THE EVOLUTION OF THE FAMILY AMERONOTHRIDAE (ACARI : ORIBATEI)

II. ECOLOGICAL ASPECTS

BY

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Introduction

A unification of the genera *Alaskozetes, Podacarus, Halozetes, Antarcticola, Pseudantarcticola* and *Ameronothrus* to one family has been conceived (Weigmann and Schulte 1977). Together with the morphological aspects of the genera, the ecological aspects influence the discussion of the evolution of the Ameronothridae. Ecological arguments are supported by the terrestrial distribution of *Alaskozetes, Podacarus, Antarcticola* and *Pseudantarcticola* (Wallwork, 1973, Balogh, 1970), by the limnetic distribution of *Aquanothrus* in South Africa (Engelbrecht, 1975) and by the bipolar distribution of *Halozetes* and *Ameronothrus* (Schuster, 1966) in the marine intertidal zones. Based on an ecological and morphological monograph of *Ameronothrus* species (Schubart, 1975, Schulte, 1970, Schulte et alii., 1975) a comparision can be made with the species of the southern hemisphere. Terrestrial, transitional and marine species can also be compared. The correlation between monotypical genera and terrestrial biotops (vice-versa polytypical genera and marine biotops) should be tested.

Terrestrial species

Each genus of the Ameronothridae family is represented in terrestrial biotops (Tab. 1). Species of *Aquanothrus, Pseudantarcticola* and *Podacarus* live exclusively terrestrial. With the exception of *Antarcticola* (*A. meyeri, A. georgiae*) the genera are monotypical. *Alaskozetes, Ameronothrus* and *Halozetes* have terrestrial species, species that approach the coast (transition species) and species that live only on the coast (intertidal species). The terrestrial species are distributed predominant in the polar regions. Only *Pseudantarcticola tropica* and *Aquanothrus montanus* live more towards the equator. *P. tropica* is found in New Guinea at an elevation of 3 900 metres and *A. montanus* is found in freshwaters of South Africa. The latter probably belongs to the small number of oribatids that live totally immersed under water. The polar and subpolar terrestrial species live in the montains as well as on the tundra. *Alaskozetes coriaceus* was collected in the Brooks Range (Northern Alaska), *Ameronothrus lapponicus* was found in the Sarek Range (Northern Sweden) and in the St. Elias Mountains (Canada, Yukon). It can be recognized that *Ameronothrus lapponicus* in the northern hemisphere and *Alaskozetes antarcticus*, *Podacarus auberti* and *Halozetes belgicae* in the southern hemisphere reveal a circumpolar distribution. Only *Alaskozetes* is found in the southern as well as in the northern hemisphere (SCHUSTER, 1966). Contrary to the ameronothrid species of the northern hemisphere, some terrestrial species of the antipodal areas are restricted to local islands (e. g. *Halozetes fulvus*).

ameronothrid species	terrestrial				marine		ecological type	zoogeographic type
	inland	alpine	limnetic	seaward	supratidal	intertidal		
Ameronothrus schusteri	-	-	-	-	-	+		mediterranean
Ameronothrus schubarti	-	-	-	-	-	+	intertidal	californian
Ameronothrus bilineatus	-	-	-	-	-	+	species	boreal-antiboreal
Ameronothrus schneideri	-	-	-	-	(+)	+		boreal-mediterranean
Ameronothrus marinus	-	-	-	-	(+)	+		boreal
Ameronothrus nigrofemoratus	-	-	+	+	+	+		arctic-boreal
Ameronothrus lineatus	-	-	+	+	+	+	transition	arctic-boreal
Ameronothrus maculatus	-	-	+	+	+	-	species	subarctic-mediterranean
Ameronothrus lapponicus	+	+	-	(?)	-	-		subarctic
Alaskozetes coriaceus	+	+	-	-	-	-		subarctic/arctic
Aquanothrus montanus	-	(+)	+	-	-	-		antiboreal
Pseudantarcticola tropica	-	+	-	-	-	-		tropic
Antarcticola meyeri	+	-	-	-	-	-		antarctic
Antarcticola georgiae	+	-	-	-	-	-		antarctic maritim
Alaskozetes antarcticus antarcticus	+	-	-	-	-	-		antarctic/antarctic maritim
Podacarus auberti occidentalis	+	-	-	-	-	-	terrestrial	subantarctic
Podacarus auberti auberti	+	-	-	+	-	-	species	subantarctic
Podacarus auberti grandjeani	+	-	-	+	-	-		subantarctic
Halozetes belgicae belgicae	+	-	-	+	-	-		antarctic maritim/subantarctic
Halozetes macquariensis	+	-	-	+	-	-		subantarctic
Halozetes fulvus	+	-	-	+	-	-		subantarctic
Alaskozetes antarcticus intermedius	+	-	-	+	+	-		antarctic maritim/subantarctic
Alaskozetes antarcticus grandjeani	+	-	-	+	+	-		subantarctic
Halozetes belgicae brevipilis	+	-	-	+	(+)	-	transition	subantarctic
Halozetes crozetensis	+	-	-	+	+	-	species	subantarctic
Halozetes intermedius	-	-	-	+	+	+		subantarctic
Halozetes necrophagus	-	-	-	(?)	+	-		antarctic maritim
Halozetes marionensis	-	-	-	(+)	+	-		subantarctic
Halozetes littoralis	-	-	-	-	+	+	intertidal	subantarctic
Halozetes marinus marinus	-	-	-	-	+	+	species	subantarctic
Halozetes marinus devilliersi	-	-	-	-	-	+		subantarctic

