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Standard Paper

A new species of *Thelocarpon* from Dutch quarries, with a worldwide key to the species of the genus

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Abstract

Thelocarpon periphysatum sp. nov. is described from marl quarries in the Netherlands. The species is characterized by perithecioid ascomata that have a green-yellowish ring around the ostiole, abundant periphyses and periphysoids that are up to 120 µm long, the absence of paraphyses and the wide, oblong and often somewhat asymmetrical ascospores. The perithecia are immersed in black cyanobacterial crusts on calcareous rocks. A worldwide key is provided to the 30 species of *Thelocarpon* that are currently accepted.

Keywords: algicolous; *Ascomycota*; biodiversity; lichenology; lichens; *Pezizomycotina*; taxonomy

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Introduction

Species of *Thelocarpon* Nyl. are free living or lichenized fungi with minute perithecioid or apothecioid ascomata. Many species within the genus appear as pioneers, settling on bare or temporary substrata such as pebbles, clay or wood and typically disappear quickly again due to succession and subsequent competition or life-cycle completion (Kocourková-Horáková 1998). As a result, even though some species are widespread (e.g. Hafellner 2017), most species are rarely collected. Species descriptions, especially in the early days, have resulted in numerous synonyms, most of which were resolved by Salisbury (1966).

The ascomata of *Thelocarpon* species typically contain flask-shaped multispored asci with colourless single-celled ascospores, although exceptions exist such as cylindrical asci (e.g. *Thelocarpon lichenicola* (Fuckel) Poelt & Hafellner) and 8-spored asci with 3-septate spores (*Thelocarpon triseptatum* Aptroot & M. Cáceres). Important characteristics that are used to distinguish species within *Thelocarpon* are the presence or absence of an algal sheath, periphyses and paraphyses. Some species develop verrucae with an algal sheath around the ascomata, but other species are only loosely associated with algae or not associated with algae at all. This variation in lichenization at times blurs the demarcation between free-living fungi and lichens within the genus. Filaments can be present in the ostiolar canal (periphyses), inside on the sides of the excipulum (periphysoids) and between the asci as interascal filaments (paraphyses) (Navarro-Rosinés *et al.* 1999), and their shape and presence are important characteristics that define the species.

Salisbury (1966) monographed the genus and recognized 13 *Thelocarpon* species, but many new species have been described since then. The type species of the genus, *Thelocarpon laureri* (Flot.) Nyl., has perithecioid ascomata that are enclosed within a verruca containing algae. Species with an exposed disc (e.g. *Thelocarpon impressellum* Nyl.) were transferred to the genus *Ahlesia* Fuckel (Salisbury 1966), but are today again placed in *Thelocarpon* since the division of the genus based on disc exposure alone is considered arbitrary (Poelt & Hafellner 1975). However, the genus is probably heterogenous and several distinct subgroups can be distinguished (Salisbury 1966; Navarro-Rosinés *et al.* 1999). Currently, DNA sequences from only a small number of species are available, and the phylogenetic position of the genus within the *Pezizomycotina* is still uncertain (Reeb *et al.* 2004; Lumbsch *et al.* 2009).

In the Netherlands, lichenologists have frequently collected and studied *Thelocarpon* species. For example, seven different species were reported by Aptroot & Sparrius (2000) in a single year. In recent years, *Thelocarpon laureri* and *T. lichenicola* have been collected in the Netherlands most often, both being recorded at around 20 localities since 2010. Species recorded in the Netherlands since then are *Thelocarpon coccosporum* Lettau, *T. epibolum* Nyl., *T. impressellum*, *T. intermediellum* Nyl., *T. magnussonii* G. Salisb., *T. olivaceum* B. de Lesd. and *T. pallidum* G. Salisb. In November 2021, an unknown species of *Thelocarpon* was found in a marl (soft calcareous rock) quarry in the Netherlands. It was different from other *Thelocarpon* species by having immersed brown perithecia with a green-yellowish ring around the ostiole, remarkably abundant and long periphyses and periphysoids, and wide, oblong and often somewhat asymmetrical ascospores. The same species was later found on marlstone at two different locations. The three collections consistently showed the same diagnostic characteristics, and hence the species is formally described here. Furthermore, since the monograph of Salisbury (1966), there has not been an up to date worldwide overview of *Thelocarpon*, therefore a key to all currently accepted *Thelocarpon* species is provided here.

