

***Stephanonectria*, a new genus of the Hypocreales (Bionectriaceae), and its sporodochial anamorph**

Hans-Josef Schroers¹, Gary J. Samuels² & Walter Gams¹

¹ Centraalbureau voor Schimmelcultures, P. O. Box 273, 3740 AG Baarn, Netherlands

² United States Department of Agriculture, Agricultural Research Service, Systematic Botany and Mycology Laboratory, Rm. 304, B-011A, BARC-West, Beltsville, Maryland 20705-2350

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A new unispecific genus of the Bionectriaceae, *Stephanonectria*, is described for *Nectria keithii*. *Stephanonectria* is characterised by brown, smooth perithecia that do not change colour in KOH and by a peculiar crown-like structure around the ostiole. The ascospores are covered with short striae that are more or less parallel with the long axis of the spore. The ascospores of different collections vary considerably in length but the differences are not indicative of infraspecific differences or particular geographical patterns. The anamorph shows features typical of several genera, and is here identified as *Myrothecium*-like. Perithecia of *Stephanonectria keithii* have been found on dead parts of *Brassica* sp. and various dead woody substrata in Europe, New Zealand, and possibly also in tropical regions. The anamorph has been isolated from European soil as well.

Keywords: Ascomycota, *Bionectria*, *Nectria*, *Myrothecium*, systematics.

Nectria (Fr.) Fr. as currently understood includes over 600 described species. The diversity of this genus has long been recognised. Booth (1959) and subsequent workers (e.g. Samuels, 1976) divided the genus into several informal groups based on morphology of the teleomorph and on the anamorph. More recently, data derived from sequences of rDNA (e.g. Guadet et al., 1989; Rehner and Samuels, 1994, 1995) have confirmed the heterogeneity of *Nectria* while also supporting restriction of *Nectria* s. str. to a rather small group of species (Rossman, 1989). Rossman et al. (1999) give formal recognition of some of the informal groups as natural genera. Nonetheless, several species cannot be retained easily in *Nectria* because of unusual apomorphies. They are certainly not congeneric with *N. cinabarina* (Tode : Fr.) Fr., nor can they be placed in any of the recently recognised genera. One such species is *Nectria keithii* Berk. & Br. This fungus was formerly classified in the *Nectria ochroleuca* group (Booth, 1959), which today is accepted at genus level as *Bionectria*

Speg. (Schroers & Samuels, 1997; Schroers et al., 1999; Schroers, unpublished). *Nectria keithii* cannot be classified in either *Bioneectria*, *Nectria* or any other genus known to us because of deviating perithecial wall anatomy and, in particular, because of a conspicuous differentiation around the ostium. Consequently a new genus is proposed for the teleomorph. The sporodochial anamorph of *Nectria keithii*, on the other hand, comprises characters of several hyphomycetous genera such as *Gliocladium* Corda, *Clonostachys* Corda, and *Myrothecium* Tode : Fr. and is identified here as being 'Myrothecium-like,' because the holomorph is sufficiently tagged by its teleomorphic name (Article 59.1; Greuter et al., 1994).

Material and methods

Specimens from various herbaria (K, IMI, PDD, BPI, CBS, NY) and one permanent slide containing longitudinal 5 μm thick sections (from K) were examined (abbreviations according to Holmgren et al., 1990). Anatomy of the perithecia and, in particular, the perithecial wall was studied from herbarium specimens, and longitudinal sections of ca. 10 μm thickness were prepared using a Damon IEC CTF microtome cryostat (for details see Schroers et al., 1999). Sections were mounted in lactic acid. Single ascospores from fresh material were isolated using a micromanipulator and grown on artificial media. Living strains are kept at the culture collection of the Systematic Botany and Mycology Laboratory (SBML, USDA, Beltsville, Maryland, U.S.A.) or at the Centraalbureau voor Schimmelcultures (CBS, Baarn, The Netherlands).

