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**Population dynamics of *Laboulbenia clivinalis* THAXTER  
(Ascomycetes, Laboulbeniales)  
and sex-related thallus distribution on its host  
*Clivina fossor* (LINNAEUS, 1758) (Coleoptera, Carabidae)**

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**Summary**

Aspects of the population dynamics of *Laboulbenia clivinalis* on its host *Clivina fossor* were studied during a complete year-cycle in a series of rivulet associated grasslands. Host activity, fungal prevalence, thallus density and fungal population maturity were determined at regular intervals. Changes in prevalence of the fungus were caused by changes in the host population structure. Thallus density was correlated with host activity. Thallus density reached highest values during the mating-season of the host. Host behavior and microclimatic preferences for relatively high temperature and humidity in the mating-season, provided optimal conditions for the transmission, reproduction and development of *L. clivinalis*. The main reproductive period of the fungus corresponded with the mating season of the host during spring. Thalli of *L. clivinalis* were found on all parts of the integument. Hosts with different behavior (sex, generation) had significantly different thallus density and thallus distribution. Differences in thallus distribution between male and female hosts were significant in the mating-season. Fungus transmission by mating was of major quantitative importance as it affected the entire infection pattern.

*L. clivinalis* is new for Belgium. A list of localities is given as well as suggestions for further research.

Key words: Laboulbeniales, prevalence, thallus density, infection pattern, Carabidae.

### Samenvatting

Aspekten van de populatiedynamica van *Laboulbenia clivinalis* op zijn gastheer *Clivina fossor* werden bestudeerd over een jaarcyclus. Gastheer-activiteit, infectiefrequentie, thallusdensiteit en de maturiteit van de schimmelpopulatie werden bepaald op regelmatige tijdstippen. Veranderingen van de infectiefrequentie van de fungus zijn het gevolg van veranderingen in de populatiestructuur van de gastheer.

Thallus densiteit was gecorreleerd met gastheeractiviteit. Thallusdensiteit bereikt zijn hoogste waarde tijdens de reproductieperiode van de gastheer. Het gedrag en microklimatologische preferenties van de gastheer, met name relatief hoge temperaturen en hoge luchtvochtigheid tijdens de reproductieperiode, vormen ideale omstandigheden voor de transmissie, reproductie en ontwikkeling van *L. clivinalis*. De belangrijkste reproductieperiode van de fungus in het voorjaar stemt overeen met die van de gastheer. Thalli van *L. clivinalis* komen op alle integumenten voor. Gastheren met verschillend gedrag (geslacht of generatie) hebben significant verschillende thallusdensiteit en infectiepatroon. Verschillend infectiepatroon bij mannelijke en vrouwelijke loopkevers werd enkel vastgesteld tijdens de reproductieperiode. De transmissie van de fungus is het grootst tijdens de paring van de loopkevers, het ganse infectiepatroon wordt erdoor bepaald.

*L. clivinalis* is nieuw voor België. Een lijst van localiteiten en suggesties voor verder onderzoek worden gegeven.

### Introduction

Laboulbeniales are obligate epizoic entomogenous Ascomycetes which are exclusively found on Arthropoda, mainly Hexapoda. Their thalli are small and of determinate growth, bearing antheridia and perithecia on a receptacle with appendages (TAVARES, 1985). There is no mycelium and only sexual stages are known. Infection takes place by means of two-celled adherent ascospores which germinate on the surface of the host. Most genera form minute haustoria and cause little or no structural damage to the integument, although SCHELOSKE (1969) showed that Laboulbeniales can extract substances from the haemocoel. Nevertheless, most of the Laboulbeniales are considered harmless (SCHELOSKE, 1969; BENJAMIN, 1971 and TAVARES, 1979 & 1985).

Laboulbeniales are host-specific and their ability to infect and reproduce on a particular host depends on the host's behavior (SCHELOSKE, 1969), its geographical distribution (HULDÉN, 1983; HEDSTRÖM, 1994), habitat preference (SCHELOSKE, 1969; ANDERSEN & SKORPING, 1991), density (DE KESEL, 1993), physico-chemical characters of haemolymph and integument (TAVARES, 1979).

Laboulbeniales are transmitted indirectly by ascospores left on the substrate (LINDROTH, 1948; MEIJER, 1971; ANDERSEN & SKORPING, 1991) or directly by contact with contaminated congeners (SCHELOSKE, 1969). Expe-

perimental studies revealed that direct-infection is much more important than auto-infection (grooming) and substrate-infection (DE KESEL, 1993).

