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Acidophilic Collembola: Living Fossils?

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ABSTRACT The existence of two groups of acidophilic (mostly present in soils at pH less than 5) and acid-intolerant Collembolan species has been demonstrated concurrently by several authors in the course of biocoenotic studies. The examination of morphological features points to a strong relationship between acidophily and hypothetical phyletic relationships between both groups. In the light of Earth history I postulate that acidophilic springtails are relicts from the time when adaptive radiation took place within Collembola, i.e. before the Carboniferous age. At this time soils were poor in nutrients, vegetation was of the acidifying type, and the atmosphere was richer than now in carbon dioxide. Thus Paleozoic environmental conditions were quite similar to those now prevailing in the most acid soils.

KEY WORDS Collembola / soil acidity / Living fossils

Introduction

It has been claimed time and again that ecology and systematics should be better linked in a synergistic approach to evolutionary processes, but surprisingly few examples have been given in soil invertebrates. Moreover, it seemed that ecological adaptations were long time considered as masking true phyletic relationships (Gisin, 1967a). Nevertheless, on the basis of ecophysiological and morphological studies Betsch and Vannier (1977), Betsch et al. (1980) and Vannier (1987) postulated that in terrestrial arthropods the passage from soil to aerial habitats was strongly linked to morphological and physiological adaptations to changing conditions prevailing in the porosphere, an obligate intermediary host between water and air which embraces soil and related habitats. Resistance to desiccation and tolerance to carbon dioxide were considered by these authors as physiological properties basic to the development of surface- and deep-living invertebrate communities, respectively.

Recently the importance of ecology for understanding the mechanisms involved in evolutionary processes has been fully recognized. Price (1988) argued that mutualisms between plants, microbes and animals were the source of terrestrial evolution. Soil foodwebs are considered as the natural sites where such mutualisms took place during the Paleozoic. Accordingly, the role of soils in the evolution of early terrestrial arthropods has been stressed by Dunger (1987).

In the present paper I intend to present some arguments based on my own studies on collembolan communities (Ponge, 1980; Ponge & Prat, 1982; Ponge 1983; Arpin et al., 1984; Poursin & Ponge, 1984; Ponge, 1993), which seem to indicate that the present distribution of Collembolan species relative to soil acidity reflects their evolutionary status within several lineages.

Acidophilic and acid-intolerant species

Gisin (1943) described biocoenoses of Collembola living in the Swiss Jura and recognized soil acidity as one of the most important factors explaining the distribution of species, along with light and humidity. Surprisingly soil acidity was neglected by authors such as Haybach (1959), Cassagnau (1961), Szeptycki (1967) and Nosek (1969), who studied Collembolan communities in varying soil conditions. For these authors the nature of the rocky substrate (siliceous, dolomitic or calcareous) and the composition of the plant cover seemed more important than the physico-chemical and biochemical conditions prevailing in the immediate environment of soil animals. However the presence of limestone in the subsoil does not preclude the establishment of strongly acidic conditions in the topsoil, provided acidifying vegetation (coniferous forest, ericaceous heath) is present or that the parent rock does not weather easily (Gobat et al., 1998). I came to the same opinion as Gisin concerning the importance of soil acidity on the basis of a wide sampling program embracing all kinds of vegetation and soil types present in a lowland temperate forest of western Europe (Ponge 1980). Multivariate analysis allowed me to determine that there are two groups of soil-dwelling species according to their attraction to or avoidance of acidic conditions. Further analyses on the same data indicated a threshold at pH 5, whatever the humus form and the vegetation (Ponge, 1983, 1993). Above this level the species composition was quite unaffected by pH, calcareous soils not differing basically from moderately acidic soils. Several authors working in different European countries (Hågvar & Abrahamsen, 1984; Pozo, 1986; Gerdsmeier & Greven, 1992) later had similar results. Although confirmed by experimental acidification or liming (Hågvar & Abrahamsen, 1980; Abrahamsen et al., 1980; Bååth et al., 1980; Hågvar & Kjøndal, 1981; Huhta et al., 1983; Hågvar, 1984; Heungens & Van Daele, 1984; Vilkamaa & Huhta, 1986; Hågvar, 1987; Geissen et al., 1997) and by the observation of acidification gradients (Kopeszki, 1992a, 1992b, 1993, 1997), the mechanisms causing this phenomenon remain unstudied to the present. Soil acidification is a complex matter (Ulrich, 1983; Bonneau et al., 1987) which embraces accumulation of humified organic matter (Bernier & Ponge, 1994; Bernier, 1996; Ponge et al., 1997), presence of heavy metals and aluminum in the soil solution (Nair & Prenzel, 1978; Reddy et al., 1995; Geissen et al., 1997), presence of a high amount of small undissociated phenolics (Appel, 1993; Stevenson, 1994; Northup et al., 1998), increase in carbon dioxide and other toxic gases in the soil atmosphere (Verdier, 1975; Sexstone & Mains, 1990). Acidophily in plants may be due to tolerance to aluminum and phenolic compounds rather than to pH itself (Clarkson, 1969; Kuiters & Sarink, 1987; Wheeler & Dodd, 1995). We know the sensitivity of soil animals, in particular Collembola, to carbon dioxide (Ruppel, 1953; Klingler, 1959; Moursi, 1962; Zinkler, 1966; Vannier, 1983), heavy metals (Bengtsson et al., 1983; Hågvar & Abrahamsen, 1990; Tranvik et al., 1993;

