Species diversity of rainborne hyphomycete conidia from living trees

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Rainwater from live trees was collected in forests of Germany, Hungary, Romania and Sweden between July 2003 and September 2005 and analysed for hyphomycete conidia. Stauro- and scolecoconidia of 62 species comparable to those of the so-called aquatic hyphomycetes were recorded in stemflow and throughfall samples collected from 25 trees. The number of species per tree ranged from 3 to 20. Stauroconidia occurred in much greater numbers than scolecoconidia. The most frequent was *Trifurcospora irregularis*, which occurred in 72% of the samples. *Retiarius bovicornutus* was recovered from all tree species. A rich variety of conidia of *Dwayaangam* and *Trinacrium* species were observed. A great number of unknown kinds of conidia were also found. Some of these forms had formerly been recorded in stream water or foam. Further evidence of the wide distribution in canopies of a group of hyphomycetes, tentatively termed as "arboreal" or "terrestrial aquatic hyphomycetes" is discussed.

Key words: arboreal aquatic hyphomycetes, canopy, living tree, rainwater, scolecoconidia, stauroconidia, terrestrial aquatic hyphomycetes

Introduction

The taxonomy and ecology of aquatic hyphomycetes have been extensively studied since the initial discovery of 16 species in streams by Ingold (1942). We know little, however, about a group of hyphomycetes with mostly stauroconidia strikingly similar to those of the Ingoldian fungi (Descals *et al*., 1995), and which live in tree canopies. However, while the saprotrophic habit of aquatic hyphomycetes is evident, we do not know if species in canopies are saprobionts or epiphytes. Many of these hyphomycetes in canopies remain so far unexplored.

Bandoni (1981) reported conidia of aquatic hyphomycetes in rainwater draining from living trees, including those of some well-known, stream-dwelling Ingoldian fungi and those of *Tripospermum* and of some unknown

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species. Mackinnon (1982) in a one-year study of stemflow and throughfall from red alder-trembling aspen forest in British Columbia found conidia of numerous hyphomycete species. He recorded *Clavariopsis aquatica, Gyoerffyella biappendiculata, Gy. gemellipara, Lateriramulosa uniinflata* and species belonging to *Flabellospora*, *Tetracladium, Tricladium* and a number of conidia of unknown identity. He found that seasonal sporulation of most fungi had positively been correlated with precipitation. Carroll (1981) proposed the existence of a guild of fungi that may "function in canopies much as classical Ingoldian aquatic hyphomycetes in streams". He called this group „canopy fungi or arboreal aquatic hyphomycetes". In a series of papers Ando and Tubaki (e.g. 1984a,b), described several new hyphomycete genera and species which were later termed "terrestrial aquatic hyphomycetes" by Ando (1992). Ando and Tubaki (1984a) were of the opinion that these hyphomycetes may live on intact leaf surfaces and are capable of using several forms of water (rain, fog, dew) for sporulation. These studies and their intriguing hypotheses have received little attention in the past decade.

Czeczuga and Orlowska (1999) recorded 57 mainly dematiaceous and aero-aquatic hyphomycetes and some Ingoldian aquatic hyphomycete species, e.g. *Articulospora prolifera*, *Colispora elongata*, *Pleuropedium tricladioides* and *Sigmoidea prolifera*, in rainwater draining from trees. In two recent studies, hyphomycete conidia resembling in their structure to those of the Ingoldian fungi were reported from water-filled treeholes and from rainwater draining from living trees (Gönczöl and Révay, 2003, 2004). In a more recent study (Magyar *et al*., 2005) stauro- and scolecoconidia (most of them previously reported from rainwater draining from living trees) were discovered in commercial honeydew honeys derived from Mediterranean regions in Europe. It was hypothesized that conidia occurring on various canopy surfaces had stuck onto insect honeydew and were then accidentally gathered by honeybees. This finding is a further evidence of the wide distribution of this special fungal group in canopies.

It is common to find aquatic hyphomycetes fruiting on their substrates in streams, but we know little about the substrates of "arboreal aquatic hyphomycetes". Very few of these fungi have been seen fruiting on their natural substrates in canopies. A number of them however, could be isolated as conidia and cultured (e.g. Ando and Tubaki, 1984a,b).

It is noteworthy that none of the numerous studies on the microflora of the phylloplane report "arboreal aquatic hyphomycetes" or any other stauroconidial hyphomycetes (Dix and Webster, 1995). Although various detecting techniques have been applied to explore phyllosphere fungi, the only reports are of common, ubiquitous, saprobiontic or weakly parasitic fungi in genera such as *Alternaria*, *Botrytis, Cladosporium*, *Drechslera, Epicoccum* and some others. One of the possible reasons for this lack of records stauroconidia is that canopies were not collected in rainy weather. For example, Hudson and Sutton (1964) only encountered a few conidia of *Trisulcosporium acerinum* on dry leaves but hundreds after a prolonged wet spell.

The aims of this study were: (a) to show the great diversity of rainborne hyphomycete conidia from living trees that are similar to those of the Ingoldian fungi; and (b) to present further evidence of their wide geographic distribution in Europe.

Materials and methods

Rainwater samples were occasionally collected from live trees between July 2003 and September 2005 in Germany, Hungary, Romania and Sweden. Eight tree species were sampled. All were selected from forests except sample 21, which was from an urban environment. The tree species from which the samples were taken and the date and location of samplings are listed in Table 1.

The sampling techniques were: 1./ stemflow from broad-leaved trees was drawn with a 5 ml disposable medical, plastic syringe. During heavy rain, when the stemflow was copious, 4 ml of the suspension were collected per sample and fixed in one ml of FAA (Ingold, 1975). During small showers, a lesser quantity of water, sometimes only 1 or 2 ml, could be collected. 2./ Throughfall samples were collected from *Picea abies*, *Pinus sylvestris* and *Taxus baccata* because no stemflow appeared on their trunks even during heavy rains. Here the foliage was shaken onto a nylon sheet, coarse debris was filtered out and the clean suspension was decanted into a glass container and fixed. Water samples were membrane filtered in the laboratory, and the filters stained and scanned for fungal spores. Conidia were identified and counted. Slide preparations have been kept in the slide collection of BP.