Specific thallus distributions of Laboulbeniales were observed in several host groups and are, when related to the host sex, caused by direct transmission during copulation (BENJAMIN & SHANOR, 1952; RICHARDS & SMITH, 1955; BOYER-LEFÈVRE, 1966; WHISLER, 1968; SCHELOSKE, 1969, 1976a,b; BALAZUC & JUBERTHIE, 1983; HEDSTRÖM, 1994).

*Laboulbenia clivinalis* THAXTER is a common species and is known from Africa, Asia, USSR and 14 European countries (SANTAMARIA, BALAZUC & TAVARES, 1991). It is confined to carabid beetles of the genus *Clivina* LATREILLE. A fortuitous infection on the carabid beetle *Patrobus atrorufus* STROEM was reported by SCHELOSKE (1969). Records for species of Laboulbeniaceus parasites other than *L. clivinalis* on *Clivina fossor* L. are unknown.

The host, *C. fossor* is a predacious ground beetle that belongs to the Carabidae (Coleoptera), one of the largest families within the Hexapoda (THIELE, 1977). *C. fossor* has a circumpolar distribution (LINDROTH, 1945). It occurs on cultivated fields and grasslands, preferring open habitats with patchy and short grassy vegetation (TISCHLER, 1965; TOPP, 1972; THIELE, 1977; DESENDER, 1986). In these habitats *C. fossor* is eurytopic and more or less hygrophilic (DESENDER, POLLET & SEGERS, 1984; DESENDER & TURIN, 1989). *C. fossor* is equipped with burrowing feet and combines an epigaeic and subterranean way of life. *C. fossor* is a spring-breeder and produces one generation per year. It is mainly the adults which hibernate (DESENDER, 1983) and the population consists predominantly of one year old beetles, reproducing during one breeding season (DESENDER & POLLET, 1985). The activity pattern of *C. fossor* usually shows two peaks, one corresponding with increased activity during the mating-season, while a secondary is observed in the summer due to the activity of the new generation beetles which start emerging in June (DESENDER & POLLET, 1985). Activity is controlled by temperature rather than photoperiod (DESENDER & POLLET, 1985). In spring *C. fossor* seeks higher temperatures by showing explicit epigaeic activity (HEYDEMANN, 1962), rather than staying below the soil surface where temperatures are even and still low. The beetles are most active in the evening, when temperature is still relatively high and the humidity is increasing (DESENDER, 1983).

Our knowledge concerning the population dynamics of Laboulbeniales is poor and is based on relatively few parasite-host associations. The existing contributions illustrate that the prevalence of Laboulbeniales is associated with the emergence of the new host generation, determined by the type of life cycle and population structure of the host. The earlier the emergence, the greater the prevalence during overwintering (SCHELOSKE, 1969). Other studies showed that the upper level of prevalence was also determined by climatological factors (HULDÉN, 1983; HEDSTRÖM, 1994) and the habitat chosen by the host (MEIJER, 1971; ANDERSON & SKORPING, 1991).

The aim of this paper is to examine the population dynamics of *L. clivialis*, using fungus prevalence and host population structure, supplemented with quantitative data on host activity, thallus density, fungus population maturity and climatological data. All these parameters provide a basis for examining temporal and spatial changes of thallus density and thallus distribution of *L. clivialis* in hosts of opposite sexes.

### Materials and Methods

A large collection of 12440 specimens, belonging to 86 carabid species was used and is currently held at the Herbarium of the National Botanic Garden of Belgium (BR). The Carabidae originated from ten grasslands, all situated along waterways in the provinces of West-Vlaanderen and Oost-Vlaanderen (Belgium). A discussion concerning the relations between the habitat characteristics of these grasslands and Laboulbeniales are beyond the scope of this paper and will be given in DE KESEL *et al.* (in prep). The beetles were caught by means of continuous pitfall trapping from January 1982 until January 1983. The commonest species was *C. fossor* with a sum total of 1143 specimens occurring in nine stations.

All specimens of *C. fossor* were checked for the presence of Laboulbeniales and stored separately in 70% alcohol.