Hopkin, 1994, 1995; Filser & Hölscher, 1997), tannins (Poinsot-Balaguer et al., 1993) and terpenes (Michelozzi et al., 1997), but no one of these factors can explain by itself why so clear a pH threshold along with water availability (Vannier, 1983) seems to govern the species composition of subterranean Collembolan communities.

Hågvar (1990) used experimental studies to show the importance of competition as a key factor explaining the reaction of mites and springtails to soil acidification. Recently Salmon & Ponge (1999) demonstrated a strong attraction of the acid-intolerant springtail *Heteromurus nitidus* (Templeton) towards earthworms and its particular sensitivity to predators of Collembola prevailing in moder humus forms. In addition they observed that in the laboratory this species was able to live in soils at pH less than 5 provided enough food was present and predatory pressure was kept at a minimum. Earthworm and earthworm-conditioned soil attraction of Collembola and other arthropods has been demonstrated (Marinissen & Bok, 1988; Hamilton & Sillman, 1989; Wickenbrock & Heisler, 1997; Loranger et al., 1998) and this attraction seems species-specific. Thus factors other than pH might explain the sensitivity of some Collembola to soil acidity, despite repeated observations on the avoidance of high as well as low pH by Collembola and other arthropods when these animals are placed in pH gradients (Mertens, 1975; Jaeger & Eisenbeis, 1984; Van Straalen & Verhoef, 1997), and the well-known influence of pH on several biological parameters of Collembola (Hutson, 1978; Hopkin, 1997). The observation that soil pH seems to influence the distribution of species even in mull humus (Ponge, 1983, 1993) still needs further explanation.

Acidophily and phylogeny

Table 1 shows a list of acidophilic, acid-intolerant and pH-indifferent Collembolan species living in temperate soils of western Europe derived from my published results (Ponge, 1980; Ponge & Prat, 1982; Ponge, 1983; Arpin et al., 1984; Poursin & Ponge, 1984; Ponge, 1993), and still unpublished personal observations. At the first sight, it appears that the distinction between acidophilic and acid-intolerant taxa is at the species or genus level.

Let us try to compare closely related taxa falling into one or the other of both groups, in the light of what we know about Collembolan phylogeny. Within the genus *Pseudosinella*, the acidophilic *P. mauli* Stomp is replaced in less acid soils by *P. alba* (Packard) and *P. decipiens* Denis. The first species has 5+5 eyes, compared to 2+2 for *P. alba* and 0+0 for *P. decipiens*. According to the rules for building the phylogenic trees of the genus *Pseudosinella* erected by Gisin (1967b) and later refined by Gama (1984), the decrease in the number of eyes from the basic number 8+8 (corresponding to the ancestor genus *Lepidocyrtus*) reflects evolution in the *Lepidocyrtus pallidus* Reuter lineage. More generally any regression in the number of eyes can be considered as an evolved character (Thibaud, 1976). Thus in the sense of Gisin (1967a, 1967b), Thibaud (1976) and Gama (1984) *P. mauli* (acidophilic) seems more primitive than both *P. decipiens* and *P. alba* (acid intolerant).

