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## *Tetramelas thiopolizus* comb. nov. with a key to all known species of *Tetramelas*

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**Abstract:** The study of the type and additional material of *Buellia andicola*, *B. hypophana* and *B. reagens* has shown that these taxa are conspecific with *B. thiopoliza*. *Buellia thiopoliza* is a muscicolous species growing at middle to high altitudes in the mountains of both hemispheres. It is easily recognized by its K+ purple-red yellow pigment mainly concentrated in the hypothecium, and by the presence of xanthenes in the thallus and the apothecial tissues. The new combination *Tetramelas thiopolizus* is proposed. A key to all known *Tetramelas* species is included. The also muscicolous *Buellia hypoleuca* is reduced to synonymy with *Phaeorrhiza sareptana* var. *sphaerocarpa*.

**Key words:** *Buellia* s. lat., *Caliciaceae*, Lecanoromycetes, lichenized fungi, *Physciaceae*, taxonomy, terricolous lichens

### Introduction

As part of a revision of the genus *Buellia* in the Iberian Peninsula, several specimens previously identified as *Buellia hypophana* and *B. reagens* have been studied. These are well characterized by their xanthone content, by the presence of a K+ purple-red yellow pigment mainly located in the hypothecium and the medulla below it, and by the rather large, 1-septate ascospores with additional pseudosepta when overmature. A thorough literature search (e.g. Poelt 1969; Clauzade & Roux 1985; Wirth 1995b; Marbach 2000; Nordin 2000) revealed that, in addition to the two species mentioned above, other taxa might be involved in the Iberian flora, such as *B. andicola* Müll. Arg. ex Zahlbr., *B. hypoleuca* H. Magn. and *B. thiopoliza* (Nyl.) Boistel. A study of the type material of these taxa has shown that they are all conspecific and well accommodated in the genus *Tetramelas* Norman, except *B. hypoleuca* which is a

synonym of *Phaeorrhiza sareptana* var. *sphaerocarpa* (Th. Fr.) H. Mayrhofer & Poelt.

A second aim of this study is to provide a key for all known *Tetramelas* species, which are so far treated in many dispersed contributions (Marbach 2000; Kalb 2004; Nordin 2004; Nordin & Tibell 2005; Giralt *et al.* 2009).

### Material and Methods

This study is based on herbarium material from G, H, LISU, M, PO and from the private herbaria of J. Etayo (Spain), K. Kalb (Germany) and P. P. G. van den Boom (The Netherlands). Lichen morphology was examined by standard techniques using stereo and compound microscopes. Only free, mature ascospores lying outside the asci have been measured. Measurements were made on material mounted in water at  $\times 1000$  magnification. Mean value ( $\bar{x}$ ) and standard deviation (SD) were calculated and the results are given as (minimum value observed)  $\bar{x} \pm$  SD (maximum value observed).  $\bar{x}$ , SD and  $n$  (the total number of ascospores measured) are given in parentheses. The terminology used here for the asci follows Rambold *et al.* (1994), Nordin (2000) for the excipulum-type, Nordin (1997) for the ascospore septation and Giralt (2010) for the ascospore and ontogeny-types.

Chemical constituents were identified by thin-layer chromatography (e.g. Culberson & Ammann 1979; Culberson *et al.* 1981; Culberson & Johnson 1982) and high performance liquid chromatography (HPLC) (Elix *et al.* 2003).

