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Synoptic key and computer database for identification of species of *Ceratocystis sensu lato*

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Ceratocystis sensu lato, incorporating *Ceratocystis*, *Ophiostoma* and *Ceratocystiopsis*, includes more than a hundred species, many of which are important plant pathogens. Existing keys to the species are, however, incomplete and available only in the dichotomous format. As synoptic keys are inherently superior, a computer database program was used to compile a synoptic key to species of *Ceratocystis*, *Ophiostoma* and *Ceratocystiopsis*. The key can thus be used manually or with the aid of a computer.

Ceratocystis sensu lato, bestaande uit *Ceratocystis*, *Ophiostoma* en *Ceratocystiopsis*, sluit meer as 'n honderd spesies in, waarvan verskeie belangrike plantpatogene is. Bestaande sleutels tot spesies is egter onvolledig en slegs beskikbaar in digotome formaat. Sinoptiese sleutels is inherent beter en daarom is 'n databasisprogram gebruik om 'n sinoptiese sleutel tot spesies van *Ceratocystis*, *Ophiostoma* en *Ceratocystiopsis* op te stel. Die sleutel kan gevolglik in geskrewe of gerekenariseerde vorm gebruik word.

Keywords: *Ceratocystiopsis*, *Ceratocystis*, *Ophiostoma*, synoptic key.

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Introduction

Ceratocystis sensu lato includes the genera *Ceratocystis* Ellis & Halsted *sensu stricto*, *Ophiostoma* H. & P. Sydow and *Ceratocystiopsis* Upadhyay & Kendrick (De Hoog & Scheffer 1984). Species placed in *Ceratocystis s. l.* are generally characterized by spherical ascomata with long necks and evanescent asci (Upadhyay 1981). This statement, however, gives little indication of the complexity of these fungi. The group is large and includes more than a hundred species with anamorphs that have been placed in up to 16 genera of Hyphomycetes (Upadhyay & Kendrick 1975), though amalgamation has recently reduced this number to eight (Nag Raj & Kendrick 1992). Many of these fungi are important plant pathogens or are associated with insects that are economically important (Upadhyay 1981). Species of *Ceratocystis s. l.* have for instance been associated with blue-stain of Southern beech (Butin & Aquilar 1984), pines (Bridges & Perry 1987; Davidson 1979) and Norway spruce (Solheim 1986). Other diseases caused by these fungi include root discolouration of grand fir (Livingston & Davidson 1987), black-stain root disease of pines (Cobb 1988), die-back of larch (Redfern *et al.* 1987), vascular diseases of oak (Kowalski & Butin 1989) and especially oak wilt caused by *C. fagacearum* (Bretz 1952) and Dutch elm disease caused by *O. ulmi* (Boyce 1961). In many instances a close relationship has been reported between fungi of this group and insects, primarily bark beetles of the genera *Dendroctonus* (Bridges & Perry 1987; Davidson 1979) and *Ips* (Redfern *et al.* 1987; Solheim 1986).

Due to the economic importance and common occurrence of species of *Ceratocystis s. l.*, there is a regular need to identify these fungi. Nevertheless, there are few simple and reliable keys to this group. The only available keys are of the dichotomous kind of which that of Upadhyay (1981) is the most recent and complete. Upadhyay's key, however, did not include all species and subsequently many additional species have been described (Brasier 1991; Bridges & Perry 1987; Butin & Aquilar 1984; Constantinescu & Ryman 1989; Hutchison & Reid 1988; Kowalski & Butin 1989; Livingston & Davidson 1987; Redfern *et al.* 1987; Solheim 1986; Wingfield *et al.* 1988).

Dichotomous keys have many disadvantages. The most obvious of these is that characteristics must be provided in sequence and a lack of data at any step of the sequence results in failure of the identification process. In contrast, synoptic keys can be entered at any point and new characteristics considered in any order (Korf 1972). This allows the user to commence with more prominent features and possibly identify specimens for which only incomplete information is available. Furthermore, new taxa as well as new characteristics can easily be added as they become available. A disadvantage of synoptic keys, particularly in the case of genera containing many species, is that a multitude of numbers must be dealt with. The availability of computers to scientists and diagnosticians alleviates this problem (Kendrick 1990).

In this paper we present a synoptic key to species of *Ceratocystis s. l.* A computer database has been used to compile the key which may be utilized electronically or, in situations where a computer is not available, the key may also be used manually. Besides providing a rapid and reliable method for identifying species of *Ceratocystis s. l.*, this key includes numerous species not incorporated in previous keys.

Methods

Source of data

The data used in the key were taken from the literature and

Table 1 Species of *Ophiostoma, Ceratocystis s. st.* and *Ceratocystiopsis* with the corresponding taxon numbers used in the synoptic key. Literature sources from which descriptions of characters were obtained are indicated in the third column