Colonies of the original isolations are preserved as dried cultures together with their specimens in BPI and PDD. Other conidial isolates were obtained from the CBS collection, isolated by various researchers and isolation techniques. Living strains were described from oatmeal agar (OA) (CBS, 1996), cornmeal-dextrose agar (CMD), potato-dextrose agar (PDA) (both Difco). Colours of the colonies were determined according to Kornerup and Wanscher (1978). Photographs and drawings were made using interference contrast microscopy on a Zeiss Axioplan or Olympus BX50. Measurements in the description are given as (i) n_1 - n_2 ; (ii) n_1 - n_3 - n_2 , or, (iii) (n_1) - n_4 - n_3 - n_5 (- n_2), with n_1 = minimum value observed; n_2 = maximum value observed; n_3 = arithmetical mean; n_4/n_5 = first/third quartile. The descriptive statistics given in the description consider all the data collected. Ranges of the ascospore length of specific specimens are shown graphically in Fig. 24. Descriptive statistics were performed using the software package XLSTAT 3.5. Boxplots (Fig. 24) were prepared using the software package Systat 8.0.

Stephanonectria Schroers & Samuels, gen. nov. – Figs. 1–23.

Perithecia superficialia, gregaria vel aggregata in stromate e substratis lignosis vel herbaceis oriundo. Stroma superficiale et reductum vel per corticem erumpens. Perithecia brunnea, KOH haud mutata, levia vel asperata, minute papillata. Ostiolum corona circumdatum; paries e duabus regionibus constans: regio exterior et corona ex cellulis irregularibus, angularibus vel elongatis, dentiformibus, parietibus <2 µm crassis, coronae parietibus partim >2 µm crassis. Ascospores uniseptatae, striis brevibus ornamentatae. Anamorphosis *Myrothecii* similis.

Perithecia superficial, gregarious to crowded, arising from stroma, on dead woody or herbaceous plants. – Stroma superficial and reduced or erumpent through the outer cortex of the substratum. – Perithecia brown, not changing colour in KOH, smooth to rough, minutely papillate. – Ostiolum surrounded by a crown-like structure. – Perithecial wall consisting of two regions. Cells of the outer region and the crown irregular, angular to elongated, tooth-like; cell-walls <2 µm, those of the crowns partly thicker than 2 µm. – Ascospores 1-septate, covered with short striae.

Anamorph. – *Myrothecium*-like.

Etymology. – *Stephanonectria*, from Greek stephanos (= crown).

Type. – *Stephanonectria keithii* (Berk. & Br.) Schroers & Samuels.

Stephanonectria keithii (Berk. & Br.) Schroers & Samuels, comb. nov. – Figs. 1–23.

= *Nectria keithii* Berk. & Br., Ann. Mag. Nat. Hist., Ser. 4, 27: 144. 1876 (basionym).

= *Nectriella keithii* (Berk. & Br.) Sacc., Michelia 1: 279. 1879.