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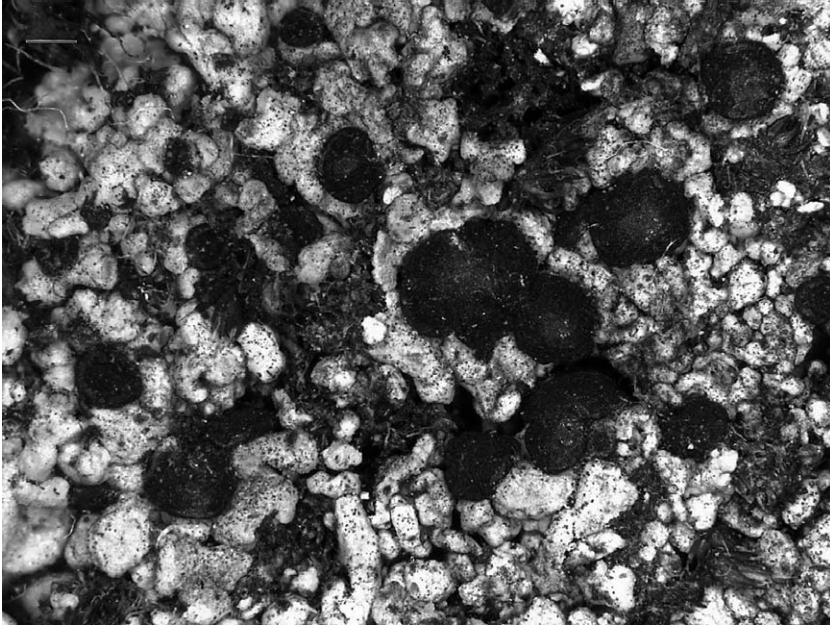


FIG. 1. *Tetramelas thiopolizus* (G 290893), habitus. Scale = 500  $\mu$ m.

The key to species has been constructed from our own data and the following literature: Nordin (1999, 2000, 2004), Giralt *et al.* (2000, 2009), Marbach (2000), Foucard *et al.* (2002), Kalb (2004), Nordin & Tibell (2005) and Bungartz *et al.* (2007).

(1925–1926); type: Chile, Anden, über Moosen, ex Herbarium Hampe 1877 (G290798—holotype!).

*Buellia reagens* H. Magn., *Broteria* **IV**: 148 (1947); type: Portugal, Beira Alta, Serra da Estrela-Caldas de Manteigas, 850 m, sur le granite moussu, 1944, *Tavares* (LISU).

### The Species

#### ***Tetramelas thiopolizus* (Nyl.) Giralt & Clerc comb. nov.**

Mycobank No.: MB561208

*Lecidea thiopoliza* Nyl., *Flora* **56**: 244 (1878); type: France, Arvernia, sur les rochers qui dominant la Bourboule près du Mont Doré, *Lamy*, 1877 (H-NYL 10368!—lectotype, selected here; H-NYL 10367—isolectotype!). Two additional specimens (H-Nyl—10366! and G—290893!) could also be original material but the collection date is 1878 or is lacking, respectively).—*Buellia thiopoliza* (Nyl.) Boistel, *Nouv. Flore Lich.* **2**: 230 & 233 (1903).

New synonyms: *Buellia hypophana* (Nyl.) Zahlbr., *Cat. Lich. Univ.* **7**: 367. (1931).—*Lecidea hypophana* Nyl. apud Hue, *Bull. Soc. Bot. France* **34**: 473 (1887); type: France, Auvergne, Cantal, à la Roquevieille, 1886, *Fuzet* (H-NYL 10648—holotype!).

*Hypoflavia andicola* (Müll. Arg. ex Zahlbr.) Marbach, *Bibliotheca Lichenologica* **74**: 292 (2000).—*Buellia andicola* Müll. Arg. ex Zahlbr., *Acta Horti Gothob.* **2**: 25

(Figs 1 & 2)

*Thallus* subsquamulose, areolate; areoles discrete and bullate to usually contiguous, sublobate, some almost lobate-effigurate, plane to verrucose, whitish grey, ochraceous, yellowish, yellowish orange to dull brown; basal part of some areoles include a yellow pigment reacting K<sup>+</sup> purple-red. *Medulla* normally I<sup>+</sup> weakly violet (microscope slide!) rarely I<sup>-</sup>.