Results and discussion

This study focused on those hyphomycete conidia, which are similar in their structure to those of Ingoldian fungi. Conidia of well-known corticicolous or foliicolous hyphomycetes (and some coelomycetes) which can regularly be seen in rainwater from living trees (e.g. *Asterosporium asterospermum*, *Cercospora* spp., *Cylindrocarpon* spp. and *Excipularia fusispora*) were omitted. It is interesting to note that spores of common phylloplane fungi such as *Alternaria, Botrytis, Cladosporium, Epicoccum* and *Stemphylium* were relatively rarely seen, and also ignored.

Table 1. The tree species investigated for fungal spores.

Serial no.	Tree species	Location		Date
1	*Fagus sylvatica*	Tübingen	Germany	4 Jul. 2003
2	*Fagus sylvatica*	Tübingen	Germany	4 Jul. 2003
3	*Fagus sylvatica*	Tübingen	Germany	4 Jul. 2003
4	*Fagus sylvatica*	Tübingen	Germany	4 Jul. 2003
5	*Fagus sylvatica*	Tübingen	Germany	4 Jul. 2003
6	*Fagus sylvatica*	Tübingen	Germany	9 Jan. 2004
7	*Fagus sylvatica*	Tübingen	Germany	9 Jan. 2004
8	*Fagus sylvatica*	Tübingen	Germany	9 Jan. 2004
9	*Fagus sylvatica*	Tübingen	Germany	9 Jan. 2004
10	*Fagus sylvatica*	Tübingen	Germany	9 Jan. 2004
11	*Prunus avium*	Tübingen	Germany	9 Jan. 2004
12	*Carpinus betulus*	Tübingen	Germany	9 Jan. 2004
13	*Alnus glutinosa*	Szokolya	Hungary	3 Jun. 2004
14	*Alnus glutinosa*	Szokolya	Hungary	3 Jun. 2004
15	*Alnus glutinosa*	Királyrét	Hungary	3 Jun. 2004
16	*Alnus glutinosa*	Királyrét	Hungary	3 Jun. 2004
17	*Quercus cerris*	Királyrét	Hungary	3 Jun. 2004
18	*Quercus cerris*	Királyrét	Hungary	3 Jun. 2004
19	*Fagus sylvatica*	Királyrét	Hungary	9 Jun. 2005
20	*Fagus sylvatica*	Királyrét	Hungary	9 Jun. 2005
21	*Taxus baccata*	Budapest	Hungary	28 Apr. 2005
22	*Picea abies*	Stockholm	Sweden	8 Sep. 2005
23	*Pinus sylvestris*	Stockholm	Sweden	8 Sep. 2005
24	*Picea abies*	Izvoras	Romania	28 Jun. 2005
25	*Picea abies*	Izvoras	Romania	29 Sep. 2005

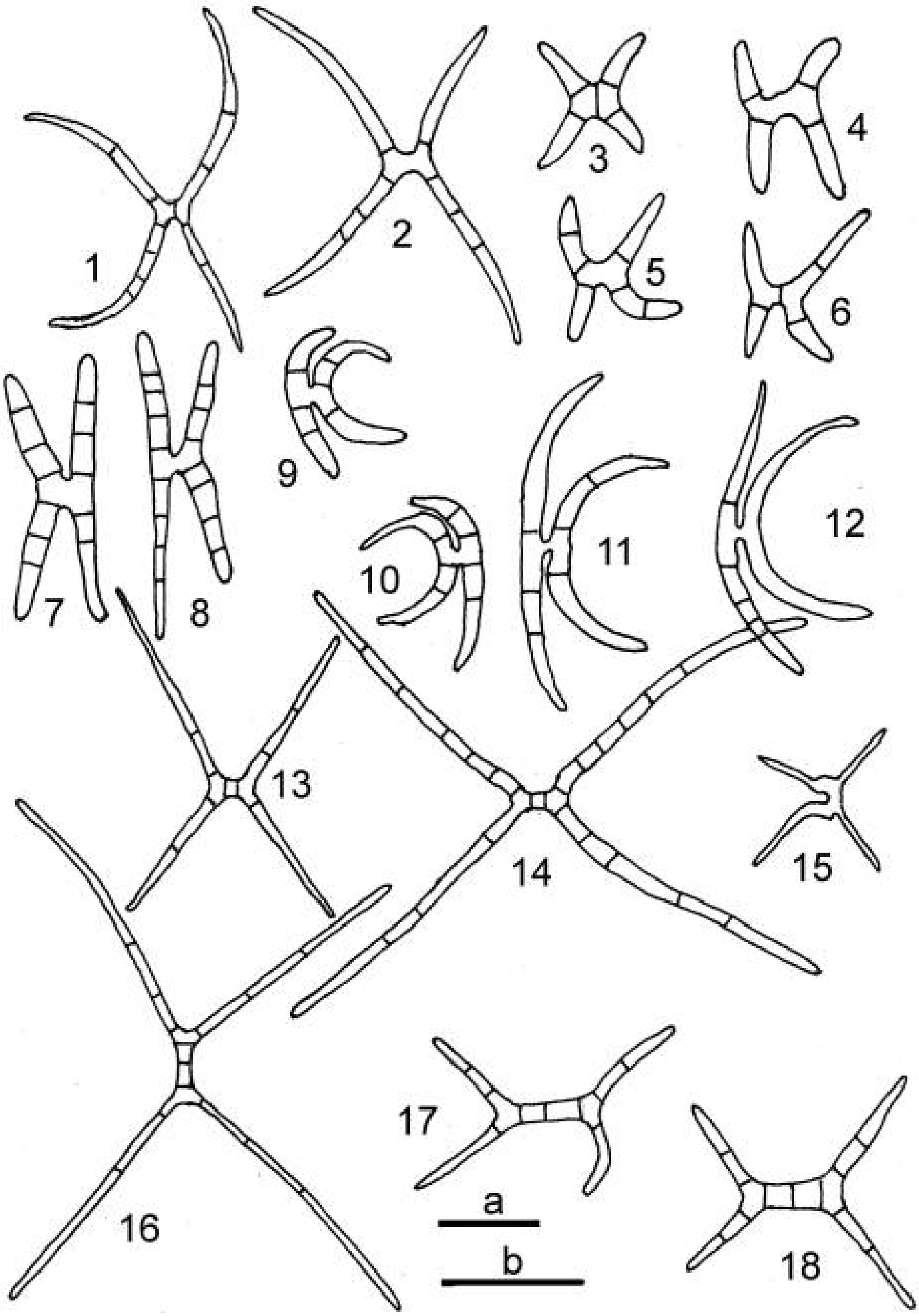
The species encountered and the numbers of conidia are listed in Table 2. Conidia of 62 hyphomycetes were detected from the 25 trees examined. The majority was moniliaceous. Stauroconidia (Figs. 1-78) occurred in much greater numbers than scolecoconidia (Figs. 79-84). The most frequent was *Trifurcospora irregularis*, which occurred in 72% of the samples. Others frequently found were Unknown sp. 14 (56%), Unknown sp. 16 (56%), *Retiarius bovicornutus* (52%), Unknown sp. 1 (52%), *Titaea complexa* (48%), *Trinacrium* sp. 1 (48%), *Trinacrium* sp. 2 (48%), *Tripospermum camelopardus* (40%) *and Tripospermum myrti* (40%). *Retiarius bovicornutus* was recovered from all tree species. *Titaea complexa* and Unknown sp. 1 were especially frequent on *Fagus*, and sometimes abundant. *Trinacrium* sp. 2 was extremely abundant on *Quercus*. More than half of the species were restricted in distribution, 12 out of 62 occurred on two trees and 24 species on single trees. The number of species per tree ranged from 3 to 20. The most species-rich sample was found in summer stemflow from a *Fagus* tree in Hungary.