Taxon	Species[a]	Source[b]
1	*O. abietinum* Marmolejo & Butin	A
2	*O. abiocarpum* (Davids.) Harring.	B
3	*C. acericola* Griffin	B
4	*O. adiposa* (Butler) D. Moreau	B
5	*C. aequivaginata* Olchow. & Reid	B
6	*O. ainoae* Solheim	C
7	*Cop. alba* (De Vay, Davids. & Moller) Upad.	B
8	*C. allantospora* Griffin	B
9	*C. angusticollis* Wright & Griffin	B
10	*O. araucariae* (Butin) De Hoog & Scheff.	B
11	*C. arborea* Olchow. & Reid	B
12	*O. aureum* (Robinson-Jeff. & Davids.) Harring.	B
13	*C. autographa* Bakshi	B
14	*O. bacillisporum* (Butin & Zimm.) De Hoog & Scheff.	B
15	*O. bicolor* Davids. & Wells	B
16	*O. brevicolla* (Davids.) De Hoog & Scheff.	B
17	*O. brunneo-ciliatum* Mathiesen-Kaarik	B
18	*C. brunneocrinita* Wright & Cain	B
19	*O. cainii* (Olchow. & Reid) Harring.	B
20	*C. californica* De Vay, Davids. & Moller	B
21	*O. canum* (Münch) I. & P. Sydow	B
22	*O. clavatum* Mathiesen	D
23	*O. clavigerum* (Robinson-Jeff. & Davids.) Harring.	B
24	*C. coerulescens* (Münch) Bakshi	B
25	*Cop. collifera* Marmolejo & Butin	A
26	*C. columnaris* Olchow. & Reid	B
27	*Cop. concentrica* (Olchow. & Reid) Upad.	B
28	*Cop. conicicollis* (Olchow. & Reid) Upad.	B
29	*O. conicolum* Marmolejo & Butin	A
30	*O. crassivaginatum* (Griffin) Harring.	B
31	*Cop. crenulata* (Olchow. & Reid) Upad.	B
32	*O. cucullatum* Solheim	C
33	*O. davidsonii* (Olchow. & Reid) Solheim	B
34	*O. deltoideospora* Olchow. & Reid	B
35	*C. denticulata* Davids.	E
36	*O. distortum* (Davids.) De Hoog & Scheff.	B
37	*O. dryocoetidis* (Kend. & Molnar) De Hoog & Scheff.	B
38	*O. epigloeum* (Guerrero) De Hoog	B
39	*C. fagacearum* (Bretz) Hunt	B
40	*Cop. falcata* (Wright & Cain) Upad.	B
41	*Cop. fasciata* (Olchow. & Reid) Upad.	B
42	*C. fimbriata* Ellis & Halst.	B
43	*O. flexuosum* Solheim	C
44	*O. francke-grosmanniae* (Davids.) De Hoog & Scheff.	B
45	*O. galeiformis* (Bakshi) Mathiesen-Kaarik	D
46	*O. grande* Samuels & Müller	F
47	*C. grandicarpa* Kowalski & Butin	G
48	*O. grandifoliae* (Davids.) Harring.	B
49	*O. huntii* (Robinson-Jeff.) De Hoog & Scheff.	B
50	*C. hyalothecium* Davids.	B
51	*C. introcitrina* Olchow. & Reid	B
52	*O. ips* (Rumbold) Nannfeldt	B
53	*C. laricicola* Redfern & Minter	H
54	*O. leptographioides* (Davids.) Von Arx	B
55	*C. leucocarpa* Davids.	B
56	*Cop. longispora* (Olchow. & Reid) Upad.	B
57	*C. magnifica* Griffin	B
58	*O. megalobrunneum* (Davids. & Toole) De Hoog & Scheff.	B
59	*O. microsporum* Davids.	B
60	*Cop. minima* (Olchow. & Reid) Upad.	B
61	*O. minus* (Hedgcock) H. & P. Sydow	B
62	*Cop. minuta* (Siemaszko) Upad. & Kend.	B
63	*Cop. minuta-bicolor* (Davids.) Upad. & Kend.	B
64	*C. moniliformis* (Hedgcock) Moreau	B
65	*O. multiannulatum* (Hedgcock & Davids.) N. Fries	B
66	*O. narcissi* Limber	B
67	*O. nigrocarpum* (Davids.) De Hoog	B
68	*O. nigrum* (Davids.) De Hoog & Scheff.	B
69	*O. nothofagi* (Butin) Rulamort	I
70	*C. novae-zelandiae* Hutchison & Reid	J
71	*O. novo-ulmi* Brasier	K
72	*O. obscura* (Davids.) Hunt	D
73	*Cop. ochracea* (Griffin) Upad.	B
74	*C. olivaceapinii* Davids.	B
75	*O. olivaceum* Mathiesen	B
76	*Cop. pallidobrunnea* (Olchow. & Reid) Upad.	B
77	*C. paradoxa* (Dade) Moreau	B
78	*O. penicillatum* (Grosmann) Siemaszko	B
79	*O. perfectum* (Davids.) De Hoog	B
80	*O. piceae* (Münch) H. & P. Sydow	B
81	*O. piceaperdum* (Rumbold) Von Arx	B
82	*O. piliferum* (Fries) H. & P. Sydow	B
83	*O. pluriannulatum* (Hedgcock) H. & P. Sydow	B
84	*O. polyporicola* Constantinescu & Ryman	L
85	*O. populicola* Olchow. & Reid	B
86	*O. populinum* (Hinds & Davids.) De Hoog & Scheff.	B
87	*C. prolifera* Kowalski & Butin	G
88	*Cop. proteae* Wingf., Van Wyk & Marasas	M
89	*C. pseudominor* Olchow. & Reid	B
90	*C. radicicola* (Bliss) Moreau	B
91	*Cop. ranaculosis* Perry & Bridges	N
92	*Cop. retusi* (Davids. & Hinds) Upad.	B
93	*O. robustum* (Robinson-Jeff. & Davids.) Harring.	B
94	*O. roraimense* Samuels & Müller	F
95	*O. rostrocoronatum* (Davids. & Eslyn) De Hoog & Scheff.	B
96	*O. rostrocylindricum* (Davids.) Von Arx	B
97	*O. sagmatospora* (Wright & Cain) Solheim	B
98	*O. serpens* (Goidanich) Von Arx	O
99	*O. seticolle* (Davids.) De Hoog & Scheff.	B
100	*O. sparsum* (Davids.) De Hoog & Scheff.	B
101	*Cop. spinulosa* (Griffin) Upad.	B
102	*O. stenoceras* (Robak) Melin & Nannfeldt	B
103	*C. stenospora* Griffin	B
104	*O. subannulatum* Livingston & Davids.	P
105	*C. tenella* Davids.	B
106	*O. tetropii* Mathiesen	B
107	*C. torticiliata* Olchow. & Reid	B
108	*O. tremulo-aureum* (Davids. & Hinds) De Hoog & Scheff.	B
109	*O. triangulosporum* Butin	B
110	*O. trinacriforme* (Parker) Harring.	B
111	*C. tubicollis* Olchow. & Reid	B
112	*O. ulmi* (Buisman) Nannfeldt	B
113	*O. valdivianum* (Butin) Harring.	I
114	*O. wageneri* (Goheen & Cobb) Harring.	Q

[a] Names of fungi listed are those which are currently held as being nomenclaturally valid for the species. Thus many species listed in *Ceratocystis* would more appropriately be transferred to *Ophiostoma* (see De Hoog & Scheffer 1984). Generic abbreviations are as follows: *O.*, *Ophiostoma*; *C.*, *Ceratocystis*; and *Cop.*, *Ceratocystiopsis*.

[b] Letters represent the literature sources from which descriptions of characters were obtained. A, Marmolejo & Butin (1990); B, Upadhyay (1981); C, Solheim (1986); D, Hunt (1956); E, Davidson (1979); F, Samuels & Müller (1978); G, Kowalski & Butin (1989); H, Redfern *et al.* (1987); I, Butin & Aquilar (1984); J, Hutchison & Reid (1988); K, Brasier (1991); L, Constantinescu & Ryman (1989); M, Wingfield *et al.* (1988); N, Bridges & Perry (1987); O, Goidanich (1936); P, Livingston & Davidson (1987); Q, Goheen & Cobb (1978).

are based on the descriptions, measurements, photographs and sketches published by the authors listed in Table 1. This key is, therefore, not based on direct examination and some characters could not be used since all authors did not describe the full range of characters available. Morphological characters for both teleomorph and anamorph states as well as ecological information were entered in a database using the 'askSam' program (askSam Systems, P.O. Box 12128, Perry, FL 32347, U.S.A.).

