

The Netherlands as an Environment for Land Mollusca

by

M. F. MÖRZER BRUIJNS, C. O. VAN REGTEREN ALTENA,
and I. J. M. BUTOT

(Institute for Nature Conservation Research (R.I.V.O.N.), Bilthoven,
and Rijksmuseum van Natuurlijke Historie, Leiden)

INTRODUCTION

The Netherlands are a small and, from a malacological point of view, apparently not very important corner of the European continent. Being part of the northwestern European lowlands, very young geologically, consisting almost entirely of holocene and pleistocene layers, the country presents but little diversity in topographical conditions. There are no mountains and but few parts which have hills of any importance. Most of the country is flat, many landscapes are almost without any relief. Such a country does not seem likely to be of much interest to the malacologist who is studying landsnails. It is true, no endemic species of this group are found here, but a more detailed ecological study of the terrestrial Mollusca of the Netherlands gives much satisfaction, because many interesting correlations appear to exist. Due to their geographical position, climate, and diversity of soil types the Netherlands have a far greater variation in life conditions than one would expect. The differentiation in various biotopes is so important that, out of the about 140 species of land molluscs known to live in northwestern Europe (ie. Denmark, the adjoining parts of Germany, the Netherlands, Great Britain and Ireland, and Belgium), certainly 87 are to be found in the Netherlands, whereas it is more or less doubtful if seven others are indigenous.

CLIMATIC CONDITIONS IMPORTANT FOR LANDSNAILS

The climate of the Netherlands is typically maritime, a so-called atlantic climate. Summers are rather cool, the average temperatures in July and August being 16.5–16.7° C. Winters are mild. The average temperature of the coldest month, January, is 1° C; the lowest means per month — 5° to — 10° C. However, extremely low temperatures, of — 16° C to — 22° C, do occur, especially in the eastern parts of the country (Fig. 1).

The prevailing winds blow from the southwest and south, bringing plenty of rain throughout the year. The average amount of precipi-

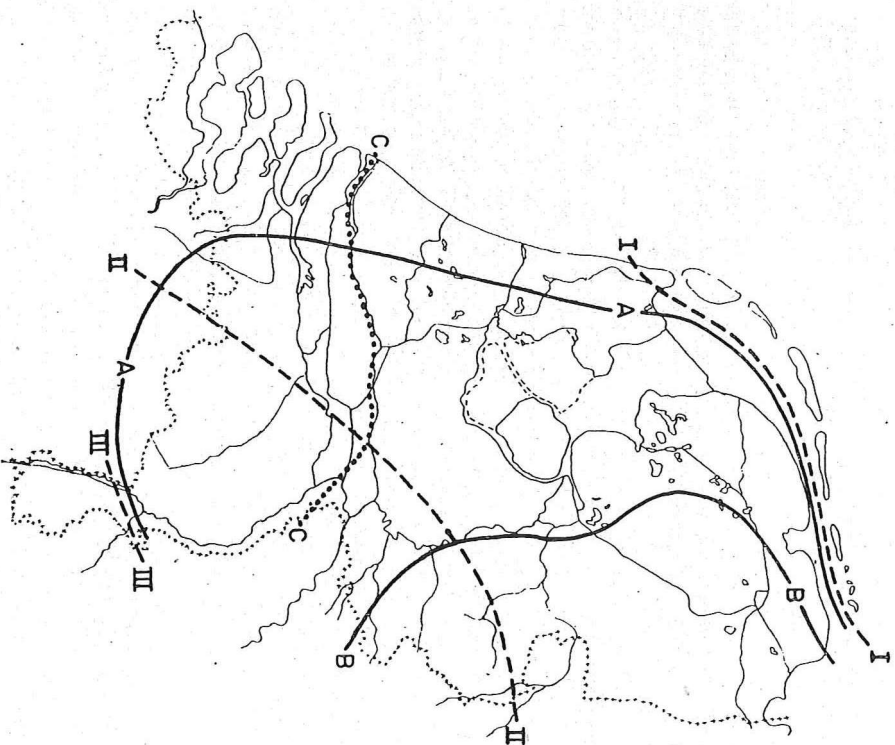


Fig. 1. Climatic regions in the Netherlands. North of I-I cool summers (less than 5 summer days); between I and II rather cool summers (5-22 summer days); between II and III rather warm summers (22-30 summer days); south of III warm summers (more than 30 summer days). West of A-A mild winters (less than 2 ice days); between A and B rather cold winters (8-12 ice days); east of B-B cold winters (more than 12 ice days). South of C-C climate milder than in the northern parts (less rain, more sunshine). Summer days are days with air temperature maxima above 25° C; ice days are days with air temperature maxima below 0° C. From Mörzer Bruijns & Westhoff, 1951.

Klimaat-gebieden in Nederland. Ten noorden van I-I koele zomers (minder dan 5 zomerdagen); tussen I en II vrij koele zomers (5-22 zomerdagen); tussen II en III vrij warme zomers (22-30 zomerdagen); ten zuiden van III warme zomers (meer dan 30 zomerdagen). Ten westen van A-A zachte winters (minder dan 8 ijisdagen); tussen A en B vrij koude winters (8-12 ijisdagen); ten oosten van B-B koude winters (meer dan 12 ijisdagen). Ten zuid van C-C zachter klimaat dan in het noorden (minder regen, meer zonneschijn). Zomerdagen zijn dagen met luchttemperatuur maxima boven 25° C; ijisdagen zijn dagen met luchttemperatuur maxima onder 0° C.

ration for the country as a whole is 713 mm. The average relative humidity in the Netherlands is rather high. It varies from 70–90%. The lowest relative humidity occurs inland, and is about 15–25% in the month of May. Diurnal variations are but slight.

Evaporation is not high. Only in summer evaporation exceeds precipitation. High dry sandy soils, and similar localities where the groundwater-table is far below the surface, form biotopes suitable for organisms adapted to life in dry surroundings. In fact in such places only these organisms are able to survive.

Although on the whole the climate of the Netherlands is a maritime one, considerable variations in climate conditions are found. They present very interesting perspectives for zoogeographical studies. Summers in the southern and especially in the southeastern parts are for instance distinctly warmer than those in the northern and northwestern parts of the country. On the other hand winters in the northeastern parts are distinctly colder than winters nearer to the sea in the northern and northwestern parts, whereas the winter in southern parts normally is milder. Especially the coastal area in the province of Zeeland and the southern parts of Limburg have relatively high summer- and winter-temperatures. Without doubt this plays a role in the occurrence of many central-European, Mediterranean and south-Atlantic faunal elements — and among them molluscs — in these areas.

Not the average but the extreme values of the climatic factors per year or per month usually are of decisive importance for the fauna, even if they occur only occasionally in a period of 5 to 10 years. One abnormal very cold (Atlantic) summer with low temperatures in the western parts of the country makes it impossible to survive in that area for species that need a certain minimum amount of sunshine and warmth during the summer, e.g. to complete their natural life cycle. In just the same way some extremely low winter temperatures in the eastern parts of the country most likely are the cause of the absence of certain types of so-called atlantic species in the east of the country, these being adapted to the very mild wintering conditions along the coast. If individuals of these species were compelled to winter in an area where the temperature, although even occasionally, drops below their relatively high tolerable minimum they would probably freeze to death.

EDAPHIC FACTORS

Apart from the effects of climate, soil conditions largely determine whether land mollusca can live in a certain place or not. For this

reason a short survey of geological data and of the most important pedological elements of the Netherlands may be given.

The superficial layers in the Netherlands belong almost entirely to the Holocene and the Pleistocene. Older strata occur at the surface almost exclusively in South Limburg, where upper cretaceous limestone crops out in the valleys which the Meuse and its tributaries have cut into the plateau. This plateau, of which the maximum height is about 200 m above sealevel, is for a great part covered by pleistocene loess loam. Most of the surface of the Netherlands is covered by pleistocene deposits. They form sandy, hilly landscapes in the eastern half of the country. The Pleistocene generally slopes down from an average of about 10-20 m above sealevel in the east to about 10-20 m below sealevel at the coast. In the western half of the country the Pleistocene, therefore, is covered by holocene formations. The pleistocene layers are mostly sediments of sand and gravel deposited by the rivers Rhine, Meuse and Scheldt. The ice-cap of the Riss glaciation influenced the pleistocene deposits in the north of the country. The glaciers pushed up the preglacial subsoil in many places, leaving behind large amounts of ground moraine.

