

## Sociology of communities invaded by *Orthodontium lineare* (*Bryophyta*) in Europe (excl. the British Isles)

Fytocenologické společenstev s *Orthodontium lineare* (*Bryophyta*) v Evropě (s výjimkou Britských ostrovů)

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Available sociological data about an adventive moss in Europe, *Orthodontium lineare*, are summarized. The communities from which *O. lineare* was described are rather heterogeneous and can be divided into four groups. No other species was present in all source data sets; most common taxa were *Cladonia* spp., *Pohlia nutans* and *Tetraphis pellucida*. Both natural and man influenced ecosystems are invaded. Differences in climate, succession status and substrate are suggested as possible reasons for this differentiation. Use of such data for the study of the *O. lineare* invasion is discussed.

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The spectacular invasion of an adventive moss, *Orthodontium lineare* SCHWAEGR. in Europe during this century is one of the few recent invasions in bryophytes and it is rather well documented (see e.g. OCHYRA 1982). The species has spread especially in oceanic and suboceanic parts of Europe and its frequency and quantity decreases in more continental Europe. The species invades mainly coniferous forests, ranging from planted spruce cultures to natural or seminatural forests.

The invasion of any organism raises obvious questions about the mechanisms which enable it to encroach on communities and possibly to replace some of their component species. However, up to now most of the published data on *O. lineare* spread have concentrated on its distribution, substrate ecology and sociology (see references in the Table 1). This allows to establish the range of biotopes invaded by *O. lineare* and identify its possible competitors among bryophytes, but it does not reveal anything about the process and mechanism(s) of invasion. The goal of this study is to overview the published sociological data from continental Europe and attempt to answer the question whether it is possible to extract from them some information for more causal research about the invasion.

Synthesis of the available relevant material (see Table 1) showed considerable heterogeneity of communities encroached by *O. lineare*. There is no species present in all 22 data sets (i.e. co-occurring with *O. lineare* through its whole European distribution area); the most common accompanying taxa are *Cladonia* spp. (19 sets), *Pohlia nutans* (16), *Tetraphis pellucida* (15), *Dicranum*