TAB. I : Terrestrial, transition and coastal ameronothrid species in the northern and southern hemisphere (after DALENIUS, 1963, ENGELBRECHT, 1974, 1975, HAMMER, 1955, SCHULTE et alii., 1975, WEIGMANN, 1975, WEIGMANN und SCHULTE, 1975, WALLWORK, 1973, BALOGH, 1970).

Terrestrial ameronothrids were chiefly taken with a berlese funnel from soil samples, meadows and moss. In addition many samples were taken by hand : *Alaskozetes antarcticus*, *Ameronothrus lapponicus* and *Aquanothrus montanus* were found on rocks and *A. lapponicus* on trees. With the exception of the arboreal *A. lapponicus* and the limnetic *A. montanus*, the other terrestrial ameronothrids are indifferent to the selection of substratum.

TRANSITION SPECIES

Between terrestrial and intertidal ameronothrids there are several species that can be found in either environment. Like the intertidal species they belong to the *Ameronothrus* and *Halozetes* genera. It is doubtfull whether the subspecies *Alaskozetes antarcticus intermedius*, *Alaskozetes antarcticus grandjeani* and *Halozetes belgicae brevipilis* are transition species, because most collection sites were located inland. Transition species can be graduated between the interior and the coast : the first group is distributed equally in both areas (e. g. *Ameronothrus maculatus*, *Halozetes crozetensis*) and the second group prefers the coast (*Ameronothrus lineatus*, *Ameronothrus nigrofemoratus*, *Halozetes intermedius*). Both *Ameronothrus* species are restricted regionally to the coast. Here is an example of an intraspecific transition between land and sea in conjunction with latitudes (SCHULTE, 1975). The transition species live like the terrestrial species in polar climates (*A. lineatus* and *A. nigrofemoratus* are circumpolar as well), but within much larger areas extending to the temperate zones. In the southern hemisphere these species extend to New Zealand (e. g. *Halozetes crozetensis*) and in the northern hemisphere they reach the tropics (*Ameronothrus maculatus*, see SCHULTE, 1975.

At their southern distribution limits *Ameronothrus lineatus* and *A. nigrofemoratus* show an ecological specialization inhabiting niches on rocky shores (*A. lineatus*) and in salt marshes (*A. nigrofemoratus*) within tidal zones. The presence of smaller sensilli in eulittoral inhabitants (e. g. *A. lineatus*, SCHULTE unpublished) and monodactyl legs in salt marsh inhabitants (*A. nigrofemoratus*, SCHUBART, 1975) can be correlated with this ecological specialization.

INTERTIDAL SPECIES

Compared to the small number of transition species that have attained coastal niches, all intertidal species have specific demands on their environment in respect to littoral zones, salinity and substratum. These species belonging to *Halozetes* and *Ameronothrus* live in the northern and southern hemisphere. The northern *Ameronothrus* species are restricted to the temperate and subtropical coastlines. The southernmost species *A. schusteri*, *A. schubarti* and *A. schneideri* attein the highest degree of specialization. A salinity of about 30 ‰, hard or soft substratum and littoral zones with longer periods of submersion are indispensible to these species. The northermost species *A. marinus* and *A. bilineatus* are also restricted to intertidal niches (hard substratum and eulittoral zones), but can withstand brackish water (SCHULTE et alii., 1975).

Allotopic ameronothrids of one genus in the northern hemisphere are distributed sympatrically (terminological explanation of allopatric/sympatric and allotopic/syntopic, see SCHULTE, 1975) :

1. The species in the marine littoral are vertically graduated. Transition species inhabit higher intertidal zones (e. g. *A. lineatus*), than the coastal species (e. g. *A. marinus*). On the rocky North Sea coast the zonation of three species has been observed : in the supralittoral *A. maculatus*, in the littoral fringe *A. lineatus* and in the eulittoral *A. marinus* (SCHULTE, 1970).
2. The species in the marine littoral are horizontally confined to hard (*A. lineatus*, *A. marinus*, *A. maculatus*) and to soft substrates (*A. nigrofemoratus*, *A. schneideri*). Within the hard substratum inhabitants there is an established restriction between *A. marinus* on sediment-free rocky shores and *A. bilineatus* on sedimentrich rocky shores.