*Apothecia* lecideine, adnate to sessile, black, up to 1.25 mm diam., often confluent. Proper margin initially thick and prominent, becoming thinner and finally  $\pm$ excluded. *Disc* plane to convex, epruinose. *Excipulum proprium* very well developed, up to 100  $\mu$ m thick, including some C<sup>+</sup> orange crystals (microscope slide!), prosoplectenchymatous, outer part brown, N<sup>-</sup>, inner part paler

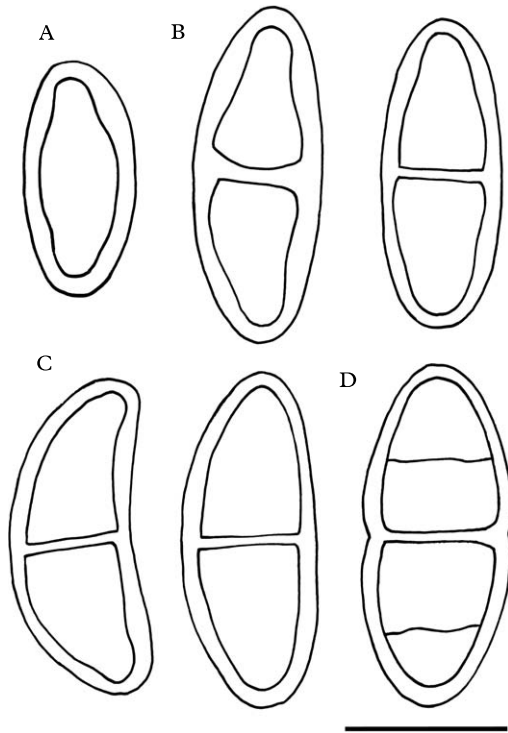


FIG. 2. *Tetramelas thiopolizus*, ascospore ontogeny and variability (hb. v. d. Boom 19535). A, immature non-septate ascospore with subapical thickenings; B, young *Callispora*-type ascospores; C, mature *Buellia*-type ascospores; D, overmature ascospore with a pseudo-septum per cell. Scale = 10  $\mu$ m.

(see Nordin 2000, Fig. 4A & B). *Epiphymenium* brown, N<sup>-</sup>, with C<sup>+</sup> orange crystals (epipsamma). *Hymenium* colourless, 60–100  $\mu$ m high, without oil droplets, often including rows of some C<sup>+</sup> orange crystals. *Hypothecium* dark brown, basal part with a yellow pigment reacting K<sup>+</sup> purple-red. *Paraphyses*, apical cells strongly swollen, up to 7  $\mu$ m diam., brown. *Asci* *Bacidia*-type. *Ascospores* (14–)17–22.5(–27)  $\times$  (6.5–)7.4–9.1(–11)  $\mu$ m [ $\bar{x}$  = 20  $\times$  8.2  $\mu$ m; SD = 2.5  $\times$  0.8  $\mu$ m;  $n$  = 190], 1-septate, apices pointed, straight or slightly curved, smooth at  $\times$ 1000; when young with subapical inner wall thickenings (*Callispora*-type, Fig. 2B), when mature without any inner wall thickening (*Buellia*-type, Fig. 2C), some showing a pseudo-septum or endospore septa (see Nordin 1997, Fig. 11) in each cell when overmature

(better seen in K) (Fig. 2D); ontogeny type C (subapical inner wall thickenings are distinct before the septum is developed, Fig. 2A).

*Conidia* bacilliform 4–6  $\times$  1  $\mu$ m.

**Chemistry.** 6-*O*-methylarthothelin, arthothelin and an unknown yellow pigment in all specimens examined except in the two known Andine specimens where arthothelin is absent [corresponding to *B. andicola* (G-holotype and hb. Kalb-29314)]. Low concentrations of several additional unknowns have also sometimes been detected. Thallus C<sup>+</sup> pale to deep orange, K<sup>+</sup> yellow-orange to orange, KC<sup>+</sup> orange to deep orange and UV<sup>+</sup> orange (the distinctness of these spot tests varies in a single thallus and must be dependent upon the concentration of xanthenes); basal part of the hypothecium and medulla below it always including the K<sup>+</sup> purple-red yellow pigment; basal part of the medulla of the areolae sometimes including the K<sup>+</sup> purple-red yellow pigment. This yellow pigment was tentatively identified by HPLC as cinnamomeic acid B (*cf.* Paz-Bermúdez & Giralt 2010).