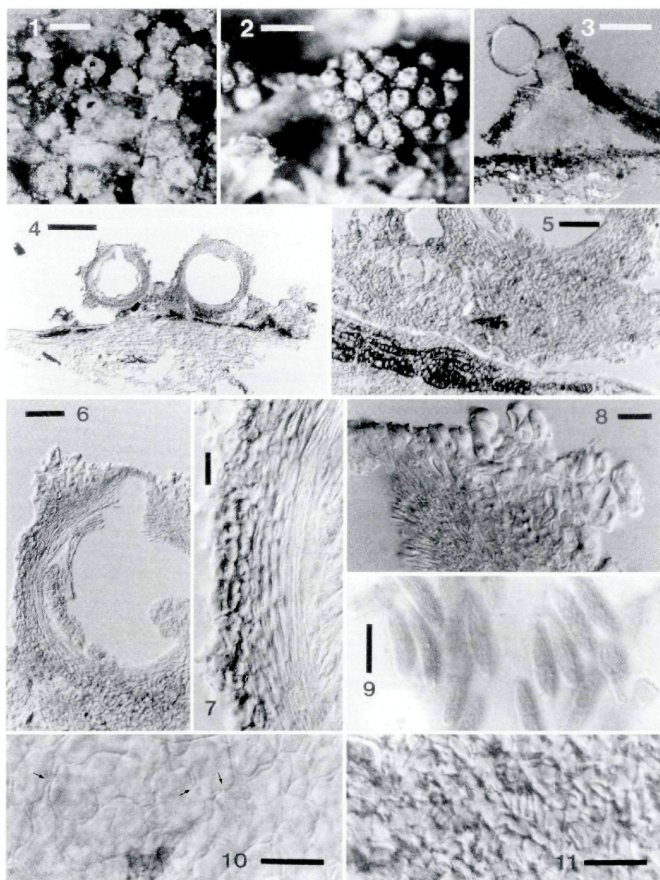
Figs. 1–11. *Stephanonectria keithii*. Teleomorphic features. – 1–4. Habit of perithecia on different substrata as seen from above and in longitudinal section. Perithecia loosely aggregated (1) on a rather superficial stroma (4) on *Brassica* sp.; perithecia crowded in large numbers (2) on a through the bark of *Elaeagnus* sp. erumpent stroma (3). – 5. Detail of the stroma as seen in longitudinal section; stroma consisting of small angular cells forming a *textura angularis*. – 6. Median longitudinal section of a perithecium showing the collar in relation to the ostiolum and the wall of the perithecium. – 7. Details of the perithecial wall, showing 2 wall regions with the outer region consisting of somewhat angular cells and an inner region consisting of flat cells. – 8. Apex of the perithecium as seen in longitudinal section, showing cells of the perithecial crown with unevenly thickened walls. – 9. Surface of ascospores showing short striae being mostly longitudinally oriented. – 10. Cells of the innermost perithecial wall region as seen in subsurface view, showing slightly lobed cells with irregularly thickened walls and pseudopores (arrows). – 11. Cells of the surface of the perithecium showing an irregular pattern of angular and ellipsoidal cells. – Bars: 1 = 300 µm; 2 = 500 µm; 3 = 250 µm; 4 = 150 µm; 5, 6 = 30 µm; 7, 8, 9 = 10 µm; 10, 11 = 20 µm. – Figs. 1, 9, 10, 11 from Broome 1877;

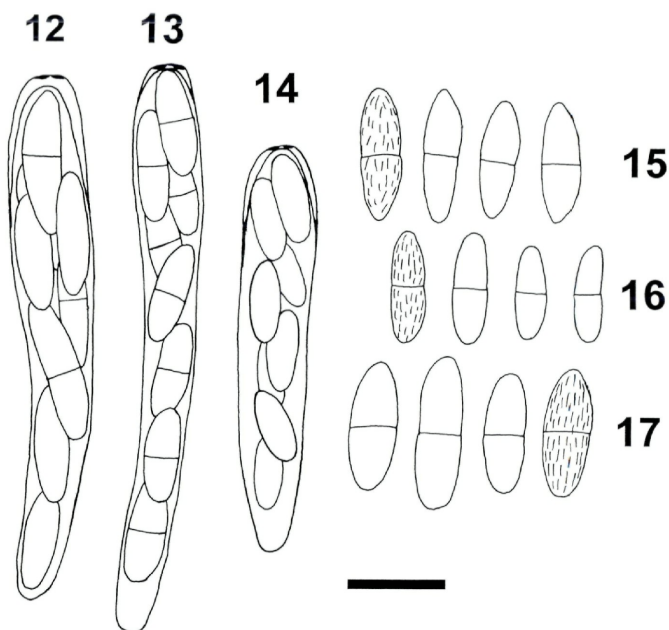
Figs. 2, 3 from BPI 802669; Figs. 4–8 from IMI 77877.

Anamorph. – *Myrothecium*-like.