Character states

The nature of this key made it necessary to establish groups or states for each characteristic and the relevant states were then used to describe the various quantitative or qualitative characteristics of species. Each character state in the database is represented by a symbol linked to the appropriate key-letters for the character. These key-letters and symbols are indicated in the synoptic key.

When establishing states, care was taken to make recognition of states as simple as possible. Users of this key should, however, take the following precautions to avoid ascribing an incorrect state to an unidentified fungus. It is advisable to examine as many isolates as possible and thus obtain mean measurements. These are more representative of the population and less dependent on the environment. Care must also be taken to examine mature structures, as immature structures, found in young cultures, could cause confusion.

Quantitative characters

Quantitative characters used to identify species of *Ceratocystis s. l.* are usually described in terms of minimum and maximum. Mid-ranges [(minimum + maximum)/2] were therefore used to distinguish species. The full spectrum of sizes (mid-ranges) occurring in the group was taken into account to set limits for the states within quantitative characters. The establishment of states for the lengths of ascomatal necks serves as an example. The mid-ranges of necklengths vary from zero, *i.e.* neck absent, to necks 10 000 μm long, with 50% of the necks shorter than 410 μm and 75% shorter than 850 μm. This implies that small differences at the lower end of the scale are just as significant as large differences at the upper end of the scale. Rather than use fixed increments or a sliding scale, we established five states which allowed a normal-type distribution of the number of taxa occurring in the different states. These states for ascomatal necks were 'absent', 'shorter than 150 μm', '150 – 899 μm', '900 – 3599 μm' and 'longer than 3600 μm'. The number of species in each of the five different states was 4, 22, 63, 20 and 4, respectively, and the neck length for one species was not available. The maximum number of states distinguished for each character was limited to five in order to restrict the effect of environmentally induced variability.

Qualitative characters

Qualitative characters were established by means of various principles. The criteria by means of which these states were selected were as follows: (i) a light microscope should be the only aid necessary for identification; (ii) operators not familiar with *Ceratocystis* should be able to use the key, and

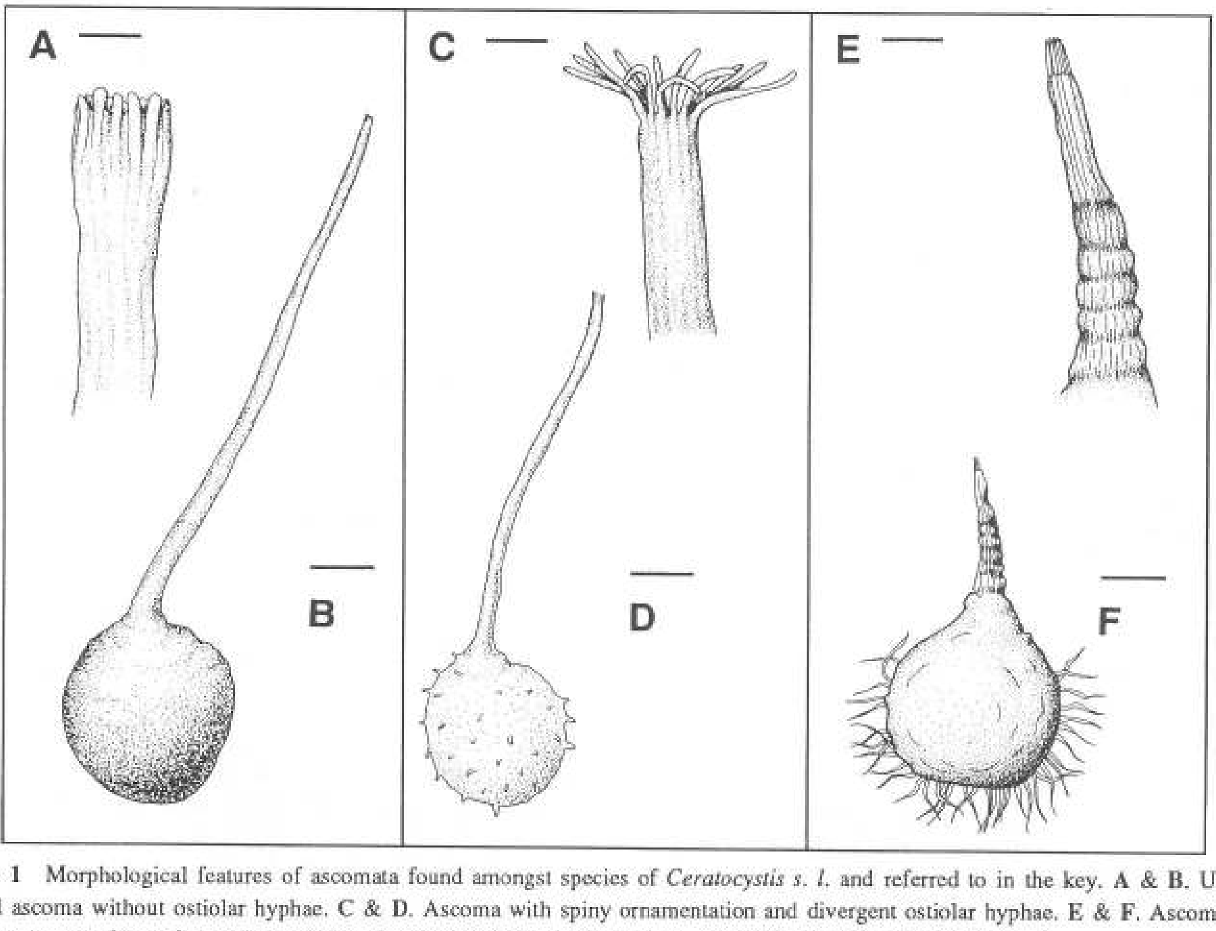

Figure 1 Morphological features of ascomata found amongst species of *Ceratocystis s. l.* and referred to in the key. **A & B.** Unornamented ascoma without ostiolar hyphae. **C & D.** Ascoma with spiny ornamentation and divergent ostiolar hyphae. **E & F.** Ascoma with hyphal ornamentation and convergent ostiolar hyphae. Scale bars: 10 μm in A, C and E and 100 μm in B, D and F.