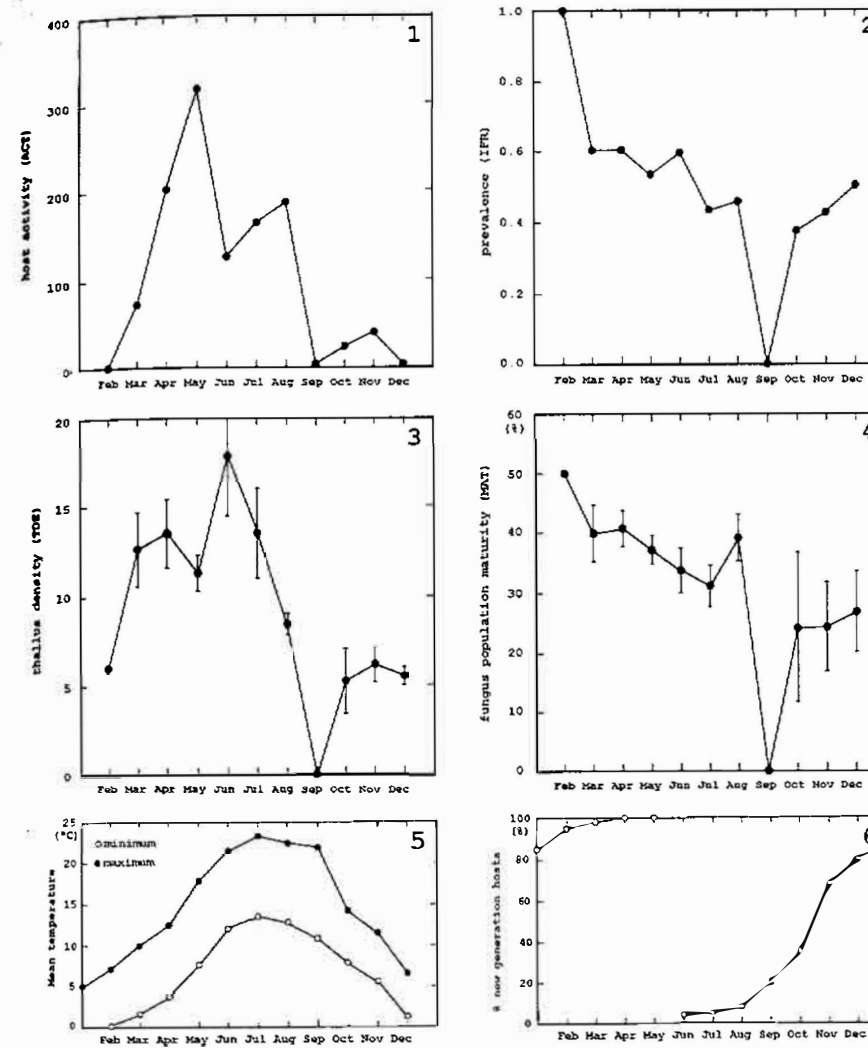
All observations of thalli as well as hosts, were made using a stereomicroscope (WILD M5A) with annular cold light source (VOLPI INTRALUX 6000).

The sex of the hosts was determined by observing the terminal segment of the abdomen in strong light and when the sex could not be distinguished by this method it was determined by dissection.

The activity (ACT) of the host was the total number of specimens caught during each month (Fig. 1). The nature of sampling implies that the measured activity concerns only epigeaic activity, subterranean activity was not determined.

The prevalence or infection-frequency (IFR) indicates the proportion of the host population being studied that was affected by the parasite at a given time (Fig. 2). The reliability of the IFR was low when small numbers of host specimens were considered.

The thallus density (TDE) or total number of thalli present on the entire exoskeleton of the host specimens was determined. All developmental stages of the thalli were taken into account, except for the remains of broken thalli. In an earlier paper, the term infection-size was used instead of thallus density (DE KESEL, 1993). These terms are identical but the latter is preferred due to possible misinterpretation of the term infection-size.



Figs 1-6. Year-cycle of *L. clivialis* on *C. fossor*, 1. Host activity (ACT) number of specimens, 2. Prevalence (IFR), 3. Thallus density (TDE ± s.e.), 4. Fungus population maturity (MAT ± s.e.), 5. Mean temperature (minimum and maximum), 6. Percentage hosts of the new generation, i.e. population structure.

The partial thallus density (PTDE) or the total number of thalli found in a specific area or integumental zone of the exoskeleton of the host specimens was also determined. The following integumental zones were distin-

gushed: antennae, upper cephalon (including eyes), pronotum, right elytron, left elytron, lower cephalon (including mouth parts), prothorax, meso- + metathorax, abdomen and legs (separately).

