

## TAXONOMIC STUDY OF THE GENUS *USNEA* (LICHENIZED ASCOMYCETES) IN JAPAN AND TAIWAN<sup>1</sup>

YOSHIHITO OHMURA<sup>2</sup>

**ABSTRACT.** The genus *Usnea* is taxonomically revised, resulting in 43 species for Japan and Taiwan. It consists of three subgenera, *Usnea*, *Eumitria* (Stirt.) Zahlbr. and *Dolichousnea* Y. Ohmura, and two sections in the subgenus *Usnea*, *Usnea* and *Ceratinae* (Motyka) Y. Ohmura. Among the species listed in the present study, *U. dendritica* Stirt., *U. hesperina* Motyka, *U. nidifica* Taylor, *U. sinensis* Motyka and *U. trichodeoides* Vain. are reported as new to Japan and Taiwan. *Usnea pygmoidea*, formerly placed under the subspecies of *U. confusa*, is elevated to species level. The subgenus *Dolichousnea* is newly proposed; it is characterized by the pendent thallus, isotomic-dichotomous branching, the presence of annular-pseudocyphellae between segments, a thicker hypothecium, and a positive iodine reaction in its axis. The subgenus *Usnea* is separated into two sections, mainly on the basis of differences in the cortical hyphal type (leptodermatous and pachydermatous types). The morphology of soralia is found to be correlated with their origins, the type of papillae, and the occurrence of soredia and/or isidiomorphs. Annular-cracks which regularly occur between segments are separated into two categories: annular-pseudocyphellae and cracks originating in the separated cortical hyphae. Cortical tissues are found to be one of four types which are *florida*-, *merrillii*-, *ceratina*-, or *baileyi*-types. The specificity of lichen substances to species is recognized. Twenty-four species show no chemical variation, while 19 species have two or three (rarely four) chemical races within a species.

### CONTENTS

Abstract . . . . .	1
I. Introduction . . . . .	2
II. Morphology and anatomy . . . . .	3
III. Chemistry . . . . .	19
IV. Taxonomic treatment . . . . .	24
Subgenus <i>Usnea</i> . . . . .	24
Section <i>Usnea</i> . . . . .	25
Section <i>Ceratinae</i> (Motyka) Y. Ohmura . . . . .	32
Subgenus <i>Eumitria</i> (Stirt.) Zahlbr. . . . .	75
Subgenus <i>Dolichousnea</i> Y. Ohmura . . . . .	80
Key to species of the genus <i>Usnea</i> in Japan and Taiwan . . . . .	88
Acknowledgements . . . . .	91
Literature cited . . . . .	92
Index . . . . .	95

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<sup>2</sup> Department of Biological Sciences, Graduate School of Science, the University of Tokyo, Hongo 7-3-1, Bunkyo-ku, Tokyo 113-0033, Japan. Present address: Center for the Study of International Cooperation in Education, Hiroshima University, 1-5-1 Kagamiyama, Higashi-Hiroshima-shi, Hiroshima 739-8529, Japan.

## I. INTRODUCTION

The genus *Usnea* is one of the most common lichenized Ascomycetes. The genus comprises of ca. 600 species and belongs to the family Parmeliaceae (Hawksworth et al. 1995). It is widely distributed, occurring in polar zones, boreal regions, temperate regions, and tropical habitats. Diagnostic features of the genus include a fruticose thallus with a cortex, medulla, and a cartilaginous central axis; the cortex always contains usnic acid.

The first comprehensive worldwide monograph of the genus *Usnea* was published by Motyka (1936–38), who reported 451 species, including 18 species for Japan and Taiwan. He recognized six subgenera (*Usnea*, *Eumitria*, *Neuropogon*, *Protousnea*, *Lethariella*, and *Chlorea*) based mainly on differences in axis structure, thallus and disc color, and species distribution patterns. Motyka reported two subgenera, *Usnea* and *Eumitria*, for Japan and Taiwan. To date Japanese and Taiwanese taxa reported for the genus *Usnea*, include 55 species, 23 subspecies, 8 varieties and 17 forms, based on Asahina's work during 1950 to 1973 and other researchers (Awasthi 1986, Clerc & Herrera-Campos 1997, James 1979, Stevens 1990, 1999). Asahina (1954, 1956) introduced the use of branching patterns, numerical treatment of the ratio of the cortex, medulla, and axis, and lichen substances into the taxonomy of *Usnea*. The following characteristics have been used for distinguishing species: thallus habit, branching patterns, thallus color, branch shape, morphology and frequency of cracks in the thallus surface, the occurrence and morphology of asexual propagules, pseudocyphellae, and papillae or tubercles, the ratio of the cortex, medulla, and axis, the axis structure, and the presence or absence of various lichen substances.

However, four taxonomic important problems have persisted in the genus *Usnea*:

(1) Distinction between similar forms of soralia between different species.

The importance of the morphology of soralia is well known in the genus *Usnea* (Clerc 1987b). However, it is difficult to distinguish similar forms, especially at the juvenile stage or when examining depressed forms between different species.

(2) Evaluation of annular cracks as a taxonomic character.

Some species of *Usnea* have annular cracks near the base of the thallus, or from the base to the apices. However, cracks may also occur randomly as a result of physical force. Unfortunately, the difference between annular cracks and random cracks has not been clarified. The nature of annular cracks needs to be reviewed from a structural and anatomical viewpoint.

(3) A lack of detailed tissue-level studies in the genus *Usnea*.

Although variations in the cortical structure have been reported (Asahina 1956, Awasthi 1986, Motyka 1936–38, Tavares 1987), cortical tissue is generally thought to be uniform within the genus (Kärnefelt et al. 1998). Tissue-level morphology is considered to be more stable and less influenced by the environmental variation than external characteristics. To date, no comprehensive evaluation of cortical tissue in *Usnea* have been completed.

(4) Specificity and variation in lichen substances.

In addition to morphological features, chemical features have also been used in characterization for the taxonomy of *Usnea*. Asahina (1956) detected various lichen substances in *Usnea* spp. through the use of microchemical tests and paper chromatography. When a chemical difference was recognized, even with the same morphology, he assumed the spec-

imen belonged to a different taxon (usually with subspecies rank). He considered chemical differences to be caused by genetic differences (Asahina 1937). However, modern instruments allow us to detect even small amounts of lichen substances. Therefore, the specificity and variation in lichen substances within a species should be revised using more accurate instruments.

The purpose of the present study is to prepare a taxonomic revision to the genus *Usnea* for Japan and Taiwan and to attempt to resolve the various problems mentioned above for the genus.

The terminology used basically follows Hawksworth et al. (1995) unless otherwise noted.

## II. MORPHOLOGY AND ANATOMY

### Materials and Methods

This study is based primarily on herbarium specimens from the National Science Museum, Tokyo (TNS), as well as specimens collected by the author between 1995 and 1999. Field trips were made to various locations in Hokkaido, Honshu, Shikoku and Kyushu in Japan. Approximately 1800 specimens were examined during this study. All collections are currently located in TNS. Various type specimens, from BG, BM, FH, G, H, LINN, M, PC, S, TNS, TUR, UPS, and W, were also examined.

Thallus morphology was examined using a dissecting microscope. The diameter of branches and the thickness of the cortex, medulla and axis were measured using well-developed thicker branches at 50× magnification. The ratio of the thickness of the cortex, medulla and axis is reported following the methods of Clerc (1984). Anatomical observations were made using a bright field microscope or a Nomarski interference microscope. Sections of apothecia and thalli were made using either a hand-razor or freezing microtome; and cross sections of thalli were cut from well-developed thicker branches. Cross sections were observed in GAW (glycerin : ethanol : water = 1 : 1 : 1).

Selected thalli of several species were chosen for scanning electron microscopy (SEM) (JEOL JSM-5410LV at 5–15 kV). Well-developed thicker branches were cut into sections of 1–2 mm from air-dried thalli in order to observe the cortex. Samples were plated with gold in a vacuum at 20 mA for 90 sec.

### Results and Discussion

#### *Thallus*

All *Usnea* species are fruticose with radially symmetrical thalli. The thallus begins to grow from the base and grows to a certain length according to species, with several possible habits (Fig. 1): 1) erect type, in which all branches are erect (e.g., *U. glabrata*, *U. koyana* and *U. orientalis*), 2) subpendent type, in which both erect and hanging branches are intermixed in the thallus (e.g., *U. aciculifera*, *U. baileyi*, *U. ceratina* and *U. subfloridana*), and 3) pendent type, in which all branches hang downward (e.g., *U. diffracta*, *U. longissima* and *U. merrillii*).

Thalli of some species are characteristically decorticated or annularly or irregularly cracked (see the section below on the cortex).

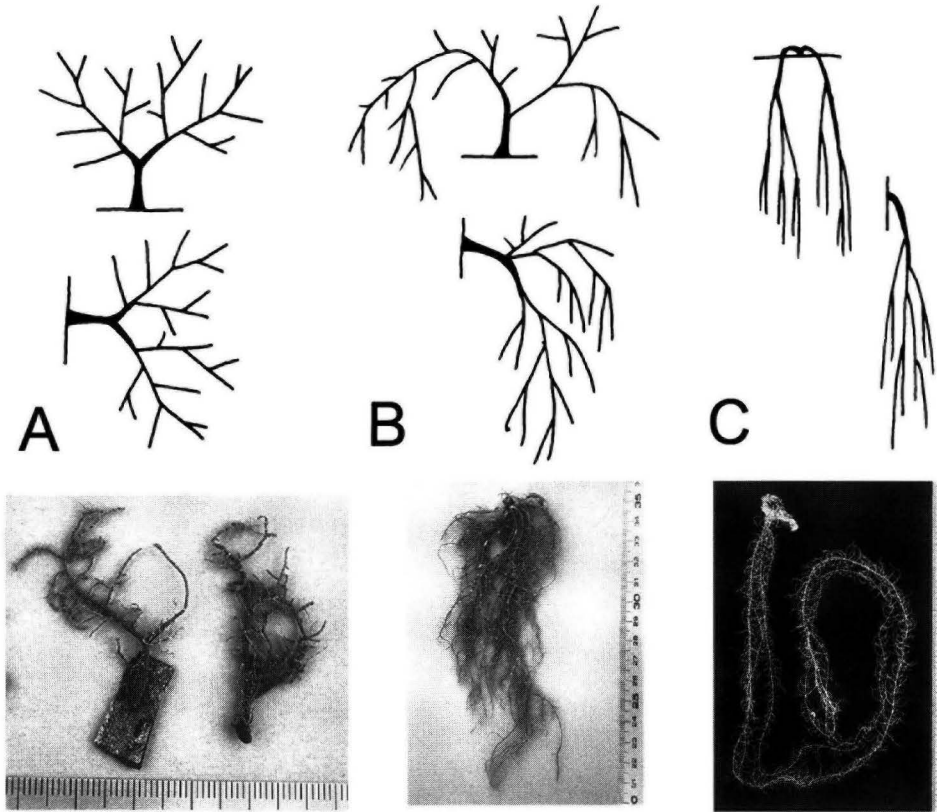


Fig. 1. Habit of *Usnea* thalli. A. Erect type [*U. koyana* (holotype)]. B. Subpendent type [*U. rubrotincta* (Y. Ohmura 3057)]. C. Pendent type [*U. trichodeoides* (Y. Ohmura 2728)].

Thallus color in fresh material is gray to grayish-green, olive-green, yellow-green, reddish, or reddish-brown. The base can be pale, concolorous with the rest of the thallus, dark brown, or jet black. Thallus color often changes to straw-yellow, chestnut-brown, brown or rusty-brown after storage (usually more than 20 years) in the herbarium. Although thallus color seems to have some taxonomic value, it is not a particularly good characteristic for use with fresh samples. However, the occurrence of reddish or reddish-brown color in thalli and a jet black base are taxonomically important, especially in separating species.

Thallus branching is dichotomous in all species. However, difference in the thickness of dichotomous branches forms the isotomic- or anisotomic-dichotomous types (Fig. 2). In the isotomic-dichotomous type, the thallus separates isotomically into branches of essentially equal thickness. Asahina (1956) described this as the “deliquescent type”. *Usnea diffracta* is an example of the isotomic-dichotomous type. In the anisotomic-dichotomous

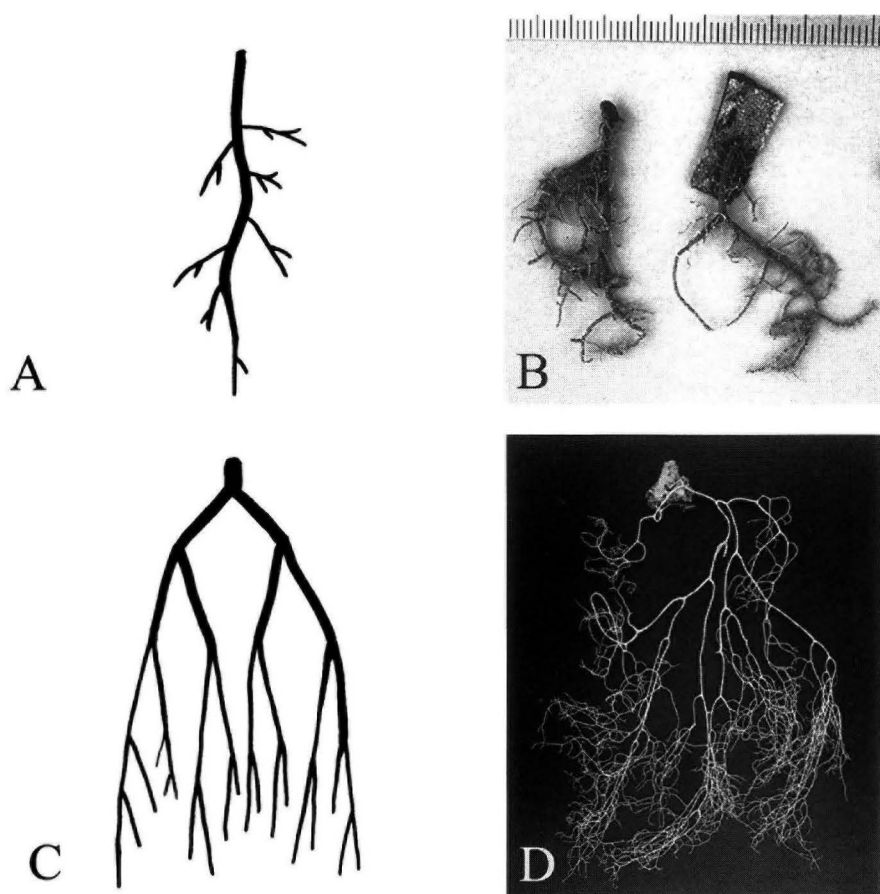


Fig. 2. Thallus branching patterns. A, B = anisotomic-dichotomous type [*Usnea koyana* (holotype)]. C, D = isotomic-dichotomous type [*U. diffracta* (Y. Ohmura 1040)].

type, the thallus separates into branches of unequal (anisotomic) thickness (termed the “excurrent type” in Asahina 1956). *Usnea koyana* is an example of this type. In addition, the terminal and subterminal branches of several species from both the isotomic- and anisotomic-dichotomous types are conspicuously elongated, and are referred to as the filamentous-dichotomous type (Hawksworth 1972), and termed the “filamentose type” by Asahina (1956). *Usnea longissima* and *U. angulata* are of this type. However, the filamentous-dichotomous habit is considered to be derivations of the isotomic- and anisotomic-dichotomous types. Therefore, this category will not be used in this study.

Branches are results of repeatedly branched thallus from the base to the apices. Although branches are more or less tapering in all species, they can be divided into two types: gradually tapering or tapering only at the apices. In the former type, the branch diameter decreases gradually toward the branch apex. This pattern is typical of most species includ-

ing e.g. *U. subfloridana*. In the latter type, the branch diameter remains constant for most of the branch length, only tapering near the apices, as demonstrated in e.g. *U. shimadai*. Branch surfaces can be matt or glossy, depending on the coarseness of the cortex, as seen using scanning electron microscopy (Fig. 3). The shape of mature branches in transverse section is terete, ridged, or flattened (Fig. 4). Terete branches are common in most species. Ridged branches, caused by uneven growth of the cortex, are found in species such as *U. angulata* and *U. himantodes*. Flattened branches, however, have their origins in the axial development, as represented by *U. trichodeoides*. Although flattened and ridged branches are never inflated, terete branches can be divided into two types, inflated (e.g., *U. glabrata*) and uninflated (e.g., *U. diffracta*). Inflated branches are caused by a wide medulla and a thin cortex. Branches can be deformed by the presence of depressions in the cortex such as foveoles or transverse furrows, as reported by Clerc & Herrera-Campos (1997), such as occasionally seen in *U. nidifica*. However, as reported by Clerc (1998), correlation between the occurrence of foveoles or transverse furrows and the thickness of the cortex is variable and seems to be of relatively low taxonomic value, though it is sometimes useful for distinguishing species.

Lateral branches arise secondarily from main branches and can be distinguished from the main branches by differences in diameter at the ramification point. The juvenile stages of lateral branches are often referred to as fibrils (Fig. 5C, I). Fibrils are simple and short and are distinguished from lateral branches by their axis which is not anchored to the central axis of a main branch as lateral branches are. For this reason, fibrils are easily detached. Once the axis of a fibril reaches and is firmly anchored to the central axis of a main branch, the fibril can grow larger and eventually reaches a point where it is called a lateral branch (Fig. 5E, F, K, L). The diagnostic feature of the base of a lateral branch is that it is cylindrical, broadened, or constricted (Fig. 6). The cylindrical type is seen in many species, including *U. aciculifera* and *U. subfloridana*. The broadened base is common in *U. longissima* and *U. trichodeoides*, while the constricted base is usually seen in the species with inflated branches, such as *U. glabrata* and *U. subintumescens*.

Papillae are small projections lacking an axis and located mainly on the surface of thicker branches. Three types of papillae are recognized (Fig. 7), as reported by Swinscow & Krog (1979): 1) the hemispherical type, which are very short and are broader than tall (e.g., *U. pygmoidea*), 2) the verrucose type, which are moderate in size and equally tall as broad (e.g., *U. confusa*), and 3) the cylindrical type, which are conspicuous, and taller than broad (e.g., *U. subfloridana*). Although the number of papillae is variable, the presence or absence of papillae is useful for distinguishing species. Larger projections, which contain medullary tissue, are called tubercles by Swinscow & Krog (1979). However, the structure are treated here as papillae, since presence or absence of medullary tissue in papillae is variable in sorediate species. The occurrence of papillae in some sorediate species is correlated with the soralia morphology (Fig. 7).

Pseudocyphellae are openings on the surface of branches with exposed medullary tissue and lacking any asexual propagules. Pseudocyphellae sometimes look like maculae (described below), but pseudocyphellae lack even a thin cortex. Two types of pseudocyphellae are recognized in the genus *Usnea*: longitudinally or irregularly elongated

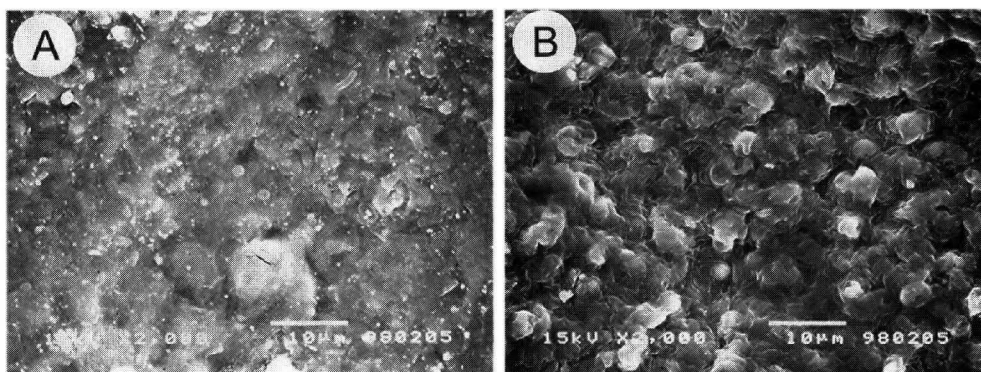


Fig. 3. Branch surface. A. Glossy surface [*Usnea pygmoidea* (Y. Ohmura 3144c)]. B. Matt surface [*U. subfloridana* (Y. Ohmura 3823)].

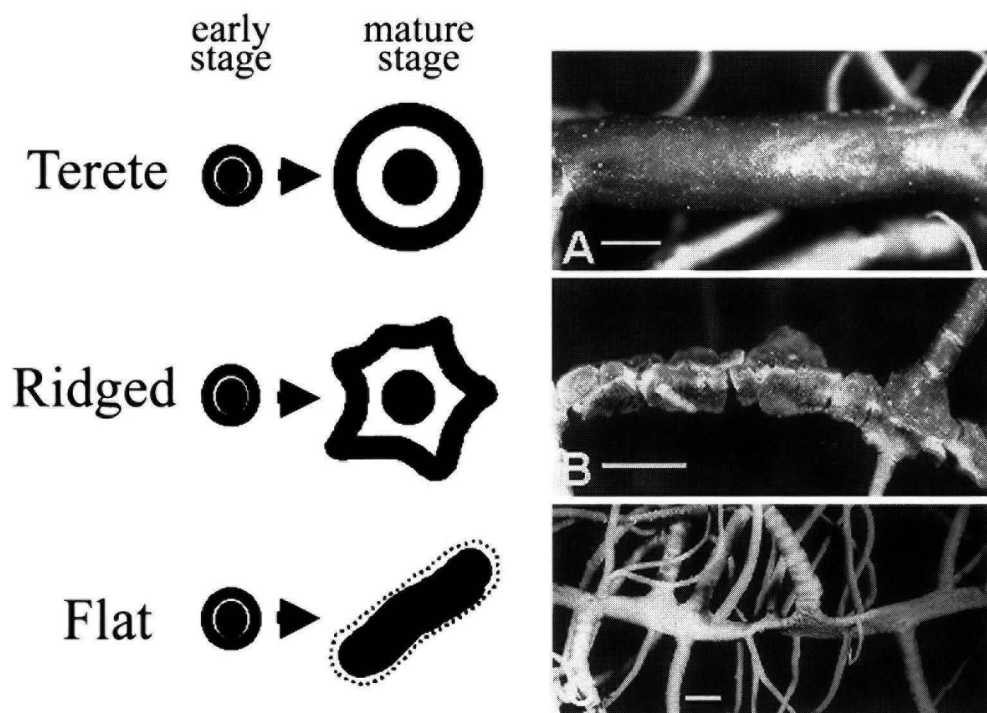


Fig. 4. Branch shape. Schematics are based on transverse sections of branches. A = terete type [*Usnea nidifica* (Y. Asahina 1201)], B = ridged type [*U. angulata* (Y. Asahina s.n.)], C = flat type [*U. trichodeoides* (S. Kurokawa 63024)]. Scales = 1 mm.

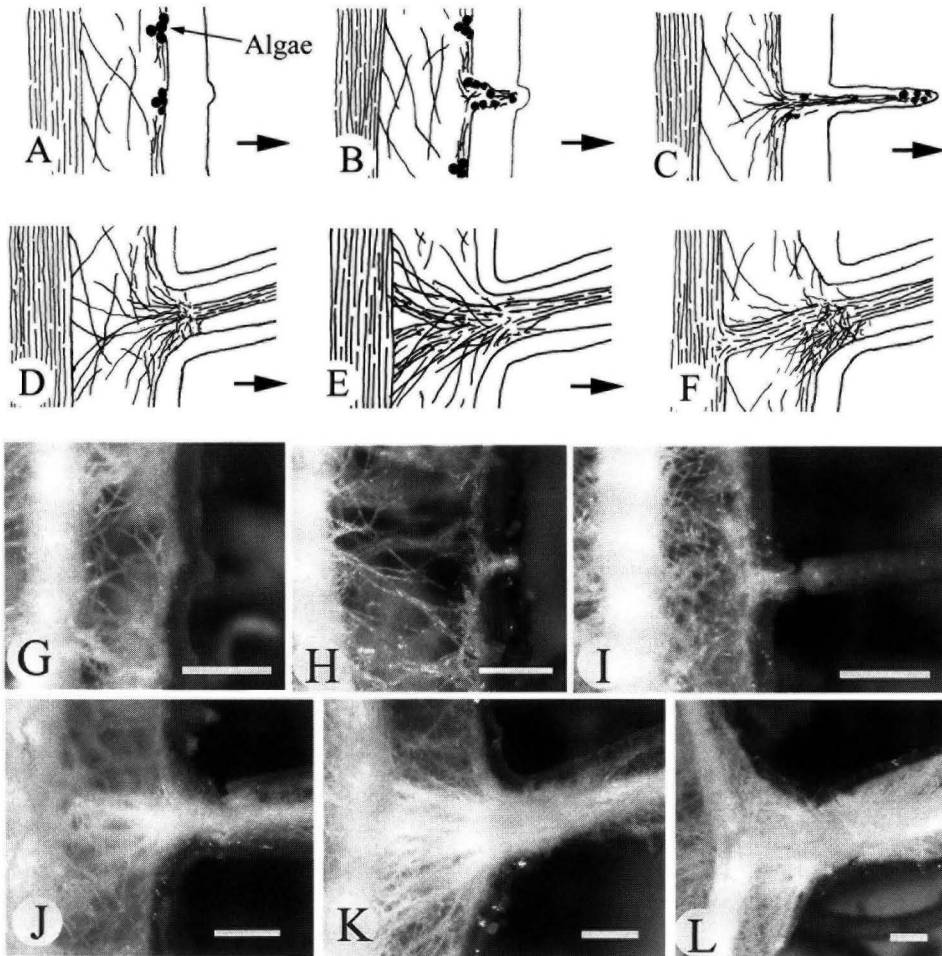


Fig. 5. Development of lateral branches [*Usnea pygmoidea* (H. Kashiwadani 13306)]. A, B, G, H = early stages of lateral branch which cannot be distinguished from papillae. C, I = fibril stage. D, J = intermediate stage between fibril and mature stage of a lateral branch. E, F, K, L = mature stage of a lateral branch. Scales: G–K = 500  $\mu\text{m}$ , L = 100  $\mu\text{m}$ .

pseudocypheallae and annular-pseudocypheallae. The former type is formed on the surface of branches (Fig. 8A), as defined by Clerc & Herrera-Campos (1997). This type is common in *U. himalayana*. The latter type resembles annular cracks (Fig. 9D–F), but the space between segments is swollen and surrounded by maculae (Fig. 8B, 9A–C). This type of pseudocypheallae differs from physical cracks, and seems to be formed due to unusual pressure from the medullary hyphae beneath the cortex (Fig. 9). The term “annular-pseudocypheallae” is a newly proposed term for this structure. This structure is one of the distinguishing features of subgenus *Dolichousnea*, such as *U. diffracta*.



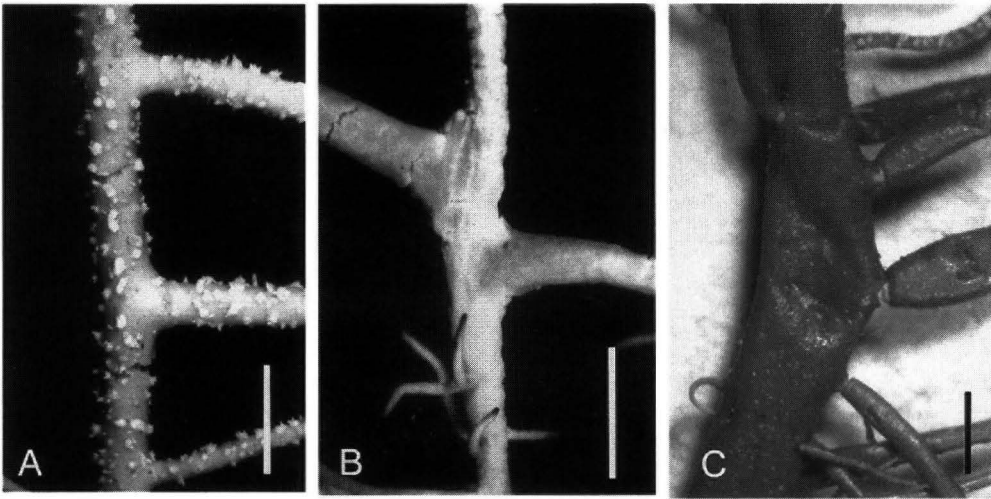


Fig. 6. Base of lateral branches. A. Cylindrical at base [*Usnea subfloridana* (Y. Ohmura 3823)]. B. Broadened at base [*U. longissima* (Y. Ohmura 2881)]. C. Constricted at base [*U. bismolliuscula* (M. Togashi s. n.)]. Scales = 1 mm.

Maculae are white blotches on the surface of branches where the cortex is thinner than in other areas. They differ from pseudocyphellae in that they are covered by cortical tissue. However, the surface of maculae is sometimes broken and connected to the medulla, which causes them to somewhat resemble pseudocyphellae. The fact that maculae sometimes give rise to soredia or isidiomorphs further documents that they are not pseudocyphellae. Shapes of maculae can be irregularly elongated (e.g., *U. merrillii*), punctiform (e.g., *U. pectinata*), or twisted (e.g., *U. longissima*) (Fig. 10).

Soralia in the genus *Usnea* are decorticated portions of the thallus where asexual propagules (i.e., soredia or isidiomorphs) develop. ["Isidiomorph," meaning on "isidia-like" structure, was defined by Clerc & Herrera-Campos (1997), as being functionally the same as isidia formed in other genera but different structurally since they are not continuous with the thallus cortex]. Soralia are formed mainly on lateral branches or thicker branches. The following four origins of soralia were reported by Clerc and his co-workers (Clerc 1987a, Clerc & Herrera-Campos 1997, Herrera-Campos et al. 1998): 1) tops of eroded papillae, 2) scars of detached fibrils, 3) cracks, and 4) cortex. All of these possibilities have been observed in Japanese and Taiwanese *Usnea*. Although the origins and morphology of soralia have been previously reported (Clerc 1987a, 1987b, Clerc & Herrera-Campos 1997, Herrera-Campos et al. 1998), the relationship between ontogeny and morphology of soralia have not been clarified. As a part of this study, this relationship was investigated. The results suggested that soralia morphology is correlated with 1) the points of origin, 2) types of papillae, and 3) the occurrence of soredia and/or isidiomorphs (Figs. 7, 11). When soralia arise from the tops of eroded papillae (Fig. 11A), they are punctiform to rounded (Fig. 11a), or they become confluent with one another to form elliptical or irregular

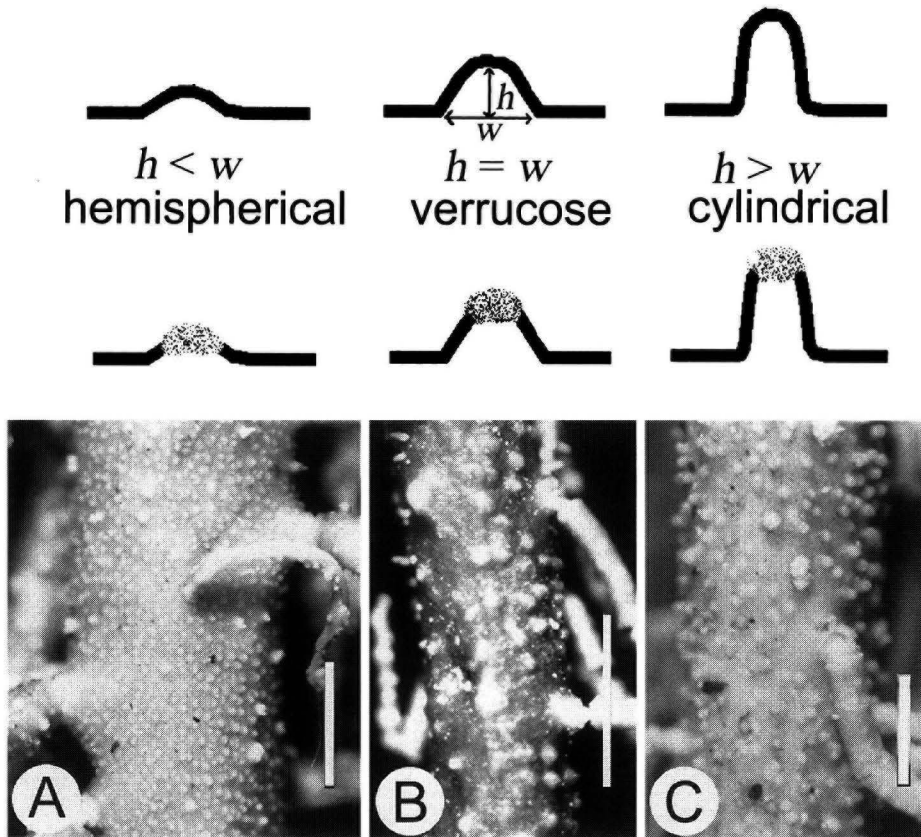


Fig. 7. Papilla types and their relationship with soralia. A. Hemispherical papillae [*Usnea pygmoidea* (Y. Ohmura 3144a)]. B. Verrucose papillae [*U. confusa* (Y. Asahina s.n.)]. C. Cylindrical papillae [*U. subfloridana* (Y. Ohmura 3823)]. Scales = 1 mm.

masses of soredia (Fig. 11b). Furthermore, soralia developing from hemispherical papillae or from an early stage of verrucose or cylindrical papillae tend to be sessile. On the other hand, soralia developing from verrucose or cylindrical papillae are usually slightly to distinctly stipitate (see Fig. 7). When soralia arise from scars of detached fibrils (Fig. 11B), they are punctiform and discrete. (Fig. 11c). Repeated regeneration of isidiomorphs from the area can increase the mass of soralia. These soralia are sessile to slightly stipitate. When they are stipitate, the stipe is originated in the left of broken fibrils. This type of soralia can be distinguished from punctiform soralia, originating from the top of eroded papillae, by the remnants of the axis. When soralia arise from cracks (Fig. 11c), the shape of the soralia is determined by the shape of the crack (Fig. 11d). The juvenile stages of this type of soralia resemble pseudocyphellae, but they produce soredia and/or isidiomorphs when mature. Soralia can also develop directly from the cortex caused by pressure from the growth of medullary hyphae and algae (Fig. 11D). In this case, the shape of the soralia is

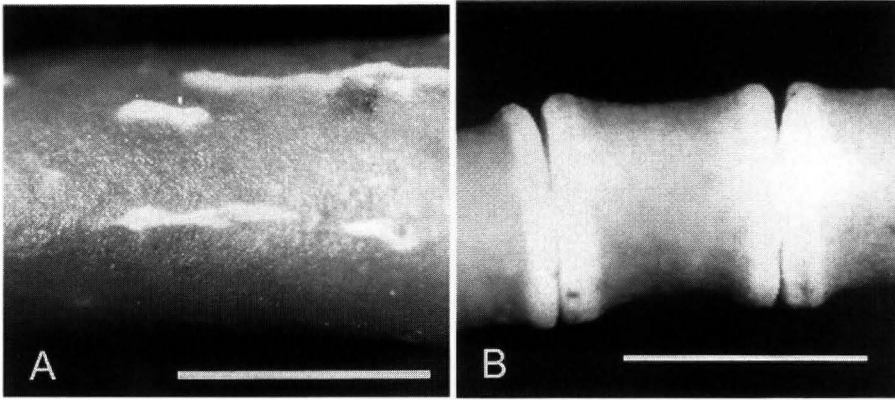


Fig. 8. Pseudocyphellae. A. Longitudinally elongated [*Usnea himalayana* (M. Togashi s.n.)]. B. Annular-pseudocyphellae which are surrounded by maculae [*U. diffracta* (Y. Ohmura 4508)]. Scales = 1 mm.

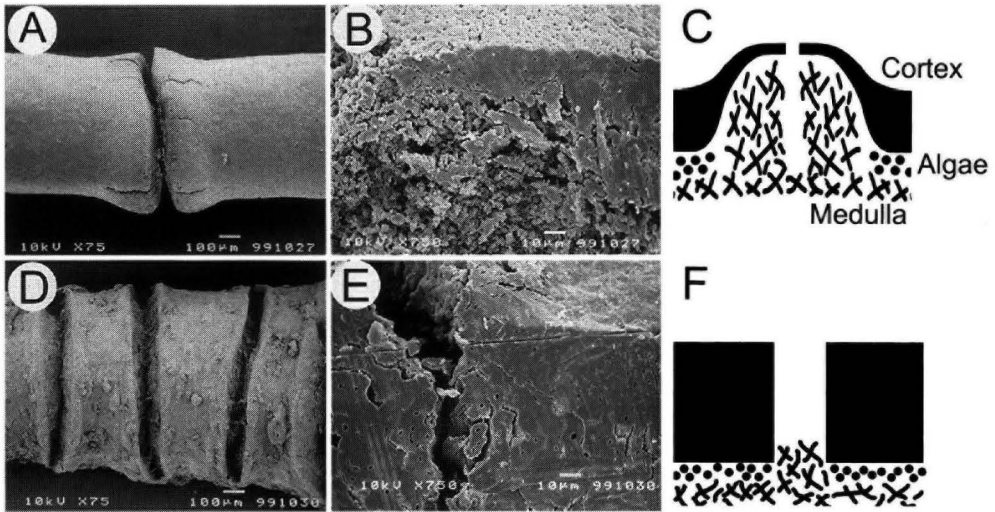


Fig. 9. An annular-pseudocyphella (A–C) and annular-cracks (D–F). A–C = *Usnea diffracta* (S. Kurokawa 67126). D–F = *U. pangiana* (M. Togashi s.n.). B, E = longitudinal sections.

initially rounded, but as they grow, they enlarge and converge to form irregular masses (Fig. 11e). They are usually slightly to distinctly stipitate, with reflexed cortical margins (Fig. 11e). The tops of soralia in the genus *Usnea* are either convex or concave. Soralia with granular soredia and a reflexed margin, are usually concave at the top (Fig. 11e). When isidiomorphs are produced by soralia, the soralia are usually convex at the top (Fig.

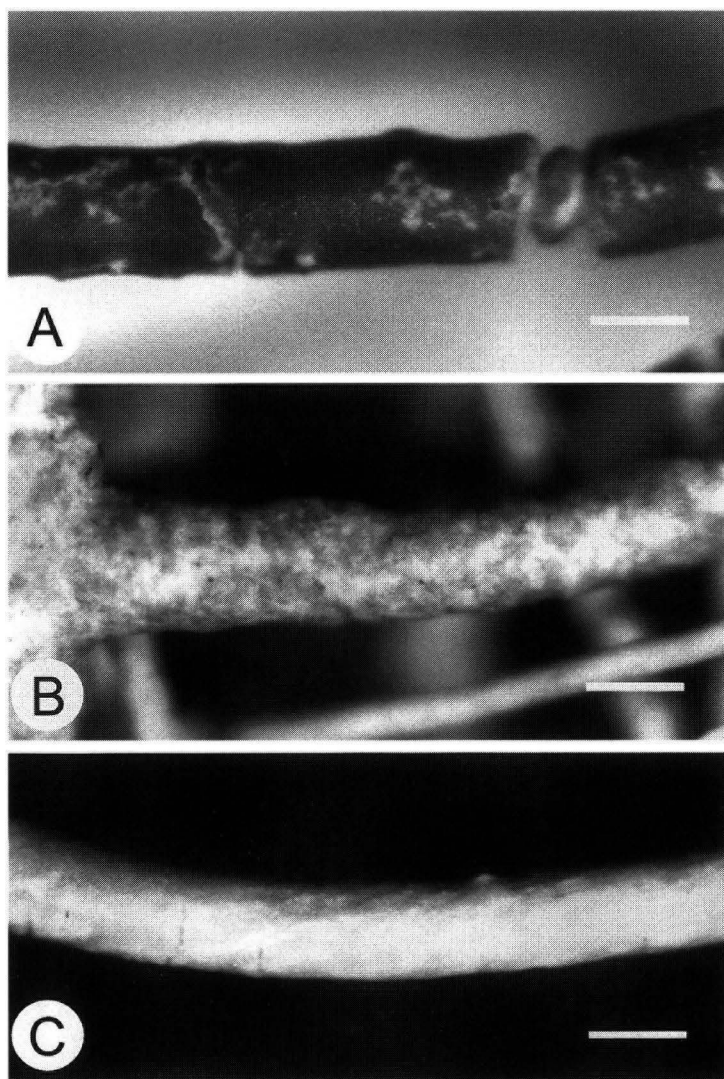


Fig. 10. Maculae on the surface of branches. A. Irregularly elongated [*Usnea merrillii* (Y. Asahina, S. Kurokawa & M. Nuno s.n.)]. B. Punctiform [*U. pectinata* (Y. Ohmura 2988)]. C. Twisted [*U. longissima* (Y. Ohmura 2881)]. Scales = 250  $\mu$ m.

