VARIATION IN THE NUMBER OF UNGUES IN
AMERONOTHRUS SCHNEIDERI (OUDEMANS),
AN ORIBATID MITE

by

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With 1 figure and 5 tables

ABSTRACT

In the present paper an analysis is made of the variation in the number of ungues in the claws of *Ameronothrus schneideri* (Oudemans), an Oribatid mite. This variation is attributable to the regression of the two lateral ungues which are completely suppressed in the course of evolution (they are either present or absent). The laws of this numerical evolution (it is a so-called vertitional evolution) appear to be statistical, and do not determine individual events precisely (as the laws of the particles in quantum mechanics). In a population, each of the claws has a probability of manifestation. The variation of this probability of manifestation shows a very interesting geographical pattern which is as yet difficult to explain. Various correlations of the evolutionary processes in the eight legs are studied, and suggestions are given for continued research.

INTRODUCTION

During his studies of the Oribatid mites of saline areas in the Dutch Wadden Sea and other parts of N.W. Europe, Mr. P. J. G. Polderman and his collaborators collected numerous specimens of *Ameronothrus schneideri* (Oudemans) at localities in Norway, Denmark, N.W. Germany, The Netherlands, France and Great Britain (cf. Polderman, 1974, 1975). Although the species was described as monodactyl (cf. Schubart, 1975), Polderman's specimens presented monodactyl, bidactyl, as well as tridactyl claws, even in one individual, a variation comparable to that studied by Grandjean (1961) and Lions (1964) in other species of Oribatid mites. A detailed analysis of the variation in the number of ungues was subsequently carried out by the first author, whilst the text of the present paper was composed by the second author. Anticipating the completion of the present paper, the second author mentioned some of the results in his paper on Numerical Changes and Evolution in Actinotrichid Mites (Van der Hammen, 1981)[1].

In his monograph of the family Ameronothridae, Schubart (1975) mentioned nine *Ameronothrus* species, among which one species of uncertain identity, that was subsequently described by Weigmann & Schulte (1975). The geographical distribution of the species was thought to be holarctic, till Weigmann (1975) published data on the occurrence of the genus in South Africa. According to Schulte, Schuster & Schubart (1975), the species of Ameronothridae fall into four ecological groups: stenotopic inhabitants of the marine littoral, eurytopic inhabitants of the littoral, holeurytopic inhabitants of the littoral, and stenotopic inland species. All stenotopic species are confined to hard substrates. The eurytopic species predominate on rocky shores (either free from, or rich in sediments), or in the salt-marsh. The holeurytopic species are indifferent to substrates. In warmer climates, the eurytopic species tend to become stenotopic. *Ameronothrus schneideri* belongs to the second ecological group (eurytopic inhabitants of the littoral).

In the genus *Ameronothrus*, claws with three ungues are predominantly found in species living on hard substrates, claws with one ungues in species living on soft substrate, although there are some notable exceptions. *Ameronothrus schneideri*, in which the number of ungues varies from three to one, is found in vegetations on soft substrate, outside the dikes, which are regularly or sporadically inundated by sea-water or by brackish water of a salinity higher than 0.05%. According to Polderman (1974), the species is a characteristic element of two communities: the Puccinellietum maritimae (especially the lower part), and the Juncetum gerardii (outside the dikes). *Ameronothrus schneideri* is known from the Atlantic coasts of Europe (from Norway to South Portugal) and from Madeira (Schulte, 1975: 344-345). The type-specimen of *Ameronothrus schneideri* (in the Oudemans Collection, Rijksmuseum van Natuurlijke Historie, Leiden) originates from Borkum island, N.W. Germany (cf. Oudemans, 1903); all legs of this specimen are monodactyl.

According to Weigmann (1973: 358), *Ameronothrus schneideri* can support long periods of inundation; in submerged condition, it clings to objects with the help of its claws, and is even able to walk among the vegetation and on the substrate. In cultures, it has been observed to feed on filamentous algae and fungi (Luxton, 1966: 168).

Reproduction in *Ameronothrus schneideri* is bisexual. Males and females are found in variable numbers. The two sexes generally present slight differences in average measurements of body and legs (cf. Schubart, 1975).

A summary of previous investigations on the variation in numbers of ungues, in Oribatid mites, was published by Van der Hammen (1981). The following passages are quoted from his paper.

The ancestral claw of Actinotrichid mites (cf. Grandjean, 1939: 539-546) was tridactyl in all stases, as still found in Endeostigmata and Palaeosomata (*Aphelacarus acarinus* (Berlese)). In most Oribatid mites, the tridactyl claw has, however, been subject to regression, and has become monodactyl in all immature stases; in the adults the claws can be mono-, bi- or tridactyl. In the

course of evolution, monodactyly can arise by suppression of the two lateral ungues (ol' and ol''), homobidactyly by suppression of the central unguis (oc), heterobidactyly by suppression of one of the lateral ungues (ol' or ol''). (The symbolic signs $'$ and $''$ denote the elements of the anterior, respectively the posterior face of the legs).