**Observations.** Phylogenetic studies based on genetic data have shown that the genus *Tetramelas* Norman constitutes a well founded segregate of *Buellia* s. lat. (Helms *et al.* 2003; Nordin & Tibell 2005). The genus was resurrected by Marbach (2000). Later, it was emended with the addition of new diagnostic characters: the presence of 6-*O*-methylarthothelin (Kalb 2004), the relative thickness of the parts of the ascospore wall (proper wall >1/2 thickness of the perispore) (Nordin 2004) and the inner wall thickenings of the ascospores ( $\pm$ *Callispora*-type) (Giralt *et al.* 2009). Since then, thirteen species have been combined into this genus and one new species has been described.

*Buellia thiopoliza* contains 6-*O*-methylarthothelin and has ascospores with *Callispora*-type thickenings. The spores are often curved, have pointed apices and may become tri-septate at maturity. The paraphyses have strongly swollen apical cells and the conidia are bacilliform. This set of characters fits well with the definition of the genus

*Tetramelas* and therefore the new combination *Tetramelas thiopolizus* is proposed here.

According to Kalb (2004), in addition to the presence of xanthones, other diagnostic characters for *Tetramelas* include the typically muscicolous habitat, the large ascospores and the arctic-antarctic or alpine-subalpine distribution. All these features are also present in *T. thiopolizus*.

*Tetramelas thiopolizus* is thus characterized by the subsquamulose-areolate thallus containing 6-*O*-methylarthothelin and usually arthothelin, the presence of a yellow K+ purple-red pigment mainly concentrated in the basal part of the hypothecium, the thick proper excipulum that is brown in the outer part and paler in the inner part, and the large, smooth, 1-septate ascospores showing *Callispora*-type thickenings when young and sometimes a pseudoseptum in each cell when overmature.

Among all *Tetramelas* species known, *T. thiopolizus* is clearly distinguished by the presence of the yellow K+ purple-red pigment. The occurrence of yellow pigments (eumitrin and secalonin acid A) was already reported in that genus in, for example, *T. graminicola* (Øvstedal) Kalb. Concerning cinnamomeic acids, they are present in the medulla of *Buellia capitata-regum* W. A. Weber (Nordin 2000).

The main differences observed between the type material of *B. andicola*, *B. hypophana* and *B. thiopoliza*, also noted in the corresponding original descriptions, lay in the ascospore size and in the intensity of the yellow colour of the thallus, that is in the intensity of the spot test reactions with C, K and KC. In our opinion, both characters are insufficient to separate taxa since large ascospores typically show a broad range of variation and since the concentration of xanthones might vary in the same thallus. *Buellia thiopoliza* has a yellowish thallus and contains arthothelin and 6-*O*-methylarthothelin whereas *B. andicola* is greyish to ochraceous and contains only 6-*O*-methylarthothelin. *Buellia hypophana* (greyish to ochraceous) has not been examined chemically due to the very scanty type material. Thalline reactions with C, K and

KC are stronger in *B. thiopoliza* than in *B. andicola* and *B. hypophana*. Concerning the ascospores, they are on average somewhat shorter in *B. andicola* and in *B. hypophana* than in *B. thiopoliza* but not significantly according to the statistical calculations: *B. andicola*: (14–)17.2–21.1(–23) × (7–)7.5–9(–10.5) μm [ $\bar{x}$  = 19 × 8.2 μm; SD = 2 × 0.7; n = 42]; *B. hypophana*: (14.5–)17–22.3(–26) × (6.5–)8–8.4(–11) [ $\bar{x}$  = 19.6 × 8.4 μm; SD = 2.7 × 0.9 μm; n = 44]; *B. thiopoliza*: (14–)17.9–23.5(–27) × (6.5–)7.2–8.7(–10) μm [ $\bar{x}$  = 20.7 × 8 μm; 2.8 × 0.8 μm; n = 48].