Table 2. Hyphomycete species found in rainwater collected from different trees. nu = numerous, * = not recorded in the previous study (Gönczöl and Révay, 2004).

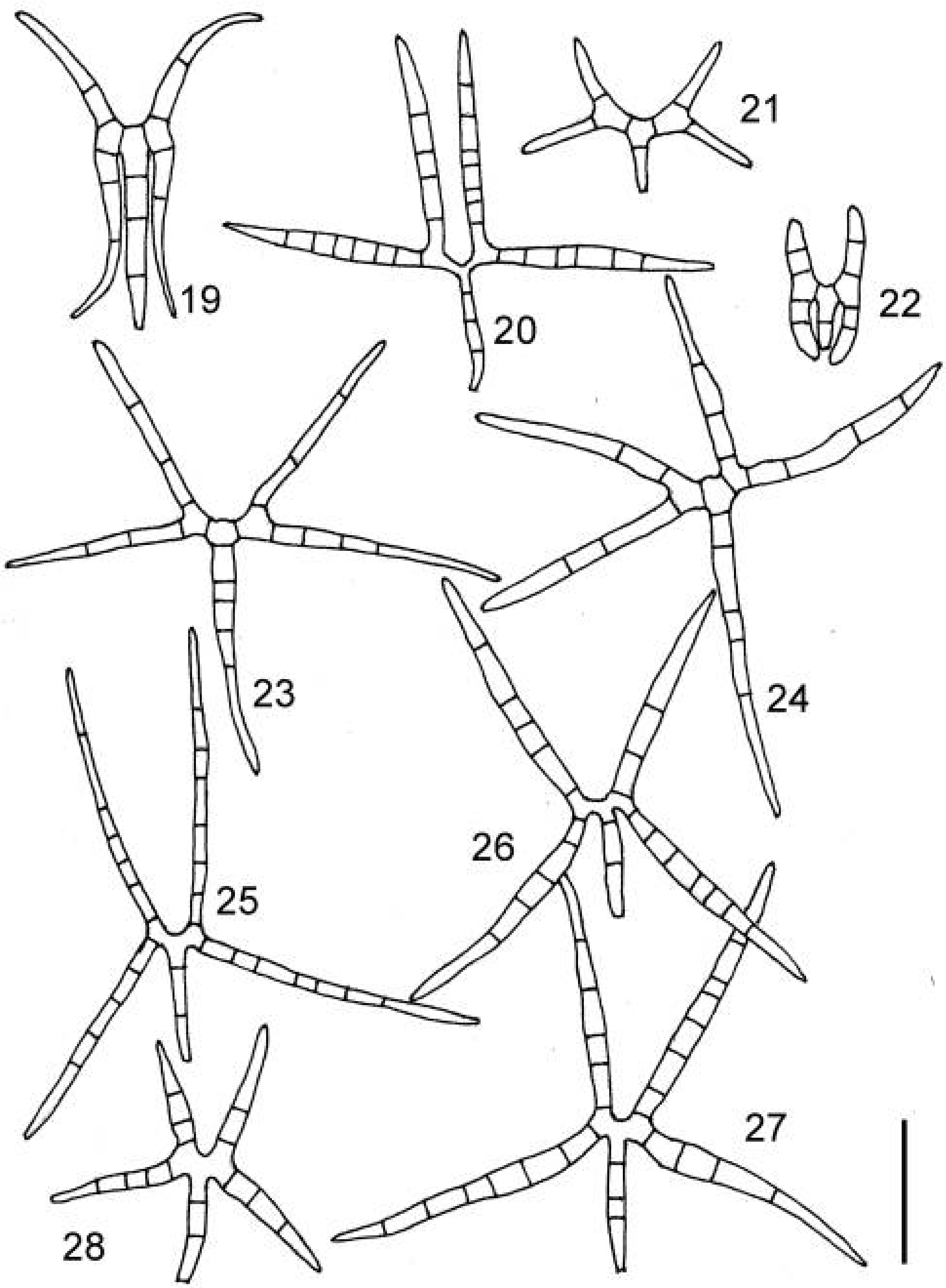
Species	Tree species																								
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
**Anguillospora crassa* Ingold																								2	
Arborispora paupera Marvanová & Bärlocher		1			2						4	20							1			3			
**Atichia millardetii* Raciborski																								6	
**Camposporium* sp.																				4					
Cephaliophora sp. ?		5	3		1	5	8									1			6	1	10				
**Ceratosporium cornutum* Matsush.																					1	5	1		
Curucispora flabelliformis Ando	1										1	1					1								
Curucispora ponapensis Matsush.	1										8												1	18	11
**Curucispora* sp.													6	7	5	9									
Diplocladiella scalaroides Arnaud ex Matsush.												1													
**Dwayaangam cornuta* Descals ?							1					1													
Dwayaangam dichotoma Nawawi												1								4					
Dwayaangam yakuensis Matsush.				7																					
**Dwayaangam* sp. 1															20	9			2	1	2				
**Dwayaangam* sp. 2						1									1										
Dwayaangam sp. 3	2																				67	2	3		
**Dwayaangam* sp. 4																						2			
**Dwayaangam* sp. 5					2																	1			
**Dwayaangam* sp. 6																						1			1
**Enantioptera* sp. ?																					1				
Isthmotricladia sp.		1			2	5				1		1													
**Magdalaenaea monogramma* G. Arnaud																			1						
Retiarius bovicornutus Olivier	1	2			2			1			10	2	1				2				3	5	20	36	4
**Retiarius* sp. ?																								30	2
**Speiropsis pedatospora* Tubaki																								18	
Titaea clarkeae Ellis & Everh.											21								1					1	
Titaea complexa Matsush. ?	8		2	8	1	18	19		1	2		4							110	37				3	
**Titaea* sp. ?					1										5	3			4	1				1	
Tricelulla aquatica Webster																				16					
**Tricladiella pluvialis* Ando & Tubaki																								7	
Tricladium castaneicola Sutton																			16	30					

Table 2 continued. Hyphomycete species found in rainwater collected from different trees.