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Methods

Three specimens of the new *Thelocarpon* species were collected between 2021 and 2023 in the Netherlands. The collections were examined with a stereo microscope (Euromex SB 1903 P StereoBlue) and a compound microscope (Euromex iScope IS.1153-PLi). All measurements and observations were made on material mounted in water, except when stated otherwise. To test colour reactions, bleach (C), 10% KOH solution (K), paraphenylenediamine solution (P) and 1% or 10% Lugol's solution (I) were used. K/I represents the I reaction after application of a 10% KOH solution.

Taxonomy

Thelocarpon periphysatum Kolk, Timans, Boers & Sparrius sp. nov.

MycoBank No.: MB 848874

Differing from *Thelocarpon immersum* Fryday and *T. opertum* J. C. David & Coppins by the longer periphyses and periphysoids, up to 120 µm, and the oblong ascospores.

Type: The Netherlands, Limburg, Berg en Terblijt, Groeve Blom, on cyanobacterial crusts on marl in abandoned quarry, 50.8570°N, 5.7927°E, 21 November 2022, *H. van der Kolk* 3271 (L—holotype; hb. H. van der Kolk—isotype).

(Figs 1 & 2)

Thallus absent. *Photobiont* absent, but perithecia immersed in cyanobacterial crusts with *Gloeocapsa*-like and other species of cyanobacteria. All parts C–, K– and P–.

Ascomata perithecioid, globose, partially to completely immersed in cyanobacterial crusts with only the apices protruding, 200–300 µm diam., without an exposed disc, opening through a small apical pore, light brown to brown, with a well-defined bright green-yellowish ring around the ostiole, with a bluish tinge in fresh material. *Excipulum* hyaline or light brown, 20–35 µm thick. *Periphyses* and *periphysoids* abundant, arranged around the ostiole and on the sides, varying in length from 20 µm in the ostiolar canal to 120 µm further down the sides, then resembling paraphyses but not occurring between the asci, 1.0–1.5 µm thick, simple. *Hymenial gel* hemiamyloid, I+ yellow (at low concentration) to I+ red (at high concentration), K/I+ blue. *Paraphyses* absent. *Asci* multispored (> 100 ascospores per ascus), flask-shaped, I–, 110–160 × 13–28 µm. *Ascospores* aseptate, oblong, often asymmetrical, hyaline, smooth-walled, mostly with one large oil droplet, sometimes with two large oil droplets or with several smaller ones, 5.5–8.5 × 3.4–4.8 µm, l/w = 1.3–2.1.

Conidiomata not observed.

Etymology. *Periphysatum*, named after the abundant and remarkably long periphyses and periphysoids.

Ecology. Perithecia are immersed in cyanobacterial crusts on well-lit marlstone in quarries, accompanied by the moss *Pseudocrossidium revolutum* (Brid.) R. H. Zander.

Distribution. Currently known only from three locations in the Netherlands.

Additional specimens examined. **The Netherlands:** *Gelderland*: Nijmegen, Heilig Landstichting, 51.818°N, 5.892°E, on cyanobacterial crusts on calcareous rocks, 19 i 2023, *M. de Winkel* s. n. (hb. H. van der Kolk 3341). *Limburg*: Berg en Terblijt, Curfsgroeve, 50.8684°N, 5.7674°E, on cyanobacterial crusts on marlstone in abandoned quarry, xi 2021, *H. van der Kolk* 2336 (hb. H. van der Kolk); *ibid*., on marlstone, xi 2022, *L. B. Sparrius* 9327 (hb. Sparrius).

Discussion

Comparison to other Thelocarpon *species*

Thelocarpon periphysatum is characterized by perithecioid ascomata that have a green-yellowish ring around the ostiole, abundant periphyses and periphysoids that are up to 120 µm long, the absence of true interascal filaments and wide, oblong and often somewhat asymmetrical ascospores. The periphysoids are very long and implanted throughout the sides of the perithecium. Consequently, in a squashed perithecium they may resemble paraphyses. Careful examination is needed to determine whether filaments in *Thelocarpon* species are implanted in between asci, or only on the inner sides of the perithecia.