Description from natural substratum:

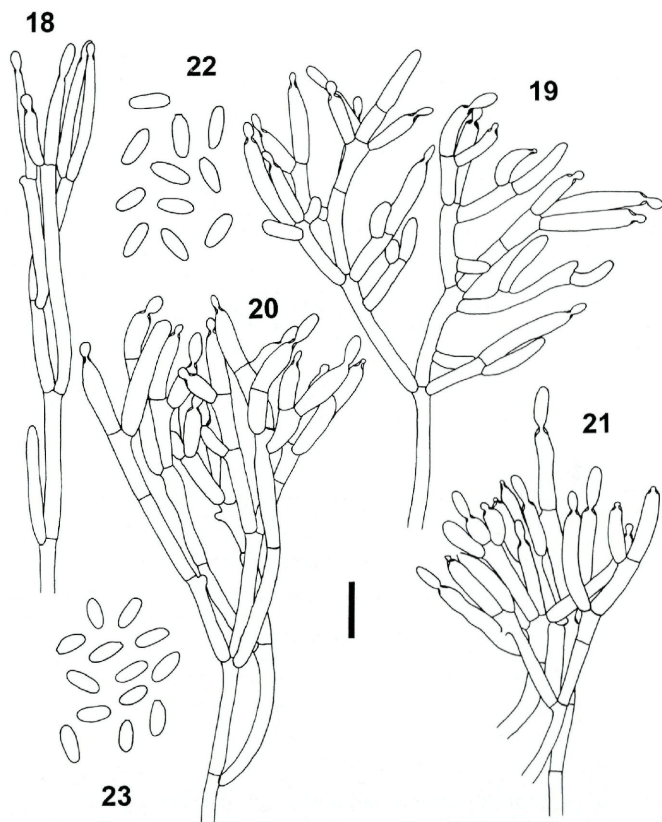
Stroma and perithecia easily removed; stroma flat, superficial to erumpent, composed of small angular cells generally not exceeding 10 μm diam (Fig. 5). – Perithecia superficial on the stroma, solitary to densely crowded (Figs. 1–5) in groups of 10(–30),





Figs. 12–17. *Stephanonectria keithii*. Asci and ascospores. – 12–14. Clavate asci showing a minute, flat apical ring. – 15–17. Ascospores (compare to Fig. 9). – Bar (12–17) = 10 μ m. – Fig. 12 from Petch 1935; Fig. 13 from BPI 802669; Fig. 14 from PDD 46245; Fig. 15 from Petch 1935; Fig. 16 from BPI 802669; Fig. 17 from PDD 46245.

ca. 300 μ m diam when seen in dried condition on the natural substratum, in median section 190–260 μ m high, 190–240 μ m diam, subglobose, golden-brown or brown, not changing colour in KOH, smooth to somewhat rough, minutely papillate, apex flat due to a crown surrounding the ostiolum (Fig. 1–4). Crown generally paler than the rest of the perithecial wall (Fig. 2), light brown, tan to pale orange; cells of the crown merging with the cells of the outer wall region, angular to oblong, tooth-like (Figs. 6, 8), sometimes hyphal-like (not shown), 5.5–19 \times 2.5–10 μ m; walls unevenly thickened, to 6 μ m thick (Fig. 8). – Perithecial wall 25–40 μ m thick (measured laterally), with two regions (Fig. 7): outer region 10–20 μ m thick, merging with the cells of the basal stroma, 3–5 cell-layers deep; cells angular to cylindrical, rarely hyphal, 4–7 \times 2.5–4.5 μ m, walls to 3 μ m



Figs. 18-23. *Stephanonectria keithii*. Conidiophores and conidia from pure culture. - 18. Infrequently occurring, convergently branched conidiophore with relatively long phialides. - 19-21. Conidiophores from sporodochial aggregates with relatively short phialides narrowed near the tip. - 19, 20. Conidiophores from young sporodochial pustules. - 21. Conidiophores from older sporodochial aggregates showing an anastomosis between two cells. - 22, 23. Conidia. - Bar (18-23) = 10 μ m. - Figs. 18, 19, 21, 22 from CBS 100007 (PDD 46342, BPI 737629), from 7-14-d-old OA-culture; Figs. 20, 23 from CBS 943.72, from 7-d-old OA-culture.

thick; inner region 15-20 μ m thick; cells slightly lobed in surface view, oblong and flat in longitudinal section, with pseudopores in the walls (surface view) (Fig. 10); cells of the inner region continuing