Species	Tree number																								
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
**Tricladium* sp. 1 ?						3																			
**Tricladium* sp. 2 ?																					12				
Trifurcospora irregularis (Matsush.) Ando & Tubaki	4	19		10	4	19	5			3	28	3		2	5	18	15	7	1	4			3	4	
Trinacrium robustum Tzean & Chen												1								2				3	
Trinacrium subtile Riess	1																				26			4	5
Trinacrium sp. 1		4	1	45	6		1	4				20	2					1	15		4			4	
Trinacrium sp. 2	30	5	5	10	8							3			10	2	nu	nu	11	15					
Trinacrium sp. 3																					5				
Trinacrium sp. 4														2					8	2					
**Trinacrium* sp. 5																					6				
Tripospermum camelopardus Ingold, Dann & McDougal	1	1			5					2								2	1	1		1	1	20	
Tripospermum myrti (Lind) Hughes	4				4			1			5	3		1				7	1	2	8				
**Tripospermum* sp.																								4	
**Triscelophorus* sp.																				1					
**Trisulcosporium acerinum* H.J. Huds. & Sutton																								18	
Unknown sp. 1	18	2	4	18	1	1	70		2	4		15							1	4	1				
Unknown sp. 2				1			11				7							1		31	13				
*Unknown sp. 3					1																				
*Unknown sp. 4															2										
*Unknown sp. 5	1			2	5																				
*Unknown sp. 6																				2					
*Unknown sp. 7					2						1														
*Unknown sp. 8														2											
*Unknown sp. 9															1										
*Unknown sp. 10																			2						1
*Unknown sp. 11	2		1																						
*Unknown sp. 12			4																						
*Unknown sp. 13	1										1				11	5			2						
Unknown sp. 14	21	5		3	7	1	4			1	4	10		nu		1		4	3	6					
Unknown sp. 15																						7	2	10	4
Unknown sp. 16	12	5	7	6	4	8	3	2	3		7	4							4	nu	4				
Number of species	16	11	8	10	18	9	9	4	3	6	12	16	3	6	9	8	4	7	19	20	15	9	7	18	7



Figs. 1-18. Stauroconidia from rainwater. **1-2.** *Curucispora ponapensis*. **3.** *Curucispora* flabelliformis. **4-6.** *Curucispora* sp. **7-8.** Unknown sp. 1. **9-12.** Unknown sp. 2. **13.** *Tricladium* sp. 1. **14.** Unknown sp. 3. **15.** Unknown sp. 4. **16.** *Tricladium* sp. 2. **17-18.** Unknown sp. 5. Bars = 20 µm, Fig. 16 with scale a, remaining to scale b.



Figs. 19-28. *Dwayaangam* species. **19.** *Dwayaangam cornuta*. **20.** *Dwayaangam dichotoma*. **21.** *Dwayaangam* sp. 1. **22.** *Dwayaangam yakuensis*. **23-24.** *Dwayaangam* sp. 2. **25-27.** *Dwayaangam* sp. 3. **28.** *Dwayaangam* sp. 4. Bar = 20 µm.

Remarks on some species

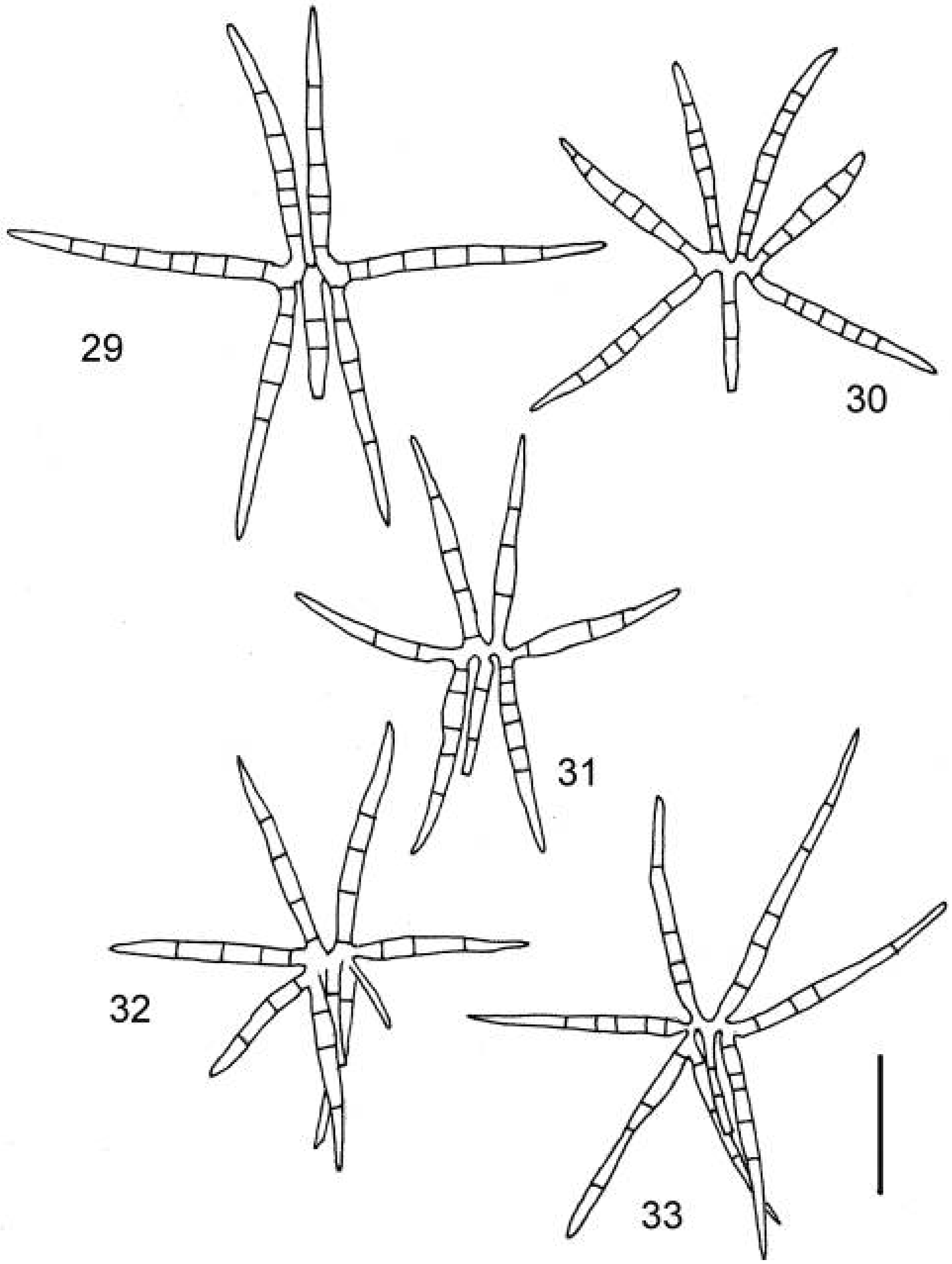
A surprisingly great variety of conidia similar in basic structure to those of *Dwayaangam* were found during this study (Figs. 19-33). The genus *Dwayaangam* was erected by Subramanian (1977) for *Triposporina quadridens*, to accommodate the nonannelidic *Triposporina*-like fungi. It is characterized by having hyaline stauroconidia that consist of a main axis branching twice dichotomously near the apex to form four secondary branches. Six species were subsequently described: *Dwayaangam yakuensis* (Matsush.) Matsush. (1981), *D. cornuta* Descals (Descals and Webster, 1982), *D. dichotoma* Nawawi (1985), *D. heterospora* Barron (1991), *D. gamundiae* Cazau, Aramb. and Cabello (1993) and *D. junci* Kohlm., Baral and Volkm.-Kohlm. (1998). During our study some conidial forms with more complicated structures than those seen so far in this genus were also recovered. For example, conidia with six secondary branches were found on *Fagus sylvatica* in Germany and *Picea abies* in Sweden (Figs. 29-31.). Conidia with seven or eight secondary branches were collected from *Picea abies* in Romania and Sweden (Figs. 32-33).