11a-d). When isidiomorphs are formed, they range from sparse to abundant.

#### *Cortex*

The cortex is composed of radially or irregularly oriented hyphae which are firmly or loosely conglutinated. The following types of hyphae and plectenchymata are found.

Two types of cortical hyphae are found in *Usnea*: the leptodermatous and the pachy-

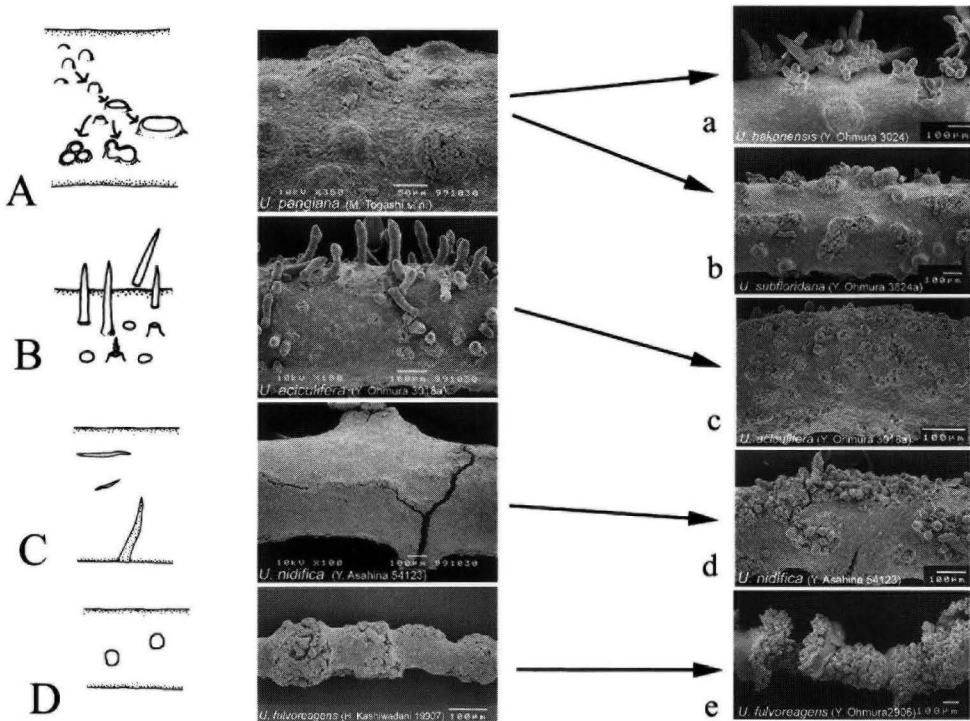


Fig. 11. Relationships between soralia origins and morphology. Origins: A. Soralia developed from the top of eroded papillae; B. Soralia developed from scars of detached fibrils; C. Soralia developed from cracks; D. Soralia directly developed from cortex. Shapes in plain view: a. rounded; b. irregular; c. punctiform; d. irregular; e. irregular. Shapes in elevation: a–d, convex with isidiomorphs; e, concave with granular soredia.

dermatous types. The hyphal diameter of both types is more or less larger than those of medullary hyphae. However, hyphae of the leptodermatous type increase mainly with regard to the mass of the lumina, and consequently, the cell walls are thin relative to the diameter of the lumina (Fig. 12A, E). This type of hyphae is found in the section *Usnea* (e.g., *U. subfloridana*). Hyphae of the pachydermatous type have distinctly thickened cell walls which are relatively thicker than the diameter of the lumina (Fig. 12 B–D, F–H), though the size of the lumina occasionally varies slightly with age. This hyphal type is common in the genus *Usnea*. It has been reported that these thick cell walls are caused by the secretion of a microfibrillar polysaccharide layer (Jacobs & Ahmadjian 1969, Peveling 1974).

Four types of cortical plectenchyma, *florida*-, *merrillii*-, *ceratina*- and *eumitria*-types (Fig. 12), are recognized with regard to following characteristics: the hyphal type; the degree of thickening of the cell wall and lumina of cortical hyphae compared with those of medullary hyphae; the degree of conglutination of adjacent hyphae; and the running direction of hyphae. In *florida*-type plectenchyma, the diameter of hyphal lumina are larger than

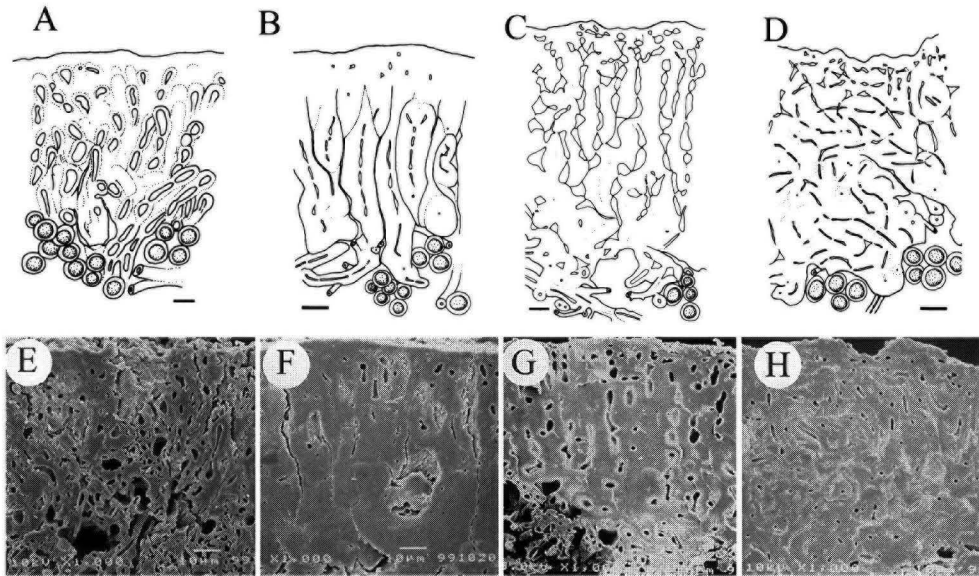


Fig. 12. Cortical types. A, E = *florida*-type plectenchyma [*Usnea glabrescens* (Y. Ohmura 3824b)]. B, F = *merrillii*-type plectenchyma [*U. pangiana* (S. Kurokawa s.n.)]. C, G = *ceratina*-type plectenchyma [C = *U. intumescens* (holotype), G = *U. ceratina* (H. Kashiwadani 8535)]. D, H = *baileyi*-type plectenchyma [*U. baileyi* (D = S. Kurokawa: Lich. Rar. Crit. Exs. 147, H = Y. Asahina F-281b)]. A–D: scales = 10  $\mu$ m.

the thickness of hyphal cell wall, and hyphae are loosely conglutinated each other (Fig. 12 A, E). This type is found in species belonging to sect. *Usnea* (e.g. *U. glabrescens*). The hyphae of *florida*-type are composed of leptodermatous hyphae, while following three types of cortical plectenchymata are composed of pachydermatous hyphae. In *merrillii*-type plectenchyma, hyphae are thickening only cell wall, and loosely conglutinated each other, which are distinctly separated at least 1/3 from medullary-side of the cortex (Fig. 12 B, F). The shape of the lumina is the same as that of the medullary hyphae, fusiform or oblong in transverse sections of the thallus. This type is found in species such as *U. merrillii*. In *ceratina*-type, hyphae are thickening both cell wall and lumina, and strongly conglutinated each other (Fig. 12 C, G). Consequently, interspaces between hyphae are indistinguishable, and only enlarged lumina are conspicuous. The shape of lumina is oblong or turbinate in transverse sections of the thallus. This type is found in species such as *U. ceratina*. *Merrillii*-type and *ceratina*-type differ in lumina size and degree of conglutination in mature specimens; however, lumina size and the degree of conglutination occasionally varies depending on the location within the thallus or the developmental stage of the specimen. Therefore, *merrillii*-type and *ceratina*-type are considered to be closely related. In *eumitria*-type, the thickness of hyphal cell wall and lumina are almost the same as those of medullary hyphae, and hyphae are loosely conglutinated each other (Fig. 12D, H). This type is found in species such as *U. baileyi*. The running direction of hyphae is basically radial in *florida*-

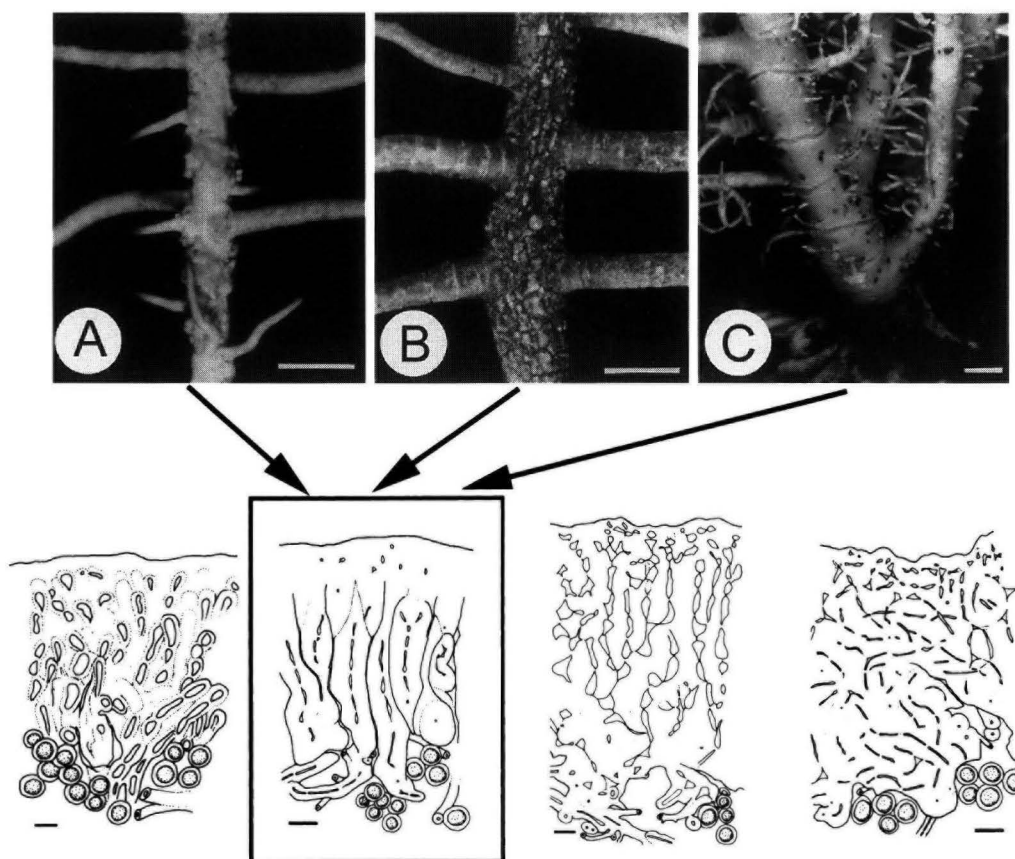


Fig. 13. *Merrillii*-type plectenchyma and its related morphology. A. Decorticate [*Usnea longissima* (Y. Ohmura 3808)]. B. Areolate cracks [*U. trichodeoides* (Y. Asahina s.n.)]. C. Annular-cracks near the base [*U. pangiana* (Y. Ohmura 3132)]. Scales: A–C = 0.5 mm, others = 10  $\mu$ m.

*merrillii*- and *ceratina*-types. Those of *eumitria*-type, however, is irregular.

The features of each type appear in the mature stage of the species, though all types show *merrillii*-type in their early stage of ontogeny. Cortex structures are stable in species and/or infrageneric group in whether fresh or old specimens. Therefore, they are considered to have taxonomic importance especially for the aspect of systematics of the genus *Usnea*.

It should be noted that the occurrence of frequent cracks and/or decortication are correlated with *merrillii*-type plectenchyma in which the hyphae are loosely conglutinated and partially or mostly separated from each other (Fig. 13). For example, *U. pangiana* usually has distinct annular cracks, especially near the base of the thallus. The cortex of this species is composed of *merrillii*-type plectenchyma, and the hyphae are distinctly separated

from each other. Similarly, branches of *U. longissima* and related species are frequently decorticated because of loosely conglutinated and separated cortical hyphae. Although the frequency of cracks or the degree of decortication is useful for distinguishing species, these characters should be used carefully when noting differences in cortical plectenchymata and hyphae.

The separated hyphae found in *merrillii*-type plectenchyma coincide with the so-called "turgid medullary hyphae" reported by Asahina (1956). Asahina (1955) and Awasthi (1986) reported the occurrence of a double-layered cortex in species such as *U. thomsonii*. The cortex was found to be composed of *ceratina*-type plectenchyma in the upper layer and prosoplectenchyma in the lower layer. However, the lower layer is composed of conglutinated medullary hyphae not cortical hyphae, and the thickness of this layer is variable. Therefore, the double-layered cortex is included as a variation of *ceratina*-type in this study, although it is useful for distinguishing species. Awasthi (1986) reported three types of cortical plectenchyma from Indian *Usnea*, including prosoplectenchyma, palisade-like plectenchyma, and semi-prosoplectenchyma. These three types were distinguished by the degree of separation of hyphae and the lumina size in tangential section. However, these features are variable, as mentioned above. Prosoplectenchyma (Awasthi 1986) can be separated into the *ceratina*-type and *baileyi*-type, and both palisade-like plectenchyma and semi-prosoplectenchyma (Awasthi 1986) belong to the *merrillii*-type plectenchyma described in the present study. Tavares (1987) reported that differences in lumina size were useful for distinguishing certain species of short and apotheciate *Usnea* from eastern North America. Although lumina size is useful as a taxonomic feature, the absolute value of lumina size is variable and difficult to determine.

When the cortex is cracked or eroded, the secondary cortex is regenerated on an exposed axis in certain species. Two types of secondary cortex are recognized: the areolate secondary cortex in *U. trichodeoides* and the globe-shaped secondary cortex in *U. merrillii*.

Pigmentation of the cortex is pale yellow or red. The pale yellow color is caused by usnic acid, while the red is caused by an unknown red pigment. The red pigment is secreted into the cell walls of hyphae in *U. rubicunda* and *U. rubrotincta*. It is also partially secreted in the cortex of *U. dorogawensis*, but mostly in the medullary hyphae immediately beneath the cortex.

### *Medulla*

The medulla, which includes a thin algal layer composed of algal cells of the genus *Trebouxia*, is a space between the cortex and the axis. It is dense or lax according to whether the hyphae are densely or loosely interwoven. Although narrow medullae are always dense, broad medullae are lax or dense. Hyphae of the medulla can be conglutinated to form bundles, lumps, or a layer, especially near the algal layer. Layers of conglutinated medullary hyphae can be a component of a double-layered cortex (see the section above on the cortex).

The pigmentation of medulla is strawberry pink or red. Two types of pigmentation in the medulla are recognized: one is caused by the accumulation of bisxanthone (such as eumitrins) outside of the cell wall of the hyphae, as seen in *U. baileyi*, *U. ceratina* and *U. mu-*



*tabilis*, while the other is caused by an unknown red pigment secreted into the cell wall of the hyphae below the cortex, as seen in *U. dorogawensis*. The location of red pigment in medulla is near the cortex (*U. baileyi*, *U. ceratina* and *U. dorogawensis*), or near the axis (*U. mutabilis*), as reported by Swinscow & Krog (1979).

#### *Axis*

The axis is a central cartilaginous strand running throughout the thallus. It is composed of prosoplectenchyma in which hyphae are conglutinated and arranged longitudinally. Two types of axes are recognized: fistulose and solid. The fistulose axis has a central hole running throughout the axis. This type is found in *U. baileyi*. The solid axis lacks a continuous hole; however, it may rarely occur a partly fistulate or dilacerate axis in older thalli. An accumulation of salazinic acid in a loose axis can make a cribose form in the transverse section, which is considered a variation of the solid type. This cribose form is found in *U. merrillii*.

#### *The ratio of the cortex, medulla, and axis*

Using the numerical ratio of the cortex, medulla and axis was first adopted as "RS value" by Asahina (1954). These values are useful for explaining subjective words such as narrow, broad, thick or thin. The cortex, medulla and axis were measured in cross sections of several parts of the thallus, however, this was a somewhat impractical method for statistical treatment. Clerc (1984) subsequently improved the technique by taking measurements along longitudinal sections. This approach yielded results that could be treated statistically. Following the method of Clerc (1984), the ratio of the cortex, medulla and axis in each species was determined. As a result, most species have a certain range of ratios, though some species, especially those with inflated branches, showed highly variable ratios (Table. 1).

#### *Apothecia, Asci, and Spores*

Apothecia are lecanorine and often have well developed fibrils. Asci are clavate containing eight spores of the *Lecanora*-type (Baral 1987). Ascospores are simple, colorless, and elliptic. The above features are genetically uniform throughout the genus and are not particularly useful for distinguishing between species. However, location and shape of apothecia, disc color, the presence of a white rim around the disc, the occurrence of pruina on the disc, the thickness of the hymenium and hypothecium, and spore size seem to be stable features of taxonomic importance. Location of apothecia is mostly lateral on branches, as reported by Kurokawa (1981). However, subterminal apothecia occur in some species such as *U. fuscorubens*. Apothecia are cup-shaped, flat, or sinuose. Discs are gray, pale yellow, or brown. The white rim around the disc is caused by the exposed proper exciple. This structure is also well known in the genus *Lobaria* (Yoshimura 1971). The disc may be covered with cineraceous pruina or epruinose. The thickness of the hymenium is (20)–50–70–(90)  $\mu\text{m}$ , depending on species. On the other hand, thickness of the hypothecium is a rather important feature for distinguishing subgenus *Dolichousnea* from other subgenera. With members of the subgenera *Usnea* and *Eumitria* ranging over (20)–30–60–(90)  $\mu\text{m}$ , while those of the subgenus *Dolichousnea* are generally thicker ranging over (70)–100–160–(200)  $\mu\text{m}$ . Spore size is ranging over (5.2)–8.3–10.3–(14)  $\times$  (3.5)–5.0–6.3–(9.0)  $\mu\text{m}$ , and a

Table 1. The ratio of thickness of the cortex, medulla and axis (CMA). Mean (italic), standard deviation and extreme values (in parenthesis) are shown,  $n$  = total number of samples examined.

Species	Cortex (% of radius)	Medulla (% of radius)	Axis (% of diameter)	Diameter of branch (mm)	$n$
<i>U. aciculifera</i>	(5.0)-6.7-9.2-12-(16)	(15)-19-23-27-(31)	(18)-29-36-43-(57)	(0.5)-0.6-0.7-0.9-(1.3)	61
<i>U. angulata</i>	(5.6)-9.2-12-15-(17)	(6.7)-8.6-14-19-(28)	(25)-40-49-57-(61)	(0.3)-0.4-0.5-0.6-(0.7)	25
<i>U. baileyi</i>	(3.3)-4.9-6.6-8.3-(9.2)	(3.0)-3.2-5.3-7.4-(12)	(58)-70-76-82-(86)	(0.8)-1.0-1.3-1.6-(1.9)	29
<i>U. bismolluscula</i>	(2.0)-2.8-4.1-5.4-(9.1)	(30)-32-35-38-(41)	(13)-17-21-25-(31)	(0.6)-0.8-1.1-1.3-(1.5)	41
<i>U. ceratina</i>	(5.3)-5.8-7.4-9-(10)	(20)-23-26-29-(29)	(29)-29-34-39-(46)	(0.6)-0.7-0.8-0.9-(1.0)	10
<i>U. confusa</i>	(3.4)-4.2-5.5-6.8-(9.3)	(28)-32-34-37-(37)	(15)-19-22-26-(31)	(0.5)-0.7-1.0-1.3-(1.8)	25
<i>U. dassea</i>	(3.3)-4.2-6.1-8.0-(12)	(19)-26-31-36-(41)	(11)-17-26-35-(52)	(0.7)-0.8-1.1-1.4-(1.9)	28
<i>U. dendritica</i>	(7.3)-9.1-(11)	(17)-25-(29)	(24)-32-(44)	(1.0)-1.2-(1.5)	6
<i>U. diffracta</i>	(4.8)-6.6-9.2-12-(15)	(15)-20-24-28-(33)	(21)-27-34-42-(55)	(4.8)-6.6-9.2-12-(15)	21
<i>U. dorogwensis</i>	(3.2)-3.9-5.3-6.7-(8.3)	(32)-33-35-37-(38)	(15)-17-19-21-(23)	(0.6)-0.7-0.9-1.2-(1.3)	12
<i>U. filipendula</i>	(8.9)-9.5-(11)	(20)-23-(25)	(32)-36-(39)	(0.6)-0.7-(1.1)	3
<i>U. florida</i>	(8.9)-11-(13)	(13)-16-(17)	(42)-46-(48)	(1.1)-1.2-(1.3)	3
<i>U. fragilesceus</i>	(3.4)-5.1-(6.4)	(29)-33-(38)	(17)-23-(28)	(0.8)-1.0-(1.2)	6
<i>U. fulvorenans</i>	(7.4)-9.2-10-12-(13)	(14)-18-22-26-(28)	(24)-28-36-44-(51)	(0.7)-0.9-1.1-1.3-(1.4)	11
<i>U. fuscorubens</i>	(3.2)-5.2-(9)	(30)-34-(38)	(17)-22-(29)	(0.9)-1.3-(1.8)	9
<i>U. glabrata</i>	(3.4)-3.9-5.6-7.3-(10)	(25)-28-32-37-(39)	(13)-17-24-31-(34)	(0.4)-0.5-0.9-1.3-(1.8)	13
<i>U. glabrescens</i>	(8.7)-11-(14)	(18)-21-(25)	(31)-37-(46)	(1.0)-1.2-(1.3)	3
<i>U. nakonensis</i>	(6.0)-7.9-9.6-11.3-(13)	(14)-21-25-29-(32)	(18)-24-31-38-(52)	(0.4)-0.6-0.9-1.2-(1.5)	24
<i>U. hesperia</i>	(5.9)-11-(16)	(12)-13-(15)	(42)-52-(64)	(0.3)-0.5-(0.7)	4
<i>U. himalayana</i>	(3.8)-4.2-5.2-6.2-(7.4)	(28)-33-36-39-(40)	(12)-12-18-24-(33)	(0.4)-0.4-0.8-1.2-(1.8)	12
<i>U. himantodes</i>	(8.6)-14-(20)	(7.4)-15-(19)	(33)-41-(46)	(0.5)-0.6-(0.8)	4
<i>U. intumescens</i>	(2.6)-3.7-5.0-6.3-(7.1)	(24)-28-32-36-(38)	(15)-17-25-33-(40)	(0.9)-1.0-1.3-1.6-(1.8)	13
<i>U. koyana</i>	(9.2)-12-(14)	(24)-28-(35)	(11)-21-(29)	(1.1)-1.4-(1.8)	9
<i>U. longissima</i>	(6.7)-7.7-10-12-(16)	(6.7)-11-15-19-(20)	(37)-40-50-60-(69)	(0.3)-0.4-0.5-0.6-(0.8)	15
<i>U. masudana</i>	3.6	3.6	21	1.7	1
<i>U. merrillii</i>	(6.8)-8.6-12-15.4-(20)	(16)-18-22-26-(27)	(26)-29-34-39-(42)	(0.3)-0.4-0.5-0.6-(0.8)	16
<i>U. mutabilis</i>	(4.4)-5.9-7.8-9.7-(12)	(22)-25-27-30-(31)	(25)-27-30-33-(36)	(0.5)-0.6-0.8-1.0-(1.3)	23
<i>U. nidifica</i>	(1.6)-2.6-4.2-5.8-(7.0)	(25)-30-35-40-(45)	(5.2)-14-22-30-(41)	(0.7)-0.8-1.4-2.0-(3.1)	27
<i>U. nipparensis</i>	(5.9)-7.1-9.7-12-(14)	(18)-18-23-28-(32)	(20)-26-35-44-(47)	(0.9)-0.9-1.2-1.5-(1.7)	10
<i>U. orientalis</i>	(2.3)-3.4-(5.1)	(32)-35-(40)	(21)-25-34-(43)	(1.0)-1.4-(2.6)	4
<i>U. pangiana</i>	(5.2)-6.3-9.2-12-(18)	(6.3)-18-24-30-(33)	(21)-25-34-43-(57)	(0.6)-0.8-1.0-1.2-(1.3)	21
<i>U. pectinata</i>	(9.4)-12-15-18-(19)	(6.6)-7.6-9.7-12-(15)	(40)-45-57-(63)	(0.3)-0.3-0.4-0.5-(0.5)	17
<i>U. pseudogatai</i>	(4.7)-5.1-(5.5)	(27)-32-(34)	(22)-27-(36)	(1.0)-1.1-(1.1)	3
<i>U. pygmaidea</i>	(3.1)-4.3-5.7-7.1-(8.1)	(26)-29-33-37-(40)	(13)-16-22-28-(33)	(0.6)-0.7-1.0-1.3-(1.6)	18
<i>U. rubicunda</i>	(5.6)-8.7-11-13-(15)	(13)-15-20-24-(28)	(24)-31-39-46-(57)	(0.7)-0.8-1.0-1.2-(1.5)	25
<i>U. rubrotincta</i>	(6.8)-8.9-11-13-(16)	(13)-17-20-24-(27)	(22)-30-37-44-(52)	(0.5)-0.7-0.9-1.1-(1.4)	30
<i>U. shimadai</i>	(4.8)-6.0-(7.1)	(16)-24-(31)	(24)-41-(58)	(0.5)-0.9-(1.3)	2
<i>U. sinensis</i>	(5.8)-8.1-10-13-(17)	(14)-16-20-25-(31)	(28)-32-39-45-(50)	(5.8)-8.1-10-13-(17)	18
<i>U. subfloridana</i>	(7.3)-9.0-11-13-(16)	(9.1)-14-18-22-(27)	(27)-34-41-48-(58)	(0.5)-0.8-1.0-1.2-(1.6)	80
<i>U. subintumescens</i>	(4.1)-5.2-(7.6)	(31)-35-(37)	(18)-20-(23)	(0.9)-1.3-(1.7)	8
<i>U. trichodeoides</i>	(2.1)-4.6-10-15-(21)	(4.0)-5.2-9.9-15-(20)	(37)-43-60-77-(85)	(16)-20-28-36-(45)	23
<i>U. wasmuthii</i>	(6.5)-9.0-11-13-(17)	(7.3)-14-18-22-(29)	(29)-37-43-49-(57)	(0.7)-0.8-1.0-1.2-(1.8)	42
<i>U. yakushimensis</i>	(8.3)-11-(14)	(9.1)-17-(22)	(31)-45-(64)	(0.7)-0.8-(1.0)	5

useful taxonomic characteristic for distinguishing certain species in the genus *Usnea* as reported by Clerc (1984).

### III. CHEMISTRY

#### Materials and Methods

The chemistry of all specimens (except for type specimens of Acharius or Linnaeus) were studied using thin layer chromatography (TLC) (Culberson & Johnson 1982), or by microchemical crystal tests (MCT) (Asahina 1956). Only solvent B system (hexane : methyl *tert.*-butyl ether : formic acid = 140 : 72 : 18) was used for TLC analysis.

Iodine tests were also performed on longitudinal axial sections with 0.5% Lugol's iodine solution. Results for iodine tests are shown in species description as "I -" for a negative reaction or "I + blue" for a positive reaction.

#### Results

Overall the following substances were detected using TLC:

1. Acetyl-polymalonyl pathway

*Dibenzofuran*: usnic acid.

*Orcinol depside*: evernic, lecanoric acids.

$\beta$ -orcinol depside: atranorin, baeomycesic, barbatic, 4-*O*-demethylbarbatic, diffractaic, squamatic, thamnolic acids.

*Orcinol depsidone*: lobaric acid.

$\beta$ -orcinol depsidone: constictic, fumarprotocetraric, galbinic, menegazziaic, norstictic, protocetraric, psoromic, 2'-*O*-demethylpsoromic (= conpsoromic), salazinic, stictic, succinprotocetraric acids.

*Bisxanthone*: eumitrin A<sub>1</sub>, eumitrin A<sub>2</sub>, eumitrin B.

*Aliphatic acids*: bourgeanic, caperatic, protolichesterinic acids, murolic acid complex, and unknown fatty acid complex (as "type I" in Asahina 1967c).

*Unidentified substances*: US1-6. R<sub>f</sub> of US<sub>n</sub>/R<sub>f</sub> of norstictic acid, R<sub>f</sub> of atranorin (spot coloration with H<sub>2</sub>SO<sub>4</sub> and heat, UV<sub>254 nm</sub>, UV<sub>366 nm</sub>, pigmentation, etc) = US1, 5/33, 85 (lemon yellow, UV<sub>254 nm</sub> + visible, UV<sub>366 nm</sub> -, no pigmentation, repelling water on TLC plate); US2, 9/33, 85 (lemon yellow, UV<sub>254 nm</sub> + visible, UV<sub>366 nm</sub> -, no pigmentation, repelling water on TLC plate); US3, 7/33, 88 (yellow, UV<sub>254 nm</sub> + visible, UV<sub>366 nm</sub> -, no pigmentation); US4, 16/33, 88 (purple, UV<sub>254 nm</sub> + visible, UV<sub>366 nm</sub> -, no pigmentation); US5, 14/23, 77 (pale, UV<sub>254 nm</sub> + visible, UV<sub>366 nm</sub> + quench, red pigmentation); US6, 35/28, 85 (pale yellow, UV<sub>254 nm</sub> + visible, UV<sub>366 nm</sub> -, no pigmentation); US7, 28/35, 74 (pale brown, UV<sub>254 nm</sub> + visible, UV<sub>366 nm</sub> -, no pigmentation; as "UF1, Ohmura et al. 2000); US8, 45/35, 74 (brown, UV<sub>254 nm</sub> + visible, UV<sub>366 nm</sub> -, no pigmentation; as "UF2", Ohmura et al. 2000).

2. Mevalonic acid pathway

*Terpenoid*: zeorin.

3. Sikkim acid pathway

Not detected.

As in most lichen species with pale yellow thalli, usnic acid is constantly produced in the cortex. This applies to all specimens tested during this study.

Atranorin is occasionally demonstrated in some *Usnea* spp. such as *U. trichodeoides* (Table 2). Although it is well known as another cortical substance in other lichen species, atranorin in *Usnea* spp. may be produced in the medulla as an intermediate metabolite of e.g. fumarprotocetraric acid (Culberson 1986). Therefore, atranorin is treated as an accessory chemical in this study.

Medullary substances show much more variety than those of the cortex.  $\beta$ -orcinol

depsides or  $\beta$ -orcinol depsidones were commonly detected, although orcinol depsides, an orcinol depsidone, bisxanthenes, aliphatic acids, a terpenoid, and other unidentified substances were also detected.

With regard to depsides, the following four biosynthetically different groups are considered: (1) diffractaic acid and related substances, (2) barbatic and 4-*O*-demethylbarbatic acids, (3) thamnolic and/or squamatic acids, and (4) evernic and lecanoric acids. Diffractaic acid basically follows barbatic, 4-*O*-demethylbarbatic, baeomycesic, and squamatic acids. According to Yoshimura & Kurokawa (1980) and Yoshimura et al. (1992), the *O*-methyl of diffractaic acid is partially substituted by H<sub>2</sub>O to form barbatic acid (= 2-*O*-demethyldiffractaic acid). Similarly the *O*-methyl of barbatic acid can be substituted by H<sub>2</sub>O to form a 4-*O*-demethylbarbatic acid. This kind of *O*-methylation substitution pattern is well known not only in lichenized fungi but also in non-lichenized fungi (Culberson 1969). Oxidation of the methyl radical of barbatic acid forms baeomycesic acid, and further oxidation of the radical of baeomycesic acid forms squamatic acid. Therefore, these substances are closely related to each other biosynthetically as well as chemically. The presence or absence of one or a few of them can have taxonomic value, even though the concentration of each substance is often variable. The biosynthetic and/or chemical relationships between squamatic and thamnolic acids have not yet been carefully studied. However, they are considered to be biosynthetically closely related substances (Culberson 1969). They often replace one another in paired races in lichens (Fiscus 1972). Although groups 1–3 belong to the  $\beta$ -orcinol depsides, the fourth group, the evernic acid group, belongs to the orcinol depsides. The orcinol depsides and  $\beta$ -orcinol depsides are similar in many ways, but differ in their structure and especially in their distribution among lichen species. It is generally thought that the orcinol and  $\beta$ -orcinol compounds are biosynthetically different (Culberson 1969).

With regard to depsidones, the following eight biosynthetically different groups are considered: (1) salazinic acid, (2) galbinic acid, (3) stictic acid, (4) norstictic acid, (5) protocetraric acid, (6) fumarprotocetraric acid, (7) psoromic acid, and (8) lobaric acid groups. Salazinic acid usually follows protocetraric, constictic, and/or norstictic acids, which have very similar chemical structures. The *O*-methyl of constictic acid (= 4-*O*-methylsalazinic acid) can be substituted with H<sub>2</sub>O to form salazinic acid. Hydrolysis of the ester bond in salazinic acid can form protocetraric acid. In addition, the 8'-position hydroxyl radical of salazinic acid can be cut by dehydration to form norstictic acid. The galbinic acid group is closely related with the salazinic acid group, since the 8'-position ester bond of galbinic acid can be easily cut by hydrolysis, which results in the formation of salazinic acid from galbinic acid. The stictic acid group usually follows constictic, menegazziaic, and norstictic acids. The 8'-position hydroxyl radical of constictic acid can be cut by dehydration to form stictic acid. The 3-position aldehyde of stictic acid can be substituted with a hydroxyl radical to form menegazziaic acid. In addition, the *O*-methyl of stictic acid can be substituted with H<sub>2</sub>O to form norstictic acid. The fourth and fifth groups, which contain no other depsidone except for norstictic or protocetraric acids, can be derived from groups 1–3. The sixth group includes fumarprotocetraric and succinprotocetraric acid, which have similar chemical structures, differing only in the bond pattern between the 2''- and 3''-positions.

The seventh group includes psoromic and 2'-*O*-demethylpsoromic acids, which are related in their *O*-methylation pattern. Although groups 1–7 belong to the  $\beta$ -orcinol depsidones, the eighth group (lobaric acid) belongs to the orcinol depsidones. They are considered a biosynthetically different group, as in the case of the orcinol depsides such as evernic acid.

The presence of bisxanthone, eumitrin A<sub>1</sub>, A<sub>2</sub>, and/or B, which belong to a different chemical group from the depsides or depsidones, is very useful for distinguishing species, since they exhibit a red color in the medulla.

Aliphatic acids are also useful for distinguishing species. However, they vary greatly in quantity, and are sometimes difficult to detect in low concentration.

Zeorin is synthesized through the mevalonic acid pathway, while depsides, depsidones, bisxanthone, and aliphatic acids are produced through the acetyl-polymalonyl pathway. This substance is found in *U. baileyi* and *U. fulvorangeans*, but these two species are distantly related morphologically as well as genetically (Fig. 14). Therefore, the occurrence of zeorin in the genus *Usnea* is considered to be a useful character only at the species level.

Besides the substances mentioned above, eight unidentified chemicals commonly occur on TLC plates with certain species. Although several other unidentified substances occur rarely, they do not seem to have any specific taxonomic value because they do not correlate with any morphological or ecological features. The characteristics of the eight common unidentified substances are as follows: US1 is R<sub>f</sub> class 2, lower than salazinic acid, repelling water on the TLC plate and exhibiting a lemon yellow color after heating; US2 is similar to US1, except that it is R<sub>f</sub> class 2, higher than salazinic acid; US3 is R<sub>f</sub> class 2 and yellow and always appears with fumarprotocetraric acid; US4 is R<sub>f</sub> class 3, lower than succinprotocetraric acid and closely related to protocetraric acid, judging from its grayish purple color and R<sub>f</sub> value; US5 is R<sub>f</sub> class 3, lower than eumitrin A<sub>1</sub>, red pigmentation; US6 is R<sub>f</sub> class 4–5, pale yellow, and always appears with lobaric acid; US7 (R<sub>f</sub> class 3–4) and US8 (R<sub>f</sub> class 5) are only detected from *U. fragilescens* collected in the present area (see Ohmura et al. 2000).

Twenty-four of 43 species have constant chemical constituents, but the remaining 19 species produce different chemical substances which are closely or distantly related biosynthetically within a single species (Table 2). In the latter case, no morphological or ecological differences were rooted among individuals of a species. This suggests that chemical differences do not necessarily warrant species designation. Therefore, in this study chemical differences found in the 19 species are treated as chemical races.

The iodine reaction of the axis can be either positive or negative. A positive reaction is blue or dirty blue, as observed in the subgenus *Dolichousnea* or rarely in *U. himantodes* and *U. pectinata*, but species belonging to the subgenus *Usnea* show a negative reaction. Although a positive iodine reaction in lichens is caused by various polysaccharides or rarely lichen substances such as stictic acid (Common 1991), the nature of this reaction in the axis of *Usnea* has not been clear. *Usnea himantodes* and *U. pectinata* occasionally accumulate abundant stictic acid in the axis. Therefore, the positive iodine reaction for these species is thought to be caused by stictic acid, while the iodine reaction in species of the subgenus *Dolichousnea* is likely caused by a polysaccharide, since these taxa do not contain stictic acid.