Thelocarpon periphysatum should especially be compared with *T. immersum* and *T. opertum*. Both species are similar to *T. periphysatum* in having perithecia that are immersed in cyanobacterial crusts, with a green-yellowish ring around the ostiole, hemiamyloid hymenial gel and long unbranched (or sparingly branched) periphyses (or paraphyses as described in *T. immersum*). *Thelocarpon immersum*, a species recently described from Alaska (Spribille *et al.* 2020), is a much smaller species than *T. periphysatum*, which is apparent in the size of the perithecia (up to 300 µm in *T. periphysatum* vs up to 120 µm in *T. immersum*), and the size of the asci (110–160 × 13–28 µm in *T. periphysatum* vs 75–90 × 15–17 µm in *T. immersum*). Moreover, the species differ in ascospore shape (oblong 5.5–8.5 × 3.4–4.8 µm in *T. periphysatum* vs globose 5–7 µm diam. in *T. immersum*). *Thelocarpon opertum* (David & Coppins 1997; but see also the updated description in Smith *et al.* (2009)) differs in ascospore shape (oblong 5.5–8.5 × 3.4–4.8 µm in *T. periphysatum* vs globose 3–5.5 um diam. in *T. opertum*) and length of the periphyses and periphysoids (up to 120 µm long in *T. periphysatum* vs up to 70 µm long in *T. opertum*). In *T. opertum*, the periphyses and periphysoids may generally be less abundant or significantly shorter than 70 µm, since the original description mentions periphyses up to 20 µm (the presence of periphyses up to 70 µm was mentioned only in the updated description in Smith *et al.* (2009)). In *T. periphysatum*, however, the periphysoids in all collections were always abundant and very long.

Thelocarpon cyaneum Olech & Alstrup, *T. intermediellum* and *T. saxicola* (Zahlbr.) H. Magn., differ from *T. periphysatum* by having shorter periphyses (up to 25 µm long) and smaller (especially narrower) ascospores (smaller than 7 × 3 µm). *Thelocarpon epibolum* differs from *T. periphysatum* by having perithecia that are not immersed and which are yellow-pruinose also on the sides, and by the presence of paraphyses and narrower ascospores. *Thelocarpon citrum* (Wallr.) Rossman and *T. superellum* Nyl. differ from *T. periphysatum* by having perithecia that are yellow-pruinose also on the sides, and by having paraphyses, I+ blue asci and I– hymenial gel. *Thelocarpon impressellum* differs from *T. periphysatum* by having a slightly exposed disc, true paraphyses that form an epithecium, and asci with an I+ blue and K/I+ blue apex.