Mean TDE with standard errors (Fig. 3) and mean PTDE (Table 3) were calculated for each month. The uninfected host specimens (real zeros) were excluded since they contained no information about the variation in thallus density. As Laboulbeniales show cycles of recolonisation when the new host generation emerges, it is obvious that inclusion of zero infections would bias the measured variability. Since young thalli can easily be overlooked it was difficult to distinguish between a true zero (no thalli present on the host) and zeros that were due to errors in observation. Quantifying the infection was performed at high magnification (50X) and was improved by observing the beetles while they were immersed in 80% alcohol solution which made the thalli more conspicuous.

Fungus population maturity (MAT) indicates the proportion of the fungus population being studied that was in a mature stage at a given time (number of mature thalli/total number of thalli) (Fig. 4). Mean MAT with standard errors was calculated for each period excluding uninfected specimens. Two thallus maturity-levels were recognised and distinction between them was based on the capability of producing and releasing spores. Thalli ranging from a germinating spore to a receptacle with a small perithecium and large trichogyne were considered immature (not producing spores). Thalli with full-grown, inflated and pigmented perithecia were considered mature (able to produce and release spores). Distinction of thallus maturity by measurement was found to be too time-consuming considering the high thallus densities and position dependent thallus polymorphism from *L. clivinalis* (DE KESEL, in prep.).

Table 1. Distribution of *L. clivinalis* in Belgium, sampled stations are marked with (\*).

Host	Locality	UTM (Station)	Slide (Date)	
<i>C. fossor</i>	Galmaarden (*)	ES62 (Station G1)	ADK534 (05.05.1982)	
	Galmaarden (*)	ES62 (Station S2)	ADK753 (05.05.1982)	
	Viane (*)	ES62 (Station L5)	ADK728 (17.05.1982)	
	Smeerebbe (*)	ES62 (Station D3)	ADK752 (07.04.1982)	
	Smeerebbe (*)	ES62 (Station R9)	ADK716 (05.05.1982)	
	Hertsberge (*)	ES16 (Station H4)	ADK755 (21.04.1982)	
	Oostkamp (*)	ES16 (Station Z0)	ADK756 (21.04.1982)	
	Poeke (*)	ES35 (Station P7)	ADK754 (17.05.1982)	
	Mere (*)	ES74 (Station E8)	ADK751 (25.08.1982)	
	Zwijnaarde	ES54	ADK335a,b,c (1979)	
	Knokke-Heist	ES29 (Het Zwin)	ADK750 (15.05.1993)	
	<i>C. collaris</i>	Meise	ES86 (BR)	ADK701 (22.04.1992)

Monthly mean minimum and maximum temperatures were obtained from the nearest meteorological stations of the Koninklijk Meteorologisch Instituut (KMI) (Fig. 5).

The population structure of *C. fossor* (Fig. 6) was not determined from the studied material but came from a study of a *C. fossor* population from a relatively dry and intensively grazed pasture (DESENDER & POLLET, 1985). The material in this study came from relatively wet grasslands and extrapolations concerning populations structure and winter-migration should be considered with care. The emergence of the new generation was determined by the presence of teneral beetles.

Graphs and statistical analyses were made using SYSTAT (WILKINSON, 1988a) and SYGRAPH (WILKINSON, 1988b) software.

Differences in thallus density (total or partial) between males and females were tested using the Mann-Whitney U test (SIEGEL, 1956). The degree of association between various infection parameters and host activity was tested with the Spearman rank correlation test (SIEGEL, 1956).

Carabid nomenclature follows DESENDER (1985), whilst the nomenclature of Laboulbeniales follows SANTAMARIA *et al.* (1991).

## Results

### Host range and distribution

*L. clivinalis* was found on *C. fossor* and *C. collaris* Herbst. A list of the localities in Belgium, UTM gridnumbers and most relevant slide references are given in Table 1.

### Parameters

Host epigeic activity or ACT (Fig. 1) shows two peaks, the first in May and a less pronounced one in August. The first tenerals were caught in June which corresponds with observations made by (DESENDER & POLLET, 1985).