Table 2. Frequency (%) of lichen substances in each species. Usn = usnic acid, Nor = norstictic acid, Sal = salazinic acid, PrC = protocetraric acid, CSt = constictic acid, Sti = stictic acid, Men = menegazziaic acid, ScP = succinprotocetraric acid, Fum = fumarprotocetraric acid, Gal = galbinic acid, dPs = 2'-O-demethylpsoromic acid, Pso = psoromic acid, Lob = lobaric acid, Thm = thamnolic acid, Squ = squamatic acid, Bae = baeomycesic acid, Dif = diffractaic acid, Bar = barbatic acid, dBr = 4-O-demethylbarbatic

Species	Dibenzofuran	Depsidone													Depside								
	Usn	Nor	Sal	PrC	CSt	Sti	Men	ScP	Fum	Gal	dPs	Pso	Lob	Atr	Thm	Squ	Bae	Dif	Bar	dBr	Eve	Lec	
<i>U. aciculifera</i>	100	100			100	100	100							13									
<i>U. angulata</i>	100	100																					
<i>U. baileyi</i> CR1	100			77	66									2					9	9			
<i>U. baileyi</i> CR2	100													17	100				17	17			
<i>U. bismolliuscula</i> CR1	100	100				100	100	100						7		4							
<i>U. bismolliuscula</i> CR2	100														100								
<i>U. ceratina</i> CR1	100																100	100	100	100			
<i>U. ceratina</i> CR2	100																				100	100	
<i>U. confusa</i> CR1	100			100	100	57								17									
<i>U. confusa</i> CR2	100				100																		
<i>U. dasaea</i> CR1	100		100	100	30									13									
<i>U. dasaea</i> CR2	100		100	100							100												
<i>U. dasaea</i> CR3	100		100	100							100	100	100										
<i>U. dendritica</i>	100	100	100	100																	100	100	
<i>U. diffracta</i> CR1	100													1		100	100	100	100				
<i>U. diffracta</i> CR2	100			100												100	100	100	100				
<i>U. diffracta</i> CR3	100															100	100			100	100		
<i>U. diffracta</i> CR4	100																						
<i>U. dorogawensis</i>	100	100				80	100						100	10		10							
<i>U. filipendula</i>	100		100	100																			
<i>U. florida</i>	100														100								
<i>U. fragilescens</i>	100		100	100																	100	100	
<i>U. fulvoviregens</i> CR1	100	100																					
<i>U. fulvoviregens</i> CR2	100	100												14		100	100	100	100	100	100		
<i>U. fuscorubens</i>	100		100		40									20									
<i>U. glabrata</i>	100		29	100	50	29																	
<i>U. glabrescens</i>	100		100	100																			
<i>U. hakonensis</i> CR1	100		100	3	3									3									
<i>U. hakonensis</i> CR2	100													25									
<i>U. hesperina</i> CR1	100				100									50									
<i>U. hesperina</i> CR2	100			100	100																		
<i>U. himalayana</i>	100		18	100	18									18									
<i>U. himantodes</i>	100	100				100	100	100															
<i>U. intumescens</i> CR1	100		100	75																			
<i>U. intumescens</i> CR2	100											80	100	20									
<i>U. koyana</i>	100													17	100								
<i>U. longissima</i> CR1	100													3		42			100	100			
<i>U. longissima</i> CR2	100													3		64	64	100	42	14			
<i>U. longissima</i> CR3	100													5		10						100	100
<i>U. masudana</i>	100		100	100																			
<i>U. merrillii</i>	100		100	47	6																		
<i>U. mutabilis</i>	100													38									
<i>U. nidifica</i>	100		100	100	93	4																	
<i>U. nipparensis</i> CR1	100													20									
<i>U. nipparensis</i> CR2	100		33			50	100	33															
<i>U. orientalis</i>	100		100	29	57																		
<i>U. pangiana</i> CR1	100		16	100	57	14								6		6							
<i>U. pangiana</i> CR2	100		31	100	64	8								4		49			100	100			
<i>U. pectinata</i>	100		100			100	100	100															
<i>U. pseudogatai</i>	100		100	100	100																		
<i>U. pygmoidea</i> CR1	100		73	100	41	14								5									
<i>U. pygmoidea</i> CR2	100		100			62	100	62						5									
<i>U. rubicunda</i> CR1	100		100			100	100	100						15		13							
<i>U. rubicunda</i> CR2	100		100			100	100	100						17		17							
<i>U. rubicunda</i> CR3	100		100	100	100																		
<i>U. rubrotincta</i> CR1	100		100	100	97									25		3							
<i>U. rubrotincta</i> CR2	100		100			100	100	100															
<i>U. shimadai</i>	100		100	100							100												
<i>U. sinensis</i>	100		100	26																			
<i>U. subfloridana</i> CR1	100														100								
<i>U. subfloridana</i> CR2	100															100							
<i>U. subfloridana</i> CR3	100															100	100						
<i>U. subfloridana</i> CR4	100		100																				
<i>U. subintumescens</i>	100		100	40	100																		
<i>U. trichodeoides</i> CR1	100		100	62	3									33									
<i>U. trichodeoides</i> CR2	100								67	100				85									
<i>U. trichodeoides</i> CR3	100													100									
<i>U. wasmuthii</i> CR1	100		100																				
<i>U. wasmuthii</i> CR2	100		100																		100	100	
<i>U. wasmuthii</i> CR3	100															100							
<i>U. yakushimensis</i>	100															100	100						



## IV. TAXONOMIC TREATMENT

*Usnea* Adans., Fam. Pl. 2: 7, 1763.

Type species: *U. florida* (L.) F. H. Wigg.

Thallus fruticose, erect to pendent, up to several meters long, grayish-green to yellow-green or red when fresh, changing to brown in some species, pale to black at the base, continuous or cracked at the base; branching isotomic- or anisotomic-dichotomous; branches matt to glossy on the surface, with or without pseudocypbellae, annular-pseudocypbellae and/or maculae, terete, ridged, or flat in transverse section, inflated or uninflated, gradually tapering or tapering only near the apices, with few to many fibrils and lateral branches; lateral branches cylindrical, broadened, or constricted at the base; papillae absent or present; soralia absent or present, if present, formed on lateral branches, thicker branches, or whole branches, developed from cortex, maculae, cracks, scars of detached fibrils or lateral branches, or the top of eroded papillae, discrete or confluent each other, punctiform, rounded, elliptic, irregular in shape, sessile to stipitate, concave to convex at the top, with or without isidiomorphs and/or granular soredia. Cortex with or without red pigment, *florida*-, *merrillii*-, *ceratina*-, or *baileyi*-type plectenchymatous; hyphae pachydermatous or leptodermatous, lumina oblong, fusiform or turbinate. Medulla lax to dense, red pigment present or absent, located near the axis or cortex, secreted into or out to hyphal cell wall. Axis fistulose or solid, I – or + blue or dirty blue. Apothecia lateral or subterminal on lateral or terminal branches, cup-shaped, flat, or sinuose in shape; thalloid exciple with few to many fibrils; disc pruinose or epruinose, gray, pale yellow, pale brown, or brown, with or without white rim; asci 8-spored, elongate-clavate, *Lecanora*-type; spores simple, ellipsoid, colorless. Chemistry usnic acid in the cortex of all species, the medulla with range of depsides, depsidones, fatty acids or terpenoid. Ecology corticolous and/or saxicolous.

The genus *Usnea* is clearly separated from other genera of Parmeliaceae by the fruticose thallus having central axis and usnic acid in the cortex.

Key to the subgenera and sections of the genus *Usnea*

- 1a. Annular-pseudocypbellae present between segments; hypothecium (70)–100–160–(200)  $\mu\text{m}$  thick. . . . . Subgen. *Dolichousnea*
- 1b. Annular-pseudocypbellae absent; hypothecium (20)–50–70–(90)  $\mu\text{m}$  thick. . . . . 2.
  - 2a. Axis fistulose . . . . . Subgen. *Eumitria*
  - 2b. Axis solid . . . . . 3. Subgen. *Usnea*
- 3a. Cortical hyphae leptodermatous . . . . . Sect. *Usnea*
- 3b. Cortical hyphae pachydermatous . . . . . Sect. *Ceratinae*

Descriptions in each species are based on Japanese and Taiwanese specimens.

#### Subgenus *Usnea*

Type species: *U. florida* (L.) F. H. Wigg.

Thallus erect to pendent; branching anisotomic-dichotomous or isotomic-dichotomous; annular-pseudocypbellae absent; hypothecium (20)–50–70–(90)  $\mu\text{m}$  thick; axis I –.

The subgenus *Usnea* is separated from subgenus *Dolichousnea* by the absence of annular-pseudocypbellae, the thinner hypothecium, and I – reaction on axis; and from subgenus *Eumitria* by the solid axis. Although morphological distinguishing features between



subgenus *Usnea* and *Eumitria* are not always clear in some species, the separation between these subgenera is strongly suggested by the molecular phylogenetic results (Ohmura 2001).

### Section *Usnea*

Type species: *U. florida* (L.) F.H.Wigg.

*Usnea* subgen. *Usnea* sect. *Barbatae* Motyka subsection. *Comosae* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 1: 255, 1936. Type species: *U. subfloridana* Stirt. (selected here).

*Usnea* subgen. *Usnea* sect. *Barbatae* Motyka subsection. *Dasyypogae* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 1: 181, 1936. Type species: *U. filipendula* Stirt. (selected here).

*Usnea* subgen. *Usnea* sect. *Barbatae* Motyka subsection. *Floridae* Motyka, nom. illeg., Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 1: 231, 1936.

Cortex *florida*-type plectenchymatous, hyphae leptodermatous.

The section *Usnea* is distinguished from other sections by the *florida*-type plectenchymatous cortex and leptodermatous cortical hyphae.

#### 1. *Usnea filipendula* Stirt., Scott. Natur. 6: 104, 1881.

Holotype: America borealis, *Roy s.n.* (BM!). Chemistry: usnic and salazinic acids.

*Usnea plicata* (L.) F. H. Wigg. var. *dasyypoga* Ach., Method. Lich. 312, 1803. – *U. barbata* (L.) F. H. Wigg. var. *dasyypoga* Ach., Lich. Univ., 624, 1810. – *U. barbata* var. *dasyypoga* Röhl., Deutschl. Fl. 3: 144, 2. Abth., 1813 [= *U. dasyypoga* (Ach.) Röhl., in Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 1: 189, 1936]. Holotype: Sweden, collector unknown (H-ACH 1873!; isotype in BM!). Chemistry: usnic and salazinic acids (annotated by P. James in 1974).

Thallus fruticose, pendent, up to 26 cm long, color unknown when fresh, straw-yellow to yellowish-brown in herbarium specimens, jet black at the base; branching anisotomic-dichotomous; branches matt to slightly glossy on the surface, lacking pseudocypheae and maculae, terete, uninflated, gradually tapering, elongated towards distal branches, with many fibrils and lateral branches, 0.6–1.1 mm in diam.; lateral branches cylindrical at the base; papillae common on thicker branches, cylindrical; soralia common, formed mainly on terminal and lateral branches, developed from the top of eroded papillae, ± discrete, rounded in shape, smaller than branch diam., often distinctly stipitate, not reflexed with cortical margin, convex at the top with isidiomorphs, lacking granular soredia. Cortex 8.9–11% of the radius, *florida*-type plectenchymatous; hyphae leptodermatous with oblong lumina. Medulla moderate to dense, 20–25% of the radius, lacking red pigment. Axis solid, 32–39% of the diameter, I–. Apothecia not seen.

Chemistry. Usnic, protocetraric (trace) and salazinic acids.

The distinguishing features of *U. filipendula* are (1) the pendent thallus with anisotomic-dichotomous branching, (2) the jet black base, (3) the cylindrical papillae on thicker branches, (4) the slender elongated terminal branches, (5) the rounded soralia which are convex at the top, (6) the absence of granular soredia, (7) the *florida*-type plectenchymatous cortex, and (8) the presence of salazinic acid as major substance.

The general habit of *U. filipendula* is different from other species of the sect. *Usnea* in having a pendent thallus with elongated terminal branches.

*U. filipendula* has only been collected at one locality in Hokkaido in the present area, although this species is widely distributed in boreal to temperate regions such as North

America, Europe and Russia (Motyka 1936–38).

Specimen examined. JAPAN. Hokkaido. Prov. Kitami: Oketo, Tokoro-gun, 10.1922, *Y. Asahina* 2210.

2. *Usnea florida* (L.) Weber ex F. H. Wigg., Pr. Fl. Holsat., 91, 1780.

*Lichen floridus* L., Sp. Pl. 1: 1156, 1753.

Lectotype (selected by Clerc 1984): Sweden?, *Linnaeus?* (LINN!). Chemistry: alectorialic (in apothecia), bourgeanic, hypothamnolic, thamnolic and usnic acids (Jørgensen et al. 1994).

Thallus fruticose, erect, up to 6.5 cm long, color unknown when fresh, straw-yellow to yellowish-brown in herbarium specimens, jet black at the base, with annular cracks; branching anisotomic-dichotomous; branches matt on the surface, lacking pseudocyphellae and maculae, terete, uninflated, gradually tapering, with numerous fibrils and lateral branches, 1.1–1.3 mm in diam.; lateral branches cylindrical at the base; papillae common on thicker branches, cylindrical; soralia absent. Cortex 8.9–13% of the radius, *florida*-type plectenchymatous; hyphae leptodermatous, lacking red pigment, with oblong lumina. Medulla dense, narrow, 13–17% of the radius, lacking red pigment. Axis solid, thick, 42–48% of the diameter, I–. Apothecia common, subterminal on terminal and lateral branches, up to 6.5 mm in diam., flat; thalloid exciple with many fibrils; disc pruinose, pale yellow to gray, lacking white rim; epihymenium 4–15  $\mu\text{m}$  thick; hymenium 56–70  $\mu\text{m}$  thick; hypothecium 30–60  $\mu\text{m}$  thick; spores 8–10 $\times$ 4–6  $\mu\text{m}$  long.

Chemistry: usnic and thamnolic acids.

The distinguishing features of *U. florida* are (1) the erect thallus with anisotomic-dichotomous branching, (2) the jet black base, (3) the uninflated branches with cylindrical papillae on the surface, (4) the absence of soralia, (5) the common occurrence of apothecia, (6) the *florida*-type plectenchymatous cortex, and (7) the presence of thamnolic acid.

In the lectotype of the present species, Jørgensen et al. (1994) reported the occurrence of alectorialic (in apothecia), bourgeanic and hypothamnolic acids as well as usnic and thamnolic acids. The former three substances, which are not detected in the specimen from the present area, can be considered to be accessory as pointed out by Clerc (1984). A specimen collected in Taiwan agrees morphologically with the type and coincides with the description given by Clerc (1984).

*U. florida* may be confused with *U. dendritica*, *U. fuscorubens*, *U. masudana*, *U. orientalis*, *U. shimadai* and *U. sinensis*, since they form similar fertile thalli without soralium. However, it is distinguished from the other six by the jet black base of the thallus and the production of thamnolic acid.

Asahina (1968a) first reported the occurrence of *U. florida* from Taiwan where it grew on tree bark at ca. 2000 m alt. This is the only record for the species in the present area, though it is widely distributed in Europe (Clerc 1984).

Specimen examined. TAIWAN. Prov. Taitung: Mt. Dai-wu, on tree bark, c. 2000 m, 9.1958, *collector unknown* 106.

3. *Usnea fulvoreagens* (Räsänen) Räsänen, Lich. Fenn. Exs. 13, 1935.

*Usnea glabrescens* (Nyl.) Vain. var. *fulvoreagens* Räsänen, Flecht. Estlands I, 34: 20, 1931.

Holotype: Russia, Karelian Republic, Kl. Kurkijoki, Lapinlahti, 22.8.1923, *Räsänen s.n.* (H!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids, and zeorin.

Thallus fruticose, erect to subpendent, up to 16 cm long, grayish-green to yellowish green when fresh, straw-yellow to yellowish-brown in herbarium specimens, jet black at the base, often with transverse cracks near the base; branching isotomic- or anisotomic-dichotomous; branches matt on the surface, lacking pseudocyphellae and maculae, terete, uninflated, gradually tapering, with many fibrils and lateral branches, 0.7–1.4 mm in diam.; lateral branches cylindrical at the base; papillae common to sparse on thicker branches, cylindrical to verrucose; soralia common, formed mainly on terminal and lateral branches, developed from cortex, confluent each other to form irregular mass of soredia, larger than the branch diam., sessile or often slightly stipitate, cortical margin distinctly reflexed, concave at the top with granular soredia, lacking isidiomorphs, deeply excavating often into nearly central axis. Cortex 7.4–13% of the radius, *florida*-type plectenchymatous; hyphae leptodermatous with oblong lumina. Medulla moderate to dense, 14–28% of the radius, lacking red pigment. Axis solid, 24–51% of the diameter, I –. Apothecia not seen.

Chemistry: Race 1, usnic, norstictic acids and zeorin; Race 2, usnic, norstictic and diffractaic acids, zeorin, and trace amounts of barbatic, 4-*O*-demethylbarbatic, baeomycesic, and squamatic acids, and atranorin ( $\pm$ ).

The distinguishing features of *U. fulvoreagens* are (1) the erect to subpendent thallus, (2) the jet black base, (3) the uninflated branches with cylindrical papillae on the surface, (4) the deeply excavating soralia which cortical margins are distinctly reflexed, (5) the presence of granular soredia and lacking isidiomorphs, (6) the *florida*-type plectenchymatous cortex, and (7) the presence of norstictic acid and zeorin.

Two chemical races were recognized within *U. fulvoreagens* from the present area as shown above. As no morphological or ecological difference was found between Race 1 and Race 2, the chemical differences found in this species are considered to have no taxonomic value. Although diffractaic acid is always present in the thalli of Race 2, its concentration is not uniform even within one thallus. When two or three different parts of the thallus were examined, the concentration of the acid is apparently variable, being detected as a distinct or a pale ambiguous spot on TLC plate.

Although menegazziac, stictic and constictic acids were detected in the holotype specimen of *U. fulvoreagens*, they were not detected from specimens in the investigated area. However, no morphological difference was observed between the type and other specimens. It is noted that Race 1 and Race 2 of *U. fulvoreagens* in the present paper are also known from Europe and North America (Clerc 1992, Halonen et al. 1998, Purvis et al. 1992).

*U. fulvoreagens* is distinguished from other related species by having deeply excavating soralia without isidiomorph, and by presence of norstictic acid and zeorin.

In Japan, *U. fulvoreagens* is distributed in Hokkaido to central Honshu, where it grows on bark of trees such as *Abies*, *Larix* and *Salix* at elevations between 50 and 1800 m (at lower elevation in Hokkaido and at higher elevations in central Honshu). In Taiwan, it was found on tree bark at elevations between 1500 and 2600 m.

Representative specimens examined. Race 1. JAPAN. Hokkaido. Prov. Nemuro: Ochiishi, on *Abies sachalinensis*, c. 50 m, 1.9.1965, *S. Kurokawa* 65808. Honshu. Prov. Shinano: Mt. Yatsugatake, Suwa-gun, c. 1600 m, 22.7.1972, *H. Kashiwadani* 9929b. Prov. Kai: Tokusa Pass, 7.8.1953, *S. Kurokawa* 521244. TAIWAN. En

route from Ssu-yuan to To-chia-tun Shanm, Mt. Nanhuta Shan, Hoping, on *Salix* sp., 1900–2250 m, 9.11.1989, *H. Kashiwadani* 35767.

Race 2. JAPAN. Honshu. Prov. Shinano: c. 3 km ESE of Azusayama, Kawakami-mura, Minamisaku-gun, on *Larix kaempferi*, 1460–1500 m, 9.12.1996, *Y. Ohmura* 2906; Mt. Tateshina. 30.5.1967, *M. Togashi* s.n. TAIWAN. Mt. Nan-Fu-Ta-San, 1500–2400 m, 19.1.1964, *S. Kurokawa* 963.

#### 4. *Usnea glabrescens* (Nyl.) Vain., Med. Soc. Fa. Fl. Fenn. 48: 173, 1925.

*Usnea barbata* (L.) F. H. Wigg. var. *glabrescens* Nyl. in Vainio, Med. Soc. Fa. Fl. Fenn. 2: 46, 1878.

Holotype: Finland, Tavastia australis, Korpilahti, Tianeä, 1873, *E. Lang* s.n. (TUR!). Chemistry: usnic, norstictic, protocetraric (trace) and salazinic acids, and atranorin.

Thallus fruticose, erect to subpendent, up to 16 cm long, grayish-green to yellowish-green when fresh, straw-yellow to yellowish-brown in herbarium specimens, jet black at the base, with transverse cracks near the base; branching isotomic-dichotomous; branches matt on the surface, lacking pseudocyphellae and maculae, terete, uninflated, gradually tapering, with sparse fibrils and lateral branches, 1.0–1.3 mm in diam.; lateral branches cylindrical at the base; papillae common on thicker branches, verrucose; soralia common, formed mainly on terminal and lateral branches, developed from cortex,  $\pm$  discrete each other, rounded in shape, growing to larger than branch diam., sessile or often slightly stipitate, cortical margin usually slightly reflexed, concave at the top with granular soredia rarely with isidiorhymorphs, slightly excavating. Cortex 8.7–14% of the radius, *florida*-type plectenchymatous; hyphae leptodermatous, with oblong lumina. Medulla moderate to dense, 18–25% of the radius, lacking red pigment. Axis solid, 31–46% of the diameter, I–. Apothecia not seen.

Chemistry: usnic, norstictic and salazinic acids.

The distinguishing features of *U. glabrescens* are (1) the erect to subpendent thallus with isotomic-dichotomous branching, (2) the jet black base, (3) the uninflated branches with papillae on the surface, (4) the rounded soralia, (5) the presence of granular soredia, (6) the *florida*-type plectenchymatous cortex, (7) the presence of norstictic acid, and (8) the absence of zeorin.

Although atranorin and a trace amount of protocetraric acid were detected in the holotype specimen of *U. glabrescens*, they were not detected in specimens in the investigated area. However, no morphological difference was observed between the type and other specimens. The presence or absence of these chemicals seems to have no taxonomic value.

Asahina (1959a, 1959b) reported three subspecies under *U. glabrescens* which were separated by the chemistry: (1) subsp. *glabrescens* characterized by norstictic acid, (2) subsp. *asiatica* Asahina by salazinic acid, and (3) subsp. *pseudocolorans* Asahina by thamnolic acid. In the present paper, however, subsp. *asiatica* and subsp. *pseudocolorans* are treated as synonyms of *U. wasmuthii* (see note under *U. wasmuthii*).

*U. glabrescens* resembles *U. fulvorangeans* in having concave top soralia and in the presence of norstictic acid. However, it is distinguished from *U. fulvorangeans* by the discrete soralia with slightly excavating surface. It also differs in the absence of zeorin which is constantly produced in *U. fulvorangeans*.

In Japan, *U. glabrescens* is found in central Honshu, where it grows on tree bark (e.g., *Salix*) at elevations between 1440 and 1800 m. In Taiwan, this species grows on twigs (e.g.,

*Osmanthus*) at elevations between 2400 and 2600 m. *U. glabrescens* is widely distributed in boreal to temperate regions in Europe, eastern Asia and North America (Halonen et al. 1998, Ohmura & Kashiwadani 2000, Purvis et al. 1992).

Representative specimens examined. JAPAN. Honshu. Prov. Shinano: en route from Gyozya-goya to Minoto-sanso, Yatsugatake Mts., Chino-city, on *Salix* sp., 1740–1800 m, 29.8.1997, Y. Ohmura 3824b. Prov. Kai: Tokusa Pass. 7.8.1953, S. Kurokawa 521244. TAIWAN. Mt. Nan-Fu-Ta-San, on twigs of *Osmanthus bioritsuensis*, 2400–2600 m, 20.1.1964, S. Kurokawa 1088.

5. *Usnea subfloridana* Stirt., Scott. Natur. 6: 294, 1882.

Holotype: Scotland, Perthshire, Killin, 19.7.1881, *Stirton s.n.* (BM!). Chemistry: usnic and thamnolic acids.

*Lichen comosus* Ach., Kgl. Vetensk. Acad. Nya Handling., 209, tab. 8, fig. 1, 1795. – *Usnea plicata* (L.) F. H. Wigg. var. *comosa* (Ach.) Ach., Method. Lich., 311, 1803. – *U. florida* (L.) F. H. Wigg. var. *comosa* (Ach.) Biroli, Flora Asconiens 2: 199, 1808. – *U. comosa* (Ach.) Vain., in Norrl. and Nyl., Herb. Lich. Fenn. exs. No. 457, 458, 1921; Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars. Syst. 1: 264, 1936; non *U. comosa* Pers., 1826. Holotype: Sweden, *Acharius?* (H!).

*Usnea comosa* subsp. *colorans* Asahina, Lich. Jap. 3: 94, 1956. Lectotype (selected by Ohmura & Kashiwadani 2000): Japan, Honshu, Prov. Kai, Yoshida-guchi 1-gome, Mt. Fuji, 10.8.1952, M. Togashi s.n., pr.maj.p. (TNS!). Chemistry: usnic and thamnolic acids.

*Usnea comosa* subsp. *praetervisa* Asahina, Lich. Jap. 3: 95, 1956. – *U. subfloridana* subsp. *praetervisa* (Asahina) P. Clerc, in Fos & Clerc, Lichenologist 32: 67–88, 2000. Lectotype (selected by Ohmura & Kashiwadani 2000): Japan, Honshu, Prov. Kai, Asahigaoka, Lakeside of Yamanaka, Nakano-mura, Minami-Tsuru-gun, 30.7.1954, S. Kurokawa 540328 (TNS!). Chemistry: usnic and norstictic acids.

Thallus fruticose, erect to subpendent, up to 13.5 cm long, grayish-green to yellowish-green when fresh, straw-yellow to yellowish-brown in herbarium specimens, jet black at the base, often with transverse cracks near the base; branching anisotomic- or isotomic-dichotomous; branches matt on the surface, lacking pseudocyphellae and maculae, terete, uninflated, gradually tapering, usually with numerous fibrils and lateral branches, 0.5–1.6 mm in diam.; lateral branches cylindrical at the base; papillae common on thicker branches, verrucose to cylindrical; soralia common, formed mainly on terminal and lateral branches, developed from the top of eroded papillae, confluent each other forming irregular mass of asexual propagule, sessile or often distinctly stipitate, usually smaller than branch diam., cortical margin not reflexed, convex at the top, usually with many isidiomorphs, lacking granular soredia. Cortex 7.3–16% of the radius, *florida*-type plectenchymatous; hyphae leptodermatous, lacking red pigment, with oblong lumina. Medulla moderate to dense in density, 9.1–27% of the radius, lacking red pigment. Axis solid, 27–58% of the diameter, I –. Apothecia very rare, lateral on terminal and lateral branches, up to 3.0 mm in diam., cup-shaped; thalloid exciple with many fibrils; disc pruinose, pale yellow, lacking white rim; epihymenium 6–18  $\mu\text{m}$  thick; hymenium 60–80  $\mu\text{m}$  thick; hypothecium 60–90  $\mu\text{m}$  thick; spores 8–10  $\times$  4–6  $\mu\text{m}$  long.

Chemistry. Race 1, usnic and thamnolic acids; Race 2, usnic and squamatic acids; Race 3, usnic, thamnolic and squamatic acids; Race 4, usnic and norstictic acids.

The distinguishing features of *U. subfloridana* are (1) the erect to subpendent thallus, (2) the jet black base, (3) the uninflated branches with cylindrical papillae on the surface, (4) the soralia having convex top, (5) the *florida*-type plectenchymatous cortex, and (6) the presence of thamnolic, squamatic or norstictic acids.

Although this species has been well known as *U. comosa* (Ach.) Vain. (1921) by

Japanese lichenologists, the name is a later homonym of *U. comosa* Pers. (1826). It is replaced by the name *U. subfloridana* Stirt. which has priority [Art. 58.1 (Greuter et al. 1994)] (Laundon 1965).

*U. subfloridana* is easily distinguished morphologically from the related species by having convex top soralia. Four chemical races were recognized in *U. subfloridana* from the present area as shown above. The most common race was the Race 1 (thamnolic acid, 74%); Race 2 (squamic acid, 16%) and Race 4 (norstictic acid, 9%) were frequently found, but only one specimen of Race 3 (both thamnolic and squamic acid, 1%) was found. No morphological or ecological difference was found among the four chemical races. Races 1–3 produce biosynthetically closely related chemical substances. Therefore, they can be considered to belong to a single species. Even though Race 4 produces norstictic acid, a depsidone, a biosynthetically distant compound from depsides produced in Races 1–3, no notable difference was found among them as mentioned above. Thus, Race 4 is tentatively treated as a race of *U. subfloridana* in the present paper, and final taxonomic decision should be made when more material has been studied.

Asahina (1956) reported four subspecies under *U. comosa* (Ach.) Vain. nom. illeg., which were separated by the chemistry: (1) subsp. *comosa* (as *eucomosa* Motyka, nom. illeg.) characterized by squamic acid, (2) subsp. *colorans* Asahina by thamnolic acid, (3) subsp. *praetervisa* Asahina by norstictic acid, and (4) subsp. *melanopoda* Asahina by salazinic acid. Although subsp. *comosa*, subsp. *colorans*, and subsp. *praetervisa* are treated as synonyms of *U. subfloridana*, subsp. *melanopoda* is treated under *U. wasmuthii* (see note of this species).

In Japan, *U. subfloridana* is distributed in Hokkaido to central Honshu, where it grows on twigs or bark of coniferous trees such as *Larix* and *Tsuga*, or deciduous trees such as *Acer*, *Betula* and *Prunus*. It is found at elevations between 50 and 2000 m (at lower elevations in Hokkaido and at higher elevations in central Honshu). In Taiwan, it grows on bark at high elevations between 2400 and 3300 m. This species has also been collected from China and Korea. *U. subfloridana* is widely distributed in northern boreal to temperate regions in Europe, Asia and North America (Awasthi 1986, Halonen et al. 1998, Motyka 1936–38, Ohmura & Kashiwadani 2000).

Representative specimens examined. Race 1. JAPAN. Honshu. Prov. Musashi: Mt. Mitsumine, Chichibu, 30.8.1951, *S. Kurokawa* 510069. Prov. Shinano: Ikenodaira, Takato-machi, Kamiina-gun, on *Larix kaempferi*, 1620 m, 29.6.1997, *Y. Ohmura* 3144b; en route from Gyozya-goya to Minoto-sanso, Yatsugatake Mts., Chino-city, on *Salix* sp., 1740–1800 m, 29.8.1997, *Y. Ohmura* 3823. Prov. Kai: Yoshida-guchi 1-gome, Mt. Fuji, 10.8.1952, *M. Togashi* s.n. Prov. Suruga: Umagaeshi, Gotemba-guchi Route, Mt. Fuji, on *Acer* sp., c. 1000 m, 15.10.1980, *H. Kashiwadani* 16784. TAIWAN. Mt. Chien-San, Mt. Shin-Kao-San, 3100–3300 m, 1.1.1964, *S. Kurokawa* 279. KOREA. Kanko, 1934, *H. To* s.n.

Race 2. JAPAN. Hokkaido. Prov. Kitami: Nakasaroma, 2.7.1953, *M. Tatewaki* s.n. Honshu. Prov. Shimosuke: W Lakeside of Yunoko, Nikko, on *Prunus ssiiori*, c. 1480 m, 16.7.1995, *Y. Ohmura* 1122. Prov. Shinano: Daimon Pass, 22.5.1959, *Y. Asahina* [59522], *S. Kurokawa* & *M. Nuno*. Prov. Kai: Yoshida-guchi 1-gome, Mt. Fuji, 10.8.1952, *M. Togashi* s.n. CHINA. Kanto, Kinso, Konshun, 16.5.1943, *S. Asahina* s.n. (herb. *Y. Asahina* 43516).

Race 3. JAPAN. Honshu. Prov. Shinano: en route from Azusayama to Jyumonji Pass, Minamisaku-gun, on *Tsuga diversifolia*, 1860–2030 m, 9.12.1996, *Y. Ohmura* 2863b.

Race 4. JAPAN. Hokkaido. Prov. Tokachi: Shimozuka, 3.7.1953, *Y. Asahina* & *M. Togashi* s.n. Honshu.

Prov. Shinano: Shin-yu Hot Spring, Mt. Tateshina, 21.5.1959, *Y. Asahina* [59524], *S. Kurokawa* & *M. Nuno*. TAIWAN. Mt. Chien-San, Mt. Shin-Kao-San, 3100–3300 m, 1.1.1964, *S. Kurokawa* 287. CHINA. Kanto, Kinso, Konshun, 16.5.1943, *S. Asahina s.n.*

6. *Usnea wasmuthii* Räsänen, *Flecht. Estlands I*, 34: 19. 1931.

Holotype: Esthonia, Tallinna, Kakumae, on *Picea*, 1908, *Wasmuth s.n.* (H!). Chemistry: usnic and barbatic acids (Clerc 1992).

*Usnea comosa* (Ach.) Vain. subsp. *melanopoda* Asahina, *Lich. Jap.* 3: 94, 1956. Lectotype (selected by Ohmura & Kashiwadani 2000): Japan, Honshu, Prov. Kai, Yoshida-guchi 1-gome, Mt. Fuji, 10.8.1952, *M. Togashi s.n.* (herb. *Y. Asahina* 52810 pr.min.p., TNS!). Chemistry: usnic and salazinic acids.

*Usnea glabrescens* (Nyl.) Vain. subsp. *asiatica* Asahina, *J. Jpn. Bot.* 34: 229, 1959. Lectotype (selected by Ohmura & Kashiwadani 2000): Japan, Honshu, Prov. Shinano, Shin-yu Hot Spring, Mt. Tateshina, 21.5.1959, *Y. Asahina* [59530], *S. Kurokawa* & *M. Nuno* (TNS!). Chemistry: usnic, barbatic, 4-*O*-demethylbarbatic and salazinic acids.

*Usnea glabrescens* subsp. *pseudocolorans* Asahina, *J. Jpn. Bot.* 34: 292, 1959. Holotype: Japan, Honshu, Prov. Shinano, en route from Yanagawa to Kitazawa, Yatsugatake Mts. 25.7.1959, *M. Togashi* & *S. Kurokawa s.n.* (herb. *Y. Asahina* 59725, TNS!). Chemistry: usnic and thamnolic acids.

Thallus fruticose, erect to subpendent, up to 24 cm long, grayish-green to yellowish-green when fresh, straw-yellow to yellowish-brown in herbarium specimens, jet black at the base, often with transverse cracks; branching anisotomic- or isotomic- dichotomous; branches matt on the surface, lacking pseudocyphellae and maculae, terete, usually uninflated but rarely slightly inflated, gradually tapering, with sparse to dense fibrils and lateral branches, 0.7–1.8 mm in diam.; lateral branches cylindrical at the base; papillae irregularly distributed on thicker branches, verrucose to cylindrical; soralia common, formed mainly on terminal and lateral branches, developed from cortex, confluent each other forming elliptic to irregularly rounded mass of soredia, sometimes becoming larger than branch diam., sessile or often slightly stipitate, cortical margin sometimes slightly reflexed, concave at the top with granular soredia and isidiomorphs, slightly excavating. Cortex moderate in thickness, 6.5–17% of the radius, *florida*-type plectenchymatous; hyphae leptodermatous, lacking red pigment, with oblong lumina. Medulla moderate to dense, narrow to moderate in width, 7.3–29% of the radius, lacking red pigment. Axis solid, moderate in thickness, 29–57% of the diameter, I –. Apothecia very rare, lateral on terminal and lateral branches, up to 4.8 mm in diam., cup-shaped; thalloid exciple with many fibrils; disc pruinose, pale yellow, lacking white rim; epihymenium 4–12  $\mu\text{m}$  thick; hymenium 48–64  $\mu\text{m}$  thick; hypothecium 30–50  $\mu\text{m}$  thick; spores 10–12  $\times$  6–7  $\mu\text{m}$  long.

Chemistry: Race 1, usnic and salazinic acids; Race 2, usnic, barbatic, 4-*O*-demethylbarbatic and salazinic acids; Race 3, usnic and thamnolic acids.

The distinguishing features of *U. wasmuthii* are (1) the erect to subpendent thallus, (2) the jet black base, (3) the uninflated branches with cylindrical papillae on the surface, (4) the elliptic soralia with concave top, (5) the presence of granular soredia, (6) the *florida*-type plectenchymatous cortex, and (7) the presence of barbatic, thamnolic or salazinic acids as major substance.

Three chemical races were recognized within *U. wasmuthii* collected in the present area as shown above. Race 1 (45%) and Race 2 (50%) were commonly found, but Race 3 is rather rare (5%). Race 3 contains thamnolic acid, a depside, which is biosynthetically dis-

tantly related to depsidone. However, it is treated as one of chemical races of *U. wasmuthii* in the present paper, since no morphological difference has been found between Races 1–2 and Race 3. It should be noted that Race 3 has been also known in Europe (Clerc 1992).

*U. wasmuthii* resembles *U. subfloridana*, from which it can be distinguished by the concave soralia. It also resembles *U. fulvorenans* and *U. glabrescens*, because they all have concave top soralia. However, it can be distinguished from *U. fulvorenans* by having isidiomorphs and the absence of norstictic acid, and from *U. glabrescens* by the confluent soralia and the absence of norstictic acid. The slender form of *U. wasmuthii* resembles *U. filipendula*. It is distinguished from *U. filipendula* by having concave soralia.

In Japan, *U. wasmuthii* is distributed in Hokkaido to central Honshu, where it grows on twigs or barks of coniferous trees such as *Abies*, *Larix*, *Picea* and *Tsuga*, or broadleaf trees such as *Betula* and *Salix*. It is found at elevations between 330 and 2030 m (at lower elevation in Hokkaido and higher elevations in central Honshu). In Taiwan, it grows on twigs or barks such as *Osmanthus* at elevations between 1500 and 3300 m. This species has also been collected from China and Korea. *U. wasmuthii* has been also reported from Europe and North America (Clerc 1992, Halonen 2000).

Representative specimens examined. Race 1: JAPAN. Hokkaido. Prov. Tokachi: Shimonozuka, 3.7.1953, *Y. Asahina* s.n. Honshu. Prov. Shinano: en route from Azusayama to Jyumonji Pass, Minamisaku-gun, on *Tsuga diversifolia*, 1860–2030 m, 9.12.1996, *Y. Ohmura* 2863a. Prov. Kai: Mt. Mizugaki, 5.8.1953, *S. Kurokawa* 521148. TAIWAN. Mt. Nan-Fu-Ta-San, 1500–2400m, 19.1.1964, *S. Kurokawa* 962. CHINA. Pref. Koanhoku, E of Yakesi, 29.5.1949, *Y. Asahina* s.n.

Race 2: JAPAN. Hokkaido. Prov. Kitami: Tokusyoppe, Furuume, Bihoro-cho, Abashiri-gun, on twigs of *Abies sachalinensis*, c. 330 m, 26.7.1997, *Y. Ohmura* 3602b pr.p. Honshu. Prov. Shinano: Daimon Pass, 22.5.1959, *Y. Asahina*, *S. Kurokawa* & *M. Nuno* s.n. TAIWAN. Mt. Chien-San, Mt. Shin-Kao-San, 3100–3300 m, 1.1.1964, *S. Kurokawa* 286. KOREA. Kankyo-Nando: Kanchi-in, 2.8.1934, *F. Fujikawa* s.n. CHINA. Kanto, Kinso, Konshun, 16.5.1943, *S. Asahina* s.n.

Race 3: JAPAN. Honshu. Prov. Shinano: c. 3 km ESE of Azusayama, Kawakami-mura, Minamisaku-gun, on *Larix kaempferi*, 1460–1500 m, 9.12.1996, *Y. Ohmura* 2900b.

### Section *Ceratinae* (Motyka) Y. Ohmura, comb. nov.

*Usnea* sect. *Elongatae* Motyka subsect. *Ceratinae* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 353, 1938. Type species: *U. ceratina* Ach. (selected here).

*Usnea* sect. *Glabratae* Motyka subsect. *Glabratae*. – *Usnea* sect. *Glabratae* Motyka subsect. *Pycnocladae* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 484, 1938. Type species: *U. glabrata* (Ach.) Vain. (selected here).

*Usnea* sect. *Glabratae* Motyka subsect. *Ciliiferae* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 535, 1938. Type species: *U. ciliifera* Motyka (selected here).

*Usnea* sect. *Setulosae* Motyka subsect. *Setulosa*. – *Usnea* sect. *Setulosae* Motyka subsect. *Densirostrae* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 305, 1938. Type species: *U. setulosa* Motyka (selected here).

*Usnea* sect. *Stramineae* Motyka subsect. *Stramineae*, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 447, 1938. Type species: *U. straminea* Müll. Arg. (selected here).

*Usnea* sect. *Setulosae* Motyka subsect. *Rubigineae* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 331, 1938. Type species: *U. rubicunda* Stirt. (selected here).

Thallus pale to dark brown at the base, axis solid, cortex *merrillii*-type or *ceratina*-type plectenchymatous, cortical hyphae pachydermatous.