The Holocene in the west is formed by a sandy shorewall with dunes along the coast, by old and young sea-clay deposits behind these shorewalls, and by large areas of peat, which developed locally on the sea clay (fig. 2). In the east the Holocene is developed in several places as large peatbog complexes on top of the pleistocene subsoil, as sandy and clayish sediments in eroded river, rivulet, and brook valleys, and very locally as inland dunes on fine sandy loamless pleistocene formations.

The soil of the Netherlands developed out of these superficial layers throughout the centuries under the influences of the slightly podsolizing climate, the often high groundwater-table, the vegetation, the fauna, and human activity. There are rich soils consisting mostly of clay and loam, and poor soils consisting mainly of sand or bog peat. The distinction between rich and poor as made by pedologists is very important for the study of the habitats of land Mollusca. Pedologically rich soils are normally also rich in land Mollusca, which often are scarce on poor soils.

The position of the groundwater-table is of great importance for the quality of the soil and for the molluscan fauna as well. The high water-table which is found in large areas of the Netherlands (fig. 3) is generally considered favourable to molluscan life.

The Soil Survey Institute at Wageningen distinguishes 9 soil associations in the Netherlands. Although each of these associations is subdivided into many soil types, only the soil associations will be

lake bottoms, and the young sea-clay soils, which are more or less recently reclaimed saltmarsh soils, are found along the coasts of the North Sea and the former Zuiderzee. They are rich also from the malacologists point of view, although they are not especially rich in lime.

The river-loam soils, which are found almost exclusively in the valleys of the rivers Meuse and Oude IJssel, and the river-clay soils, occurring in all other river valleys, although pedologically very different, both are rich soils to the malacologist.

Among the river-clay soils, the high river levee soils of the ridges formed by the sedimentation of coarser materials along stream courses must be mentioned especially. In the river-systems of the Rhine and IJssel these deposits are calcareous. The occurrence of many organisms (among them several species of land snails) which distinctly prefer habitats rich in lime and which do not live in other habitats in the vicinity, is here restricted to these calcareous deposits.

Nowadays the peat soils in the Netherlands are nearly all reclaimed, mostly as grass land. In most cases they are rich, which is partly due to cultivation, but only exceptionally they are attractive as habitats for Mollusca. The *Sphagnum* peat soils which still exist locally, are extremely poor, with very little terrestrial Mollusca living on them. Still poorer are the peat soils of *Sphagnum* raised bogs on the pleistocene sand in the east. No molluscs are found there.

Dune and beach-bank sandy soils only occur along the coast of the North Sea. The dunes south of Bergen in the province of Noord-Holland are rich in lime, the dunes north of Bergen are poor in lime. This contrast is very remarkable. The composition of the land Mollusca fauna in both districts differs accordingly. In the calcareous dunes many species are living in moist as well as in dry localities. In the sand dunes poor in lime molluscan life is much scarcer.

The pleistocene sandy soils generally are poor in lime and also relatively poor in land Mollusca. Especially poor are the "acid" podsolized heath soils and the inland sand dunes. Richer are the brown forest soils and the loamy brook soils occurring along brooks and rivulets in the pleistocene area. There again a good number of land Mollusca can be found.

The loessloam soils belong to the richest soils in the Netherlands. The south of Limburg is almost entirely covered with loess. These loess soils are very interesting for the malacologist, although they are not rich in lime. In the southern part of Limburg where the calcareous senonic substratum is locally found at the surface the "residual limestone soils" occur. These soils lend a special character to this part of the Netherlands. Together with the calcareous dunes

SOIL ASSOCIATIONS IN THE NETHERLANDS

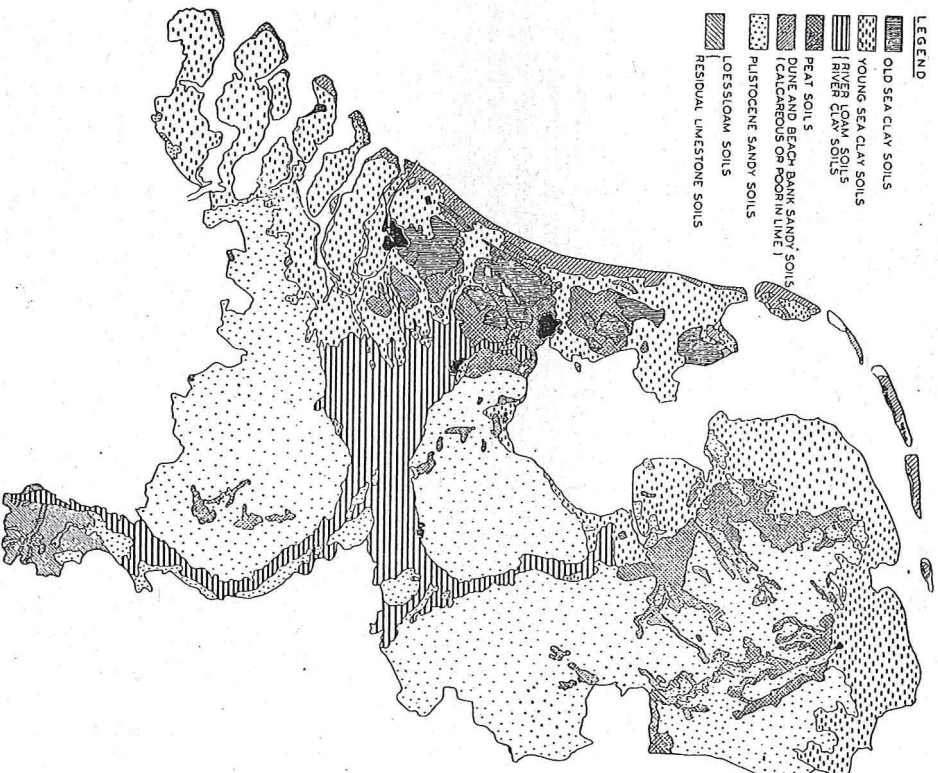


Fig. 4. Soil associations in the Netherlands, according to the Provisional Soil Map, Soil Survey Institute, Wageningen.
Bodem-gezelschappen in Nederland, naar de voorlopige bodemkaart, Instituut voor Bodemkartering, Wageningen.

along the North Sea coast and some more or less calcareous river-dunes along the Rhine and the IJssel they form the only calcareous soils in the country. The high lime content of these soils in combination with the climatic conditions in these areas plays an interesting part in the distribution of several species of land Mollusca in the Netherlands.

LAND MOLLUSCA IN THE NETHERLANDS
AS ZOOGEOGRAPHICAL ELEMENTS

Differences in climate and edaphic conditions are of special importance for those organisms that live at or near the limit of their distribution area. It is generally acknowledged for many cases that organisms living in an environment where they are just able to maintain themselves under the prevailing climatic conditions can do so only in biotopes where the other circumstances are as favourable as possible. Soil conditions and microclimate, then, are highly important. In the Netherlands with their chilly northern Atlantic summers organisms which have their optimum life conditions e.g. in central or southern Europe occur almost only on dry, relatively warm soils, preferring the calcareous ones. Organisms adapted to the relatively cool summers and mild winters of the Atlantic coast of western Europe generally are not able to withstand low winter temperatures. In the Netherlands they avoid the colder eastern and northeastern parts, sometimes they even live in the North Sea coastal area only.

On the other hand species living mainly in areas with a climate colder than that in the Netherlands are likely to be found here in relatively cool biotopes.

There is a rather great number of continental land Mollusca which live in the Netherlands at the northwestern border of their natural distribution area. Consequently, their main distribution is found southeast of this country.

Of these species *Orchella doliolem*, *Clansilia lineolata*, *Cl. parvula*, and *Milax rusticus* occur in southern Limburg only, where the two clausiliids and *Milax rusticus* are restricted to the calcareous soils. They are not found further to the northwest and do not occur in Great Britain.

Helicella unfiasciata and *Helicigona lapicida*, of which only the latter occurs in England, are almost restricted to the calcareous soils of southern Limburg. Besides, *Helicella unfiasciata* occurs in the calcareous dunes near Beverwijk and *Helicigona lapicida* on the old seadike near Hoorn. Probably these occurrences are due to transportation by man. Although this enlargement of the distribution area is not a natural one, the snails have managed to maintain themselves in these localities for years.

Comparable with the species mentioned above are *Cochlicopa minima*, *Vitrina diaphana*, *V. major*, and *Monacha incarnata*. *Cochlicopa minima* and *Vitrina major* also have their main distribution southeast of the Netherlands. In this country they are mainly found

in southern Limburg. *Cochlicopa minima*, however, also occurs in the calcareous dune area. Here it does not live so near to the border of its range, for it also occurs in Great Britain. *Vitrina diaphana* and *Monacha incarnata* are not known from Great Britain. The localities in the Netherlands, therefore, form the northwestern limit of their natural area. *Vitrina diaphana* occurs in a few places on the pleistocene sands in the provinces of Gelderland and Limburg. *Monacha incarnata* is rather common in many places in the east and southeast, even up to the centre of the country, but is hardly found in the west (fig. 5).

