The genus Acanthostigma (Tubeufiaceae, Pleosporales)

Martina Réblová¹ & Margaret E. Barr²

 ¹ Institute of Botany, Dept. Plant Taxonomy and Biosystematics, Academy of Sciences, CZ-252 43 Průhonice, Czech Republic
 ² 9475 Inverness Road, Sidney, British Columbia, V&L 5G8 Canada

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The genus Acanthostigma is redescribed on the basis of the re-examination of type material of A. perpusillum, type species of the genus. It is placed in the Tubeufiaceae and is characterized by having dark, setose ascomata, cellular pseudoparaphyses, bitunicate asci, hyaline, multiseptate, cylindrical-fusiform to elongate fusiform ascospores, Helicosporium and Helicomyces anamorphs and occurrence on rotten wood or on stromata of other ascomycetes. Six species are accepted in Acanthostigma. Acanthostigma ellisii, A. longisporum, A. perpusillum, A. revocatum, A. minutum and A. scopulum are redescribed and illustrated on the basis of re-examination of type material. A new combination for A. longisporum is proposed. A key to species in Acanthostigma is provided. Acanthostigma filisporum is excluded and its affinity to the Niessliaceae is discussed. Acanthostigmina is relegated to synonymy with Acanthostigma. Two species previously referred to Acanthostigmina and one to Tubeufia sect. Acanthostigmina are not accepted in Acanthostigma and are transferred to Taphrophila in the Tubeufiaceae and proposed as three new combinations T. hebridensis, T. miscanthi and T. trichella.

Keywords: Ascomycetes, *Helicosporium*, *Helicomyces*, mycosaprobe, Niessliaceae, *Taphrophila*, Tubeufiaceae, systematics.

The systematic position of *Acanthostigma* De Not. (De Notaris, 1863) in relation to the nature of asci and hamathecium has been addressed several times (Müller, 1965; von Arx & Müller, 1975; Barr, 1977; 1980; 1990; Eriksson & Hawksworth, 1998). The discrepancies in the literature, i.e. whether the fungus possesses unitunicate or bitunicate asci were a consequence of the impossibility to examine the type material of *Acanthostigma perpusillum* De Not., the type species of the genus, that von Arx & Müller (1975) considered lost.

De Notaris (1863) described *A. perpusillum* from inner side of the bark of *Cerasus* sp. from Italy. The fungus was characterized by superficial, setose ascomata with a fragile wall and cylindrical-clavate asci containing eight, hyaline, 5-septate, ca. 30 μ m long ascospores. Later, Saccardo (1883) gave full sizes for asci (70 × 5 μ m) and ascospores (28–30 × 5.5–5 μ m). He was probably the last to examine

the type material of *A. perpusillum*. Berlese (1894) based his description and illustration of *A. perpusillum* on type material of *A. decastylum* (Cooke) Sacc. (Tab. 102, fig. 2. 'Ex specimen orig. *Acanth. decastyli* a cl. Cooke benevole communicatis'). Berlese (1894) gave sizes for asci ($65-75 \times 10-12 \mu$ m) and ascospores ($22-25 \times 4-5 \mu$ m) and listed *Acanthostigma decastylum* [\equiv *Chaetosphaeria decastyla* (Cooke) Réblová & W. Gams, Réblová & Gams, 1999], *Lasiosphaeria subvelutina* Ellis & Everh. and *Zignoëlla cariosa* (Cooke & Ellis) Sacc. [= *Chaetosphaeria ovoidea* (Fr.) Constantinescu & al., Réblová & Gams, 1999] as synonyms of *A. perpusillum*.

According to the original illustration of *A. perpusillum* (De Notaris, 1863), von Arx & Müller (1975) suggested that *Acanthostigma* might be a synonym of a leaf biotroph *Nematostoma* H. Syd. & P. Syd. of the Pseudoperisporiaceae (Barr, 1997). Müller (1965) and Barr (1990; 1993; 1997) interpreted the asci of *A. perpusillum* as unitunicate and placed *Acanthostigma* in the Trichosphaeriaceae.

A recent examination of the newly discovered type material of Acanthostiqma perpusillum (RO) revealed that the fungus possesses minute, dark, deeply collapsing pseudothecia covered with short, opaque pointed setae, numerous cellular pseudoparaphyses, clavate, bitunicate asci and eight hyaline, transversely multiseptate ascospores. It matches the circumscription of Acanthostigmina Höhn. Acanthostigmina was erected by Höhnel (1909) for a single species Lasiosphaeria minuta Fuckel and was considered closely related to Acanthostigmella Höhn. Later, von Arx & Müller (1975) considered Acanthostigmina and Acanthostigmella to be synonymous with Tubeufia Penzig & Sacc. Barr (1980) accepted Acanthostigmina as a synonym of Tubeufia in the Tubeufiaceae and distinguished it as an independent section among the three others as Tubeufia sect. Acanthostigmina (Höhn.) M. E. Barr, while Acanthostigmella with the type species A. genuflexa Höhn. proved different from Tubeufia and was attributed to the Herpotrichiellaceae (Barr, 1977; Crane & al., 1998). Recently, Crane & al. (1998) returned Acanthostigmina to generic rank within the Tubeufiaceae. Because both Acanthostigma and Acanthostigma perpusillum (De Notaris, 1863) have priority as generic name and specific epithet over Acanthostigmina (Höhnel, 1909) and Acanthostigmina minuta [Basionym: Lasiosphaeria minuta (Fuckel, 1870)], therefore, Acanthostigmina is relegated to synonymy.

Acanthostigma is a well-characterized genus in the Tubeufiaceae. It encompasses lignicolous saprobes or mycosaprobes with minute, setose, dark ascomata, dark, thick-walled setae, bitunicate asci, narrow cellular pseudoparaphyses and hyaline, cylindrical-fusiform to elongate fusiform, transversely multiseptate ascospores arranged in fascicles. The *Helicosporium aureum* (Corda) Linder anamorph has been linked to *Acanthostigma scopulum* (Cooke & Peck) Peck [as *Tubeufia scopula* (Cooke & Peck) M. E. Barr; Barr, 1980], and *Helicomyces* sp. is linked to *A. minutum* (Fuckel) Sacc. in the present study.