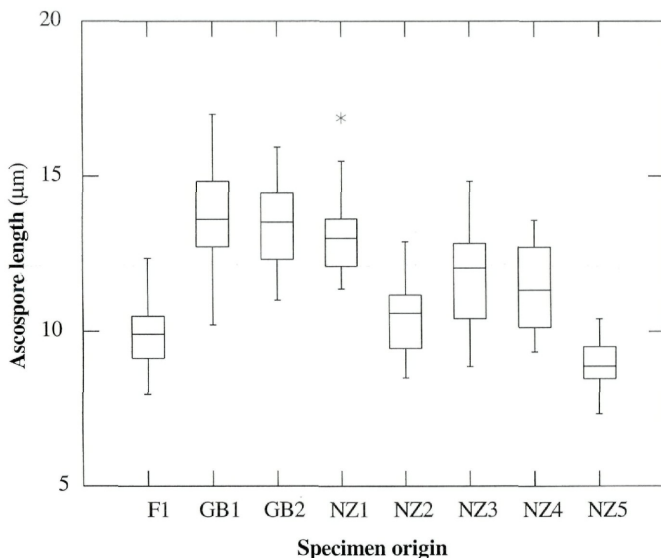


Fig. 24. – Boxplot display of the ascospore length of selected specimens. GB: specimens from Europe (Great Britain); F: specimens from Europe (France); NZ: specimens from New Zealand. F1: BPI 802669; GB1: Broome 1877; GB2: Petch 1935; NZ1: PDD 46245; NZ2: PDD 46284; NZ3: PDD 46342; NZ4: PDD 46344; NZ5: PDD 46416. – The hinges (upper and lower limits) of the boxes indicate the 75th and the 25th percentiles, respectively. The centre horizontal line marks the median of the sample. The whiskers show the range of values that fall within the inner fences. The value plotted with an asterisk may be interpreted as a potential outlier.

into the cells of the ostiolar apparatus, and continuing subapically inwards into brick-like, thin-walled cells that bear periphyses. – Ascii clavate, (38–)43–48–53(–64) × (5.5–)6.4–7.4–8(–11.5) µm (n = 51), 8-spored, apex broadly rounded, rarely flat, with a barely visible refractive ring (Figs. 12–14). – Ascospores ellipsoidal, 1-septate, more or less evenly 2-celled, colourless, with short, more or less longitudinally oriented striae or appearing smooth, particularly when still in the ascus, (7.5–)10–11.6–13.1(–17) × (2.4–)3.1–3.6–4.1(–5.6) (n = 221), biseriolate above, uniseriate below, almost completely filling the ascus (Figs. 9, 15–17).

Sporodochia flat to cup-shaped, to 300 µm diam, composed of dense, parallel conidiophores; hymenium consisting of densely arranged phialides. – Conidial masses brownish orange, or white

to pale orange. Conidia within the conidial masses arranged in disconnected linear or somewhat imbricate chains (not shown). – Conidia $(2.9-4.4-4.9-5.4(-7.6) \times (1.6-1.8-3.3(-5.2) \mu\text{m}$ ($n = 226$), 1-celled, hyaline, smooth, ellipsoidal, symmetrical (homopolar, polysymmetrical) or asymmetrical with a slightly laterally displaced hilum (heteropolar, bilateral symmetry). – Sterile mycelium on the substratum visible or not, typically not observed close to mature perithecia.