A second group of landsnails reached the Netherlands rather from the southern and southwestern parts of Europe. One species of these Mediterranean-southern Atlantic species is *Helicodoma obvolata*, which has its northern border-line in southern Limburg, the only part of the Netherlands where it is found. Other species of this group living in the same area also occur in Great Britain, and in some cases range as far as Denmark. Among these *Pomatias elegans*, *Clansilia rolphi*, *Cl. lamina*, and *Milax gagates* are found only in calcareous biotopes of southern Limburg, and *Ena obscura* here almost reaches its northern border-line. *Euhadra fruticosa*, certainly a southern Atlantic species, lives also further to the north. *Helicella ericetorum*, another species from south and south-west Europe, is found in southern Limburg as well as in the calcareous dunes along our coast. It occurs all over Great Britain and Ireland, and also in north-western Germany.

The distribution area of *Vertigo moulinsiana* appears to be that of an Atlantic species. Its life conditions must be rather specialised, since in the Netherlands it occurs only in very few localities, again in the southeastern part of the country.

The third interesting group of land snails are those that have their main populations not only south and southwest, but also in the western parts of Europe. They occur only in the western half of the Netherlands. *Lanina cylindracea* is one of them. It is found only in a few places in the calcareous dunes along the North Sea. *Theba cantiana* is rather common in some parts of the calcareous dune area (fig. 5). *Lanina* and *Theba cantiana* also occur in northwestern Germany and in Denmark. *Theba carthusiana*, another representative of this group, however, reaches its northern border-line here, occurring only in a few inland localities. Possibly *Oxychilus diaphanali*, a species from southern Europe, also belongs to the same group. This species is found in south Limburg in a few places, but it is more common in the western half of the country. It seems to extend its area, partly as a result of transportation by man.

Apart from the central European, and the Mediterranean and southern Atlantic species a few land molluscs are found whose distribution is interesting because the localities in the Netherlands form the eastern limit of their distribution area.

One of them is *Succinea arenaria* (fig. 5). In Ireland this species lives along the coast as well as inland. In England, Belgium, the Netherlands, and Germany it occurs only along the North Sea coast, in Scandinavia also in the mountains.

Helicella caperata is common in Great Britain, occurring on the continent only along the coast of the Atlantic from Spain up to Denmark. In the Netherlands this species lives almost exclusively in the dune area along the North Sea coast. Inland the species is found only in one locality, namely on the St. Pietersberg near Maastricht in the calcareous district of southern Limburg. A few inland occurrences are known also from Belgium in comparable localities.

In the Netherlands *Helicella herpensis* is a species characteristic of the southwestern parts, especially of the calcareous dune area (fig. 5). This area, having relatively warm summers and mild winters, gives species such as *Helicella herpensis* the opportunity to extend their area of distribution from the south and southwest to the north as far as the Netherlands. Other comparable species range further, into northwestern Germany or even into Scandinavia.

It is possible that the distribution of *Helicella virgata*, a species living mainly along the Atlantic coast in France and in Great Britain, may be compared with that of *Helicella caperata* and *H. herpensis*. *Helicella virgata*, however, does not occur in the dune-area of the Netherlands, but only in one place, namely on a dike of the former Zuiderzee near Medemblik in Noord-Holland. It seems likely that the species arrived there accidentally. However, it has managed to maintain itself in this place for more than 75 years.

In southern and western Europe *Pythia myosotis* is living along the coast, where brackish water is present. In the Netherlands *Pythia myosotis* is not rare along the North Sea coast, occurring mostly in salt and brackish marsh-vegetations, where it finds the eastern limit of its range in this part of its area. Further to the north it is known from the North Sea coast in northwestern Germany and from a single locality in Denmark.

Ovatella bidentata has its main distribution in southwestern Europe and occurs as far as the Channel coasts of France and southern England, and the east coast of England. No living individuals of the species have been found in Belgium. In the Netherlands it is known from a few places along the North Sea-coast, but almost only as empty shells on the beach. If the species would really prove to be a

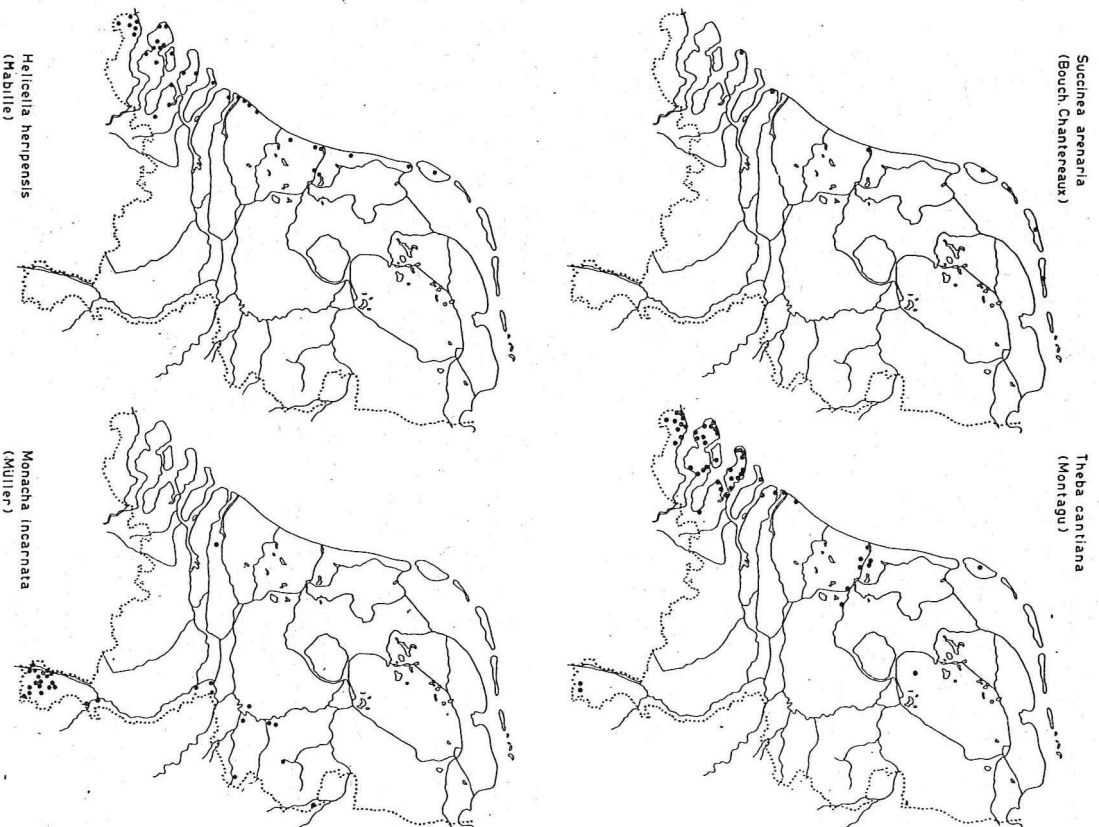


Fig. 5. Distribution of four species of land Mollusca in the Netherlands. Verspreiding van vier soorten landslakken in Nederland.

permanent member of the Dutch fauna, it would reach the north-western border-line of its distribution area here.

Still another species which has its easternmost localities in the Netherlands is *Zonitoides excavatus*. This snail occurs locally in the provinces of Friesland, Drente, Gelderland, and Noord-Brabant, and in one locality in the western part of the country. The species has its main distribution in the British Isles. On the continent it is only known from two localities in northern Belgium, from the Netherlands, and from one locality in northwestern Germany.

Two more species must be mentioned here because their distribution in the Netherlands is interesting: *Clansilia dubia* and *Monacha rubiginosa*. In the Netherlands *Clansilia dubia* is found only in the valleys of the Rhine and IJssel, not along the Meuse although it occurs in that valley in Belgium and France. It is living on the bark of trees (*Salix* and *Populus* spp.) in the river foreland only. The snails hide in crevices and live mostly about 2 m above the soil. The species must have reached the Netherlands from the east and was probably brought here by the Rhine. *Monacha rubiginosa* also is characteristic of river valleys. It occurs in many localities in the river foreland of the Rhine and its branches in the Waal and the IJssel, and has been recorded from two places in the valley of the Meuse not far from the Belgian frontier. It has, however, not (yet?) been found in the valley of that river in Belgium or France. It exclusively inhabits the soil of the wet grasslands of the river foreland. The occurrences of the species in the Netherlands are the most western outposts of its distributional area, which comprises central and eastern Europe.