According to the treatments of Acanthostigma by Berlese (1894), Ellis & Everhart (1892), Saccardo (1883; 1891; 1895; Saccardo in Mussat, 1901; Saccardo in Trotter, 1926), Saccardo & Sydow (1899), Saccardo & Traverso (1910) and Saccardo & Trotter (1913), the genus accommodated ca. 75 rather unrelated elements. Some were recently placed in Loculoascomycetes, e.g. *Chaetothyrium* Speg. (Barr, 1993), *Nematostoma* Syd. & P. Syd. including *Aphanostigme* Syd. as its synonym (Barr, 1968; 1977; Müller, 1965; Rossman, 1987) and *Acanthophiobolus* Berl. (Walker, 1972; 1980), or Hymenoascomycetes, e.g. *Cercophora* Fuckel (Barr, 1993), *Chaetosphaeria* Tul. & C. Tul. (Réblová & Gams, 1999) and *Niesslia* Auersw. (Winter, 1887). Other species that were placed in the genus require further revision and possibly also reclassification.

The goal of this study is the clarification of the systematic position of Acanthostigma on the basis of the re-examined type material of A. perpusillum. In the present paper, six species of Acanthostigma are accepted. A new combination is proposed for Acanthostigma longisporum (Remler) Réblová & M. E. Barr. Acanthostigma ellisii Sacc & Syd., A. longisporum, A. perpusillum, A. revocatum Sacc., A. minutum and A. scopulum are redescribed and illustrated on the basis of their type material.

Acanthostigma filisporum M. E. Barr is excluded from the genus and its affinity to the Niessliaceae is discussed. Two species referred by Crane & al. (1998) to Acanthostigmina and another one referred by Hsieh & al. (1998) to Tubeufia sect. Acanthostigmina are saprobes with a strong preference for culms and leaves of Cyperaceae and Poaceae. These species are not accepted in Acanthostigma and are transferred to the closely related Taphrophila in the Tubeufiaceae as T. hebridensis (Dennis) Réblová & M. E. Barr, T. miscanthi (W. H. Hsieh, C. Y. Chen & A. Sivan.) Réblová & M. E. Barr and T. trichella (Sacc., E. Bommer & M. Rousseau) Réblová & M. E. Barr.

Material and methods

Ascomata from herbarium specimens were rehydrated in 3% KOH. The asci, ascospores and interthecial filaments were studied in lactic acid, water and Melzer's reagent. Measurements were taken in Melzer's reagent. The structure of the perithecial wall was studied from freehand sections of dried material cut under the dissecting microscope and mounted in lactic acid.

Taxonomy

Acanthostigma De Not., Sfer. Ital., Cent. I, Fasc. 1, 2: 85, 1863.

= Acanthostigmina Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math. – Naturwiss. Cl., Abt. 1, 118: 1499, 1909.

Pseudothecia superficial, globose to subglobose or conical, vinaceous or reddish-brown to dark brown, sometimes covered with protruding cells, setose, noncollapsing or collapsing upon drying. – Setae mostly 1-celled or rarely 1-septate, thick-walled, dark brown, opaque, acute to obtuse at the tips. – Pseudothecial wall leathery, formed of brown, thick-walled, polyhedral to brick-like cells. – Hamathecium consisting of cellular pseudoparaphyses. – As co bitunicate, cylindrical-fusiform or cylindrical-clavate or clavate, thickened at the apex, short-stipitate, 8-spored. – As cospores cylindrical-fusiform, fusiform or elongate fusiform, straight or curved, hyaline, transversely multiseptate, often one or two inner cells slightly broader, arranged in fascicles in the ascus.

Type species. - Acanthostigma perpusillum De Not.

Anamorphs. - *Helicosporium* C. G. Nees & F. Nees, *Helicomyces* Link.

Habitat. – Saprobes on decaying wood and bark or mycosaprobes on stromata of other ascomycetes.

Distribution. - Cosmopolitan.

Key to the species accepted in Acanthostigma

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3.	Ascospores usually up to 40 µm long	4
3*.	As cospores usually more than 40 μm long $\hdots models model$	5

- 5. Ascospores more than $3.5 \ \mu\text{m}$ wide, $40-55(-63) \times (5-)6-7(-7.5) \ \mu\text{m}$; long-fusiform, straight or slightly curved, one of the middle cells slightly broader; *Helicomyces* anamorph

Species accepted in Acanthostigma

- Acanthostigma ellisii Sacc. & Syd., Syll. Fung. 14: 591, 1899. Fig. 1.
 - Acanthostigma parasiticum Ellis & Everh., Proc. Acad. Nat. Sci. Philad. 45: 443, 1893. Nom. Illeg. Art. 53.1.] non Acanthostigma parasiticum (R. Hartig) Sacc., Syll. Fung. 9: 855, 1891 = Nematostoma parasiticum (R. Hartig) M. E. Barr, Mycotaxon 64: 167, 1997.

Anamorph. - Unknown.

Teleomorph. – Pseudothecia superficial, scattered to gregarious, globose to subglobose, 150–230 μ m diam, 160–210 μ m high, brown, densely setose, noncollapsing. – Setae 0–1-septate, thick-walled, dark brown, opaque, acute, 20–85 μ m long, 4–4.5(-6) μ m wide at the base. – Pseudothecial wall 26–37.5 μ m thick, of polyhedral, pale to mid brown, thick-walled cells, cells becoming more brick-like and paler towards interior. – Cellular pseudopara-physes numerous among asci, branching, anastomosing, 1.5–2.5 μ m wide. – Asci bitunicate, clavate, (63–)84–90×14–15 μ m, broadly rounded and thickened at the apex, short-stipitate, 8-spored. – Ascospores cylindrical-fusiform to long-fusiform, (38–)48–64.5×4–4.5 μ m, straight or slightly curved, rounded at the proximal end, tapering at the distal end to ca. 2–2.5 μ m, one or two middle cells near the proximal end slightly broader than the others, 6–12-septate, nonconstricted at the septa, hvaline, 4–8-seriate in the ascus.

Specimen examined. – USA: New Jersey, Newfield, parasitic on stroma of *Diatrype stigma*, 25 Nov. 1892 (holotype of *Acanthostigma ellisii*, NY).



Fig. 1. Acanthostigma ellisii (holotype, NY). – a. Ascus containing ascospores. – b. Cellular pseudoparaphyses. – c. Ascospores. – d. Setae covering pseudothecia.