Section *Ceratinae* is distinguished from section *Usnea* by the pachydermatous hyphae in cortex. Most of species in the genus *Usnea* belong to this section.



7. *Usnea aciculifera* Vain., Bot. Mag. Tokyo 35: 45, 1921.

Lectotype (selected here): Japan, Honshu, Prov. Kozuke, in arboribus, 8.8.1913, *A. Yasuda 195* (TUR-V 00620!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

*Usnea aciculifera* f. *abbreviata* Asahina, Lich. Jap. 3: 74, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Kai, Yatsugatake Mts., 4.10.1930, *F. Fujikawa s.n.* (herb. *Y. Asahina 1401*, TNS!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

Thallus fruticose, erect to subpendent, up to 20 cm long, straw-yellow to olive-green when fresh, rusty- to chestnut-brown in herbarium specimens, concolorous with thallus or pale at the base, sometimes partially decorticate especially near the base; branching isotomic-dichotomous; branches slightly glossy on the surface, lacking pseudocypbellae and maculae, terete, uninflated, 0.5–1.3 mm in diam., gradually tapering, with sparse lateral branches and few fibrils; lateral branches cylindrical; papillae absent; soralia common, formed on whole branches especially on near the apices, developed from scars of detached fibrils, punctiform, discrete each other, sessile or rarely slightly stipitate, flat to slightly convex at the top with many isidiomorphs, lacking granular soredia. Cortex thick, 5–16% of the radius, lacking red pigment, *ceratina*-type plectenchymatous; hyphae pachydermatous, lumina turbinate. Medulla dense, 15–31% of the radius, lacking red pigment. Axis solid, 18–57% of the diameter, I –. Apothecia very rare, lateral on terminal branches, up to 3.0 mm in diam., cup-shaped; thalloid exciple with sparse fibrils; disc pruinose, whitish gray, lacking white rim; epihymenium 10–14  $\mu\text{m}$  thick; hymenium 56–66  $\mu\text{m}$  thick; hypothecium 18–28  $\mu\text{m}$  thick; spores 10–12 $\times$ 6–9  $\mu\text{m}$  long.

Chemistry. Usnic, norstictic, menegazziaic, stictic and constictic acids, and atranorin ( $\pm$ ).

The distinguishing features of *U. aciculifera* are (1) the erect to subpendent thallus with isotomic-dichotomous branching, (2) the uninflated branches, (3) the presence of punctiform soralia and isidiomorphs on the surface of branches, (4) the absence of papillae, (5) the absence of granular soredia, (6) the *ceratina*-type plectenchymatous cortex, and (7) the presence of stictic acid as major substance.

When Vainio (1921) described *U. aciculifera* Vain., he cited two specimens, Prov. Kozuke ("*Yasuda 195*") and Prov. Mimasaka ("*Yasuda 233*"). The former specimen "*Yasuda 195*" has been cited as a lectotype (e.g., Awasthi 1986); although it was annotated as a lectotype by Asahina in 1965, he did not published it. The specimen of "*Yasuda 195*" agrees well morphologically and chemically with the protologue. Therefore, it is designated as the lectotype.

When Asahina (1956) described *U. aciculifera* f. *abbreviata* Asahina, he cited one specimen to show RS and A.Q.-values of this taxon. Although he did not designate the type in the protologue, this specimen [Japan, Honshu, Prov. Kai, Yatsugatake Mts., 4.10.1930, *F. Fujikawa s.n.* (herb. *Y. Asahina 1401*)] should be accepted as the holotype according to Art. 9.1 note 1 of Tokyo Code (Greuter et al. 1994). According to Asahina (1956), this taxon was different from f. *aciculifera* in the small thallus (3–5 cm long) with short branches which are crowded toward apices. However, these features belong to the natural range of variation of *U. aciculifera*. Therefore, f. *abbreviata* is reduced to a synonym of *U. aciculifera*.

In Japan, *U. aciculifera* is distributed from northern Honshu to Kyushu, where it grows on bark of coniferous trees such as *Larix*, *Picea* and *Pinus*, or broadleaf trees such as *Carpinus*, *Prunus*, *Quercus* and *Salix*. It also rarely grows on rocks. It is found at elevations between 260 and 1600 m. In Taiwan, it grows on tree bark at elevations between 800 and 2200 m. This species is also known from China, India and Nepal (Asahina 1972, Awasthi 1986), and its distribution pattern is considered to belong to the typical Himalayan-Japan element as reported by Asahina (1972).

Representative specimens examined. JAPAN. Honshu. Prov. Rikuchu: Hiraizumi, 21.10.1954, *M. Togashi s.n.* Prov. Rikuzen: Matsubara, Takada-cho, Kesen-gun, 30.3.1928, *G. Toba s.n.* Prov. Hitachi: Tukuba-san shrine, Mt. Tsukuba, Tsukuba-city, on tombstone in the cemetery, c. 270 m, 23.7.1998, *Y. Ohmura 4441*. Prov. Shimotsuke: Nishi-Iwasaki, Nasu, 4.8.1965, *the Empress Nagako 57*. Prov. Kozuke: Numata, Tone-gun, 14.4.1921, *A. Tsunoda s.n.* (herb. *Y. Asahina 1406*). Prov. Kazusa: Ichinomiya, 30.3.1952, *Y. Asahina 1413*. Prov. Musashi: Chichibu, 21.7.1933, *Y. Asahina s.n.* Prov. Sagami: Hakone, Lakeside of Ashinoko, 15.7.1952, *M. Togashi s.n.* (herb. *Y. Asahina 52716*). Prov. Sado: Kompon Temple, Niibo-mura, 10.3.1953, *Y. Asahina s.n.* Prov. Shinano: Todai, Hase-mura, Kami-ina-gun, on *Pinus densiflora*, c. 1040 m, 27.6.1997, *Y. Ohmura 3115*. Prov. Kai: Lakeside of Yamanaka, Mt. Fuji, 11.8.1952, *M. Togashi s.n.* Prov. Suruga: Subashiri-guchi, Mt. Fuji, 6.4.1932, *F. Fujikawa s.n.* Prov. Izu: Mt. Amagi, 13.4.1952, *M. Togashi s.n.* Prov. Tohtomi: shrine, Kuma-mura, Iwata-gun, 23.3.1969, *M. Togashi s.n.* Prov. Mikawa: Mt. Horaiji, 6.1.1956, *Y. Asahina s.n.* Prov. Ohmi: Kami-Niyu, Samegai-mura, Sakata-gun, 24.4.1962, *M. Togashi s.n.* Prov. Yamashiro: Koshihata, Ukyo-ku, Kyoto, 3.4.1967, *M. Togashi s.n.* Prov. Ise: Yachi, Misugi-mura, Ichishi-gun, c. 120 m, *S. Nagano 6*. Prov. Shima: Oshibuchi, Nansei-cho, Watarai-gun, 19.3.1966, *M. Togashi s.n.* Prov. Yamato: Murou Temple, Murou-mura, Uda-gun, 13.9.1953, *M. Togashi s.n.* Prov. Kii: Mt. Koya, 23.8.1952, *Y. Asahina s.n.* Prov. Settsu: Arima-guchi, Mt. Rokko, on *Pinus thunbergii*, 4.10.1953, *M. Togashi s.n.* Prov. Inaba: Nagi-mura, Yazu-gun, 26.10.1930, *N. Hiratsuka s.n.* (herb. *Y. Asahina 1407*). Prov. Izumo: Mt. Makuragi, Matsue City, 420 m, *H. Kashiwadani 8809a*. Prov. Iwami: Mt. Sanbe, Ohda city, 600 m, *H. Kashiwadani 5616*. Prov. Bingo: Kamiyama-mura, Sera-gun, 3.1.1933, *T. Sato s.n.* (herb. *Y. Asahina 1418*). Shikoku. Prov. Awa: Mt. Kenzan, 24.6.1952, *S. Togawa s.n.* Prov. Iyo: Nakasone-mura, Uma-gun, c. 500 m, 5.10.1952, *K. Ochi s.n.* Prov. Tosa: Mt. Dohgamori, Hata-gun, on *Pinus densiflora*, 16.6.1955, *S. Kurokawa 550616c*. Kyushu. Prov. Buzen: Ipponkunugi, Yabakei, 17.4.1942, *Y. Asahina 1416*. Prov. Bungo: Egomori, Yabakei-machi, Shimoge-gun, on *Prunus yedoensis*, c. 420 m, 4.3.1997, *Y. Ohmura 3013*. Prov. Hyuga: Suki-son, Nishi-Morokata-gun, 15.3.1947, *M. Togashi s.n.* Prov. Hizen: Kashinokibaru Marsh, Kashinokibaru, Ikebaru, Nanayama-mura, Higashi-matsuura-gun, on *Pinus densiflora*, c. 590 m, 9.8.1996, *Y. Ohmura 2487 & 2490*. Prov. Higo: Uchinomaki, Aso-gun, 27.3.1954, *M. Togashi s.n.* TAIWAN. Prov. Chiayi: Mt. Ali, 2200m, 6.1.1964, *S. Kurokawa 585*. Prov. Ilan: Piyanan, 1100–1300 m, 15.1.1964, *S. Kurokawa 762*. Prov. Kaohsiung: Mt. Nanfong, 800–1300 m, 7.2.1965, *S. Kurokawa 2843*. Prov. Nantou: Keitau, 1936, *H. Masuda s.n.* (herb. *Y. Asahina 36009*). CHINA. Kiemgsi, Lushan, 26.9.1942, *F. Fujikawa s.n.* INDIA. Sikkim: Darjeeling, 18.4.1960, *M. Togashi s.n.*; Gontok, c. 1900 m, 15.6.1960, *M. Togashi s.n.* NEPAL. East Nepal: Bilbatay Bhanjang, c. 2200 m, 25.10.1963, *M. Togashi s.n.*

## 8. *Usnea angulata* Ach., Synops. Lich., 307, 1814.

Holotype: America septentrionalis, *Mühlenberg 22–2* (H-ACH 1880!). Chemistry: norstictic acid [TLC was demonstrated by O. Vitikainen (Awasthi 1986)].

*Usnea asahinai* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 393, 1938. – *U. torquescens* Stirt. var. *asahinai* (Motyka) Asahina, J. Jpn. Bot. 46: 262, 1971. Isotype: Japan, Honshu, Prov. Musashi, Mt. Takao, 4.4.1926, *Y. Asahina 2201* (TNS!). Chemistry: usnic, norstictic and caperatic acids.

*Usnea sulcata* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 478, 1938. Lectotype (selected by Awasthi 1986): Brazil, Minas Geraes Stitio, 1885, *E. A. Vainio*, Lich. Bras. Exs. 388 (TUR-V 00450!). Chemistry: usnic, norstictic and caperatic acids.

*Usnea torquescens* Stirt. in Transact. New Zealand Instit. 30: 391, (1897) 1898. Isotype: Australia, New South Wales, Illawara, on rocks, 14.9.1882, *Bullii s.n.* (BM!). Chemistry: usnic, norstictic and caperatic acids.

Thallus fruticose, pendent, up to 50 cm long, color unknown when fresh, straw-yellow to olive-green or rusty in herbarium specimens, concolorous with thallus or pale at the base; branching anisotomic-dichotomous; branches slightly glossy on the surface, lacking pseudocyphellae and maculae, ridged to alate when mature, uninflated, tapering only near the apices, elongated towards distal branches, with many fibrils and lateral branches, 0.4–0.9 mm in diam.; lateral branches cylindrical at the base; papillae absent; soralia occasional, formed mainly on lateral branches, developed from scars of detached fibrils or lateral branches, punctiform, smaller than branch diam., sessile or often slightly stipitate, cortical margin not reflexed, slightly convex at the top, rarely with isidiomorphs, lacking granular soredia. Cortex 5.6–17% of the radius, lacking red pigment, *ceratina*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina slightly enlarged to form oblong or elliptic in shape. Medulla dense, narrow, 6.7–29% of the radius, lacking red pigment. Axis solid, 25–61% of the diameter, I –. Apothecia not seen.

Chemistry. Usnic, norstictic and caperatic acids.

*U. angulata* is a distinctive species and it is readily distinguished from other species by (1) the pendent thallus with anisotomic-dichotomous branching, (2) the ridged to alate branches, (3) the absence of granular soredia, (4) the *ceratina*-type plectenchymatous cortex, and (5) the presence of norstictic and caperatic acids.

Although caperatic acid has not been known from the type specimen of *U. angulata*, it was constantly detected in all examined materials including the type specimens of *U. asahinai*, *U. sulcata* and *U. torquescens* in the present study. The chemistry of type specimen of *U. angulata* needs to be revised. However, no morphological difference was observed between the type and the others. Therefore, *U. asahinai*, *U. sulcata* and *U. torquescens* are treated as synonyms of *U. angulata*.

In Japan, *U. angulata* is distributed in Honshu and Shikoku, where it grows on tree bark such as *Picea* at elevations between 10 and 1000 m. In Taiwan, it grows on tree bark at elevations between 1100 and 1300 m. This species is widely distributed in temperate to subtropical regions in East Asia, Oceania, North and South America and South Africa (Asahina 1971, Awasthi 1986, Herrera-Campos et al. 1998, Motyka 1936–38, Stevens 1999, Stirton 1881).

Exsiccata examined. JAPAN. Honshu. Prov. Rikuzen: Kitagama Seashore, 20.5.1967, *M. Togashi s.n.* (S. Kurokawa, Lich. Rar. Crit. Exs. 294). Prov. Kai: Lakeside of Yamanaka, Mt. Fuji, on *Picea polita*, c. 1000 m, 11.8.1952, *Y. Asahina s.n.* (S. Kurokawa & H. Kashiwadani, Lich. Rar. Crit. Exs. 550).

Representative specimens examined. JAPAN. Honshu. Prov. Rikuzen: Kitagama Seashore, 20.5.1967, *M. Togashi s.n.* Prov. Musashi: Mt. Takao, 4.4.1926, *Y. Asahina 2201*. Prov. Kai: Lakeside of Yamanaka, Mt. Fuji, 6.6.1956, *Y. Asahina s.n.* Prov. Kii: Mt. Koya, 23.8.1952, *Y. Asahina s.n.* Shikoku. Prov. Tosa: Nagasawa Water Fall, Higashitsuno-mura, Takaoka-gun, c. 600 m, 26.3.1983, *H. Kashiwadani 19842*. TAIWAN. Prov. Ilan: Piyanan, 1100–1300 m, 15.1.1964, *S. Kurokawa 759*.

## 9. *Usnea bismolliuscula* Zahlbr., Cat. Lich. Univ. 6: 542, 1923.

*U. molliuscula* Vain., Bot. Mag., Tokyo 35: 45, 1921, nom. illeg.; non *U. molliuscula* Stirt., Scott. Natur. 7: 77, 1883.

Holotype: Japan, Prov. Harima, on *Pinus densiflora*, 19.11.1916, *A. Yasuda 232* (TUR-V 00880!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

*Usnea bismolliuscula* f. *subramulifera* Asahina, Lich. Jap. 3: 65, 1956, syn. nov. Holotype: Japan, Honshu, Prov.

- Kazusa, Ichinomiya, 30.3.1952, *Y. Asahina s.n.* (TNS!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.
- Usnea bismolliuscula* f. *turgescens* Asahina, Lich. Jap. 3: 65, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Kazusa, Ichinomiya, 30.3.1952, *Y. Asahina 52330* (TNS!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.
- Usnea bismolliuscula* subsp. *pseudomolliuscula* Asahina, Lich. Jap. 3: 66, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Sagami, Hakone, Lakeside of Ashinoko, 9.10.1951, *M. Togashi s.n.* (herb. *Y. Asahina 1311*, TNS!). Chemistry: usnic and thamnolic acids.
- Usnea leucospilodea* Nyl., J. Linn. Soc. London, Bot. 20: 30, 1883, syn. nov. Holotype: Insula Penang pr. Malay Peninsula, Government Hill, ad arbores valde elatas, 1865, collector unknown (BM!). Chemistry: not examined.
- Usnea pygmea* Motyka, Lich. Gen. *Usnea* Stud. Monogr. 2: 499, 1938. Holotype: Japan, Jochohama (Yokohama), on *Cryptomeria*, 1868–1871, *Wawra 1590* pr.maj.p. (W, not seen). Chemistry: usnic acid and stictic acid complex (Awasthi 1986).

Thallus fruticose, erect to subpendent, up to 16 cm long, straw-yellow to yellowish-green when fresh, brownish in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches glossy on the surface, lacking pseudocypbellae and maculae, terete, with perforations on thicker branches, inflated, gradually tapering, with many fibrils and lateral branches, 0.6–1.5 mm in diam.; lateral branches constricted at the base; papillae very rare, hemispherical; soralia common, formed mainly on lateral branches, developed from scars of detached fibrils or the top of eroded papillae, confluenting each other to form irregular mass of asexual propagules, smaller than branch diam. but sometimes surrounding the branch, sessile to slightly stipitate, cortical margin not reflexed, slightly convex at the top often with numerous isidiomorphs, lacking granular soredia. Cortex thin, 2.0–6.3% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina slightly enlarged to be turbinate or fusiform. Medulla lax, wide, 30–40% of the radius, lacking red pigment. Axis solid, thin, 14–31% of the diameter, I–. Apothecia rare, lateral on lateral and terminal branches, up to 5.2 mm in diam., cup-shaped; thalloid exciple with sparse fibrils; disc pruinose, gray, lacking white rim; epihymenium 0–8  $\mu\text{m}$  thick; hymenium 40–64  $\mu\text{m}$  thick; hypothecium 40–60  $\mu\text{m}$  thick; spores 7.2–9.6  $\times$  4.8–6.4  $\mu\text{m}$  long.

Chemistry. Race 1, usnic, norstictic, menegazziaic, stictic, constictic and squamatic acids ( $\pm$ ), and atranorin ( $\pm$ ); Race 2, usnic and thamnolic acids.

The distinguishing features of *U. bismolliuscula* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the inflated branches which are glossy, smooth and perforated on the surface (Fig. 14), (3) the soralia which are confluenting each other to form irregular in shape and smaller than branch diam., (4) the absence of granular soredia, (5) the *merrillii*-type plectenchymatous cortex, and (6) the presence of stictic acid or thamnolic acid as major substance.

Two chemical races are recognized in the present area. Race 1 (stictic acid, 98%) is commonly found, and Race 2 (thamnolic acid, 2%) is rarely found. No morphological difference was found between them. Therefore, *U. bismolliuscula* subsp. *pseudomolliuscula*, which coincides with Race 2, is treated as a synonym of *U. bismolliuscula*.

Asahina (1956) separated *U. bismolliuscula* f. *subramulifera* from *U. bismolliuscula* by having the perpendicular fibrils, and f. *turgescens* by the large thallus and distinct artic-

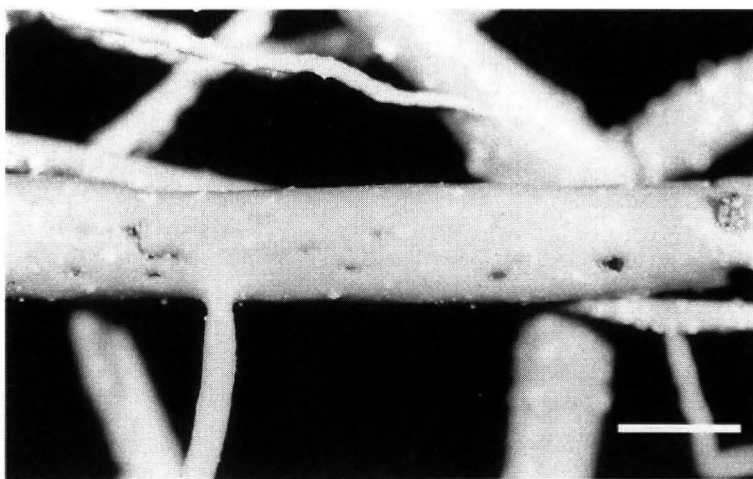


Fig. 14. Perforations in the thallus of *Usnea bismolliuscula* (*M. Togashi s.n.*).  
Scale = 1 mm.

ulation on the branches. However, they belong to the natural range of variation of *U. bismolliuscula*. Therefore, they are treated as synonyms of *U. bismolliuscula*.

*U. bismolliuscula* resembles *U. himalayana*, *U. nidifica* and *U. pygmoidea* in having inflated branches with soralia. However, it can be distinguished from the others by the presence of perforations on the branches.

In Japan, this species is distributed in Honshu, Shikoku and Kyushu, where it grows on bark of trees such as *Cryptomeria*, *Pinus* and *Quercus*. It also rarely grows on rocks. This species is found at elevations between 150 and 1000 m. In Taiwan, it is found at elevations between 400 and 1000 m. *U. bismolliuscula* is also known from India and Australia (Awasthi 1986, Stevens 1999).

Exsiccata examined. Race 1. JAPAN. Honshu. Prov. Kazusa: Ichinomiya, 30.3.1952, *Y. Asahina 52330* (S. Kurokawa; Lich. Rar. Cri. Exs. 295).

Representative specimens examined. Race 1. JAPAN. Honshu. Prov. Rikuzen: Ohkawa-mura, Monou-gun, 24.6.1931, *S. Murai s.n.* (herb. *Y. Asahina 1306*). Prov. Hitachi: Tsukuba-san shrine, Mt. Tsukuba, Tsukuba-city, on stone work, c. 270 m, 23.7.1998, *Y. Ohmura 4434*. Prov. Shimofusa: Cape Inubo, 28.12.1931, *F. Fujikawa s.n.* (herb. *Y. Asahina 1301*). Prov. Awa: Mt. Kiyosumi, 1.1.1958, *M. Togashi s.n.* (herb. *Y. Asahina 5811*). Prov. Sagami: Hakone, Lakeside of Ashinoko, 9.10.1951, *M. Togashi s.n.* Prov. Sado: Konpon Temple, Niibo-mura, 10.5.1953, *Y. Asahina s.n.* Prov. Shinano: Mt. Tateshina, 9.10.1955, *M. Togashi s.n.* Prov. Kai: Asahigaoka, Lakeside of Yamanaka, Minami-tsuru-gun, c. 980 m, 25.7.1957, *S. Kurokawa 57101*. Prov. Suruga: Mt. Kuno-san, 8.7.1951, *S. Kurokawa 51100*. Prov. Izu: Kamogahora, Vicinity of Mishima, 12.8.1929, *Y. Asahina 1310*. Prov. Tohtomi: Mt. Kohmyo, 24.3.1888, *M. Miyoshi s.n.* (herb. *Yatabe 297*). Prov. Mikawa: Taguchi-machi, Kita-shitara-gun, c. 500 m, 30.10.1965, *M. Togashi s.n.* Prov. Owari: Inuyama, 26.8.1938, *Y. Asahina 1312*. Prov. Ohmi: Mt. Ibuki, 14.8.1935, *Y. Asahina 1308*. Prov. Yamashiro: Koshihata, Kyoto, 3.4.1967, *M. Togashi s.n.* Prov. Ise: Oshibuchi, Nansei-cho, Watarai-gun, 19.3.1966, *M. Togashi s.n.* (herb. *Y. Asahina 66319*). Prov. Yamato: Dorogawa, Tenkawa-mura, Yoshino-gun, 12.6.1952, *M. Togashi s.n.* Prov. Kii: Mt. Koya, 23.8.1952, *Y. Asahina s.n.* Prov. Settsu: Mt. Myoken, 7.9.1952, *M. Togashi s.n.* Prov. Tanba: Mt. Koganei, Nishiki-cho, Taki-gun, on tree bark, c. 300 m, 10.7.1967, *H. Kashiwadani 3174*; Ryuzoji Temple, Manamijo, Taki-gun, 11.6.1957, *M. Togashi s.n.* Prov. Tango: Nariaiji, Miyazu-city, 7.7.1956, *M. Togashi s.n.* Prov. Izumo: Izumo Temple, 24.8.1952, *F. Fujikawa s.n.*

(herb. *Y. Asahina* 52824). Prov. Aki: Shiwa-higashi, Shiwa-cho, Kamo-gun, on *Pinus thunbergii*, 30.5.1968, *H. Kashiwadani* 3474. Prov. Suo: Dadoko, Nakasu-kita, Tokuyama-city, c. 400 m, 23.4.1978, *H. Kashiwadani* 14524. Shikoku. Prov. Awa: Jinryo-mura, Myozai-gun, 25.7.1952, *T. Inobe s.n.* Prov. Sanuki: Kankake, 5.10.1952, *M. Togashi s.n.* Prov. Iyo: Mt. Onigajo, 14.6.1955, *S. Kurokawa s.n.* Prov. Tosa: Mt. Dohgamori, Hata-gun, 17.6.1955, *S. Kurokawa s.n.* Kyushu. Prov. Bungo: Shingai, Tsukinoki, Yamakuni-machi, Shimoge-gun (33°27'N, 130°59'E), on *Cryptomeria japonica*, c. 330 m, 3.3.1997, *Y. Ohmura* 2968. Prov. Hyuga: Agata, Nichinan-city, 21.3.1954, *S. Hattori s.n.* Prov. Hizen: Kashinokibaru Marsh, Kashinokibaru, Ikebaru, Nanayama-mura, Higashi-matsuura-gun (33°25'N, 130°10'E), on *Pinus densiflora*, c. 590 m, 18.7.1992, *Y. Ohmura* 218. Prov. Higo: Uchinomaki, Aso-gun, 27.5.1954, *M. Togashi s.n.* (herb. *Y. Asahina* 53527). Prov. Satsuma: Ibusuki, 1.1.1938, *Y. Asahina* 1314. TAIWAN. Prov. Taitung: Antung Pass, 400–995 m, 27.1.1965, *S. Kurokawa* 2666. INDIA. Takuda, Darjeeling, 18.4.1960, *M. Togashi s.n.*

Race 2. JAPAN. Honshu. Prov. Bitchu: Takahashi, 8.11.1931, *Yoshino s.n.*

#### 10. *Usnea ceratina* Ach., Lich. Univ., 619, 1810.

Lectotype (selected here): (Poland), Silesia, *Mosig s.n.* (H-ACH 1890!). Chemistry: usnic, diffractaic, barbatic and squamtic acids (Herrera-Campos et al. 1998).

*Usnea creberrima* Vain. var. *fitulescens* Asahina, Lich. Jap. 3: 109, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Settsu, Kazan-in, Miwa-machi, Arima-gun, on *Cryptomeria japonica*, 30.8.1953, *M. Togashi s.n.* (herb. *Y. Asahina* 1905, TNS!). Chemistry: usnic, barbatic, diffractaic, baeomycesic and squamatic acids, and US5.

*Usnea creberrima* var. *simplicior* Asahina, Lich. Jap. 3: 108, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Kai, Lakeside of Yamanaka, Mt. Fuji, on *Picea polita*, 11.8.1952, *M. Togashi s.n.* (herb. *Y. Asahina* 1903, TNS!). Chemistry: usnic, barbatic, diffractaic, baeomycesic and squamatic acids, and US5.

*Usnea roseola* Vain., Bot. Mag. Tokyo 35: 46, 1921, syn. nov. Holotype: Japan, Prov. Rikuzen, Sendai, 22.6.1913, *A. Yasuda* 138 (TUR-V 00875!). Chemistry: usnic, diffractaic, barbatic, baeomycesic and squamatic acids, and US5.

*Usnea roseola* subsp. *pseudoroseola* Asahina, Lich. Jap. 3: 105, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Suruga, Subashiri-guchi 1-gome, Mt. Fuji, 21.6.1925, *Y. Asahina* 17071 (TNS!). Chemistry: usnic, barbatic and 4-*O*-demethylbarbatic acids, and US5.

*Usnea subroseola* Asahina, Lich. Jap. 3: 106, 1956, syn. nov. – *U. roseola* f. *subroseola* (Asahina) Asahina, J. Jpn. Bot. 40: 226, 1965. Holotype: Japan, Honshu, Prov. Tanba, Oyama-mura, Taki-gun, 14.7.1927, *Y. Asahina* 1704 (TNS!). Chemistry: usnic, barbatic, diffractaic, baeomycesic and squamatic acids, and US5.

Thallus erect to subpendent, up to 25 cm long, grayish-green when fresh, brownish in herbarium specimens, pale to concolorous with thallus at the base; branching anisotomic-dichotomous; branches slightly glossy on the surface, lacking pseudocyphellae and maculae, terete, uninflated, gradually tapering, usually with many lateral branches, 0.6–1.0 mm in diam.; lateral branches cylindrical at the base; papillae sparse, verrucose; soralia common, formed mainly on lateral and terminal branches, developed from at the top of eroded papillae, ± discrete, rounded in shape, up to branch diam., distinctly stipitate, cortical margin slightly reflexed, convex at the top often with isidiomorphs, lacking granular soredia. Cortex 5.3–10% of the radius, *ceratina*-type plectenchymatous, hyphae pachydermatous, lacking red pigment, with oblong or turbinate lumina. Medulla moderate in density, 23–29% of the radius, with red pigment near the cortex. Axis solid, 29–36% of the diameter, I –. Apothecia rare, lateral on lateral and terminal branches, up to 5.4 mm in diam., flat in shape; thalloid exciple with sparse fibrils; disc pruinose, pale yellow to gray, lacking white rim; epihymenium 0–18 μm thick; hymenium 35–50 μm thick; hypothecium 16–35 μm thick; spores 9–10 × 5–6 μm long.

Chemistry. Race 1, usnic, barbatic, diffractaic, baeomycesic and squamatic acids,

and US5; Race 2, usnic, barbatic and 4-*O*-demethylbarbatic acids, and US5.

The distinguishing features of *U. ceratina* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the rounded soralia which are stipitate and convex at the top often with isidiomorphs, (3) the presence of red pigment (US5) in the medulla near the cortex, and (4) the presence of diffractaic or barbatic acids as the major substance.

When Acharius (1810) described *U. ceratina*, he cited two specimens in the protologue, one collected from Silesia by Mosig, and the another from Gallia by Persoon. Although the former specimen has been cited as the holotype (Herrera-Campos et al. 1998), the lectotype should be selected according to Art. 9.2 of Tokyo Code (Greuter et al. 1994). The former specimen agrees well with the protologue, but the latter does not belong to this species, since the red color in the medulla of this specimen is not caused by US5. Therefore, the specimen collected from Silesia is designated here as the lectotype of *U. ceratina*.

When Asahina (1956) described *U. creberrima* Vain. var. *simplicior* Asahina, he did not designate the holotype. However, in the protologue, he mentioned this taxon was only collected once in the forest of Mt. Fuji. Only one specimen is located in TNS, and the measurements of the ratio of the cortex, medulla and axis in the packet is identical with the values shown in the protologue. The thallus of the specimen is also identical with the photograph shown in the protologue. Thus, this specimen agrees with the protologue, and can be accepted as the holotype of *U. creberrima* var. *simplicior*.

Two chemical races were recognized in the present area. Race 1 (diffractaic acid, 91%) was commonly found. Only one specimen of Race 2 (barbatic acid) was found. No morphological and ecological differences were found between them. Therefore, *U. roseola* subsp. *pseudoroseola*, which coincides with Race 2, is treated as a synonym of *U. ceratina*.

*U. ceratina* is variable in morphology, especially in thallus size, flexure of branches, and fissure in axis. The variations of these features belong to the natural range of *U. ceratina*. Therefore, *U. creberrima* var. *simplicior* having large thallus, *U. creberrima* var. *fistulescens* having fissure in the axis, *U. roseola* having small thallus, and *U. subroseola* having flexuous branches are treated under the synonyms of *U. ceratina*.

*U. ceratina* resembles *U. mutabilis* in having red pigment in the medulla. However, it can be distinguished from the latter by the location of red pigment in the medulla: the red pigment of *U. ceratina* is located near the cortex in the medulla, and that of *U. mutabilis* is located near the axis in the medulla. Furthermore, the chemistry is different: *U. ceratina* contains diffractaic or barbatic acids as major substance, but *U. mutabilis* is lacking them.

In Japan, *U. ceratina* is distributed in Honshu, Shikoku and Kyusyu, where it grows on bark of *Cryptomeria* at ca. 1000 m alt. In Taiwan, it is found on tree bark at elevations between 2000 and 2600 m. Taiwanese specimens are often fertile, though Japanese specimens are all sterile. This species is widely distributed in the temperate to subtropical regions such as Asia, Europe, East Africa, North America and Oceania (Halonen et al. 1998, Stevens 1999, Swinscow & Krog 1979).

Representative specimens examined. Race 1. JAPAN. Honshu. Prov. Shinano: Yatsugatake Mts., 5.1958, Y. Asahina & M. Togashi s.n. Prov. Yamato: Dorogawa, Tenkawa-mura, Yoshino-gun, 12.6.1952, M. Togashi s.n. (herb. Y. Asahina 1810b). Prov. Kii: en route from Ichinobashi to Okunoin, Mt. Koya, on *Cryptomeria japonica*, c. 800 m, 1.4.1999, Y. Ohmura 4492. Prov. Tanba: Komakura, Johnan-mura, Taki-gun, 22.6.1952, S. Satake s.n. (herb. Y. Asahina 1708). Shikoku. Prov. Iyo: Kawase-mura, Kami-ukena-gun, 28.9.1965, M. Togashi s.n. (herb. Y.

*Asahina 65928*); Mt. Iwayaji, Kami-ukena-gun, on *Cryptomeria japonica*, c. 500 m, 21.10.1970, *H. Kashiwadani 8535*. Kyushu. Prov. Bungo: Tsue, Yufuin-cho, Ohita-gun, 1.6.1954, *M. Togashi s.n.* TAIWAN. Prov. Taitung: Chokakurai, 1936, *H. Masuda 36007*.

Race 2. JAPAN. Honshu. Prov. Musashi: Mt. Mitsumine, Chichibu, 30.8.1951, *S. Kurokawa 510067*.

11. *Usnea confusa* Asahina, Lich. Jap. 3: 97, 1956.

Lectotype (selected here): Japan, Honshu, Prov. Suruga, Subashiri-guchi, Mt. Fuji, 7.7.1952, *Y. Asahina 5277* (TNS!). Chemistry: usnic, salazinic and constictic acids.

*Usnea confusa* subsp. *rubroreagens* Asahina, Lich. Jap. 3: 98, 1956, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Kai, Lakeside of Shoji-ko, Mt. Fuji, 9.1952, *M. Togashi s.n.* (herb. *Y. Asahina 52901*, TNS!). Chemistry: usnic and protocetraric acids.

Thallus fruticose, erect, up to 9 cm long, grayish-green when fresh, brownish to rusty in herbarium specimens, concolorous with thallus at the base, sometimes with annular cracks especially near the base; branching anisotomic-dichotomous; branches slightly glossy on the surface, lacking pseudocypbellae and maculae, terete, inflated, gradually tapering, with many fibrils and lateral branches, 0.5–1.8 mm in diam.; lateral branches constricted at the base; papillae sparse to common, hemispherical to verrucose; soralia common, formed mainly on lateral branches, developed from the top of eroded papillae,  $\pm$  discrete, rounded, larger than branch diam., sessile to slightly stipitate, cortical margin not reflexed, slightly convex at the top often with isidiomorphs, lacking granular soredia. Cortex thin, 3.4–9.3% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina almost the same as medullary hyphae. Medulla lax to moderate in density, wide, 28–37% of the radius, lacking red pigment. Axis solid, thin, 15–31% of the diameter, I –. Apothecia not seen.

Chemistry. Race 1, usnic, salazinic, protocetraric (trace) and constictic acids ( $\pm$ ), and atranorin ( $\pm$ ); Race 2, usnic and protocetraric acids.

The distinguishing features of *U. confusa* are (1) the erect thallus with anisotomic-dichotomous branching, (2) the inflated branches which are constricted at the base, (3) the rounded soralia which are formed on lateral branches, (4) the absence of granular soredia, (5) the *merrillii*-type plectenchymatous cortex, and (6) the presence of salazinic or protocetraric acids as the major substance.

When Asahina (1956) described *U. confusa*, he did not cite any specimens in the protologue; however, he showed the ratio of the cortex, medulla and axis. The measurements of the ratio of the specimen, labeled as Japan, Honshu, Prov. Suruga, Subashiri-guchi, 7.7.1952, *Y. Asahina 5277*, is identical with the protologue. In addition, the specimen is marked as "Typus" on the herbarium packet by Asahina. Therefore, this specimen is selected here as the lectotype.

When Asahina (1956) described *U. confusa* subsp. *rubroreagens* Asahina, he did not cite any specimens in the protologue. However, he showed a photograph of thalli in the protologue. The thalli in the specimen, labeled as Japan, Honshu, Prov. Kai, Lakeside of Shoji-ko, Mt. Fuji, 9.1952, *M. Togashi s.n.* (herb. *Y. Asahina 52901*), are identical with the photograph; they agree well with the protologue morphologically and chemically. Therefore, this specimen is selected as the lectotype.

Two chemical races of *U. confusa* are recognized in the present area. Race 1 (salazinic



acid, 85%) was commonly found, and Race 2 (protocetraric acid, 15%) was occasionally found. As no morphological and ecological differences were found between them, the chemical differences found in this species are considered to have no taxonomic value. Although Stevens (1999) reported the occurrence of diffractaic, fumarprotocetraric, galbinic and norstictic acids from this species in Australia, these substances were not detected from the present area.

*U. confusa* resembles *U. dasaea*, *U. glabrata*, *U. hakonensis* and *U. pygmoidea* in having inflated branches with soralia. However, *U. confusa* is distinguished from *U. dasaea* and *U. pygmoidea* by the rounded soralia and the absence of norstictic acid, from *U. glabrata* by the absence of granular soredia, and from *U. hakonensis* by the *merrillii*-type plectenchymatous cortex and the absence of US1 and US2.

In Japan, *U. confusa* is distributed in Hokkaido, Honshu and Shikoku, where it grows on bark of trees such as *Abies*, *Cryptomeria* and *Larix* at elevations between 100 and 1300 m. In Taiwan, it is found at elevations between 1100 and 2200 m. This species has been also collected from India, Nepal and Indonesia. In addition, this species has been reported from Oceania by Stevens (1999).

Representative specimens examined. Race 1. JAPAN. Hokkaido. Prov. Kushiro: along Route 44, Akkeshi-cho, Akkeshi-gun, on *Abies sachalinensis*, c. 100 m, 3.9.1996, *Y. Ohmura* 2754. Honshu. Prov. Rikuzen: Kitagama Seashore, 20.5.1967, *M. Togashi* s.n. (herb. *Y. Asahina* 67520). Prov. Shinano: 4.3 km SW of Lake Chiyoda, Fujisawa, Takato-machi, Kami-ina-gun (35°47'N, 138°08'E), on *Larix kaempferi*, 1220 m, 28.6.1997, *Y. Ohmura* 3129. Prov. Kai: Lakeside of Shoji, Mt. Fuji, 15.9.1952, *M. Togashi* s.n. (herb. *Y. Asahina* 52915). Prov. Suruga: Subashiri-guchi, 1-gome, 16.7.1952, *Y. Asahina* s.n. Prov. Mikawa: Mt. Horaiji, 6.1.1956, *Y. Asahina* s.n. Prov. Yamato: Murou Temple, Murou-mura, Uda-gun, 10.10.1954, *Y. Tanaka* 937. Prov. Kii: Mt. Koya, 23.8.1952, *Y. Asahina* s.n. Prov. Settsu: Arima-guchi, Mt. Rokko, 4.10.1953, *M. Togashi* s.n. Prov. Tanba: Mananjo, Jonan-mura, Taki-gun, 5.10.1952, *S. Satake* s.n. Prov. Bingo: Ueyama-mura, Sera-gun, 3.1.1933, *T. Sato* 89b. Shikoku. Prov. Awa: Jinryo-mura, Myozai-gun, 1.1.1940, *T. Inobe* s.n. Prov. Sanuki: Kankake, Shodo-shima Island, 15.8.1953, *M. Togashi* s.n. (herb. *Y. Asahina* 53815). TAIWAN. Prov. Chiayi: Mt. Ali, 2200 m, 6.1.1964, *S. Kurokawa* 583. Prov. Ilan: Piyanan, 1100–1300 m, 15.1.1964, *S. Kurokawa* 763. Prov. Nantou: Chitou, 30.1.1964, *S. Kurokawa* 1409. INDIA. Phalut, Darjeeling, 10.5.1960, *M. Togashi* s.n. NEPAL. East Himalaya, 1.12.1963, *M. Togashi* s.n. INDONESIA. Java, Garden of Tjibodas, c. 1400 m, 12–13.3.1964, *S. Kurokawa* 2228.