The last species to be mentioned as an interesting zoogeographical element is *Acmibinula lamellata*, a northern Atlantic species. It occurs in Norway up to lat. 59°–60°, in south Sweden, Denmark, northwestern Germany, Scotland, the north of England, and in Ireland. In the Netherlands it is known only from one locality in the northeast of the country in the province of Drente, where it lives in a little forest. This locality is really one of the coolest ones in the Netherlands. It is the southernmost locality of the species on the continent.

BIOTIC COMMUNITIES AS HABITATS FOR LAND MOLLUSCA

Land Mollusca living near the border-line of their distribution area generally are more particular about their habitats than those living nearer to the centre of that area. But the habitat of all ter-

restrial Mollusca should answer certain requirements typical of each species.

Many species can be found in many places all over the country, but even the most common and eurykous species do not live everywhere, i.e. in all biotopes of a landscape. All species without exception prefer special biotopes as habitats, avoiding others. Some biotopes are always rich in molluscs, some always poor. These differences are due to the conditions of soil, groundwater-table, microclimate, vegetation, and the specific demands of the species concerned. Therefore, in a landscape with a great variation of different biotopes the malacologist finds many combinations or associations of mollusc species, each combination being characteristic of the biotope in which it lives.

Plant ecology has taught us in which way plant communities or phytocoenoses are characteristic of and can be used as indicators of environmental conditions. These plant communities, therefore, are a great help to the malacologist studying the biology of molluscs. In the following paragraphs a short survey is given of the most characteristic vegetation types of the Netherlands described as units according to the French-Swiss Phytosociologist School, with an enumeration of the land Mollusca which are associated with them.

- The following communities will be dealt with:
1. Swamps and marshes;
 2. Saltmarshes;
 3. Grasslands;
 4. Sea dunes;
 5. Arable land and human settlements;
 6. Heath-formations; moorland and bogs;
 7. Woodlands.

Swamps and marshes

Although since about 1500 A.D. most of the larger swamps and lakes in the Netherlands have been reclaimed, some large swamps still exist. They occur mainly in two complexes, one in the low parts of the provinces of Zuid-Holland, Noord-Holland and Utrecht, the other in Friesland and the northern part of Overijssel. Together, they cover an area of about 50,000 ha.

In both complexes many biotopes with their characteristic communities exist, different according to the depth of the water, the content of nutrient salts, the degree of salinity, etc. The most important phytocoenoses described are: freshwater plant-communities of the Potamoion eurosibericum, reed swamp-communities of the Phragmitoion eurosibericum, the communities of the tall sedges: the

Magnocaricion, and the swampy communities mainly consisting of the smaller sedges (Caricion fuscae). Apart from quite a number of freshwater Mollusca, land Mollusca are well represented in these habitats.

Even in the freshwater plant communities of the Potamion eurosibericum i.e. in the Hydrocharo-Stratiotetum, (characteristic plant species *Syratotes aloides* and *Hydrocharis morsus-ranae*) land Mollusca are already present, although generally one or two species only: *Succinea Pfeifferi*, and *S. sarsi*.

Along the shallow shores of eutrophic lakes, broads etc. the reed vegetations of the Scirpeto-Phragmitetum are widely spread in the Netherlands. Characteristic plant species are *Schoenoplectus lacustris*, *Phragmites communis*, *Glyceria maxima*, *Typha angustifolia*, *Ranunculus lingua*, etc. In these communities *Succinea Pfeifferi* and *S. sarsi* are often present, creeping on the stems and leaves above the water. More rarely *Succinea patris* can be found also. As soon as parts of the peaty soil emerge above water-level typical hydrophilic species such as *Zonitoides nitidus*, *Carychium minimum* and *Agriolimax laevis* may be expected, and with them *Retinella hammonis* and *Eucornutus trochiformis*.

In mesohalinic, brackish circumstances, for instance in the estuaries in the provinces of Zealand and Zuid-Holland, (the so-called delta area), in other places along the North Sea coast, along the coast of the Wadden Sea, and in a few localities along the coast of the IJsselmeer (former Zuiderzee) the Phragmiton is developed as Scirpetum maritimi, with *Scirpus maritimus*, *Aster triploium* and *Schoenoplectus tabernaemontani* as characteristic plant species.

In this habitat normally *Arsminea grayana* is found, in some cases with *Hydrobia ulvae*, occasionally with *Alderia modesta* and *Limnoria depressa*, but never with the molluscs known from other Phragmiton communities. The swamp vegetations which in zonation and in succession generally succeed the Phragmiton are characterized by the dominance of tall sedges (*Carex* spp.). The phreatic level, which in the Phragmiton normally is above that of the soil, is as high as the surface in the Magnocaricion elatae vegetation. Tall sedges as *Carex vesicaria*, *C. pseudocyperus*, *C. riparia*, *C. acutiformis*, *C. paniculata*, *C. gracilis*, and *C. disticha* form several types of Magnocaricion plant communities under different conditions. Some of these typify eutrophic, others mesotrophic or oligotrophic environments. Many land Mollusca are recorded from these habitats: *Zonitoides nitidus* and *Vertigo antiovertigo* occur in great numbers, other species being *Carychium minimum*, *Agriolimax laevis*, *Succinea Pfeifferi*, *S. sarsi*, *S. patris*, *Retinella hammonis*, *Eucornutus trochiformis*, and

Arianta arbustorum, which are still found together with *Lymnaea truncatula*, *Planorbis contortus*, *Segmentina nitida*, and *Lymnaea palustris*.

Vertigo moulinsiana, only known from a few localities in Limburg, is living also in a Magnocaricion vegetation, and *Vivrina diaphana* occurs in comparable surroundings. In Magnocaricion vegetations in mesotrophic environment only *Retinella hammonis*, *Arianta arbustorum*, and *Agriolimax laevis* are still present.

The trembling swamps of the "Parvocaricion"- or Caricion fuscae-vegetations are characterized by the growth of small sedges, such as *Carex diandra*, *C. stolonifera*, *C. lasiocarpa*, and species as *Galium palustre*, *Comarum palustre*, *Pedicularis palustris*, *Viola palustris*, etc. They have the phreatic level below, although very near to the surface. These vegetations are rare in the Netherlands, because most of the original swampy grassland, used as pasture land, is improved and ameliorated as Lolero-Cynosuretum grassland. The Caricion fuscae-communities generally have the same landmollusc fauna as the Magnocaricion coenoses have, although species that have their optimal conditions in dryer places sometimes occur, e.g. *Arron rufus*.

Saltmarshes

The saltmarshes are completely different from the freshwater swamps and marshes. In the Netherlands they are found in the delta area, near the coast, and in the Wadden Sea. The lower saltmarsh-communities the Salicornio-Spartinetum (with *Salicornia europaea* and *Spartina maritima* ssp. *glabra* as characteristic plant species) and the Puccinellietum maritimae (characterized by *Puccinella maritima*, *Obione pedunculata* and other halophytes) are almost daily submerged by high tide. In these communities a few specimens of *Physia myosotis* and *Arsminea grayana* are sometimes living, next to large numbers of *Hydrobia ulvae* and some *Littorina littorea* and *Alderia modesta*. Perhaps *Physia* prefers saltings with a brackish character, as *Arsminea* does. The higher saltings, less often flooded, covered with Arnetion maritimae vegetations, and characterized by species of plants like *Juncus gerardi*, *Festuca rubra* var. *littoralis*, *Armeria maritima*, *Glaux maritima*, *Cochlearia anglica*, *Carex extensa*, etc., are normally developed as a closed and homogeneous grass mat. This is often a favourable habitat for *Arsminea grayana*, which is sometimes found there with a density of more than 300 living individuals per square metre. It may be accompanied by a single *Pubilla marcorum*, which has its optimum higher up.

Quarella bidentata has hardly ever been found alive in the Netherlands. If colonies of this species are actually living in this country, this probably will turn out to be in the saltmarshes of the delta area.

Grasslands

About a quarter of the surface of the Netherlands is occupied by grasslands. There is a great variety of types. Several of these are of great interest for the malacologist.

For our purpose we use the following phytosociological units:

- a. Wet and sodden not intensively cultivated poor grasslands, mostly in use as hayfields (Molinietalia coenuleae).
- b. Moist, normally intensively cultivated grasslands, manured and eutrophic (Arrhenatherion elatioris).
1. pastures (Lolieto-Cynosuretum);
2. hayfields (Arrhenatherum elatioris and related communities).
- c. Dry grasslands, rich in lime, except those of the calcareous dunes (Bromion erecti).
- d. Dry grasslands on pleistocene sandy soils poor in lime (Thero-Airion and Corynephorion).