The type material of *B. reagens* (LISU) was not available for study. However, according to the original description (Tavares 1947), *B. reagens* “seems exceedingly well characterized by the chemical reactions”. These reactions are the “K+ intensely (violet) red” hypothecium and the “K+ yellowish and C+ intensely orange yellowish-grey thallus”. The measurements given for the ascospores are “15–17(–20) × 8–9 μm”. Material studied here and mentioned in the protologue (LISU), as well as the specimen collected close to the type locality (hb. v. d. Boom-17327), have ascospores (16–)17.8–22.5(–25) × (6.5–)7.5–9.3(11) μm [ $\bar{x}$  = 20.2 × 8.4 μm; SD = 2.4 × 0.9 μm; n = 55].

Two features distinguish the Andine specimens (corresponding to *B. andicola*) from all other specimens examined. They lack arthothelin and the I+ medullar violet reaction. However other *Tetramelas* taxa may or may not contain arthothelin in addition to 6-*O*-methylarthothelin [e.g. *T. chloroleucus* (Körb.) A. Nordin, *T. concinnus* (Th. Fr.) Giralt and *T. insignis* (Nägeli ex Hepp) Kalb, see Giralt *et al.* 2000 and Bungartz *et al.* 2004, 2007]. Moreover, xanthones, especially when present in traces, are difficult to detect with routine thin-layer chromatography (TLC). HPLC is a far more sensitive method of detection and identification for this category of compounds. As with other chemical data given for *Tetramelas* species, those included here for *B. andicola* are based only on TLC analyses. Concerning the medullar reaction with iodine, it has been shown to be variable in other species of *Tetramelas*, as, for example, in *T. concinnus*



(cf. Scheidegger 1993; Bungartz *et al.* 2004 and Giralt *et al.* 2009).

Except for the differences mentioned, all specimens studied here are congruent in the following characters: the ecology (on mosses in alpine/sub-alpine/montane habitats), the thalline morphology, the anatomy and pigmentation of the proper excipulum, the morphology and ontogeny of the ascospores, the presence of the yellow K<sup>+</sup> purple-red pigment in the hypothecium, the large apical cells of the paraphyses and the shape and size of the conidia.

It should be noted that Poelt (1969) had already tentatively proposed to synonymize *B. hypophana* with *B. thiopoliza*. He probably did so because of the very similar original descriptions.

The genus *Hypoflavia* Marbach was segregated from *Buellia* s. lat. by Marbach (2000). According to this author, the main diagnostic character of the genus *Hypoflavia* is the presence of a yellow pigment in the hypothecium and the excipulum which reacts K<sup>+</sup> yellow-orange or violet. Additional generic diagnostic features are the occurrence of norstictic acid and the presence of subapical wall thickenings in the ascospores (*Callispora*-type). The genus includes two species, the generic type *Hypoflavia velloziae* (Kalb) Marbach and *H. andicola* (Müll. Arg. ex Zahlbr.) Marbach. The former is known from three Brazilian localities including the type; the latter from the type locality in Chile and one additional locality in Venezuela (hb. Kalb 29314).

According to our investigations, the two known specimens of *Hypoflavia andicola* have a yellow pigment in the thallus and apothecia which reacts K<sup>+</sup> purple-red but instead of norstictic acid, as described by Marbach (2000), they contain 6-*O*-methylarthothelin. They fit well with the generic concept of *Tetramelas* and indeed correspond well to *T. thiopolizus*.