From the 1143 specimens 596 were infected with *L. clivinalis*. The prevalence or IFR (Fig. 2) generally fluctuated between 0.37 and 0.60 which indicated that at least 35% of the active host population was infected throughout the year. A decrease in the prevalence was observed in June, which corresponded with the emergence of the new host generation (Fig. 6). Highest values were observed from December to June. Extremes, i.e. zero prevalence in September and 100% in February, are based on very few specimens and should be considered carefully.

Thallus density or TDE (Fig. 3) generally fluctuated between 5 and 20 thalli per beetle, with a maximum value of 300 thalli per insect detected once. The TDE was low in Autumn and Winter, began increasing in Fe-

bruary and peaked in June. TDE increased simultaneously with temperature (Fig. 5) and host activity (Fig. 1). A decrease was observed from June until September, which corresponded with the emergence of the new host generation (Fig. 6). The teneral were always found free of Laboulbena and the rate of appearance of *L. clivinalis* on the new host generation was low and remained low during the Autumn and early Winter as stated earlier.

Fungus population maturity or MAT (Fig. 4) fluctuated between 20% and 50%. The fungus population always consisted of at least 50% immature thalli with the highest maturity level (40%-50%) observed in February. A gradual decrease, theoretically indicating fungus reproduction, was observed from February to October. Maturity increased from September to February suggesting a decline in the reproduction of the fungus during winter.

**Correlations**

Spearman rank correlation coefficients ( $r_s$ ) between host activity (ACT), prevalence (IFR), thallus density (TDE) and fungus population maturity (MAT) are given in Table 2.

Table 2. Spearman rank correlation coefficients ( $r_s$ ) between host activity (ACT), prevalence (IFR), mean thallus density (TDE) and mean fungus population maturity (MAT). Significant  $r_s$ : \*  $p < 0.05$ ; \*\*  $p < 0.01$ .

	TDE	MAT	ACT	IFR
TDE	1.000			
MAT	0.436	1.000		
ACT	0.610 *	0.342	1.000	
IFR	0.591	0.836 **	0.178	1.000
Number of periods = 11				

Thallus density (TDE) and host activity (ACT) were positively correlated ( $r_s = 0.610$ ;  $p < 0.05$ ). Host activity (ACT) and prevalence (IFR) were not ( $r_s = 0.178$ , n.s.). Prevalence (IFR) was positively correlated with the maturity of the fungus population (MAT) ( $r_s = 0.836$ ;  $p < 0.01$ ).

**Thallus distributions**

Thallus density on hosts of opposite sex for the entire year-cycle and for each period separately as well as the Mann-Whitney U statistic is given in the first row of Table 3.

Table 3. Mean TDE and mean PTDE of males and females per period: Partial thallus density (PTDE) for AN = antennae, CU = upper cephalon, PRO = pronotum, EL = left elytron, ER = right elytron, CL = lower cephalon, PT = prothorax, MT = meso+metathorax, AB = abdomen, Legs = pairnumber (1,2 or 3)+R(right) or L(left), N = number of obs., U = Mann-Whitney U values, significant values were underlined, level of significance: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ . January, February and September were omitted (insufficient data to compute test).