Nearly all grasslands of the Netherlands belong to category b, the categories a, c and d covering less than 1% of the total grassland area.

The sodden grassland of the Molinietalia are becoming rare in the Netherlands, due to reclamation and drainage. Characteristic plant species are *Filipendula ulmaria*, *Lyimnacha vulgaris*, *Angelica sylvestris*, *Lolus uliginosus*, *Cirsium palustre*, *Valeriana dioica*, *Thalictrum flavum*, *Bromus racemosus*, *Galba palustris*. These grasslands are good habitats for Mollusca, especially for hygrophilous species: *Zonitoides nitidus*, *Vitrea crystallina*, *Carychium minimum*, *Succinea putris*, *Succinea oblonga*, *Retinella hammonis*, *Eucomilus trochiformis*, and *Agriolimax laevis*. *Airion rufus* is regularly found here, often in great numbers. *Airion circumscriptus*, *A. intermedium*, *A. subfuscus*, *Agriolimax reticulatus*, *Punctum pygmaeum*, and *Gonyodiscus romundatus* are also recorded from these habitats. These species, however, have their optimum in other biotopes.

Nearly all the grasslands of the Netherlands are intensively pastured, regularly manured with a carefully regulated groundwater-table. These grasslands, so typical for the Netherlands, belong to the Lolieto-Cynosuretum in its various forms. Characteristic plant species are *Lolium perenne*, *Cynosurus cristatus*, *Pleium pratense*, *Trifolium repens*. The Lolieto-Cynosuretum is poor in molluscs. This is probably due to the management and the intensive trampling down, which is

normal for this habitat. Only species like *Agriolimax reticulatus* and *A. laevis* often live there in numbers. Other mollusc species seem to be mere invaders from other biotopes.

Much richer are the moist Arrhenatherion grasslands, mostly used as hayfields, also well developed along roadsides and on dikes on river-clay and loam soils. Characteristic plant species of these communities are:

Arrhenatherum elatius, *Hieracium spondylium*, *Trisetum flavescens*, and *Pastinaca sativa*. A relatively long list of land Mollusca is known from these habitats. *Valtonia excentrica* and *Fruiticicola hispida* are often the most numerous species. *Pupilla muscorum*, *Valtonia pulchella*, *V. costata*, *Vitrea belluicida*, *Retinella hammonis*, *Succinea oblonga*, *Agriolimax reticulatus*, *Airion circumscriptus* and *Verrugo pygmaea* are regular inhabitants, but also *Agriolimax laevis*, *Succinea putris*, *Carychium bidentatum*, *Eucomilus trochiformis*, *Verrugo substriata*, *Airion intermedium*, *A. subfuscus*, *A. rufus*, *Arionta arbatorum*, and *Vitrea crystallina* occur. Below the surface *Cecilioides acicula*, and especially along roads *Gonyodiscus romundatus* are known to live in Arrhenatherion biotopes. In the southwestern part of the country (province of Zeeland) also *Thelba caniana* and *Helicella berpensis* can be added to the list of species. In the river foreland in low wet places Rumicion crispi grasslands occur, which are closely related to the Arrhenatherion-vegetations. For these habitats, where *Ranunculus repens* and *Alopecurus geniculatus* are typical plant species, *Monacha rubiginosa*, *Lymanea truncatula*, *Succinea Pfeifferi*, *S. carvi*, *S. putris*, *S. oblonga* and *Agriolimax reticulatus* form a characteristic combination.

The "Bromion" grasslands on dry calcareous soils are ecologically related to the Arrhenatherion, but dryer and more calcareous. In the Netherlands these communities are restricted to the lightly pastured Medicago-Avenum pubescentis association on dry sandy places along the rivers, with *Medicago falcata*, *Avena pubescens*, *Thalictrum minus*, etc. as characteristic plant species and to the Mesobrometum erecti vegetations of the residual limestone soils in south Limburg, where *Brachypodium pinnatum*, *Koeleria* spp., and *Bromus erectus* characterize the vegetation.

Molluscs from these biotopes are: *Valtonia excentrica*, *Pupilla muscorum*, *Cochlicopa lubrica*, *Valtonia pulchella*, *V. costata*, *Cecilioides acicula*, *Verrugo pygmaea*, *Columella edentula*, *Vitrea belluicida*, *Agriolimax reticulatus*, and perhaps as exclusive species *Cochlicopa minima* and *Truncatella cylindracea*. On the warm southern hill slopes of the Mesobrometum in south Limburg there live some thermophilous species, which are only known from this part of the

country or from the calcareous open and grassy vegetations of the calcareous dunes, e.g. *Orcula dolium*, *Helicella unifasciata*, *H. erise-torum*, and *H. beripensis*.

The Thero-Airion grasslands are dry grasslands typical of the pleistocene sands poor in lime. Characteristic plant species of these grasslands are: *Festuca rubra* var. *arenaria*, *Aira praecox*, *Festuca ovina*, *Trifolium arvense*, *Campylosia rotundifolia*. Although not as rich as the grasslands on the clay soils, the Thero-Airion vegetations are not extremely poor, especially when the soil is more or less loamy. Molluscs typical of this environment are: *Cochlicopa lubrica*, *Vallonia excentrica*, *V. pulchella*, *Vitrina bellucida*, *Pupilla muscorum*, *Eucornutus trochiformis*, *Retinella hammonis*, *Succinea oblonga*, *Airion subfuscus*, and *A. intermedius*. Although they can live in the mesotrophic conditions of these grasslands, they never occur in great numbers.

In the extremely dry, open vegetations of the Corynephorion typical of the inland sand dunes poor in lime molluscs do not live.

Sea dunes

In comparison with dune areas in other European countries the dune area in the Netherlands is well developed and full of variation.

The dune district south of the village of Bergen (Noord-Holland) is rich in lime (CO₂ content about 3-29%) as are the dunes of Belgium and France. The dunes of the Wadden district, north of Bergen, including the West-Frisian islands, are poor in lime (CO₂ about 0.2-1%) as are the dunes of Germany and the Danish coast. This difference in CO₂ content and the climatic gradient from south to north are of great importance for the mollusc fauna. The differences between dune district and Wadden district are but slight in the outer dunes. In the first dune ridge where wind, drifting sand, and salt are the dominating factors and *Agropyron junceum*, *Ammophila arenaria* and *Elymus arenarius* form plant communities of the Ammophilion building up the dunes, practically no living land Mollusca are found.

Many land Mollusca, however, are living in the moist, always more or less calcareous outer dune valleys of both districts. In wet places biotic communities of the Littorellion uniflorae, on dryer spots communities of the Caricion davallianae are developed.

Littorella uniflora, *Juncus bulbosus*, *Mentha aquatica*, *Carex trinervis*, *Hydrocotyle vulgatis* and communities of *Phragmites communis* and *Scirpus maritimus* related with the *Scirpetum maritimi* grow in the lower wet places. In higher, only temporarily submerged, bare dune soil, vegetations of the Caricion davallianae develop with *Pan-*

PLANTENGEOGRAFISCHE DISTRICTEN VAN NEDERLAND

- Wadden d.
- ▨ Drenthe d.
- ▧ Drenthe d.
- ▩ Drenthe d.
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- Drenthe d.
- ▬ Goiders d.
- ▭ Vlaams d.
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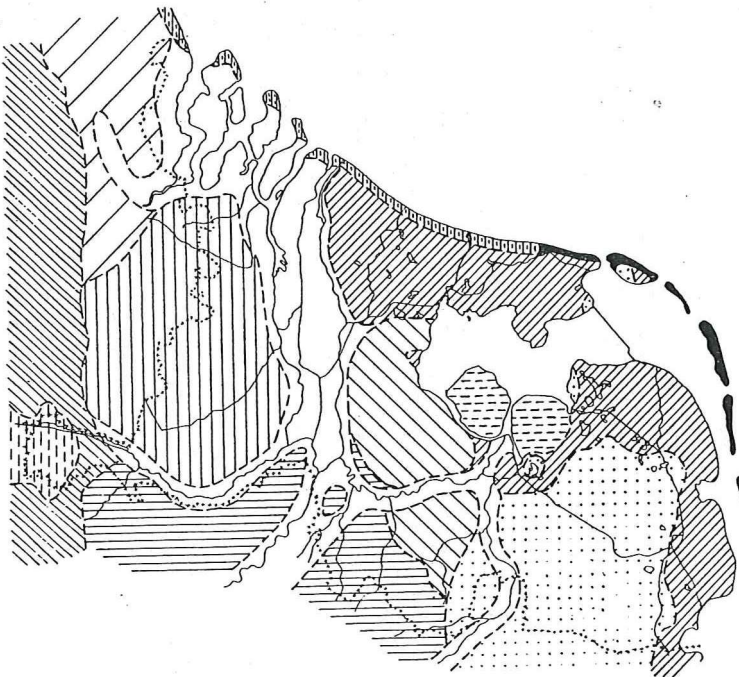