On the other hand syntopic ameronothrids of one genus in the northern hemisphere are distributed allopatrically (SCHULTE, 1975) :

1. Latitudinal vicariance is known between species inhabiting boreal salt marshes (*A. nigrofemoratus*) and those inhabiting the atlantic-lusitanian salt marshes (*A. schneideri*). Compa-

rable vicariance is known from rocky shores between the northern *A. lineatus* and the southern *A. bilineatus.*

2. Longitudinal vicariance between species inhabiting the californian rocky shore (*A. schubarti*) and those inhabiting the mediterranean rocky shore (*A. schusteri*).

Comparable ecological studies do not exist for the ameronothrids of the southern hemisphere. Nevertheless ecological conclusions can be drawn concerning collection data from the antarctic and the subantarctic. To this day *Halozetes marinus marinus, Halozetes marinus devilliersi* and *Halozetes marionensis* seem to be restricted only to rocky shores. Furthermore it can be concluded from the data of ENGELBRECHT (1974) that the subspecies *H. marinus devilliersi* inhabits a lower eulittoral zone in the northern Marion Island than *H. marinus marinus* found further to the south.

There are indications showing that allotopic species live sympatrically in the littoral zones of the southern hemisphere :

1. Vertical zonation is possible for the species *Halozetes intermedius, H. crozetensis, H. littoralis* and *H. marinus.*
2. Horizontal zonation is to be expected, because *H. marinus* requires a hard substratum.

There are other indications that syntopic species live allopatrically in the subantarctic islands :

1. Latitudinal vicariance is possible between *Halozetes marinus marinus* inhabiting the cooler intertidal zones of the subantarctic and *H. marinus minor* inhabiting the warmer intertidal zones of Cambell Island near New Zealand.
2. Longitudinal vicariance is possible respective to the subantarctic islands as a special distribution (see WALLWORK, 1973).

species	ecological specializations	morphological specializations	physiological specializations
transition species			
Ameronothrus maculatus	soft/hard substrates terrestrial-supratidal holeuryhalin	with sensillus tridactyl normal rutellum	lichenovorous circadian rhythm
Ameronothrus lineatus	(soft)/hard substrates terrestrial-intertidal holeuryhalin	long/small sensillus tridactyl normal rutellum	algae/fungivorous circadian and tidal rhythms
Ameronothrus nigrofemoratus	soft/(hard) substrates terrestrial-intertidal holeuryhalin	with sensillus monodactyl short rutellum	fungivorous circadian rhythm
coastal species			
Ameronothrus marinus	hard substrates (sedimentfree) intertidal euryhalin	without sensillus tridactyl long rutellum	algaevorous circadian and tidal rhythms
Ameronothrus schneideri	soft substrates intertidal euryhalin	rudim. sensillus tridactyl/monodactyl short rutellum	fungivorous circadian rhythm
Ameronothrus bilineatus	hard substrates (sedimentrich) intertidal euryhalin	without sensillus monodactyl short rutellum	algae/fungivorous tidal rhythm
Ameronothrus schubarti	hard substrates intertidal stenohalin	with sensillus tridactyl long rutellum	algaevorous circadian and tidal rhythms ?
Ameronothrus schusteri	hard substrates intertidal stenohalin	with sensillus tridactyl long rutellum	algaevorous circadian rhythm

TAB. 2 : Intertidal specializations in the genus Ameronothrus.

These ecological specializations (Tab. 2) of the intertidal ameronothrids combine morphological and physiological adaptations (SCHUBART, 1975, SCHULTE 1976 a). In conjunction with a salt marsh existence the legs become monodactyl and the rutella are shorter (SCHUBART, 1975). Species with short rutella which live in salt marshes are fungivorous and species with long rutella which live on rocky shores are algaevorous. In conjunction with an intertidal existence the sensilli are reduced or are not present. This phenomenon has already been described for the limnetic oribatids (TARMAN, 1961).

Tidal activity can be regarded as a specialization of intertidal *Ameronothrus* species (see SCHULTE, 1973, SCHULTE 1976 b). Similarly it is known, that the sensilli in the *Halozetes* genus are very small and lacking entirely in some juvenile stages.