Several cases of numerical regression of the claws have been investigated in detail. Grandjean (1939, 1961, 1965) studied the regression of the ungues of the claws in *Nothrus silvestris* Nicolet, an Oribatid mite of which the reproduction is parthenogenetic. He based his study on material from various parts of France, Switzerland and Italy. In the genus *Nothrus*, the lateral ungues can be subject to numerical regression. Adults of *Nothrus silvestris* are, generally, bidactyl (the ungues mostly found are ol' and oc; ol' is stronger than ol''); specimens with monodactyl and tridactyl claws are, however, also found (monodactyl claws are regularly found, the occurrence of tridactyl claws is rare, and appears to be restricted, in a specimen, to one leg at the utmost). The evolution of the ungues is vertitional[1]): regression manifests itself partly asymmetrical; in many cases different legs present different claws; the specimens of one population seldom belong to one claw-type. Bidactyly appears to be statistically predominant in wooded areas, monodactyly in open country. Statistically, the lateral ungues of legs I and II disappear before those of legs III and IV.

According to Grandjean (1965: 109), unguis ol'' is stronger than ol' in the case of *Nothrus anauniensis* Canestrini & Fanzago (ol' is stronger in the case of *Nothrus silvestris*). In *Nothrus anauniensis*, specimens generally present tridactyl claws; bidactyl claws are, however, also found, whilst specimens with monodactyl claws are extremely rare.

Lions (1964: 41-65) studied the variation of the numbers of ungues in *Rhysotritia ardua* (C. L. Koch), an Oribatid mite. The reproduction of this species is probably also parthenogenetic. Lions based his investigations on material from three different biotopes in the surroundings of Aix-en-Provence, in France. *Rhysotritia ardua* is predominantly bidactyl at leg I and tridactyl at legs II-IV. Regression has, consequently, started at leg I. In bidactyl claws of this species, the ungues are mostly ol'' and oc. Monodactyl claws are also found. Claw-types are, generally, distributed over the legs in a more or less asymmetrical and apparently irregular way; evidently the variations must be attributed to vertitional evolutions. Homonychia (the occurrence of one claw-type in all legs of a specimen; the term is introduced here on the analogy of heteronychia) appeared to be more common in specimens from the open country, heteronychia (the oc-

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[1]) A vertition is a discontinuous individual variation of presence-absence, pertaining to an idionymous organ observed in specimens of the same species, at the same stase, provided that this variation is fundamentally unilateral, and has an evolutionary significance. Generally, vertitions are repeated in part of the offspring; they are not immediately hereditary (in the offspring they have a certain probability of manifestation). Vertitions are probably the result of gene regulation. (The laws of this type of evolution are similar to those of the particles in quantum mechanics.) References to the literature on the subject are given by Van der Hammen (1980: 167).

currence of various claw-types in the legs of one specimen) appeared to be more common in shaded country. The order of regression, in the legs, presented differences of a very complex nature.

Matsakis (1967) made a mathematical analysis of the data collected by Lions. He discovered the existence of distinct, although very complicated connections between the variations; a number of elementary processes appeared to have acted together and in superposition. Statistically, *ol″* appeared to be stronger than *ol′*; there was, however, also a double priority because the lateral ungues of legs II and III were statistically stronger than those of legs I and IV. Matsakis discovered also the presence of a certain balance (association of opposite and mutually compensatory variations) between *ol′* and *ol″* in neighbouring symmetrical or adjacent legs. Evidently, we are dealing here with the effects of a balanced distribution of some regulatory material, present in a restricted quantity.

MATERIAL

As mentioned above, the material on which the present study is based was collected (by extraction from samples taken from the soil, 10 cm in diameter, to a depth of 5 cm, including the vegetation) in Norway, Denmark, N.W. Germany, The Netherlands, France and Great Britain. Data with reference to stations and samples are given in table 1. The numbers of the stations are indicated on the map of fig. 1. The distribution of these localities is partly determined by the distribution of salt-marshes. The occurrence of important gaps is, however, also connected with the incidental character of the collecting done in Norway, France and Great Britain. All the material analysed for the present study (with the exception of a few specimens that got lost) is in the collection of the Rijksmuseum van Natuurlijke Historie, Leiden.

