Host preference of Cisidae (Coleoptera) on tree-inhabiting fungi in northern Norway.

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Fruiting bodies of tree-inhabiting "macrofungi" (Polyporaceae, Hymenochaetaceae, Corticiaceae and Tremellaceae) were collected in 1993–1996 in Troms county, northern Norway for investigation of host specificity of Cisidae species. Three methods of estimating the amount of fruiting bodies were compared: 1) dry weight, 2) calculation of volume and 3) measure of volume. They were all highly correlated (R = 0.79–0.96), but only method 1) and 3) were applicable irrespective of shape and therefore used in the statistical analyses concerning host preferences. 31 different species and more than 1 000 units of tree-living fungi were investigated and yielded about 15 500 individuals and 13 species of Cisidae. The cisid species showed preference for one single genus or species of fungi. *Cis boleti, Cis hispidus* and *Octotemnus glabriculus* preferred *Trametes* spp., *Cis comptus* preferred *Cerrena unicolor, Cis lineatocribratus* and *Cis jacquemarti* preferred *Fomes fomentarius*, while *Cis punctulatus* preferred *Trichaptum* spp. *Orthocis festivus* and *Ropalodontus strandi* appeared to be even more specific, with occurrence exclusively in *Stereum rugosum* and *Fomes fomentarius,* respectively. *Cis bidentatus* showed no specific host selection (polyphagous). A spatial segregation of the cisids *R. strandi, C. jacquemarti and C. lineatocribratus* was evident regarding height above ground of the fungus *F. fomentarius.* Microclimatic factors cannot explain the host selection of the species, but *Sulcacis affinis, Sulcacis fronticornis* and *Ennearthron cornutum* were exclusively found in fungi in warm and dry positions.

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1. Introduction

Fungivorous insects are faced with a variable resource. Thus, the quality and durability of the resource varies with species and the stage of sporophore development. Furthermore, the temporal and spatial occurrence of the resource is often variable. The spatial distribution of fruiting bodies in many species of fungus is markedly aggregated, with the sporophores growing in tight clusters, while in others the sporophores occur singly and more or less randomly.

There seems to be a varying degree of host specificity among insect species inhabiting Basidiomycetes. Insect species adapted to fungi with short-living fruiting bodies, e.g. most fungi spe-

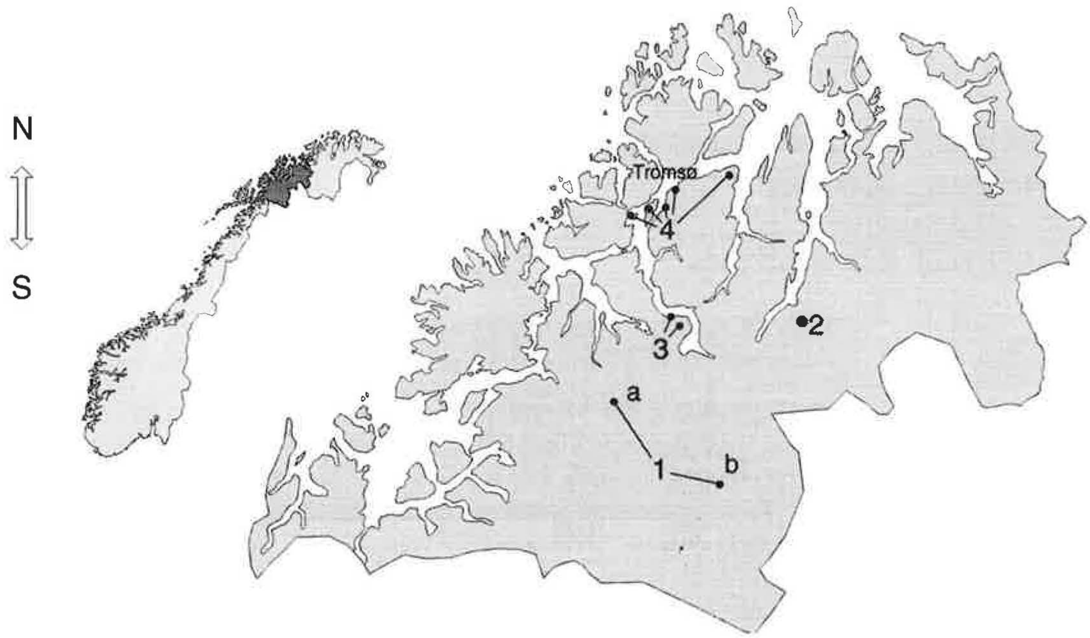

Fig. 1. Map showing the location of the four fields: 1: Målselvdalen and Dividalen; 2: Skibotn; 3: Balsfjord; 4: Tromsø.

cies occurring on the forest floor, generally show weak host specificity (Crowson 1981, Jonsell & Nordlander 1995). On the contrary, the large number of insect species adapted to tree-living fungi (Gilbertson 1984) may be more specialized (Jonsell & Nordlander 1995). The tenebrionid beetle *Bolitophagus reticulatus* (L.) for example, has the polypore *Fomes fomentarius* (L.: Fr.) Kickx as the main host (Krasutskiy 1996, Midtgaard 1996). Several studies of the species of the family Cisidae, which seem to be well adapted to tree-living fungi, indicate that they may be quite host specific (Saalas 1923, Benick 1952, Graves 1960, Paviour-Smith 1960a, Matthewman & Pielou 1971, Lawrence 1971, 1973, Ackerman & Shenefeldt 1973, Kaila *et al.* 1994, Thunes 1994, Jonsell & Nordlander 1995, Økland 1995, Krasutskiy 1996).

However, common for all the studies done so far on host preference of the family Cisidae and other tree-fungus living insects, is the lack of a quantitative measure of the host sample size. The total number of investigated fruiting bodies alone gives no information of quantity (volume, weight) examined. Intuitively this is assumed to be important when the purpose is to find out to what extent species show preferences to certain fungi. Therefore, in the present study, we have aimed at making quantitative measurements for each fungus unit.

The purpose of this study is: 1) to find a useful way of measuring the volume of fruiting bodies, thereby comparing methods of estimating volume to find a valid/useful measure of size to rank order, 2) examine if the species of the family Cisidae established in northern Norway show host preference, 3) examine whether height above ground of sporocarps (only for *F. fomentarius*) and microclimatic factors affect the spatial distribution of the species.