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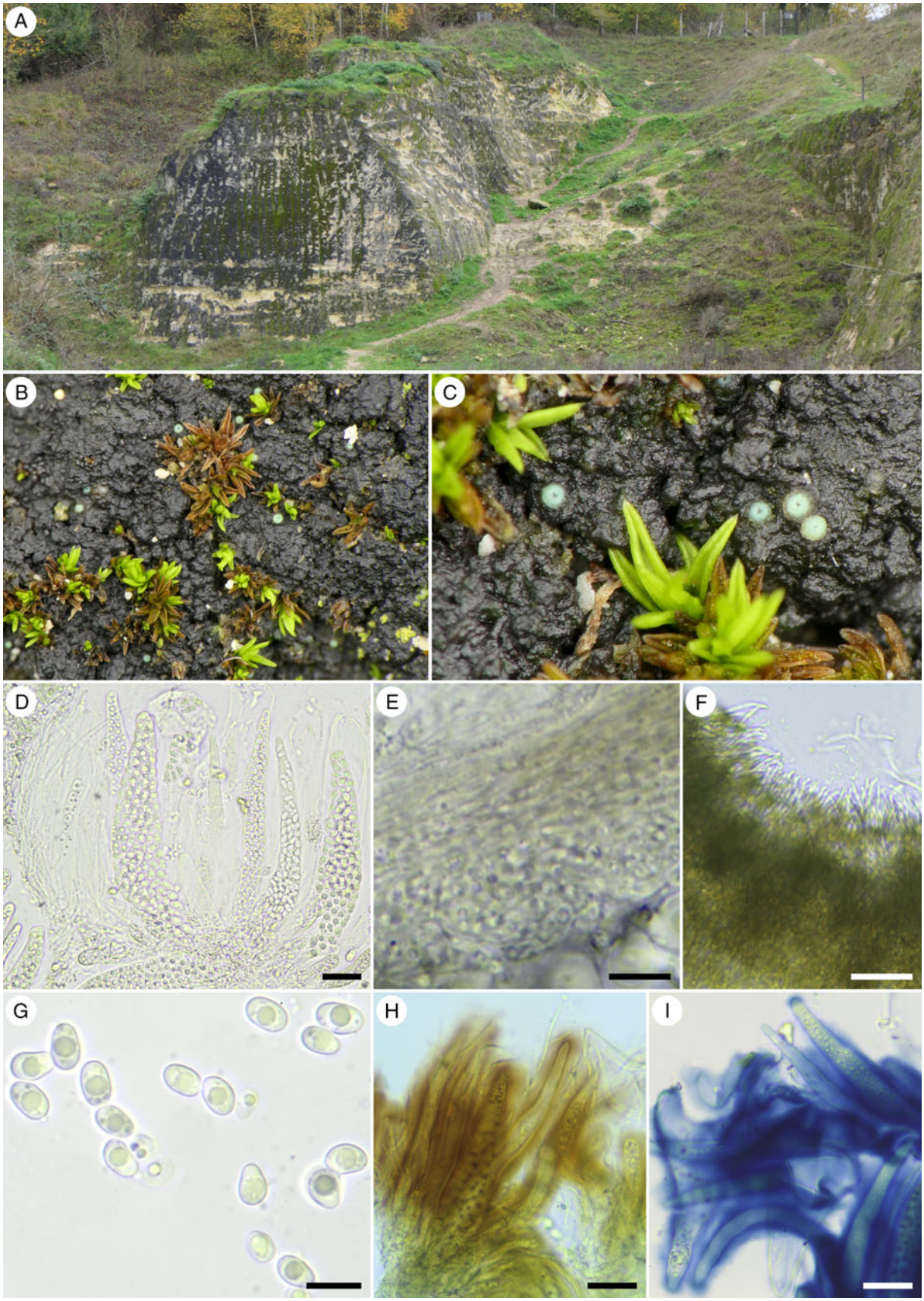

Figure 1. *Thelocarpon periphysatum*. A, habitat, marble walls in abandoned quarry. B & C, perithecia with distinct green-yellowish ring with bluish tinge immersed in crust of cyanobacteria. D, asci (note the long periphysoids on the left and the