Table 1. — Communities with *Orthodontium lineare* in Europe

| Relevé set                        | 1       | 2       | 3       | 4       | 5       | 6      | 7       | 8      | 9       |
|-----------------------------------|---------|---------|---------|---------|---------|--------|---------|--------|---------|
| no. of relevé                     | 7       | 2       | 1       | 8       | 3       | 31     | 15      | 24     | 2       |
| no. species/relevé                | 4.3     | 5.0     | 5.0     | 3.8     | 6.0     | 5.0    | 3.2     | 3.5    | 6.0     |
| Substrates (%):                   |         |         |         |         |         |        |         |        |         |
| rotten wood                       | 100     |         |         |         |         | 21     | 67      | 10     |         |
| humus                             |         | 100     | 100     | 100     | 100     | 31     | 33      | 24     | 100     |
| epiphytic                         |         |         |         |         |         | 48     |         | 66     |         |
| sand                              |         |         |         |         |         |        |         |        |         |
| <i>Orthodontium lineare</i>       | 100(14) | 100(34) | 100(33) | 100(45) | 100(45) | 80(r5) | 100(15) | 75(+5) | 100(55) |
| <i>Cladonia</i> spp.              | 71(14)  | 50(++)  | .       | 25(+2)  | 33(++)  | 38(r4) | 40(r+)  | 33(r4) | 100(22) |
| <i>Plagiothecium lactum</i> s.l.  | 14(++)  | .       | .       | 50(+2)  | 67(+2)  | 16(r1) | .       | 21(r2) | .       |
| <i>Tetraphis pellucida</i>        | 85(+5)  | 50(rr)  | .       | 25(11)  | 67(11)  | 64(24) | 13(rr)  | 92(r3) | 100(+1) |
| <i>Lophocolea heterophylla</i>    | 14(++)  | 50(rr)  | .       | 13(++)  | 33(++)  | .      | 6(rr)   | .      | .       |
| <i>Lepidozia reptans</i>          | 29(14)  | 100(24) | 100(22) | 63(+1)  | 100(11) | 90(r4) | 80(r4)  | 4(rr)  | 100(22) |
| <i>Calypogeia integristipula</i>  | .       | .       | 100(22) | .       | .       | 38(r2) | 12(r2)  | 8(++)  | .       |
| <i>Calypogeia muelleriana</i>     | .       | 50(11)  | .       | 37(++)  | 67(++)  | .      | .       | .      | .       |
| <i>Leucobryum</i> spp.            | .       | .       | .       | .       | 67(++)  | 32(r3) | 6(++)   | 21(r1) | .       |
| <i>Cephalozia bicuspidata</i>     | 43(+2)  | 50(33)  | .       | .       | .       | 3(22)  | .       | .      | .       |
| <i>Adontschisma denudatum</i>     | 43(25)  | .       | .       | .       | .       | 3(11)  | .       | .      | .       |
| <i>Jazzania trilobata</i>         | .       | .       | .       | .       | .       | 38(r4) | .       | 4(rr)  | .       |
| <i>Dicranodontium denudatum</i>   | .       | .       | .       | .       | .       | 3(++)  | .       | .      | .       |
| <i>Sphenobolus minutus</i>        | .       | .       | .       | .       | .       | 6(r+)  | .       | .      | .       |
| <i>Pohlia nutans</i>              | .       | 50(11)  | .       | 37(++)  | 33(++)  | 16(r+) | 20(r3)  | 12(r2) | .       |
| <i>Dicranum scoparium</i>         | .       | .       | .       | 25(++)  | .       | 3(++)  | .       | 4(rr)  | 50(rr)  |
| <i>Hypnum cupressiforme</i> s.l.  | .       | .       | .       | .       | 33(++)  | .      | .       | 1(rr)  | .       |
| <i>Dicranum montanum</i>          | .       | .       | .       | .       | .       | .      | .       | .      | .       |
| <i>Hypogymnia physodes</i>        | .       | .       | .       | .       | .       | .      | .       | .      | .       |
| <i>Lecanora gonizacoides</i>      | .       | .       | .       | .       | .       | .      | .       | .      | .       |
| <i>Dicranella heteromalla</i>     | 14(22)  | .       | .       | .       | .       | 16(r3) | 13(r2)  | 4(rr)  | 100(+2) |
| <i>Polytrichum formosum</i>       | .       | .       | .       | .       | .       | 3(rr)  | 6(++)   | .      | .       |
| <i>Campylopus flexuosus</i>       | .       | .       | .       | .       | .       | .      | .       | 17(r+) | .       |
| <i>Lecidea</i> spp.               | .       | .       | .       | .       | .       | 22(+1) | .       | 12(r1) | .       |
| <i>Cephaloziella divaricata</i>   | .       | .       | .       | .       | .       | .      | 6(11)   | .      | .       |
| <i>Paraleucobryum longifolium</i> | .       | .       | .       | .       | .       | 12(r+) | .       | .      | .       |
| <i>Ptilidium pulcherrimum</i>     | .       | .       | .       | .       | .       | .      | .       | .      | .       |
| <i>Pleurozium schreberi</i>       | .       | .       | .       | .       | .       | .      | .       | .      | .       |
| <i>Campylopus pyriformis</i>      | .       | .       | .       | .       | .       | .      | .       | .      | .       |
| <i>Herzogiella seligeri</i>       | .       | .       | .       | .       | .       | .      | .       | .      | .       |
| <i>Novellia curvifolia</i>        | .       | .       | .       | .       | .       | .      | .       | .      | .       |
| <i>Lophocolea bidentata</i>       | .       | .       | .       | .       | .       | .      | 13(r+)  | .      | .       |
| <i>Cephalozia lunulifolia</i>     | .       | .       | 100(22) | .       | .       | .      | .       | .      | .       |
| <i>Aulacomnium androgynum</i>     | .       | .       | .       | 25(++)  | .       | .      | .       | .      | .       |
| <i>Plagiothecium denticulatum</i> | .       | .       | .       | .       | .       | .      | .       | .      | .       |