Habitat. – Mycosaprobe on stromata of other ascomycetes (*Diatrype stigma*).

Distribution. - North America: USA (New Jersey).

Acanthostigma ellisii seems intermediate between A. minutum and A. scopulum. However, the shape and size of ascospores clearly distinguish all three species. The two latter have ascospores with symmetrical narrowly rounded ends. Moreover, A. minutum has ascospores often with one of the middle cells slightly broader and pseudothecia that are covered with setae and protruding cells mostly on the upper half. Acanthostigma scopulum has much narrower ascospores steady wide along the whole length and typically curved or bent in the lower third.

Acanthostigma ellisii was introduced as a nomen novum for A. parasiticum Ellis & Everh. non (R. Hartig) Sacc. (Saccardo & Sydow, 1899), therefore, it is used here as the correct name.

Crane & al. (1998) cited Acanthostigma ellisii to be synonymous with A. perpusillum (as Acanthostigmina minutum). However, the type material of A. ellisii contains a fungus that is clearly different from A. perpusillum in having longer asci and longer ascospores with asymmetrical ends with one or two inner cells near the proximal end slightly broader. Therefore, A. ellisii is considered a separate species and is redescribed and illustrated based on the present re-examination of the type material.

2. Acanthostigma longisporum (Remler) Réblová & M. E. Barr, comb. nov. – Fig. 2.

Bas.: Herpotrichiella longispora Remler, Bibl. Mycol. 68: 94, 1979.

- ≡ Acanthostigmina longispora (Remler) J. L. Crane & al., Can. J. Bot. 76: 606, 1998.
- = Tubeufia alpina L. Holm & Nograsek, Bibl. Mycol. 133: 221, 1990.
 - ≡ Acanthostigmina alpina (L. Holm & Nograsek) J. L. Crane & al., Can. J. Bot. 76: 606, 1998.

Anamorph. - Unknown.

Teleomorph. – Pseudothecia erumpent to superficial, often the lower third immersed in the substratum, scattered, globose to subglobose, 150–260 μ m diam, 160–250 μ m high, brown, densely setose, non-collapsing. – Setae 0–1-septate, thick-walled, mid brown, straight to slightly curved, translucent in transmitted light, obtuse at the tips, 30–90 μ m long, 3.5–4 μ m wide in the middle. – Pseudothecial wall 15–20 μ m thick, of polyhedral, pale to mid brown, thick-walled cells, cells becoming more brick-like and paler towards interior. – Cellular pseudoparaphyses numerous among asci,



Fig. 2. Acanthostigma longisporum (holotype, GZU 145.80). – a. Ascus containing ascospores. – b. Cellular pseudoparaphyses. – c. Ascospores. – d. Setae covering pseudothecia.

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branching, anastomosing, ca. 2.5 μ m wide. – Asci bitunicate, cylindrical-clavate, 73–85(–94) × 10–15 μ m, broadly rounded to obtuse and thickened at the apex, short-stipitate, 8-spored. – Ascospores long-fusiform, (29–)38–51 × 4–4.5(–5) μ m, straight or inequilateral, broadly rounded at the proximal end, tapering and narrowly rounded, often curved at the distal end, ca. 1.5 μ m wide, (4–)6–8-septate, non-constricted or slightly constricted at the septa, hyaline, 4-seriate in the ascus.

Specimens examined. – AUSTRIA: Carinthia [Kärnten], Alps Mts., Kreuzeck Mts. [Kreuzeck-Grouppe], between Emberger Alm and Naßfeldtörl, 2100–2200 m a.s.l., on dead branch of *Rhododendron ferrugineum*, 14 Jul. 1978, P. Remler (holotype of *Herpotrichiella longispora*, GZU 145-80). – NORWAY: Oppland, Dovre, Grimsdalen, ca. 1200 m a.s.l., on dead stem of *Dryas octopetala*, 22 Aug. 1985, L. Holm & K. Holm 3700b (holotype of *Tubeufia alpina*, UPS).

Descriptions and illustrations. - Remler (1979: 94, Tab. 2, Fig. 4); Nograsek (1990: 221, Figs. 137, 138).

Habitat. – Saprobe on woody stems or bark of dead thicker branches.

Known hosts. – Calluna vulgaris, Dryas octopetala, Rhododendron ferrugineum, R. hirsutum, Rhodothamnus chamaecistus, Vaccinium myrtillus, Vaccinium uliginosum.

Distribution. - Europe: Austria, Norway.

Acanthostigma longisporum most closely resembles A. ellisii in the ascospore morphology. However, the latter differs in having longer asci, dark brown opaque, acute setae and somewhat longer ascospores merely tapering, narrowly rounded and not curved at the distal end and with one or two inner cells near the proximal end somewhat broader.

The ascospores of *A. longisporum* with tapered, narrowly rounded distal end are strongly reminiscent of those of *Rebentischia* P. Karsten of the Tubeufiaceae. However, the ascospores of the latter are bicolorous, having the middle cells brown and the appendagelike end-cells hyaline.

- Acanthostigma perpusillum De Not., Sfér. Ital., Cent. I, Fasc.1, 2: 85, 1863. – Fig. 3.
- = *Lasiosphaeria perpusilla* (De Not.) Sacc. sensu Saccardo, Nuovo Giorn. Bot. Ital. 7: 327, 1875.
 - ≡ Acanthostigma revocatum Sacc., Syll. Fung. 2: 208, 1883].
- = Sphaeria clintonii Peck, Ann. Rep. New York State Mus. 30: 65, 1878.
 - = Acanthostigma clintonii (Peck) Sacc., Syll. Fung. 2: 210, 1883.
 - = Tubeufia clintonii (Peck) M. E. Barr, Mycotaxon 12: 163, 1980.

Anamorph. – Unknown.

Teleomorph. – Pseudothecia superficial, scattered, globose to subglobose, 150–155 μ m diam and 100–110 μ m high, reddishbrown to dark brown, sparsely setose on the upper part, collabent inwards when dry. – Setae 1-celled, dark brown, opaque, acute, (10–)28–97 μ m long and 5–6 μ m wide at the base. – Pseudothecial wall 15–22 μ m thick, of polyhedral, pale to mid brown, thick-walled cells arranged into 3–4 rows. – Cellular pseudoparaphyses numerous among asci, branching, anastomosing, 2–3.5 μ m wide. – Asci bitunicate, clavate, 77–79×14–16 μ m, broadly rounded and thickened at the apex, short-stipitate, 8-spored. – Ascospores fusiform, narrowly rounded at both ends, one of middle cells often broader than the others, 30.5–35.5(–42)×5–6 μ m, (5–)6–7(–8)-septate, straight or slightly curved, non-constricted or slightly constricted at the septa, hyaline, 2–4-seriate in the ascus.