Surprisingly, the known specimens of *Hypoflavia velloziae* lack the yellow pigment in the hypothecium and the excipulum considered by Marbach (2000) as the main diagnostic character for the genus *Hypoflavia*. The K<sup>+</sup> yellow-orange reaction described by

Marbach (*op. cit.*) for these apothecial parts of *H. velloziae* is the typical reaction given by norstictic acid before the formation of red crystals. Furthermore *H. velloziae* contains norstictic acid also in the thallus, lacks xanthonones, has slightly enlarged apical cells of the paraphyses [(2–)3–4 µm diam.] and fusiform conidia (6–9 × 1–1.5 µm), a character hitherto unknown for this species and which, according to Marbach (2000), is diagnostic for the genus *Gassicurtia*. All characters mentioned above do not accommodate *H. velloziae* in the genus *Tetramelas*. Consequently, only *H. velloziae* is retained in the genus *Hypoflavia*, which now includes only this species.

*Ecology and distribution.* *Tetramelas thiopolizus* grows on mosses or plant debris on rocks or earth, at medium to high altitudes in the mountains of both hemispheres. In the Southern Hemisphere, it is known from the Andes of Chile (type locality) and Venezuela (Marbach 2000: sub *Hypoflavia andicola*). In the Northern Hemisphere, it occurs in the mountains of the Iberian Peninsula (Rico 1992; Terrón-Alfonso *et al.* 2000; van den Boom & Jansen 2002; van den Boom 2003; Pérez-Ortega & Álvarez-Lafuente 2006; Paz-Bermúdez & Giralt 2010: sub *B. hypophana*; and Tavares 1947: sub *B. reagens*); Austria (Türk & Hafellner 1993, 1999: sub *B. hypophana*); France (type localities of *Lecidea thiopoliza* and *L. hypophana*); Germany (Wirth 1995a: sub *B. thiopoliza*); and Italy (Nimis & Martellos 2008: sub *B. hypophana*). According to Nimis & Martellos (*op. cit.*) the species occurs also in Siberia (Russian Federation).

*Tetramelas thiopolizus* also grows on mosses at altitudes of 1600–1900 m in Macaronesia from where it has been reported as *B. hypophana* from two localities in Madeira by Kalb & Hafellner (1992) and from one locality in Gran Canaria (Canary Islands) by Hafellner (1995).

The records of *B. hypophana* by Etayo (1990a, b) from the western Pyrenees (Navarra, Spain) refer to *Tetramelas chloroleucus* and those by Beauchamp *et al.* (2007) from Switzerland (Valais) with filiform conidia,

probably to *Buellia punctata* f. *muscolica* Hepp ex Koerb. em Arnold (cf. Poelt 1969: 141), because of the small ascospores and the muscicolous habitat.

*Additional specimens examined.* **Portugal:** *Minho:* Castro Laboreiro, musgos do penedo no castelo, 1915, *Sampaio* (487L, PO) (sub *Buellia insignis* var. *geophila*). *Beira Alta:* Serra da Estrela-Sra. do Desterro, Cabeça da Velha, sobre o granito musgoso, 950 m, 1946, *Tavares* (LISU); Serra da Estrela-Sra. do Desterro, sobre os blocos graníticos de um pinhal, sobre o granito musgoso, 800 m, 1945, *Tavares* (LISU-71); Serra da Estrela-Entre as Lagoas Escurra e Comprida, sobre *Andreaea* em granito, c. 1600 m, 1947, *Tavares* (LISU-2223); Serra da Estrela, SW of Manteigas, NE of Lagoa Comprida, Lagoa Redonda, N exposed steep granite, 1625 m, 1995, *van den Boom* (hb. v. d. Boom-17327) [sub *B. reagens* H. Magn. (= *B. pulchella* C. Tav. non Tuck.)]. *Trás-Os-Montes:* N of Bragança, Montesinho, path to storage lake with *Pinus* and granite outcrops, small *Quercus* wood and *Betula* near source, sheltered S exposed granite ± horizontal, 6°45'2"W; 41°56'5"N, 1200 m, 7 viii 1997, *van den Boom* (hb. v. d. Boom-19535).— **Spain:** *Extremadura:* 41 km ENE of Plasencia, N of Jarandilla, 1–3 km N of Guijo de Santa Bárbara, along path E of river Jaranda, acid rock on SW slope, 1400 m, 1989, *van den Boom* (hb. v. d. Boom-8880) [sub *B. hypophana*].— **Venezuela:** *Mérida:* Libertador, Pico Espejo, SE von Mérida, Loma Redonda,