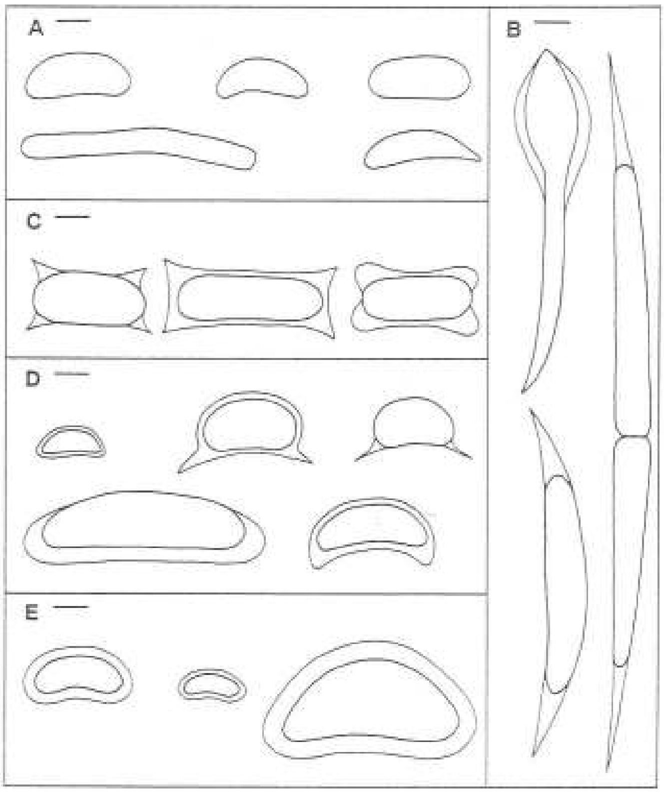

Figure 2 Range of ascospore shapes and sizes in side view encountered amongst species of *Ceratocystis s. l.* and representative of the five states used in the key. **A.** 'Sheath not visible'. **B.** 'Falcate'. **C.** 'Rectangular'. **D.** 'Cucullate or sheath irregular'. **E.** 'Sheath uniform'. Scale bars: 1 μm.

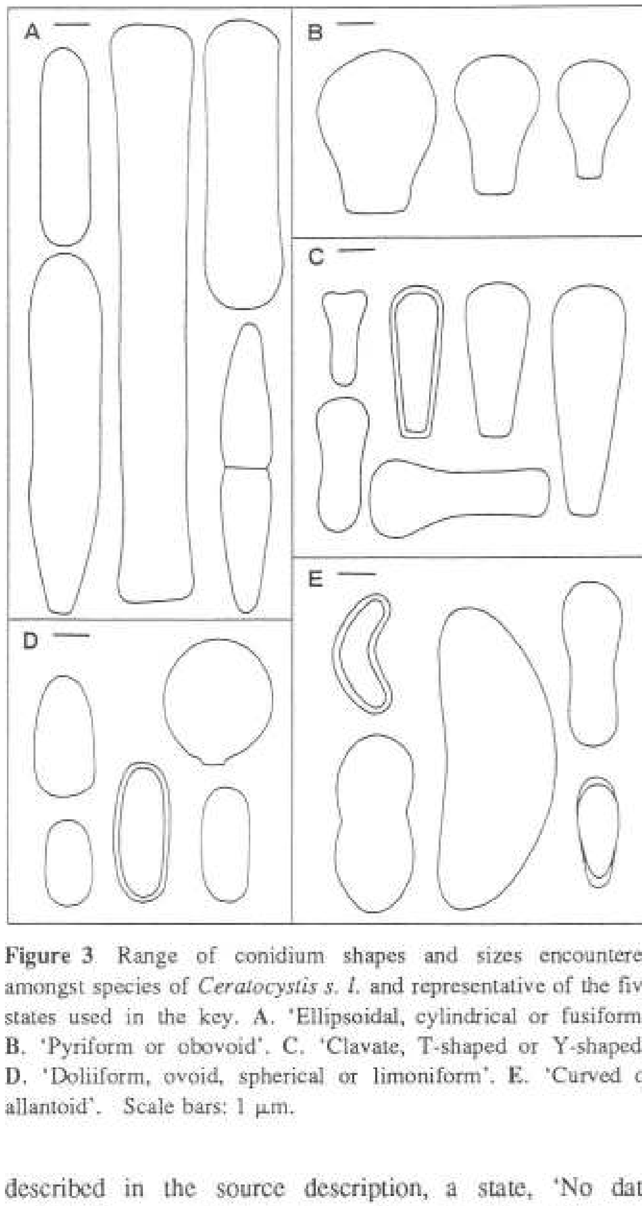

Figure 3 Range of conidium shapes and sizes encountered amongst species of *Ceratocystis s. l.* and representative of the five states used in the key. **A.** 'Ellipsoidal, cylindrical or fusiform'. **B.** 'Pyriform or obovoid'. **C.** 'Clavate, T-shaped or Y-shaped'. **D.** 'Doliiform, ovoid, spherical or limoniform'. **E.** 'Curved or allantoid'. Scale bars: 1 μm.

(iii) the number of states should be kept to a minimum. Qualitative characters dealt with on the basis of these preconditions were: ostiolar hyphae, ascoma base colour, ascomatal ornamentation, ascospore shape and conidium shape. For example, the ostiolar hyphae may be absent, convergent or divergent. In cases where they have been described as 'parallel', we treated them as convergent and where they were described as 'spirally curved', we treated them as divergent. The colour of ascomatal bases ranges from hyaline to white to yellowish-brown to brown or black. In our key, ascomata were regarded as either light or dark in colour. Ornamentation of the ascoma was considered to be 'absent', 'spiny' or 'hyphal' (Figure 1). This characteristic often develops only at maturity and must thus be treated with some circumspection.

Ascospores of *Ceratocystis s. l.* vary greatly in both size and shape (Figure 2). The states into which ascospore shape are divided are based on the optical outline of the ascospore as well as the shape of the sheath as it would appear under the light microscope. A similar approach was used in establishing states for conidium shapes (Figure 3). The classification of basic ascospore and conidium shapes into states is shown in Figures 2 and 3. Some species displayed features which might be placed in more than one state, as in the case of 'ellipsoid to clavate' conidia. In such cases both states were entered into the database and the taxon number included under both states in the written key. To accommodate taxa for which a certain character had not been described in the source description, a state, 'No data available', was added in the written key. To utilize this feature, taxon numbers occurring under 'No data available' must be considered as if they had fitted the description. Anamorph generic names are included in the database and in some cases where the anamorph is known it can be used to speed up the identification process. Consequently, the six primary anamorph genera occurring in *Ceratocystis s. l.* are illustrated in Figure 4.