Specimens examined. – FRANCE: Noidan, Côte d'Or, on decayed wood of *Quercus* sp., Feb. 1899, F. Fautrey (PAD). – ITALY: Lombardia, Turbigo, on inner side of bark of *Cerasus* sp. (associated with *Calosphaeria pulchella*), Gené (holotype of *Acanthostigma perpusillum*, RO). – USA: New York, Buffalo, Erie Co. (Alden in protologue), on decaying wood, Nov. 1876, G. W. Clinton (holotype of *Sphaeria clintonii*, NYS).

Descriptions and illustrations. – De Notaris (1863: 85, Tab. 95); Peck (1878: 65, Plate 2, Figs. 19–23); Berlese (1894: 103, Tab. 100, Fig. 3); Barr (1980: 163, Figs. 16–18).

Habitat. - Saprobe on decayed wood of deciduous trees.

Known hosts. - Cerasus sp., Elletaria sp., Quercus sp.

 Distribution. – Europe: Austria, Italy, Switzerland, France;
 North America: USA (Louisiana, Massachusetts, New Hampshire and New York); Canada (Ontario and Quebec); South America: Grenada, Venezuela; Asia: Java.

Acanthostigma perpusillum is characterized by minute, setose, collapsing pseudothecia and hyaline, (5-)6-7(-8)-septate, fusiform ascospores narrowly rounded at both ends, usually with one of the middle cells somewhat broader. The species is well documented by Barr (1980) as *Tubeufia clintonii* (Peck) M. E. Barr. Upon the revision of the type material of *Sphaeria clintonii* and other herbarium material, Barr (1980) described the ascospores as (2-)5-7(-11)-septate and somewhat longer $[(19-)32-45(-54) \times (2.5-)3.5-5.5(-6) \text{ µm}]$ than those in the type material of *A. perpusillum* and material of taxa referred by Barr (1980) to *T. clintonii* are identical. As was indicated in the key of species in *Acanthostigma*, the species concept of *A. perpusillum* should be re-



Fig. 3. Acanthostigma perpusillum (holotype, RO). – a. Ascus containing ascospores. – b. Cellular pseudoparaphyses. – c. Ascospores. – d. Habit sketch, median longitudinal section of pseudothecium. – e. Habit sketch of pseudothecia on the natural substratum.

stricted to taxa with ascospore length up to $40 \ \mu m$. Those taxa with longer ascospores should be compared with *A. minutum* (see below).

Acanthostigma perpusillum is related to A. revocatum that differs in having smaller asci and smaller ascospores that are broadly rounded at each end. Acanthostigma minutum resembles A. perpusillum generally in the shape of ascospores but differs in having the ascospores always longer than 40 μ m and broader, usually 6–7 μ m wide.

De Notaris primarily marked the type collection of A. perpusillum (RO) as Sphaeria stictica, an unpublished herbarium name. Later, when De Notaris (1863) described a new genus Acanthostigma with a new species A. perpusillum he based the descriptions on this material that he renamed and chose as a type. In the protologue De Notaris (1863) cited Sphaeria eres Berk. & C. Broome [= Venturia eres (Berk. & C. Broome) Ces. & De Not.; Cesati & De Notaris, 1863], Sphaeria dickiei Berk. & C. Broome [= Metacoleroa dickiei (Berk. & C. Broome) Petr.; Petrak, 1927] and Sphaeria chaetomium Corda [= Niesslia exilis (Alb. & Schw. : Fr) G. Winter; G. Winter, 1887] to have an affinity with A. perpusillum.

Barr (1993) cited two herbarium specimens to represent A. perpusillum in North America. The first collection bearing the unpublished name Acanthostigma atrobarbum (Cooke & Ellis) Ellis Everh. var. piniolum (CANADA: Ontario, Ottawa, on rotten pine wood, 23 Jul. 1897, NY 428) represents a species of Chaetosphaeria, known as Chaetosphaeria crustacea (Sacc.) Réblová & W. Gams (Réblová & Gams, 1999); the Chloridium-Cylindrotrichum anamorph is abundantly present. The other collection bearing the name Sphaeria barbirostris Dufour (USA: New Jersey, Vineland, on inner surface of cast off bark of Acer saccharum, J. B. Ellis, N.A.F. 186) preserved in NY did not contain any pseudothecia of A. perpusillum.

- 4. Acanthostigma revocatum Sacc., Syll. Fung. 2: 208, 1883. Fig. 4.
 [≡ Lasiosphaeria perpusilla (De Not.) Sacc. sensu Saccardo, Nuovo Giorn. Bot. Ital. 7: 327, 1875. Fungi Ital. autograph. del., Fasc. 1–4, t. 141, 1877.]
 non Acanthostigma perpusilum De Not. Sfór Ital. Cent. J. Fasc. 12, 255
 - non Acanthostigma perpusillum De Not., Sfér. Ital., Cent. I, Fasc. 1, 2: 85, 1863.
- = Acanthostigma minutum (Fuckel) Sacc. var. brachysporum Sacc., Syll. Fung. 2: 209, 1883.

Anamorph. - Unknown.

Teleomorph. - Pseudothecia superficial, gregarious, globose, 120-150 μm diam, 120-140 μm high, dark brown, densely setose, non-collapsing. - Setae 1-celled, thick-walled, dark brown, opaque, acute, 15–20 μm long, 2.5–3.5 μm wide at the base. – Pseudothecial wall 27–30 μm thick, of polyhedral, mid brown, thickwalled cells. – Cellular pseudoparaphyses numerous among asci, branching, anastomosing, ca. 2.5 μm wide. Asci bitunicate, cylindrical-clavate, 40–50 × 13–15 μm , broadly rounded and thickened at the apex, short-stipitate, 8-spored. – Ascospores cylindrical to fusiform, 22–27 × 3–3.5 μm , straight or slightly curved, broadly rounded at both ends, 5(–9)-septate, nonconstricted at septa, hyaline, 4-seriate in the ascus.