The ecological data mentioned in table 1, include either references to the plant-communities (Puccinellietum maritimae, Juncetum gerardii, Artemisietum maritimae; nomenclature according to Westhoff & Den Held, 1969) or references to the species of plants present in the samples (in some cases, data were lacking, or were restricted to other information). The following names of plants are included in the table. Higher plants: *Agrostis stolonifera* L., *Armeria maritima* (Mill.) Wildl., *Aster tripolium* L., *Cochlearia anglica* L., *Elytrigia pungens* (Pers.) Tutin, *Epilobium parviflorum* Schreb., *Festuca rubra* L., *Glaux maritima* L., *Halimione portulacoides* (L.) Aellen, *Juncus gerardii* Loisl., *Juncus maritimus* Lamk., *Limonium vulgare* Mill., *Plantago maritima* L., *Puccinellia maritima* (Huds.) Parl., *Salicornia europaea* L., *Solanum dulcamara* L., *Spergularia marina* (L.) Griseb., *Spergularia media* (L.) C. Presl., *Spergularia* spec., *Suaeda maritima* (L.) Dum., *Suaeda* spec., *Triglochin maritima* L. Mosses: *Funaria hygrometrica* Hedw. Chlorophyceae: *Rhizoclonium riparium* (Roth) Harv. Rhodophyceae: *Bostrychia scorpioides* (Huds.) Mont., *Catenella* spec.
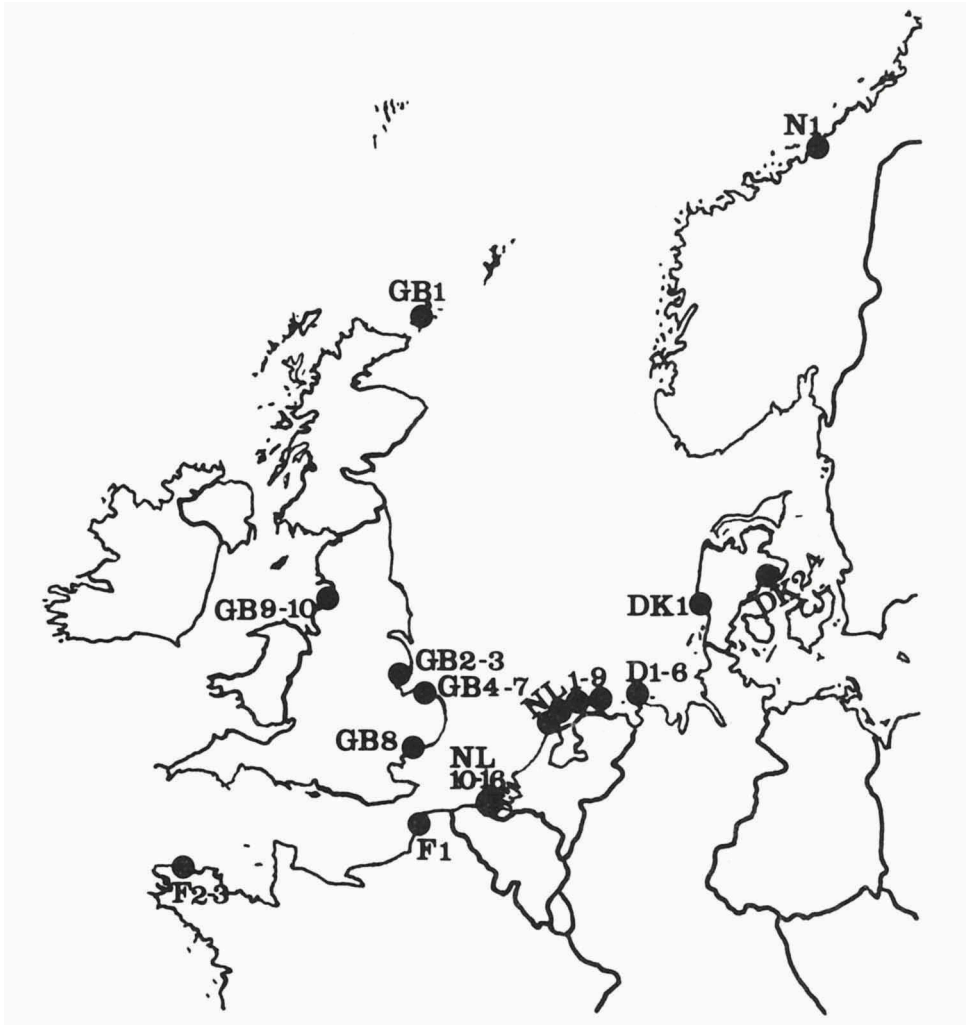
Fig. 1. Sketch-map of N.W. Europe, showing the localities (with station-numbers) in which material of *Ameronothrus schneideri* (Oudemans) was collected.

RESULTS

In the 89 samples listed in table 1, a total number of 838 adults of *Ameronothrus schneideri* was found (38 from Norway, 317 from Denmark, 78 from Germany, 243 from The Netherlands, 108 from France, and 54 from Great Britain). In these specimens, a total number of 6704 claws was investigated, and the variability was represented by using the following symbols, introduced by Lions (1964): T = tridactyl claw, consisting of the central unguis *oc*, the anterior lateral unguis *ol'*, and the posterior lateral unguis *ol"*; B' = bidactyl claw, consisting of

oc and *ol'*; B" = bidactyl claw, consisting of *oc* and *ol"*; M = monodactyl claw, consisting of *oc*. The eight legs were represented by the usual symbols: Il = left leg I; Ir = right leg I; etc. The complete results are represented in table 2.

DISCUSSION

At first sight, the most conspicuous character of table 2 seems to be constituted by the chaotic distribution of claw-types in the material. All claw-types (T, B', B", M) can be found in one population, as well as simultaneously in one specimen; in a population, each of the legs can present all claw-types. On closer examination the variation appears, however, to present statistical regularities which form part of the vertitional, regressive evolution of the two lateral claws (*ol'* and *ol"*). The regression evidently takes place by complete suppression: each of the lateral claws is either present or absent (without transition). The suppression forms part of an evolutionary tendency in the genus *Ameronothrus*, directed towards the development of species which are completely monodactyl at the adult level.

A few remarks must be made here, before we can enter on a further discussion of the results. From a first study of the material, it has appeared that there is no connection between claw-type and sex, no linear connection between claw-type and leg-number, and no connection between claw-type and biotope. Anomalous claws appeared to be very rare; the single anomaly observed, referred to a lateral unguis (in a bidactyl specimen) which was too small.