Fig. 6. Phytogeographic regions in the Netherlands (Wadden, Dune, Haf, Drente, Gueltern, Flemish, Subcentro-european, Löss, Cretaceous, Campina, Fluviale, and Flevo Region). According to Van Soest in: Heukels & Wachter, Schooflora.

massia palustris, *Juncus anceps*, *Centaurium vulgare*, *Schoenus nigricans*, and *Epipactis palustris*. Land Mollusca in these valleys are *Lymnaea truncatula* (often very numerous), *Succinea Pfeifferi*, *S. arenaria*, *Zonitoides nitidus*, *Carychium minimum*, *Vertigo antiveritgo*, *V. pygmaea*, *Arrianta arbastorum*, *Vallonia pulchella*, *Eucornulus trochiformis*, *Punctum pygmaeum*, and under *Scirpus maritimus* rarely *Assiminea gratiana*.

In the Netherlands, at least, *Succinea arenaria* is characteristic of the Caricion davallianae vegetations, especially of the *Schoenenum nigricans*.

Shrub vegetations of *Hippophae rhamnoides* are dominant in the calcareous dunes behind the coastal range in the dune district; these vegetations form communities which are different in moist and dry places. Many snails are found here, especially on moist soils, e.g.: *Zonitoides nitidus*, *Vertigo antiveritgo*, *Cochlicopa lubrica*, *Arrianta arbastorum*, *Fruitticola hispida*, *Vallonia pulchella*, *V. costata*, *Cepaea nemoralis*, *Retinella nitidula*, *Columnella edentula*, *Eucornulus trochiformis*, *Virrina pellucida*, *Theba cantiana*, *Oxychilus cellarius*, *O. allarius*, *Punctum pygmaeum*, and in dryer places *Vertigo pygmaea*, *Pupilla muscorum*, and *Vallonia excentrica*.

In the more or less open shrubless dune grasslands on calcareous sand, which are "pastured" by rabbits, sheep, goats, etc., vegetations with *Carex arenaria*, *Pbleium arenarium*, *Koeleria abersceni*, *Saxifraga triaetlii*, *Ononis repens*, and sometimes the very characteristic moss *Tortula muralis* var. *arenaria*, form Koelerion albescentis habitats for associations of species which are able to live in dry surroundings: *Vallonia excentrica*, *Pupilla muscorum*, and *Virrina pellucida*. *Cepaea nemoralis* is also found here. These biotopes are the typical habitats of *Helicella ericetorum*, *H. berpensis*, *H. caperata*, *H. unifasciata*, *Theba cantiana*, *Cochlicopa minima*, and *Truncatellina cylindrica*, as far as their occurrence in the dunes is concerned.

In the island of Walcheren *Lamria cylindracea* is found in dry grassland, and in a habitat which is a transition of a dry open dune slope to dry woodland such as occurs on the rich sandy soil in the area behind the dunes. This type of woodland with its characteristic molluscan fauna will be described with the woodland habitats.

The dunes of the Wadden district are poor in lime, and generally very poor in terrestrial Mollusca. Just behind the coastal range hardly any molluscs are found, at least as compared with the abundance in the calcareous dune district. In the *Hippophae*, dwarfshrub, and other dune vegetations at a little distance behind the outer dune ridge *Virrina pellucida*, *Vertigo pygmaea*, *Cochlicopa lubrica*, and *Vallonia excentrica* are found, although often locally, and never in great

numbers. Locally also *Vallonia pulchella*, *Pupilla muscorum*, *Columnella edentula*, *Punctum pygmaeum*, and *Agriolimax laevis* occur in small numbers, and only on Texel: *Helicella berpensis* and *Theba cantiana*. Further inland, in the dry Corynephorion dune, no molluscs are present, and in the dune heath vegetation only species such as *Arion intermedius* are known to occur.

Arable land, gardens, and human settlements

At least in the Netherlands arable land is a bad habitat for terrestrial Mollusca. This is probably due to farming. Even on rich soils the arable land is poorer in molluscs than the intensively pastured grasslands of the Lolieto-Cynosuretum on poor sandy soils. Snails and slugs which are sometimes found in arable land are normally invaders from neighbouring communities, such as hedges, verges, roadsides, grasslands, etc.

Gardens, however, frequently are rich in slugs and snails, probably because they often have corners which serve as refuge areas. Species such as *Agriolimax reticulatus*, *Arion borrensis*, *A. rufus*, *A. circumscriptus*, *Limax maximus*, and *Helix aspersa* are often found living in gardens, and sometimes they even are a pest. *Oxychilus draparnaldi*, *O. cellarius*, *Fruitticola hispida*, and *Goniodiscus rotundatus* are also inhabitants of gardens, and all these species are characteristic of areas near human settlements, such as fallow ground in towns and villages, roadsides, etc. Though they occur more locally, *Fruitticola striolata*, *Theba cantiana*, *Th. carthusiana*, *Milax gagates*, and *M. soverbii* also belong to this group of anthropochorous species.

From the local occurrence of some species, viz., *Helix aspersa* (mostly in and about towns in the west of the country), *Fruitticola striolata* (at Veere), *Milax gagates* (in three localities on roadsides in southern Limburg), and *M. soverbii* (in gardens in Amsterdam and Utrecht) it appears that these species probably do not belong to the endemic fauna, but have been introduced, the first-mentioned species intentionally so because it is edible. *Helix pomatia* is another species that must have been introduced into the Netherlands, even into the calcareous district of southern Limburg, where at present it would seem to be an indigenous species, because all fossil records are lacking. *Limax flavus* too must have been introduced, for this species is not able to maintain itself outside of human habitations. It is mostly met with in cellars, a habitat sometimes also occupied by *L. maximus*. *L. flavus* originates from the eastern part of the mediterranean area.

Fruitticola hispida and *Oxychilus cellarius* are common species distributed all over the country and, therefore, strike one as being

indigenous. In 1930 it appeared, however, that they did not occur in the province of Drenthe (except for *Fruinicola hispida* in one locality), even in many seemingly suitable localities. Attention should be paid to a possible settlement of these species in this area.

Other snails likely to be dispersed by man are the species of *Helicella*, which are able to survive long periods of unfavourable conditions. Thus transportation, probably by man, must be the cause of the occurrence of *Helicella unistasciata* in the dunes near Velsen and of *H. virgata* on the dike near Medemblik. *Helicigona lapicida* may have reached the neighbourhood of Hoorn along with the stones used to reinforce the dike on which it is living. Some records of species not belonging to our fauna show that introduced specimens are not always able to establish more or less permanent colonies. Thus *Abida secale* was never found again near Zeist or Driebergen, nor *Chondrina arenacea* near Haarlem or Sassenheim, nor *Ena monina* near Bloemendaal, in which places they were each found on one occasion. The occurrence of *Helicodiscus singleyanus inermis*, a North American species, in four localities in Europe, two of which are situated in the Netherlands, is still a mystery, but it seems possible that it is due to introduction by man.

Displacement of certain species occasionally seems to influence the occurrence of others. Thus there are indications that *Oxyechilus cellarius* and *Limax cinereomiger* vanish where *O. draparnaldi* and *L. maximus* respectively, are introduced.

Heath formations, moorland, and bogs

Heath, moorland, and bogs form biotopes which are very characteristic of the Netherlands. They are found mainly on the pleistocene sandy soils, and in the more inland parts of the dunes poor in lime in the Wadden district. Nowadays a great part of the heath and moorland is reclaimed, and only very little is left of the enormous peatbog areas which formerly existed in the northeastern parts of the country, and in the provinces of Noord-Brabant and Limburg. These communities have a characteristic flora and fauna which is very interesting to the ecologist. To the malacologist, however, they are of little interest. Only very few terrestrial Mollusca are able to live in these habitats, which are moist enough, but which have a very acid litter and soil.