Species occurring only in one relevé set (less than three times): 1: *Cephalozia connivens* 14(+); 3: *Calypogeia trichomanis* 100(2); 11: *Bryum flaccidum* 3(+), *Cephalozia hampeana* 5(22), *Ceratodon purpureus* 3(+), *Ptilidium ciliare* 3(1); 12: *Campylopus pyriformis* 100(+), *Dicranoweisia cirrata* 100(+); 13: *Calypogeia fissa* 6, *Gymnocolea inflata* 6, *Plagiothecium nemorale* 12; 14: *Dicranum fuscens* 2, *Polytrichum longisetum* 4, *Brachythecium plumosum* 2, *Mnium hornum* 2; 16: *Barbilophozia attenuata* 14(+).

The nomenclature follows ZITTOVÁ et al. (1982), except for *Bryum flaccidum*. In accordance with IRELAND (1969), *P. curvifolium* was included into *P. lactum*.

Source references (Any source material was divided into several separate entries only when such division was implied already in the original work): 1 — the Netherlands, BARKMAN (1962); 2 — Hautes Fagnes, Belgium, DEZUTTERE et SCHUMACKER (1980); 3 — Thüringen, DDR, MARSTALLER (1984); 4 — NW-Germany, von HÜBSCHMANN (1976); 5 — NW-Germany, von HÜBSCHMANN (1970), rel. 8, 9, 12; 6 — sandstones in Czechoslovakia, HERBEN (1987b), table 3.4, entries 42, 51, 53; 7 — Hautes Fagnes, Belgium, HERBEN ms. (1985); 8 — sandstones in Czechoslovakia, HERBEN (1987b), table 3.4, entries 21, 61; 9 — LAUER (1975); 10 — sandstones in Czechoslovakia, HERBEN (1987b), table 3.4, entries 12, 31; 11 — Thüringen, DDR, MARSTALLER (1987); 12 — Hautes Fagnes, Belgium, DEZUTTERE et SCHUMACKER (1980); 13 — surroundings of Muenster, NEU (1962); 14 — Skåne, Sweden, HEDENÄS et al. (1989), table 5, entry B; 15 — Rheinbacher Wald, BRD, BREUER (1979); 16 — Brdy Mts., Czechoslovakia, HERBEN ms. (1986);