lack of true interascal filaments). E, excipulum. F, periphyses around the ostiole. G, ascospores. H, reaction of hymenial gel in I (Lugol's solution). I, reaction of hymenial gel in K/I. Scales: D–F, H & I = 20 μm; G = 10 μm. In colour online.

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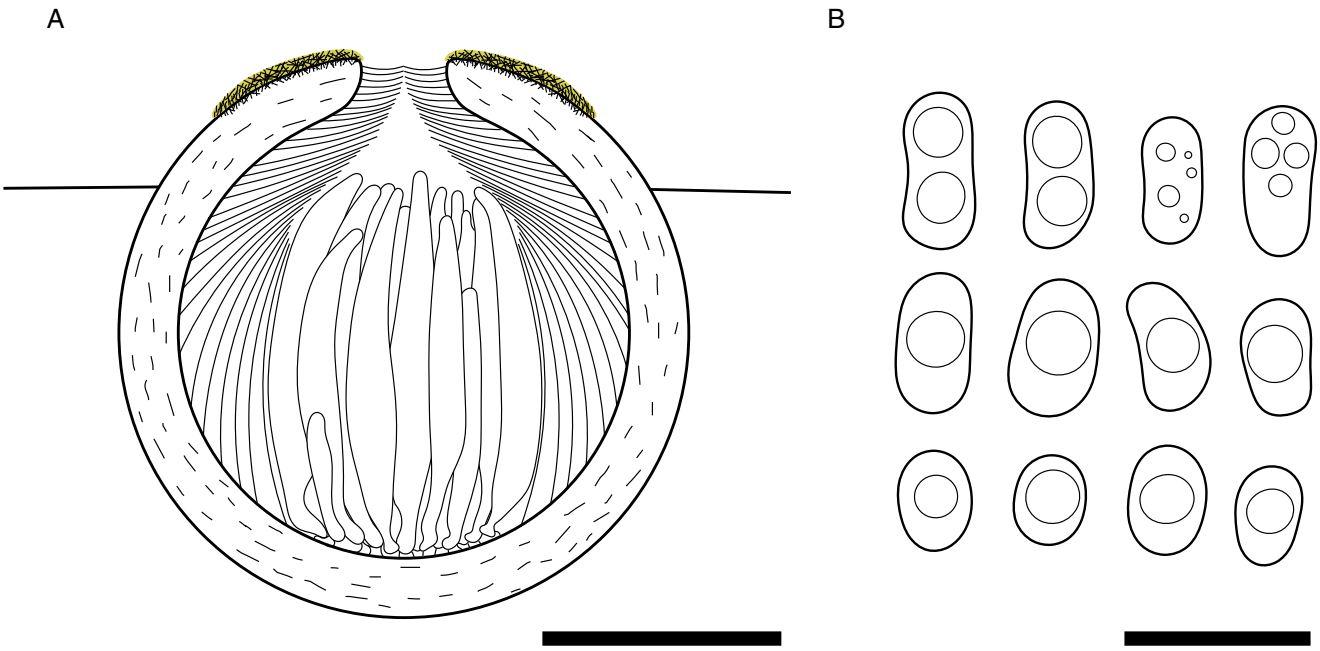