It appears that *Dwayaangam* may be worldwide in distribution as fungi assignable to this genus have been reported from widely separated geographical locations, e.g. Argentina (Cazau *et al*., 1993) Britain (Ingold, 1974), Hungary (Gönczöl and Révay, 2004), Japan (Ando and Tubaki, 1984a; Matsushima, 1989), New Zealand (Aimer and Segedin, 1985; Barron, 1991) and Uganda and Zimbabwe (Ingold, 1958). During the present study conidia of different *Dwayaangam* species were collected in all of the four European countries.

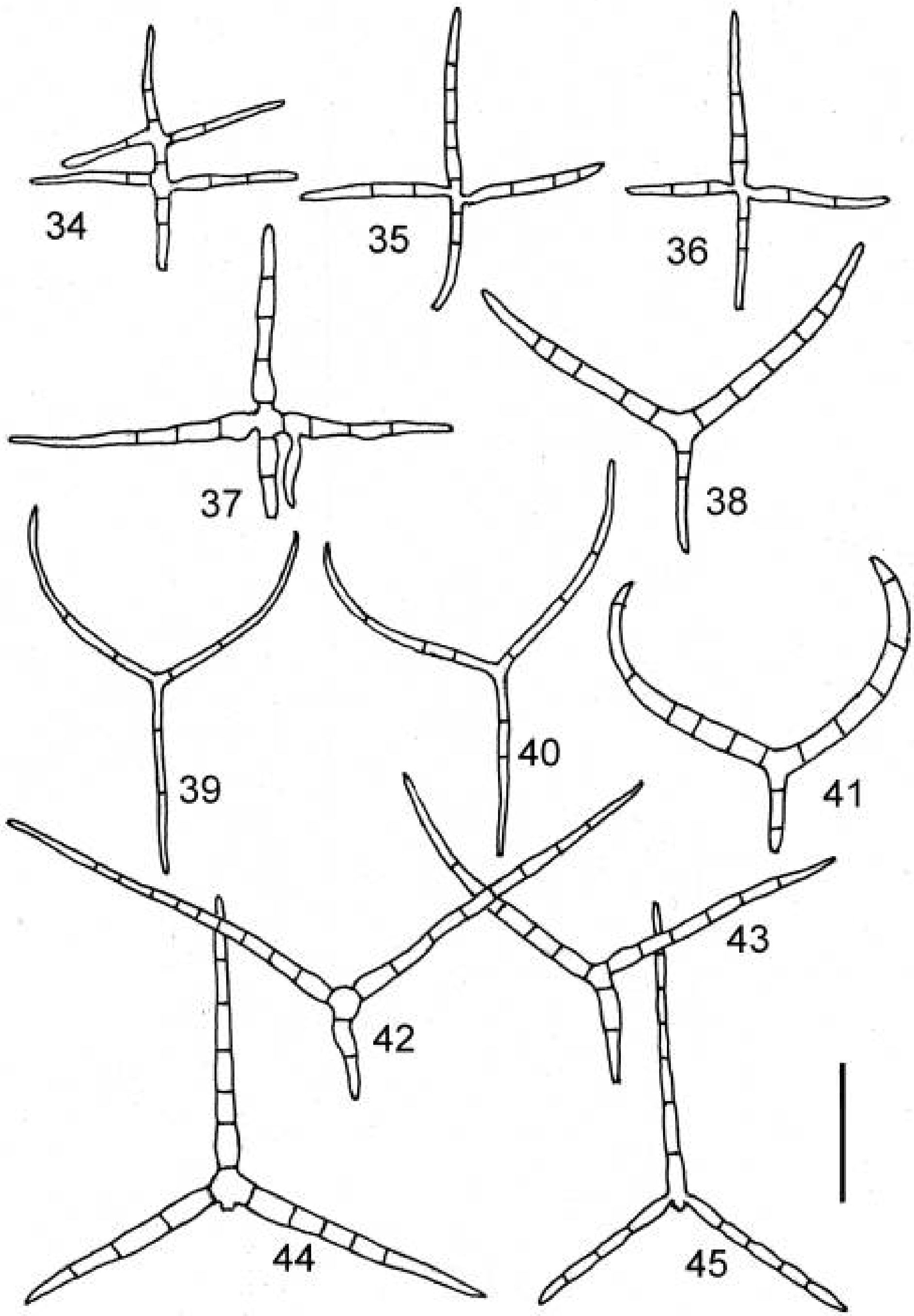
A rich variety of conidia of *Trinacrium* species was also found (Figs. 46-55). *Trinacrium robustum* and *T. subtile* were recognized, but other forms could only be tentatively adscribed to this genus. A great variety of *Trinacrium* species in rainwater from living trees and in water from treeholes and from honeydew honeys has been reported in recent studies (Gönczöl and Révay, 2003, 2004; Magyar *et al.,* 2005). These findings suggest that canopies are an important habitat for *Trinacrium* spp.