The present study is limited to tree-living "macrofungi" species.

2. Study area and the taxa of fungi

Four main sites (field 1–4), located in Troms county, northern Norway, were investigated (Fig. 1). They include inland, fjord as well as coastal districts: field 1, Målselvdalen and Dividalen (site 1a and 1b); field 2, Skibotndalen; field 3, Balsfjord (site 3a and 3b); field 4, Tromsø.

Site 1a was searched both at the bottom and on the hill-side of the valley, facing south or southwest, except one sampling site in Målselvdalen where the slope was facing north. The selected area contained mainly Scots pine (*Pinus sylvestris* L.), and birch (*Betula pubescens* Ehrh.), but there were also some willows (*Salix* spp.), aspen (*Populus tremula* L.) and alder (*Alnus incana* L.). The forest in the investigated area was old with a few clearcuts and had a high density of dead wood.

Field 2 was on the hillside of the valley, either facing southwest or in flat terrain. In this field *P. sylvestris* was dominating, but *B. pubescens* was also present.

In field 3, site a, investigations were done either on a north-facing or in a weakly southwest-facing position. *B. pubescens* was the dominating tree species in most of the area.

In field 4, five different sites were examined: Tromsøya, where the examined area had a weakly northwest facing or flat position; Håkøybotn at Kvaløya, where the slope was facing east; Tønsvikdalen, where the investigation was done in almost flat terrain along the river, but also in a steep southwest facing slope; Oldervikdalen, where the investigated area had a steep south-east facing position; and Tromsdalen, where the slope was facing southwest or northwest. In all these sites samples were also taken from flat terrain. All the sites in field 4 contain deciduous forests, dominated by *B. pubescens*. *A. incana* and *Salix* spp. predominated along brooks and rivers in all the four fields. Within each of the fields 1 and 3 an area of a given size was selected (termed 1b and 3b). Site 1b was situated in an old forest of mainly *P. sylvestris* and *B. pubescens*, on a slope facing southwest. Site 3b was partly situated in old wood predominated by *B. pubescens* and *A. incana*, partly in a clearcut with many stumps and twigs. The terrain is flat or weakly southwest-facing.

A summary and a brief description of the fungi taxa sampled are given in Table 1. The taxonomy follows Ryvarden (1991). Identifications are based on keys and descriptions in Ryvarden (1976, 1978), Eriksson *et al.* (1984) and Ryvarden and Gilbertson (1993).

3. Material and methods

The field investigation was carried out from the middle of July to late November 1993, and from early April to late October in 1994–1996. Sporocarps were cut at their base and brought to the laboratory. Usually not all the fungus material of an unit (trunk, twig or stump) was removed. For species with very small sporocarps, e.g. *Trichaptum* spp., bark infected with mycelium was also collected. No division of successional stages of fungi for the material collected in 1993–1994 was done to avoid loss of cisid species due to succession, as Paviour-Smith (1960b) and Klimaszewski and Peck (1986) showed for *Piptoporus betulinus* and *Polyporus squamosus,* respectively. However, our results from 1993–1994 indicated that only dead parts of the fruiting bodies of woody hard species were usually attacked by cisids, whereas the species with soft sporocarps may be attacked when still alive (see also Graves 1960, Ackerman & Shenefeldt 1973). Consequently, alive and uninfected sporocarps were not sampled in site 1b in 1994 and in field 3b in 1995–1996. Therefore the sporocarps sampled in site 1b and 3b are in a more comparable stage than the rest of the material.

For the 1994–1996 samples, height above ground, exposure (exposed/shady), ground moisture (dry/humid) and topography (slope/flat terrain) parameters were noted for each sample.

The sampling in site 1b was performed from 12 to 23 September 1994, in 3b 19–20 September and 4–5 October 1995. Dead and/or attacked sporocarps from all units infected with fungi were collected. In field 1b, however, only 50% of the sporocarps of *Phellinus* spp. and *Fomes fomentarius* were sampled.

Different methods were used to extract the beetles depending on fungus species. Fungi with soft tissue were picked to pieces and all beetles were collected. Some samples were laid on a grate on top of a collecting jar and placed under a 60-W table lamp to force the inhabitants out of the fungus. Emerging insects were sampled once a day, but when the number of emerging individuals declined to zero, the fungi were investigated to insure that all adult specimens were taken.

Because of the woody or leathery fruiting bodies of *F. fomentarius*, *P. betulinus* and *Phellinus* spp., these fungi were placed in plastic funnels standing in glass jars, and the emerging insects were picked once a week until the number of specimen declined to zero.

All samples were stored for eclosion and investigated three times during the winter. Thus, all the specimens that were eggs, larvae, pupae or beetles when the fungi were collected, were sampled. In addition, a new generation of beetles was sampled. Since the fruiting bodies of *F. fomentarius,* and *Phellinus* spp. were not picked to pieces, there is a possibility that individuals of cisidae may have remained inside the hosts and hence that their abundance was underestimated in these fungi species. Cisids were identified by means of keys and descriptions in Hansen (1951), Freude *et al.* (1967) and Fjellberg (1985) and preserved in 70% ethanol. The nomenclature follows Lundberg (1995).

The dry weights of all the fungi collected in 1994–1996 were recorded after one week at room temperature (R.H. = 17–20%). For the fungi collected in 1994, the volume of *F. fomentarius*, *P. betulinus* and the genus *Phellinus* was calculated by measuring maximum length (distance from

Table 1. Description of the tree-living fungi species sampled in 1993-96. Equal numbers (given behind genus) indicate a close relationship between the respective genera. Different numbers (1, 2, 3, 5, 6 and 9) indicate that the genera are separated in distinct groups of the family Polyporaceae (Ryvarden 1991). a and p denotes annual and perennial, respectively.