Specimen examined. – ITALY: Selva, Treviso, on decayed wood of Salix vitellina, 1873, P. A. Saccardo (holotype of Acanthostigma revocatum, PAD).

Descriptions and illustrations. - Saccardo (1883: 208); Berlese (1894: 104, Tab. 101, Fig. 3; Tab. 102, Fig. 1); Podlahová (1974: 180, Fig. 61).

Habitat. - On decayed decorticated wood of deciduous trees.

Known hosts. - Quercus sp., Salix vitellina.

Distribution. - Europe: Italy.

Acanthostigma revocatum is characterized by short, 22–27 μ m long, cylindrical to fusiform ascospores with broadly rounded ends. It resembles *A. perpusillum* in ascospores and overall habitat of pseudothecia but the latter differs in that the ascospores are longer, usually up to 40 μ m long, tapering at both ends, usually containing more septa, slightly constricted at the septa and with one of the middle cells often slightly broader.

Saccardo (1883) distinguished A. minutum var. brachysporum from the type variety (as A. perpusillum in the present study) in having smaller ascospores $(25-32 \times 4-4.5 \ \mu\text{m})$. Berlese (1894) examined the type material of var. brachysporum and illustrated the ascospores as 8–9-septate and fusiform with broadly rounded ends. Upon the present search in PAD neither the type material of the variety nor any other herbarium material could be found. The A. minutum var. brachysporum apparently represents a counterpart of A. perpusillum having smaller-sized ascospores. Judging from the protologue it matches well the circumscription of A. revocatum (Saccardo, 1883). Therefore, A. minutum var. brachysporum is relegated to synonymy.



Fig. 4. Acanthostigma revocatum (holotype, PAD). – a. Ascus containing ascospores. – b. Cellular pseudoparaphyses. – c. Ascospores. – d. Habit sketch, median longitudinal section of pseudothecium.

- Acanthostigma minutum (Fuckel) Sacc., Syll. Fung. 2: 209, 1883. Figs. 5,6.
 - = Lasiosphaeria minuta Fuckel, Jahrb. Nassau. Ver. Naturk. 23–24: 148, 1870.
 - = Acanthostigmina minuta (Fuckel) Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Math.–Naturwiss. Cl., Abt. 1, 118: 1499, 1909.
- = Acanthostigma nectrioideum Penzig & Sacc., Malphigia 11: 530, 1897.
- = Acanthostigma scleracanthum (Sacc.) Sacc., Syll. Fung. 2: 209, 1883.
 - = Lasiosphaeria scleracantha Sacc., Michelia 1: 46, 1878.
- = Tubeufia setosa A. Sivan. & W.H. Hsieh, Mycol. Res. 99: 928, 1995.

Anamorph. - Helicomyces sp. (described here).

Teleomorph. - Pseudothecia superficial, scattered to gregarious, globose to subglobose, 120-230 um diam, 150-250 um high, brown, densely setose mostly on the upper half, covered with dark brown, opaque protruding cells, non-collapsing. – Setae 1-celled or rarely 1-septate, thick-walled, dark brown, opaque, acute, 28–100 µm long, $4.5-5 \mu m$ wide in the middle, $7-8 \mu m$ wide at the bulbous base. - Pseudothecial wall 26-37 μm thick, of polyhedral, mid brown, thick-walled cells. - Cellular pseudoparaphyses numerous among asci, branching, anastomosing, ca. 1.5-2.5 µm wide. - Asci bitunicate, cylindrical-clavate, 75–95(–126)×18–23 μm, broadly rounded and thickened at the apex, short-stipitate, 8-spored. - Ascospores long-fusiform, tapering at both ends and narrowly rounded, straight or slightly curved, one of the middle cells slightly broader, $40-55(-63) \times (5-)6-7(-7.5)$ µm, 10-14-septate, non-constricted or slightly constricted at the septa, hyaline, (4-5-)8-seriate in the ascus.

Anamorph on the natural substratum (Fig. 6). – Colony effuse, yellowish to pale brown. – Mycelium subhyaline to pale brown; hyphae septate, branching, 5.5–6.5 μ m wide. – Setae absent. – Conidiophores erect, simply branched, septate, pale brown, up to 55 μ m long, 5.5–6.5 μ m wide in the middle, bearing sparse minute denticles. – Conidia holoblastic on denticles, hyaline, multiseptate, coiled in two planes, ca. 3.5 μ m wide, the diameter of the coil 19–21 μ m.

Specimens examined. – FRANCE: Noidan, Côte d'Or, on decaying wood of *Populus* sp., Feb. 1899, F. Fautrey (neotype of *Acanthostigma scleracanthum*, PAD; designated here). – SWITZERLAND: Jura, on decayed wood of *Quercus* sp., Morthier (holotype of *A. minutum*, G). – CANADA: British Columbia, Sidney, on *Gaultheria shallon*, 21 Jul. 1995, M. E. Barr 9033 (DAOM). – TAIWAN: Anmashan, Taichung Hsien, on decaying wood (associated with *Helicomyces* sp.), A. Sivanesan 71 (holotype of *Tubeufia setosa*, IMI 354620, as IMI 354621 in protologue). – USA: Connecticut, 1 mi south of Canaan, on decayed wood (associated with *Hemitrichia clavata*), 2 Nov. 1959, C. T. Rogerson (as *Acanthostigma decastylum*, NY).



Fig. 5. Acanthostigma minutum (A. scleracanthum, neotype PAD). – a. Asci containing ascospores. – b. Cellular pseudoparaphyses. – c. Ascospores. – d. Setae covering pseudothecia.



Fig. 6. Acanthostigma minutum, Helicomyces sp. anamorph (IMI 354620). – a. Conidiophores and mycelium. – b. Conidia. From nature.

Exsiccatae. – Rehm: Ascomyceten (No. 1568. GERMANY: Alps Mts., ca. 1200 m a.s.l., on decayed wood of branch of *Fagus sylvatica*, Jun. 1904, H. Rehm, as *Acanthostigma minutum*, PAD).

Descriptions and illustrations. - Saccardo (1878: 46); Hsieh & al. (1995: 928, Figs. 40-43); Teng (1996: 70, Fig. 100a).

Habitat. – Saprobe on decaying wood of deciduous trees and woody, dicotyledonous shrubs.