|         |         |         |         |     |         |         |         |         |     |         |     |        |
|---------|---------|---------|---------|-----|---------|---------|---------|---------|-----|---------|-----|--------|
| 10      | 11      | 12      | 13      | 14  | 15      | 16      | 17      | 18      | 19  | 20      | 21  | 22     |
| 28      | 38      | 1       | 16      | 85  | 7       | 7       | 10      | 7       | 58  | 6       | 33  | 28     |
| 5.5     | 5.6     | 7.0     | 4.2     | 4.0 | 3.4     | 4.0     | 3.0     | 1.7     | 2.9 | 2.2     | 2.1 | 2.5    |
| 9       |         |         |         | 91  | 100     |         | 10      |         | 66  | 83      | 82  | 7      |
| 38      |         | 100     |         |     |         | 100     | 30      |         |     | 17      |     | 21     |
|         |         |         | 100     | 9   |         |         |         | 100     | 34  |         | 18  |        |
| 53      |         |         |         |     |         |         | 60      |         |     |         |     | 72     |
| 64(+5)  | 100(+5) | 100(33) | 100(25) | 26  | 100(15) | 100(24) | 100(15) | 100(35) | 28  | 100(35) | 94  | 82(r5) |
| 53(r1)  | 63(r3)  | .       | .       | 7   | 85(+5)  | 71(r1)  | 70(+3)  | 57(+1)  | 55  | 83(r2)  | 33  | 68(r4) |
| 32(r1)  | 42(+4)  | .       | .       | 68  | .       | 28(r1)  | 20(++)  | .       | 19  | .       | 21  | 7(rr)  |
| 57(r5)  | .       | .       | 25      | 24  | .       | 28(11)  | 10(33)  | .       | 5   | .       | .   | 7(11)  |
|         | 45(+4)  | .       | 31      | 84  | 85(+4)  | .       | .       | .       | 5   | .       | 24  | .      |
| 21(r3)  | 11(+2)  | .       | .       | 2   | .       | 28(r+)  | .       | .       | 12  | .       | .   | .      |
| 28(r2)  | .       | .       | .       | .   | .       | .       | .       | .       | .   | .       | .   | .      |
|         | 5(++)   | .       | .       | .   | .       | .       | .       | .       | .   | .       | .   | .      |
| 35(r1)  | 3(++)   | .       | .       | .   | .       | .       | 30(++)  | .       | .   | .       | .   | 11(r1) |
| .       | 3(++)   | .       | .       | .   | .       | .       | .       | .       | .   | .       | .   | .      |
| 25(r3)  | .       | .       | .       | .   | .       | .       | .       | .       | .   | .       | .   | .      |
| 7(+1)   | .       | .       | .       | .   | .       | .       | .       | .       | .   | .       | .   | .      |
| 14(r1)  | .       | .       | .       | .   | .       | .       | .       | .       | .   | .       | .   | .      |
| 100(r5) | 74(+4)  | 100(11) | 62      | 34  | .       | 71(r4)  | 30(r1)  | 14(++)  | 7   | 18(++)  | .   | .      |
| 50(r3)  | 42(+4)  | 100(++) | 25      | 32  | .       | 42(rr)  | 30(+1)  | 29(++)  | 36  | .       | .   | 4(++)  |
| 3(rr)   | 34(+2)  | 100(++) | .       | 38  | 57(+3)  | .       | 10(++)  | 42(++)  | 17  | .       | 6   | .      |
| .       | 11(13)  | .       | .       | 11  | 14(44)  | .       | .       | .       | .   | .       | .   | .      |
| .       | 3(++)   | .       | .       | 8   | .       | .       | .       | 29(++)  | 53  | .       | 3   | .      |
| .       | .       | .       | .       | 4   | .       | .       | .       | .       | 16  | .       | 9   | .      |
| 3(11)   | 16(+2)  | 100(22) | 60      | 9   | .       | .       | .       | .       | 3   | .       | .   | 4(rr)  |
| .       | 16(+1)  | .       | .       | 2   | .       | .       | .       | .       | .   | .       | .   | 1(++)  |
| 17(r4)  | .       | .       | 12      | .   | .       | .       | .       | .       | .   | .       | .   | 4(++)  |
| 25(r1)  | .       | .       | .       | 25  | .       | .       | .       | .       | 12  | .       | 15  | 64(r3) |
| 7(+1)   | .       | .       | .       | .   | .       | .       | .       | .       | .   | .       | .   | .      |
| .       | .       | .       | .       | .   | .       | .       | 14(++)  | .       | .   | .       | .   | .      |
| 3(++)   | .       | .       | .       | 1   | .       | .       | .       | .       | .   | .       | .   | 4(rr)  |
| .       | .       | .       | .       | 5   | .       | .       | .       | .       | 2   | .       | .   | .      |
| .       | .       | 100(++) | .       | .   | .       | .       | .       | .       | .   | .       | .   | .      |
| .       | .       | .       | .       | 5   | .       | .       | .       | .       | .   | .       | .   | .      |
| .       | .       | .       | .       | 6   | .       | .       | .       | .       | 5   | .       | .   | .      |
| .       | .       | .       | .       | .   | .       | .       | .       | .       | .   | .       | .   | .      |
| .       | 5(+1)   | .       | .       | .   | .       | .       | .       | .       | .   | 17(++)  | .   | .      |
| .       | .       | .       | .       | .   | .       | .       | .       | .       | .   | .       | .   | .      |
| .       | 13(+3)  | .       | .       | .   | .       | .       | .       | .       | .   | .       | .   | .      |

17 — Hel peninsula, Poland, HERBEN ms. (1986); 18 — NW-Germany, VON HÜBSCHMANN (1970), rel. 1, 3, 4, 5, 6, 10, 11; 19 — Skåne, Sweden, HEDENÄS et al. (1989), table 5, entry C; 20 — Mecklenburg, DDR, DOLL (1981); 21 — Skåne, Sweden, HEDENÄS et al. (1989), table 5, entry D; 22 — sandstones in Czechoslovakia, HERBEN (1987b), table 3.4, entry 41.