A combination of chaetotaxy features induced Gama (1988) to place *Xenylla* *tullbergi* Börner (acidophilic) at a lower evolutionary distance from the common ancestor of the genus than *X. grisea* Axelson (acid intolerant).

In a recent work, D'Haese & Weiner (1998) applied cladistic methods to the genus *Willemia*, and they found that *W. anophthalma* Börner and *W. intermedia* Mills (both acidophilic) were more primitive than *W. buddenbrocki* Hüther (acid-intolerant).

Only these three cases, provide evidence from phylogeny for genera present in Table 1. Nevertheless, if we apply to other genera the same rules as for *Pseudosinella*, *Xenylla* and *Willemia*, we can observe some interesting properties, in tune with the above mentioned patterns. In the genus *Mesaphorura* (formerly included in *Tullbergia*) the chaetotaxy has been used to classify species (Zimdars & Dunger, 1994), following the pioneer work of Rusek (1967, 1971). While still waiting for cladistic studies within this genus, it can be postulated that primitive species are those which conform the best to the basic chaetotaxy scheme, i.e. with full series of setae in the three rows present on each thoracic and abdominal tergite. Following this rule, *Mesaphorura yosiii* (Rusek) and other members of the *yosiii* group such as *M. tenuisensillata* Rusek (Zimdars & Dunger, 1994), with a1, a2 and a3 in the anterior row of the fifth abdominal tergite, and l'2 present along the anal lobes, can be considered as more primitive than species of the *sylvatica* group such as *M. hylophila* Rusek and *M. jarmilae* Rusek, which lack a2 on Abd. V and than species of the *krausbaueri* group such as *M. krausbaueri* (Börner) and *M. italica* (Rusek), which lack l'2 on the anal lobes. *M. macrochaeta*, which belongs

Table 1. A list of acidophilic, acid-intolerant and pH-indifferent Collembolan species living in temperate soils of western Europe.

Acidophilic	Acido-intolerant	Indifferent
Pseudosinella mauli	*Pseudosinella decipiens*	*Heteromurus major*
Pogonognathellus flavescens	*Pseudosinella alba*	*Tomocerus minor*
Proisotoma minima	*Heteromurus nitidus*	*Orchesella cincta*
Friesea mirabilis	*Tomocerus botanicus*	*Orchesella villosa*
Micranurida pygmaea	*Folsomides parvulus*	*Parisotoma notabilis*
Willemia anophthalma	*Folsomia penicula*	*Isotomiella minor*
Willemia intermedia	*Monobella grassei*	*Folsomia manolachei*
Xenylla tullbergi	*Anurida sensillata*	*Friesea truncata*
Micraphorura absoloni	*Xenylla grisea*	*Mesaphorura macrochaeta*
Protaphorura furcifera	*Willemia buddenbrocki*	*Pseudachorutes parvulus*
Protaphorura subuliginata	*Onychiurus pseudogranulosus*	*Dicyrtoma fusca*
Protaphorura lata	*Onychiurus jubilarius*	*Dicyrtomina minuta*
Protaphorura eichhorni	*Kalaphorura burmeisteri*	*Megalothorax minimus*
Protaphorura armata	*Metaphorura affinis*	
Mesaphorura yosiii	*Stenaphorura denisi*	
Mesaphorura tenuisensillata	*Wankeliella pongei*	
Sminthurinus signatus	*Mesaphorura italica*	
Arrhopalites sericus	*Mesaphorura jarmilae*	
Lipothrix lubbocki	*Mesaphorura hylophila*	
	Mesaphorura krausbaueri	
	Sminthurinus aureus	
	Arrhopalites caecus	
	Megalothorax incertus	

to the *yosii* group, is indifferent to soil acidity (Table 1), but it has been found more abundantly in acid soils and was even classified as acidophilic in Ponge (1980). Thus the same pattern can be found in the genus *Mesaphorura,* i.e. acidophilic species exhibit more primitive characters than acid-intolerant species.