Figure 2. *Thelocarpon periphysatum*. A, schematic section of a perithecium; the periphysoids are more appressed to the exciple than appears in the drawing. B, ascospores. Scales: A = 100 μm; B = 10 μm. In colour online.

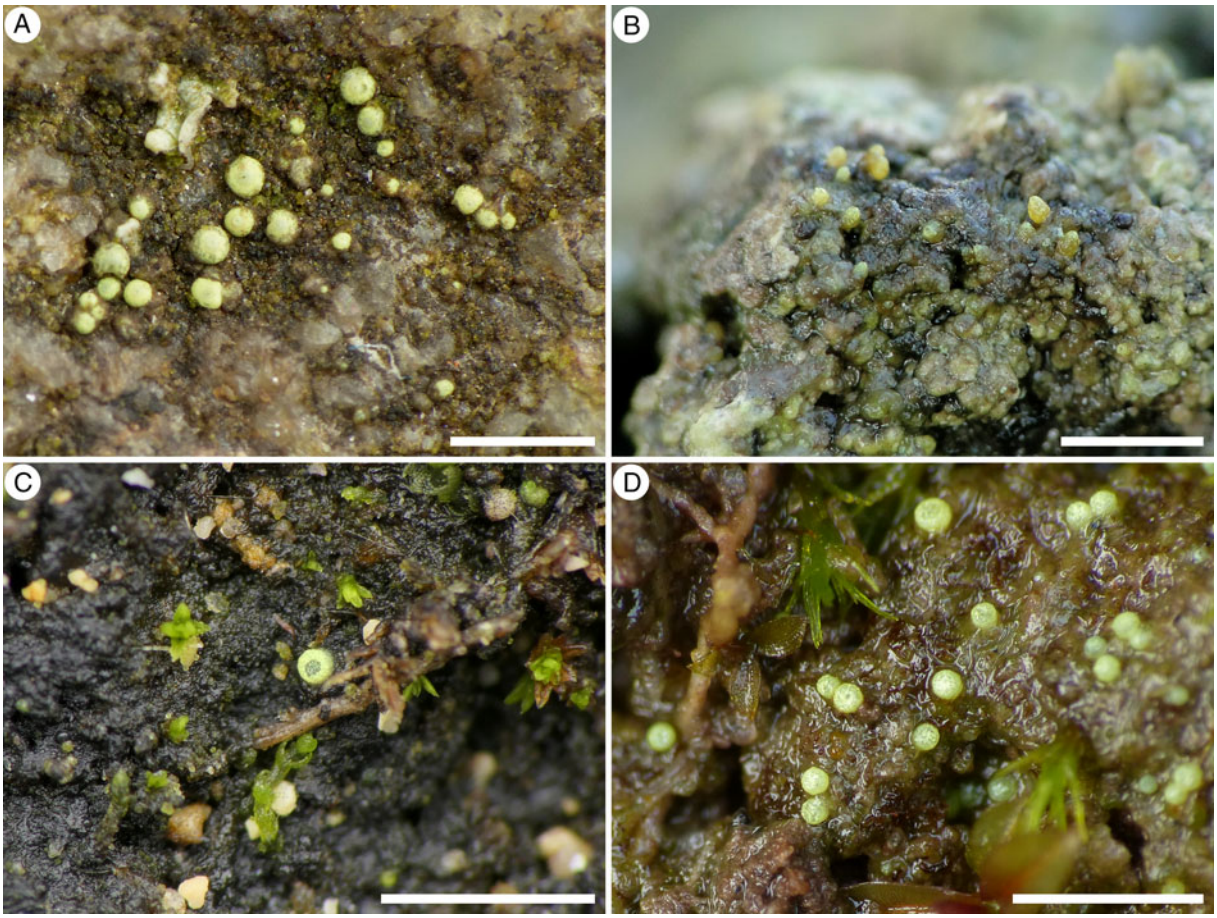

Figure 3. Variation in morphological appearance of fresh material of some *Thelocarpon* species occurring in the Netherlands. A, *Thelocarpon laureri*, 23 x 2021, coll. *H. van der Kolk* 2319. B, *Thelocarpon epibolum*, 16 i 2015, coll. *H. van der Kolk* 0320. C, *Thelocarpon impressellum*, 21 xi 2022, coll. *H. van der Kolk* HK 3272. D, *Thelocarpon lichenicola*, 22 i 2021, coll. *H. van der Kolk* 2050. Scales: A–D = 1 mm. In colour online.

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A worldwide key to the species of *Thelocarpon*

Including *Thelocarpon periphysatum*, the presented key includes 30 species. Although many more *Thelocarpon* names have been published, many were later synonymized or not considered to belong in *Thelocarpon*, and therefore are not included in the key (for a list of synonyms see Supplementary Material Table S1, available online). The type material of *Thelocarpon hassei* B. de Lesd. (Bouly de Lesdain 1930) and *Thelocarpon cinereum* Eitner (Magnusson 1936) was destroyed during World War II (Salisbury 1966), and therefore both species are also not included in the key (see notes in Supplementary Material Table S1). For each species included in the key, at least one literature reference is provided that includes a detailed description.

Keys for the genus *Thelocarpon* typically use a set of microscopic characteristics, specifically 1) presence or absence of an algal sheath, 2) presence or absence of yellowish pruina, 3) presence and shape of paraphyses, 4) presence and shape of periphyses and periphysoids, 5) I and K/I reactions of asci and hymenial gel, and 6) ascospore shape and size. The presented key also makes use of these, and aims to focus on characteristics that are most easy to observe. Hence, the divisions in the key do not reflect the subgroups that can be distinguished within the genus (e.g. Navarro-Rosinés *et al.* 1999). For example, *Thelocarpon opertum* and *T. periphysatum* are probably closely related, but separated early in the key by ascospore shape.

While examining *Thelocarpon* species, care is needed to distinguish different types of filaments. Especially long periphysoids that are implanted on the side of the excipulum may resemble paraphyses when ascomata are squashed. We recommend preparing multiple sections of ascomata to judge the length, shape and positions of filaments present.

The colours revealed by the I-reaction depend on the concentration used. We recommend observing the colour change of the asci and hymenial gel while gradually increasing the amount of Lugol's solution added, and also do the same in a section that is pre-treated with KOH.

Field characteristics may be more helpful than current identification keys suggest. Many *Thelocarpon* species show small but consistent differences from each other in the size, colour and shape of the ascomata (Fig. 3). The lack of published *Thelocarpon* images makes these characteristics still of limited use, especially for unexperienced observers; as a result, most identifications will rely on microscopic characteristics alone. Since field characteristics may also be useful for identification, we encourage future authors to include high quality pictures of fresh specimens of *Thelocarpon* species in their publications.

Although the presented key now gives an overview of the species currently included in *Thelocarpon*, future revisions may divide the species over multiple genera. DNA sequencing in particular may resolve which morphological characteristics reflect phylogeny. It will, however, be challenging to sequence a large number of different species, since most species are rarely recorded, are short-lived and minute, and grow on unstable substrata.