Race 2. JAPAN. Prov. Kii: en route from Ichinobashi to Okunoin, Mt. Koya, on *Cryptomeria japonica*, c. 800 m, 1.4.1999, *Y. Ohmura* 4487. TAIWAN. Prov. Taitung: Chokakulai, 1936, *H. Masuda* s.n. (herb. *Y. Asahina* 36004).

## 12. *Usnea dasaea* Stirt., Scott. Natur. 6: 104, 1881.

Holotype: Madeira, Funchal, *Payne* (BM!). Chemistry: usnic, norstictic, galbinic and salazinic acids.

*Usnea confusa* Asahina subsp. *subconfusa* Asahina, J. Jpn. Bot. 43: 130, 1968, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Kai, Lakeside of Yamanaka, Mt. Fuji, 11.8.1952, *M. Togashi* s.n. (TNS!). Chemistry: usnic, protocetraric (trace) and salazinic acids.

*Usnea galbinifera* Asahina, J. Jpn. Bot. 38: 257, 1963. Holotype: India, Darjeeling, en route from Phalut to Sandakphu, 10.5.1960, *M. Togashi* s.n. (TNS!). Chemistry: usnic, norstictic, galbinic and salazinic acids.

*Usnea galbinifera* f. *subfibrillosa* Asahina, in Hara, Fl. Eastern Himalaya, 602, 1966, syn. nov. Lectotype (selected here): Nepal, East Nepal, Bibatay Bhanjang, 2200 m, 25.10.1963, *M. Togashi* s.n. (TNS!). Chemistry: usnic, norstictic, galbinic and salazinic acids.

*Usnea kinkiensis* Asahina, J. Jpn. Bot. 33: 257, 1958, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Yamashiro, Koshihata, Ukyo-ku, Kyoto, 3.4.1958, *Y. Asahina* 58411 (TNS!). Chemistry: usnic, norstictic and salazinic acids.

*Usnea kinkiensis* Asahina f. *gracilior* Asahina, J. Jpn. Bot. 33: 258, 1958, syn. nov. Lectotype (selected here):

- Japan, Honshu, Prov. Yamashiro, Koshihata, Ukyo-ku, Kyoto, 29.6.1958, *Y. Asahina 58629a* (TNS!). Chemistry: usnic, norstictic and salazinic acids.
- Usnea kyotoensis* Asahina, J. Jpn. Bot. 33: 259, 1958, syn. nov. Holotype: Japan, Honshu, Prov. Yamashiro, Koshihata, Ukyo-ku, Kyoto, 20.11.1957, *M. Togashi s.n.* (herb. *Y. Asahina 57112*, TNS!). Chemistry: usnic, norstictic and galbinic acids.
- Usnea pygmaea* (non Motyka) Asahina subsp. *kitamiensis* Asahina, Lich. Jap. 3: 99, 1956, syn. nov. – *U. confusa* subsp. *kitamiensis* (Asahina) Asahina, J. Jpn. Bot. 43: 130, 1968. Lectotype (selected here): Japan, Hokkaido, Prov. Kitami, Bihoro Pass, 27.6.1953, *Y. Asahina s.n.* (TNS!). Chemistry: usnic, psoromic, 2'-*O*-demethylpsoromic, norstictic, galbinic and salazinic acids.
- Usnea spinigera* Asahina, Lich. Jap. 3: 85, 1956. Holotype: Japan, Honshu, Prov. Kazusa, Ichinomiya, 30.3.1952, *Y. Asahina 52330* (TNS!). Chemistry: usnic, norstictic and salazinic acids.
- Usnea spinigera* f. *subnuda* Asahina, Lich. Jap. 3: 86, 1956. Holotype: Japan, Honshu, Prov. Kazusa, Ichinomiya, 30.3.1952, *Y. Asahina 52330b* (TNS!). Chemistry: usnic, norstictic and salazinic acids.
- Usnea undulata* Stirt., Scott. Natur. 6: 104, 1881. Holotype: Madeira, Funchal, *Payne s.n.* (BM!). Chemistry: usnic, norstictic, galbinic and salazinic acids (Clerc & Herrera-Campos 1997).

Thallus fruticose, erect to subpendent, up to 21 cm long, grayish-green when fresh, straw-yellow to rusty in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches matt to slightly glossy on the surface, lacking pseudocyphellae and maculae, terete, inflated, gradually tapering, with many spinulose fibrils and lateral branches, 0.7–1.9 mm in diam.; lateral branches slightly constricted at the base; papillae sparse, hemispherical; soralia common, formed mainly on lateral branches, developed from scars of detached fibrils, partially confluent each other to form irregular mass of asexual propagules, smaller than branch diam. but sometimes surrounding the branch, slightly stipitate, cortical margin not reflexed, convex at the top with numerous isidiomorphs, lacking granular soredia. Cortex 3.3–12% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina slightly enlarged to be fusiform to oblong or turbinate in shape. Medulla lax to moderate in density, 23–41% of the radius, lacking red pigment. Axis solid, 11–32% of the diameter, I –. Apothecia very rare, lateral on terminal branches, up to 2.3 mm in diam., cup-shaped; thalloid exciple with many fibrils; disc pruinose, gray, lacking white rim; epihymenium 2.0–12  $\mu\text{m}$  thick; hymenium 56–66  $\mu\text{m}$  thick; hypothecium 22–40  $\mu\text{m}$  thick; spores not seen.

Chemistry. Race 1, usnic, norstictic, salazinic and protocetraric acids ( $\pm$ ), and atranorin ( $\pm$ ); Race 2, usnic, norstictic and galbinic acids; Race 3, usnic, psoromic, 2'-*O*-demethylpsoromic, norstictic, galbinic and salazinic acids.

The distinguishing features of *U. dasaea* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the inflated branches often with many spinulose fibrils, (3) the irregular shaped soralia which are developed from the detached fibrils, (4) the absence of granular soredia, (5) the *merrillii*-type plectenchymatous cortex, and (6) the presence of salazinic or galbinic acids as the major substance.

When Asahina (1968b) described *U. confusa* subsp. *subconfusa*, he did not cite any specimens in the protologue. The protologue shows only chemical constituent and color reaction with K and PD. The authentic specimen of this taxon labeled as Japan, Honshu, Prov. Kai, Lakeside of Yamanaka, Mt. Fuji, 11.8.1952, *M. Togashi s.n.* examined by Asahina agree well with the protologue morphologically and chemically. Therefore, this specimen is selected as the lectotype of *U. confusa* subsp. *subconfusa*.

When Asahina (1966) described *U. galbinifera* var. *subfibrillosa*, he selected a specimen, collected from Nepal, East Nepal, Bibatay Bhanjang, 2200 m, 25.10.1963, *M. Togashi s.n.*, as the type. According to the protologue, the specimen, however, was divided into two specimens, one housed in TNS and the other in TI. At that time, he did not designate which specimen was holotype or isotype. The specimen housed in TNS agrees well with the protologue morphologically as well as chemically. Therefore, the former specimen is designated as the lectotype of *U. galbinifera* var. *subfibrillosa*.

The type specimen of *U. kinkiensis* Asahina is comprised of four individuals in the packet. They agree with the protologue morphologically, but they are chemically heterogeneous. One of them contains usnic, norstictic and salazinic acids, but the other three contain galbinic acid in addition. The former individual is selected here as the lectotype of *U. kinkiensis* in order to avoid the further confusion in the typification.

When Asahina (1958) described *U. kinkiensis* f. *gracilior* Asahina, he did not cite any specimen in the protologue. However, he showed the ratio of the cortex, medulla and axis of this taxon in the protologue. The specimen, labeled as Japan, Honshu, Prov. Yamashiro, Koshihata, Ukyo-ku, Kyoto, 29.6.1958, *Y. Asahina 58629a*, is considered to have been used for showing the value. Therefore, this specimen is designated as the lectotype of *U. kinkiensis* f. *gracilior*.

When Asahina (1956) described *U. pygmea* (non Motyka) Asahina subsp. *kitamiensis* Asahina [later transferred to *U. confusa* subsp. *kitamiensis* (Asahina) Asahina], he did not designate the type specimen in the protologue. However, the specimen marked as "Typus" of this taxon is housed in TNS, which is labeled as Japan, Hokkaido, Prov. Kitami, Bihoro Pass, 27.6.1953, *Y. Asahina s.n.* This specimen agrees with the protologue of *U. pygmea* subsp. *kitaminensis* morphologically, although small amount of additional substances (psoromic, 2'-*O*-demethylpsoromic, and galbinic acids) along with usnic and norstictic acids were detected by TLC in the present study. Therefore, this specimen is selected as the lectotype of *U. pygmea* subsp. *kitamiensis*.

*U. dasaea* is very variable in morphology, especially the amount of spinulose fibrils. The fibrils are easily detached and may act as asexual propagules, from which soralia arise with many isidiomorphs. The spinulose form and the sorediate form of this species look very different. Therefore, many taxa were described as shown in the synonyms. However, there is no discontinuity among them, and they can all be treated as synonyms of *U. dasaea*.

Three chemical races were recognized in the present area. Race 1 (62%) is more common than Race 2 (37%), though Clerc & Herrera-Campos (1997) reported most of the collections of this species from North America were Race 2. Only one specimen of Race 3 (psoromic acid containing race, 1%) was found. As no morphological and ecological differences were found among them, the chemical differences found in this species are considered to have no taxonomic value.

*U. dasaea* very much resembles *U. confusa*, *U. glabrata*, *U. hakonensis* and *U. pygmoidea* in having the inflated branches with soralia. However, it can be distinguished from *U. glabrata* and *U. pygmoidea* by the absence of granular soredia, and from *U. confusa* and *U. hakonensis* by irregular shaped soralia enlarged by repeated growth of isidiomorphs.

In Japan, *U. dasaea* is distributed in Hokkaido, Honshu, Shikoku and Kyushu, where it grows on tree barks such as *Larix*, *Pinus*, *Prunus* and *Quercus* at elevations between 50 and 1500 m. In Taiwan, it is found at elevations between 1500 and 2600 m. This species is widely distributed in temperate to subtropical regions such as Asia, North and South America, Europe and Africa (Clerc & Herrera-Campos 1997).

Representative specimens examined. Race 1. JAPAN. Hokkaido. Prov. Nemuro: Ochiishi, c. 50 m, 2.9.1965, *S. Kurokawa* 65833. Prov. Hidaka: Monbetsu, on *Quercus dentata*, 4.7.1951, *M. Tatewaki* s.n. Honshu. Prov. Rikuzen: Otomo-mura, Kesen-gun, 28.9.1901, *G. Toba* s.n. Prov. Kazusa: Ichinomiya, 30.3.1952, *Y. Asahina* 52330. Prov. Sagami: Lakeside of Ashinoko, Hakone, 15.7.1952, *M. Togashi* s.n. Prov. Shinano: Todai, Hase-mura, Kami-ina-gun (35°47'N, 138°08'E), on *Pinus densiflora*, c. 1040 m, 27.6.1997, *Y. Ohmura* 3113. Prov. Kai: Lakeside of Yamanaka, Mt. Fuji, 6.5.1956, *M. Togashi* s.n. Prov. Suruga: Gotenba, 14.4.1952, *Y. Asahina* 52441. Prov. Izu: Honryuji Temple, Nirayama, 9.4.1958, *S. Kurokawa* 58015. Prov. Tohtomi: Kuma-mura, Iwata-gun, 23.3.1969, *M. Togashi* s.n. Prov. Mikawa: Mt. Horaiji, Kadoya, Horai-cho, Minami-shitara-gun (34°58'N, 137°35'E), on twigs of *Prunus* sp., c. 340 m, 5.12.1996, *Y. Ohmura* 2842. Prov. Ohmi: Ohno-mura, Koga-gun, c. 240 m, 31.5.1952, *S. Kurokawa* 520012. Prov. Yamashiro: Mt. Kurama, 4.4.1939, *Y. Asahina* s.n. Prov. Yamato: Murou Temple, Murou-mura, Uda-gun, 13.11.1953, *M. Togashi* s.n. Prov. Kii: Mt. Koya, 23.8.1952, *Y. Asahina* s.n. Prov. Settsu: Sengari, Dohjo-mura, Arima-gun, 30.11.1952, *T. Satake* s.n. (herb. *Y. Asahina* 52113). Prov. Izumi: Mt. Makinoo, Yokoyama-mura, Senboku-gun, 26.11.1950, *M. Mizutani* s.n. Prov. Tanba: Ido, Yamakuni-mura, Kita-kuwada-gun, 7.11.1955, *M. Togashi* s.n. (herb. *Y. Asahina* 55171). Prov. Aki: Haji, Yachiyo-cho, Takata-gun, c. 260 m, 10.4.1971, *H. Kashiwadani* 8725. Shikoku. Prov. Awa: Jinryo-mura, Myozai-gun, 25.7.1952, *T. Inobe* s.n. Prov. Iyo: Mt. Iwayaji, Kami-ukena-gun, c. 500 m, 21.10.1970, *H. Kashiwadani* 8535c. Kyushu. Prov. Bungo: Egomori, Yabakei-machi, Shimoge-gun (33°21'N, 131°12'E), on *Quercus acutissima*, c. 420 m, 4.3.1997, *Y. Ohmura* 3018b. TAIWAN. Mt. Nan-Fu-Ta-San, 1500–2400 m, 19.1.1964, *S. Kurokawa* 968b.

Race 2. JAPAN. Hokkaido. Prov. Hidaka: Monbetsu, Saru-gun, 4.7.1951, *M. Tatewaki* s.n. (herb. *Y. Asahina* 5174). Honshu. Prov. Musashi: Mikuni Pass, Chichibu, 23.8.1952, *S. Kurokawa* 520752. Prov. Shinano: Nakamichi, Izumino-mura, Suwa-gun, 4.5.1958, *Y. Asahina* [5846] & *M. Togashi*. Prov. Kai: Lakeside of Yamanaka, Nakano-mura, Minami-tsuru-gun, 30.7.1954, *S. Kurokawa* 540324. Prov. Izu: Tanaka-mura, Tagata-gun, 28.8.1951, *Y. Asahina* s.n. Prov. Yamashiro: Koshihata, Kyoto, 3.4.1958, *Y. Asahina* [58408a] & *M. Togashi*. Prov. Settsu: Sengari, Dohjo-mura, Arima-gun, 30.11.1952, *T. Satake* s.n. (herb. *Y. Asahina* 52113). Prov. Kawachi: Yodoshi, Chihaya-mura, Minami-Kawachi-gun, 23.12.1954, *M. Togashi* s.n. (herb. *Y. Asahina* 5423). Shikoku. Prov. Tosa: Mt. Dohgamori, Hata-gun, on *Pinus densiflora*, 17.6.1955, *S. Kurokawa* s.n. TAIWAN. Mt. Nan-Fu-Ta-San, 1500–2400 m, 19.1.1964, *S. Kurokawa* 960. Prov. Chiayi: Mt. Ali, 24.12.1925, *Y. Asahina* F-282b. Prov. Nantou: Keitau, 30.10.1933, *H. Masuda* s.n. (herb. *Y. Asahina* 33103).

Race 3. Only the type specimen of *U. pygmaea* (non Motyka) *Asahina* subsp. *kitamiensis* *Asahina*.

### 13. *Usnea dendritica* Stirt., Scott. Natur. 6: 296, 1882.

Holotype: (India, W. Bengal, Darjeeling district), Tongloo, c. 3000 m, alt., 6.1881, *G. Watt* 14, C (BM!). Chemistry: usnic, barbatic, 4-*O*-demethylbarbatic, norstictic, protocetraric and salazinic acids.

*Usnea ogatai* *Asahina*, J. Jpn. Bot. 45: 129, 1970, syn. nov. Holotype: India, Darjeeling, Senchal, 6.4.1960, *M. Togashi* s.n. (TNS!). Chemistry: usnic, barbatic, 4-*O*-demethylbarbatic, norstictic, protocetraric and salazinic acids.

Thallus erect to subpendent, up to 8 cm long, color unknown when fresh, brown to rusty in herbarium specimens, concolorous with thallus at the base, with annular cracks especially near the base; branching anisotomic-dichotomous; branches matt on the surface, lacking pseudocyphellae and maculae, terete, uninflated, gradually tapering, usually with many fibrils and lateral branches, 1.0–1.5 mm in diam.; lateral branches cylindrical at the base; papillae common, cylindrical; soralia rare, formed on thicker branches, developed from the top of eroded papillae, discrete, punctiform to irregularly rounded in shape, small-

er than branch diam., distinctly stipitate, cortical margin not reflexed, slightly convex at the top rarely with isidiomorphs, lacking granular soredia. Cortex 7.3–11% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, with fusiform to oblong lumina. Medulla moderate in density, 17–29% of the radius, lacking red pigment. Axis solid, 24–44% of the diameter, I–. Apothecia common, subterminal on lateral or terminal branches, up to 5.2 mm in diam., flat to sinuose in shape; thalloid exciple with few fibrils; disc epruinose, brown, marginated by white rim; epihymenium 6–16  $\mu\text{m}$  thick; hymenium 80–90  $\mu\text{m}$  thick; hypothecium 50–60  $\mu\text{m}$  thick; spores 10–11  $\times$  6–8  $\mu\text{m}$  long.

Chemistry. Usnic, barbatic, 4-*O*-demethylbarbatic, norstictic, protocetraric and salazinic acids.

The distinguishing features of *U. dendritica* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the annular cracks especially near the base, (3) the cylindrical papillae which produce few soralia at the top, (4) the absence of granular soredia, (5) the flat to sinuose apothecia with few fibrils along the margin, (6) the brown disc which are marginated by white rim, (7) the *merrillii*-type plectenchymatous cortex, and (8) the presence of barbatic and salazinic acids as major substances.

*U. dendritica* resembles other richly fertile species such as *U. florida*, *U. orientalis* and *U. pseudogatai*. However, it is distinguished from others by the flat to sinuose shaped apothecia which have few fibrils and possess a white rim on the disc, and by the presence of barbatic and salazinic acid as major substances. *U. dendritica* is considered to have a close relationship with *U. pangiana*, since the morphology and their chemistry are similar each other except for soralia morphology.

*U. dendritica* has not been collected from Japan. In Taiwan, this species grows on tree bark at ca. 2000 m alt.

Representative specimens examined. TAIWAN. Prov. Chiayi: Mt. Ali, 2200 m, 30.12.1963, *S. Kurokawa* 46. Prov. Nantou: Keitau, 25.12.1933, *Y. Asahina* 33125. Prov. Taitung: Mt. Lachialachiaerh, c. 1800 m, 22.1.1965, *S. Kurokawa* 2508. INDIA. Darjeeling, Takuda, 18.4.1960, *M. Togashi* s.n.

14. *Usnea dorogawensis* Asahina, J. Jpn. Bot. 28: 228, 1953.

Lectotype (selected here): Japan, Honshu, Prov. Yamato, Dorogawa, Amakawa-mura, Yoshino-gun, 12.6.1952, *M. Togashi* s.n. (TNS!). Chemistry: usnic, lobaric, norstictic, stictic and constictic acids, and US6.

Thallus erect, up to 6 cm long, color unknown when fresh, reddish-brown in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches glossy on the surface, lacking pseudocyphellae and maculae, terete, inflated, tapering only near the apices, with many lateral branches and fibrils, 0.6–1.3 mm in diam.; lateral branches constricted at the base; papillae absent; soralia common, formed mainly on lateral and terminal branches, developed from cortex, rounded in shape or confluenting each other to form irregular in shape, larger than branch diam., distinctly stipitate, cortical margin distinctly reflexed, concave at the top with granular soredia and rarely with isidiomorphs. Cortex thin, 3.2–8.3% of the radius, *ceratina*-type plectenchymatous; hyphae pachydermatous, secreted red pigment in the cell wall in part, with oblong or turbinate lumina. Medulla lax, wide, 32–38% of the radius, hyphae near the cortex thickened and secreted red pigment in the cell wall. Axis solid, thin, 15–23% of the diameter, I–. Apothecia not seen.

Chemistry. Usnic, lobaric, norstictic, stictic, constictic ( $\pm$ ) squamatic acids ( $\pm$ ), US6 ( $\pm$ ), and atranorin ( $\pm$ ).

The distinguishing features of *U. dorogawensis* are (1) the erect thallus with anisotomic-dichotomous branching, (2) the inflated branches, (3) the concave soralia with granular soredia and few isidiomorphs, (4) the presence of red pigment secreted in the hyphal cell wall in the medulla near the cortex, and (5) the presence of stictic and lobaric acids.

When Asahina (1953) described *U. dorogawensis* Asahina, he cited two specimens in the protologue: one is collected from Prov. Yamato, Dorogawa, and the other is from Prov. Kii, Mt. Koya. Although he did not designate the type specimen in the protologue, the specimen collected from Dorogawa was marked as "Typus". Therefore, the former specimen is designated here as the lectotype of *U. dorogawensis* according to Art. 9.9 and recommendation 9A.3. of Tokyo Code (Greuter et al. 1994).

Although *U. dorogawensis* resembles *U. glabrata* (Ach.) Vain. morphologically, it can be distinguished from the latter by the presence of red pigment in hyphal cell walls in the medulla. The secreted pattern of red pigment of this species is similar with *U. rubicunda* Stirt. and *U. rubrotincta* Stirt. However, *U. dorogawensis* secretes red pigment mainly in the medullary hyphae near the cortex, while *U. rubicunda* and *U. rubrotincta* secrete it in the cortex, never in the medulla. Morphological features of *U. dorogawensis* are not close to *U. rubicunda* and *U. rubrotincta*, though Asahina (1956) treated *U. dorogawensis* as belonging to sect. *Setulosae* subsect. *Rubigineae* (*sensu* Motyka 1936–38) regarding the nature of secretion of the red pigment as an important characteristic.

This species is endemic to central Japan, where it grows on bark of *Cryptomeria* and *Pinus* at elevations between 500 and 1000 m.

Representative specimens examined. JAPAN. Honshu. Prov. Mikawa: Chichiiwa, Minami-shitara-gun, 1.4.1960, *Y. Asahina*, *S. Kurokawa* & *M. Nuno* s.n. Prov. Ohmi: Kaminyu, Samegai-mura, Sakata-gun, 24.4.1962, *M. Togashi* s.n. Prov. Yamato: Murou Temple, Murou-mura, Uda-gun, 2.3.1958, *M. Togashi* s.n. Prov. Kii: Mt. Koya, 19.12.1954, *Y. Tanaka* 982. Prov. Tanba: Yamakuni-mura, Kita-kuwata-gun, 7.11.1955, *M. Togashi* s.n.

15. *Usnea fragilescens* Havaas ex Lynge, Vid. Selsk. Skr. I. M.-N. Kl. 7: 230, 1921.

Lectotype (selected by Clerc 1987a): Norvegia occidentalis, Inter Manger i Hallandsvand insulae Radoen, rupicola, 15.8.1909, *Havaas* (O not seen; isolectotype in BG!). Chemistry: norstictic, cryptostictic, stictic and menegazziaic acids (Clerc 1987a).

*Usnea mollis* Stirt., Scot. Natur. 6: 109, 1881, nom. illeg., non Baumg. (1790). – *U. florida* var. *mollis* Vain., Etud. Lich. Brésil 1: 4, 1890. – *U. malacea* Zahlbr., Cat. Lich. Univ. 6: 588, 1930, nom. illeg., non *U. malacea* (Stirt.) Zahlbr. (1930). – *U. fragilescens* var. *mollis* (Vain.) P.Clerc, Nord. J. Bot. 7: 492 (1987). Lectotype (selected by Clerc 1987a): Scotland, New Galloway, *Mc Andrew* (BM!). Chemistry: stictic, constictic and cryptostictic acids (Clerc 1987a).

Thallus fruticose, erect to subpendent, up to 6.5 cm long, grayish-green when fresh, straw-yellow in herbarium specimens, jet black at base; branching anisotomic-dichotomous; branches slightly glossy on surface, lacking pseudocyphellae and maculae, terete, inflated, gradually tapering, with sparse fibrils and lateral branches especially towards the apices, 0.8–1.2 mm in diam.; lateral branches constricted at base; papillae common, verrucose; soralia common, formed mainly on lateral and terminal branches, developed from the top of eroded papillae,  $\pm$  discrete, rounded, becoming as large as the branch diam., slightly stipitate, cortical margin not reflexed, slightly concave at top with granular soredia and

rarely with isidiomorphs. Cortex thin, 3.4–6.4% of the radius, *ceratina*-type plectenchymatous, lacking red pigment, with oblong or turbinate lumina. Medulla lax, wide, 29–38% of the radius, lacking red pigment. Axis solid, thin, 17–28% of the diameter, I –. Apothecia not seen.

Chemistry. Usnic, barbatic, 4-*O*-demethylbarbatic, protocetraric and salazinic acids (trace), US7 and US8.

*U. fragilescens* is characterized by the following morphology: (1) erect to subpendent thallus with anisotomic-dichotomous branching, (2) jet black base, (3) inflated branches which are constricted at base, (4) slightly excavated, rounded soralia with granular soredia, which become as large as the branch diam., and (5) non-reflexed cortical margin around soralia.

The major chemical substances of all Japanese specimens included barbatic, 4'-*O*-demethylbarbatic and protocetraric acids; in addition, small amounts of salazinic acid and various unidentified substances were detected. These substances were consistently detected in all specimens, with some variation in concentration. Although six chemical strains have been reported for the species including (1) usnic, norstictic, cryptostictic, stictic,  $\pm$  constictic,  $\pm$  menegazziaic, and  $\pm$  fatty acids, (2) usnic,  $\pm$  cryptostictic, stictic, and  $\pm$  menegazziaic acids, (3) usnic, salazinic acids,  $\pm$  stictic acid aggregate, and  $\pm$  atranorin, (4) usnic, psoromic, and  $\pm$  2'-*O*-demethylpsoromic acids, (5) usnic and squamatic acids, and (6) usnic acid only, the chemical strain from Japan has not been reported for either Europe or North America (Clerc 1987a, Halonen et al. 1998). Chemical differences suggest that the Japanese population is geographically isolated from the other strains. However, no morphological differences between Japanese specimens and those collected from other regions are reported. Therefore, Japanese specimens simply represent a new chemical strain of *U. fragilescens*.

According to Clerc (1987a), *U. fragilescens* grows on both rocks and tree bark in Europe. Saxicolous specimens tend to have thinner and fusiform bases, with sparsely branched thalli, while corticolous specimens tend to have thicker bases, with richly branched thalli. These differences fall within the natural morphological variation for this species, and do not deserve taxonomic distinction.

The inflated branches and excavated soralia with granular soredia typical of *U. fragilescens* resembles somewhat similar features in *U. glabrata* (Ach.) Vain. However, *U. fragilescens* can be distinguished from *U. glabrata* by its jet black base. In addition, the soralia of *U. fragilescens* are slightly concave at the top with non-reflexed cortical margins, while the soralia of *U. glabrata* are deeply excavated with distinctly reflexed cortical margins. The jet black base and excavated soralia with granular soredia of *U. fragilescens* also resemble similar features in *U. fulvovireagens*, *U. glabrescens* and *U. wasmuthii*; however, *U. fragilescens* can be distinguished from these taxa on the basis of its inflated branches which are constricted at the base and slightly glossy branch surfaces.

In Japan, *U. fragilescens* has only been collected from Akkeshi, in southeast Hokkaido, where it occurs on bark of *Abies sachalinensis* and *Picea glehnii* at elevations between 20 and 75 m. No saxicolous material has been found. Akkeshi is located in a highly humid maritime area, one of the foggiest areas in Japan. This species has also been collected from

similar habitats in western Europe and British Columbia (Clerc 1987a, Halonen et al. 1998).

Exsiccata examined. Brodo, Lich. Can. Exs. 71 & 215; Havaas, Lich. Norveg. Occid. Exs. 102; Vezda, Lich. Sel. Exs. 571.

Representative specimens examined. JAPAN. Hokkaido. Prov. Kushiro: c. 1.5 km E of Rokubansawa, Hamanaka-cho, Akkeshi-gun (43°04'N, 140°04'E), on *Picea glehnii*, c. 40 m, 9.7.1997, *S. Arakawa 1694*; Hillside facing Kiritappu Marsh, Hamanaka-cho, Akkeshi-gun (43°04'N, 145°02'E), on *Abies sachalinensis*, 20–40 m, 2.9.1999, *K. H. Moon 4217*; Fukushima, Biwase-mura, Hamanaka-cho, Akkeshi-gun (43°06'N, 145°00'E), on decayed wood of *Abies sachalinensis*, c. 75 m, 1.9.1999, *K. H. Moon 4136*; c. 6 km from Chiripumura to Akkeshi-cho, Akkeshi-gun (43°01'N, 145°02'E), on *Abies sachalinensis*, c. 70 m, 3.9.1999, *K. H. Moon 4484*.

16. *Usnea fuscrobens* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 546, 1938.

Holotype: Insula Mauritius, *Simony s.n.* (W!). Chemistry: usnic, norstictic, protocetraric and salazinic acids. *Usnea pseudorientalis* Asahina, J. Jpn. Bot. 44: 355, 1969, syn. nov. Holotype: (Malaysia), Sabah, Ascending Mesilau Trail from W. Mesilau River, c.1700 m alt., Kinabalu National Park, 8.1964, *M. E. Hale 28267* (TNS!). Chemistry: usnic, protocetraric, salazinic and constictic acids.

Thallus fruticose, erect to subpendent, up to 9 cm long, color unknown when fresh, straw-yellow to brown in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches glossy on the surface, lacking pseudocyphe-lae and maculae, often foveolate, terete, inflated, gradually tapering, with many fibrils and lateral branches, 1.1–1.8 mm in diam.; lateral branches slightly constricted at the base; papillae common on thicker branches, cylindrical; soralia absent. Cortex thin, 3.6–7.5% of the radius, *ceratina*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina distinctly enlarged to be oblong in shape. Medulla lax in density, wide, 28–37% of the radius, lacking red pigment. Axis solid, thin, 18–29% of the diameter, I –. Apothecia common, subterminal on terminal and lateral branches, up to 1.1 cm in diam., cup-shaped at least when juvenile stage; thalloid exciple with many fibrils; disc pruinose, gray to pale brown, lacking white rim; epihymenium 6–12  $\mu\text{m}$  thick; hymenium 54–72  $\mu\text{m}$  thick; hypothecium 30–54  $\mu\text{m}$  thick; spores 9–11  $\times$  6–7  $\mu\text{m}$  long.

Chemistry. Usnic, salazinic and constictic acids ( $\pm$ ).

The distinguishing features of *U. fuscrobens* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the inflated branches with cylindrical papillae, (3) the absence of soralia, (4) the cup-shaped apothecia, (5) the gray to pale brown disc which are not margined by white rim, and (6) the presence of salazinic acid as the major substance.

Although *U. fuscrobens* strongly resembles *U. orientalis*, it is distinguished by the cup-shaped apothecia at least when juvenile.

*U. fuscrobens* is one of rare species in Japan, and has been known from central Japan, where it grows on tree bark at ca. 1500 m alt. In Taiwan, it also grows on tree bark at elevations between 2000 and 3000 m.

Exsiccata examined. TAIWAN. Prov. Ilan: Mt. Nanfuta-san, on twigs of *Osmanthus biorituensis*, 2400–2600 m, 20.1.1964, *S. Kurokawa 1099* (*S. Kurokawa*: Lich. Rar. Cri. Exs. 150; as *U. orientalis*).

Representative specimens examined. JAPAN. Honshu. Prov. Musashi: Ippai-mizu, Nippara, 13.9.1955, *M. Togashi s.n.* (herb. *Y. Asahina 55913*). TAIWAN. Prov. Nantou: Keitai, 24.12.1933, *Y. Asahina 33421*.



17. *Usnea glabrata* (Ach.) Vain., Ann. Acad. Sci. Fenn. ser. A, 6(7): 7, 1915

*U. plicata* (L.) F. H. Wigg. var. *glabrata* Ach., Lich. Univ., 624, 1810.

Holotype: Switzerland (Helvetia), *Schleicher 318* (H-ACH 1854A!). Chemistry: usnic and fumarprotocetraric acids [demonstrated by P. W. James in Myllys (1994)].

*Usnea glabrata* (Ach.) Vain. subsp. *pseudoglabrata* Asahina, Lich. Jap. 3: 95, 1956, syn. nov. Holotype: Japan, Hokkaido, Prov. Kitami, Bihoro Pass, 27.6.1953, *Y. Asahina s.n.* Chemistry: usnic and salazinic acids.

Thallus fruticose, erect, up to 18 cm long, grayish-green when fresh, brownish to rusty- or chestnut-brown in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches glossy on the surface, lacking pseudocypbellae and maculae, terete, inflated, gradually tapering, with many fibrils and lateral branches, 0.4–1.8 mm in diam.; lateral branches constricted at the base; papillae sparse to common, verrucose; soralia common, formed mainly on lateral branches, developed from cortex, confluent each other to form irregular mass of soredia, larger than branch diam., distinctly stipitate, cortical margin reflexed, concave at the top with granular soredia and rarely with isidiomorphs. Cortex thin, 3.4–10% of the radius, *ceratina*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, with oblong lumina. Medulla lax, wide, 13–34% of the radius, lacking red pigment. Axis solid, thin, 13–34% of the diameter, I–. Apothecia not seen.

Chemistry. Usnic, salazinic, norstictic ( $\pm$ ), protocetraric ( $\pm$ ) and constictic ( $\pm$ ) acids.

The distinguishing features of *U. glabrata* are (1) the erect thallus with anisotomic-dichotomous branching, (2) the inflated branches which are constricted at the base, (3) the concolorous base with the thallus, (4) the concave soralia with granular soredia, (5) the reflexed cortical margin of soralia, (6) the *ceratina*-type plectenchymatous cortex, and (7) the presence of salazinic acid as a major substance.

Although type specimen of this species contains fumarprotocetraric acid [demonstrated by P. W. James, in Myllys (1994)], this substance was not detected in the specimens from the present area. No morphological difference was found between the type specimen and the materials from the present area.

*U. glabrata* resembles *U. confusa* in having sorediate inflated branches and same chemistry. However, it is readily distinguished from *U. confusa* by the concave soralia with granular soredia and the *ceratina*-type plectenchymatous cortex. *U. glabrata* also resembles *U. fragilescens*, but it can be distinguished by the concolours base with thallus and chemistry from the latter species.

In Japan, *U. glabrata* is distributed in Hokkaido and central Honshu, where it grows on barks such as *Abies* and *Larix*, or rarely on rocks. It is found at elevations between 800 and 2400 m. In Taiwan, it is found at elevations between 2000 and 3300 m. *U. glabrata* is widely distributed in boreal to temperate region such as eastern Asia, Europe and North America (Asahina 1956, Halonen et al. 1998, Myllys 1994).

Representative specimens examined. JAPAN. Hokkaido. Prov. Kushiro: Lakeside of Mashu, 28.7.1953, *Y. Asahina & M. Togashi s.n.* Honshu. Prov. Mutsu: Sui-ren-numa, Mt. Hakkoda, on twigs of *Abies mariesii*, c. 950 m, 5.8.1985, *K. Sasaki 7246*. Prov. Shinano: Nyukasa Pasture Land, NW slope of Mt. Nyukasa, Takato-machi, Kami-ina-gun (35°54'N, 138°10'E), on *Larix kaempferi*, 1780 m, 30.6.1997, *Y. Ohmura 3216*. Prov. Kai: Shogen Pass, Chichibu Mts., 12.8.1953, *S. Kurokawa 521294*. Prov. Suruga: Mt. Arakawa, en route from Niken-goya

lodge to the Senmai-goya lodge, 1300–2700 m, 5.8.1974, *H. Kashiwadani 12764*. Prov. Yamashiro: Koshihata, Kyoto, 3.4.1958, *Y. Asahina s.n.* Prov. Kii: Mt. Koya, 23.8.1952, *Y. Asahina s.n.* Prov. Tanba: Ido, Yamakuni-mura, Kita-kuwata-gun, 7.11.1955, *M. Togashi s.n.* TAIWAN. Mt. Nan-Fu-Ta-San, 2400–2600 m, 20.1.1964, *S. Kurokawa 1072*; Mt. Chien-San, Mt. Shin-Kao-San, 3100–3300 m, 1.1.1964, *S. Kurokawa 282*.

18. *Usnea hakonensis* Asahina, Lich. Jap. 3: 77, 1956.

Holotype: Japan, Honshu, Prov. Sagami, Hakone, Lakeside of Ashinoko, 15.7.1952, *M. Togashi s.n.* (TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids, US1 and US2.

*Usnea hakonensis* f. *inactiva* Asahina, Lich. Jap. 3: 77, 1956, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Sagami, Hakone, Lakeside of Ashinoko, 15.7.1952, *M. Togashi s.n.* (TNS!). Chemistry: usnic acid, US1 and US2.

Thallus fruticose, erect, up to 12 cm long, grayish green when fresh, straw-yellow to chestnut-brown in herbarium specimens, concolorous with thallus or dark brown at the base; branching anisotomic-dichotomous; branches glossy on the surface, lacking pseudocyphellae and maculae, terete, inflated, gradually tapering, with many fibrils and lateral branches, 0.4–1.5 mm in diam.; lateral branches constricted at the base; papillae sparse or absent, hemispherical to verrucose; soralia common, formed mainly on lateral branches, developed from the top of eroded papillae,  $\pm$  discrete, rounded, smaller than branch diam., sessile to distinctly stipitate, cortical margin not reflexed, convex at the top often with numerous isidiomorphs which can grow up to fibrils as they are attached on soralia, lacking granular soredia. Cortex 6.0–13% of the radius, *ceratina*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, with oblong or turbinate lumina. Medulla lax to moderate in density, 14–32% of the radius, lacking red pigment. Axis solid, 18–52% of the diameter, I–. Apothecia not seen.

Chemistry. Race 1, usnic and norstictic acids, US1, US2, salazinic ( $\pm$ ) and protocetraric acids ( $\pm$ ), and atranorin ( $\pm$ ); Race 2, usnic acid, US1, US2 and atranorin ( $\pm$ ).

The distinguishing features of *U. hakonensis* are (1) the erect thallus with anisotomic-dichotomous branching, (2) the inflated branches which are glossy on the surface and with few papillae, (3) the rounded soralia often with numerous isidiomorphs or fibrils, and (4) the presence of US1 and US2.

When Asahina (1956) described *U. hakonensis* f. *inactiva*, he did not designate the type specimen. The authentic specimen marked as "Typus" of this taxon housed in TNS (labeled as Japan, Honshu, Prov. Sagami, Hakone, Lakeside of Ashinoko, 15.7.1952, *M. Togashi s.n.*) is identical with the protologue morphologically and chemically. In addition, the ratio of the cortex, medulla and axis shown in the protologue is identical with the note in the specimen. Therefore, this specimen is selected as the lectotype of *U. hakonensis* f. *inactiva*.