Results and Discussion

Use of the database and key

The database in askSam can be used independently of the written key to achieve synoptic identification of species of *Ceratocystis s. l.* in a manner similar to the method described for identification of gilled fungi by Kendrick (1990). Species of *Ceratocystis s. l.* can be identified using the computer by entering the appropriate key-letters and symbols (indicated in the written key) for each character. For example, an unidentified specimen having a dark ascoma with a diameter of 370 μm, a neck 1300 μm long, no ostiolar hyphae and ascospores with uniform sheaths would be treated as follows: enter **bc-d**, **bd-l**, **nl-l**, **oh-0** and

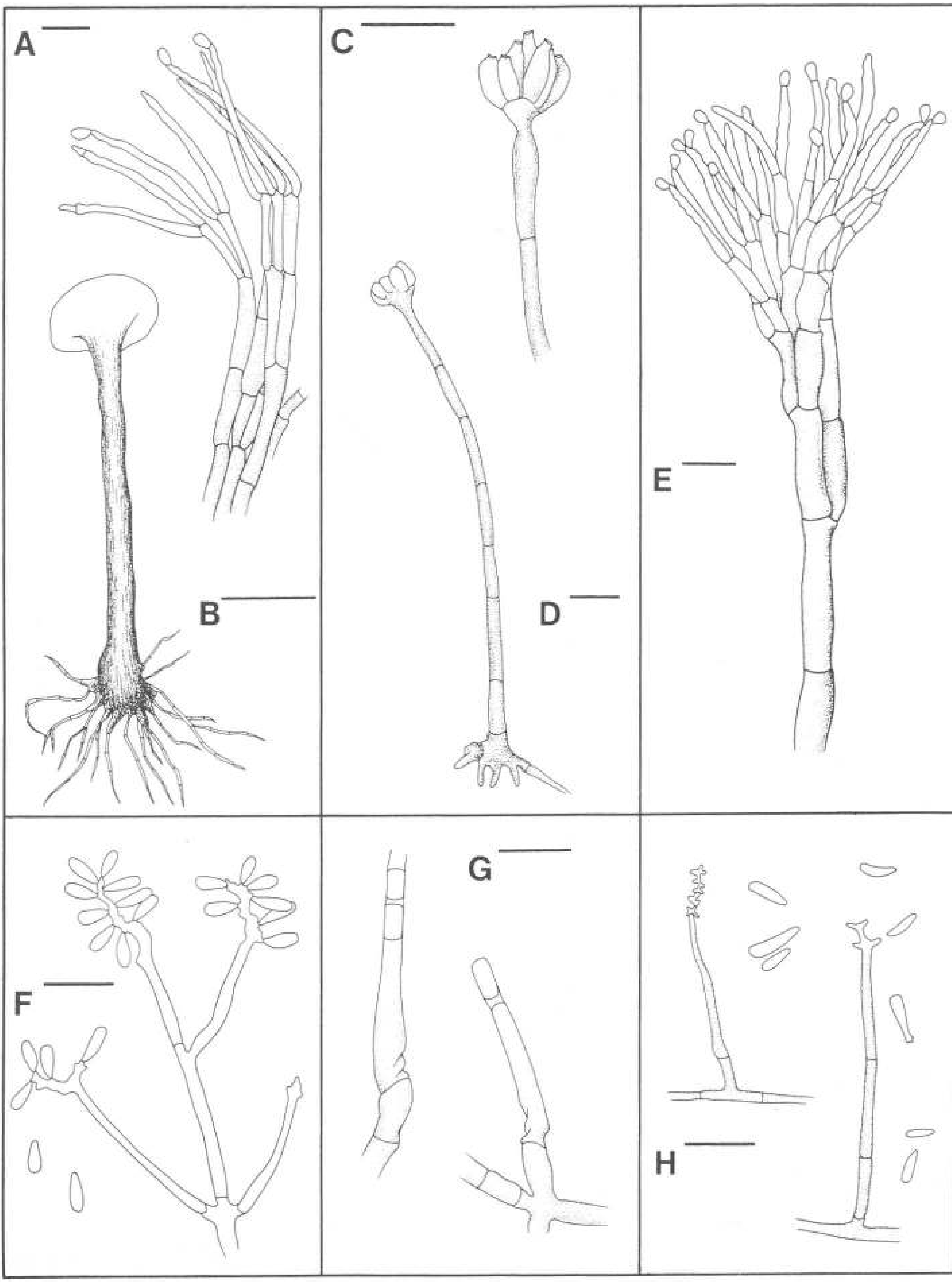

Figure 4 Morphology of anamorph genera occurring in *Ceratocystis s. l.* and referred to in the database. **A**. *Graphium* (synnema). **B**. *Knoxdaviesia* (mononema). **C**. *Leptographium* (mononema). **D**. *Hyalorhinocladiella* (simple conidiophore). **E**. *Chalara* (simple conidiophore). **F**. *Sporothrix* (simple conidiophore). Scale bars: 10 μm in A and C – H and 100 μm in B.

as-e in the query line. The record of *C. magnifica* would then be retrieved in the following form:

HOLOMORPH:	H[*Ceratocystis magnifica*] N[057]
PERITHECIUM NECK:	LENGTH (1210) **nl-l** WIDTH/B (85) nb-l
	WIDTH/A (17.5) na-m
	OSTIOLAR HYPHAE (absent) **oh-0**
PERITHECIUM BASE:	COLOUR (dark brown/ black) **bc-d**
	DIAMETER (407.5) **bd-l**
	ORNAMENTATION (absent/hyphal) or-0 or-h
	PERIDIAL CELLS (10.25) pc-m
ASCOSPORE:	SHAPE (orange section) **as-e**
	WIDTH (1) aw-s LENGTH (2.25) al-s
CELL WALL:	CHITOSAN () ch-0 ch-p
	CELLULOSE () ce-0 ce-p
HOST:	*Abies*
ANAMORPH 1:	
CONIDIUM:	DEVELOPMENT () cd-e cd-h
	SHAPE () cs-a cs-b cs-c cs-d cs-e
	SEPTATION (0) se-0 WIDTH (3.5) cw-l
	LENGTH (8.25) cl-l
CONIDIOPHORE:	AGGREGATION (mononema) ca-m
	LENGTH (275) ml-l WIDTH (6.5) mw-l

Note: Bold key letters and symbols are those recognized in the computer search.

The user is able to obtain a list of the taxon numbers and names in the database by entering ' N[H[' in the query line and printing the list. An introduction and list of references is retrieved by entering ' INTRODUCTION ' and ' REFERENCES ', respectively.

Advantages

The advantages of the 'askSam'-based key over other computer keys were discussed in detail by Kendrick (1990). A major advantage of this database is that the organism is not merely identified, but a complete description of the identified species is retrieved to confirm identification. Furthermore, information can be added without difficulty, since it is only necessary to 'update' existing records or to 'add a record' for new species. The appropriate taxon numbers must then also be added under the correct states in the written key. As is true of all synoptic keys, a disadvantage is the multitude of taxon numbers to which certain character states apply. The tedious effort of writing down all the taxon numbers can be avoided by using the computer database.

The key makes it possible to identify species which are not fully described as these taxa were included in all character states. However, correct identification with any key is subject to the input of correct data, often dependent on environmental influence on morphology. Incorrect interpretation of characters and states by operators can also result in errors. However, such errors should be curtailed with this key since great care was taken in setting limits for qualitative character states and establishing groups for qualitative states. An important advantage of both the written key and the database is, therefore, that it can be used by operators who are not familiar with this group of fungi. This key is not merely an updated version of existing keys, but it enables faster and correct identification of *Ceratocystis s. l.*

We are willing to supply copies of this database on preformatted diskettes for IBM-compatible computers to registered owners of askSam and we would be grateful for any suggestions regarding additions or changes to the database.