Description from pure culture:

Colony diameter after 7 d (24°C, darkness) 9–12 mm (CMD, OA). – Colony surface on CMD transparent, aerial mycelium sparse, tufted; on OA and PDA somewhat felty to cottony, with aerial mycelium in fine tufts, more strongly developed than on CMD. – Sporodochia formed on all media within 21 d, more abundantly on OA and PDA than on CMD, initially from small tufts of aerial mycelium, later confluent and in concentric rings if incubated in day/night rhythm. – Colony reverse transparent or orange-white to pale orange (5A23), with time developing pale brown hues. – Conidiophores (Figs. 19–21) monomorphic, penicillate, sporodochial, or, towards the margin of the colony, solitary or sparsely aggregated, particularly in young sporodochia rather irregularly and loosely joined; branches overall diverging, sometimes joined by anastomoses (Fig. 21); conidiophores irregularly penicillate, not showing regular patterns, with 1–5 phialides on each supporting cell. – Phialides cylindrical, sometimes widening in the middle or in the upper part, typically becoming narrower just underneath the apex, with apical periclinal thickening visible, without collarette, $(8.5-11-12.8-14.1(-20.5) \mu\text{m}$ long, from $(1.6-1.9-2.2-2.4(-2.7) \mu\text{m}$ at the base widening to $(1.7-2.2-2.5-2.8(-3.4) \mu\text{m}$ at the widest point, and tapering to $(0.6-1-1.2-1.3(-1.9) \mu\text{m}$ wide at the tips ($n = 80$). – Sparingly and convergently branched conidiophores rarely observed, with longer phialides of 10–18.5–23 μm (Fig. 18). – Conidial masses orange brown to brown, not changing colour in lactic acid or KOH, initially watery slimy, later tough slimy, formed in hemispherical masses on the sporodochia, or confluent on adjacent sporodochia. – Conidia (Figs. 22, 23) 1-celled, hyaline, smooth, ellipsoidal, hilum median, slightly laterally displaced, or not visible, $(3.4-4.8-5.4-5.9(-7.7) \times (1.8-2.1-2.4-2.6(-3.1) \mu\text{m}$ ($n = 259$).

Habitat. – On ?dead material of diverse plants; teleomorph known from dead stems of *Brassica* sp., bark of trees, e.g. *Elaeagnus* sp., on rotting inflorescence of *Rhopalostylis sapida*, ?and on basidomes of *Amuroderma* sp.; conidial isolates known from soil.

Known distribution. – Possibly cosmopolitan; perithecia found in Europe (England, France), Japan, New Zealand, French Guiana (specimen immature, tropical distribution needs confirmation); conidial isolates from The Netherlands.

Holotype of *Stephanonectria keithii*. – Great Britain. Forbes, on decorticated stems of cabbage, Rev. J. Keith, IMI 77877. No perithecia remain on the specimen but a slide ex type collection containing sections through perithecia, labeled "Herb. Berk. 1879, 5 μ sections, *N. keithii*, Ex Type coll., 77877", together in one package with a slide containing a squash preparation of *Nectria keithii* (sections possibly prepared by T. Petch). These slides are apparently all that remains of the holotype.

Additional specimens/isolates examined. – GREAT BRITAIN: Batheaston, on cabbage stalk, Mar. 1877, C. E. Broome. North Wootton, on stalks of *Brassica*, Nov. 1935, T. Petch (IMI 76120, slide). – France: Pyrénées Atlantiques. Ilot de Sauveterre 64, on bark of *Elaeagnus* sp., 2 Nov. 1992, F. Candoussau 253, G. J. Samuels culture 92-133, CBS 100005 (BPI 802669). – THE NETHERLANDS: Utrecht, Berenkuil, soil, CBS course Sep. 1972 (CBS 943.72). Oostelijk Flevoland, agricultural soil, under permanent potato, J. W. Veenbaas-Rijks, Oct. 1969 (CBS 434.70). – NEW ZEALAND: Northland, vic. Mangamuka Bridge, vic. forest H.Q., on indet. tree, 11 May 1983, G. J. Samuels, Samuels culture 83-86 (dried, dead, PDD 46284). Northland, vic. Mangamuka Bridge, Omahuta State Forest, Kauri Reserve, on bark of indet. tree, 8 May 1983, G. J. Samuels et al., Samuels culture 83-215 (dried, dead, PDD 46416; BPI 737627). Gisborne, Lake Waikaremoana, Ngamoko Trail, on *Beilschmiedia tawa*, 30 May 1983, G. J. Samuels et al., Samuels culture 83-167 (dried, dead) (PDD 46344). Gisborne, Lake Waikaremoana, Ngamoko Trail, on *Beilschmiedia tawa*, 30 May 1983, G. J. Samuels et al., Samuels culture 83-165, CBS 100007 (PDD 46342; BPI 737629). Auckland, Waitakere Ra., Cowan Trail, on rotting inflorescence of *Rhopalostylis sapida*, 27 Apr. 1983, G. J. Samuels et al., Samuels culture 83-36 (dried, dead) (PDD 46245; BPI 737630). – JAPAN: Kakuma valley, Sanado-Town, Nagano-prefecture, 1036 m, 13 Aug. 1997, H.-J. Schroers et al., Schroers culture and specimen 244, CBS 100289 (remaining sterile). – FRENCH GUIANA: Upper Marouini River, 2 km N of Oumanfou-Langa Soula, 02°53' N, 54°00' W, 150 m alt., Aug. 1987, on *Amauroderma* sp., G. J. Samuels et al., formerly identified as *Hypomyces amaurodermatis* (NY; G.J.S. 5969; immature).