Family Genus	Species	Life cycle	Fruiting body	Host trees	Distribution in Troms	Hyphal system
Polyporaceae						
Polyporus (1) s. str Fr.	*melanopus* Fr.	a	soft when fresh	dead deciduous wood	scattered, but not rare	dimitic
	squamosus Fr.	a	fleshy when fresh	living or dead deciduous trees	not common	dimitic
	varius Fr.	a	tough when fresh	living or dead deciduous trees	common	dimitic
Pleurotus (1) (Fr.) Kumm.	*pulmonarius* (Fr.) Quel	a	soft	deciduous *Betula*	common	dimitic
Trametes (2) Fr.	*hirsuta* (Fr.) Pilát	a	soft	deciduous	common	trimitic
	pubescenc (Fr.) Pil	a	soft	deciduous	rather rare	trimitic
	ochracea (Fr.) Pil.	a	soft	deciduous	common	trimitic
Pycnoporus (2) Karst.	*cinnabarinus* (Jacq.: Fr.) Karst.	a	tough and fibrous	deciduous wood	scattered, not common	trimitic
Cerrena (2) S. F. Gray	*unicolor* (Fr.) Murr.	p	tough to corky	deciduous, mostly *Betula*	common, follows *Betula*	trimitic
Trichaptum (2) Murr.	*abietinus* (Fr.) Ryv.	a	soft when fresh	coniferous wood	scattered, not common	dimitic
	fusco-violaceus (Ehrenberg) Donk.: Fr. Ryv.	a	soft when fresh	coniferous wood	common	dimitic
	laricinus (Karst.) Ryv.	p	soft when fresh	coniferous wood	rare	dimitic
Gloeophyllum (3) Karst.	*sepiarium* (Fr.) Karst.	a-p	tough and flexible	both coniferous and deciduous woods, but most frequent on the former	scattered, not common	trimitic
Piptoporus (3) Karst.	*betulinus* (Fr.) Karst.	a	elastic when fresh	weakened or dead *Betula*	common	di(tri)mitic
Fomitopsis (3) Karst.	*pinicola* (Fr.) Karst.	p	corky to woody hard	common on *Picea*	rather rare	trimitic

Continues ...

Table 1. Continued.

Family Genus	Species	Life cycle	Fruiting body	Host trees	Distribution in Troms	Hyphal system
Oxyporus **(5)** Donk	*populinus* (Bourdot & Galzin) Donk	a	soft when young, hard when dry	deciduous trees	rather rare	monomitic
Hapalopilus **(6)** Karst.	*nidulans* (Fr.) Karst.	a	soft and watery when fresh	dead deciduous wood	rather rare	monomitic
Bjerkandera **(6)** Karst.	*adusta* (Willd.: Fr.) Karst.	a	soft and pliable when fresh	dead deciduous wood	rather rare	monomitic
Fomes **(9)** *(Fr.) Fr.*	*fomentarius* (L.: Fr.) Kickx	p	woody hard	deciduous	very common	trimitic
Hymenochaetaceae						
Phellinus Quél.	*igniarius* (Fr.) Quél.	p	woody hard	deciduous	common	dimitic
	lundellii Niemelä	p	woody hard	dead deciduous wood	common	dimitic
	nigricans (Fr.) Karst.	p	woody hard	deciduous	scattered, not rare	dimitic
Inonotus Karst.	*obliquus* (Fr.) Pilat	a	soft when fresh	deciduous wood	common	monomitic
Corticiaceae						
Stereum Pers.	*rugosum* (Pers.: Fr.) Fr.	p	coriciaceous to very hard	deciduous	common	monomitic
	sanguinolentum (Alb. & Schw.:Fr.) Fr.	a-p	tough when fresh,hard when dry	coniferous wood	common	monomitic
	subtomentosum Po.	a	tough when fresh, hard when dry	deciduous, *Alnus* spp.	rather rare	monomitic
	hirsutum (Willd.: Fr.) S. F. Gray	a	tough when fresh, hard when dry	deciduous	common	monomitic
Plicatura Karst.	*nivea* (Sommerf.: Fr.) Karst.	a	soft when fresh	deciduous wood	common	monomitic
Chondrostereum Po.	*purpureum* (Pers.: Fr.) Po.	a	tough	deciduous *Betula*	scattered, not rare	monomitic
Tremellaceae						
Exidia Fr.	*glandulósa* Fr.	a	soft when fresh	deciduous wood	common	
Tremélla Fr.	*foliácea* Pers. ex. Fr.	a	soft when fresh	deciduous wood	common	

trunk outwards when the sporophores were viewed on the tree), width (from side to side) and height (from apex to lower surface) by using a ruler. "Apex" is used according to the description by Matthewman & Pielou (1971).

To get an exact measure of volume, each sample from site 1b and 3b, was placed in a thin plastic bag. The air was removed by a vacuum pump. Then each vacuumpacked fungus was dipped into a jar completely filled with water, which was placed into another collecting jar where the surplus water was collected. This surplus water was measured, giving the volume of each sample. This method is termed "measure of volume".

Correlations between weight and volume (calculated and measured) were tested for data sampled in field 1b, using Spearman Rank Order Correlations.

The frequency of each cisid species in the fungi deviated significantly from a normal distribution (d between 0.3892 and 0.5235, $p < 0.01$, Kolmogorov-Smirnov one sample tests). Kruskal-Wallis tests were therefore used in the statistical analysis. When this test gave significant differences between groups, Mann-Whitney U tests (with corrections for tied variables, vide Sokal & Rohlf (1981)),were used in the further statistical analyses.

The six data sets (Table 2–7) were treated separately when testing for host preference, using individuals per gram fungi (Table 2–5) or individuals pr. ml fungi (Table 6 and 7). For each cisid species, the fungus taxon with the highest number of individuals was tested for difference in density against all others. Taxa of fungi inhabited by less than ten individuals of a particular species, or taxa with less than four attacks, were not included. We did not control significance levels for multiple comparisons, because this significantly increases the probability of dismissing real patterns (Rothman 1990).

In *F. fomentarius*, the effect of height above ground on density of beetles (individuals per gram) was tested with Mann-Whitney U tests for three beetle species, and Chi-square tests were used to test pairwise differences in prevalence between the species.