One of the first things observed, after a closer investigation of the results of table 2, is the statistical occurrence of a certain geographical variation. In table 3, the numbers for the claw-types (T, B', B", M) are arranged according to geographical region, and according to separate legs. It appears that the number of tridactyl legs is relatively high in material from Norway (48.4%); this number decreases progressively along the coasts in southern direction: W. Denmark, 23%; E. Denmark, 8.3%; N.W. Germany, 1.4%; N. Netherlands, 1.2%; S. Netherlands, 0.3%; N. France, 0%. At the same time the number of monodactyl legs increase from 16.8% in Norway, to 98% in N. France. (In the complete material, 13% of the legs present tridactyl claws, 71.4% of the legs monodactyl claws). South of the Strait of Dover, the number of tridactyl claws is again considerably higher (Brittanny, 69.5%). On a smaller scale, the same variation is found in material from Great Britain, although the number of specimens in our collection is too small for a definite conclusion; there appeared to be a decrease in the number of tridactyl specimens from Orkney to The Wash (Lincolnshire, Norfolk) and to the Lancashire coast, and an increase further southward, on the Essex coast.

It stands to reason that, in a detailed analysis of the vertitional regression of the claws, both ungues (*ol'* and *ol"*) have to be studied separately. In table 3, the average presence of *ol'* and *ol"* is given for each geographical region, expressed in values ranging from 1.0 (absolute presence) to 0 (absolute absence). (The

value for ol' is computed by dividing the sum of T and B $'$ by the total number of legs; the value for ol'' is computed by dividing the sum of T and B $''$ by the total number of legs). Table 3 demonstrates that the presence of ol' decreases, from Norway to N. France, from 0.71 to 0.01, and suddenly increases in the material from Brittany (0.86); the values for ol'' are respectively 0.61, 0.01 and 0.77. (Evidently, ol' is stronger than ol''; it offers more resistance to regression). Similar values are found in the material from Great Britain.

In table 4, the total number of the four claw-types, and the presence of the two lateral ungues, are given for each of the eight legs and for each of the four pairs of legs. This table demonstrates again that ol' is stronger than ol''. Table 4 demonstrates also that, statistically, there is little difference between the presence of ol' and ol'' on the left and on the right side. The presence of ol' is lowest in the case of leg II (the presence increases in, respectively, legs I, III, and IV); the presence of ol'' is lowest in the case of leg I (the presence increases in, respectively, legs II, III, and IV). The position of the claw with reference to the plane of symmetry of the body, i.e. either paraxial (ol' in the case of legs I and II, ol'' in the case of legs III and IV) or antiaxial (ol'' in the case of legs I and II, ol' in the case of legs III and IV), evidently has no influence on the regressive evolution.

The presence of homonychia (i.e. the occurrence of one claw-type in all legs of one specimen) has been computed in table 5. The presence of homonychous tridactyl specimens (representing the starting-point of the regressive evolution) decreases from 0.13 in Norway to 0 in N.W. Germany, The Netherlands and N. France, and subsequently increases to 0.19 in Brittanny. The presence of homonychous monodactyl specimens (representing the final stage in the regressive evolution) increases from 0 in Norway to 0.87 in N. France, and subsequently decreases to 0 in Brittanny. Similar data, although on a much smaller scale, are obtained from the material collected in Great Britain.

Among the total number of specimens, 2.6% appears to present tridactyl homonychia, 45.2% monodactyl homonychia. Bidactyl homonychia (B $'$ or B $''$) has not been found; both bidactyl claw-types represent a transitional stage in the regression from tridactyl to monodactyl claws; apparently, these transitional stages are hardly ever attained by all legs at the same time.

A detailed comparative study of table 2 suggests that there could be a certain balance between ol' and ol'' in the manifestation of regression in the eight legs, i.e. an association of opposite and mutually compensatory variations, in neighbouring symmetrical or adjacent legs. An analysis, similar to that executed by Matsakis (1967), is required to confirm this first impression.

The geographical variation in presence of ol' and ol'' is difficult to explain. Apparently, an unknown external factor has influenced the regressive evolution, southward along the coast, as far as the Strait of Dover. The different grades along the coast could be connected, in some way, with differences in evolutionary time and changes in the North Sea at the end of the Pleistocene. Although the material collected in Great Britain is numerically too small to arrive at a more definite conclusion, the general pattern agrees with the results

from other parts of N.W. Europe; the increase in number of tridactyl claws, however, has apparently already started on the Essex coast.

Evidently, the present investigation is but a first orientation, and should be repeated on a much larger scale. Additional material should, in the first place, be collected along the Norwegian coast, in the neighbourhood of the Strait of Dover, and along the Atlantic coast of France and Portugal. Besides that, material should be studied, collected along the Baltic and Irish coasts. A much more numerous material from Great Britain will also be required for a better understanding of the variation.

It will certainly be interesting to study also the occurrence of vertitions (certainly rare) in other *Ameronothrus* species: the vertitional absence of lateral claws in predominantly tridactyl species, and the vertitional presence in predominantly monodactyl species. Schubart (1975) recorded the occurrence of one bidactyl claw in a specimen of *Ameronothrus lineatus* (Thorell), a predominantly tridactyl species.