On higher, and relatively drier soils the *Calluna* heath is dominant, with various communities of the Calluneto-Genisterum. Characteristic species of plants are: *Calluna vulgaris*, *Genista anglica*, *G. pilosa*, *Caschia epithymum*, *Juncus communis*, *Pleurozium schreberi*, and in the north of the country also *Empetrum nigrum*. On wet sandy

soils the *Erica tetralix* heath forms moorland communities with *Erica tetralix*, *Trichoforum caespitosum*, *Juncus squarrosus*, *Narbecium ossifragum*, and *Sphagnum compactum* as characteristic plant species. The *Sphagnum* bogs are extremely wet. Sphagnum europaeum vegetations are locally found in Ericetum moorland areas on the Pleistocene, and in some larger complexes in Noord-Brabant, Twente, and Drenthe. Characteristic plant species are: *Sphagnum* spp., *Eriophorum angustifolium*, *Rhynchospora alba*, *Rh. fusca*, and *Drosera intermedia*.

Land Mollusca are very rare in these surroundings. *Arion subfuscus* is the most common species. It is, however, found only in the *Calluna* heath, and with an extremely low density. The other species, *Arion intermedius* and *Retinella hammonis*, which are still more scarce, also are found only in Calluneto-Genisterum vegetations.

Woodlands

Only about 7.5% of the area of the Netherlands is covered by woodland, i.e. about 250,000 ha. Most of this, viz. 2/3 or 175,000 ha, is coniferous forest consisting of plantations of *Pinus sylvestris*, *P. nigra*, *Picea excelsa*, *Pseudotsuga taxifolia*, and *Larix leptolepis* on the poor pleistocene sands, 29,000 ha is deciduous forest of oak, beech, and poplar, and 45,000 ha is copice wood of oak or willow.

Those plots of woodland which may be supposed to be the last representatives of the "natural" forest types are the most interesting to the malacologist. Nothing is left of the original wild woodland in the Netherlands, and plots of more or less natural woodland, viz. woodland with a fauna which is supposed to be natural, are rare, especially on richer soil types. About 6,000 ha of the deciduous and copice woodland are scientifically important.

Plant-ecologists divide the woodlands of the Netherlands into three categories (classes), which are ecologically different. These classes are characterized by their floristic composition. This division is valuable also for the malacologist:

I, woodland of mostly richer soils (pH > 7; Querco-Fagetea);
II, woodland of poor sandy soils (pH < 7; Vaccinio-Picetea);
III, woodland of wet, peaty soils (Alnetea glutinosae).

The Querco-Fagetea, in most cases developed as oak forests, are characterized by the following plant species: *Acer pseudoplatanus*, *A. platanoides*, *Corylus avellana*, *Fraxinus excelsior*, *Acer campestris*, *Helera helix*, *Paris quadrifolia*, *Circaea lutetiana*, *Prunella elatior*, *Anemone nemorosa*, *Arum maculatum*, *Allium ursinum*, *Geranium robertianum*, etc.

The Vaccinio-Picetea, comprising a small percentage of oak forests and much coniferous plantations, are characterized by the following

Plant species: *Betula pendula*, *B. pubescens*, *Sorbus aucuparia*, *Populus tremula*, *Fraxinus alnus*, *Vaccinium myrtillus*, *V. vitis-idaea*, *Myrica themum bifolium*, *Laetia lazuloides*, *L. sylvatica*, *Melampyrum pratense*, *Polypodium vulgare*, *Dryopteris austriaca*, and *Blechnum spicant*. The *Alnetea glutinosa*, mostly alder woodland on marshy soils, are characterized by *Alnus glutinosa*, *Salix cinerea*, *S. aurita*, *Calluna-groxis canescens*, *Ribes nigrum*, *Ornithogalum vulgare*, *Solanum dulcamara*, and *Humulus lupulus*, along rivulets also by *Carex elongata*, in the western parts of the Netherlands by *Dryopteris austriaca*, and on poor, more acid peat soils by *Myrica gale*.

Classes are subdivided into orders, which again are subdivided into smaller units. As it is well known that several species of terrestrial Mollusca are found in special types of forest vegetation, some details of the phytosociological division of the classes are given here. The woodlands on the richer soils (*Querceto-Fagetea*) are divided into three groups:

1. *Fagetalia*: deciduous forests, mostly of oak, on well-differentiated soil profiles. For the Netherlands the following plant species may be mentioned: *Prunus avium*, *Carpinus betulus*, *Polygonatum multiflorum*, *Carex sylvatica*, *Sanicula europaea*, *Poa nemoralis*, *Oxalis acetosella*, *Asperula odorata*, *Laminium galeobdolon*, *Vinca minor*, etc.

2. *Populetalia*: deciduous forest on young homogeneous soil profiles, in the Netherlands for instance along rivulets, rivers, etc. Characteristic plant species are: *Populus alba*, *Prunus padus*, *Sambucus nigra*, *Melanchium diurnum*, *Stachys sylvatica*, *Festuca gigantea*, *Impatiens noli-tangere*.

3. *Prunetalia spinosae*: plant communities typical of hedges, shrub vegetation, verges of forests, etc. Characteristic plant species are: *Prunus spinosa*, *Crataegus monogyna*, *Cr. oxyacantha*, *Viburnum opulus*, *Elaeagnus europaeus*, *Cornus sanguinea*, *Rosa canina*, and *Vicia sepium*.

Further differentiation is possible owing to differences in the vegetation due to the level of the groundwater-table, the lime content of the soil, etc. The vegetations of southern Limburg and the calcareous dunes, therefore, have their own specific forest associations. The forest communities of the *Querceto-Fagetea* category are very rich in land Mollusca and count among the habitats which are the most important to the malacologist, not only as to the number of species concerned, but also as to the number of individuals.

In the eutrophic forests of the Netherlands the following land Mollusca are found regularly: *Carychium tridentatum*, *Succinea oblonga*, *Cochlicopa lubrica*, *Colymbella edentula*, *Vertigo substriata*, *V. pusilla*, *Acanthinula aculeata*, *Vallonia pulchella*, *V. costata*, *Balea*

perversa, *Punctum pygmaeum*, *Gonyodiscus rotundatus*, *Vitrea contracta*, *Retinella hammonis*, *R. pura*, *R. nitidula*, *Oxychilus cellarius*, *O. albarius*, *Vitrina pellicula*, *Atrion vulvus*, *A. subfuscus*, *A. circumscriptus*, *A. borrensis*, *A. intermedius*, *Limax maximus*, *L. cinereoniger*, *Lebmanium marginata*, *Eucornutus trochiformis*, *Monacha inarrata*, *Fruiticola bipida*, *Arionta arbustorum*, *Cepaea nemoralis*, and *C. borrensis*. *Agrioninae reticulatus* and *A. laevis* occur exceptionally in these types of woodland.

Of the species mentioned *Oxychilus albarius* is restricted to the northern and western parts of the country, *Cepaea borrensis* to the eastern parts. In wet places *Carychium minimum* and *Vitrea crystallina* replace *C. tridentatum* and *V. contracta*, respectively. Both pairs of species have a zone of overlap, which is the larger in that of *Vitrea*.

An average abundance of 100-400 individuals per square metre is normal for *Querceto-Fagetea* forests. In some cases the density even amounts to 1000 or more per square metre. *Zonitoides nitidus* and *Succinea puris* occur only in the very moist types of the *Querceto-Fagetea*. They are more typical of the *Alnetea glutinosa* forests. *Vallonia excentrica* is sometimes found in forests, but rarely, and only in dry biotopes and in the transition zone to the open field. In many places *Clausilia biplicata* shows a preference for *Prunetalia spinosae* associations. In the valleys of the Rhine and the IJssel *Clausilia dubia*, *Cl. bidentata*, and *Balea perversa* are confined to *Populetalia* sites. The forests on richer soils in the dune area are more or less characterized by the occurrence of *Trocheta cantiana*, *Acanthinula aculeata*, *Vitrea contracta*, and *Clausilia bidentata*.

Southern Limburg is privileged by edaphic and climatic conditions especially favourable for molluscan life. Here the plots of woodland are habitats for the following species which are not found in other parts of the country: *Pomatias elegans*, *Ena obscura*, *Clausilia rolphi*, *Cl. lineolata*, *Cl. parvula*, *Cl. laminata*, *Milax rusticus*, and *Ealora fuscum*.

The woodlands on the poor sandy soils (Vaccinea-Piceeta)

In the first place the coniferous forests belong to this category (class). In the Netherlands they have been planted on the poor, sandy soils of the pleistocene deposits. The oak-birch forest (*Querceto-Betulium* association), differentiated in several communities according to soil conditions and groundwater-table, and the birch-fenforest vegetation (*Betulium pubescens*) on wet, poor, acid soils are more important to the biologist. However, as a whole they cover only a very small area of the Netherlands.