*scoparium* (14), *Lepidozia reptans* (14) and *Plagiothecium laetum* s.l. (13). Though there are apparently many intergradations between them, there seem to be four basic sociological groups of (micro-) communities from which *O. lineare* is reported:

(1) Species rich communities of species typical mainly of rotten wood (with *Tetraphis pellucida*, hepatics like *Lepidozia reptans*, *Calypogeia* spp., *Cephalozia bicuspidata* etc.). Such communities can be satisfactorily placed into the *Tetraphido-Aulacomnion* alliance (see VON HÜBSCHMANN 1986), though they are not necessarily confined to rotten wood (entries 1—9).

(2) Communities of larger mosses (*Dicranum scoparium*, *Hypnum cupressiforme*, *Pohlia nutans* and others) of the forest floor (entries 10—17).

In these communities the species of rotten wood are poorly represented; out of them only more generalist species like *Tetraphis pellucida*, *Lophocolea heterophylla* and *Plagiothecium laetum* occur more frequently. Such communities show relations to both alliances *Hylocomion* and *Tetraphido-Aulacomnion* (see VON HÜBSCHMANN 1986).

(3) Communities of mosses and lichens of acid bark of mainly coniferous trees (e.g. with *Hypogymnia physodes* and *Lecanora conizaeoides*). In this group most of the *Tetraphido-Aulacomnion* species are missing; only some ubiquitous mosses are present. The number of species per sample is very low (entries 18, 19).

(4) Extremely species poor communities, where *O. lineare* is accompanied almost only by *Cladonia* species, mainly *C. coniocraea*, *C. digitata* (entries 20–22).

Several authors have already observed that on a local scale, *O. lineare* may occur in several microcommunity types (BARKMAN 1962, VON HÜBSCHMANN 1970, DEZUTTERE et SCHUMACKER 1980, HEDENÄS et al. 1989). It is interesting that a similar heterogeneity appears also on a larger scale (also noted by BARKMAN 1962), since the process of summarizing often fragmentary regional data rather tends to conceal local sociological and ecological differences.

The views on the syntaxonomical treatment of communities with *O. lineare* vary. VON HÜBSCHMANN (1970) holds that *O. lineare* occurs in several community types and cannot thus serve as a characteristic species of any association. However, in his subsequent works (VON HÜBSCHMANN 1976, 1986) he rejected this view and considered *O. lineare* to be a characteristic species of the association *Orthodontietum linearis*. This opinion was shared e.g. by MARSTALLER (1987). HEDENÄS et al. (1989) take the opposite view because of the large variability of communities with *O. lineare* in Southern Sweden. In my opinion, the large variability of these communities on both local (VON HÜBSCHMANN 1970, HEDENÄS et al. 1989, HERBEN 1987b) and regional (BARKMAN 1962, Table 1) scales and unknown dynamic relationships within the communities do not permit to treat *O. lineare* as a characteristic species of an association.

Irrespective of the syntaxonomic treatment, the existence of such a heterogeneity is intriguing and needs further explanation. It may be due to many factors (substrate, climate, successional age, surrounding vegetation, etc.), which, in addition, may enter complicated interactions.

First, the observed community groups seem not to be evenly represented in different parts of Europe. Communities of the first group (rich in hepatics) tend to occur in oceanic part of Europe (and sandstone formations in central Europe); in suboceanic areas, *O. lineare* occurs mainly in communities rich in larger mosses and *Cladonia* species, probably because *Tetraphido-Aulacomnion* communities occur here at places too dark for *O. lineare* (see ZITTOVÁ-KURKOVÁ 1984). This might mean that in different parts of Europe *O. lineare* invades slightly different communities.