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TABLE 1. Stations and samples

Country	Station	Locality	Date	Sample	Ecological data
Norway	M1	Stjörnfjord	17.8.73	X756	Juncetum gerardii
				X757	Juncetum gerardii
				X758	Juncetum gerardii
				X759	Juncetum gerardii
Denmark	DK1	Skallingen	28.4.72	787	Halimione portulacoides, Puccinellia maritima
				792	Juncetum gerardii
				800	Juncetum gerardii
	DK2	Kalø	17.4.72	790	Puccinellia maritima
				794	Juncetum gerardii
	DK3	Hestehave	10.4.72	X501	Puccinellietum maritimae
	DK4	Kysingfjord, Norsminde	20.4.72	791	Puccinellietum maritimae
Germany	D1	Langeoog, "Oosterkwelder"	1.5.75	797	Artemisietum maritimae
				798	Puccinellietum maritimae
				978	Puccinellia maritima, Halimione portulacoides, Bostrychia scorpioides, Salicornia europaea,
				979	Puccinellia maritima, Rhizoclonium riparium
	D2	Langeoog, "Westerdeich"	1.5.75	975	Puccinellia maritima, Aster tripolium
	D3	Baltrum	30.4.75	964	Salicornia europaea,
	D4	Norderney, airport	29.4.75	953	Puccinellia maritima,
				954	Puccinellia maritima,
	D5	Norderney, harbour	6.8.74	60	Festuca rubra
	D6	Juist	5.8.74	X922	
The Netherlands	NL1	Schiermonnikoog, E. of ferry-harbour	30.1.74	X788	Puccinellia maritima, Salicornia europaea
	NL2	Ameland, "de Griend"	28.6.72	X516	Puccinellia maritima, Glaux maritima, Limonium vulgare
	NL3	Terschelling, "Oslleval"	21.7.72	X430	Puccinellia maritima, Catanella spec.
	NL4	Terschelling, "de Kom"	31.10.72	X481	Catanella spec.
				X482	
				X483	Puccinellietum maritimae

TABLE 1. Stations and samples (continued)

Country	Station	Locality	Date	Sample	Ecological data
The Netherlands (continued)	NL5	Vlieland, "Posthuis"	5.8.72	X431	Puccinellietum maritimae
	NL6	Vlieland, "Westerveld"	6.7.71	X580	Puccinellia maritima
	NL7	Texel, "de Eendracht"	13.4.71	X559	Puccinellia maritima
			14.6.77	X560	Puccinellia maritima
				X561	Halimione portulacoides
	NL8	Texel, "Mokbaai"	1.8.72	X563	Puccinellia maritima
			23.8.71	X564	Puccinellia maritima
			8.11.71	X566	Juncus gerardii
				X569	Puccinellia maritima
				X570	Festuca rubra, Juncus gerardii
	NL9	Balgzand	4.1.74	X571	Juncus gerardii
	NL10	Goeree, "Springersgors"	5.1.72	X777	Juncus maritimus
			9.11.72	X543	Puccinellia maritima
				X504	former creek
				X505	Sueda maritima, Halimione portulacoides
			14.3.73	X506	Festuca rubra, moss
				X656	Festuca rubra,
				X657	Spergularia spec., Sueda spec.,
				X665	Puccinellia maritima
			21.9.73	X720	Puccinellia maritima, Limonium vulgare, Glaux maritima,
				X723	Spergularia marina, Funaria hygrometrica Sueda maritima, Solanum dulcamara
			15.6.74	X818	Puccinellia maritima, Aster tripolium, Epilobium parviflorum
				X822	Festuca rubra, Limonium vulgare
	NL11	Schouwen, Oosterland	25.8.72	X439	Puccinellietum maritimae

TABLE 1. Stations and samples (continued)

Country	Station	Locality	Date	Sample	Ecological data
The Netherlands (continued)	NL12	St. Philipsland	15.6.74	X843	Limonium vulgare, Aster tripolium, Elytrigia pungens
				X844	Puccinellia maritima, Triglochin maritima, Aster tripolium
	NL13	N. Beveland, 's-Gravenhoek	5.7.72	X438	Puccinellietum maritimae
			25.8.72	X441	
			5.7.72	X442	
	NL14	"de Braakman", E. of Biervliet	14.7.74	X851	Puccinellia maritima
	NL15	Cadzand, "Zwarte polder"	13.7.74	X854	Salicornia europaea, Puccinellia maritima, Glaux maritima, Spergularia spec., Suaeda maritima, Limonium vulgare
				X835	Salicornia europaea, Puccinellia maritima, Spergularia maritima, Juncus gerardii, Suaeda maritima, Limonium vulgare, Spergularia media
	NL16	Retranchement, "het Zwin"	14.7.74	X829	Puccinellia maritima
				X832	Salicornia europaea, Halimione portulacoides, Suaeda maritima
				X833	Salicornia europaea, Halimione portulacoides
France	F1	Slack estuary, near Ambleteuse	15.5.72	X454	Puccinellia maritima, Halimione portulacoides, Armeria maritima, Cochlearia anglica
	F2	Pensé, near St. Pol de Léon (Finistère)	1.7.75	X1092	Puccinellia maritima, Halimione portulacoides
				X1093	Puccinellia maritima, Spergularia media
				X1094	Puccinellia maritima, Triglochin maritima

TABLE 1. Stations and samples (continued)