Known hosts. – Fagus sylvatica, Gaultheria shallon, Populus sp., Quercus sp.

Distribution. – Europe: France, Germany, Switzerland; North America: Canada (British Columbia), USA (Connecticut); Asia: China, Taiwan.

Acanthostigma minutum is characterized by minute pseudothecia that are setose and covered with protruding cells mostly on the upper half and long-fusiform, 7-10(-13)-septate ascospores with symmetrical narrowly rounded ends. It is related to *A. ellisii* that differs in having 6-12-septate narrower ascospores with asymmetrical ends; A. scopulum that possesses 10–14-septate, longer and narrower ascospores and A. perpusillum that has ascospores of similar shape but shorter and narrower.

The type material of *A. scleracanthum* (ITALY: Consiglio, on decayed wood of *Fagus sylvatica*, Oct. 1875, P. A. Saccardo, PAD) is apparently lost (present search in PAD). Podlahová (1974) examined the type material of *A. scleracanthum* and provided detailed description and illustration that are in full agreement with our observation.

Another specimen identified by Saccardo as *A. scleracanthum* was collected by F. Fautrey in 1899 in France and was preserved in PAD. This material matches well the circumscription of *A. scleracanthum* given by Saccardo (1878) and Podlahová (1974) on the basis of the holotype. The material collected by F. Fautrey is designated here as a neotype.

Upon the examination of the type material, *Tubeufia setosa* (as sect. *Acanthostigmina*; Hsieh & al., 1995) is relegated to synonymy. Although Hsieh & al. (1995) did not report any associated anamorph, effuse yellowish to pale brown colonies of *Helicomyces* sp. were observed around pseudothecia on the natural substratum. The conidiophores and mycelium that were found growing from the perithecia initials and mature perithecia as well as from the surface of the substratum are described and illustrated here.

- Acanthostigma scopulum (Cooke & Peck, Bull. New York State Mus. 1: 22, 1887. – Fig. 7.
 - ≡ Sphaeria scopula Cooke & Peck, Ann. Rep. New York State Mus. 32: 51, 1880.
 - ≡ Lasiosphaeria scopula (Cooke & Peck) Sacc., Syll. Fung. 9: 852, 1891.
 - ≡ Tubeufia scopula (Cooke & Peck) M. E. Barr, Mycotaxon 12: 164, 1980.

Anamorph. – *Helicosporium aureum* (Corda) Linder, Ann. Missouri Bot. Gard. 16: 279, 1929.

Teleomorph. – Pseudothecia superficial, scattered to gregarious, globose to subglobose to conical, 165–310 μ m diam, 180– 300 μ m high, brown to vinaceous brown, densely setose, non-collapsing. – Setae 1-celled, thick-walled, dark brown, opaque, acute, 37– 90 μ m long, 4.5–5 μ m wide in the middle, 6–7.5 μ m wide at the base. – Pseudothecial wall 25–35 μ m thick, of polyhedral, mid brown, thick-walled cells. – Cellular pseudoparaphyses numerous among asci, branching, anastomosing, ca. 1.5–2.5 μ m wide. – Asci bitunicate, cylindrical-clavate, (67–)86–110(–130) \times 12–15 (–22) μ m, broadly rounded and thickened at the apex, short-stipitate, 8-spored. – Ascospores long-fusiform to cylindrical-fusiform,



Fig. 7. Acanthostigma scopulum (holotype, NYS). – a. Asci with ascospores and cellular pseudoparaphyses. – b. Ascospores. – c. Setae covering pseudothecia.

 $(40-)56-78(-95)\times(2-)2.5-3(-3.5)$ µm, tapering and narrowly rounded at both ends, often bent or slightly curved in the lower third, 10–14-septate, non-constricted at the septa, hyaline, 5–8-seriate in the ascus.

S p e c i m e n s e x a m i n e d. – AUSTRIA: Wiener Wald, decaying wood, 21 May 1903, F. Höhnel (FH). – USA: New York, Adirondack Mts., on wood of *Tsuga* sp., Aug. 1878, C. H. Peck (holotype of *Sphaeria scopula*, NYS); New Jersey, Newfield, Sep. 1878, J. B. Ellis (FH); New Jersey, Newfield, Oct. 1880, J. B. Ellis (NY); Florida, Grasmere, 30 Mar. 1893, W. C. Sturgis (FH, NY); Alabama, Tuskegee, 26 Aug. 1901, G. W. Carver (FH).

Exsiccatae. – J. B. Ellis: North American Fungi [No. 184. USA: Louisiana, on decaying wood of *Pinus* sp. (associated with *Helicosporium aureum*), as *Sphaeria scopula*, NY].

Descriptions and illustrations. - Berlese (1894: 103, Tab. 101, Fig. 1); Barr (1980: 164, Figs. 19-21).

Habitat. – Saprobe on decayed decorticated wood of conifers, rarely on wood of deciduous trees.

Known hosts. - Fagus sylvatica, Pinus sp., Tsuga sp.

Distribution. – Europe: Austria; North America: USA (Alabama, Florida, New Jersey, and New York).

Acanthostigma scopulum is characterized by 10–14-septate, long-fusiform to cylindrical-fusiform ascospores that are often bent or slightly curved in the lower third, tapering and narrowly rounded at both ends and a strong preference for decayed wood of coniferous trees, but occasionally it can grow on wood of deciduous trees. It is mostly known from North America although one collection was made in Central Europe. Acanthostigma scopulum can be compared with A. minutum that differs in having somewhat shorter and broader and only slightly curved ascospores. Acanthostigma ellisii resembles A. scopulum in long-fusiform to cylindrical-fusiform ascospores and number of septa, however, the former clearly differs in that the ascospores have asymmetrical ends with one or two inner cells near the proximal end slightly broader.

Excluded species

Acanthostigma filisporum M. E. Barr, Mycotaxon 46: 63, 1993. – Fig. 8.

Anamorph. - Unknown.