Conidia belonging to species of *Curucispora*, *Titaea*, *Trifurcospora*, *Tripospermum*, plus those of Unknown sp. 1 and Unknown sp. 2 were also regularly found in the present and previous studies.

Conidia of *Curucispora flabelliformis* were found in stemflow from *Carpinus betulus*, *Fagus sylvatica* and *Prunus avium* in Germany and from *Quercus cerris* in Hungary (Fig. 3). During our former study it was frequently seen from *Chamaecyparis lawsoniana*, *Koelreuteria paniculata*, *Platanus*



Figs. 29-33. *Dwayaangam* species. **29-31.** *Dwayaangam* sp. 5. **32-33.** *Dwayaangam* sp. 6. Bar = 20 μm.

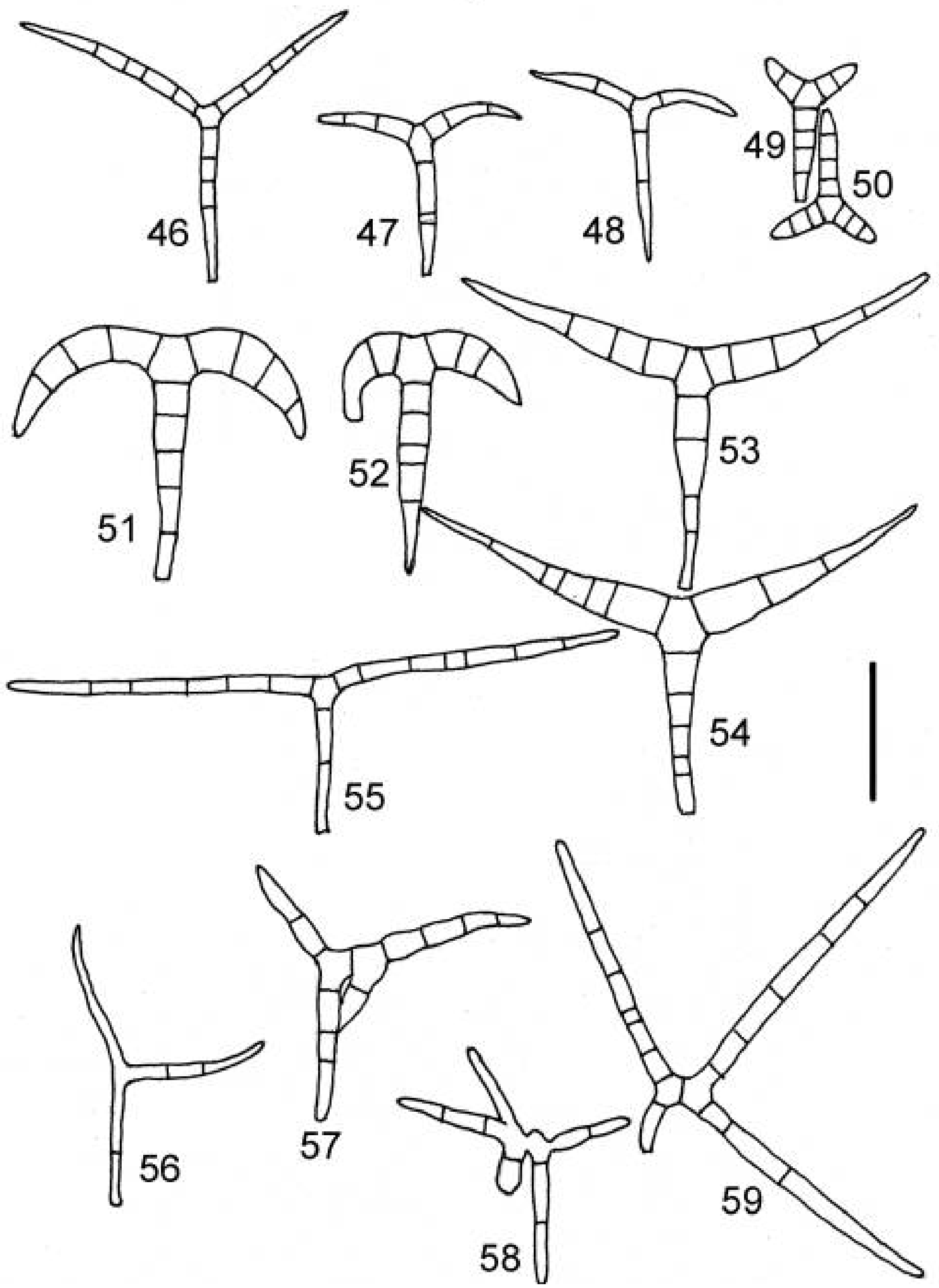


Figs. 34-45. Stauroconidia from rainwater. **34.** *Enantioptera* sp. **35-36.** *Arborispora paupera*. **37.** Unknown sp. 6. **38.** *Retiarius bovicornutus*. **39-40.** *Retiarius* sp. **41.** *Ceratosporium cornutum*. **42-43.** Unknown sp. 7. **44.** *Trifurcospora irregularis*. **45.** *Trisulcosporium acerinum*. Bar = 20 µm.