Two chemical races were recognized in the present area. Race 1 (88%) is more common than Race 2 (12%). As no morphological and ecological differences were found among them, the chemical differences found in this species are considered to have no taxonomic value. Therefore, *U. hakonensis* f. *inactiva*, which was separated from *U. hakonensis* only by the chemical reaction, is treated under a synonym of *U. hakonensis*.

*U. hakonensis* resembles *U. confusa*, *U. dasaea*, *U. fragilescens*, *U. glabrata* and *U. pygmoidea* in having the inflated branches with soralia. However, it is readily distinguished

from them by the presence of unidentified substances (US1 and US2).

*U. hakonensis* is known only from central to western Japan, where it grows on rocks (granite) or tree bark such as *Cryptomeria*, *Salix* and *Quercus* at elevations between 600 and 1000 m.

Representative specimens examined. Race 1. JAPAN. Honshu. Prov. Sagami: Tanzawa, 5.5.1987, *Y. Kon s.n.* Prov. Kai: Lakeside of Yamanaka-ko, Mt. Fuji, on *Larix leptolepis*, c. 1000 m, 5.4.1996, *K. H. Moon 634*. Prov. Suruga: Sengen Shrine, Gotenba, 14.7.1953, *M. Togashi s.n.* Prov. Kii: Kondo Temple, Mt. Koya, on *Cryptomeria japonica*, c. 800 m, 1.4.1999, *Y. Ohmura 4498*. Prov. Settsu: Ono-mura, Arima-gun, 1.11.1953, *M. Togashi s.n.* Prov. Tanba: Mt. Koganegatake, Sasayama-cho, Taki-gun (35°07'N, 135°16'E), on rock (granite), 650–700 m, 23.8.1998, *Y. Ohmura 4482*. Shikoku. Prov. Awa: Jinryo-mura, Myozai-gun, 1.1.1940, *T. Inobe s.n.* Prov. Tosa: Mt. Dohgamori, Hata-gun, 17.6.1955, *S. Kurokawa s.n.* Kyushu. Prov. Buzen: Takasumi shrine, Mt. Hikosan, Soeda-machi, Tagawa-gun, on *Cryptomeria japonica*, c. 800 m, 8.10.1996, *H. Kashiwadani [39687]* & *Y. Umezū*. Prov. Bungo: Kyusui-kei Gorge, Kokonoe-machi, Kusu-gun (33°10'N, 131°13'E), on *Quercus acutissima*, c. 720 m, 4.3.1997, *Y. Ohmura 3024*. Prov. Hizen: Kashinokibaru Marsh, Kashinokibaru, Ikebaru, Nanayama-mura, Higashi-matsuura-gun, on *Pinus densiflora*, c. 590 m, 9.8.1996, *Y. Ohmura 2489*. Prov. Higo: Mt. Aso, 27.6.1972, *Y. Hamada s.n.*

Race 2. JAPAN. Honshu. Prov. Tanba: Mt. Koganegatake, Sasayama-cho, Taki-gun (35°07'N, 135°16'E), on rock (granite), 650–700 m, 23.8.1998, *Y. Ohmura 4482* pr.p. Kyushu. Prov. Buzen: Bonji-iwa, SW slope of Mt. Hikosan, Soeda-machi, Tagawa-gun, on *Pinus densiflora*, c. 850 m, 9.10.1996, *H. Kashiwadani [40028b pr.p.]* & *Y. Umezū*. Prov. Bungo: Kyusui-kei Gorge, Kokonoe-machi, Kusu-gun (33°10'N, 131°13'E), on *Quercus acutissima*, c. 720 m, 4.3.1997, *Y. Ohmura 3024* pr.p.

19. *Usnea hesperina* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 383, 1937, nom. cons. prop. (by Clerc 1999).

Neotype (selected by Clerc 1997): Espagne (Spain), Iles Canaries, Tenerife, La Laguna, Monte Las Mercedes, Lomo del Boqueron, 740–780 m alt., dans la pente boisée en exp. SW, Laurisylva-Fayal-Brezal, sur les branches de *Laurus*, 12.9.1986, *P. Clerc s.n.* (G!). Chemistry: usnic and protocetraric acids (Clerc 1997).

*Usnea capilliformis* Asahina, Lich. Jap. 3: 73, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Kii, Mt. Koya, 23.8.1952, *Y. Asahina s.n.* (TNS!). Chemistry: usnic and protocetraric acids.

Thallus fruticose, pendent, up to 20 cm long, grayish-green when fresh, straw-yellow to brownish in herbarium specimens, concolorous with thallus at the base, with annular cracks especially near the base; branching anisotomic-dichotomous; branches usually matt but rarely slightly glossy on the surface, lacking pseudocypellae, with the punctiform to irregular-shaped maculae on the surface, terete, uninflated, gradually tapering, with many fibrils and lateral branches, 0.4–1.2 mm in diam.; lateral branches cylindrical at the base; papillae absent to rare, hemispherical; soralia common, formed on lateral branches and thicker branches, developed from maculae, discrete, punctiform to rounded in shape, smaller than branch diam., sessile to slightly stipitate, cortical margin not reflexed, convex at the top, rarely with isidiomorphs, lacking granular soredia. Cortex thin to thick, 5.9–16% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina almost the same as medullary hyphae. Medulla dense, thin, 12–15% of the radius, lacking red pigment. Axis solid, thick, 42–64% of the diameter, I –. Apothecia not seen.

Chemistry. Race 1, usnic and protocetraric acids; Race 2, usnic, protocetraric and salazinic acids.

The distinguishing features of *U. hesperina* are (1) the pendent thallus with anisotomic-dichotomous branching, (2) the annular cracked base which is concolor with the thallus,

(3) the uninflated branches with punctiform to irregular shaped maculae on the surface, (4) the punctiform to rounded soralia, (5) the solid axis, (6) the absence of granular soredia, (7) the *merrillii*-type plectenchymatous cortex, and (8) the presence of protocetraric and/or salazinic acids as the major substance.

When Asahina (1956) described *U. capilliformis*, he did not cite any specimens in the protologue, but he mentioned that this species was only collected once from Mt. Fuji. This specimen could not be found in TNS; only one authentic specimen is housed in the herbarium, which is labeled as Japan, Honshu, Prov. Kii, Mt. Koya, 23.8.1952, *Y. Asahina s.n.* The specimen was marked as "Typus" by Asahina, and the annotations of morphological and chemical features examined by Asahina is identical with the protologue except for locality. Therefore, the distribution in the protologue is considered as erroneous. The specimen collected from Mt. Koya is accepted as the holotype of *U. capilliformis* according to Art. 9.1 and Recommendation 9A.1 (Greuter et al. 1994).

*U. hesperina* Motyka (1937) is proposed to conserve the name against *U. schadenbergiana* Göpp. & Stein (1883) by Clerc (1999). However, the latter taxon which contains stictic acid as a major substance is only distributed in Asia. Further research should be made on the relationship between these taxa from ecological and phylogenetical viewpoints.

Two chemical races were recognized in the present area, but no morphological and ecological differences were found among them. Therefore, they are treated as same species in the present study.

*U. hesperina* may be confused with *U. diffracta*, *U. himantodes*, *U. longissima*, *U. merrillii*, *U. pangiana*, *U. pectinata*, *U. trichodeoides* and *U. yakushimensis*. However, *U. hesperina* can be distinguished from *U. diffracta*, *U. longissima*, *U. himantodes* and *U. pectinata* by the presence of protocetraric and/or salazinic acids. It is distinguished from *U. merrillii* by the solid axis which is never to be cribose, and from *U. pangiana* and *U. yakushimensis* by the presence of maculae on the surface of the branches. It is also distinguished from *U. trichodeoides* by the terete branches, the cortex which is not areolately cracked on the thicker branches, and the negative iodine reaction in the axis.

*U. hesperina* is a rare species in Japan and Taiwan, where it grows on tree bark at ca. 1800 m alt. This species is widely distributed in the temperate to tropical regions such as North America and Africa (Clerc 1997).

Specimens examined. Race 1. TAIWAN. Prov. Taitung: Mt. Lachialachiaerh, c. 1800 m, 22.1.1965, *S. Kurokawa 2500*.

Race 2. JAPAN. Honshu. Prov. Rikuchu: Hachimantai, 15.10.1954, *M. Togashi s.n.*

## 20. *Usnea himalayana* C. Bab., Hook. J. Bot. 4: 243, 1852.

Lectotype (*vide* Awasthi 1986): Himalaya (India, Uttar Pradesh), Kumaon, Binsar, c. 2300 m alt., *R. Strachey & J. E. Winterbottom s.n.* (H-Nyl, not seen; isolectotype in BM!). Chemistry: usnic and salazinic acids.

*Usnea dichotoma* Fr., Syst. Orb. Veget. 1: 282, 1825 (non Hoffm. ex anno 1796). Holotype: India Orient., E. Nepal, *Vahl s.n.* (UPS!). Chemistry: usnic acid and stictic acid complex (Awasthi 1986).

*Usnea flexilis* Stirt., Scott. Natur. 6: 106, 1881. Lectotype (selected here): India Orientalis, Neilgherries, *G. Watt s.n.* (GLAM, not seen; isolectotype in BM!). Chemistry: usnic and salazinic acids.

*Usnea himalayana* f. *major* Asahina, J. Jpn. Bot. 42: 258, 1967, syn. nov. Lectotype (selected here): East Nepal, en route from Batasay to Bhupate Danra via Halhale Bhanjang, on tree bark, ca. 2500 m alt., 1.12.1963, *M. Togashi s.n.* (*S. Kurokawa & H. Kashiwadani: Lich. Rar. Cri. Exs.*, 341, TNS!). Chemistry: usnic, protoce-

tralic and salazinic acids.

*Usnea subflexilis* Stirt., Scott. Natur. 6: 106, 1881. Holotype: India, Himalaya, Darjeeling, *J. Thomson s.n.* (GLAM, not seen; isotype in BM!). Chemistry: usnic acid and stictic acid complex (Awasthi 1986).

Thallus fruticose, pendent, up to 40 cm long, grayish-green when fresh, straw-yellow to brownish in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches glossy on the surface, with pseudocyphellae which are usually longitudinally elongated or rarely irregular in shape, lacking maculae, terete, inflated, gradually tapering, with sparse fibrils and lateral branches, 0.4–1.8 mm in diam.; lateral branches constricted at the base; papillae absent; soralia absent. Cortex thin, 2.2–7.4% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina almost the same as medullary hyphae. Medulla lax, wide, 28–45% of the radius, lacking red pigment. Axis solid, thin, 6.6–33% of the diameter, I –. Apothecia not seen.

Chemistry. Usnic, salazinic, norstictic ( $\pm$ ) and protocetraric ( $\pm$ ) acids, and atranorin ( $\pm$ ).

The distinguishing features of *U. himalayana* are (1) the pendent thallus with anisotomic-dichotomous branching, (2) the inflated branches with pseudocyphellae on the glossy surface, (3) the absence of soralia, (4) the *merrillii*-type plectenchymatous cortex, and (5) the presence of salazinic acid as a major substance.

When Stirton (1881) described *U. flexilis*, he cited three specimens collected from Neilgherries, South Africa and Fernando Po. Therefore, the lectotype should be selected from them, although the specimen collected from Neilgherries was cited as a holotype by Awasthi (1986). Although the specimen housed in GLAM was not seen by the present author, its duplicate housed in BM coincides well with the protologue. Therefore, the specimen collected from Neilgherries is selected here as the lectotype of *U. flexilis*.

When Asahina (1967b) described *U. himalayana* f. *major* Asahina, he cited six specimens and the photograph of the thallus in the protologue. One of them, labeled as East Nepal, en route from Batasay to Bhuspate Danra via Halhale Bhanjang, on tree bark, ca. 2500 m alt., 1.12.1963, *M. Togashi s.n.*, is identical with the photograph. Therefore, this specimen is designated as the lectotype of *U. himalayana* f. *major*.

*U. himalayana* is a variable species, especially on the amount of fibrils and CMA. All the species listed in synonyms belong to natural range of *U. himalayana*. Although type specimens of *U. dichotoma* (non Hoffm.) Fr. and *U. subflexilis* contain stictic acid as a major substance, their morphology and distributions belong to the *U. himalayana*. A stictic acid containing race was not found in the present area.

Although *U. himalayana* resembles *U. nidifica*, it is readily distinguished by the absence of soralia.

In Japan, *U. himalayana* is distributed in Honshu, Shikoku and Kyushu, where it grows on tree bark at ca. 1000 m alt. In Taiwan, it grows on bark at elevations between 2000 and 2500 m. This species has also been collected from India, Nepal, Malaysia and Philippines.

Representative specimens examined. JAPAN. Honshu. Prov. Kai: Goten-niwa, Mt. Fuji, c. 900 m, 25.10.1976, *H. Kashiwadani 13809*. Prov. Kii: Mt. Koya, 21.4.1926, *Y. Numajiri s.n.* (herb. *Y. Asahina 26421*). Prov. Yamato: Muroo Temple, Muroo-mura, Uda-gun, 13.9.1953, *M. Togashi s.n.* (herb. *Y. Asahina 53913*). Shikoku. Prov. Iyo: Mt. Ishizuchi, 29.9.1965, *M. Togashi s.n.* Kyushu. Prov. Ohsumi: Kurio, Yakushima Island,

27.7.1933, *F. Fujikawa s.n.* (herb. *Y. Asahina 1219a*). TAIWAN. Mt. Nan-Fu-Ta-San, on twigs of *Osmanthus bitoritsuensis*, 2400–2600 m, 20.1.1964, *S. Kurokawa 1054*. Prov. Chiayi: Mt. Ali, 25.12.1925, *Y. Asahina F-279*. INDIA. Phalut, Darjeeling, c. 3000 m, 9.5.1960, *M. Togashi s.n.*; Sikkim, Migothang-Nayathang, 1.6.1960, *M. Togashi s.n.* NEPAL. Khumbu, Lamjura La (27°35'N, 86°30'E), on *Rhododendron* sp., c. 3300 m, 10.3.1999, *A. Shimizu s.n.* (herb. *Y. Ohmura 4503*). MALAYSIA. Sabah, along summit trail, Kinabalu National Park, on tree in sparse forest, c. 3500 m, 23.12.1997, *M. Kato s.n.* (herb. *Y. Ohmura 4374*). PHILIPPINES. Mt. Data, c. 2000 m, *M. E. Hale [26049a] & Banaag*.

21. *Usnea intumescens* Asahina, Lich. Jap. 3: 81, 1956.

Holotype: Japan, Honshu, Prov. Kai, Lakeside of Yamanaka, Mt. Fuji, 11.8.1952, *Y. Asahina [52816] & M. Togashi* (TNS!). Chemistry: usnic, protocetraric and salazinic acids.

*Usnea intumescens* f. *condensata* Asahina, Lich. Jap. 3: 83, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Shinano, Kyowa-mura, Kita-saku-gun, 27.12.1921, *K. Chino s.n.* (herb. *Y. Asahina 211227*, TNS!). Chemistry: usnic, protocetraric and salazinic acids.

*Usnea pseudintumescens* Asahina, Lich. Jap. 3: 83, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Rikuzen, Matsubara, Takata-cho, Kesen-gun, 30.3.1928, *G. Toba s.n.* (herb. *Y. Asahina 28330*, TNS!). Chemistry: usnic, psoromic and 2'-*O*-demethylpsoromic acids.

Thallus fruticose, erect to subpendent, up to 20 cm long, grayish-green to olive-green when fresh, olive green to brown in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches matt to slightly glossy on the surface, lacking pseudocyphellae and maculae, terete, slightly inflated, 0.9–1.8 mm in diam., gradually tapering, with many lateral branches and fibrils; lateral branches broadened at the base, but constricted when cracked; papillae absent; soralia common, formed on whole branches, developed from scars of detached fibrils, punctiform, discrete each other, sessile, flat to slightly convex at the top with numerous isidiomorphs, lacking granular soredia. Cortex thin, 2.6–7.1% of the radius, lacking red pigment, *ceratina*-type plectenchymatous; hyphae pachydermatous, with turbinate or oblong lumina. Medulla lax to moderate in density, 24–38% of the radius, lacking red pigment. Axis solid, 15–40% of the diameter, I–. Apothecia not seen.

Chemistry. Race 1, usnic, salazinic and protocetraric acids ( $\pm$ ); Race 2, usnic, psoromic and 2'-*O*-demethylpsoromic ( $\pm$ ) acids, and atranorin ( $\pm$ ).

The distinguishing features of *U. intumescens* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the slightly inflated branches lacking papillae, (3) the lateral branches which are broadened at the base, (4) the punctiform soralia with numerous isidiomorphs, (5) the absence of granular soredia, (6) the *ceratina*-type plectenchymatous cortex, and (7) the presence of salazinic or psoromic acids as the major substance.

Two chemical races are recognized in the present area. Although salazinic acid of Race 1 and psoromic acid of Race 2 are distantly related substances within depsidone, no morphological difference was found between Race 1 and Race 2. Therefore, chemical differences found in this species are treated as chemical strains.

*U. intumescens* resembles *U. aciculifera* and *U. subintumescens* in having punctiform soralia developed from scars of detached fibrils. However, *U. intumescens* is distinguished from *U. aciculifera* by the inflated branches and the presence of salazinic acid, and from *U. subintumescens* by the lateral branches which are broadened at the base, and the absence of constrictic acid.

*U. intumescens* is a rare species restricted in central Japan, where it grows on bark of trees such as *Larix* and *Zelkova* at elevations between 800 and 1600 m.

Specimens examined. Race 1. JAPAN. Honshu. Prov. Shinano: Izumino-mura, Suwa-gun, 15.10.1957, *T. Matsuoka s.n.* (herb. *Y. Asahina 57105a*); Suguri-daira, Kotoh-mura, Suwa-gun, 3.8.1958, *S. Kurokawa 58275*. Prov. Kai: Asahiga-oka, Lakeside of Yamanaka, Minami-tsuru-gun, c. 980 m, 25.7.1957, *S. Kurokawa 57100*. Prov. Yamashiro: Koshihata, Ukyo-ku, Kyoto city, 3.4.1958, *Y. Asahina 58412*.

Race 2. JAPAN. Honshu. Prov. Shinano: Ikenodaira, Takato-machi, Kami-ina-gun (35°55'N, 138°10'E), on *Larix kaempferi*, 1620 m, 29.6.1997, *Y. Ohmura 3149*; Izumino-mura, Suwa-gun, 4.5.1958, *M. Togashi s.n.* (herb. *Y. Asahina 5854*); precinct in small shrine, en route from Nakakawara to Tsuetsuki Pass, Chino-city (35°59'N, 138°09'E), on *Zelkova serrata*, 870 m, 27.6.1997, *Y. Ohmura 3112*. Prov. Yamashiro: Koshihata, Ukyo-ku, Kyoto-shi, 29.6.1958, *Y. Asahina 58628*.

22. *Usnea koyana* Asahina, Lich. Jap. 3: 78, 1956.

Holotype: Japan, Honshu, Prov. Kii, Mt. Koya, 23.8.1952, *Y. Asahina & M. Togashi s.n.* (TNS!). Chemistry: usnic and thamnolic acids, US1 and US2.

Thallus fruticose, erect, up to 5 cm long, color unknown when fresh, brown to chestnut-brown in herbarium specimens, concolorous with thallus or dark brown at the base; branching anisotomic-dichotomous, almost simple; branches slightly glossy on the surface, lacking pseudocyphellae and maculae, terete, inflated, gradually tapering, with sparse fibrils and lateral branches, 1.1–1.8 mm in diam.; lateral branches cylindrical at the base; papillae sparse to common, hemispherical; soralia common, formed mainly on lateral and terminal branches, developed from the top of eroded papillae or cortex,  $\pm$  discrete, rounded, smaller than branch diam., sessile to distinctly stipitate, cortical margin not reflexed, convex at the top usually with many isidiomorphs and fibrils. Cortex thick, 9.2–14% of the radius, *ceratina*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina enlarged to be fusiform, oblong or turbinate in shape. Medulla lax to moderate in density, 24–35% of the radius, lacking red pigment. Axis solid, thin, 11–29% of the diameter, I –. Apothecia not seen.

Chemistry. Usnic and thamnolic acids, US1 ( $\pm$ ), US2 ( $\pm$ ), and atranorin ( $\pm$ ).

The distinguishing features of *U. koyana* are (1) the erect thallus with anisotomic-dichotomous branching, which is almost simple, (2) the inflated branches with thick cortex, (3) the rounded soralia with many isidiomorphs and fibrils, (4) the absence of granular soredia, (5) the *ceratina*-type plectenchymatous cortex, and (5) the presence of thamnolic acid as a major substance.

*U. koyana* strongly resembles *U. hakonensis* morphologically. However, *U. koyana* is distinguished from *U. hakonensis* by the presence of thamnolic acid, and its simple thallus.

*U. koyana* is known only from Mt. Koya, central Japan, where it grows on *Cryptomeria japonica* at ca. 800 m alt.

Specimens examined. JAPAN. Honshu. Prov. Kii: Mt. Koya, 23.8.1952, *Y. Asahina 52823*.

23. *Usnea masudana* Asahina, J. Jpn. Bot. 45: 132, 1970.

Holotype: Taiwan (Formosa), Prov. Taitung, Chokakulai, 1936, *H. Masuda 36001* (TNS!). Chemistry: usnic, norstictic and salazinic acids.

Thallus erect to subpendent, up to 7 cm long, color unknown when fresh, brown to reddish-brown in herbarium specimens, concolorous with thallus at the base, with annular

cracks especially near the base; branching anisotomic-dichotomous; branches slightly glossy on the surface, lacking pseudocyphellae and maculae, terete, inflated, gradually tapering, usually with many crisp fibrils and sparse lateral branches, 1.1–1.7 mm in diam.; lateral branches cylindrical at the base; papillae sparse, verrucose to cylindrical; soralia absent. Cortex thin, 3.6–7.5% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina almost the same as medullary hyphae. Medulla moderate in density, wide in width, 28–36% of the radius, lacking red pigment. Axis solid, 21–28% of the diameter, I–. Apothecia common, subterminal on lateral or terminal branches, up to 8.5 mm in diam., cup-shaped; thalloid exciple with many crisp fibrils; disc epruinose, brown, lacking white rim; epihymenium 4–12  $\mu\text{m}$  thick; hymenium 70–80  $\mu\text{m}$  thick; hypothecium 30–40  $\mu\text{m}$  thick; spores 10–12  $\times$  6–8  $\mu\text{m}$  long.

Chemistry. Usnic, norstictic and salazinic acids.

The distinguishing features of *U. masudana* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the inflated branches with sparse verrucose to cylindrical papillae, (3) the absence of soralia, (4) the crisp fibrils on the branches and the margin of apothecia, (5) the brown colored disc without white rim, (6) the *merrillii*-type plectenchymatous cortex, and (7) the presence of salazinic acid as a major substance.

*U. masudana* resembles other richly fertile and esorediate species such as *U. dendritica*, *U. fuscobubens* and *U. orientalis*. However, it can be distinguished from them by the crisp fibrils on the branches and the thalloid exciple of the apothecia, and by the brown colored disc with no white rim.

This species has been collected only once from Taiwan, where it grows on tree bark.

Specimens examined. Only the type specimen.

24. *Usnea merrillii* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 371, 1938.

Lectotype (*vide* Herrera-Campos et al. 1998): U.S.A., Maine, Matinicus Island, 1909, *G. K. Merrill*, Lich. Exs. G. K. Merrill Nr. 64, *U. ceratina* (W!). Chemistry: usnic and salazinic acids (Herrera-Campos et al. 1998). *Usnea cribrosa* Asahina, Lich. Jap. 3: 71, 1956. Holotype: Japan, Honshu, Prov. Shinano, Shimo-Ina, collector unknown (TNS!). Chemistry: usnic, salazinic and constictic acids.

Thallus fruticose, subpendent to pendent, up to 30 cm long, grayish-green when fresh, brown to rusty-brown in herbarium specimens, concolorous with thallus or dark brown at the base, regenerated globe-shaped secondary cortex between the segments; branching anisotomic-dichotomous; branches glossy with scattered irregular shaped maculae on the surface, lacking pseudocyphellae, gradually tapering, with many fibrils and lateral branches, 0.3–0.8 mm in diam.; lateral branches cylindrical at the base; papillae very rare, hemispherical; soralia common, formed on whole branches especially on lateral branches, developed from maculae or cortex,  $\pm$  discrete, rounded, smaller than branch diam., sessile to slightly stipitate, cortical margin not reflexed, flat to slightly convex at the top often with isidiomorphs, lacking granular soredia. Cortex 6.8–20% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina almost the same as medullary hyphae. Medulla moderate to dense in density, 16–27% of the radius, lacking red pigment. Axis solid but hyphae loosely conglutinated each other to form cribose in shape, 26–42% of the diameter, I–. Apothecia not seen.

Chemistry. Usnic, salazinic, protocetraric ( $\pm$ ) and constictic ( $\pm$ ) acids, and US2.



The distinguishing features of *U. merrillii* are (1) the subpendent to pendent thallus with anisotomic-dichotomous branching, (2) the presence of regenerated globe-shaped secondary cortex between segments, (3) the irregular shaped maculae on the surface of branches, (4) the absence of granular soredia, (5) the *merrillii*-type plectenchymatous cortex, (6) the cribose axis, and (7) the presence of salazinic acid.

*U. merrillii* somewhat resembles *U. hesperina* and *U. yakushimensis* in having a slender thallus with anisotomic-dichotomous branching, and rounded soralia. However, *U. merrillii* is easily distinguished from them by the regeneration of the globe-shaped secondary cortex between the segments, and the cribose axis.

Herrera-Campos et al. (1998) consider the type specimen of *U. cribrosa* Asahina described from Japan to belong to *U. malmei* Motyka. Although *U. malmei* contains unknown substances of UP1 and UP2 (Herrera-Campos et al. 1998), the type specimen of *U. cribrosa* does not contain them. Morphological and chemical features of the type specimen of *U. cribrosa* coincide well with *U. merrillii* as reported by Asahina (1965b), and it is treated as a synonym of *U. merrillii* in the present study.

In Japan, *U. merrillii* is distributed from central Honshu to Kyushu, where it grows on bark of trees such as *Picea*, *Pinus* and *Sorbus* at elevations between 500 and 1000 m. This species is also known from North America (Motyka 1936–38, Herrera-Campos et al. 1998).

Exsiccata examined. JAPAN. Shikoku. Prov. Iyo: Mt. Onigajo, Kita-uwa-gun, on *Pinus densiflora*, c. 1000 m, 19.11.1972, S. Kurokawa 72270 (S. Kurokawa & H. Kashiwadani; Lich. Rar. Cri. Exs. 343, as *U. japonica*).

Representative specimens examined. JAPAN. Honshu. Prov. Shinano: Daimon Pass, Ikenotaira, 22.5.1959, Y. Asahina, S. Kurokawa & M. Nuno s.n. Prov. Kai: Aokigahara-marubi, Kamikuishiki-mura, Nishi-yashiro-gun, on bark of dead conifer tree, c. 1000 m, 8.5.1998, Y. Ohmura 4397. Prov. Mikawa: Taguchi-cho, Kita-shitara-gun, c. 500 m, 30.10.1965, M. Togashi s.n. Prov. Kii: Mt. Koya, 23.8.1952, Y. Asahina & M. Togashi s.n. Prov. Settsu: Mt. Myoken, 1.9.1952, M. Togashi s.n. Prov. Tanba: Kaibara-mura, Hikami-gun, 14.7.1927, Y. Asahina s.n. Prov. Aki: Mt. Kamakuraji, Takata-gun, on *Sorbus japonica*, c. 500 m, 17.5.1970, H. Kashiwadani 7444. Shikoku. Prov. Iyo: Kawase-mura, Kami-ukena-gun, 28.9.1965, M. Togashi s.n. Kyushu. Prov. Buzen: Mt. Hikosan, 18.11.1962, S. Kurokawa 62485. Prov. Higo: Nishize, Kuma-gun, 9.12.1928, K. Mayebara s.n. Prov. Ohsumi: Kurio, Yakushima Island, 27.7.1933, F. Fujikawa s.n.

## 25. *Usnea mutabilis* Stirt., Scott. Natur. 6: 107, 1881.

Holotype: U.S.A., Alabama, Cedar villa, *Hawley s.n.* (BM, not seen). Chemistry: no substance [demonstrated by M. E. Hale 1977, *vide* Clerc (1994)].

*Usnea croceorubescens* Vain. f. *tenuiramea* Asahina, Lich. Jap. 3: 112, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Musashi, Asagawa-mura, Minami-tama-gun, 19.5.1940, I. Sasaki s.n. (TNS!). Chemistry: usnic acid, murolic acid complex and eumitrin A<sub>2</sub>.

Thallus erect to subpendent, up to 18 cm long, grayish-green to olive-green when fresh, dirty ochreous in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches matt on the surface, lacking pseudocyphellae and maculae, terete, uninflated, gradually tapering, with many fibrils and lateral branches, 0.5–1.3 mm in diam.; lateral branches cylindrical at the base; papillae sparse, hemispherical; soralia common, formed on lateral and terminal branches, developed from the top of eroded papillae, confluent each other to form irregular mass of asexual propagules, smaller than branch diam., distinctly stipitate, cortical margin not reflexed, convex at the

top usually with many isidiomorphs, lacking granular soredia. Cortex 4.4–12% of the radius, *ceratina*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina slightly enlarged at both ends. Medulla moderate in density, 22–31% of the radius, with red pigment near the axis. Axis solid, 25–36% of the diameter, I –. Apothecia not seen.

Chemistry. Usnic acid, murolic acid complex, eumitrin A<sub>2</sub> and atranorin (±).

The distinguishing features of *U. mutabilis* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the irregular shaped soralia which are distinctly stipitate and convex at the top with many isidiomorphs, (3) the absence of granular soredia, (4) the *ceratina*-type plectenchymatous, (5) the presence of red pigment (eumitrin A<sub>2</sub>) in the medulla near the axis and murolic acid complex, and (6) the solid axis.

*U. mutabilis* is readily distinguished from other species in the subgenus *Usnea* by the presence of the red pigment (eumitrin A<sub>2</sub>) in the medulla near the axis.

Asahina (1965a) treated *U. croceorubescens* Vain. as a synonym of *U. mutabilis*, but the holotype of *U. croceorubescens* belongs to *U. pangiana* Stirt.

In Japan, *U. mutabilis* is distributed in Hokkaido, Honshu and Shikoku, where it grows on bark of trees such as *Cryptomeria*, *Larix* and *Quercus* at elevations between 100 and 1500 m. This species is widely distributed in temperate regions in Japan, Europe and North America (Clerc, 1994).

Exsiccata examined. JAPAN. Honshu. Prov. Rikuzen: Kitagama Seashore, 20.5.1967, *Y. Asahina s.n.* (S. Kurokawa; Lich. Rar. Cri. Exs. 297). Prov. Kai: Lakeside of Yamanaka, Nakano-mura, Minami-tsuru-gun, 30.7.1954, *S. Kurokawa s.n.*, (*Y. Asahina*; Lich. Jap. Exs. fasc. 4, 189; as *U. croceorubescens* Vain.); Uchino, Oshino-mura, Minami-tsuru-gun, on *Larix leptolepis*, c. 950 m, 5.6.1980, *H. Kashiwadani* [16029], *M. Togashi* & *T. Nakamura*. Prov. Ohmi: Kaminyu, Samegai-mura, Sakata-gun, on *Cryptomeria japonica*, c. 200 m, 24.4.1962, *M. Togashi s.n.* (S. Kurokawa & H. Kashiwadani; Lich. Rar. Cri. Exs. 549).

Representative specimens examined. JAPAN. Hokkaido. Prov. Kushiro: Chikushikoi, Akkeshi-gun, c. 100 m, 5.8.1970, *H. Kashiwadani* 7590. Honshu. Prov. Rikuchū: Chusonji Temple, Hiraizumi, 6.10.1954, *S. Kurokawa* 54106. Prov. Musashi: Asakawa-mura, Minami-tama-gun, 19.5.1940, *I. Sasaki s.n.* Prov. Kii: en route from Ichinobashi to Okunoin, Mt. Koya, on *Cryptomeria japonica*, c. 800 m, 1.4.1999, *Y. Ohmura* 4493. Shikoku. Prov. Iyo: Mt. Iwayaji, Kami-ukena-gun, on *Cryptomeria japonica*, c. 500 m, 21.10.1970, *H. Kashiwadani* 8535b.

## 26. *Usnea nidifica* Taylor, London J. Bot. 6: 191, 1847.

Holotype: Norfolk Island, *C. Babington* & *Thomas s.n.* (FH!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea japonica* Vain., Bot. Mag. Tokyo 32: 154, 1918, syn. nov. Holotype: Japan, Prov. Rikuzen, Shobuta, 10.5.1914, *A. Yasuda* 67 (TUR-V 00580!; isotype in TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea japonica* var. *boninensis* Asahina, Lich. Jap. 3: 59, 1956, syn. nov. Holotype: Japan, Bonin Islands, Haha-jima Island, 20.7.1926, *M. Ogata* 1217 (TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea kurokawae* Asahina, Lich. Jap. 3: 80, 1956, syn. nov. Holotype: Japan, Kyushu, Prov. Hyuga, Ebara-mura, Minami-naka-gun, 11.7.1955, *S. Kurokawa s.n.* (TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea kushiroensis* Asahina, Lich. Jap. 3: 60, 1956, syn. nov. Holotype: Japan, Hokkaido, Prov. Kushiro, Chinbe, Akkeshi-gun, 19.7.1953, *M. Tatewaki s.n.* (TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea nidularis* Asahina, J. Jpn. Bot. 44: 3, 1969, syn. nov. Holotype: Japan, Honshu, Prov. Iwaki, Matsukawaura, Souma-gun, 18.7.1958, *S. Kurokawa* 58098b (TNS!). Chemistry: usnic, norstictic, protocetraric and

salazinic acids.

*Usnea nidularis* var. *subnuda* Asahina, J. Jpn. Bot. 44: 4, 1969, syn. nov. Holotype: Japan, Honshu, Prov. Iwaki, Matsukawa-ura, Souma-gun, 18.7.1958, S. Kurokawa 58718 (TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea societatis* Vain., Univ. California Pub. Bot. 12(1): 4, 1924, syn. nov. Holotype: Tahiti, Punaruu River, on trees, 15.6.1922, W. A. Setchell & H. E. Parks s.n. (TUR-V 00498!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea straminea* Müll.Arg., Flora 62: 162, 1879, syn. nov. Holotype: Mauritius, 1876, Robillard s.n. (G!). Chemistry: usnic, norstictic, salazinic and protocetraric acids ( $\pm$ ).

Thallus fruticose, subpendent to pendent, up to 60 cm long, grayish-green when fresh, straw-yellow to brownish in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches glossy on the surface, lacking pseudocyphellae and maculae, terete, inflated, gradually tapering, with sparse to many fibrils and lateral branches, 0.7–3.1 mm in diam.; lateral branches broadened at the base, but constricted when cracked; papillae absent; soralia common, formed on whole branches especially on lateral branches, developed usually from cracks or rarely directly from cortex, partially confluent each other to form irregular mass of asexual propagules, smaller than branch diam. but sometimes surrounding the branch, sessile to distinctly stipitate, cortical margin not reflexed, slightly convex at the top often with many isidiomorphs, lacking granular soredia. Cortex thin, 1.6–6.4% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina almost the same as medullary hyphae. Medulla lax, wide, 30–45% of the radius, lacking red pigment. Axis solid, thin, 5.2–31% of the diameter, I –. Apothecia very rare, lateral on lateral branches, up to 4.0 mm in diam., cup-shaped; thaloid exciple with many fibrils; disc pruinose, gray, lacking white rim; epihymenium 0–36  $\mu$ m thick; hymenium 50–64  $\mu$ m thick; hypothecium 46–60  $\mu$ m thick; spores 9.0–11  $\times$  5.0–7.0  $\mu$ m long.

Chemistry. Usnic, norstictic, protocetraric and salazinic acids.

The distinguishing features of *U. nidifica* are (1) the pendent thallus with anisotomic-dichotomous branching, (2) the inflated branches which is glossy and lacking papillae on the surface, (3) the irregular shaped soralia which are developed from cracks of cortex, (4) the absence of granular soredia, (5) the *merrillii*-type plectenchymatous cortex, and (6) the presence of norstictic and salazinic acids as major substances.

This species is very variable in morphology especially the shape of soralia which arise from cracks on the surface of branches and between segments, and directly from cortex. Therefore, the shape of soralia varies in shape (e.g. rounded, elliptic, elongated or irregular). In addition, the lateral branches sometimes arise partially abundant, e.g. at near the base, or near the apices, which makes the thallus appear very different. The amount of lateral branching and the ratio of the cortex, medulla and axis are also variable. Therefore, all the taxa mentioned above in synonyms belong to the natural range of variation of *U. nidifica*. Stevens (1999) discussed about the relationship between *U. grandis*, *U. intercalaris*, *U. japonica*, *U. neocaledonica*, *U. nexilis*, *U. societatis* and *U. straminea*, and supposed they all belong to *U. nidifica* at species or subspecies rank.

*U. nidifica* resembles *U. bismolliuscula* and *U. himalayana*. However, it is distinguished from *U. bismolliuscula* by the absence of perforations on the thicker branches and

the presence of salazinic acid. It is distinguished from *U. himalayana* by the absence of pseudocyphellae on the surface of branches.

In Japan, *U. nidifica* is distributed in Honshu and Shikoku, where it grows on bark of trees such as *Pinus* at elevations up to 600 m especially near the coast. In Taiwan, it is found at elevations between 2000 and 2500 m. This species is widely distributed in subtropical to tropical regions of Asia, Africa and Oceania (Stevens 1991).

Exsiccata examined. JAPAN. Honshu. Prov. Rikuzen: Kitagama Seashore, 20.5.1967, *M. Togashi s.n.* (S. Kurokawa: Lich. Rar. Cri. Exs. 296). Prov. Hitachi: Suda-Shinden, Wakabayashi-mura, Kashima-gun, on tree bark, c. 20 m, 2.4.1968, *M. Togashi s.n.* (S. Kurokawa & H. Kashiwadani: Lich. Rar. Cri. Exs. 342).

Representative specimens examined. JAPAN. Honshu. Prov. Rikuzen: Kitagama Seashore, 20.5.1967, *M. Togashi s.n.*; Gamou, Miyagi-gun, 5.1.1921, *Y. Asahina 1201*. Prov. Iwaki: Matsukawa-ura, Souma-gun, 18.7.1958, *S. Kurokawa 58098*. Prov. Kazusa: Yatsumi-mura, Chousei-gun, 9.12.1923, *Y. Asahina 1212*. Prov. Tanba: Kaibara-cho, Hikami-gun, 14.7.1927, *Y. Asahina 1205*. Shikoku. Prov. Awa: Mt. Tairyuji, Anan-city, c. 580 m, 6.5.1979, *H. Kashiwadani [15074]* & *S. Kurokawa*. Prov. Tosa: Nagasawa Water Fall, Higashi-tsuno-mura, Takao-ka-gun, c. 600 m, 26.3.1983, *H. Kashiwadani 19841*. Sulphur Island, *M. Kikuchi s.n.* (herb. *Y. Asahina 1216*). Bonin Islands, *Yatabe 298*. TAIWAN. Mt. Nan-Fu-Ta-San, 2400–2600 m, 20.1.1964, *S. Kurokawa 1091*. Prov. Chiayi: Nimandaira, Mt. Ali, 25.12.1925, *Y. Asahina F-297*.

27. *Usnea nipparensis* Asahina, Lich. Jap. 3: 91, 1956.

Holotype: Japan, Honshu, Prov. Musashi, Nippara, 4.6.1927, *Y. Asahina 3101* (TNS!). Chemistry: usnic, norstictic, caperatic and stictic acids.