Discussion

The teleomorph. – Booth (1959) corrected the status of *N. keithii* formerly listed as synonym of *Nectria subquaternata* Berk. & Br. by Petch (1938), and an error of the original authors who apparently mistook conidia from the natural substratum for ascospores and described 1-celled ascospores. We follow Booth's interpretation.

The holotype of the species is in poor condition. No perithecia are left. Our concept of *S. keithii* is in accordance with the description provided by Booth (1959) and is supported by slide IMI 77877 that is labelled "ex type coll." (Figs. 4-8), containing sections of perithecia showing the characteristic collar and wall anatomy of the

species redescribed here. Interestingly, Broome in 1877, one year after the original description of *N. keithii*, labelled another specimen of the same species "Nectria", without epithet and one could argue that Broome should have recognised the species he had described himself. Nevertheless, it is possible that Broome left the identification uncertain because of the 1-septate ascospores that he clearly illustrated on the package of the 1877 specimen but that were obviously overlooked in the original description.

Ascospores of *S. keithii* are striate, but the striae are short and mostly oriented longitudinally on the surface of the ascospores (Figs. 9, 15–17). This ornamentation may also be interpreted as elongated warts that have a cylindrical shape. The ascospore length is variable, covering a range of 7.5–17 μm . However, although both specimens from Great Britain (Broome 1877, Petch 1935) have comparably large ascospores (Fig. 24), spore measurements in general show a continuous range, with strong variation within a specimen. The variation therefore is not indicative of infraspecific differences or a pattern of geographical distribution.

The most characteristic feature of *S. keithii* are its perithecia, particularly of the ostiolar crown (Figs. 1–4, 6, 8). Such ostiolar discs, collars or crowns are rare in hypocrealean fungi. In *Nectriella coronata* Juel [*Pseudonectria coronata* (Juel) Lowen (Rossman et al., 1993)] the collar is inconspicuous, composed of mostly 1-septate, up to 30 μm long hyphae loosely surrounding the ostiolum (Juel, 1925, Fig. 2). Differences to *S. keithii* are also the anamorph (*Sesquicillium*) and the substratum (*Buxus* leaves). In *Nectria coronata* Penzig & Saccardo (anamorph *Cylindrocarpon* sp.) the small cells of the outer perithecial region continue into the collar surrounding the ostiolum and only the top cells of the crown are conspicuously large, saccate, and thin-walled (Samuels et al., 1990, Fig. 18A). Perithecia in the genus *Ijuhya* Starbäck typically have a crown around the apex. The crown of *Ijuhya* is formed of intertwined hyphae that sometimes project as short, triangular hyphal constructions giving the perithecia an aspect somewhat similar to *S. keithii*. However, the perithecial wall anatomy, anamorph (*Acremonium* species) and substratum (mainly monocotyledonous plant debris) of *Ijuhya* species differ from those of *S. keithii* and we do not see a close relationship between *Ijuhya* and *Stephanonectria*.