Country	Station	Locality	Date	Sample	Ecological data
France (continued)				X1095	Puccinellia maritima, Spergularia media, Agrostis stolonifera, Halimione portulacoides
				X1096	Salicornia europaea, Puccinellia maritima
				X1097	Puccinellia maritima, Halimione portulacoides, Armeria maritima, Cochlearia anglica
				X1098	Puccinellia maritima, Triglochin maritima
				X1099	Puccinellia maritima
				X1100	Halimione portulacoides
				X1101	Puccinellia maritima
	F3	Térénez (Finistère)	13.11.73	X766	Puccinellietum maritimae
Great Britain	GB1	Orkney Mainland, Loch Stenness	30.7.73	930	
	GB2	Gibraltar Point, Lincolnshire	16.4.73	912	Puccinellietum maritimae
	GB3	Freiston, Lincolnshire	10.73	X768	Puccinellietum maritimae
	GB4	Scolt Head Island, Norfolk	9.5.73	910	
	GB5	Overy Staithe, Norfolk	2.4.74	X803	
				X804	
				X805	
				X806	
	GB6	Holkham, Norfolk	30.4.73	913	
	GB7	Morston, Norfolk	10.73	X769	Halimione portulacoides
				X770	Puccinellietum maritimae
	GB8	Manningtree, Essex	22.2.75	956	Plantago maritima
			2.4.74	X808	
	GB9	Morecambe, Lancashire	25.7.75	987	Puccinellietum maritimae
	GB10	Pilling, Lancashire	25.7.75	986	Puccinellietum maritimae

TABLE 2, Distribution of claw-types in the material
(mentioned separately for each species)

Station	Sample	Il	Ir	Ill	IIr	IIll	IIlr	IVl	IVr
N1	X756								
	X757								
	X758								
	X759								

TABLE 2, Distribution of claw-types in the material
(continued)

Station	Sample	Il	Ir	Ill	IIr	IIll	IIlr	IVl	IVr
	X759 (cont.)								
DK1	787								
	792								
	800								

TABLE 2, Distribution of claw-types in the material
(continued)

Station	Sample	Il	Ir	Ill	IIr	IIll	IIlr	IVl	IVr
	800 (cont.)								
DK2	790								
	794								
DK3	X501								

TABLE 2. Distribution of claw-types in the material (continued)

Station Sample I1 Ir III IIr I1I1 IIIr IVl IVr

X501 (cont.)

DK4   791

TABLE 2, Distribution of claw-types in the material
(continued)

Station	Sample	I1	Ir	I11	IIr	I111	IIIr	IV1	IVr
791 (cont.)									

TABLE 2, Distribution of claw-types in the material
(continued)

Station	Sample	I1	Ir	I11	IIr	I111	IIIr	IV1	IVr
791 (cont.)									

TABLE 2, Distribution of claw-types in the material
(continued)

Station	Sample	I1	Ir	III	IIr	IIII	IIIr	IVl	IVr
791 (cont.)									

TABLE 2. Distribution of claw-types in the material (continued)

TABLE 2. Distribution of claw-types in the material (continued)

TABLE 2. Distribution of claw-types in the material (continued)

TABLE 2. Distribution of claw-types in the material (continued)

Station Sample   Il   Ir   Ill   IIr   IIIl   IIIr   IVl   IVr

95A (cont.)

D5   60

TABLE 2. Distribution of claw-types in the material (continued)

Station Sample   Il   Ir   Ill   IIr   IIIl   IIIr   IVl   IVr

D6   60 (cont.) X922

NL1   X788

NL2   X516
NL3   X430

NL4   X481
     X482

TABLE 2. Distribution of claw-types in the material (continued)

Station Sample   Il   Ir   Ill   IIr   IIIl   IIIr   IVl   IVr

X482 (cont.)

X483

NL5   X431
NL6   X580
NL7   X559
     X560
     X561

NL8   X563
     X564
     X566

     X569

TABLE 2, Distribution of claw-types in the material
(continued)

Station	Sample	I1	Ir	I1	IIr	II11	III1	IIIr	IV1	IVr
NL9	X569									
	(cont.)									
	X570									
	X571									
	X777									
NL10	X543									
	X504									
	X505									
	X506									
	X656									

TABLE 2, Distribution of claw-types in the material
(continued)

Station	Sample	I1	Ir	I1	IIr	II11	III1	IIIr	IV1	IVr
	X656									
	(cont.)									
	X657									
	X665									
	X720									
	X723									
	X818									
	X822									
	X439									
NL11										
NL12	X843									

TABLE 2, Distribution of claw-types in the material
(continued)

Station	Sample	I1	Ir	I1	IIr	II11	III1	IIIr	IV1	IVr
	X843									
	(cont.)									

TABLE 2. Distribution of claw-types in the material (continued)

Station	Sample	Il	Ir	IIl	IIr	IIIl	IIIr	IVl	IVr
	X844	x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
NL13	X438	x	x	x	B"	x	B"	x	x
		x	x	B"	x	x	x	x	x
		x	x	x	x	x	x	B'	x
		x	B"	x	x	x	x	x	x
		x	x	B"	x	x	x	x	x
		x	x	x	x	x	x	B"	x
		x	x	x	x	x	x	x	x
		B"	x	x	x	B"	B"	x	x
		x	x	x	x	x	x	x	x
		x	B"	x	B'	B'	x	B'	B'
		B'	x	x	x	x	x	x	B"
		x	x	x	x	x	x	x	x
		B"	x	B'	x	x	B'	x	x
		B"	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	B'	x	x	x	B'	B"	x
	X441	B"	x	x	x	x	x	x	x

TABLE 2. Distribution of claw-types in the material (continued)