*Usnea nipparensis* f. *reagens* Asahina, J. Jpn. Bot. 47: 257, 1972. Holotype: Japan, Honshu, Prov. Kai, Lakeside of Yamanaka, Mt. Fuji, 16.8.1952, *Y. Asahina 52816* (TNS!). Chemistry: usnic, norstictic, menegazziaic, stictic, constictic and caperatic acids.

Thallus erect to subpendent, up to 31 cm long, grayish-green when fresh, brown to rusty brown in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches slightly glossy on the surface, lacking pseudocyphellae and maculae, terete, uninflated, gradually tapering, usually with many fibrils and lateral branches, 0.9–1.7 mm in diam.; lateral branches slightly constricted at the base; papillae common, usually hemispherical rarely verrucose; soralia common, formed mainly on lateral and terminal branches, developed from the top of eroded papillae,  $\pm$  discrete, rounded to irregularly rounded in shape, grow up to larger than branch diam., often distinctly stipitate, cortical margin not reflexed, convex at the top often with isidiomorphs, lacking granular soredia. Cortex 5.9–14% of the radius, *ceratina*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, with oblong lumina. Medulla moderate to dense in density, 18–32% of the radius, lacking red pigment. Axis solid, 20–47% of the diameter, I–. Apothecia not seen.

Chemistry. Race 1, usnic and caperatic acids, and atranorin ( $\pm$ ); Race 2, usnic, caperatic, stictic, norstictic ( $\pm$ ), menegazziaic ( $\pm$ ) and constictic acids ( $\pm$ ).

The distinguishing features of *U. nipparensis* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the rounded soralia which are distinctly stipitate and their cortical margins are not reflexed, (3) the absence of granular soredia, (4) the *ceratina*-type plectenchymatous cortex, and (5) the presence of caperatic acid, occasionally with stictic acid, as a major substance.

Two chemical races are recognized in the present area. Both Race 1 (stictic acid lack-

ing, 45%) and Race 2 (stictic acid containing, 55%) are commonly found. As no morphological and ecological differences were found between them, the chemical differences found in this species are considered to have no taxonomic value.

*U. nipparensis* may sometimes be confused with *U. hakonensis* in having rounded soralia which are distinctly stipitate. However, it is readily distinguished from the latter species by the presence of caperatic acid and the absence of US1 and US2. Herbarium specimens of *U. nipparensis* resemble *U. pangiana* in color and habit of thallus. It is distinguished from *U. pangiana* by the rounded and stipitate soralia growing up to branch diam., the *ceratina*-type plectenchymatous cortex, and the presence of caperatic acid.

In Japan, *U. nipparensis* is distributed in central Honshu, where it grows on tree bark such as *Salix* at elevations between 800 and 1800 m. In Taiwan, it is found at elevations between 1600 and 1900 m. This species is also recorded from Korea, India and Nepal.

Representative specimens examined. Race 1. JAPAN. Honshu. Prov. Musashi: Nippara, 25.11.1969, *M. Togashi s.n.* (herb. *Y. Asahina 69112*). Prov. Shinano: en route from Gyozya-goya to Minoto-sanso, Yatsugatake Mts., Chino-city, on *Salix* sp., 1740–1800 m, 29.8.1997, *Y. Ohmura 3825*. Prov. Kai: Momonoki Mineral Spring, Ashiyasu-mura, c. 900 m, 19.12.1982, *M. Nuno et al. s.n.* Prov. Suruga: Ohmiyaguchi 2-gome, Mt. Fuji, 24.6.1933, *Y. Asahina 3324*. TAIWAN. Prov. Ilan: Piyanan Pass, 1600–1900 m, 16.1.1964, *S. Kurokawa 832*. NEPAL. E. Nepal, Walunchung, Gola-Zongi, c. 3500 m, 11.11.1963, *M. Togashi s.n.*

Race 2. JAPAN. Honshu. Prov. Musashi: Ohtaki-mura, Chichibu-gun, 16.8.1949, *M. Omura s.n.* (herb. *Y. Asahina 3102*). Prov. Kai: Oshino-mura, Minami-tsuru-gun, 3.5.1968, *M. Togashi s.n.* (herb. *Y. Asahina 6853R*); Sengen Shrine, Fuji-yoshida, 1952, *Y. Asahina 2591*. Prov. Kii: Mt. Koya, 19.10.1952, *Y. Asahina s.n.* KOREA. Kanchi-in, 2.8.1934, *F. Fujikawa s.n.* (herb. *Y. Asahina 3482*). INDIA. Phalut, Darjeeling, 9.5.1960, *M. Togashi s.n.*

## 28. *Usnea orientalis* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 547, 1938.

Holotype: China, Prov. Setschwan austro-occid., in regionis temperatae tergorum supra vicum Fumadi ad flumen Wolo-ho inter Yenyuen et Yungning, Cotoneastere, ca. 3300 m alt., 15.6.1914, *Handel-Mazzetti 3035* (Diar. Nr. 559, W!). Chemistry: usnic, norstictic, galbinic and salazinic acids.

*Usnea orientalis* f. *esorediosa* Asahina, Lich. Jap. 3: 100, 1956, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Musashi, Nippara, 29.10.1922, *Y. Asahina 1903* (TNS!). Chemistry: usnic and salazinic acids.

Thallus fruticose, erect, up to 7 cm long, color unknown when fresh, yellowish-brown to chestnut-brown in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches glossy on the surface, lacking pseudocyphellae and maculae, terete, inflated, tapering only near the apices especially on lateral branches, with many fibrils and lateral branches, 1.0–1.2 mm in diam.; lateral branches short, spinulose, cylindrical at the base; papillae common on thicker branches, cylindrical; soralia absent. Cortex thin, 2.3–5.1% of the radius, *ceratina*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina distinctly enlarged to be elliptic to rounded in shape. Medulla lax in density, wide, 32–40% of the radius, lacking red pigment. Axis solid, thin, 16–26% of the diameter, 1–. Apothecia common, subterminal on terminal and lateral branches, up to 1.7 cm in diam., flat; thalloid exciple with many fibrils; disc pruinose, gray to pale brown, lacking white rim; epihymenium 2–16  $\mu\text{m}$  thick; hymenium 70–80  $\mu\text{m}$  thick; hypothecium 20–50  $\mu\text{m}$  thick; spores 8–11  $\times$  6–7  $\mu\text{m}$  long.

Chemistry. Usnic, salazinic, protocetraric ( $\pm$ ) and constictic ( $\pm$ ) acids.

The distinguishing features of *U. orientalis* are (1) the erect thallus with anisotomic-

dichotomous branching, (2) the inflated branches with glossy surface, (3) the cylindrical papillae on thicker branches, (4) the absence of soralia, (5) the flat apothecia through the juvenile to mature stages, (6) the disc without the white rim, (7) the *ceratina*-type plectenchymatous, and (8) the presence of salazinic acid as a major substance.

Although the type specimen of *U. orientalis* contains galbinic acid, this substance was not detected from specimens of the present area. As no morphological difference was found between the type and specimens from the present area, the chemical differences between them are considered to have no taxonomic value.

When Asahina (1956) described *U. orientalis* f. *esorediosa*, he cited two specimens to show the ratio of the cortex, medulla and axis in the protologue. Both of them agree well with the protologue. One of them, “*Y. Asahina 1903*”, is selected as the lectotype of *U. orientalis* f. *esorediosa*.

Although *U. orientalis* resembles *U. fuscorubens*, it is distinguished by the flat apothecia through the juvenile to mature stages.

In Japan, *U. orientalis* is a rare species known from central Japan and Shikoku, where it grows on tree bark at ca. 1500 m alt. In Taiwan, it grows on tree bark at elevations between 1900 and 2900 m.

Representative specimens examined. JAPAN. Honshu. Prov. Musashi: Ippai-mizu, Nippara, 13.9.1955, *M. Togashi* s.n. (herb. *Y. Asahina 55913*). Prov. Kai: Tokusa Pass, 7.8.1953, *S. Kurokawa 521245*. Shikoku. Prov. Awa: Mt. Kenzan, 27.8.1908, *J. Nakai 50604*. TAIWAN. Taichung Hsien, en route from Ssu-yuan to To-chia tun Shan, Mt. Nanhuta Shan, Hoping, 1900–2250 m, 9.11.1989, *H. Kashiwadani 35769*.

29. *Usnea pangiana* Stirt., Scott. Natur. 7: 77, 1883.

Holotype: India, Himalaya, Lingalelah Range, 2000–2300 m alt., *G. Watt 7051* (BM!). Chemistry not examined.

*Usnea cineraria* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 3: 618, 1938, syn. nov. Holotype: Himalaya, Kataphar bei Darjeeling, on *Cryptomeria stämmen*, 2500 m, 6.1915, *A. K. Gebauer* s.n. (W!). Chemistry: usnic, barbatic, 4-*O*-demethylbarbatic and salazinic acids.

*Usnea croceorubescens* Vain., Bot. Mag., Tokyo 35: 46, 1921, syn. nov. Holotype: Japan, Prov. Kushiro, in arbore, 21.8.1918, *A. Yasuda 234* (TUR-V 00877!). Chemistry: usnic, barbatic, 4-*O*-demethylbarbatic and salazinic acids

*Usnea hondoensis* Asahina, Lich. Jap. 3: 87, 1956, syn. nov. – *U. pangiana* Stirt. subsp. *hondoensis* (Asahina) Asahina, J. Jpn. Bot. 47: 134, 1972. Holotype: Japan, Honshu, Prov. Musashi, Nippara, 10.1922, *Y. Asahina 115* (TNS!). Chemistry: usnic, protocetraric and salazinic acids.

*Usnea hondoensis* subsp. *inflata* Asahina, Lich. Jap. 3: 89, 1956, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Kai, Lakeside of Shoji, Mt. Fuji, 9.1952, *M. Togashi* s.n. (herb. *Y. Asahina 5290*, TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea hondoensis* subsp. *inflata* f. *fujisanensis* Asahina, Lich. Jap. 3: 89, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Suruga, Subashiri-guchi, Mt. Fuji, 16.7.1952, *Y. Asahina 52716* (TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea hondoensis* subsp. *lacunosula* Asahina, Lich. Jap. 3: 90, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Musashi, Hikawa-machi, Nishi-tama-gun, 4.5.1952, *Y. Asahina 3015* (TNS!). Chemistry: usnic, barbatic, 4-*O*-demethylbarbatic, norstictic, protocetraric and salazinic acids.

Thallus erect to subpendent, up to 25 cm long, grayish-green when fresh, brown to rusty brown in herbarium specimens, concolorous with thallus at the base, often with distinct annular cracks especially near the base; branching anisotomic-dichotomous; branches matt on the surface, lacking pseudocyphellae and maculae, terete, usually uninflated or

rarely inflated, gradually tapering, usually with many fibrils and lateral branches, 0.6–1.3 mm in diam.; lateral branches cylindrical at the base; papillae sparse, hemispherical; soralia common, formed on whole branches especially on lateral branches, developed from the top of eroded papillae or scars of detached fibrils, discrete, punctiform, smaller than branch diam., usually sessile but rarely slightly stipitate, cortical margin not reflexed, flat to slightly convex at the top rarely with isidiomorphs. Cortex 5.2–18% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina almost the same as medullary hyphae. Medulla lax to dense in density, 6.3–33% of the radius. Axis solid, 21–53% of the diameter, I–. Apothecia rare, subterminal on lateral or terminal branches, up to 6.0 mm in diam., cup-shaped; thalloid exciple with sparse fibrils; disc pruinose, gray, lacking white rim; epihymenium 8–30  $\mu\text{m}$  thick; hymenium 60–80  $\mu\text{m}$  thick; hypothecium 50–60  $\mu\text{m}$  thick; spores 9–14 $\times$ 6  $\mu\text{m}$  long.

Chemistry. Race 1, usnic, salazinic, norstictic ( $\pm$ ), protocetraric ( $\pm$ ), constictic ( $\pm$ ) and squamatic acids ( $\pm$ ), and atranorin ( $\pm$ ); Race 2, usnic, salazinic, barbatic and 4-*O*-demethylbarbatic, norstictic ( $\pm$ ), protocetraric ( $\pm$ ), constictic ( $\pm$ ) and squamatic acids ( $\pm$ ), and atranorin ( $\pm$ ).

The distinguishing features of *U. pangiana* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the annular cracks especially near the base, (3) the punctiform soralia, (4) the absence of granular soredia, (5) the *merrillii*-type plectenchymatous cortex, and (6) the presence of salazinic acid and/or barbatic acids as major substances.

The type specimen of *U. hondoensis* subsp. *inflata* includes three individuals in a herbarium packet. Two of them coincide very well with the morphological features shown in the protologue, but the rest is *U. dasaea*. TLC tests for the former two individuals show that barbatic and 4-*O*-demethylbarbatic acids are present in one, and, in addition, norstictic and protocetraric acids are detected in the other. The occurrence of these substances was not mentioned by Asahina (1956). The latter two substances are chemically close to salazinic acid, but barbatic and 4-*O*-demethylbarbatic acids are distantly related with salazinic acid. In the present paper, therefore, one individual containing norstictic, protocetraric and salazinic acids along with usnic acid is designated as the lectotype of subsp. *inflata*, especially to avoid further confusion in the typification of the subspecies.

Two chemical races are recognized from the present area as shown above. Both Race 1 (salazinic acid, 53%) and Race 2 (salazinic and barbatic acids, 47%) are commonly found. As no morphological and ecological differences were found between them, the chemical difference found in this species is considered to have no taxonomic value.

*U. pangiana* is a variable species, especially in the ratio of the cortex, medulla and axis, and the frequency of annular cracks near the base. Therefore, this species may be confused with some specimens of *U. confusa* which has inflated branches and sometimes has annular cracks near the base. However, it can be distinguished by the punctiform soralia instead of rounded soralia. *U. pangiana* is also similar to *U. yakushimensis* in morphology, but it is distinguished from *U. yakushimensis* by the presence of salazinic acid.

In Japan, *U. pangiana* is distributed in Hokkaido, Honshu, Shikoku and Kyushu, where it grows on bark of coniferous trees such as *Abies*, *Larix*, *Picea* and *Pinus*, or

broadleaf trees such as *Carpinus*, *Fagus*, *Fraxinus* and *Quercus*. It is found at elevations between 100 and 1800 m (at lower elevations in Hokkaido and at higher elevations in Honshu, Shikoku and Kyushu). In Taiwan, it grows on bark at elevations between 800 and 3300 m. This species is also recorded from India, Nepal and Thailand.

Exsiccata examined. Race 2. JAPAN. Honshu. Prov. Shinano: Daimon Pass, Chiisagata-gun, on trunk of trees, c. 1400 m, 22.5.1959, *Y. Asahina et al.* (S. Kurokawa: Lich. Rar. Cri. Exs. 200; as *U. pangiana* Stirt. subsp. *hondoensis* Asahina).

Representative specimens examined. Race 1. JAPAN. Hokkaido. Prov. Kushiro: along Route 44, Akkeshi-cho, Akkeshi-gun, on *Abies sachalinensis*, c. 100 m, 2.9.1996, *Y. Ohmura* 2720. Prov. Tokachi: Shimonozuka, 2.7.1953, *Y. Asahina s.n.* Honshu. Prov. Mutsu: Sarukura Hot Spring, Mt. Hakkoda, on *Fagus crenata*, c. 900 m, 1.8.1985, *K. Sasaki* 7249. Prov. Musashi: Hikawa-machi, Nishi-tama-gun, 4.5.1952, *Y. Asahina* 3015. Prov. Sagami: Hakone, Lakeside of Ashinoko, 15.7.1952, *M. Togashi s.n.* (herb. *Y. Asahina* 52715). Prov. Shinano: Ikenodaira, Takato-machi, Kamiina-gun (35°55'N, 138°10'E), on *Larix kaempferi*, 1620 m, 29.6.1997, *Y. Ohmura* 3144d. Prov. Kai: Lakeside of Yamanaka, Minami-tsuru-gun, c. 980 m, 26.7.1957, *S. Kurokawa* 57117-b; Lakeside of Yamanaka, Mt. Fuji, 9.7.1967, *M. Togashi s.n.* Prov. Suruga: Subashiri-guchi, Mt. Fuji, 16.7.1952, *Y. Asahina s.n.* Prov. Izu: Mt. Amagi, 29.4.1933, *F. Fujikawa s.n.* Prov. Ise: Mt. Gozaisho-dake, 1952, *T. Harada s.n.* (herb. *Y. Asahina* 3011). Shikoku. Prov. Iyo: Sumino-machi, Nii-gun, 27.3.1943, *K. Ochi s.n.* (herb. *Y. Asahina* 3006). Kyushu. Prov. Bungo: en route from Hanamura to Oike, Shonai-cho, Ohita-gun (33°08'N, 131°17'E), on *Quercus serrata*, c. 960 m, 5.3.1997, *Y. Ohmura* 3044. Prov. Hyuga: Suki-son, Nishi-morokata-gun, 15.5.1947, *M. Togashi s.n.* Prov. Hizen: Mt. Unzen, 31.8.1958, *Y. Asahina s.n.* Prov. Ohsumi: Kosugidani, Yakushima Island, on *Cryptomeria japonica*, 30.5.1998, *Y. Sakuma s.n.* (herb. *Y. Ohmura* 4511). TAIWAN. Mt. Nan-Fu-Ta-San, 2400–2600 m, 20.1.1964, *S. Kurokawa* 1109. INDIA. Lopdui, Darjeeling, 28.4.1960, *M. Togashi s.n.*

Race 2. JAPAN. Hokkaido. Prov. Kitami: Tokusyoppe, Furu-ume, Bihoro-cho, Abashiri-gun, on *Abies sachalinensis*, c. 330 m, 2.9.1996, *Y. Ohmura* 2682. Prov. Nemuro: Bettouga, c. 50 m, 1.9.1965, *S. Kurokawa* 6574d. Prov. Kushiro: along Route 44, Akkeshi-cho, Akkeshi-gun, on *Abies sachalinensis*, c. 100 m, 3.9.1996, *Y. Ohmura* 2755. Prov. Tokachi: Shimonozuka, 2.7.1953, *Y. Asahina* 53729. Prov. Iburi: Mt. Tarumae, c. 250 m, 10.11.1977, *H. Kashiwadani* 14481. Honshu. Prov. Sagami: Hakone, Lakeside of Ashinoko, 15.7.1952, *M. Togashi s.n.* (herb. *Y. Asahina* 111). Prov. Shinano: 4.3 km SW of Lake Chiyoda, Fujisawa, Takato-machi, Kami-inagun (35°47'N, 138°08'E), on *Larix kaempferi*, 1220 m, 28.6.1997, *Y. Ohmura* 3132. Prov. Kai: Tokyo University Forest, Asahigaoka, Minami-tsuru-gun, on weathered bark of *Fraxinus mandshurica* var. *japonica*, c. 1500 m, 8.5.1998, *Y. Ohmura* 4409. Prov. Suruga: Ohmiya-guchi 1-gome, Mt. Fuji, 19.10.1924, *Y. Asahina* 3008. Prov. Izu: Mt. Amagi, 29.4.1933, *F. Fujikawa s.n.* (herb. *Y. Asahina* 3016). Prov. Mikawa: Mt. Chausu, Kita-shitara-gun, *N. Takaki* 349 pr.p. Prov. Yamashiro: Mt. Hiei, 25.10.1954, *S. Kurokawa s.n.* Shikoku. Prov. Awa: Hirono, Kisawason, Naka-gun, 23.11.1968, *M. Togashi s.n.* (herb. *Y. Asahina* 681123). Prov. Iyo: Sumino-machi, Nii-gun, 27.3.1943, *K. Ochi* 80a. Kyushu. Prov. Bungo: Kyusui-kei Gorge, Kokonoe-machi, Kusu-gun (33°10'N, 131°13'E), on *Quercus acutissima*, c. 720 m, 4.3.1997, *Y. Ohmura* 3024 pr.p. Prov. Hyuga: Suki-son, Nishi-morokata-gun, 15.5.1947, *M. Togashi s.n.* Prov. Higo: en route from Senomoto to Kurokawa, Minami-oguni-mura, Aso-gun, 31.5.1954, *M. Togashi s.n.* TAIWAN. Prov. Taitung: Mt. Lachialachiaerh, c. 1800 m, 22.1.1965, *S. Kurokawa* 2502. INDIA. Darjeeling, 2.4.1960, *M. Togashi s.n.* NEPAL. Khumbu, Near Lukla (27°40'N, 86°43'E), on bark, c. 3500 m, 18.3.1999, *A. Shimizu s.n.* (herb. *Y. Ohmura* 4506). THAILAND. Prov. Chiang Mai: Doi Sutep, 1000–1676 m, 16.2.1964, *S. Kurokawa* 1688.

### 30. *Usnea pseudogatai* Asahina, J. Jpn. Bot. 45: 131, 1970.

Holotype: Taiwan (Formosa), Prov. Chiayi, Mt. Ali, 1935, *M. Ogata* 203 (TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

Thallus fruticose, erect to subpendent, up to 11 cm long, color unknown when fresh, brown in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches slightly glossy on the surface, lacking pseudocypbellae and maculae, terete, inflated, gradually tapering, with many fibrils and lateral branches, 1.0–1.1 mm



in diam.; lateral branches cylindrical at the base; papillae common on thicker branches, cylindrical; soralia absent. Cortex thin, 4.7–5.5% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina slightly enlarged to be fusiform, oblong or turbinate. Medulla lax to moderate in density, wide, 27–34% of the radius, lacking red pigment. Axis solid, 22–36% of the diameter, I –. Apothecia common, subterminal on terminal and lateral branches, up to 6.4 mm in diam., flat to sinuose; thal-  
loid exciple with few fibrils; disc pruinose, gray to pale brown, marginated by white rim; epihymenium 2–8  $\mu\text{m}$  thick; hymenium 54–76  $\mu\text{m}$  thick; hypothecium 26–40  $\mu\text{m}$  thick; spores 8–10 $\times$ 5–6  $\mu\text{m}$  long.

Chemistry. Usnic, norstictic, protocetraric and salazinic acids.

The distinguishing features of *U. pseudogatai* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the inflated branches with cylindrical papillae, (3) the absence of soralia, (4) the flat to sinuose apothecia with few fibrils along the thal-  
loid exciple, (5) the brown colored disc marginated by white rim, (6) the *merrillii*-type plectenchymatous cortex, and (7) the presence of salazinic acid as a major substance.

Although *U. pseudogatai* resembles *U. dendritica*, it is distinguished by the wide medulla and the absence of barbatic acid.

This species has only been collected from Taiwan, where it grows on tree bark at elevations between 1900 and 2600 m.

Representative specimens examined. TAIWAN. Prov. Chiayi: Mt. Ali, 24.12.1925, *Y. Asahina* 2512. Prov. Ilan: Mt. Nanfuta-san, 2400–2600 m, 20.1.1964, *S. Kurokawa* 1112. Prov. Taitung: Mt. Wunitoparu, c. 1900 m, 23.1.1965, *S. Kurokawa* 2621a.

### 31. *Usnea pygmoidea* (Asahina) Y. Ohmura, stat. nov.

*U. pygmea* (non Motyka) Asahina, nom. illeg., Lich. Jap. 3: 98, 1956. – *U. confusa* Asahina subsp. *pygmoidea* Asahina, J. Jpn. Bot. 43: 130, 1968.

Holotype: Japan, Honshu, Prov. Kai, Yoshida-guchi 1-gome, Mt. Fuji, 10.8.1952, *M. Togashi* s.n. (TNS!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

*Usnea kushiroensis* Asahina subsp. *subasiriensis* Asahina, Lich. Jap. 3: 61, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Suruga, Subashiri-guchi, Mt. Fuji, 8.8.1933, *Y. Asahina* 1218 (TNS!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

Thallus fruticose, erect to subpendent, up to 18 cm long, grayish-green when fresh, brownish-, rusty- or chestnut-brown in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches glossy on the surface, lacking pseudocyphellae and maculae, terete, inflated, gradually tapering, with many fibrils and lateral branches, 0.6–1.6 mm in diam.; lateral branches constricted at the base; papillae common, hemispherical to verrucose; soralia common, formed mainly on lateral branches, developed from the top of eroded papillae, elongated and confluenting each other to form irregular mass of asexual propagules, smaller than branch diam. but sometimes surrounding the branch, distinctly stipitate, cortical margin not reflexed, convex at the top with isidiomorphs and granular soredia. Cortex 3.1–8.1% of the radius, *ceratina*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, with fusiform or oblong lumina. Medulla lax to moderate in density, 26–40% of the radius, lacking red pigment. Axis solid, 13–33% of the diameter, I –. Apothecia not seen.

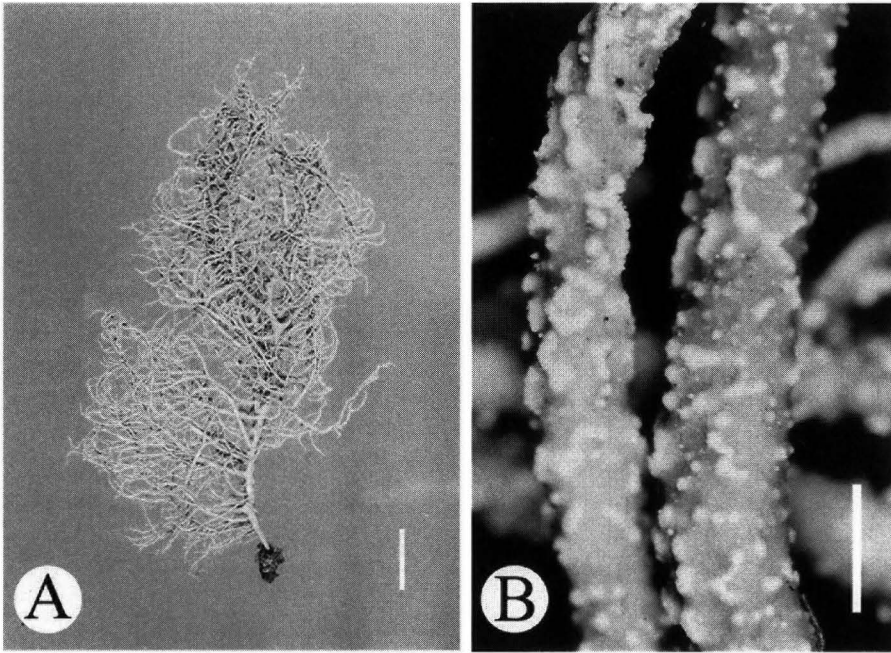


Fig. 15. *Usnea pygmoidea* (Asahina) Y. Ohmura, (*Y. Ohmura 3144a*). A. Thallus. B. Soralia which are confluent and form irregular masses of soredia; and are distinctly stipitate. Scales: A = 1 cm; B = 1 mm.

Chemistry. Race 1, usnic, salazinic, norstictic ( $\pm$ ), protocetraric ( $\pm$ ) and constictic ( $\pm$ ) acids, and atranorin ( $\pm$ ); Race 2, usnic, norstictic, stictic, menegazziaic ( $\pm$ ) and constictic acids ( $\pm$ ), and atranorin ( $\pm$ ).

The distinguishing features of *U. pygmoidea* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching (Fig. 15A), (2) the inflated branches which are glossy on the surface, (3) the stipitate and irregularly elongated soralia (Fig. 15B), (4) the presence of granular soredia together with isidiomorphs, (5) the *ceratina*-type plectenchymatous cortex, and (6) the presence of salazinic or stictic acids as major substances.

Asahina (1956) identified some Japanese specimens of *Usnea* as *U. pygmea* Motyka based only on the protologue of this species; but the type specimen of *U. pygmea* belongs to *U. bismolliuscula*, as reported by Asahina (1965b). Therefore, the specimen used for making the description of *U. pygmea* (non. Motyka) Asahina should be given another name. Asahina (1968b) treated it as a subspecies of *U. confusa*, and published it as *U. confusa* subsp. *pygmoidea* Asahina. Although he did not designate the type specimen in the protologue of *U. pygmea* (non Motyka) Asahina and *U. confusa* subsp. *pygmoidea* Asahina, the specimen, labeled as Japan, Honshu, Prov. Kai, Yoshida-guchi 1-gome, Mt. Fuji, 10.8.1952, *M. Togashi s.n.* which is used to show the ratio of the cortex, medulla and axis in the protologue of *U. pygmea* (non Motyka) Asahina, can be accepted as the holotype of

*U. confusa* subsp. *pygmoidea* according to Art. 9.1 note 1 of Tokyo Code (Greuter et al. 1994). This taxon, however, is apparently a distinct species as mentioned above. In this way, *U. pygmoidea* is newly reported as a species.

Two chemical races are reported in the present area. Race 1 and Race 2 are commonly found, frequency of each being 50%. As no morphological and ecological differences were found between them, the chemical differences found in this species are considered to have no taxonomic value.

*U. pygmoidea* strongly resembles *U. confusa*, *U. dasaea*, *U. glabrata* and *U. hakonensis* in having inflated branches with soralia. However, *U. pygmoidea* is distinguished from them by the stipitate soralia which are elongated and irregular in shape, although juvenile stages of *U. pygmoidea* are very similar to *U. confusa* and *U. dasaea*. Race 2 of *U. pygmoidea* is readily distinguished from them by the presence of stictic acid.

In Japan, *U. pygmoidea* is distributed in Hokkaido, Honshu and Kyushu, where it grows on bark of trees such as *Abies*, *Alnus*, *Cryptomeria*, *Larix*, *Picea*, *Pinus* and *Ulmus* at elevations between 100 and 2600 m. In Taiwan, it is found at elevations between 2000 and 2500 m.

Representative specimens examined. Race 1. JAPAN. Hokkaido. Prov. Kushiro: along Route 44, Akkeshi-cho, Akkeshi-gun, on *Abies sachalinensis*, c. 100 m, 2.9.1996, *Y. Ohmura 2736*. Honshu. Prov. Awa: Mt. Kiyosumi, on *Pinus* sp., 3.11.1998, *Y. Kon s.n.* (herb. *Y. Ohmura 4509*). Prov. Musashi: E Valley of Ohchigawa River, Chichibu, 1.9.1951, *S. Kurokawa 510157*. Prov. Shinano: N slope of Mt. Nyukasa, Fujimi-cho, Suwa-gun (35°54'N, 138°10'E), on *Larix kaempferi*, 1800–1920 m, 30.6.1997, *Y. Ohmura 3206*; Ikenodaira, Takato-machi, Kami-ina-gun (35°55'N, 138°10'E), on *Larix kaempferi*, 1620 m, 29.6.1997, *Y. Ohmura 3144a*. Prov. Kai: Shogen Pass, Chichibu Mts., 12.8.1953, *S. Kurokawa 521293*. Prov. Ohmi: Mt. Hiei, 13.11.1953, *M. Togashi s.n.* Prov. Yamashiro: Mt. Hiei, 13.11.1953, *M. Togashi s.n.* Prov. Kii: en route from Ichinobashi to Okunoin, Mt. Koya, on *Cryptomeria japonica*, c. 800 m, 1.4.1999, *Y. Ohmura 4485*. Kyushu. Prov. Hizen: Mt. Unzen, 31.5.1956, *H. Muroi s.n.*

Race 2. JAPAN. Hokkaido. Prov. Kitami: Tokushoppe, Furu-ume, Bihoro-cho, Abashiri-gun, on *Abies sachalinensis*, c. 330 m, 2.9.1996, *Y. Ohmura 2679*. Prov. Tokachi: Shimozuka, 2.7.1953, *Y. Asahina s.n.* Honshu. Prov. Musashi: Akazawa, Ohtaki-mura, Chichibu-gun, 16.8.1949, *M. Omura s.n.* (herb. *Y. Asahina 1307*). Prov. Shinano: Ikenodaira, Takato-machi, Kami-ina-gun (35°55'N, 138°10'E), on *Larix kaempferi*, 1620 m, 29.6.1997, *Y. Ohmura 3144c*; Mt. Nyukasa, c. 1900 m, 6.7.1976, *H. Kashiwadani 13306*. Prov. Kai: Oshino-mura, Minami-tsuru-gun, 3.5.1968, *M. Togashi s.n.* (herb. *Y. Asahina 68503b*). Prov. Kii: Mt. Koya, 23.8.1952, *M. Togashi s.n.* Prov. Yamato: Ryusenji Temple, Dorogawa, Yoshino-gun, 12.6.1952, *M. Togashi s.n.* TAIWAN. Prov. Chiayi: Mt. Ali, 2200 m, 6.1.1964, *S. Kurokawa 586*. Prov. Nantou: Chitou, 30.1.1964, *S. Kurokawa 1399*. Mt. Nan-Fu-Ta-San, 2400–2600 m, 20.1.1964, *S. Kurokawa 1106*.

### 32. *Usnea rubicunda* Stirt., Scott. Natur. 6: 102, 1881.

Holotype: England, 27.6.1879, *E. M. Holmes s.n.* (BM!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

*Usnea pensylvanica* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 351, 1938, syn. nov. Holotype: Pennsylvania, collector unknown (H-ACH 1853!). Chemistry: not examined.

*Usnea rubicunda* subsp. *aberrans* Asahina, Lich. Jap. 3: 116, 1956, syn. nov. – *U. pseudorubicunda* Asahina, J. Jpn. Bot. 44: 260, 1969. Holotype: Japan, Shikoku, Prov. Sanuki, Kankake, Shodoshima Island, on rock (granite), c. 600 m, 15.7.1953, *M. Togashi s.n.* (TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

Thallus fruticose, erect to subpendent, up to 14 cm long, red to reddish-brown or greenish-gray with a few red flecks, concolorous with thallus or dark brown at the base; branching anisotomic-dichotomous; branches matt to slightly glossy on the surface, lack-

ing pseudocyphellae and maculae, terete, uninflated, 0.7–1.5 mm in diam., gradually tapering, with few to many lateral branches and fibrils; lateral branches cylindrical at the base; papillae rare to common on thicker branches, hemispherical to verrucose; soralia common, formed mainly on thicker branches but absent or rare on fibrils, developed from the top of eroded papillae,  $\pm$  discrete, rounded in shape, smaller than branch diam., slightly to distinctly stipitate, cortical margin not reflexed, convex at the top with numerous isidiomorphs, lacking granular soredia. Cortex thick, 5.6–15% of the radius, *ceratina*-type plectenchymatous cortex; hyphae pachydermatous, secreted red pigment in the cell wall, lumina slightly enlarged to be fusiform or oblong. Medulla dense, 13–28% of the radius, lacking red pigment. Axis solid, 24–57% of the diameter, I–. Apothecia very rare, lateral on lateral or terminal branches, up to 4.5 mm in diam., flat to sinuate; thalloid exciple with many fibrils; disc pruinose, whitish gray to pale brown, lacking white rim; epihymenium 2–36  $\mu\text{m}$  thick; hymenium 20–60  $\mu\text{m}$  thick; hypothecium 36–60  $\mu\text{m}$  thick; spores 10–11  $\times$  5–6  $\mu\text{m}$  long.

Chemistry. Race 1, usnic, norstictic, stictic, menegazziaic, constictic and squamatic ( $\pm$ ) acids, and atranorin ( $\pm$ ); Race 2, usnic, norstictic, stictic, menegazziaic, constictic, psoromic and 2'-*O*-demethylpsoromic acids ( $\pm$ ), and atranorin ( $\pm$ ); Race 3, usnic, norstictic, salazinic and protocetraric acids.

The distinguishing features of *U. rubicunda* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the presence of red pigment in cortex, (3) the stipitate and rounded soralia on thicker branches with many isidiomorphs, (4) the absence of soralia on fibrils, (5) the absence of granular soredia, (6) the *ceratina*-type plectenchymatous cortex, and (7) the presence of stictic acid (very rarely salazinic acid).

Three chemical strains were recognized. Race 1 was commonly found (93%); Race 2 (6%) and Race 3 (1%) were rarely found. As no morphological differences were found among them, chemical differences found in this species are considered to have no taxonomic value.

*U. rubicunda* strongly resembles *U. rubrotincta* Stirt. morphologically and chemically. However, it is distinguished from *U. rubrotincta* by (1) the absence of soralia on fibrils and (2) rounded and stipitate soralia which are formed on thicker branches and developed from the top of eroded papillae.

In Japan, *U. rubicunda* is distributed in Hokkaido, Honshu, Shikoku and Kyushu, where it grows on bark of coniferous trees such as *Cryptomeria*, *Larix*, *Pinus* and *Thuja*, or deciduous trees such as *Prunus*. It also grows on rocks. It is found at lower elevations up to 1500 m. In Taiwan, it is found at elevations between 1000 and 3000 m. Although many researchers reported this species from various locality through the world, such as Asia, East Africa, Europe, North and South America and Oceania (Clerc & Herrera-Campos 1997, Swinscow & Krog 1979, Motyka 1936–38, Purvis et al. 1992, Stevens 1999), taxonomic review should be carried out on the related species.

Exsiccata examined. Race 1. AUSTRALIA. Queensland: Beechmont, on tree bark, c. 540 m, 2.11.1965, *S. Kurokawa s. n.* (*S. Kurokawa*; Lich. Rar. Cri. Exs. 348).

Representative specimens examined. Race 1. JAPAN. Hokkaido. Prov. Nemuro: Attoko, 4.7.1953, *M. Togashi s. n.* Honshu. Prov. Rikuchu: Mt. Hayachine, Hienuki-gun, en route from Dake to Mt. Hayachine via Mt. Keito, c. 570 m, 10.8.1971, *H. Kashiwadani 9238*. Prov. Iwaki: Yoshida-hama, 6.12.1964, *S. Kurokawa 64476*.