The perithecial crown of *S. keithii* could be taken to be apical warts. Warted perithecia are common in unrelated genera of the Hypocreales, but in none of them are the warts restricted to the ostiolar region as in *S. keithii*.

The Hypocreales comprise four families, the Hypocreaceae, the Nectriaceae, the Bionectriaceae, and Niessliaceae (Samuels & Barr, 1997; Rossman et al., 1999). Taxa with perithecia formed super-

ficially on a stroma, on the substratum, or, more rarely, on a subiculum are classified in the Nectriaceae or Bionectriaceae. The Nectriaceae can roughly be characterised by red perithecia that do change colour in KOH (positive KOH reaction) while perithecia of the Bionectriaceae lack any colour reaction in KOH (negative KOH reaction). Both families contain anamorphs classified in numerous different genera. The lack of a KOH reaction in *S. keithii* and the relatively thin perithecial wall point to its classification in the Bionectriaceae.

The anamorph. – *Stephanonectria keithii* possesses a distinctive anamorph of densely aggregated, sporodochial conidiophores. The penicilli of the conidiophores are irregularly branched, with phialides arising from several levels or even scattered along the cells of the penicillus. Although the conidiophores, at least in pure culture, appear to be densely aggregated, the term sporodochium is applied with some hesitation because the conidiophores are not produced from a clearly differentiated base or a morphologically distinct subhymenium (Seifert, 1985). On the natural substratum the perithecia of some specimens are, however, associated in morphologically distinct, somewhat cup-shaped sporodochia.

The phialides are conspicuous in form, almost cylindrical, typically widening in the middle or in the upper part, and typically becoming narrower just underneath the tips (Figs. 19–21). In this regard, this anamorph resembles some species of *Myrothecium* (Tulloch, 1972). Furthermore, the conidiophores of *S. keithii* are often joined laterally by short bridges, as they are in the equally *Myrothecium*-like anamorph of *N. pityrodes* (Montagne) Montagne. For these reasons, conidial isolates of *S. keithii* have been previously identified as an undescribed species of *Myrothecium*. However, neither the anamorph of *S. keithii* (nor the anamorph of *N. pityrodes*) belong to *Myrothecium* in the sense of Tulloch (1972) because sterile marginal hairs are lacking from the sporodochia and, in *S. keithii*, conidial masses are brown and not green. That notwithstanding, we do not wish to describe a new genus for the anamorph of this distinctive ascomycete. Designation as *Myrothecium*-like appears to be the best solution. We emphasise, however, that no natural relatedness of *S. keithii* to *Myrothecium inundatum* Tode : Fr., the type species of *Myrothecium*, should be inferred from our use of this descriptive term.

Pale brown conidia of *S. keithii* are unusual in the Hypocreales, but not unheard of. The species that have brown conidia are not closely related to each other. These include the *Calostilbella calostilbe* Höhnelt anamorph of *Calostilbe striispora* (Ellis & Everh.) Seaver, and the two anamorphic members of the order, *Trichoderma*

flavofuscum (Miller et al.) Bissett and an undescribed species in *Clonostachys*.

Ecology and distribution. – All specimens collected in England were found on *Brassica*, which might be indicative of some host preference. Because all other collections (France, New Zealand, Japan) were found on the bark of various woody plants, *N. keithii* is better considered as a non-specialised saprotroph.

The morphological pattern of the teleomorph is consistent in specimens collected in Europe (UK and France) and New Zealand. The species therefore might be considered to have a temperate to subtropical distribution. The collection cited from French Guiana is immature and identified as *S. keithii*, based on the morphology of the still immature asci (not shown) and some details of perithecial wall anatomy. However, the perithecia of this specimen are more orange than brown, were found on *Amauroderma* sp., and lack a crown. Occurrence of *S. keithii* in tropical regions therefore is possible, but not confirmed. Perithecia in the specimen cited for Japan are somewhat smaller than is typical but are otherwise indistinguishable from other specimens of *S. keithii*. Single ascospore isolates from this specimen remained sterile.

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Autor(en)/Author(s): Schroers Hans-Josef, Gams Walter, Samuels Gary J.

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