1 Lichenized, algal sheath around ascomata present, in some species forming distinct verrucae 2
Not or doubtfully lichenized, sometimes algal cells loosely associated with or present around the ascomata, but never forming a distinct algal sheath 9

2(1) Paraphyses absent; periphyses present, up to 25 µm and often branched 3
Paraphyses present; periphyses absent or present 5

3(2) Ascospores 7–9 × 3.5 µm; ascomata colourless or light yellow . . . . . **T. pallidum** (Lit.: Salisbury 1966)
Ascospores smaller than 4.5 × 2 µm 4

4(3) Ascomata colourless or brownish throughout, lacking yellow pruina; asci I−; hymenial gel I+ red, K/I+ blue; ascospores 3.5–4.5 × 1.2–2 µm . . . . . **T. magnussonii** (Lit.: Salisbury 1966)
Ascomata at least around the apex yellow-pruinose; asci I+ blue; hymenial gel I+ red, K/I+ blue, but often only scarcely present; ascospores 2.5–3.5 × 1.5–2 µm . . . . . **T. olivaceum** (Lit.: Salisbury 1966; Kocourková-Horáková 1998)

5(2) Paraphyses branched 6
Paraphyses unbranched 7

6(5) Thallus squamulose to placodioid, covered with yellow pruina; ascospores 4–5.5 × 2.5–3 µm . . . . . **T. andicola** (Lit.: Flakus & Kukwa 2014)
Thallus limited to forming verrucae around the perithecia, each verruca enclosing a single perithecium; ascospores 1.5–4 × 1.5–2 µm . . . . . **T. laureri** (Lit.: Salisbury 1966; Poelt & Hafellner 1975; Kocourková-Horáková 1998; Hafellner 2017)

7(5) Ascospores 11–17 × 5.5–9 µm; verrucae whitish to ochraceous, often crowded and resembling a more or less continuous thallus; asci I+ blue; hymenial gel I+ yellow . . . . . **T. albidum** (Lit.: Salisbury 1966)
Ascospores smaller than 5 × 4 µm 8

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8(7) Ascospores 2.5–3.8 × 3.8 µm, simple; verrucae appearing black, not pruinose . . . . . **T. palniense**
(Lit.: Awasthi & Singh 1975)
Ascospores 3–4 × 2–2.5 µm, simple or 1-septate; verrucae appearing brownish or yellowish, yellow-brown pruina present . . . . . **T. ulleungdoense**
(Lit.: Kondratyuk *et al.* 2016)

9(1) Ascospores globose 10
Ascospores oblong 15

10(9) Ascomata apothecioid, with a (sometimes narrowly) exposed hymenial disc; paraphyses present, simple 11
Ascomata perithecioid 12

11(10) Ascospores 4.5–6.0 µm diam. . . . . **T. sphaerosporum**
(Lit.: Salisbury 1966)
Ascospores 1.5–1.7 µm diam. . . . . **T. depressulum**
(Lit.: Magnusson 1936)

12(10) Ascospores 1.5–2 or 5–7 µm diam.; paraphyses present 13
Ascospores 3.0–5.5 µm diam.; paraphyses absent (but long periphyses sometimes present) 14

13(12) Ascospores 5–7 µm diam.; perithecia immersed . . . . . **T. immersum**
(Lit.: Spribille *et al.* 2020)
Ascospores 1.5–2 µm diam.; perithecia sessile . . . . . **T. microsporum**
(Lit.: van den Boom 2016)

14(12) Perithecia 120–200 µm, with yellow-green pruina, slightly immersed; asci 70–120 × 12–20 µm . . . . . **T. coccosporum**
(Lit.: Salisbury 1966)
Perithecia 200–300 µm, without yellow-green pruina, but sometimes greenish around the ostiole, immersed; asci 130–170 × 14–21 µm . . . . . **T. opertum**
(Lit.: David & Coppins 1997)

15(9) Asci with 8 ascospores; ascospores 3-septate . . . . . **T. triseptatum**
(Lit.: Cáceres & Aptroot 2016)
Asci with more than 8 ascospores; ascospores 0–1-septate 16

16(15) Outer part of ascoma wall partially carbonized, showing as dark green pigmentation giving the perithecia a blackish appearance; ascospores 9–12 × 5–6 µm . . . . . **T. nigrum**
(Lit.: Moon & Aptroot 2009; Aptroot & Schumm 2012)
Ascomata wall not carbonized, with light brown or light greenish pigmentation or translucent 17