8°35'N; 71°00'W, 4200 m, 1989, *Kalb & Kalb* 29314 (hb. Kalb) (sub *B. andicola*).

*Specimens of Hypoflavina velloziae studied for comparison.* **Brazil:** *Bahia:* Chapada diamantina, Serra do Tombador, etwa 1 km vor der Stadt Morro do Chapéu, 1000 m, an *Vellozia*, 1980, *Kalb* (K. Kalb: *Lichenes Neotropici* n° 363, holotype, hb. Kalb); zwischen Mundo Novo und Morro Chapéu, 1000 m, 1980, *Kalb* 28758 (hb. Kalb). *Minas Gerais:* Serra do Espinhaço, Serra do Caraça, umbegung des Klosters Caraça (Hauptsammelgebiet von Vainio), 1978, *Kalb & Plöbst* 28952 (hb. Kalb); NW-Hangdes Berges Carapuça, Groutas do P. Trombert, in feuchtem, dunklem Primärwald, 1978, *Kalb & Plöbst* 28730 (hb. Kalb).

**Phaeorrhiza sareptana (Tomin) H. Mayrhofer & Poelt var. sphaerocarpa (Th. Fr.) H. Mayrhofer & Poelt**

*Nova Hedwigia* 30: 793 (1979) [1978].

*New synonym:* *Buellia hypoleuca* H. Magn., *Bot. Not.* 109: 150 (1956); type: Austria, Südtirol, Wintschgau, trockene Felsen oberhalb Graun am Reschensee, on earth, 1955, *J. Poelt* (M—holotype!).

For additional data on this taxon see Magnusson (1956, sub *B. hypoleuca*), Mayrhofer & Poelt (1978) and Mayrhofer & Moberg (2002).

**Key to all known species of *Tetramelas***

- 1 Lichenicolous, on foliose *Physciaceae*; thallus absent (endokapilic) . . . . . 2  
Not lichenicolous or, if lichenicolous, thallus present . . . . . 3
- 2(1) Ascospores 3-septate. . . . . **T. pulverulentus (Anzi) A. Nordin & Tibell**  
Ascospores 1-septate. . . . . **T. phaeophysciae A. Nordin & Tibell**
- 3(1) Thallus sorediate; ascospores (1–)3-septate, 24–40 × 7–11.5 µm; containing 6-O-methylarthothelin and traces of the anthraquinones eumitrin and secalonic acid A; on plant debris; known only from South Georgia . . . . .  
. . . . . **T. graminicola (Øvstedal) Kalb**  
Thallus not sorediate; ascospores smaller; eumitrin and secalonic acid A always lacking . . . . . 4
- 4(3) Hypothecium with a yellow pigment reacting K+ purple-red. Ascospores 1-septate, (14–)17–22.5(–27) × (6.5–)7.4–9.1(–11) µm, when overmature showing sometimes an additional pseudoseptum per cell; on mosses growing on rock or ground; mountains of both hemispheres. . . . . **T. thiopolizus (Nyl.) Giralt & Clerc**  
Hypothecium without yellow pigment, K– . . . . . 5
- 5(4) Thallus without xanthonenes C–, KC–, UV–, white and chalky containing only atranorin (K+ yellow); ascospores 1-septate, 15–25 × 7–10 µm; muscicolous and saxicolous; mountains of northern Europe . . . **T. papillatus (Sommerf.) Kalb**  
Thallus always containing xanthonenes (C+ or KC+ or UV+ orange), not white and chalky; atranorin present or not. . . . . 6