Contrary to the forests on richer soils the Vaccinea-Piceeta are generally poor in molluscs. Nevertheless they are interesting to the malacologist because they form a pessimum, and within these groups a transition can be studied from habitats with mesotrophic conditions, where a fairly large number of molluscs is still living, to purely oligotrophic environments without any molluscs.

The coniferous forests of *Pinus*, *Picea*, *Pseudotsuga*, or *Larix* are among the poorest habitats. It is rather an exception when one meets with molluscs there, especially when no undergrowth or herb layer is present. The few species which may be expected are: *Arion subfuscus*, *A. intermedius*, and *Limax tenellus*. They live on fungi and in most cases they are found eating toadstools (e.g. *Boletus*, *Russula*, and *Amanita* species).

When there is some undergrowth of *Molinia coerulea* and other herbs, often because the soil conditions are slightly better, *Retinella hammonis*, *Eucomilus trochiformis*, *Columella edentula*, and *Agriolimax laevis* may also be present in such woodlands. The average abundance of the total molluscan fauna exceptionally reaches 25 individuals per square metre. The oak-birch forests are richer habitats for terrestrial molluscs; *Retinella hammonis* and *Eucomilus trochiformis* are the most numerous species, while *Arion intermedius*, *A. subfuscus*, *Columella edentula*, *Limax tenellus*, *L. cinereoniger*, and *Agriolimax laevis* are normally present. *Limax maximus* is not known to occur in these habitats. On richer soils *Cochlicopa lubrica*, *Lebmanina marginata*, *Punctum pygmaeum*, *Gonyodiscus rotundatus*, and sometimes *Retinella nitidula* also occur more or less regularly. *Zonitoides excavatus* is typical of this sort of woodland, but it occurs only locally. *Acambinula lamellata* lives in a forest which is an example of a "rich" Querceto-Betuleum, with transitions to Querceto-Fagea woodland. The average density of the total mollusc population in 26 oak-birch woodlands proved to be 70 individuals per square metre.

The birch-fenwoodland (Betuleum pubescens) on sandy and peaty, very poor and acid soils on which often *Sphagnum* growth occurs are very poor in molluscs. Only *Arion intermedius*, *Agriolimax laevis*, *Retinella hammonis*, and *Eucomilus trochiformis* occur in these biotopes, where the snails develop very thin and fragile shells.

Woodland of wet peaty soils (*Alnetea glutinosae*)

The *Alnetea glutinosae* communities consist of woodlands on rich (eutrophic) to poorer (mesotrophic) wet peaty soils, which are never very poor and oligotrophic. When the soil is very poor the Betuleum pubescens (*Vaccinio-Piceeta*) is taking its place. Three communities

have been distinguished, which all three are interesting to the malacologist: the alder fenwood (*Alnetum glutinosae*), the *Alnetum Cardaminetosum amarae*, and the Betuleto-Salicetum.

The *Alnetum glutinosae* is to be found all over the country in places with a high groundwater-table of eutrophic water. The phreatic level is very near to the surface, locally even above the surface. This type of woodland is closely related to the Magnocaricion, from which it often originated in the succession. Nearly always *Alnus glutinosa*, *Salix* spp., *Iris pseudacorus*, *Lycopus europaeus*, and *Scutellaria galericulata* are present. Many species of molluscs are found here, which is comprehensible for habitats which are wet and eutrophic. Even freshwater Mollusca are present, e.g.: *Planorbis leucostoma*, *Lymnaea truncatula*, *L. palustris*, and *Physidium* spp. Land Mollusca regularly found in these alder woods in the Netherlands are: *Zonitoides nitidus*, *Retinella hammonis*, *Vitrea crystallina* (not *V. contracta*), *Carychium minimum* (not *C. tridentatum*), *Succinea putris*, *S. oblonga*, *Cochlicopa lubrica*, *Vertigo antiveritigo*, *V. substriata*, *Columella edentula*, *Eucomilus trochiformis*, *Punctum pygmaeum*, *Arion rufus*, *A. subfuscus*, *A. circumscriptus*, *Agriolimax reticulatus*, *A. laevis*, *Retinella pura*, *R. nitidula*, *Furticicola hispida*, *Arianta arbustorum*, and *Cepaea nemoralis*.

In the alder woodland of the *Alnetum cardaminetosum*, the characteristic woodland vegetation growing along little streams, and in and near springs, generally the same species of Mollusca may be found. These biotopes are moreover the habitats of some species which are rare in the Netherlands: for instance *Vitina diaphana* is found in such "spring alder-woodlands" in the southeast of the Netherlands. Characteristic plant species of this alder woodland are: *Cardamine amara*, *Carex remota*, *Chrysosplenium oppositifolium*, and *Chr. albertifolium*.

The communities of the Betuleto-Salicetum fenwoodland, growing under mesotrophic conditions, are poorer. Characteristic plant species are: *Salix aurita*, *Myrica gale*, and *Ornanda regalis*. Here *Retinella hammonis*, *Arion intermedius*, *Eucomilus trochiformis*, *Arianta arbustorum*, and *Zonitoides nitidus* are still rather numerous, while *Succinea putris*, *Punctum pygmaeum*, *Columella edentula*, *Arion subfuscus*, and *Agriolimax laevis* are present but in small numbers only, just as *Carychium minimum*, *Vitrea crystallina*, *Arion circumscriptus*, and *Agriolimax reticulatus*. *Zonitoides excavatus* is recorded from such a vegetation in one locality in the west of the country.

THE VERTICAL DISTRIBUTION OF TERRESTRIAL MOLLUSCA

By vertical distribution we here mean the distribution in relation to the surface of the soil. Most species of land Mollusca are living on the soil, under the herb layer and in the litter. Under the influence of external conditions they may move in vertical direction; generally a moist atmosphere and warmth favour upward movement, drought and cold makes them hide deeper into the soil. In Vitrinidae the reaction to temperature is the opposite; they hide in the soil in summer, when they are young, while the adults appear creeping at the surface in winter, even when it is freezing.

Some few species are living deeper in the soil, and rarely appear at the surface. *Truncatellina cylindrica* is living just below the surface in relatively dry calcareous grasslands, for instance in the root system of *Thalictrum minus*. *Cochlicoides acicula* is found deeper in the soil. Its presence in grasslands on rich soils sometimes appears from specimens brought to the surface in mole-hills.

When the atmosphere is damp, a number of the inhabitants of the soil will ascend the stalks and leaves of the vegetation. This is mostly the case in *Succinea Pfeifferi* and *S. saxii*, and sometimes in *Vertigo moulinsiana*, which are living near the waterside. It may, however, also be observed in *Succinea putris*, *Columella edentula*, and *Fruticola hispida*. The species of *Helicella* are able to remain on herbs and small shrubs even during days of bright sunshine, and *Cepaea* and *Helix* species will ascend walls and trees and remain in a high position withdrawn in their shells during the dry hours of the day. Among the slugs *Lehmanna marginata* is a well-known tree climber, while *Limax maximus* occasionally is found climbing walls and trees.

While some clausiliids, such as *Clausilia rolyhi* and *Cl. laminata*, are always found on the soil, others, such as *Cl. lineolata*, *Cl. bidentata*, and *Cl. parvula*, occasionally ascend trees when these have a smooth bark, or are found living more or less permanently on old walls, cretaceous rocks, or trees with a rough bark. In the Netherlands *Balea perversa* and *Clausilia dubia* are normally inhabiting trees, where they hide in the crevices of the bark or in between moss cushions during periods of dry weather. Specimens of these species are never found on the soil.

PROTECTION OF THE NATURAL MOLLUSCAN FAUNA

Most species of Dutch land Mollusca are living in many places, and there is no danger that reclamation, improvement of the land, etc. will exterminate them in this country. A number of species, and

among them the stenokous ones, need special care because the biotopes in which they live are rare or even very rare. These biotopes are often threatened by reclamation. For that reason surveys are being made of the habitats of species such as *Vertigo moulinsiana*, *Acanthinula lamellata*, *Vitrina diaphana*, *Succinea arenaria*, *Lauria cylindracea*, *Vertigo angustior*, etc., in order to know which localities are of special scientific interest and deserve protection, e.g. as nature reserves. On the other hand the policy of the nature conservation in the Netherlands is aiming at the conservation of reserves which include specimens of all still existing natural biotic communities. In these reserves the survival of the autochthonous molluscan fauna of the Netherlands is ensured.

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¹⁾ An extensive list of references to the older literature is to be found in Van Benthem Jutting, 1933. Papers and notes on the Dutch molluscan fauna mostly appeared in the journals De Levende Natuur, Natuurhistorisch Maandblad, and Basteria.