DISCUSSION

Together with the morphological aspects (WEIGMANN and SCHULTE, 1977) the ecological aspects leed to a hypothesis for the evolution of the ameronothrids : We are of the opinion, that terrestrial oribatids were the ancestors of the ameronothrids. The terrestrial live style of *Ameronothrus lapponicus* and the *Podacarus* and *Alaskozetes* genera strengthen this hypothesis. *Ameronothrus lapponicus* has a larger number of plesiomorphic characteristics than the other species of the same genus. *Halozetes* has more apomorphic characteristics than Podacarus and Alaskozetes. The recent ecology of terrestrial ameronothrids replicates the possible ancestral ecology. The ancestors may have inhabited wet and cold soils with a preference for the surface and they may have fed upon microphytes. The ancestral species may have occupied a considerably larger portion of the world's land masses. A warming of the world's athmosphere scattered these mites to ccoler locations. Survival of the species was possible in alpine biotops (e. g. *Pseudantarcticola* in the tropical alpine region of New Guinea) or in polar regions (e. g. *Antarcticola meyeri*). The oribatid mite *Muconothrus nasalis* has thus survived under similar circumstances (TRAVÉ, 1973). From scattered terrestrial locations the ancestors invaded cool aquatic biotops. Mountainous waters (e. g. *Aquanothrus montanus* in South Africa) as well as arctic and antarctic coastlines (*Ameronothrus* and *Halozetes*) were conquered. This successful invasion of the polar coastlines can be attributed to the glaciation of the terrestrial biotops (vgl. WALLWORK, 1973). The chances of survival were increased near the warmer sea.

During glaciation terrestrial ameronothrids were afforded a few possibilities for survival : on nunataks (e. g. *Ameronothrus lapponicus* in the Sarek Range and the St. Elias Mountains) or on large unglaciated land masses (*Alaskozetes coriaceus* in the Brooks Range).

Meanwhile, the terrestrial and monotypical genera were restricted and therefore unable to leave the relict biotops, the coastal species spread themselves throughout various littoral zones, substrates, etc. This spreading was convergent in the arctic marine littoral by *Ameronothrus* and in the antarctic marine littoral by *Halozetes*. Special morphological and ecological characteristics evolved in several species. Furthermore coastal species couldt have spread along the coast to warmer climates. Stenotopic ameronothrids are found in the marine littoral zones near the subtropics (SCHULTE, 1975). In the subtropic zones it became impossible for the coastal immigrants to return to the terrestrial interior. Returning emigrants to the terrestrial interior are found today only in the polar and subpolar regions (e. g. several *Halozetes* species in the subantarctic, see WALLWORK, 1973). While migrating south *Ameronothrus* species probably crossed over the equator (*A. bilineatus* have been found in South Africa : WEIGMANN, 1975).

The spread of ameronothrids from the southern hemisphere to the equator has not been studied. The northernmost species of *Halozetes* are found today in New Zealand, on Marion Island and in southern Chile. (Mrs. E. Clasing took the South American samples from the island Chiloe in 1976. The material has not been examinated.)

ABSTRACT

The monotypical ameronothrid genera *Alaskozetes, Aquanothrus, Podacarus, Pseudantarcticola* and *Antarcticola* (2 species) are restricted to wet and cold, polar and alpine (mountainous) terrestrial habitats.

The polytypical ameronothrid genera *Halozetes* and *Ameronothrus* comprise transitional species living in terrestrial environments and in the marine littoral. Within several species of these genera ecological specializations have been established regarding adaptations to littoral substrates, submersion and salinity. A hypothesis of the evolution of the Ameronothridae was suggested. From scatterd relict terrestrial biotops, ameronothrids invaded aquatic habitats including mountainous freshwaters and polar coastlines. Terrestrial species were restricted and therefore unable to leave the relict habitats. The coastal species spread themselves throughout various littoral zones along continental shores.

Zusammenfassung

Die monotypischen Ameronothriden-Gattungen *Alaskozetes, Aquanothrus, Podacarus, Pseudantarcticola* und *Antarcticola* (2 Arten) sind auf kalte und nasse, polare und alpine (montane) terrestrische Lebensräume beschränkt. Die polytypischen Ameronothriden-Gattungen *Halozetes* und *Ameronothrus* enthalten Übergangsarten, die in terrestrischen Lebensräumen und im marinen Litoral leben, und zahlreiche Arten mit ökologischer Spezialisation hinsichtlich der Substrate, der Überflutung und des Salzgehaltes im marinen Litoral. Eine Hypothese zur Evolution der Familie Ameronothridae wird aufgestellt. Aus zersplitterten, terrestrischen Reliktbiotopen sind die Ameronothriden in aquatische Ledensräume vorgedrungen, und zwar sowohl in montane Süßgewässer als auch an polare Küsten. Während die terrestrischen Arten in ihren Reliktbiotopen gebunden waren, und sie nicht verlassen konnten, drangen die Kustenarten entlang der Kontinente in verschiedene Litoralzonen vor.

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