Synoptic Key

LENGTH OF ASCOMA NECK

Neck absent (nl-0)
  12; 23; 93; 110
< 150 μm (nl-s)
  7; 25; 27; 28; 30; 34; 40; 41; 56; 60-62; 73; 76; 85; 87; 89; 91; 92; 101; 103; 111
150 - 899 μm (nl-m)
  1; 3; 5; 6; 8–11; 13–16; 18–20; 22; 24; 26; 29; 31–33; 35–39; 43–45; 48; 49; 51–55; 63; 64; 66–68; 71; 72; 74; 75; 78; 79; 88; 90; 95–100; 104; 105; 107; 108; 112–114
900 – 3599 μm (nl-l)
  2; 4; 17; 21; 42; 46; 57–59; 77; 80–84; 86; 94; 102; 106; 109
≥ 3600 μm (nl-xl)
  47; 65; 69; 70
No data available
  50

WIDTH OF ASCOMA NECK AT THE BASE

Neck absent (nb-0)
  12; 23; 93; 110
< 34 μm (nb-s)
  1; 3; 5; 9–11; 13; 18; 20; 21; 25; 27; 30–36; 40–42; 44; 53; 56; 62–64; 66; 67; 70; 71; 72; 74–76; 79; 80; 82; 83; 85; 87; 88; 91; 95; 101; 104; 105; 107–109; 111; 113; 114
34 – 67 μm (nb-m)
  2; 4; 6–8; 14–17; 19; 22; 24; 26; 28; 29; 37; 38; 43; 45; 48; 49; 51; 52; 54; 59–61; 65; 68; 73; 77; 78; 81; 84; 86; 89; 90; 92; 96–100; 102; 103; 106; 112
≥ 68 μm (nb-l)
  39; 47; 55; 57; 58; 69
No data available
  46; 50; 94

WIDTH OF ASCOMA NECK AT THE APEX

Neck absent (na-0)
  12; 23; 93; 110
< 15.9 μm (na-s)
  1; 3; 5; 7; 9–11; 18; 20–22; 24–28; 30–32; 34–36; 40–43; 56; 59; 61; 63–67; 70; 71; 76; 79; 80; 82; 83; 85 87; 89; 101–105; 111–113
15.9 – 47.6 μm (na-m)
  4; 6; 8; 13–17; 19; 29; 33; 37; 38; 44; 45; 48; 49; 51–54; 57; 58; 60; 62; 68; 72; 73; 75; 77; 78; 81; 84; 86; 90; 92; 95–98; 100; 106–109; 114
≥ 47.7μm (na-l)
  39; 47; 55; 69; 74; 99
No data available
  2; 46; 50; 88; 91; 94

OSTIOLAR HYPHAE

Absent (oh-0)
2; 3; 8–10; 12; 15; 19; 21; 23; 26; 35; 37; 38; 40; 45; 49–52; 57; 59; 66–69; 78; 81; 84; 91; 93; 94; 96; 100; 103; 110; 111; 114

Convergent (oh-c)
7; 16; 25; 27; 28; 36; 41; 42; 47; 56; 60; 62; 63; 72; 74–77; 99; 101

Divergent (oh-d)
1; 4–6; 11; 13; 14; 17; 18; 20; 22; 24; 29–34; 36; 39; 43; 44; 48; 53–55; 58; 61; 64; 65; 67; 68; 70; 73; 77; 79; 80; 82; 83; 85–90; 92; 95–97; 102; 104–109; 112; 113

No data available
46; 71; 98

DIAMETER OF ASCOMA

< 85 μm (bd-s)
9; 25; 27; 30; 31; 33; 40; 41; 56; 60; 62; 63; 67; 73; 76; 87; 101; 103; 105

85 – 249 μm (bd-m)
1–3; 5–8; 10; 11; 13; 14; 16; 18–22; 24; 26; 28; 29; 32; 34–38; 42–45; 48; 51; 54; 55; 61; 64–66; 68; 70–72; 74; 75; 77–83; 85; 86; 88; 89; 91; 92; 95–97; 99; 100; 102; 104; 107–109; 111–114

≥ 250 μm (bd-l)
4; 12; 15; 17; 23; 39; 46; 47; 49; 50; 52; 53; 57–59; 69; 84; 90; 93; 94; 98; 106; 110

COLOUR OF ASCOMA BASE

Dark (bc-d)
1–6; 8–14; 16–31; 33–49; 51–54; 56–62; 64–72; 74–78; 80–114

Light (bc-l)
7; 15; 29; 32–34; 50; 54; 55; 63; 73; 79; 92

ORNAMENTATION OF ASCOMA

Absent (or-0)
1; 2; 5–7; 9; 11; 12; 15; 16; 18–20; 22; 23; 26–28; 30; 32; 33; 35; 37–39; 44; 46; 48; 54; 56–58; 62; 63; 66; 69; 70; 72–75; 78; 79; 81; 84; 85; 88; 91–98; 100; 103; 105; 107; 109; 110; 113; 114

Hyphal (or-h)
3; 4; 8; 10; 13; 17; 21; 24; 29; 31; 36; 40–43; 45; 47; 49–53; 55; 57; 59; 61; 67; 68; 70; 71; 80; 82; 83; 87; 89; 99; 102; 104; 106; 108; 112

Spiny (or-s)
14; 34; 60; 64; 65; 76; 77; 86; 90; 101; 111

Collar (or-c)
25

DIAMETER OF PERIDIAL CELLS

< 5.5 μm (pc-s)
5; 7; 10; 25; 31; 38; 41; 44; 46; 53; 60; 62; 67; 73; 76; 92–94; 103

5.5 – 11.5 μm (pc-m)
1; 3; 8; 9; 11–17; 19; 20; 23; 24; 26–30; 32–34; 36; 40; 43; 48; 51; 52; 54–57; 61; 63; 79–86; 89; 95–97; 99; 101; 105–108; 110–112

≥ 12 μm (pc-l)
2; 4; 18; 21; 37; 39; 42; 49; 58; 59; 64–66; 68; 74; 75; 77; 78; 90; 100; 102; 109

No data available
6; 22; 35; 45; 47; 50; 69–72; 87; 88; 91; 98; 104; 113; 114

SHAPE OF ASCOSPORE (IN SIDE VIEW)

Sheath not visible (as-a)
1; 2; 8–10; 14; 20–22; 29; 35; 38; 46; 47; 51; 55; 58; 61; 65–67; 69; 70; 71; 79; 80; 82–84; 86; 87; 89; 94; 95; 102; 104–106; 108; 112–114