The following classification was used to elucidate the

Table 2. Mean number of cisids pr. 10 gram fungi found in fruiting bodies of *Trametes* spp., *Fomes fomentarius*, *Phellinus* spp., *Piptoporus betulinus*, *Cerrena unicolor*, *Stereum sanguinolentum* and *Trichaptum* spp. sampled in Dividalen and Målselvdalen. Total number of cisids is given in brackets while the number of fungi in which they were found is given by the following number. Sampled fungi without attack and N ≤ 7 are not considered in the table: *Gloeophyllum sepiarium* (N = 7), *Polyporus* spp. (N = 6), *Fomitopsis pinicola* (N = 3), *Stereum* spp. (N = 2), *Oxyporus populinus* (N = 2), *Exidia* spp. (N= 2) and *Plicatura nivea* (N= 1). Host preference for fungi species was tested with Mann-Whitney U Test for all cisid species pr. gram fungi exceeding ten individuals in at least one fungus species. Figures with asterics denote that the abundance is significantly higher than in all the other fungus species ($p < 0.05$).

Fungi name:	*Tram.*	*F. fom.*	*Phell.*	*P. bet.*	*C. unic.*	*S. sang.*	*Tric.*
N:	52	92	76	43	22	21	32
n:	48	52	6	15	11	3	27
Fungi group:	(2)	(9)		(3)	(2)		(2)
Cisidae							
Cis bidentatus	**0.02** (2) 1	**0.21** (54) 9	**0.02** (2) 1	* **2.48** (151) 12	**0.13** (9) 3	**0.06** (1) 1	**0**
Cis jacquemarti	**0**	* **3.04** (785) 41	**0.03** (4) 4	**1.18** (72) 6	**0.09** (6) 1	**0**	**0**
Cis lineatocribratus	**0**	* **0.28** (73) 12	**0.22** (30) 2	**0.03** (2) 2	**0.01** (1) 1	**0.11** (2) 1	**0**
Cis comptus	**0.51** (46) 5	**0**	**0**	**0**	* **6.16** (420) 9	**0.06** (1) 1	**0.01** (2) 1
Cis boleti	* **12.13** (1100) 33	**0**	**0**	**0**	**0**	**0**	**0**
Cis hispidus	* **11.49** (1042) 30	**< 0.01** (1) 1	**0**	**0**	**0**	**0**	**0**
Cis punctulatus	**0**	**0**	**0**	**0**	**0**	**0**	* **0.84** (113) 27
Octotemnus glabriculus	* **3.34** (303) 21	**0**	**0**	**0**	**0**	**0**	**0**
Sulcacis fronticornis	**3.57** (324) 2	**0**	**0**	**0**	**0**	**0**	**0**
Sulcacis affinis	**0.20** (1) 1	**0**	**0**	**0**	**0**	**0**	**0**
Ennearthron cornutum	**0**	**0.04** (11) 1	**0**	**0**	**0**	**0**	**0**
Ropalodontus strandi	**0**	* **3.25** (841) 14	**0**	**0**	**0**	**0**	**0**
Number of species	7	6	3	3	4	3	2
Volume (cal.)•	–	18579	8276	4500	–	–	–
Weight (g.)	907	2582	1342	610	682	175	<<1352

N: total number of fungi sampled, n: number of attacked fungi, •: volume calculated (cm^3).

Note Table 2-7: For large species of fungi (e.g. *Fomes fomentarius, Phellinus* spp., *Piptoporus betulinus*) N denotes one sporocarp, while for small species of fungi (e.g. *Trametes* spp., *Cerenna unicolor, Stereum* spp., *Trichaptum* spp.) it denotes number of units (tree, trunk, stump or twig).

host selection of the cisid species:

1. Optimal host, where the individuals feed and reproduce, and the highest density of each species is found.
2. Suboptimal host, where the species feed and may reproduce, but have a lower density and prevalence than in 1).
3. Fungi where only stragglers are found, e.g. occasionally in fungi of the "wrong" species. The term "straggler" is used in cases where the total number of individuals found in each fungus species is less than ten, and when less than four fungi units were found attacked. No sign of reproduction is evident, but the individuals may feed.
4. Fungi where no individuals were found.

4. Results

There was a highly significant ($p < 0.005$) and positive correlation ($R \geq 0.79$) between weight and volume, both with regard to each fungus and all fungi combined, and whether volume was measured or calculated. This gives the opportunity to use one of three methods: 1) dry weight; 2) calculation of volume; or 3) measure of volume.

In total, four fungi families, 20 genera and 31 fungi species were found and investigated. The family Polyporaceae is divided into 12 groups (Ryvarden 1991, Table 1). Fungi from six of these groups were examined. (1) The Polyporus group: *Polyporus* and *Pleurotus*; (2) the Trametes group: *Trametes, Pycnoporus, Cerrena* and *Trichaptum*; (3) the Daedalea group: *Gloeophyllum, Piptoporus* and *Fomitopsis*; (5) the Rigidoporus group: *Oxyporus*; (6) the Tyromyces group: *Bjerkandera* and *Hapalopilus,* and (9) the Fomes group: *Fomes.*

Totally, 13 cisid species of the 29 recorded from Norway (Lundberg 1995), were found in nine taxa of fungi.

A significant difference in density was evident for all cisid species tested statistically across taxa of fungi (Table 2–7). Most of the cisid species showed a similar host occurrence regardless of geographical location, although the composition of cisid and polypore species varied.

Cis boleti (Scopoli), *Cis hispidus* Payk. and *Octotemnus glabriculus* (Gyll.) were most abundant in *Trametes* spp., whereas *Cis comptus* Gyll. was most common in *Cerrena unicolor. Cis punctulatus* Gyll. occurred exclusively in *Trichaptum* spp. *Cis jacquemarti* Mell. and *Cis lineatocribratus* Mell.

Table 3. Mean number of cisids pr. 10 gram fungi found in fruiting bodies of *Trametes* spp., *Phellinus* spp., *Cerrena unicolor, Stereum sanguinolentum, Trichaptum* spp., *Piptoporus betulinus, Stereum hirsutum* and *Pleurotus pulmonarius* sampled in Skibotndalen. Total number of cisids is given in brackets while the number of fungi in which they were found is given by the following number. Sampled fungi not considered in the table: *Fomes fomentarius* (N = 1), *Gloeophyllum sepiarium* (N = 2), *Exidia* spp. (N = 2) and *Hapalopilus nidulans* (N = 1). For further explanation see Table 2.