Similar observations can be made in several other instances, if we consider the differentiation of setae into sensillae or spines as an evolved character, as well as plurichaetosis or regression of several organs, *Arrhopalites caecus* (Tullberg), whose females have spines alternating with differentiated flame-like macrochaetae on the lesser abdomen and spine-like setae on the forehead, is acid-intolerant and can be considered more evolved than the acidophilic *A. sericus* Gisin, whose females have normal fine setae on their lesser abdomen and on the forehead. The acid-intolerant *Heteromurus nitidus* exhibits a regression in the number of eyes with 2+2 compared with 8+8 in *H. major* (Moniez), which is indifferent to acidity. The toothed mucro of *M. incertus* (Börner), which is acid-intolerant, can accordingly be considered more evolved than the smooth mucro of *M. minimus* (Willem), which is indifferent to pH.

The case of the Onychiuridae differs from the above mentioned patterns, since tolerance or intolerance to soil acidity seems to be shared by members of the same genus. If we consider the complexity of the structure of the post-antennal organ and the regression or even the disappearance of the furcula as signs of evolution within this family, then the acidophilic genera *Micraphorura,* represented here by *M. absoloni* (Börner), and *Protaphorura,* represented here by 5 species, are more primitive than members of the acid-intolerant genus *Onychiurus,* represented by *O. pseudogranulosus* Gisin and *O. jubilarius* Gisin.

Acidophiliy and history of the earth

Despite the small number of known fossil Collembola, it is now admitted that this group appeared as soon as the Silurian age and was strongly diversified at the Devonian age (Kevan et al., 1975; Rolfe, 1985; Dunger, 1987). What conditions did primitive springtails find in their immediate environment at this period, i.e. what conditions prevailed at the time most evolutionary processes took place within this group? Before the Mesozoic era, and even before the Cretaceous age, we can postulate that most terrestrial vegetation had an acidifying character, with a strong production of organic acids and terpenes, and recalcitrant litter, if we judge from actual lichens, bryophytes, pteridophytes and gymnosperms. Probable consequences at the ecosystem level were a scarcity of nutrients available to decomposer and saprophagous species and strong acidity of the environment (Kuiters, 1990; White, 1994; Northup et al., 1995, 1998). It was not before the Cretaceous age that nutrient-rich (angiosperm) vegetation and litter was present in terrestrial ecosystems (Elmi & Babin, 1996; Lethiers, 1998). This evolution of the plant kingdom was probably associated with an increase in the content of soils in major elements such as calcium and nitrogen. It can be postulated that the calcium content of terrestrial habitats increased in the course of Paleozoic then Mesozoic times, following the emergence of marine sediments during successive orogeneses. Nitrogen progressively accumulated in terrestrial habitats through the slow fixation of atmospheric nitrogen by bacteria and cyanobacteria. The immobilization of calcium in algal and animal exoskeletons and in wood was the main mechanism by which the atmosphere (and consequently precipitation) was progressively de-acidified in the course of Paleozoic times. All these arguments (nutrient-poor soils, acid rain, acidifying vegetation) point to the existence of acid environmental conditions prevailing at the time most Collembolan lineages diverged.

The above mentioned views are in conflict with the idea of calcareous soils as an obligate intermediary habitat in the passage from aquatic to aerial habitats during the evolution of invertebrates (Vannier, 1983, 1987). This author considered that calcareous soils shared several properties with water, in particular they regulate the partial pressure of carbon dioxide to a level low enough to be compatible with the life of carbon dioxide sensitive organisms. On the contrary, acid soils, as well as the aboveground atmosphere, were unable to control the partial pressure of carbon dioxide in the presence of a source such as respiration (Verdier, 1975). Although this view was satisfactory from the point of view of ecophysiology, it does not agree with what we know and what we can postulate of the environmental conditions which prevailed on Earth during Paleozoic times.

Conclusion

If my hypothesis is correct, then extant acidophilic species can be considered as living fossils still surviving from the Paleozoic era, thus having kept genetic structure giving them resistance against acidobiosis. No proof can be given of that in the absence of studies in both ecophysiology and molecular biology. Studies on the tolerance of some Collembolan populations to heavy metals gave encouraging results (Joosse & Buker, 1979; Frati et al., 1992; Tranvik et al., 1993; Posthuma et al., 1993), but they pointed only on differences between populations rather than on differences between species or genera, which would be more useful to understand pH-related distributions of species.

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