Differences in substrate do not play a larger role at a regional level. Only communities of the group 3 differ from the rest by their tendency to occur on bark at the basis of living conifers. Apart from this, there do not seem to be many other substrate differences when a synthesis is made on the European scale (see Table 1). However, there is a considerable substrate differentiation

at a local level (VON HÜBSCHMANN 1970, HERBEN 1987b, HEDENÄS et al. 1989).

Finally, there is some indication that this heterogeneity of communities may be partly due to their different successional status. *O. lineare* was shown to overgrow successfully mainly *Tetraphis pellucida*, *Plagiothecium laetum*, *Lepidozia reptans*, *Lophocolea heterophylla*, i.e. the species in the first group of communities; conversely, it is regularly overgrown by *Cladonia* spp. and also by *Pohlia nutans*, *Dicranum scoparium* and *Hypnum cupressiforme* s.l. (HEDENÄS et al. 1989, HERBEN 1987a, b). Hence, the difference between some communities of groups 1 and 2 (or 1 and 4) may be due to a difference in the time since invasion. Again, this phenomenon is likely to be important mainly on the local scale; since the competitive relations differ between areas and substrates (HERBEN 1987b), the regional differences remain a matter of speculation.

The microcommunities invaded by *O. lineare* cannot be unequivocally classified as natural or anthropogenous; most of them have rather wide amplitude and can occur in a large range of ecosystems from almost natural ones (in some sandstone areas in Czechoslovakia) to artificial cultures of alien conifers (Belgian Ardennes). At the European scale, the species then does not lend support to the idea that alien species tend not to invade natural communities (ORLIANS 1986 and references therein), though at the local scale this may be true in some areas (see also HEDENÄS et al. 1989).

It is important to note that the floristic composition of the invaded communities tells us very little about the change of vegetation due to the invasion. There are two reasons for this:

1. The succession status of all communities and the status of the invading species in them is unknown. Hence it cannot be said without further evidence (permanent plots, removal experiments) whether such communities (only without *O. lineare*) are directly invaded by *O. lineare*, or whether their structure and composition are the result of its invasion.

2. The inherent difficulty of studies, which report on sociology of one species, is that they tend to sample only vegetation with this species, often without proper attention to variability of similar communities without that species. The only study treating this shortcoming properly is that of HEDENÄS (1981). However, the definition how large the studied group of communities should be is itself a problem. Unless the dynamics of invasion is well understood, it is hard to select a "control" group, with which to compare the invaded communities. However, in such a case there is no longer a need for making such comparisons.

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#### SOUHRN

V článku jsou shrnuty dostupné údaje o fytoocenologii adventivního mechu *Orthodontium lineare* v Evropě. Společenstva, v nichž se tento druh vyskytuje, jsou poměrně heterogenní. Žádný doprovodný druh se nevyskytuje ve všech snímkových souborech, nejčastější doprovodné

druhy jsou *Cladonia* spp., *Pohlia nutans* a *Tetraphis pellucida*. Tato společenstva mohou být rozdělena do čtyř skupin:

- (1) společenstva s druhy tlejícího dřeva, rozšířená hlavně v oceánické části Evropy a v pískovcových oblastech ve střední Evropě,
- (2) společenstva s mechy přízemního patra acidofilních lesů,
- (3) druhově chudá společenstva s epifytickými druhy typickými pro kyselou borku,
- (4) velmi chudá společenstva s *Cladonia* spp.

Vzhledem k této heterogenitě nelze *O. lineare* považovat za charakteristický druh žádné asociace.

Příčiny této sociologické diferenciacce společenstev s *O. lineare* nejsou zcela jasné. Pravděpodobně zde kromě klimatických rozdílů hrají roli rozdíly v substrátu a pravděpodobně i sukcesní stádi společenstev. Vzhledem k neznámým dynamickým procesům ve společenstvech a nedostatečným údajům o společenstvech bez *O. lineare* nelze sociologických údajů použít k výpovědi o vlivu invazního druhu na změnu struktury společenstev.

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