Fungi name:	*Tram.*	*Phell.*	*C. unic.*	*S. sang.*	*Tric.*	*P. bet.*	*S. hirs*	*Pleur.*
N:	19	11	3	15	23	10	2	5
n:	17	1	2	1	14	0	1	1
Fungi group:	(2)		(2)		(2)	(3)		(1)
Cisidae								
Cis bidentatus	**0**	**0.11** (3) 1	**0**	**0.70** (3) 1	**0.11** (3) 2	**0**	**0.53** (2) 1	**0**
Cis punctulatus	**0**	**0**	**0**	**0**	* **2.86** (75) 14	**0**	**0**	**0**
Cis comptus	**0.32** (18) 3	**0**	**0.70** (4) 1	**0**	**0.11** (3) 1	**0**	**0**	**0**
Cis boleti	* **13.53** (748)16	**0**	**6.50** (37) 1	**0**	**0**	**0**	**0**	**0.10** (1) 1
Cis hispidus	* **13.65** (755) 11	**0**	**1.23** (7) 1	**0**	**0**	**0**	**0**	**0.10** (1) 1
Orthocis festivus	**0**	**0**	**0**	**0**	**0**	**0**	**0.26** (1) 1	**0**
Octotemnus glabriculus	**0.33** (18) 2	**0**	**1.05** (6) 1	**0**	**0**	**0**	**0**	**0**
Sulcacis affinis	**0.29** (16) 3	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Number of species	5	1	4	1	3	0	2	2
Volume (cal.)•	–	1643	–	–	–	1371	–	–
Weight (g.)	553	280	57	43	< 262	342	38	94

N: total number of fungi sampled. For further explanation see Table 2. n: number of attacked fungi, •: volume calculated (cm^3).

were most abundant in *Fomes fomentarius*. *Ropalodontus strandi* Lohse was exclusively found in *F. fomentarius* whereas *Orthocis festivus* (Panzer) almost exclusively occurred in *Stereum rugosum*. *Cis bidentatus* (Olivier) occurred in eight taxa, but it was most common in *F. fomentarius*, *C. unicolor*, *P. betulinus* and *S. rugosum*.

Sulcacis affinis (Gyll.), *Sulcacis fronticornis* (Panzer) and *Ennearthron cornutum* (Gyll.) were not tested statistically for host preferences due to the criteria mentioned in section 3. However, *E. cornutum* was exclusively found in *F. fomentarius*. Although low-numbered, the find of two dead adult specimens in one sporocarp, might indicate breeding and reproduction. The present results for *S. affinis* and *S. fronticornis* indicate that these species might be host specific, due to their occurrence exclusively in *Trametes* spp.

Trametes spp. were commonly infected with *C. boleti*, *C. hispidus* and *O. glabriculus* regardless of whether the fungi occurred in shady and moist, or exposed and dry positions. The same was true for *R. strandi*, *C. jacquemarti* and *C. lineatocribratus* in *F. fomentarius*, for *C. comptus* in *C. unicolor* and for *C. punctulatus* in *Trichaptum* spp. However, the spatial distribution of *S. fronticornis*, *S. affinis* and *E. cornutum* seems to be influenced by microclimatic factors. They were exclusively found in fruiting bodies sampled in a warm environment (exposed and south-west facing slopes with dry ground). *O. festivus* and its host, *S. rugosum*, were always found in moist and shady or semiexposed positions.

R. strandi was most common in fruiting bodies of *F. fomentarius* growing above ground (Mann-Whitney U test, $p = 0.00006$) in contrast to *C. lineatocribratus* and *C. jacquemarti* (Fig. 2). Pairwise tests gave significant differences between *R. strandi* and *C. lineatocribratus* ($\chi^2 = 45.78$, df = 1, $p < 0.0001$) and between *R. strandi* and *C. jacquemarti* ($\chi^2 = 83.93$, df = 1, $p < 0.0001$). A significant difference was also evident when *C. lineatocribratus* vs. *C. jacquemarti* was tested pairwise ($\chi^2 = 9.25$, df = 1, $p < 0.0024$). *C. lineatocribratus* was almost exclusively found in fruiting bodies sampled on ground (Mann-Whitney U test, $p < 0.0000001$, see Fig. 2). *C. jacquemarti* was found abundant in fungi sampled in both heights, but a

Table 4. Mean number of cisids pr. 10 gram fungi found in fruiting bodies of *Trametes* spp., *Fomes fomentarius*, *Phellinus* spp., *Piptoporus betulinus*, *Cerrena unicolor*, *Polyporus* spp. and *Stereum rugosum* sampled in Balsfjord. Total number of cisids is given in brackets while the number of fungi in which they were found is given by the following number. Sampled fungi not considered in the table: *Stereum* spp. (N = 7), *Pycnoporus cinnabarinus* (N = 3), *Oxyporus populinus* (N = 5), *Pleurotus pulmonarius* (N = 7), *Exidia* spp. (N = 1), *Plicatura nivea* (N = 1), *Chondrostereum purpureum* (N = 4), *Inonotus obliquus* (N = 2), *Bjerkandera adusta* (N = 4) and *Tremella foliácea* (N = 1). For further explanation see Table 2.

Fungi name:	*Tram.*	*F. fom.*	*Phell.*	*P. bet.*	*C. unic.*	*Polyp.*	*S. rug.*
N:	31	64	29	19	15	39	19
n:	25	43	4	4	13	2	16
Fungi groups:	(2)	(9)		(3)	(2)	(1)	
Cisidae							
Cis bidentatus	**0.03** (1) 1	**0.26** (92) 9	**0.83** (4) 3	**3.70** (56) 4	**0.12** (6) 2	**0.26** (2) 2	**0.05** (3) 2
Cis jacquemarti	**0**	* **1.50** (521) 21	**0**	**0**	**0**	**0**	**0**
Cis lineatocribratus	**0.03** (1) 1	* **1.06** (372) 22	**0**	**0**	**0.02** (1) 1	**0**	**0**
Cis comptus	**0**	**0**	**0**	**0**	* **5.12** (263) 13	**0**	**0**
Cis boleti	* **18.40** (583) 24	**0**	**0**	**0**	**0.06** (3) 1	**0**	**0**
Cis hispidus	* **5.86** (186) 14	**0**	**0**	**0**	**0.06** (3) 1	**0**	**0**
Orthocis festivus	**0**	**0**	**< 0.01** (1) 1	**0**	**0**	**0**	* **3.06** (188) 16
Octotemnus glabriculus	* **1.30** (41) 8	**0**	**0**	**0**	**0**	**0**	**0**
Number of species	5	3	2	1	5	1	2
Volume (cal.)•	–	4585	5834	5068	–	–	–
Weight (g.)	317	3492	1020	671	511	78	614

N: total number of fungi sampled. For further explanation see Table 2. n: number of attacked fungi, •: Volume calculated (cm^3).

significant (Mann-Whitney U test, p = 0.04) difference was found regarding height above ground (Fig. 2). Thus, *C. lineatocribratus* shows a stronger attraction for fruiting bodies on the ground than does *C. jacquemarti* (Fig. 2).