TDE and PTDE sex	Mar	Apr	May	Jun	Jul	Aug	Oct	Nov	Dec	Year
Entire	♂ 13.79	20.05	13.25	17.32	12.25	8.05	2.67	5.78	5	13.67
exoskeleton	♀ 12.07	9.78	9.78	18.38	14.49	4.09	6.50	6.63	6	10.52
	U 256	<u>2169.5*</u>	<u>3950.5</u>	<u>760.5</u>	<u>689.5</u>	<u>1304**</u>	4.5	32	0	<u>50573.5**</u>
AN	♂ 0	0.14	0.06	0.13	0	0	0	0	0	0.06
	♀ 0	0	0.01	0	0	0	0	0	0	0.003
	U 210	1755	3516	740	624	893	9	36	0.5	43993
CU	♂ 0.43	0.66	0.38	0.42	0.34	0.21	0	0.67	1	0.42
	♀ 0.27	0.37	0.26	0.43	0.13	0.04	0.67	0.13	0	0.26
	U 215	1767	3708	730	649	952	7.5	36	1	45297
PRO	♂ 0.86	1.32	1.00	1.05	0.75	0.53	1.33	0.22	2	0.93
	♀ 2.17	1.01	1.42	2.22	1.87	0.81	1.50	1.00	2	1.44
	U 169	1640	<u>3078.5</u>	569	487	827	8.5	26.5	0.5	<u>38067.5**</u>
EL	♂ 1.64	1.41	1.56	2.47	1.91	0.84	0	0.56	0	1.54
	♀ 2.43	1.80	2.20	3.32	1.59	0.87	1.83	2.63	3	2.00
	U 190	<u>1304.5*</u>	<u>3030.5</u>	<u>597.5</u>	524	<u>925.5</u>	1.5	17	0	<u>36621**</u>
ER	♂ 1.86	2.11	1.62	1.29	1.03	0.32	0.33	1.11	2	1.37
	♀ 3.43	2.80	2.75	3.14	2.87	0.83	1.33	2.88	0	2.58
	U 140	<u>1413.5</u>	<u>2606.5**</u>	<u>484*</u>	<u>464*</u>	<u>677.5*</u>	5	28	1	<u>32979**</u>
CL	♂ 0.86	0.89	0.60	0.50	0.88	0.53	0	0	0	0.64
	♀ 0.10	0.18	0.02	0.11	0	0.00	0	0	0	0.07
	U 257*	<u>2079**</u>	<u>4403**</u>	<u>829*</u>	<u>799.5**</u>	<u>1128**</u>	9	36	0.5	<u>52972**</u>
PT	♂ 2.50	3.68	2.19	2.63	2.50	2.03	0	1.33	0	2.47
	♀ 1.23	0.90	0.64	1.65	2.15	0.11	0	0	0	0.93
	U 276.5*	<u>2394**</u>	<u>4689**</u>	816	<u>805*</u>	<u>1418**</u>	9	44	0.5	<u>58232**</u>
MT	♂ 1.50	2.09	1.25	2.11	1.16	1.05	0.67	0.89	0	1.46
	♀ 0.23	0.54	0.41	0.76	0.87	0.06	0.33	0	0	0.45
	U 293**	<u>2338.5**</u>	<u>4128**</u>	<u>890.5**</u>	<u>786*</u>	<u>1230**</u>	10.5	44	0.5	<u>55150**</u>
AB	♂ 0.57	1.02	0.63	1.40	0.19	0.05	0.33	0	0	0.63
	♀ 0.30	0.28	0.16	1.97	0.46	0.06	0	0	0	0.41
	U 233.5	<u>2129.5**</u>	<u>3967**</u>	798	585	861	12	36	0.5	<u>47664**</u>
1R	♂ 0.57	0.39	0.30	0.40	0.19	0.16	0	0	0	0.29
	♀ 0.10	0.13	0.18	0.16	0.41	0.04	0	0	0	0.16
	U 205.5	<u>1935.5*</u>	3723	776.5	667	989.5	9	36	0.5	<u>46823.5**</u>
2R	♂ 0.79	1.57	1.03	0.79	0.69	0.68	0	0.22	0	0.93
	♀ 0.17	0.42	0.49	0.62	1.39	0.28	0.33	0	0	0.52
	U 290**	<u>2144**</u>	<u>4280.5**</u>	756	591	1045.5	7.5	40	0.5	<u>50569.5**</u>
3R	♂ 0.79	0.98	0.53	1.00	0.84	0.47	0	0.11	0	0.70
	♀ 0.43	0.55	0.45	0.78	0.56	0.32	0	0	0	0.48
	U 240.5	1985.5	3858	828.5	653.5	1001.5	9	40	0.5	<u>48436.5**</u>
1L	♂ 0.50	1.07	0.38	0.42	0.50	0.18	0	0	0	0.48
	♀ 0.23	0.28	0.22	0.81	0.36	0.02	0	0	0	0.28
	U 240	1854	<u>3700.5</u>	<u>692.5</u>	<u>680.5</u>	<u>992*</u>	9	36	0.5	<u>46317.5**</u>
2L	♂ 0.43	1.36	1.03	1.71	0.78	0.53	0	0.67	0	1.01
	♀ 0.33	0.30	0.37	1.57	0.95	0.26	0.27	0	1	0.52
	U 266*	<u>2172.5**</u>	3698	810	650	1010	7.5	40	0	<u>48946.5**</u>
3L	♂ 0.50	1.16	0.69	1.00	0.50	0.47	0	0	0	0.71
	♀ 0.63	0.23	0.23	0.84	0.87	0.38	0	0	0	0.42
	U 214.5	<u>2077**</u>	<u>4060.5**</u>	772	634	1019	9	36	0.5	<u>48617.5**</u>
N	♂ 14	44	73	38	32	38	3	9	1	254
	♀ 30	78	96	37	39	47	6	8	1	342

Thallus density was significantly higher in males than in females. Significant differences between TDE of males and females were observed in April and August, in both cases the male TDE was higher than the female TDE.