Station	Sample	Il	Ir	IIl	IIr	IIIl	IIIr	IVl	IVr
	X442	x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
NL14	X851	B'	x	x	x	B'	x	x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
NL15	X834	x	x	x	x	x	x	x	x
	X835	x	x	x	x	x	x	x	x
NL16	X829	x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
	X832	x	B'	x	B"	x	B'	x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x

TABLE 2. Distribution of claw-types in the material (continued)

Station	Sample	Il	Ir	IIl	IIr	IIIl	IIIr	IVl	IVr
	X832 (cont.)	x	x	x	x	x	x	B'	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	x	B"	x	x	x	x	x
	X853	x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	B'	x	x	x	x	x	x
	X454	x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x

TABLE 2, Distribution of claw-types in the material (continued)

Station	Sample	Il	Ir	III	IIr	IIIl	IIIr	IVl	IVr

TABLE 2, Distribution of claw-types in the material (continued)

Station	Sample	Il	Ir	III	IIr	IIIl	IIIr	IVl	IVr

TABLE 2, Distribution of claw-types in the material (continued)

Station	Sample	Il	Ir	III	IIr	IIIl	IIIr	IVl	IVr

TABLE 2. Distribution of claw-types in the material
(continued)

Station	Sample	I1	Ir	III	IIr	IIIl	IIIr	IVl	IVr
	912 (cont.)	x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x
		B"	B"	T	B"	B'	x	B"	T
		x	x	x	x	B"	x	B"	x
		x	x	x	x	B"	x	x	x
GB3	x768	x	x	x	x	x	x	x	x
GB4	910	x	x	x	x	x	T	x	x
GB5	x803	x	B'	x	x	x	x	x	x
	x804	x	x	x	x	x	x	x	x
	x805	x	x	x	x	x	x	x	x
	x806	x	B"	x	x	x	x	x	x
GB6	913	x	x	x	x	x	x	x	x
GB7	x769	x	x	x	x	x	x	x	x
	x770	x	x	x	B'	x	x	x	x
	956	B'	x	x	x	x	x	x	B"
		x	x	x	x	x	x	x	x
		x	x	x	x	x	x	N.	x
GB8	x808	B'	x	x	x	B"	B'	B'	B"

TABLE 2. Distribution of claw-types in the material
(continued)

Station	Sample	I1	Ir	III	IIr	IIIl	IIIr	IVl	IVr
	x808 (cont.)	T	T	T	B'	T	T	T	T
		T	T	T	T	T	B"	T	T
GB9	987	B'	T	B"	T	B'	x	B"	B'
		x	x	x	x	x	x' x	x
		x	x	x	x	x	x	x	x
		x	x	x	x	x	B'	x	x
GB10	986	x	B'	x	x	B'	x	B'	B'
		x	x	x	x	x	x	x	x

TABLE 3. Claw-types, individual legs and geographical distribution

Stations	Number of samples	Number of specimens	Legs	T	B'	B"	M	Average presence cl'	Average presence cl"
M1	4	38	Il	9	15	1	13	0.65	0.26
			Ir	11	15	3	9	0.68	0.37
			III	18	5	7	8	0.60	0.66
			IIr	17	9	6	6	0.68	0.60
			IIIl	21	6	6	5	0.71	0.71
			IIIr	22	9	4	3	0.82	0.68
			IVl	22	9	8	3	0.71	0.80
			IVr	27	5	2	4	0.84	0.76
			Total	147	69	37	51	0.71	0.61
DK1	3	32	Il	3	6	3	20	0.28	0.19
			Ir	7	6	2	17	0.40	0.28
			III	7	3	2	20	0.31	0.28
			IIr	7	3	1	21	0.31	0.25
			IIIl	8	4	3	17	0.38	0.34
			IIIr	11	4	1	16	0.47	0.38
			IVl	10	4	1	17	0.44	0.34
			IVr	6	6	3	17	0.38	0.28
			Total	59	36	16	145	0.37	0.29
DK2-4	6	285	Il	15	44	19	207	0.21	0.12
			Ir	14	50	17	204	0.22	0.11
			III	23	41	22	199	0.22	0.16
			IIr	22	30	25	208	0.18	0.16
			IIIl	34	32	22	197	0.23	0.20
			IIIr	26	40	23	196	0.23	0.17
			IVl	28	39	28	190	0.24	0.20
			IVr	28	42	22	193	0.25	0.18
			Total	190	318	178	1594	0.22	0.16

TABLE 3. Claw-types, individual legs and geographical distribution (continued)

Stations	Number of samples	Number of specimens	Legs	T	B'	B"	M	Average presence cl'	Average presence cl"
D1-6	8	78	Il	1	9	4	64	0.13	0.06
			Ir	2	4	4	68	0.08	0.08
			III	1	6	2	69	0.07	0.04
			IIr	0	3	3	71	0.05	0.04
			IIIl	3	1	7	67	0.05	0.13
			IIIr	0	8	2	68	0.10	0.03
			IVl	1	3	6	68	0.05	0.09
			IVr	1	7	1	69	0.10	0.03
			Total	9	42	29	544	0.08	0.06
M1-9	19	74	Il	1	5	1	67	0.08	0.03
			Ir	1	4	2	67	0.07	0.04
			III	2	1	2	70	0.04	0.04
			IIr	0	4	0	70	0.05	0.00
			IIIl	0	6	4	64	0.06	0.05
			IIIr	1	7	2	64	0.11	0.04
			IVl	0	7	1	66	0.09	0.01
			IVr	2	4	0	68	0.08	0.03
			Total	7	38	11	536	0.08	0.03
M10-16	22	169	Il	0	7	7	155	0.04	0.04
			Ir	0	4	3	162	0.02	0.02
			III	0	4	5	160	0.02	0.03
			IIr	0	4	2	163	0.02	0.01
			IIIl	3	7	2	157	0.06	0.03
			IIIr	0	8	5	156	0.05	0.03
			IVl	0	7	5	157	0.04	0.03
			IVr	1	4	0	162	0.03	0.02
			Total	4	45	31	1272	0.04	0.03