5. Discussion

Previous studies on fungi-species preferences of insects included the number of insect specimens per fruiting body (e.g. Økland 1995). This method gives equal values to each unit of fungi regardless of volume or weight, which differs within and between species. However, density measures of insect specimens by means of estimates of the size of each fruiting body are considered to be important in preference studies of fungivorous species.

Calculation of volume makes sense only when the fruiting bodies are pileate. Dry weight is applicable on all types of fruiting bodies. Vacuum packed fungi dipped in water (measure of volume) gives a precise measure of the volume at the same time as the technique can be used on all types of fruiting bodies, whether it is pileate, imbricate or resupinate. Since the results of the last two methods were highly correlated, both may be adequate in quantitative studies of fungivorous species.

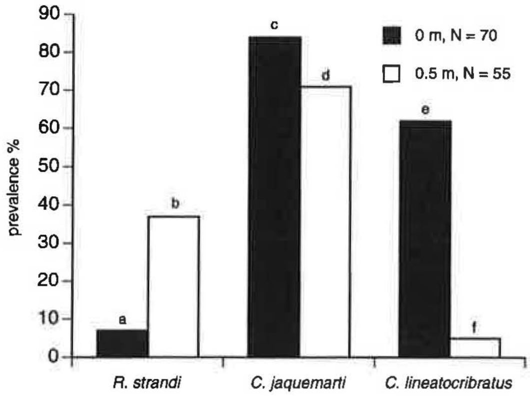

Fig. 2. Prevalence of cisids associated with *Fomes fomentarius* according to height above ground: 0 m = fruiting bodies sampled from logs on the ground; 0.5 m = fruiting bodies sampled from 0.5–2 m on standing trunks; N = number of fruiting bodies. The number of individuals pr. gram fruiting body were tested statistically. Significance in difference is given above each bar as small letters. Different letters within each species represent significant differences (p < 0.05) (Mann-Whitney U test). Pairwise comparison (Chi-square tests) revealed significant differences (p < 0.05) in prevalence between the three cisid species.

The sporocarps sampled in field 1b and 3b are

Table 5. Mean number of cisids pr. 10 gram fungi found in fruiting bodies of *Trametes* spp., *Phellinus* spp., *Piptoporus betulinus, Cerrena unicolor, Stereum rugosum, Pycnoporus cinnabarinus* and *Polyporus* spp. sampled in Tromsø. Total number of cisids is given in brackets while the number of fungi in which they were found is given by the following number. Sampled fungi not considered in the table: *Fomes fomentarius* (N = 2), *Inonotus obliquus* (N = 1), *Pleurotus pulmonarius* (N = 3) and *Stereum* spp. (N = 7). For further explanation see Table 2.

Fungi name:	*Tram.*	*Phell.*	*P. bet.*	*C. unic.*	*S. rug.*	*P. cin.*	*Polyp.*
N:	56	54	5	13	33	14	11
n:	47	0	1	2	1	0	0
Fungi group:	(2)		(3)	(2)		(2)	(1)
Cisidae							
Cis bidentatus	**0**	**0**	**3.00** (51) 1	**0.14** (9) 2	**0.07** (5) 1	**0**	**0**
Cis boleti	* **28.16** (2321) 46	**0**	**0**	**0**	**0**	**0**	**0**
Cis hispidus	* **5.87** (484) 18	**0**	**0**	**0**	**0**	**0**	**0**
Octotemnus glabriculus	* **4.04** (333) 17	**0**	**0**	**0**	**0**	**0**	**0**
Sulcacis affinis	**0.23** (19) 3	**0**	**0**	**0**	**0**	**0**	**0**
Number of species	4	0	1	1	1	0	0
Volume (cal.)•	–	15680	–	–	–	617	–
Weight (g.)	824	1401	169	657	720	70	75

N: total number of fungi sampled. For further explanation see Table 2. n: number of attacked fungi, •: Volume calculated (cm^3).

in a more comparable stage than the rest of the material. Nevertheless, the results from Tables 2–5 are in agreement with the results from 1b and 3b (Tables 6 and 7).

Paviour-Smith (1960a), Matthewman & Pielou (1971), Lawrence (1973), Thunes (1994) and Økland (1995), divided taxa of fungi in host preference groups in which cisids are found. Paviour-Smith (1960a) proposed that the beetle species and the species of fungi should be separated into two mutually exclusive breeding groups.

Host selection and a classification of the different taxa of fungi in which each cisid species is found are summarized in Table 8. A division of fungi into three "host preference groups" could be made: (*i*) the Trametes group, (*ii*) the Fomes and Daedalea group and (*iii*) the genus *Stereum*. Despite this grouping, most of the cisids tend to prefer single genera, and two species appear to be species-specific (*O. festivus* and *R. strandi*) (Table 8).

Taxonomically closely related cisid species tend to select the same taxa of fungi. Accordingly, *C. lineatocribratus* and *C. jacquemarti* are closely related and prefer *F. fomentarius*. *C. boleti, C. hispidus* and *C. comptus* are also closely related and select *Trametes* spp. or the closely related *C. unicolor*. The species of *Orthocis* probably prefer species of fungi other than Polyporaceae. This is evident for *O. festivus* (Table 8) and it is also likely for the two other species of the genus occuring in Troms: *Orthocis alni* (Gyll.) and *Orthocis linearis* (Sahlb.). Thus, *O. alni* is one of the most common cisid species found in window traps in Dividalen (Ø. Huse, pers. comm.) indicating that it must be quite common. Nevertheless, we have not found it amongst the fungi species we have examined (Table 1), although Koch (1989) mentioned *Exidia glandulosa* and *Stereum rugosum* as hosts for *O. alni*. It remains to be found what types of fungi these two *Orthocis* species prefer.