Falcate (as-b)
7; 25; 27; 28; 31; 40; 41; 56; 60; 62; 63; 73; 76; 88; 91; 92; 101

Rectangular (as-c)
11; 13; 15; 17; 18; 26; 34; 43; 50; 52; 54; 68; 99; 100; 111

Cucullate or Sheaths Irregular (as-d)
11; 12; 19; 22–24; 32; 36; 42; 44; 45; 48; 49; 54; 59; 64; 72; 74; 75; 78; 81; 85; 93; 97; 109; 110

Sheath Uniform (as-e)
3–6; 9; 11; 16; 22; 24; 30; 33; 36; 37; 39; 44; 48; 53; 57; 74; 77; 90; 96; 103; 107; 114

No data available
98

WIDTH OF ASCOSPORE

< 1.26 μm (aw-s)
7; 14; 20; 25; 27; 31; 34; 40 41; 53; 55–63; 67; 70; 71; 76, 83; 84; 89; 102; 106; 107; 112

1.26 – 2.49 μm (aw-m)
1–3; 5; 6; 8–11; 13; 17; 18; 21; 22; 26; 29; 30; 35; 36; 38; 42; 43; 46–49; 51; 52; 65; 66; 68; 72; 74; 79; 80; 85–87; 91; 92; 94–96; 98; 100; 101; 103–105; 108; 109; 111; 113

≥ 2.50 μm (aw-l)
4; 12; 15; 16; 19; 23; 24; 28; 32; 33; 37; 39; 44; 45; 50; 54; 69; 73; 75; 77; 78; 81; 82; 88; 90; 93; 97; 99; 110

No data available
64; 114

LENGHT OF ASCOSPORE

< 3.5 μm (al-s)
5; 11; 22; 51; 55; 57; 59; 66; 69; 84; 89; 96; 106; 107

3.5 – 6.5 μm (al-m)
1–3; 6; 8–10; 12; 13; 15–21; 23; 26; 29; 32–38; 42–50; 52–54; 58; 61; 65; 67; 68; 70–72; 74; 75; 78–83; 85–87; 93–95; 97–100; 102–105; 108–113

≥ 7.0 μm (al-l)
4; 7; 14; 24; 25; 27; 28; 30; 31; 39–41; 56; 60; 62; 63; 73; 76; 77; 88; 90–92; 101

No data available
64; 114

CONIDIUM SHAPE

Ellipsoidal, Cylindrical or Fusiform (cs-a)
1; 2; 8; 9; 12; 16; 17; 19; 20; 23; 24; 26; 30; 39; 42; 52–54; 56; 59; 62; 64; 67; 71; 74; 76; 77; 79; 80; 82–84; 86; 90–92; 94; 95; 100; 110; 111; 114

Pyriform or Obovoid (cs-b)
21; 43; 46; 49; 52; 61; 64; 66; 89; 99; 104; 109

Clavate, T-shaped or Y-shaped (cs–c)
6; 7; 11; 15–21; 23; 26–28; 31–38; 40; 41; 43; 52; 54–56; 58; 61; 63; 65–71; 84; 87; 91; 96–98; 101; 102; 105; 107; 108; 111–113

Doliiform, Spherical or Limoniform (cs-d)
4; 5; 8; 10; 13; 14; 21; 22; 25; 29; 31; 37; 42; 44–48; 51; 68; 71; 72; 74; 76; 77; 81; 93; 96; 97; 100–102; 106; 107; 109; 110; 113; 114

Curved or allantoid (cs-e)
9; 13; 17; 41; 47; 60; 68; 70; 75; 78; 81; 85; 87; 88

No data available
3; 50; 57; 73; 103

SEPTATION OF CONIDIA

Absent (se-0)
1; 2; 4–49; 51–72; 74–102; 104–114

Present (se-p)
23; 42; 94

No data available
3; 50; 73; 103

WIDTH OF CONIDIUM

< 3 µm (cw-s)
1; 2; 5; 6; 8–14; 16–20; 22; 23; 25–28; 30–34; 36; 38–40; 43; 45–48; 51; 52; 54–56; 58–71; 74–76; 79; 80; 82–87; 89; 91; 92; 94–96; 98–102; 104–108; 110–114

⩾ 3 µm (cw-l)
4; 7; 15; 21; 23; 29; 35; 37; 41; 42; 44; 49; 52; 57; 64; 72; 77; 78; 81; 88; 90; 93; 97; 109

No data available
3; 24; 50; 53; 73; 103

LENGTH OF CONIDIUM

< 3.75 µm (cl-s)
10; 13; 18; 23; 25; 27; 41; 45; 48; 51; 68; 85; 98; 107; 112

3.75 – 7.95 µm (cl-m)
1; 5–11; 13–17; 19; 21; 22; 24; 26; 28–36; 38; 40; 43–47; 49; 52; 54–56; 58–70; 72; 74–76; 81; 82; 87–89; 91–93; 95–97; 99–102; 104–114

⩾ 8 µm (cl-l)
2; 4; 12; 20; 23; 24; 37; 39; 42; 47; 52; 57; 64; 71; 77–80; 83; 84; 86; 90; 94

No data available
3; 50; 53; 73; 103

CONIDIUM DEVELOPMENT

Enteroblastic (cd-e) (*Chalara*)
4; 13; 24; 26; 33; 39; 40; 42; 44; 53; 64; 75; 77; 90; 97

Holoblastic (cd-h)
1; 2; 5–21; 23; 25; 27–32; 34; 36–38; 41; 43; 45–49; 51; 52; 54–56; 58–63; 65–72; 74; 76; 78–89; 91–96; 98–102; 104–114

No data available
3; 22; 35; 50; 57; 73; 103

TYPE OF CONIDIOPHORE

Simple (ca-0) (no specialization)
8; 13; 18; 35; 36; 45; 46; 53; 58; 64; 68; 71; 84; 91; 94; 99; 105; 106; 113

Mononema (ca-m)
1; 2; 4; 5; 7; 9; 10; 12; 14; 16; 20; 23–25; 27–31; 34; 37–45; 47–49; 52; 54–57; 59–63; 65–70; 76–83; 85–96; 98; 101; 102; 108; 109–114

Synnema (ca-s)
6; 10; 11; 17; 19; 21–23; 26; 32; 33; 45; 51; 52; 70–72; 74; 75; 80; 97; 100; 107; 112

No data available
3; 15; 50; 73; 103; 104

WIDTH OF SIMPLE CONIDIOPHORE

< 3 µm (hw-s)
13; 18; 45; 46; 64; 68; 84; 99

⩾ 3 µm (hw-l)
8; 53; 94

No data available
35; 36; 58; 71; 91; 105; 106; 113

WIDTH OF MONONEMA

< 3 µm (mw-s)
1; 5; 9; 10; 14; 25; 27; 28; 31; 34; 38; 39; 41; 43; 44; 56; 59; 60; 62; 63; 65; 66–69; 76; 79; 80; 82; 85; 86; 92; 95; 101; 102; 108; 109; 111; 112