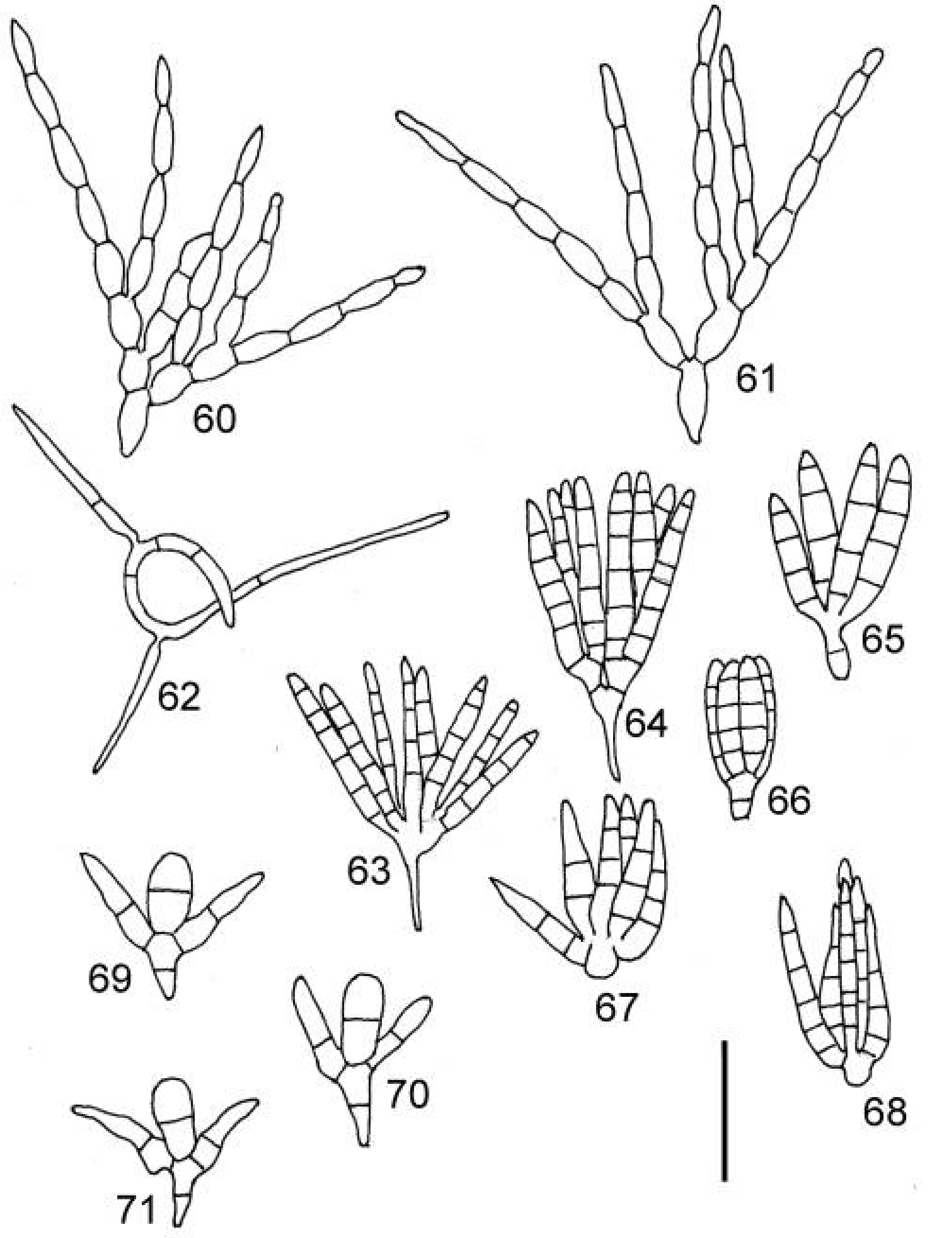
hybrida and *Tilia cordata* in Hungary and it was referred to as an unknown form (Gönczöl and Révay, 2004, Fig. 13). The present and previous records suggest that *Curucispora flabelliformis* is widely distributed in canopies. Ando (1993) isolated this fungus from fallen leaves in Japan, which suggests a litter inhabiting species. Another conidial form, referred to as *Curucispora* sp. (Figs. 4-6) is similar in size to those of *Curucispora flabelliformis*, but it is somewhat different in shape and septation. *Curucispora* sp. is also similar to *Curucispora ponapensis*, but with conidia smaller and wider. *Curucispora* sp. is restricted to *Alnus glutinosa* in Hungary.

In this study 34 species had not been reported in our previous study (Gönczöl and Révay, 2004). A great number of unknown kinds of conidia have also been found. The majority had to our best knowledge not been figured elsewhere. Two conidia of Unknown sp.4 (Fig. 15) were found on *Alnus*. Similar conidia were illustrated by Ingold, who had been found in great numbers in a foam sample from Britain (Ingold, 1974, Fig. 7A).