Several factors seem to contribute to the fungus choice of cisid species: differences of the fruit-

Table 6. Mean number of cisids pr. 10 ml fungi found in dead and/or attacked fruiting bodies of *Trametes* spp., *Fomes fomentarius*, *Phellinus* spp. and *Piptoporus betulinus* sampled in Dividalen (site 1b) between 12–23 September 1994. Sampled fungi without attack and N ≤ 7 are not considered in the table: *Cerrena unicolor* (N = 2). Total number of cisids is given in brackets while the number of fungi in which they were found is given by the following number. Host preference for fungi species was tested with Mann-Whitney U Test for all cisid species pr. ml fungi exceeding ten individuals in at least one fungus species. Figures with asterics denote that the abundance is significantly higher than in all the other fungus species ($p < 0.05$).

Fungi name:	*Tram.*	*F. fom.*	*Phell.*	*P. bet.*
N:	11	27	28	16
n:	11	24	1	0
Fungi group:	(2)	(9)		(3)
Cisidae				
Cis bidentatus	**0.02** (1) 1	**0.01** (8) 4	< **0.01** (1) 1	**0**
Cis jacquemarti	**0.02** (1) 1	* **0.12** (72) 13	**0**	**0**
Cis lineatocribratus	**0**	**0.04** (22) 2	**0**	**0**
Cis boleti	* **2.45** (143) 9	**0**	**0**	**0**
Cis hispidus	* **9.00** (524) 9	**0**	**0**	**0**
Octotemnus glabriculus	* **6.91** (403) 7	**0**	**0**	**0**
Sulcacis affinis	**0.02** (1) 1	**0**	**0**	**0**
Ennearthron cornutum	**0**	< **0.01** (3) 3	**0**	**0**
Ropalodontus strandi	**0**	* **0.68** (408) 18	**0**	**0**
Number of species	6	5	1	0
Volume (cal.)•	–	11208	11177	3191
Volume (ms.)♦	583	6018	4939	1500
Weight (g.)	129	1540	2657	663
% sampled *f*	100	50	50	100

f: % of total number of fungi in the investigated area. N: total number of fungi sampled. For further explanation see Table 2. n: number of attacked fungi, •: volume calculated (cm^3), ♦: volume measured (ml).

ing bodies in the durational stability (Hanski 1989, Økland 1995), in hyphal structure (Paviour-Smith 1960a), or hardness (Klopfenstein & Graves 1989, Økland 1995), or differences in mouth morphology and feeding strategy between the cisid species (Lawrence 1989). The durational stability of most Polyporaceae is obviously sufficient to support many cisid species. Although *Trametes* spp. are annual, their fruiting bodies persist for a long time after death (2–3 years), and they harbour more cisid species than any other fungi taxa do (Table 8). Species of the *Phellinus igniarius* group may be too hard to be attacked by cisid species since hardly any of them use *Phellinus* spp. as hosts (Table 8, see also Økland 1995). However, despite that *F. fomentarius* is a comparatively hard species, it is used as a host by almost as many species as *Trametes* spp. According to our opinion, therefore, a hypothesis involving softness and durability of the host to explain species richness of insects in fungi is of limited applicability to cisids.

The fact that several cisids found in *Trametes* spp. have been extracted exclusively from soft bodied fungi (*Trametes* spp., *C. unicolor* and *Trichaptum* spp.), may indicate that their mandibles are adapted to chew relatively soft fungi. The species associated with hard fungi seem to have heavily developed mandibles adapted to chew such fungi (Entwhistle 1955, unpubl.). However, it is reasonable that the species adapted to chew woody fungi are able to chew softer fungi as well. Nevertheless, the species preferring *F. fomentarius* mostly occur as stragglers in soft bodied fungi (Tables 4, 6, 7 and 8).

It is likely that olfactory stimuli play a major role when cisids locate the host (Lawrence 1973), as it does for bark beetles (Wood & Bushing 1963, Wood 1982). Paviour-Smith (1960a) argued that it seems very unlikely that the answer to the question about the choice of fungi will be found by the postulation of special chemical attractants or repellents in the fruiting bodies themselves. She suggested that a general odour from decaying wood could work as a stimulus to the cisid species. However, the specialized host preference shown by most of the cisids, indicates rather a response to volatiles from fungi than to a general odour of a decaying tree (see also Jonsell & Nordlander (1995)). This is also in accordance with the following: the cisid species select fungus species across tree species. For example, several cisid

Table 7. Mean number of cisids pr. 10 ml fungi found in dead and/or attacked fruiting bodies of *Trametes* spp., *Fomes fomentarius, Phellinus* spp., *Stereum rugosum*, sampled in Balsfjord September–October 1995. Sampled fungi without attack and N ≤ 7 are not considered in the table: *Pleurotus pulmonarius* (N = 5) and *Oxyporus populinus* (N = 1). Total number of cisids is given in brackets while the number of fungi in which they were found is given by the following number. For further explanation see Table 6.