TABLE 3. Claw-types, individual legs and geographical distribution (continued)

Stations	Number of samples	Number of specimens	T	B'	B"	M	Average presence cl'	Average presence cl"	Legs
F1	1	31	0	0	0	31	0.00	0.00	I1
			0	2	1	28	0.06	0.03	Ir
			0	0	0	31	0.00	0.00	I11
			0	0	0	31	0.00	0.00	IIr
			0	0	0	31	0.03	0.00	I111
			0	1	0	30	0.00	0.00	IIIr
			0	0	0	31	0.00	0.00	IV1
			0	0	1	30	0.00	0.03	IVr
			0	3	2	243	0.01	0.01	Total
F2-3	11	77	39	24	4	10	0.82	0.56	I1
			39	25	5	8	0.82	0.57	Ir
			57	4	10	6	0.80	0.87	I11
			57	10	4	6	0.87	0.80	IIr
			54	12	7	4	0.84	0.80	I111
			55	12	5	5	0.87	0.78	IIIr
			58	10	8	1	0.88	0.86	IV1
			69	4	1	3	0.95	0.90	IVr
			428	101	44	43	0.86	0.77	Total
GB1	1	6	0	1	0	5	0.17	0.00	I1
			0	0	2	4	0.00	0.33	Ir
			1	2	0	3	0.50	0.17	I11
			0	1	0	5	0.17	0.00	IIr
			1	2	2	3	0.50	0.17	I111
			0	2	2	2	0.33	0.33	IIIr
			2	0	2	2	0.33	0.67	IV1
			1	1	2	2	0.33	0.50	IVr
			5	9	8	26	0.29	0.27	Total

TABLE 3. Claw-types, individual legs and geographical distribution (continued)

Stations	Number of samples	Number of specimens	T	B'	B"	M	Average presence cl'	Average presence cl"	Legs
GB2-7	11	34	0	1	1	32	0.03	0.03	I1
			0	2	2	30	0.06	0.06	Ir
			1	0	0	33	0.03	0.03	I11
			0	0	2	32	0.00	0.06	IIr
			0	2	2	30	0.06	0.06	I111
			1	1	0	32	0.06	0.03	IIIr
			0	0	1	33	0.00	0.03	IV1
			1	0	1	32	0.03	0.06	IVr
			3	6	9	254	0.03	0.04	Total
GB8	1	4	2	2	0	0	1.00	0.50	I1
			3	0	0	1	0.75	0.75	Ir
			2	0	1	1	0.50	0.75	I11
			2	1	0	1	0.75	0.50	IIr
			3	0	1	0	0.75	1.00	I111
			2	2	0	0	1.00	0.50	IIIr
			2	1	1	0	0.75	0.75	IV1
			3	0	1	0	0.75	1.00	IVr
			19	6	4	3	0.80	0.72	Total
GB9-10	2	10	0	0	0	10	0.00	0.00	I1
			0	1	0	9	0.10	0.00	Ir
			0	0	0	10	0.00	0.00	I11
			0	0	0	10	0.00	0.00	IIr
			0	1	0	9	0.10	0.00	I111
			0	1	0	9	0.10	0.00	IIIr
			0	1	1	8	0.10	0.10	IV1
			0	2	0	8	0.20	0.00	IVr
			0	6	1	73	0.08	0.01	Total

TABLE 4. Total numbers of the four claw-types and of the two lateral claws for each of the eight legs and for each of the four pairs

	T	B'	B"	M	ol'	ol"
Il	70	114	40	614	184	110
Ir	77	113	41	607	190	118
IIl	112	66	50	610	178	162
IIr	105	66	43	624	171	148
IIIl	127	73	54	584	200	181
IIIr	117	94	46	581	211	163
IVl	123	77	62	576	200	183
IVr	139	75	36	588	214	175
Total	870	678	372	4784	1548	1242
I	147	227	81	1221	374	228
II	217	132	93	1234	349	310
III	244	167	100	1165	411	344
IV	262	152	98	1164	414	360

Total number of specimens 838
Total number of legs 6704

TABLE 5. Homonychia

Stations	Number of specimens	Homonychia and ratio of occurrence T	M
N1	38	5 (0.13)	0
DK1	32	1 (0.03)	11 (0.34)
DK2-4	285	0	83 (0.29)
D1-6	78	0	51 (0.65)
NL1-9	74	0	50 (0.65)
NL10-16	169	0	126 (0.75)
F1	31	0	27 (0.87)
F2-3	77	15 (0.19)	0
GB1	6	0	0
GB2-7	34	0	24 (0.71)
GB8	4	1 (0.25)	0
GB9-10	10	0	7 (0.70)