The difference in thallus distribution between males and females, based on the partial thallus densities (PTDE), is also presented in Table 3. The extent of the considered PTDE for males and females is presented in figure 7.

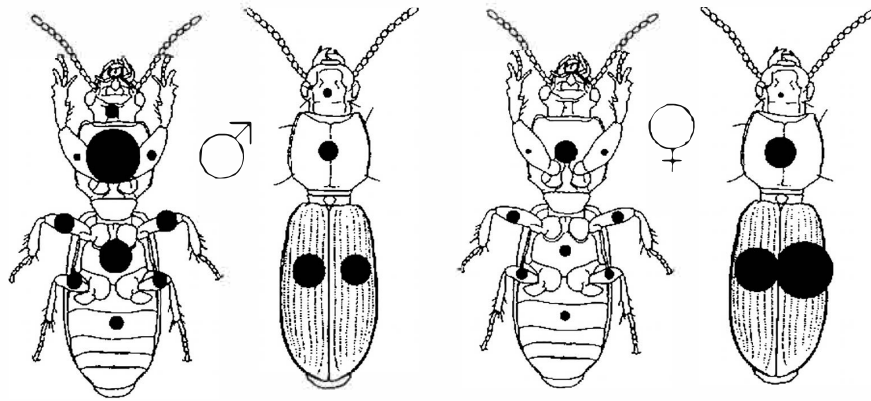


Fig. 7. Partial thallus densities (PTDE) of *L. clivinalis* on upper and lower integuments of males (♂♂) and females (♀♀). Diameter of circles correspond with PTDE-values in table 3 (year-column).

All parts of the exoskeleton of *C. fossor* can be infected by *L. clivinalis*. All the PTDE of males and females, from the entire year-cycle, were significantly different (excepting antennae and upper cephalon). Male and female beetles showed similar thallus distributions from September to February and significantly different thallus distributions from March to August. Maximal qualitative difference in infection patterns of males and females was observed in April and May with respectively 9 and 7 significantly different PTDE.

### Discussion

#### *Differences between opposite sexes*

*L. clivinalis* has significantly different infection patterns on males and females of *C. fossor* as illustrated in figure 7. The observed temporal changes in these infection patterns correspond with the mating season of the host and major significant differences occur only in this period and shortly after. Sex-related infection patterns are frequently encountered on hosts infected with Laboulbeniales (SCHELOSKE, 1969; BENJAMIN, 1971). Mating partners show different infection patterns, as a consequence of

their different behavior and position during mating. While hosts copulate, the parasite transmission is directional and spores from thalli growing on the elytra of the female are transmitted towards the lower integumental areas of the male and vice-versa. Figure 7 shows, by the extent of the PTDE, that direct infections caused by mating were of major importance and dominated the entire thallus distribution of *L. clivinalis*.

#### *Population dynamics of L. clivinalis*

The prevalence and thallus density of *L. clivinalis* were affected by the differential emergence of uninfected new generation imagines in June. This phenomenon was already recognised in other Laboulbeniales (SCHELOSKE, 1969), and it is probably true for most Laboulbeniales parasitizing terrestrial hosts. SCHELOSKE (1969) assumed that spring-breeding hosts with late generation overlap (July-October), which corresponds with *C. fossor*, have a low parasite prevalence in winter. HULDÉN (1983) stated that this was due to the fact that there was not enough time for the majority of the new generation beetles to become infected before winter. In this case time may have been important but other factors, especially when related to the host and its biology, are probably of even greater significance. The prevalence of *L. clivinalis* reached its maximal value in winter which may have been due to enhanced direct- and substrate-infection. The importance of substrate-infection, although small compared to direct-infection (DE KESEL, 1993), must not be underestimated since *C. fossor* leads a mainly subterranean way of life. In relatively dry conditions *C. fossor* shows no winter migration (DESENDER *et al.*, 1981) and both generations stay and hibernate in the contaminated burrows for several months. In relatively wet conditions, i.e. with eventual inundations, both generations of *C. fossor* probably migrate (DESENDER, pers. comm.) towards winter-refugia.