Fungi name:	*Tram.*	*F. fom.*	*Phell.*	*S. rug.*
N:	27	31	32	7
n:	27	24	1	7
Fungi group:	(2)	(9)		
Cisidae				
Cis bidentatus	**0**	**0**	**0.02** (2) 1	* **0.27** (16) 4
Cis jaquemarti	**0.04** (4) 3	* **0.53** (407) 21	**0**	**0**
Cis lineatocribratus	**0.05** (5) 4	* **1.63** (1240) 20	**0**	**0**
Cis boleti	* **4.38** (420) 24	**0**	**0**	**0**
Cis hispidus	* **2.48** (238) 15	**0**	**0**	**0**
Orthocis festivus	**0**	**0**	**0**	* **0.73** (43) 6
Octotemnus glabriculus	* **3.02** (290) 22	**0**	**0**	**0**
Rhopalodontus strandi	**0**	**< 0.01** (1) 1	**0**	**0**
Number of species	5	3	1	2
Volume (ms.)♦	959	7615	1059	587
Weight (g.)	148	2401	615	123
% sampled *f*	100	100	100	100

f: % of total number of fungi in the investigated area. N: total number of fungi sampled. For further explanation see Table 2. n: number of attacked fungi, ♦: volume measured (ml).

species (e.g. *C. boleti, C. hispidus, O. glabriculus*) prefer *Trametes* spp., but these fungi grow on a wide variety of deciduous trees (*Betula, Alnus, Populus, Salix*) whereas *P. betulinus*, which exclusively grows on *Betula*, is completely unattacked by the same cisid species. Furthermore, a fresh fruiting body probably emits stronger and more specific odours than older ones and decaying trees. Together with old, decomposed fruiting bodies, newly formed ones are usually found on the same site (stem, twig, stump). The reason for this is that the mycelium exists for many years inside the wood, producing fruiting bodies over several years. Cisids may therefore orientate to a new site using chemical cues emitted from fresh fruiting bodies although dead sporocarps within the site usually are used as breeding places.

Pheromones produced (perhaps in the feces) by the first colonizing specimens, which would attract other members of the species, may also play a role in host detection (Lawrence 1973).

The present results indicate that microclimatic factors have no crucial effect on the host selection of most of the cisids since they were usually found in the same fungi species irrespective of exposure and moisture. *S. affinis, S. fronticornis* and *E. cornutum*, however, occurred only in fungi associated with a warm and dry environment although their hosts, *Trametes* spp. and *F. fomentarius,* were sampled in all microclimatic categories.

The cisid species preferring *F. fomentarius* select sporocarps at different heights above ground (Fig. 2). *R. strandi* mostly colonizes fungi above ground whereas *C. lineatocribratus* is found almost exclusively in fungi sampled on the ground. *C. jacquemarti* occurred in fungi sampled from both heights, but it was found in significantly more fungi sampled on the ground than off the ground (Fig. 2). It is possible, therefore, that *R. strandi* colonizes the fungi before *C. jacquemarti* and the latter species before *C. lineatocribratus*. Another possibility is that *C. lineatocribratus* prefers wetter sporocarps than the other two cisid species, irrespective of their age or successional stage. Thus, sporocarps which have grown near the ground are usually wet, contrary to those present on standing trees (Paviour-Smith 1960a). One consequence of this division of the host may be that *C. jacquemarti* and especially *C. lineatocribratus* locate hosts when crawling on the ground. *C. li-*

Table 8. Utilization categories of cisids summarized according to associated fungi. Optimal host: the species feed and reproduce; Suboptimal host: the species feed and may reproduce, but have a lower density and prevalence than the former; Straggler: the species may feed, but no sign of reproduction; Zero: no individuals found. ? is added when the given category might be too high. Figures underlined indicate eclosion (1: larvae or pupae were found as adults in a later investigation of a sample or 2: teneral specimens).

Fungi species:	*Pleurotus pulmonarius*	*Polyporus* spp.	*Trametes* spp.	*Cerrena unicolor*	*Trichaptum* spp.
Fungi group:	(1)	(1)	(2)	(2)	(2)
Cisidae					
Cis bidentatus	zero	straggler	straggler	suboptimal ?	straggler
Cis jaquemarti	zero	zero	straggler	straggler	zero
Cis lineatocribratus	zero	zero	straggler	straggler	zero
Cis comptus	zero	zero	suboptimal	<u>optimal</u>	straggler
Cis boleti	straggler	zero	<u>optimal</u>	suboptimal	zero
Cis hispidus	straggler	straggler	<u>optimal</u>	suboptimal	zero
Cis punctulatus	zero	zero	zero	zero	<u>optimal</u>
Orthocis festivus	zero	zero	zero	zero	zero
Octotemnus glabriculus	zero	zero	<u>optimal</u>	straggler	zero
Sulcacis fronticornis	zero	zero	optimal ?	zero	zero
Sulcacis affinis	zero	zero	<u>optimal ?</u>	zero	zero
Ennearthron cornutum	zero	zero	zero	zero	zero
Ropalodontus strandi	zero	zero	zero	zero	zero

Continues ...

neatocribratus is frequently found in pitfall traps (Thunes 1994), supporting this hypothesis.

Contrary to *C. lineatocribratus*, *R. strandi* may mostly orientate in flight, prior to landing. Catches from traps designed by Kaila (1993) agree with the hypothesis that *R. strandi* prefers fruiting bodies growing above ground on standing trees (Olberg, unpublished data).

Tømmerås & Mustaparta (1989), tested single cell responses to volatiles from host and nonhost species in the ambrosia beetle *Trypodendron lineatum* (Oliver). Their results suggested that odour cells respond to one or a few compounds and that minor constituents are rather important. Similar experiments ought to be conducted on cisids by using volatiles extracted from different polypore species to elucidate the host preference/selection mechanisms in these species.

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Table 8. Continued.

Fungi species:	*Piptoporus betulinus*	*Fomes fomentarius*	*Phellinus spp.*	*Stereum hirsutum*	*Stereum rugosum*	*Stereum sanguinolentum*
Fungi group:	(3)	(9)				
Cisidae						
Cis bidentatus	optimal	suboptimal ?	straggler	straggler	optimal ?	straggler
Cis jaquemarti	suboptimal	optimal	straggler	zero	zero	zero
Cis lineatocribratus	straggler	optimal	suboptimal ?	zero	straggler	straggler
Cis comptus	zero	zero	zero	zero	zero	straggler
Cis boleti	zero	zero	zero	zero	zero	zero
Cis hispidus	zero	straggler	zero	zero	zero	zero
Cis punctulatus	zero	zero	zero	zero	zero	zero
Orthocis festivus	zero	zero	straggler	straggler	optimal	zero
Octotemnus glabriculus	zero	zero	zero	zero	zero	zero
Sulcacis fronticornis	zero	zero	zero	zero	zero	zero
Sulcacis affinis	zero	zero	zero	zero	zero	zero
Ennearthron cornutum	zero	optimal ?	zero	zero	zero	zero
Ropalodontus strandi	zero	optimal	zero	zero	zero	zero

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