- 6(5) Apothecia with norstictic acid, K+ red (forming crystals); ascospores (1–)3-septate, 26–34 × 8–10 μm; usually on calciferous ground, rarely lignicolous; arctic-alpine . . . . . **T. terricola (A. Nordin) Kalb**  
 Apothecia without norstictic acid, K– (no red crystals) . . . . . 7
- 7(6) Saxicolous . . . . . 8  
 Corticolous, lignicolous, terricolous, muscicolous or on plant debris . . . . . 9
- 8(7) Ascospores 1(–)3-septate, 13–21 × 6–10 μm; thallus with arthothelin and often 6-*O*-methylarthothelin; Northern Hemisphere . . . **T. concinnus (Th. Fr.) Giralto**  
 Ascospores (1–)3-septate, 17–28 × 8–11.5 μm; thallus only with 6-*O*-methylarthothelin; Southern Hemisphere (antarctic) . . . . .  
 . . . . . **T. granulosis (Darb.) A. Nordin**
- 9(7) Corticolous or lignicolous . . . . . 10  
 Terricolous, muscicolous or on plant debris . . . . . 14
- 10(9) Ascospores 3-septate . . . . . 11  
 Ascospores 1-septate, rarely 1(–)3-septate . . . . . 12
- 11(10) Ascospores 19–27.5 × 7.5–10.5 μm; thallus only with arthothelin; subalpine; Northern Hemisphere . . . . . **T. triphragmoides (Anzi) A. Nordin & Tibell**  
 Ascospores 23–38 × 6–13 μm; thallus only with 6-*O*-methylarthothelin; arctic-(sub)alpine; Northern Hemisphere . . . . . **T. geophilus (Sommerf.) Norman**
- 12(10) Ascospores 13–23 × 6–11 μm; thallus with 6-*O*-methylarthothelin and rarely traces of arthothelin; alpine-subalpine; Northern Hemisphere . . . . .  
 . . . . . **T. chloroleucus (Körb.) A. Nordin**  
 Ascospores larger, > 23 μm . . . . . 13
- 13(12) Ascospores 1-septate, 27–31 × 10–11 μm; thallus with 6-*O*-methylarthothelin, atranorin and lobaric acid; high tropical mountains . . . . .  
 . . . . . **T. regiomontanus Marbach**  
 Ascospores 1(–)3-septate, 23–32 × 9–13 μm; thallus with 6-*O*-methylarthothelin and rarely traces of arthothelin; high European mountains . . . . .  
 . . . . . **T. insignis (Nägeli ex Hepp) Kalb**
- 14(9) Ascospores 3-septate . . . . . 15  
 Ascospores 1-septate or 1(–)3-septate . . . . . 16
- 15(14) Ascospores 26–34 × 8–10 μm; apothecia containing norstictic acid (K+ red crystals); thallus with atranorin, arthothelin and rarely 6-*O*-methylarthothelin; arctic-alpine . . . . . **T. terricola**  
 Ascospores 23–38 × 6–13 μm; apothecia without norstictic acid; thallus containing only 6-*O*-methylarthothelin; arctic-(sub)alpine . . . . . **T. geophilus**
- 16(14) Ascospores 13–25 × 5–7.5 μm; thallus containing atranorin and 6-*O*-methylarthothelin; known only from New Zealand . . **T. confusus A. Nordin**  
 Ascospores larger, > 25 × 7.5 μm . . . . . 17
- 17(16) Ascospores 1-septate, 27–31 × 10–11 μm; thallus with 6-*O*-methylarthothelin, atranorin and lobaric acid; high tropical mountains . . . . . **T. regiomontanus**  
 Ascospores 1(–)3-septate, 23–32 × 9–13 μm; thallus with 6-*O*-methylarthothelin and rarely arthothelin; high European mountains . . . . . **T. insignis**

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