17(16) Paraphyses absent (but long periphyses sometimes present which may resemble paraphyses when squashed) 18
Paraphyses present 22

18(17) Periphyses up to 120 µm long; ascospores 5.5–8.5 × 3.4–4.8 µm . . . . . **T. periphysatum**
Periphyses much shorter, up to 40 µm long 19

19(18) Ascospores 7–14 × 4–5.5 µm; ascomata completely immersed except for tops of dark apices; asci I+ pale blue . . . . . **T. imperceptum**
(Lit.: Salisbury 1966)
Ascospores on average smaller than 7 × 3 µm 20

20(19) Perithecia yellow-pruinose; asci or hymenial gel I+ 21
Perithecia blue-green around ostiole; asci and hymenial gel I−; ascospores 4–5 × 1.8–2.2 µm . . . . . **T. cyaneum**
(Lit.: Olech & Alstrup 1990)

21(20) Asci I+ light blue; hymenial gel I−; ascospores 3–4 × 1–1.5 µm . . . . . **T. intermediellum**
(Lit.: Salisbury 1966; Poelt & Hafellner 1975; Kocourková-Horáková 1998)
Asci I−; hymenial gel I+ red, K/I+ blue; ascospores 4–7 × 2–3 µm . . . . . **T. saxicola**
(Lit.: Salisbury 1966)

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22(17) Ascomata perithecioid, opening through a small pore; paraphyses loose, not forming an epithecium (if asci cylindrical see 29) 23
Ascomata (somewhat) apothecioid, with at least a small disc exposed; tips of paraphyses clustering to form an epithecium 25

23(22) Hymenial gel I+ red, K/I+ blue; asci I−; ascospores 4–6 × 1.7–2 µm or in some varieties 8–10 × 3 µm . . . . . **T. epibolum** (Lit.: Salisbury 1966; Poelt & Hafellner 1975; Kocourková-Horáková 1998)
Hymenial gel I−, K/I−; asci I+ blue 24

24(23) Ascospores 8–13 × 3.5–5 µm, often with one or two pseudosepta (if growing on *Sphagnum*, perithecia brick red and ascospores attenuated, compare *Carneothele sphagnicola* (Spribille *et al.* 2020)) . . . . . **T. superellum** (Lit.: Salisbury 1966; Kocourková-Horáková 1998; Olsen & Tønsberg 2016)
Ascospores 4.5–6 × 2 um, without a pseudoseptum . . . . . **T. citrum** (Lit.: Aptroot & Sparrius 2000; Salisbury 1966, as *T. vicinellum*)

25(22) Asci 10–16-spored; ascospores 9.5–12 × 5–6.5 µm . . . . . **T. macchiae** (Lit.: Nimis *et al.* 1994)
Asci with numerous ascospores, often more than 100 26

26(25) Ascospores < 3.5 µm long; ascomata whitish (if ascomata yellowish also compare *T. depressulum*) 27
Ascospores > 5 µm long; ascomata at least partially yellowish 28

27(26) Ascospores 2.5–3.5 × 2.0–2.5 µm; asci I+ light blue . . . . . **T. sandwicense** (Lit.: Magnusson 1955)
Ascospores 1.5–2.0 × 1 µm; asci I− . . . . . **T. subantarcticum** (Lit.: Øvstedal & Gremmen 2001)

28(26) Asci flask-shaped; ascomata green-yellow only at the top; hymenial gel I+ red, K/I+ blue; ascospores 6–8.5 × 4–5 µm . . . . . **T. impressellum** (Lit.: Salisbury 1966; Poelt & Hafellner 1975)
Asci cylindrical; ascomata green-yellow also on the sides; hymenial gel I−; asci I+ blue; ascospores 5–8 × 1.7–3 µm . . . 29

29(28) Ascomata globose or appressed, 0.9–2.9 times as wide as high . . . . . **T. lichenicola** (Lit.: Poelt & Hafellner 1975; Kocourková-Horáková 1998)
Ascomata cylindrical, 0.4–0.5 times as wide as high . . . . . **T. strasseri** (Lit.: Magnusson 1936)

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