | – | 20 | 12 | – | – | – | – | – | – | – | – | 2 | – | – | 1 | – | – | – | – | 1 | 2 | 1 | – | – | 349 | – | 20 | 452 |
| 45 | Blankenberge | A | 41 | 10 | – | – | – | – | – | – | 4 | – | 13 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | 1 | – | 283 | – | 9 | 363 |
| 46 | Zeebrugge | A | 1 | – | – | – | 2 | – | – | – | 2 | – | 4 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 5 | – | 4 | 18 |
| 47 | Heist | A | 12 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 6 | – | – | 18 |
| 48 | Het Zoute | S | 6 | – | – | – | 1 | – | 2 | – | 1 | – | 1 | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | 18 | – | 3 | 33 |
| 49 | Het Zoute | A | 5 | 1 | – | – | 1 | – | – | – | 1 | – | 5 | – | – | – | – | – | 1 | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 10 | – | 1 | 26 |
| 50 | Zwin | A | 14 | 6 | – | – | 26 | – | – | 1 | 28 | – | 33 | 2 | 3 | 1 | – | – | – | – | 1 | – | 1 | – | – | – | – | – | – | – | – | 5 | 3 | 1 | – | 397 | 2 | 113 | 637 |
| | Totals : | | 3.122 | 478 | 3 | 1 | 37 | 11 | 13 | 3 | 84 | 10 | 410 | 109 | 23 | 1 | 784 | 13 | 25 | 4 | 5 | 2 | 270 | 8 | 1 | 2 | 9 | 4 | 5 | 11 | 8 | 9 | 13 | 13 | 1 | 5,213 | 3 | 2,707 | 13,415 |

# Appendix II

*Collections of* C. nemoralis *classified by shell colour*

| | | Yellow | Pink | | Brown | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Locality | Habitat | Nº | % | Nº | % | Nº | % | Total |
| 1 | Westhoek | A | 497 | 98.4 | 8 | 1.6 | – | – | 505 |
| 2 | Westhoek | S | 205 | 85.8 | 34 | 14.2 | – | – | 239 |
| 3 | De Panne | S | 131 | 68.6 | 54 | 28.3 | 6 | 3.1 | 191 |
| 4 | Koksijde | H | 10 | 100.0 | – | – | – | – | 10 |
| 5 | Koksijde | H | 136 | 88.9 | 17 | 11.1 | – | – | 153 |
| 6 | Koksijde | S | 83 | 69.2 | 37 | 30.8 | – | – | 120 |
| 7 | Koksijde | S | 153 | 61.4 | 57 | 22.9 | 39 | 15.7 | 249 |
| 8 | Koksijde | A | 132 | 93.6 | 9 | 6.4 | – | – | 141 |
| 9 | Koksijde | S | 548 | 91.5 | 49 | 8.2 | 2 | 0.3 | 599 |
| 10 | Koksijde | S | 885 | 90.2 | 96 | 9.8 | – | – | 981 |
| 11 | Oostduinkerke | H | 277 | 88.8 | 35 | 11.2 | – | – | 312 |
| 12 | Oostduinkerke | H | 155 | 64.0 | 87 | 36.0 | – | – | 242 |
| 13 | Oostduinkerke | S | 185 | 50.0 | 149 | 40.3 | 36 | 9.7 | 370 |
| 14 | Oostduinkerke | S | 204 | 63.9 | 64 | 20.1 | 51 | 16.0 | 319 |
| 15 | Nieuwpoort | S | 46 | 47.9 | 19 | 19.8 | 31 | 32.3 | 96 |
| 16 | Nieuwpoort | A | 172 | 33.2 | 346 | 66.8 | – | – | 518 |
| 17 | Nieuwpoort | R | 139 | 11.5 | 1,054 | 87.0 | 19 | 1.6 | 1,212 |
| 18 | Nieuwpoort | H | 155 | 45.2 | 185 | 53.9 | 3 | 0.9 | 343 |
| 19 | Nieuwpoort | R | 62 | 36.0 | 110 | 64.0 | – | – | 172 |
| 20 | Nieuwpoort | R | 53 | 38.1 | 86 | 61.9 | – | – | 139 |
| 21 | Nieuwpoort | A | 70 | 78.7 | 16 | 18.0 | 3 | 3.4 | 89 |
| 22 | Lombardsijde | S | 208 | 85.2 | 36 | 14.8 | – | – | 244 |
| 23 | Lombardsijde | S | 66 | 72.5 | 25 | 27.5 | – | – | 91 |
| 24 | Westende | A | 106 | 93.8 | 7 | 6.2 | – | – | 113 |
| 25 | Westende | S | 82 | 100.0 | – | – | – | – | 82 |
| 26 | Westende | S | 142 | 94.7 | 8 | 5.3 | – | – | 150 |
| 27 | Westende | S | 464 | 93.9 | 30 | 6.1 | – | – | 494 |
| 28 | Westende | S | 209 | 100.0 | – | – | – | – | 209 |
| 29 | Westende | A | 333 | 100.0 | – | – | – | – | 333 |
| 30 | Middelkerke | A | 247 | 99.6 | 1 | 0.4 | – | – | 248 |
| 31 | Middelkerke | S | 157 | 100.0 | – | – | – | – | 157 |
| 32 | Raversijde | A | 344 | 100.0 | – | – | – | – | 344 |
| 33 | Oostende | A | 77 | 97.5 | 2 | 2.5 | – | – | 79 |
| 34 | Oostende | A | 445 | 79.3 | 116 | 20.7 | – | – | 561 |
| 35 | Bredene | H | 14 | 60.9 | 9 | 39.1 | – | – | 23 |
| 36 | Bredene | A | 284 | 82.6 | 60 | 17.4 | – | – | 344 |
| 37 | Bredene | S | 36 | 50.0 | 36 | 50.0 | – | – | 72 |
| 38 | De Haan | H | 67 | 94.4 | 4 | 5.6 | – | – | 71 |
| 39 | De Haan | S | 59 | 32.6 | 122 | 67.4 | – | – | 181 |
| 40 | De Haan | R | 46 | 39.0 | 72 | 61.0 | – | – | 118 |
| 41 | De Haan | H | 398 | 49.2 | 411 | 50.8 | – | – | 809 |
| 42 | Wenduine | S | 44 | 83.0 | 9 | 17.0 | – | – | 53 |
| 43 | Wenduine | A | 83 | 90.2 | 9 | 9.8 | – | – | 92 |
| 44 | Blankenberge | H | 270 | 59.7 | 182 | 40.3 | – | – | 452 |
| 45 | Blankenberge | A | 248 | 68.3 | 115 | 31.7 | – | – | 363 |
| 46 | Zeebrugge | A | 15 | 83.3 | – | – | 3 | 16.7 | 18 |
| 47 | Heist | A | 18 | 100.0 | – | – | – | – | 18 |
| 48 | Het Zoute | S | 30 | 90.9 | 3 | 9.1 | – | – | 33 |
| 49 | Het Zoute | A | 26 | 100.0 | – | – | – | – | 26 |
| 50 | Zwin | A | 499 | 78.3 | 138 | 21.7 | – | – | 637 |
| | Total : | | 9,315 | 69.44 | 3,907 | 29.12 | 193 | 1.44 | 13,415 |

A : *Ammophila* ; H : herbage ; S : scrub ; R : *Rubus*.