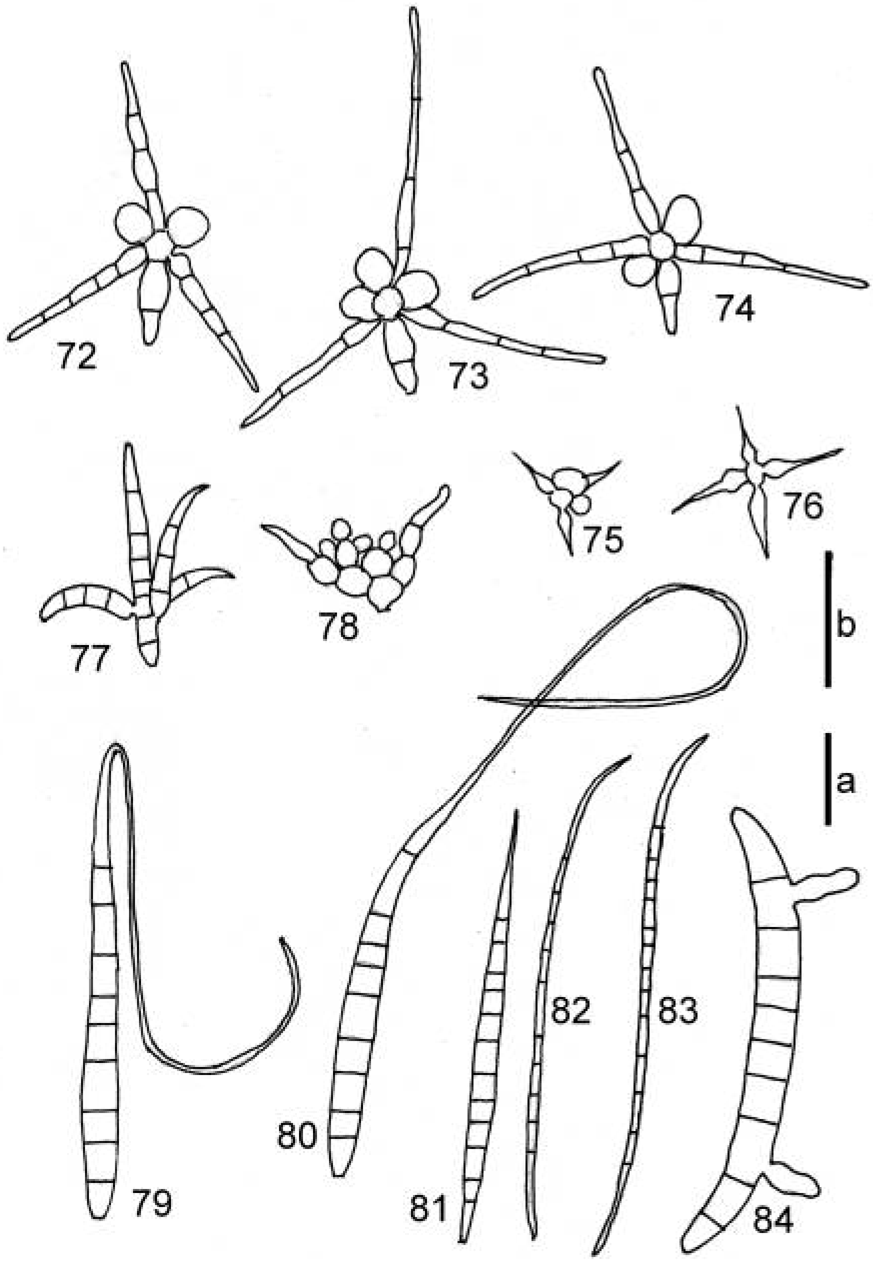
In Gönczöl and Révay (2004) only some conidia of a few Ingoldian hyphomycetes were seen in rainwater samples. This observation also applies to the present study, i.e. two typical conidia of *Anguillospora crassa*, some conidia of *Triscelophorus* sp. (Fig. 77) and *Dwayaangam cornuta* (Fig. 19) were scarely encountered in this study. This reinforces our belief that an ecological group of hyphomycetes distinct from those in lotic habitats exists and functions in canopies. This was also hypothesized by Carroll (1981) and Ando (1992). However, the natural sporulating medium of a number of these "canopy" species has remained unclear since their description. For example, *Dwayaangam dichotoma* isolated from foam in a small stream in Malaysia sporulates underwater *in vitro*. This species appeared to be a true aquatic hyphomycete in the tropics (Nawawi, 1985). *Arborispora paupera,* isolated from a stream in Canada, and "sporulating upon submergence but above water", was also believed to be a stream inhabitant (Marvanová and Bärlocher, 1989). Conidia of *Trisulcosporium acerinum* (unknown at the time) were repeatedly recorded from stream foam in Uganda and Nigeria (Ingold, 1958, 1959). Some years later such conidia were again seen on leaves of *Acer pseudoplatanus* and cultured and described as a new species by Hudson and Sutton (1964). It is important to note that sporulation of this fungus could only be obtained after colonies had been aerated in water. Ando and Tubaki (1984c) also isolated and cultured this species from rainwater on *Sasa* sp. in Japan, but no details were given on sporulation conditions. We have found numerous conidia of the three above species in our rainwater samples, implying their wide geographic distribution in canopies.



Figs. 46-59. *Trinacrium* and some other staurosporous species. **46.** *Trinacrium subtile*. **47-48.** *Trinacrium* sp. 1. **49-50.** *Trinacrium* sp. 2. **51-52.** *Trinacrium* sp. 3. **53-54.** *Trinacrium* sp. 4. **55.** *Trinacrium* sp. 5. **56.** Unknown sp. 8. **57.** *Tripospermum camelopardus*. **58.** *Tripospermum* sp. **59.** Unknown sp. 9. Bar = 20 µm.



Figs. 60-71. Stauroconidia from rainwater. **60-61.** *Speiropsis pedatospora*. **62.** *Tricladiella pluvialis*. **63-64.** Unknown sp. 10. **65-66.** Unknown sp. 11. **67-68.** Unknown sp. 12. **69-71.** Unknown sp. 13. Bar = 20 µm.



Figs. 72-84. Strauro- and scolecoconidia from rainwater. **72-74.** *Titaea* sp. **75-76.** *Titaea complexa*. **77.** *Triscelophorus* sp. **78.** *Atichia millardetii*. **79-80.** *Camposporium* sp. **81.** Unknown sp. 15. **82-83.** Unknown sp. 16. **84.** *Cephaliophora* sp. Bars = 20 µm, Figs. 81 and 84 with scale a, remaining to scale b.

Conclusions

1./ The most intriguing question is whether a distinct hyphomycete group requiring free water (rain, dew, fog appearing intermittently) for growth and sporulation, really exists in canopies. Can this fungal group play a similar role in decomposition in canopies like the aquatic hyphomycetes in continental waters?

2./ If such a hyphomycete group exists in canopies, it is questionable that its species should include those colonizing dead and/or senescent plant parts (i.e. inhabit canopy-litter), as was proposed by Carroll (1981) or those on intact leaf surfaces (i.e. epiphytes) as was emphasized by Ando and Tubaki (1984a; Ando, 1992). Appropriate terms for defining these fungal groups have to be coined. "Arboreal aquatic hyphomycetes", and likewise "terrestrial aquatic hyphomycetes" appear to be inadequate. "Aquatic hyphomycetes" in any attributive use (i.e. either preceded by "arboreal" or "terrestrial") is incorrect because "aquatic hyphomycetes" have already been assigned to surface water habitats. Stemflow and throughfall contain taxonomically and ecologically heterogeneous groups of spores. Certainly the major part of these spores derives from the canopy and the other part from the air simply washed off by rainfall. One part belongs to the "arboreal aquatic hyphomycetes or "canopy fungi" (in Carroll's sense). Until we know better the taxonomy and ecology of these different groups we propose to use the "canopy fungi" as a general term. A deeper knowledge of the taxonomy (including the completion of life cycles, i.e. the discovery of their teleomorphs), physiology (i.e. the sporulating medium) and ecology of this canopy group (e.g. substrata) may contribute to a more holistic understanding of their biology.

3./ Although very little evidence has been published for the occurrence of "true" aquatic hyphomycetes in canopies, there are nevertheless a few records. This poses a further question: Can true aquatic hyphomycetes adapt to sporulation in free water in canopies?

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