Teleomorph. – Perithecia superficial, scattered, reddishbrown to brown, subglobose to globose, 120–210 μ m diam, setose, collapsing deeply inwards upon drying. – Setae 4–6-septate, tapering, dark brown, opaque, 67–84 μ m long, 6–7 μ m wide at the base. – Perithecial wall 22–30 μ m thick, of thick-walled polyhedral cells; cells becoming thinner-walled, more flattened and paler towards the interior. – Hamathecium consisting of remnants of apical paraphyses seen as chains of saccate cells among asci, ca. 4–

 $5 \ \mu m$ wide. $-Asci unitunicate, cylindrical-clavate, <math>40.5-72 \times 7-9 \ \mu m$, apex thin-walled, without any visible discharge mechanism, short-stipitate, 8-spored. $-Ascospores \ long-fusiform, \ 33-47 \times 1.5-2 \ \mu m$, straight or curved, tapering at both ends, 3-septate, non-constricted at the septa, hyaline, in fascicle in the ascus.

Specimen examined. – USA: Massachusetts, Franklin Co., Conway, Baptist Hill, on a dead branch of *Fraxinus americanus* showing canker symptoms, 16 Dec. 1979, M. E. Barr 6648 (NY).

Barr (1990, 1993, 1997) interpreted Acanthostigma as a perithecial ascomycete genus having unitunicate asci and placed it in the Trichosphaeriaceae. In accordance with this generic concept, Barr (1993: 63, Fig. 2x, y) described a new species A. filisporum. The type material of A. filisporum could not be located in NY. The other collection (M. E. Barr 6648, NY) designated by Barr (1993) was examined.

In regard to minute, setose and deeply collapsing perithecia, unitunicate asci, apical paraphyses and hyaline ascospores A. filisporum resembles taxa of the Niessliaceae. The apical paraphyses that were seen among maturing asci in the material of A. filisporum (M. E. Barr 6648, NY) are identical to those described for Valetoniellopsis Samuels & M. E. Barr having Acremonium-like anamorph (Samuels & Barr, 1997: 2175, Fig. 41) and Cryptoniesslia Scheuer (Scheuer 1993a: 544, Fig. 3) of the Niessliaceae. Within the family A. filisporum also resembles Valetoniella claviornata Samuels & M. E. Barr in elongate fusiform ascospores and their arrangement in fascicles in the asci. Valetoniella Höhn. differs in having the perithecia ornamented with dark setae with apically forked and coronate apices and the typical habitat over or near other ascomycetous fungi. In the Niessliaceae features of the perithecial vestiture were considered to have a diagnostic value in separating genera (Samuels & Barr, 1997). In this light, it is difficult to place A. filisporum in any genus of the family. It shares features of ascospores with Valetoniella and features of dark, stiff, pointed setae with Trichosphaerella E. Bommer, M. Rousseau & Sacc. (ascospores ellipsoidal, 1-septate, disarticulating into part-spores; setae very short; acremonium-like anamorph), Niesslia Auersw. (ascospores ellipsoidal to fusiform, 1septate, nonfragmenting; setae very short; *Monocillium* anamorph) and Cryptoniesslia (perithecia immersed with setae usually in-

Fig. 8. Acanthostigma filisporum (M. E. Barr 6648, NY). – a. Asci containing ascospores. – b. Apical paraphyses formed of chains broadly inflated cells occurring among maturing asci. – c. Ascospores. – d. Habit sketch of perithecia on the natural substratum.





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tegrated in the upper half of the perithecium, setae short to elongate; ascospores ellipsoidal-fusiform, 1-septate, nonfragmenting; anamorph unknown; on monocotyledonous substrates). Of these taxa, *Niesslia* would seem to be the most appropriate taxon to accommodate *A. filisporum*. We do not accept *A. filisporum* as a species of *Acanthostigma*, however, we hesitate to accept it in *Niesslia* without cultural studies and examining type and other material.

Acanthostigma filisporum is also remarkably similar to Zignoëlla slaptonensis P. F. Cannon (Cannon, 1997) in regard to narrow and long-fusiform, hyaline 1–3-septate ascospores arranged in a fascicle in the ascus, thin-walled asci without any visible discharge mechanism and occurrence on wood of a branch showing a canker symptom [Specimen examined. – United Kingdom: England, Devon, Kingsbridge, Slapton Ley, Marsh Lane, on a dead branch of Ulmus sp. showing a canker symptom, 6 May 1994, P. F. Cannon, IMI 362466 (holotype)]. However, the ascomata of Z. slaptonensis are partly immersed, glabrous and hamathecium consists of filiform, at the septa not constricted, ca. 1.5-3 µm thick interthecial filaments observed among asci. Cannon (1997) discussed a possible relationship of Z. slaptonensis with Chaetosphaeria or Ceratosphaeria Niessl.

Discussion

According to Barr (1980) the Tubeufiaceae accommodated ten mycoparasitic or saprobic or mycosaprobic genera including *Tubeufia* that was divided into four sections (sect. *Tubeufia*, *Thaxteriella*, *Nectrioidea* and *Acanthostigmina*). The Tubeufiaceae sensu Rossman (1987) accommodated sixteen genera; the generic concept and infrageneric classification of *Tubeufia* suggested by Barr (1980) was fully adopted. According to the recent compilation of the saprobic Tubeufiaceae by Crane & al. (1998) the family encompassed ten saprobic or mycosaprobic genera including *Acanthostigmina*, *Thaxteriella* and *Tubeufia* (sect. *Nectrioidea* and *Tubeufia*) as separate genera.

Acanthostigma, including Acanthostigmina as its generic synonym, is a distinct genus in the Tubeufiaceae. In Acanthostigma, shape and size of ascospores, size of asci and morphology of setae can be exclusively used as outstanding features distinguishing taxa at the species level. The conidiogenesis has been observed merely in two species, A. minutum (anamorph Helicomyces) and A. scopulum (anamorph Helicosporium); in both the conidia are helicosporous. Although the complete life history of other species remains unknown, the conidia and conidiophore morphology might serve as an associate diagnostic character at the species level. The basic differences between Acanthostigma and Tubeufia lie in features of ascomata. They are vinaceous, reddish-brown, brown or dark brown, covered with dark brownish-black, often opaque, acute or obtuse setae in *Acanthostigma*. *Tubeufia* is characterized by ascomata that are hyaline, white, yellowish to pinkish or becoming darkened at maturity and, on drying, smooth or covered with protruding cells or thick-walled hyphal appendages or short dark setae.