Older generation beetles usually have high thallus densities (DE KESEL, 1993) and their presence during winter, continually allows opportunities for direct infections on the new host generation. Nevertheless winter-time is still a critical period for the survival of *L. clivinalis* because low temperature slows down fungal reproduction and consequently winter thallus density. Also the differential mortality of older generation beetles results in the loss of the majority of thalli in terms of the whole host population and since hosts do not mate until the next spring, an efficient spore transmission between hosts is absent.

HULDÉN (1983) presumed that host activity and prevalence were associated because enhanced host activity implies increased chances of direct infections. Although this association was observed in experiments with *Fanniomyces ceratophorus* (WHISLER) MAJEWSKI from flies by WHISLER (1968), it was not demonstrable for *L. clivinalis*. There may be an association between host activity and prevalence, but it is difficult to recognise in natural populations, considering the large number of parameters involved.

Host activity and thallus density were significantly associated but assumptions should be made carefully since changes in host population struc-

ture also affected thallus density, as stated earlier. The increasing temperature, host activity and the specific microhabitat selection of the host in spring, enhanced fungus reproduction, spore transmission and consequently thallus density. There was a direct effect of host activity on thallus density; the greater the activity of hosts, the higher the spore transmission by means of mating. However, the prevailing temperature affected both host activity and fungus reproduction. The same common cause (temperature) increased the host activity and fungus reproduction, hence increasing the correlation caused by the direct effect of host activity on thallus density. Increasing host activity in late summer did not, however, result in increasing thallus density which indicated that it was associated with the activity of non-copulating hosts, i.e. the new generation.

The correlation between prevalence and maturity of the fungus population should be considered as illusory since no reasonable direct connection between these variables can be found. Correlations that have time as a common factor and processes that change with time are frequently likely to be correlated, not because of any functional biological reason, but simply because the change with time in the two variables under consideration happens to be in the same direction (SOKAL & ROHLF, 1981).

It is beyond dispute that assumptions concerning correlations between infection parameters and host related parameters will be more reliable when endorsed by experimental results.

The study of the population dynamics of Laboulbeniales is promising, considering the wide variety of Laboulbeniales and the life-cycles of the hosts they infect. The most interesting approach, in the near future, would be to concentrate on Laboulbeniales from hosts with a similar life-cycle but different habits and preferences, in order to assess the sensitivity of the method presented here. New parameters, such as host population density and habitat characteristics should also be included because they can play an important role in the growth rate of the fungus population (DE KESEL, 1993). Some of the presented parameters, especially fungus population maturity, can probably be refined by increasing the number of considered maturity stages of thalli.

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I

**A propos du genre *Dendrocerus* RATZEBURG, 1852  
Les especes du groupe «penmaricus»  
(Hymenoptera Ceraphronoidea Megaspilidae)**

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**Summary**

The Author first exposes some general considerations on the characters important for the diagnosis, the description and the identification of the species of the genus *Dendrocerus* RATZEBURG, 1852; then, he proposes the repartition of the species, at least for the males, into 5 artificial groups, grounded on the form of the antennae. Then, he studies the species of the so defined 5<sup>th</sup> group: the «penmaricus» group. He redescribes the known species and adds three new ones, namely *Dendrocerus zoticus* (0, Mexico), *D. cyclopeus* (0, United States) et *D. tibialis* (0, 'a', Sulawesi), *n. spp.* He finally proposes dichotomic keys, one for the males, the other for the females of this group.

Key words: Megaspilidae, *Dendrocerus*, species groups, Ceraphronoidea.

**Resume**

L'auteur expose d'abord quelques considerations genera/es sur /es caracteres importants pour la diagnose, la description et /'identification des especes du genre *Dendrocerus* RATZEBURG, 1852; puis, ii propose la repartition des especes, du moins pour /es males, en 5 groupes artificiels, fondees sur /'allure des antennes. Ensuite, ii etudie /es especes du 5<sup>e</sup> groupe ainsi defini: le groupe «penmaricus». Il en redecrit /es especes connues et y ajoute 3 nouvelles, ii savoir: *Dendrocerus wticus* (0, Mexico), *D. cyclopeus* (0, Etats-Unis) et *D. tibialis* (0, 'a', Sulawesi), *n. spp.* Enfin, ii propose des tableaux dichotomiques, un pour /es males, l'autre pour /es femelles, de ce groupe.

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