⩾ 3 µm (mw-l)
2; 4; 16; 20; 23; 24; 29; 30; 37; 40; 42; 45; 48; 49; 52; 55; 57; 61; 77; 78; 81; 83; 88–90; 93; 96; 98; 110; 114

No data available
7; 12; 47; 54; 70; 87; 91; 94; 113

LENGTH OF MONONEMA

< 100 µm (ml-s)
1; 4; 5; 21; 25; 27; 28; 30; 31; 39–42; 47; 55; 61; 63; 65–68; 79; 82; 87; 89; 93; 94; 109; 112

⩾ 100 µm (ml-l)
2; 12; 16; 23; 24; 29; 37; 44; 45; 47–49; 54; 57; 77; 78; 80; 81; 88; 90; 96; 98; 110; 113; 114

No data available
7; 9; 10; 14; 20; 34; 38; 43; 52; 56; 59; 60; 62; 69; 70; 76; 83; 85; 86; 91; 92; 95; 101; 102; 108; 111

WIDTH OF SYNNEMA

< 35 µm (sw-s)
10; 21; 26; 32; 33; 80; 97; 100; 112

⩾ 35µm (sw-l)
11; 17; 19; 22; 23; 45; 51; 70; 72; 75; 107

No data available
6; 52; 71; 74

LENGTH OF SYNNEMA

< 350 µm (sl-s)
10; 11; 26; 32; 33; 45; 52; 97; 100

⩾ 350 µm (sl-l)
17; 19; 21–23; 51; 70–72; 74; 75; 80; 107; 112

No data available
6

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References

BOYCE, J.S. 1961. Forest pathology, 3rd edn. Mc Graw-Hill Book Company, New York.

BRASIER, C.M. 1991. *Ophiostoma novo-ulmi* sp. nov., causative agent of current Dutch elm disease pandemics. *Mycopathologia* 115: 151 – 161.

BRETZ, T.W. 1952. The ascigerous stage of the oak wilt fungus. *Phytopathology* 42: 435 – 437.

BRIDGES, J.R. & PERRY, T.J. 1987. *Ceratocystiopsis ranaculosus* sp. nov. associated with the Southern pine beetle. *Mycologia* 79: 630 – 633.

BUTIN, H. & AQUILAR, A.M. 1984. Blue-stain fungi from Chile – including two new species of *Ceratocystis* Ellis & Halst. *Phytopath. Z.* 109: 80 – 89.

COBB, F.W. 1988. *Leptographium wageneri*, cause of black-stain root disease: A review of its discovery, occurrence and biology with emphasis on pinyon and ponderosa pine. In: *Leptographium* root diseases on conifers, eds. T.C. Harrington & F.W. Cobb. APS Press, St Paul, Minnesota.

CONSTANTINESCU, O. & RYMAN, S. 1989. A new *Ophiostoma* on Polypores. *Mycotaxon* 34: 637 – 642.

DAVIDSON, R.W. 1979. A *Ceratocystis* associated with an ambrosia beetle in *Dendroctonus*-killed pines. *Mycologia* 71: 1085 – 1089.

DE HOOG, G.S. & SCHEFFER, R.J. 1984. *Ceratocystis versus Ophiostoma*: a reappraisal. *Mycologia* 76: 292 – 299.

GOHEEN, D.J. & COBB, F.W. 1978. Occurrence of *Verticicladiella wagenerii* and its perfect state, *Ceratocystis wageneri* sp. nov., in insect galleries. *Phytopathology* 68: 1192 – 1195.

GOIDANICH, G. 1936. Il genre di ascomyceti 'Grosmannia' G. Goid. *Boll. Staz. Patol. Veg. Roma n.s.* 16: 26 – 60.

HUNT, J. 1956. Taxonomy of the genus *Ceratocystis*. *Lloydia* 19: 1 – 58.

HUTCHISON, L.J. & REID, J. 1988. Taxonomy of some potential wood-staining fungi from New Zealand. 1. Ophiostomataceae. *N. Z. J. Bot.* 26: 63 – 81.

KENDRICK, B. 1990. A rapid, computer-based synoptic key to genera of gilled fungi. *Mycotaxon* 38: 27 – 36.

KORF, R.P. 1972. Synoptic key to the genera of the Pezizales. *Mycologia* 64: 937 – 994.

KOWALSKI, T. & BUTIN, H. 1989. Taxonomie bekannter und neuer *Ceratocystis*-arten an Eiche (*Quercus robur* L.). *J. Phytopath.* 124: 236 – 248.

LIVINGSTON, W.H. & DAVIDSON, R.W. 1987. *Ophiostoma subannulatum*, a new fungal species pathogenic to grand fir roots. *Mycologia* 79: 144 – 147.

MARMOLEJO, J.G. & BUTIN, H. 1990. New conifer-inhabiting species of *Ophiostoma* and *Ceratocystiopsis* (Ascomycetes, Microascales) from Mexico. *Sydowia* 42: 139 – 199.

NAG RAJ, T.R. & KENDRICK, B. 1992. The anamorph as generic determinant in the holomorph: The *Chalara* connection in the Ascomycetes, with special reference to the *Ophiostomatales*. In: *Ceratocystis* and *Ophiostoma*: Taxonomy, Ecology and Pathogenicity, eds. M.J. Wingfield, K.A. Siefert & J.F. Webber. APS Press, St Paul, Minnesota (in press).

REDFERN, D.B., STOAKLEY, J.T., STEELE, H. & MINTER, D.W. 1987. Dieback and death of Larch caused by *Ceratocystis laricicola* sp. nov. following attack by *Ips cembrae*. *Pl. Pathol.* 36: 467 – 480.

SAMUELS, G.J. & MÜLLER, E. 1978. Life-history studies of Brazilian Ascomycetes: Two new species of *Ophiostoma* and their *Sporothrix* anamorphs. *Sydowia* 31: 169 – 179.

SOLHEIM, H. 1986. Species of Ophiostomataceae isolated from *Picea abies* infested by the bark beetle *Ips typographus*. *Nord. J. Bot.* 6: 199 – 207.

UPADHYAY, H.P. 1981. A monograph of *Ceratocystis* and *Ceratocystiopsis*. University of Georgia Press, Athens.

UPADHYAY, H.P. & KENDRICK, B. 1975. Prodromus for a revision of *Ceratocystis* (Microascales, Ascomycetes) and its conidial states. *Mycologia* 67: 798 – 805.

WINGFIELD, M.J., VAN WYK, P.S. & MARASAS, W.F.O. 1988. *Ceratocystiopsis protea* sp. nov., with a new anamorph genus. *Mycologia* 80: 23 – 30.