Von Arx & Müller (1975) suggested Nematostoma to accommodate Acanthostigma. Although the two genera show certain superficial similarity in ascomata and ascospores they clearly differ in biology and anamorphs. Nematostoma and the Pseudoperisporiaceae are superficial biotrophs on leaf surfaces and trichomes (Rossman, 1987; Sivanesan, 1987). Where anamorphs are suspected or known, they are small pycnidia, similar to the ascomata (Barr, 1997). Acanthostigma and all members of the Tubeufiaceae include superficial saprobes usually on woody substrates or hypersaprobes on other fungi or on substrates previously colonized by other fungi or hyperparasites on foliicolous fungi or saprobes on old culms and leaves of Cyperaceae and Poaceae. Known anamorphs are dematiaceous hyphomycetes with usually helicosporous, staurosporous, phragmosporous or occasionally dictyosporous conidia (Linder, 1929; Hughes, 1958; 1978; Samuels & al., 1979; Scheuer, 1991).

Within the Tubeufiaceae, Acanthostigma can be compared with Acanthophiobolus (Barr, 1997; Crane & al., 1998) and Taphrophila (Scheuer, 1988; 1991). All three genera share minute, dark, setose ascomata, bitunicate cylindrical-clavate asci, narrow cellular pseudoparaphyses and hyaline, cylindrical-fusiform or fusiform or elongate fusiform or scolecosporous ascospores. Helicosporium and Helicomyces anamorphs have been linked to Acanthostigma. A Mirandina anamorph has been linked to Taphrophila cornu-capreoli Scheuer the life history of wich was also confirmed by cultural studies (Scheuer, 1991). Acanthophiobolus has not been vet linked to any anamorph (Walker, 1980). Acanthophiobolus is characterized by minute, superficial, globose, dark brown, setose ascomata, hvaline scolecosporous ascospores tightly coiled in a dense spiral in the ascus and a strong preference for herbaceous substrates or rarely growing on textiles of plant origin. Taphrophila was established for taxa with minute, pale brown, non-collapsing pseudothecia covered with dichotomously branched setae, pseudoparaphyses, bitunicate asci and fusiform, septate, hyaline ascospores (Scheuer, 1988). Crane & al. (1998) separated Taphrophila from Acanthostigma (as Acanthostigmina) on the basis of the nature of dark brown setae; setae that branch dichotomously before tapering to pointed apices in the former and setae that taper without branching to an apical point in the latter. In addition, Taphrophila can be also separated from

Acanthostigma by its occurrence and fructification on decaying culms and leaves of Cyperaceae and Poaceae.

Although Scheuer (1988; 1991) considered dichotomously branched setae a diagnostic generic character within the Tubeufiaceae, Tubeufia trichella (Sacc., E. Bommer & M. Rousseau) Scheuer, a species that was otherwise habitually and biologically similar to Taphrophila, was described with acute setae that were more irregularly or dichotomously branched in some collections or remain unbranched (including lectotype; Scheuer, 1993b). The ontogeny of ascomatal setae might indicate that taxa with either acute and unbranched setae or branched setae could be placed in one genus. On the other hand features of the perithecial vestiture served as a diagnostic character in separating genera, for instance, in the Niessliaceae (Samuels & Barr, 1997). On the basis of acute and unbranched setae Scheuer (1991) separated from Taphrophila another species, Tubeufia hebridensis Dennis with otherwise similar morphology and biology. Later, Crane & al. (1998) accepted the two graminicolous Tubeufia species in Acanthostigmina. Although the type species Acanthostigmina minuta was relegated to synonymy with Acanthostigma in the present paper and the majority of its species were accepted in the latter genus, we hesitate to accept Acanthostigmina trichella (Sacc., E. Bommer & M. Rousseau) J.L. Crane & al. and A. hebridensis (Dennis) J. L. Crane & al. We prefer to preserve Acanthostigma for species that are saprobes on decaying woody substrata or mycosaprobes on old ascomata or stromata of other fungi. The related Taphrophila should be retained for species with minute, light to dark brown pigmented pseudothecia covered with more irregularly or dichotomously branched or unbranched setae; bitunicate asci containing eight fusiform to elongate fusiform to cylindrical, hyaline, multiseptate ascospores sometimes coiled in the ascus; holoblastic conidiogenesis on small denticles and phragmosporous conidia, i.e. the Mirandina anamorph and occurrence on monocotyledonous substrates.

Two other species *Tubeufia setosa* A. Sivan. & W. H. Hsieh (Hsieh & al., 1995) and *T. miscanthi* W. H. Hsieh, C. Y. Chen & A. Sivan. (Hsieh & al., 1998) were described in *Tubeufia* sect. Acanthostigmina. The comments on or their re-disposition are missing in the survey of the saprobic Tubeufiaceae compiled by Crane & al. (1998). Upon the present revision of the type material, the former species is attributed to Acanthostigma and relegated to synonymy with A. minutum. The latter shares biology and morphology of setae ($300-400 \mu m$ long and $6-10 \mu m$ wide) with Acanthophiobolus and biology and morphology of elongate fusiform ascospores arranged in a fascicle with *Taphrophila*.

Although the generic delimitation of Acanthostigma and Taphrophila is very narrow, mainly based on habitat (lignicolous or herbicolous) and life history (anamorphs are mostly known for type species only), we assume that the affinity of *Tubeufia hebridensis*, *T. miscanthi* and T. *trichella* lie with *Taphrophila* rather than with *Acanthostigma* or *Acanthophiobolus* or the restricted *Tubeufia* in the Tubeufiaceae. The anamorph of *Tubeufia hebridensis* and *T. miscanthi* are unknown (Dennis, 1980; Hsieh & al., 1998) and the cultivation of *T. trichella* yielded a sterile mycelium in pure culture (Scheuer, 1991).

Therefore, we propose three new combinations:

Taphrophila hebridensis (Dennis) Réblová & M. E. Barr, comb. nov.

(Bas.: Tubeufia hebridensis Dennis, Mycol. Res. 95: 814, 1991)

Taphrophila miscanthi (W. H. Hsieh, C. Y. Chen & A. Sivan.) Réblová & M. E. Barr, comb. nov.

(Bas.: Tubeufia miscanthi W.H. Hsieh, C.Y. Chen & A. Sivan., Mycol. Res. 102: 234, 1998)

Taphrophila trichella (Sacc., E. Bommer & M. Rousseau) Réblová & M. E. Barr, comb. nov.

(Bas.: Ophiobolus trichellus Sacc., E. Bommer & M. Rousseau, Bull. Soc. Roy. Bot. Belg. 29: 259, 1890)

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