Prov. Hitachi: Daigo, Kuji-gun, on *Prunus* sp., c. 300 m, 24.10.1965, *W. Yoshitake* 76. Prov. Kazusa: Ichinomiya, 30.3.1952, *Y. Asahina* 2608. Prov. Musashi: Mt. Mitsumine, Chichibu, 30.8.1951, *S. Kurokawa* 510064. Prov. Sagami: Hakone, *Y. Asahina* 117b. Prov. Sado: Konpon Temple, Niibo-mura, 10.5.1953, *Y. Asahina* s.n. Prov. Shinano: c. 3 km ESE of Azusayama, Kawakami-mura, Minami-saku-gun, on *Larix kaempferi*, 1460–1500 m, 9.12.1996, *Y. Ohmura* 2899. Prov. Kai: Tokusa Pass, 7.8.1953, *S. Kurokawa* 521235. Prov. Suruga: Mt. Shiomidake, 9.8.1925, *H. Koidzumi* 102262. Prov. Izu: Nirayama, Tagata-gun, 15.8.1955, *Y. Asahina* s.n. Prov. Mikawa: Mt. Horaiji, 6.1.1956, *Y. Asahina* 56106. Prov. Mino: Mt. Kinka, 10.4.1889, *M. Miyoshi* s.n. (herb. *Yatabe* 299). Prov. Ohmi: Mt. Hiei, 27.9.1955, *M. Togashi* s.n. Prov. Yamashiro: Koshihata, Sakyo-ku, Kyoto-city, 3.4.1967, *M. Togashi* s.n. Prov. Yamato: Dorogawa, Yoshino-gun, 12.6.1952, *M. Togashi* s.n. Prov. Kii: en route from Ichinobashi to Okunoin, Mt. Koya, on *Cryptomeria japonica*, c. 800 m, 1.4.1999, *Y. Ohmura* 4491. Prov. Settsu: Sengari, Dohjo-mura, Arima-gun, 30.11.1952, *M. Togashi* s.n. Prov. Tanba: Sasayama-cho, Taki-gun, on *Prunus yedoensis*, c. 220 m, 22.8.1998, *Y. Ohmura* 4470. Prov. Tango: Nariaiji, Miyazu-city, 7.7.1956, *M. Togashi* s.n. Prov. Harima: Funakoshi, Mikawa-mura, Shisou-gun, 10.6.1952, *K. Utsumi* s.n. (herb. *Y. Asahina* 124). Prov. Inaba: Tottori, 20.1.1931, *K. Yasuda* s.n. Prov. Bitchu: Mt. Gagyu-san, Joubou-gun, 12.11.1920, *Z. Sasano* s.n. Prov. Bingo: Kamiyama-mura, Sera-gun, 28.11.1932, *T. Sato* s.n. Prov. Aki: Mt. Komagabayashi-dake, Miyajima Island, Saeki-gun, on *Cryptomeria japonica*, c. 500 m, 12.5.1969, *H. Kashiwadani* 5621. Prov. Suo: Teonokiri, Asahi-son, Abu-gun, 24.1.1970, *H. Kashiwadani* 7150b. Shikoku. Prov. Awa: Mt. Kenzan, 24.4.1952, *S. Togawa* s.n. Prov. Sanuki: Kankake, Shodo-shima Island, 27.5.1969, *M. Togashi* s.n. Prov. Iyo: Mt. Iwaya-san, Taketani, Mikawa-mura, Kami-ukena-gun, 400–500 m, 21.10.1970, *S. Kurokawa* 70970A. Prov. Tosa: Mt. Yokokura, 27.8.1931, *F. Fujikawa* s.n. (herb. *Y. Asahina* 2606). Kyushu. Prov. Buzen: Ipponkunugi, Yabakei, 17.4.1942, *Y. Asahina* 2601. Prov. Bungo: Tsue, Yufuin-cho, Ohita-gun, 1.6.1954, *M. Togashi* s.n. Prov. Hizen: Kashinokibaru Marsh, Kashinokibaru, Ikebaru, Nanayama-mura, Higashi-matsuura-gun (33°25'N, 130°10'E), on *Pinus densiflora*, c. 590 m, 9.8.1996, *Y. Ohmura* 2488. Prov. Higo: Senomoto, Minami-oguni-mura, Aso-gun, 31.5.1954, *M. Togashi* s.n. TAIWAN. Prov. Chiayi: Mt. Ali, 25.12.1925, *Y. Asahina* s.n. Prov. Ilan: Piyanan Pass, 1600–1900 m, 16.1.1964, *S. Kurokawa* 831a. INDIA. Sikkim, Gantok, c. 1900 m, 14.6.1960, *M. Togashi* s.n. INDONESIA. Java, Mountain Garden of Tjibodas, c. 1400 m, 12–13.3.1964, *S. Kurokawa* 2209. NEPAL. E. Nepal, Murhay- Bilbatay Bhanjang, 2200 m, 25.10.1963, *M. Togashi* s.n. NEW GUINEA. Western Highland District, Kuno Saw Mill, logging area, 24 km E of Mt. Hagen, c. 1800 m, 24.11.1965, *S. Kurokawa* 6236. PHILIPPINES. Second growth pine forest, c. 2000 m, Hill above barrio of Mt. Data, 7–8.1964, *M. E. Hale* [26202a] & *J. Banaag*. MALAYSIA. Sabah, Mt. Kinabalu, Kundasang, c. 1350 m, 27.12.1966, *M. Togashi* s.n. (herb. *Y. Asahina* 66971).

Race 2. JAPAN. Honshu. Prov. Shinano: Asama Hot Spring, 20.9.1922, *H. Koidzumi* 71169. Prov. Ohmi: Ohno-mura, Kouga-gun, c. 240 m, 31.5.1952, *S. Kurokawa* 520043. Prov. Izumi: Mt. Makinoo, Yokoyama-mura, Senboku-gun, 26.11.1950, *M. Mizutani* s.n. Shikoku. Prov. Iyo: Kawase-mura, Kita-ukena-gun, 28.9.1965, *M. Togashi* s.n. Kyushu. Prov. Hyuga: Suki-son, Nishi-morokata-gun, 15.3.1947, *M. Togashi* s.n. TAIWAN. Prov. Chiayi: Mt. Ali, 2200 m, 30.12.1963, *S. Kurokawa* 63.

Race 3. Only the type specimen of *U. rubicunda* subsp. *aberrans* Asahina.

### 33. *Usnea rubrotincta* Stirt., Scott. Natur. 6: 103, 1881.

*U. rubescens* var. *rubrotincta* (Stirt.) Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 348, 1937. Holotype: Madeira, Funchal, *J. Payne* s.n. (BM!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea ceratinella* Vain., Bot. Mag. Tokyo 35: 45, 1921, syn. nov. – *U. rubicunda* var. *ceratinella* (Vain.) Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 345, 1938. Holotype: Japan, Prov. Rikuzen, Bandai, in ramis arboris, *A. Yasuda* 230 (TUR, not seen; isotype in TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea pseudorubescens* Asahina, J. Jpn. Bot. 40: 130, 1965, syn. nov. Holotype: Formosa, Prov. Ilan, Piyanan pass, 1600–1900 m alt., 16.1.1964, *S. Kurokawa* 831a (TNS!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

*Usnea pseudorubescens* var. *anaemica* Asahina, J. Jpn. Bot. 44: 259, 1969, syn. nov. Holotype: Malaysia, Sabah, Kinabalu National Park, ascending Mesilau Trail from W. Mesilau River, ca. 1700 m alt., 8.1964, *M. E. Hale* 28286 (TNS!). Chemistry: usnic, norstictic, protocetraric, menegazziaic, stictic and constictic acids.

*Usnea rubescens* Stirt., Scott. Natur. 7: 76, 1883, syn. nov. Holotype: Australia, New South Wales, Illawara, on

rocks, 1882, *Kirton s.n.* (GLAM, not seen; isotype in BM!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea rubescens* var. *anaemica* Asahina, J. Jpn. Bot. 44: 259, 1969, syn. nov. Holotype: New Guinea, Western Highland District, Quip Saw Mill, logging area, 24 km N of Mt. Hagen, 2450 m alt., 25.11.1965, S. Kurokawa 6313 (TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea rubescens* var. *areolata* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 348, 1937, syn. nov. Isotype: Peru, Dept. Ayacucho, Pampalca between Huanta and Rio Aprimacu, ca. 3200 m alt., on sandy soil, 4,5,18.5.1929, E. P. Killip 22266 (TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

*Usnea rubescens* subsp. *aberrans* Asahina, Lich. Jap. 3: 115, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Rikuzen, Nobiru-mura, Momoo-gun, 19.7.1931, S. Murai 28. (TNS!). Chemistry: usnic, norstictic, protocetraric, menegazziac, stictic, salazinic and constictic acids.

*Usnea spilota* Stirt., Scott. Natur. 6: 294, 1882, syn. nov. – *U. rubicunda* Stirt. var. *spilota* (Stirt.) G.N.Stevens, Bibl. Lich. 72: 90, 1999. Holotype: Australia, Kings Island (between Australia and Tasmania), E. Spong 193 (BM!). Chemistry: usnic, norstictic, protocetraric and salazinic acids.

Thallus fruticose, erect to subpendent, up to 35 cm, red to reddish-brown or greenish-gray with a few red flecks when fresh, red to reddish-brown or straw-yellow with a few red flecks in herbarium specimens, pale to dark brown at the base; branching anisotomic-dichotomous, branches matt with small longitudinal furrow on the surface when well developed, lacking pseudocyphellae and maculae, terete, uninflated, gradually tapering, usually with many fibrils and lateral branches, 0.5–1.4 mm in diam.; lateral branches cylindrical at the base; papillae cylindrical; soralia common, formed mainly on lateral branches and fibrils, developed from scars of detached fibrils or lateral branches, discrete, punctiform to sinuose on lateral branches, rounded in shape on thicker branches, smaller than branch diam., sessile to distinctly stipitate, cortical margin not reflexed, convex at the top usually with numerous isidiomorphs, lacking granular soredia. Cortex thick, 6.8–16% of the radius, *ceratina*-type plectenchymatous; hyphae pachydermatous, secreted red pigment in the cell wall, lumina slightly enlarged to be fusiform or oblong. Medulla dense, 13–26% of the radius, red pigment absent. Axis solid, 22–48% of the diameter, I –. Apothecia rare, lateral on lateral and terminal branches, up to 4.2 mm in diam., flat in shape; thalloid exciple with many fibrils; disc pruinose, pale yellow, lacking white rim; epihymenium 6–20  $\mu\text{m}$  thick; hymenium 48–60  $\mu\text{m}$  thick; hypothecium 40–60  $\mu\text{m}$  thick; spores 7–10 $\times$ 5–6  $\mu\text{m}$  long.

Chemistry. Race 1, usnic, norstictic, salazinic, protocetraric ( $\pm$ ), squamatic ( $\pm$ ) and bourgeanic ( $\pm$ ) acids, and atranorin ( $\pm$ ); Race 2, usnic, norstictic, stictic, menegazziac and constictic acids.

The distinguishing features of *U. rubrotincta* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the red pigment in the cortex, (3) the sinuose soralia formed on lateral branches and fibrils, (4) the absence of granular soredia, (5) the *ceratina*-type plectenchymatous, and (6) the presence of salazinic or stictic acids as the major substance.

This species is well known to Japanese lichenologists as *U. rubescens* Stirt. However, *U. rubrotincta* Stirt. (1881) was published earlier than *U. rubescens* Stirt. (1883) and should therefore be adopted for the species according to Art. 11.3 of Tokyo Code (Greuter et al. 1994).

Two chemical races are recognized in the present area. Race 1 (salazinic acid, 98%) is more common than Race 2 (stictic acid, 2%). As no morphological and ecological differ-

ences are found among them, chemical differences found in this species are considered to have no taxonomic value. It should be noted here that one specimen of Race 1 is chemically heterogeneous, in which it is partially Race 2.

*U. rubrotincta* is variable species especially in amount of fibrils, lateral branches, and red pigment in the cortex. Although many taxa have been described, as listed in the synonyms above, they are considered to belong the natural range of *U. rubrotincta*.

Although *U. rubrotincta* strongly resembles *U. rubicunda* morphologically and chemically, it is distinguished from *U. rubicunda* by the sinuose soralia formed on fibrils and lateral branches, which develop from scars of detached fibrils, and by the rounded soralia on thicker branches which develop from scars of detached lateral branches.

In Japan, *U. rubrotincta* is distributed in Hokkaido, Honshu, Shikoku and Kyushu, where it grows on bark of coniferous trees such as *Abies*, *Cryptomeria*, *Larix* and *Pinus*, and broadleaf trees such as *Alnus*, *Quercus* and *Prunus*. It also grows on rocks (granite). It is found at relatively low altitudes between 50 and 1500 m. In Taiwan, it is found at elevations between 1000 and 3000 m. *U. rubrotincta* is widely distributed in temperate regions such as Asia, Europe, Africa and South America (Asahina 1956, Motyka 1936–38).

Exsiccata examined. Race 1. JAPAN. Honshu. Prov. Kazusa: Ichinomiya, 30.3.1952, *Y. Asahina s.n.* (H. Kashiwadani; Lich. Rar. Exs. 49, as *U. rubescens*). Prov. Kii: Mt. Koya, 23.8.1952, *Y. Asahina s.n.* (S. Kurokawa; Lich. Rar. Cri. Exs. 299, as *U. rubescens*).

Representative specimens examined. Race 1. JAPAN. Hokkaido. Prov. Kushiro: along Route 44, Akkeshi-cho, Akkeshi-gun, on *Picea glehnii*, c. 100 m, 2.9.1996, *Y. Ohmura 2732*. Prov. Hidaka: Mt. Apoi, Samani-gun, on *Pinus pentaphylla*, 250 m, 1.8.1970, *S. Kurokawa 70513*. Honshu. Prov. Rikuzen: Gamou, 5.6.1921, *A. Yasuda s.n.* (herb. *Y. Asahina 2735*). Prov. Hitachi: Hanazono, Kita-ibaraki-city, on *Cryptomeria japonica*, c. 400 m, 9.11.1997, *Y. Sakuma s.n.* (herb. *Y. Ohmura 4380*). Prov. Musashi: Hikawa-mura, Nishi-tamagun, 10.1922, *Y. Asahina s.n.* Prov. Sagami: Hakone, on bark of deciduous tree, 4.4.1999, *G. Thor 16406b*. Prov. Sado: Yahata, Sawata-machi, 5.5.1959, *M. Togashi s.n.* Prov. Kai: Aokigahara-marubi, Kamikuishiki-mura, Nishiyashiro-gun, on bark of dead conifer tree, c. 1000 m, 8.5.1998, *Y. Ohmura 4396*. Prov. Izu: Honryuji Temple, Niryama, 9.4.1958, *S. Kurokawa 58013*. Prov. Tohtomi: around Nuno-taki Waterfall, Misakubo-cho, on tree bark, 410 m, 25.9.1997, *Y. Sakuma s.n.* (herb. *Y. Ohmura 4379*). Prov. Mikawa: Mt. Horaiji, Kadoya, Horai-cho, Minamishitara-gun (38°58'N, 137°35'E), on *Prunus* sp., c. 340 m, 5.12.1996, *Y. Ohmura 2841*. Prov. Yamashiro: Koshihata, Kyoto, 3.4.1958, *Y. Asahina 58404*. Prov. Kii: en route from Ichinobashi to Okunoin, Mt. Koya, on *Cryptomeria japonica*, c. 800 m, 1.4.1999, *Y. Ohmura 4490*. Prov. Settsu: Mt. Rokko, on *Pinus thunbergii*, c. 900 m, 17.7.1966, *H. Kashiwadani 667*. Prov. Awaji: Mt. Yuzuruha-yama, Mihara-gun, c. 500 m, 18.7.1969, *H. Kashiwadani 6594*. Prov. Izumo: Mt. Makuragi, Matsue-city, on *Cryptomeria japonica*, c. 420 m, 9.5.1971, *H. Kashiwadani 8807*. Prov. Mimasaka: Mt. Yahazu, Kamo-cho, Tomata-gun, c. 750 m, 23.11.1981, *C. Igi 79*. Prov. Bingo: Kamiyama-mura, Sera-gun, 3.1.1933, *T. Sato 2720*. Prov. Suo: Daineiji, Fukawa-mura, Ohtsu-gun, on *Prunus mume*, 24.1.1970, *H. Kashiwadani 7189*. Shikoku. Prov. Awa: Kangase, Kainan-cho, Kaifu-gun, on *Prunus mume*, c. 180 m, 29.3.1978, *H. Kashiwadani 14386*. Prov. Sanuki: Kankake, Shodoshima Island, on rocks, 27.5.1969, *M. Togashi s.n.* Prov. Tosa: Befu-kyo Gorge, Monobe-son, Kami-gun, c. 500 m, 8.11.1978, *H. Kashiwadani 14934*. Kyushu. Prov. Buzen: Bonji-iwa, SW slope of Mt. Hikosan, Soeda-machi, Tagawa-gun, on rock, c. 900 m, 9.10.1996, *H. Kashiwadani [39919]* & *Y. Umezu*. Prov. Bungo: en route from Hanamura to Oike, Shonai-cho, Ohita-gun, on *Quercus acutissima*, c. 900 m, 5.3.1997, *Y. Ohmura 3057*. Prov. Hyuga: Takachiho Gorge, Nishiusuki-gun, on *Tracherospermum asiaticum*, c. 300 m, 8.4.1970, *H. Kashiwadani 7220*. TAIWAN. Prov. Kaohsiung: Shunsan, Mt. Nanfong, c. 1200 m, 8.2.1965, *S. Kurokawa 2935*. Prov. Chiayi: Mt. Ali, 2200 m, 30.12.1963, *S. Kurokawa 62*. Prov. Ilan: Piyanan Pass, 1600–1900 m, 16.1.1964, *S. Kurokawa 831*. AUSTRALIA. New South Wales: *Casuarina* and *Melaleuca* thicket, E side of the road, 21 km N of Kempsey, Pacific Highway, c. 15 m, 29.10.1965, *S. Kurokawa 5228*. NEPAL. E. Nepal, Minchin Dhap-Mul Pokhari, 29.10.1963, *S. Kurokawa & M. Togashi s.n.* PHILIPPINES. Pine forest near Barrio, Mt. Dato, 7.1964, *M. E. Hale 26202b*.

Race 2. JAPAN. Honshu. Prov. Shinano: Oiwake, Wada-mura, Chiisagata-gun, c. 1500 m, 29.8.1970, *M. Togashi s.n.* Prov. Kai: Oshino-mura, Minami-tsuru-gun, 2.5.1966, *M. Togashi s.n.* TAIWAN. Mt. Tsu-Tson-San, Mt. Ali, 2300–2900 m, 31.12.1963, *S. Kurokawa 172*. AUSTRALIA. Queensland, Beechmont, c. 540 m, 2.11.1965, *S. Kurokawa 5539*.

34. *Usnea shimadai* Asahina, J. Jpn. Bot. 45: 131, 1970.

Holotype: Taiwan (Formosa), Prov. Shinchiku, Nihonmatsu, Taiko-gun, on trees, ca. 1000 m alt., 23.6.1928, *Y. Shimada 53* (TNS!). Chemistry: usnic, norstictic, galbinic and salazinic acids.

Thallus fruticose, erect to subpendent, up to 7 cm long, color unknown when fresh, brown in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches slightly glossy on the surface, lacking pseudocyphellae and maculae, terete, slightly inflated, tapering only near the apices, with many spinulose fibrils and lateral branches, 0.9–1.3 mm in diam.; lateral branches cylindrical at the base; papillae common on thicker branches, cylindrical; soralia absent. Cortex 4.8–7.1% of the radius, *ceratina*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina slightly enlarged especially at both ends. Medulla dense, 16–31% of the radius, lacking red pigment. Axis solid, 24–58% of the diameter, I –. Apothecia common, subterminal on terminal and lateral branches, up to 1.1 cm in diam., cup-shaped; thalloid exciple with spinulose fibrils which are broadened at the base; disc pruinose, gray to brown, lacking white rim; epihymenium 4–16  $\mu\text{m}$  thick; hymenium 42–56  $\mu\text{m}$  thick; hypothecium 40–56  $\mu\text{m}$  thick; spores 8–9 $\times$ 5–6  $\mu\text{m}$  long.

Chemistry. Usnic, norstictic, galbinic and salazinic acids.

The distinguishing features of *U. shimadai* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the uninflated branches with cylindrical papillae, (3) the absence of soralia, (4) the apothecia with spinulose fibrils which are broadened at the base, (5) the *ceratina*-type plectenchymatous, (6) the brown color disc lacking white rim on the margin, and (7) the presence of galbinic acid as a major substance.

Although *U. shimadai* resembles other richly fertile and esorediate species, it is distinguished from others by the morphology of the fibrils along the thalloid exciple of apothecia.

This species has only once been collected from Taiwan, where it grows on tree bark at ca. 1000 m alt.

Specimen examined. Only the type specimen.

35. *Usnea sinensis* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 1: 248, 1936.

Holotype: China, Prov. Yunnan, in montium inter Dail (Talifu) et Hodjing regione temperata supra vicum Hsiangschuiho, 26°15', on ligno pubrido, ca. 3000–3400 m alt., 25.5.1915, *Heimr. Frh. v. Handel-Mazzetti 6527* (Diar. Nr. 1155, W!). Chemistry: usnic and caperatic acids.

*Usnea alisani* Asahina, J. Jpn. Bot. 43: 66, 1968, syn. nov. Holotype: Taiwan (Formosa), Mt. Ali, 2200 m alt., 30.12.1963, *S. Kurokawa 46* (TNS!). Chemistry: usnic, norstictic and caperatic acids.

*Usnea alisani* f. *condensata* Asahina, J. Jpn. Bot. 43: 67, 1968, syn. nov. Holotype: Taiwan (Formosa), Mt. Ali, 2200 m alt., 30.12.1963, *S. Kurokawa 46* pr. p. (TNS!). Chemistry: usnic, norstictic and caperatic acids.

Thallus fruticose, erect to subpendent, up to 30 cm long, color unknown when fresh, yellowish-brown in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches matt on the surface, lacking pseudocyphellae and mac-



ulae, terete, uninflated, gradually tapering, with many fibrils and lateral branches, 0.8–1.9 mm in diam.; lateral branches cylindrical at the base; papillae common on thicker branches, verrucose to cylindrical; soralia absent. Cortex thin, 5.7–17% of the radius, *ceratina*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina slightly enlarged to be elliptic in shape. Medulla moderate in density, 14–30% of the radius, lacking red pigment. Axis solid, 22–50% of the diameter, I –. Apothecia common, subterminal on terminal branches, up to 1.5 cm in diam., flat to sinuose; thalloid exciple with many fibrils; disc pruinose, gray, pale brown or pale yellow, lacking white rim; epihymenium 6–20  $\mu\text{m}$  thick; hymenium 44–54  $\mu\text{m}$  thick; hypothecium 38–50  $\mu\text{m}$  thick; spores 8–10 $\times$ 5–6  $\mu\text{m}$  long.

Chemistry. Usnic, norstictic, caperatic and salazinic acids ( $\pm$ ).

The distinguishing features of *U. sinensis* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the concolorous base with the thallus, (3) the uninflated branches which are matt on the surface, (4) the absence of soralia, (5) the large apothecia (up to 1.5 cm in diam.), (6) the *ceratina*-type plectenchymatous cortex, and (7) the presence of caperatic acid as a major substance.

Although norstictic acid was not detected from the type specimen of *U. sinensis*, morphological and other chemical features of *U. alisani* coincide well with *U. sinensis*. Therefore, the occurrence of norstictic acid is considered to be accessory in this species.

When Asahina (1968a) described *U. alisani*, he separated f. *condensata* by its erect form instead of subpendent form. However, the size of thallus varies from erect to subpendent; *U. alisani*, f. *alisani* and *U. alisani* f. *condensata* are therefore treated as synonyms of *U. sinensis* in the present study.

Although *U. sinensis* resembles *U. florida*, it is distinguished by the base which is concolorous with the thallus, and by the presence of caperatic acid.

*U. sinensis* has not been collected from Japan. In Taiwan, it grows on tree bark at elevations between 1500 and 2500 m.

Exsiccata examined. TAIWAN. Prov. Halien: Mt. Nan-Fu-Ta-San, 1500–2400 m, 19.1.1964, S. Kurokawa s.n. (S. Kurokawa: Lich. Rar. Cri. Exs. 146, as *U. alisani*).

Representative specimens examined. TAIWAN. Prov. Chiayi: Mt. Ali, 2200 m, 6.1.1964, S. Kurokawa 584. Prov. Ilan: Piyanan Pass, 1600–1900 m, 16.1.1964, S. Kurokawa 835. Prov. Nantou: Lisan, 17.1.1964, S. Kurokawa 883.

### 36. *Usnea subintumescens* Asahina, J. Jpn. Bot. 47: 129, 1972.

Holotype: Japan, Honshu, Prov. Shinano, Ohfuna, Izumino-mura, Chino-machi, Suwa-gun, 15.10.1957, T. Matsuoka 57105b (TNS!). Chemistry: usnic, salazinic and constictic acids.

*Usnea subintumescens* f. *olivaceoviridis* Asahina, J. Jpn. Bot. 47: 129, 1972, syn. nov. Holotype: Japan, Honshu, Prov. Shinano, Nakamichi, Izumino-mura, Suwa-gun, 5.5.1958, Y. Asahina [58550] & M. Togashi (TNS!). Chemistry: usnic, salazinic and constictic acids.

Thallus fruticose, erect to subpendent, up to 30 cm long, color unknown when fresh, straw-yellow to brown or olive-green in herbarium specimens, concolorous with thallus at the base; branching anisotomic-dichotomous; branches slightly glossy on the surface, lacking pseudocyphellae and maculae, usually foveolate, terete, inflated, 0.9–1.7 mm in diam., gradually tapering, with many lateral branches and fibrils; lateral branches constricted at

the base; papillae sparse, hemispherical; soralia common, formed on whole branches, developed from scars of detached fibrils or top of eroded papillae, punctiform, discrete, smaller than branch diam., sessile to slightly stipitate, flat to slightly convex at the top with many isidiomorphs, lacking granular soredia. Cortex thin, 4.1–7.6% of the radius, lacking red pigment, *ceratina*-type plectenchymatous; hyphae pachydermatous, lumina enlarged to be fusiform to oblong. Medulla lax, wide, 31–36% of the radius, lacking red pigment. Axis solid, thin, 18–23% of the diameter, I –. Apothecia not seen.

Chemistry. Usnic, salazinic, constictic and protocetraric acids ( $\pm$ ).

The distinguishing features of *U. subintumescens* are (1) the erect to subpendent thallus with anisotomic-dichotomous branching, (2) the inflated and foveolate branches sparsely with hemispherical papillae, (3) the lateral branches constricted at the base, (4) the punctiform soralia with many isidiomorphs, (5) the absence of granular soredia, (6) the *ceratina*-type plectenchymatous, and (7) the presence of salazinic and constictic acids as major substances.

*U. subintumescens* strongly resembles *U. intumescens* in having inflated branches and punctiform soralia. However, it can be distinguished from *U. intumescens* by the lateral branches which are never broadened at the base.

This species is a rare, and known only from central Japan, where it grows on bark at ca. 1000 m alt.

Representative specimens examined. JAPAN. Honshu. Prov. Shinano: Izumino-mura, Suwa-gun, 4.5.1958, *Y. Asahina* [5854] & *M. Togashi*; Namiai-mura, Shimo-ina-gun, c. 1000 m, 26.7.1966, *M. Togashi s.n.* (herb. *Y. Asahina* 66267). Prov. Kai: Asahigaoka, Lakeside of Yamanaka, Nakano-mura, Minami-tsuru-gun, 30.7.1954, *S. Kurokawa* 540329.

37. *Usnea yakushimensis* Asahina, Lich. Jap. 3: 72, 1956.

Holotype: Japan, Kyushu, Prov. Ohsumi, Yakushima Island, 24.7.1933, *F. Fujikawa s.n.* (herb. *Y. Asahina* 2008, TNS!). Chemistry: usnic, squamatic and thamnolic acids.

Thallus subpendent, up to 11 cm long, color unknown when fresh, brown to rusty brown in herbarium specimens, concolorous with thallus at the base, with annular-cracks especially near the base; branching anisotomic-dichotomous; branches matt on the surface, lacking pseudocyphellae and maculae, gradually tapering, with many fibrils and lateral branches, 0.6–1.0 mm in diam.; lateral branches cylindrical at the base; papillae sparse, hemispherical to verrucose; soralia common, formed mainly on lateral branches, developed from the top of eroded papillae, discrete, punctiform, smaller than branch diam., sessile to slightly stipitate, cortical margin not reflexed, flat to slightly convex at the top rarely with isidiomorphs, lacking granular soredia. Cortex 8.3–14% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina almost the same as medullary hyphae. Medulla moderate to dense in density, 9.1–22% of the radius, lacking red pigment. Axis solid, 31–64% of the diameter, I –. Apothecia not seen.

Chemistry. Usnic, squamatic and thamnolic acids.

The distinguishing features of *U. yakushimensis* are (1) the subpendent thallus with anisotomic-dichotomous branching, (2) the annular cracks especially near the base, (3) the punctiform and flat soralia which are smaller than branch diam., (4) the absence of granular soredia, (5) the *merrillii*-type plectenchymatous cortex, and (6) the presence of squa-

matic and thamnolic acids as major substances.

*U. yakushimensis* strongly resembles *U. pangiana* in having annular cracks and punctiform soralia. However, *U. yakushimensis* is distinguished from the latter species by the slender branches, the presence of squamatic and thamnolic acids, and its distribution.

This species is endemic to Yakushima Island, where it grows on tree bark at elevations between 1000 and 1400 m.

Specimen examined. JAPAN. Kyushu. Prov. Ohsumi: Hananoego, Yakushima Island, 6.12.1956, *M. Togashi s.n.*

#### Subgenus *Eumitria* (Stirt.) Zahlbr.

*Eumitria* Stirt., Scott. Natur. 6: 100, 1881. – *Usnea* subgen. *Eumitria* (Stirt.) Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 1: 49, 1936. Type species: *U. baileyi* (Stirt.) Zahlbr.

*Usnea* sect. *Elongatae* Motyka subsect. *Angulosae* Duvig., Bull. de la Soc. Bot. Belge, t. 85: 106-108, 1952. Type species: *U. gigas* Motyka.

Subgenus *Eumitria* is distinguished from subgenera *Usnea* and *Dolichousnea* by the fistulose axis; however, this feature is sometimes ambiguous in some species which were formerly placed under subgen. *Usnea* sect. *Elongata* subsect. *Angulosae* and its related species.

#### 38. *Usnea baileyi* (Stirt.) Zahlbr., in Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 83: 182, 1909.

*Eumitria baileyi* Stirt., Scott. Natur. 6: 100, 1881.

Lectotype (selected by Rogers & Stevens 1988): Australia, Queensland, near Brisbane, *F. M. Bailey 164* (BM!). Chemistry: usnic, norstictic and salazinic acids, eumitrin A<sub>2</sub>, eumitrin B, and zeorin.

*Eumitria formosa* Stirt., Scott. Natur. 6: 297, 1883. – *Usnea formosa* (Stirt.) Zahlbr., Cat. Lich. Univ. 6: 575, 1930.

Lectotype (selected by Rogers 1982): Australia, Queensland, Peak Range, *Statter s.n.* (BM!). Chemistry: usnic acid, eumitrin A<sub>1</sub>, eumitrin A<sub>2</sub> and zeorin.

*Eumitria implicita* Stirt., Scott. Natur. 6: 100, 1881. – *Usnea implicita* (Stirt.) Zahlbr., Cat. Lich. Univ. 6: 582, 1930. Lectotype (selected by Rogers & Stevens, 1988): Madeira, Funchal, *J. Payne s.n.* (BM!). Chemistry: usnic and norstictic acids, eumitrin A<sub>1</sub>, eumitrin A<sub>2</sub>, eumitrin B, and zeorin.

*Usnea baileyi* (Stirton) Zahlbr. subsp. *septentrionalis* Asahina, in Hara, Fl. Eastern Himalaya, 598, 1966, syn. nov. Holotype: India, Sikkim, Pamianche, ca.1000 m alt., 13.5.1960, *M. Togashi s.n.* (TNS!). Chemistry: usnic, norstictic, protocetraric (trace) and salazinic acids (trace), eumitrin A<sub>1</sub>, eumitrin A<sub>2</sub>, eumitrin B, and zeorin.

*Usnea creberrima* Vain., Bot. Mag. Tokyo 35: 46, 1921. – *U. implicita* f. *creberrima* Asahina, J. Jpn. Bot. 41: 161, 1966. – *U. baileyi* subsp. *septentrionalis* f. *creberrima* (Asahina) Asahina, in Hara, Fl. Eastern Himalaya, 598, 1966. Holotype: Japan, Prov. Rikuzen, Yuriage, on *Pinus thunbergii*, *A. Yasuda 137* (TUR-V 00878!). Chemistry: usnic, norstictic, salazinic, bourgeanic (trace) and caperatic acids, eumitrin A<sub>1</sub>, eumitrin A<sub>2</sub>, and zeorin.

*Usnea eizanensis* Asahina, Lich. Jap. 3: 42, 1956, syn. nov. – *U. baileyi* (Stirton) Zahlbr. subsp. *baileyi* var. *eizanensis* (Asahina) Asahina, J. Jpn. Bot. 42: 6, 1967. Holotype: Japan, Honshu, Prov. Ohmi, Anrakuritsuin Temple, Mt. Hiei, 13.11.1953, *M. Togashi s.n.* (herb. *Y. Asahina 1523*, TNS!). Chemistry: usnic, thamnolic and bourgeanic acids, eumitrin A<sub>1</sub>, eumitrin A<sub>2</sub>, eumitrin B, and zeorin.

*Usnea implicita* (Stirt.) Zahlbr. f. *subcreberrima* Asahina, J. Jpn. Bot. 41: 162, 1966, syn. nov. – *U. baileyi* subsp. *septentrionalis* f. *subcreberrima* (Asahina) Asahina, in Hara, Fl. Eastern Himalaya, 599, 1966. Holotype: Japan, Honshu, Prov. Rikuzen, Yuriagehama, Natori-gun, 3.3.1965, *M. Togashi s.n.* (TNS!). Chemistry: usnic, norstictic, protocetraric and salazinic acids, eumitrin A<sub>1</sub>, eumitrin A<sub>2</sub>, eumitrin B, and zeorin.

*Usnea implicita* var. *yokawensis* Asahina, Lich. Jap. 3: 41, 1956. – *U. baileyi* var. *yokawensis* (Asahina) Asahina, J. Jpn. Bot. 42: 6, 1967. Holotype: Japan, Honshu, Prov. Ohmi, Yokawa-chudo, Mt. Hiyei, 13.11.1953, *M. Togashi s.n.* (herb. *Y. Asahina 1520*, TNS!). Chemistry: usnic, norstictic, protocetraric, salazinic and caperatic acids, eumitrin A<sub>1</sub>, eumitrin A<sub>2</sub>, eumitrin B, and zeorin.

Thallus fruticose, erect to subpendent, up to 30 cm, gray to greenish-gray when fresh, dirty yellowish olive-green in herbarium specimens, the base concolorous with the thallus or dark brown, often with transversal cracks, sometimes partially decorticate especially near the base; branching anisotomic- or subisotomic-dichotomous; branches matt on the surface, lacking pseudocyphellae and maculae, terete, uninflated, 0.8–1.9 mm in diam., gradually tapering, with few to many lateral branches and fibrils; lateral branches cylindrical at the base; papillae verrucose; soralia common, formed mainly on lateral and terminal branches, developed from the top of eroded papillae, discrete each other forming punctiform in shape, smaller than branch diam., slightly stipitate, cortical margin not reflexed, convex at the top, often with isidiomorphs, lacking granular soredia. Cortex thin, 3.3–9.2% of the radius, lacking red pigment, *baileyi*-type plectenchymatous; hyphae pachydermatous, red pigment absent, lumina almost the same as medullary hyphae. Medulla dense, narrow, 3.0–12% of the radius, hyphae secreted red pigment outside of the cell wall near the cortex. Axis fistulose, thick, 58–86% of the diameter, I–. Apothecia rare, lateral on lateral branches, up to 5 mm in diam., flat; disc pruinose, gray, lacking white rim; ephymenium 2–10  $\mu\text{m}$  thick; hymenium 40–50  $\mu\text{m}$ ; hypothecium 40–90  $\mu\text{m}$ ; spores 8–10 $\times$ 4–5  $\mu\text{m}$  long.

Chemistry. Race 1, usnic and norstictic acids, eumitrin A<sub>2</sub>, zeorin, and protocetraric ( $\pm$ ), salazinic ( $\pm$ ), barbatic ( $\pm$ ), 4-*O*-demethylbarbatic ( $\pm$ ), bourgeanic ( $\pm$ ), protoliches-terinic ( $\pm$ ) and caperatic acids ( $\pm$ ), eumitrin A<sub>1</sub> ( $\pm$ ), eumitrin B ( $\pm$ ) and atranorin ( $\pm$ ); Race 2, usnic and thamnolic acids, eumitrin A<sub>1</sub>, eumitrin A<sub>2</sub>, zeorin, and barbatic ( $\pm$ ), 4-*O*-demethylbarbatic ( $\pm$ ) and bourgeanic acids ( $\pm$ ) and eumitrin B ( $\pm$ ).

*U. baileyi* is a distinctive species and is readily distinguished from other species by (1) the fistulose axis, (2) the punctiform soralia, (3) the presence of red pigment in the medulla near the cortex, (4) the *baileyi*-type plectenchymatous cortex, and (5) the presence of zeorin and eumittrins.

This species is very variable in morphology as well as chemistry. The density of lateral branches and fibrils varies remarkably not only among individuals but also even in a single thallus. In the chemistry, two chemical races were recognized from the present area. Race 1 contains depsidones such as norstictic, protocetraric and/or salazinic acids; Race 2 is lacking depsidones. No morphological and ecological differences were found between Race 1 and Race 2. Therefore, all taxa listed in the synonyms above are considered to belong to the natural range of variation of *U. baileyi*.

In Japan, *U. baileyi* is distributed in Honshu, Shikoku and Kyushu, where it grows on bark of coniferous trees such as *Cryptomeria* and *Pinus*, or broadleaf trees (e.g. *Rhododendron*). It also grows rarely on rocks. It is found at elevations between 10 and 800 m. In Taiwan, it grows on tree bark at elevations between 1100 and 2900 m. This species is widely distributed in temperate to tropical regions in Asia, Oceania, North and South America, and South Africa (Asahina 1967a, Awasthi 1986, Motyka 1936–38, Stevens 1991).

Exsiccata examined. Race 1. JAPAN. Honshu. Prov. Rikuzen: Kitakama, prope Yuriage, Natori-gun, on *Pinus thunbergii*, 20.5.1967, *M. Togashi s.n.* (S. Kurokawa, Lich. Rar. Crit. Exs. 147). AUSTRALIA. Queensland, Beechmont, c. 540 m, 2.11.1965, *S. Kurokawa 5541* (S. Kurokawa, Lich. Rar. Crit. Exs. 197).

Representative specimens examined. Race 1. JAPAN. Honshu. Prov. Awa: Mt. Kiyosumi, on *Rhododendron indicum*, 8.3.1998, *Y. Sakuma s.n.* (herb. *Y. Ohmura 4510*). Prov. Sagami: Hakone, 18.10.1924, *Y. Asahina*

1510. Prov. Kai: Lakeside of Yamanaka, Mt. Fuji, 10.8.1952, *M. Togashi s.n.* (herb. *Y. Asahina 1518b*). Prov. Suruga: Ohmiya-guchi, Mt. Fuji, 21.6.1925, *Y. Asahina 1511*; Subashiri-guchi, I-gome, Mt. Fuji, 21.6.1925, *Y. Asahina 1501*. Prov. Mikawa: Chichi-iwa, 1.4.1960, *Y. Asahina, S. Kurokawa & M. Nuno s.n.* Prov. Yamashiro: Mt. Ushio, Uji-gun, 30.3.1904, *I. Sono s.n.* Prov. Kii: en route from Ichinobashi to Okunoin, Mt. Koya, on *Cryptomeria japonica*, c. 800 m, 1.4.1999, *Y. Ohmura 4488*. Prov. Kawachi: Yodohshi, Chihaya-mura, Minami-kawachi-gun, 23.12.1954, *M. Togashi s.n.* (herb. *Y. Asahina 1531*). Prov. Tanba: Onigakebashi, Hikami-gun, 14.7.1927, *Y. Asahina 1515a*. Prov. Bizen: Kojima-gun, 10.8.1901, *Y. Katayama s.n.* (herb. *Y. Asahina 1506*). Prov. Aki: Mt. Chikurinji, 15.9.1931, *T. Sato s.n.* (herb. *Y. Asahina 1505*). Shikoku. Prov. Iyo: Iwaya-dera, Kawase-mura, Kamiukena-gun, 28.9.1965, *M. Togashi s.n.* Kyushu. Prov. Bungo: Oushi, Tsukinoki, Yamakuni-machi, Shimoge-gun, on rocks along Yamakuni River, c. 430 m, 2.3.1997, *Y. Ohmura 2958*. Prov. Hyuga: Shiratori Shrine, Nishimorokata-gun, 28.10.1956, *M. Togashi s.n.* (herb. *Y. Asahina 56102*). Prov. Higo: Danto, 7.8.1933, *F. Fujikawa s.n.* (herb. *Y. Asahina 1507a*). TAIWAN. Prov. Changhua: Lienhuachih (Rengechi), 30.12.1925, *Y. Asahina 25123*. Prov. Chiayi: en route from Su-Su-Lu to Fun-Chi-Fu, 1700–2000 m, 5.1.1964, *S. Kurokawa 536*. Prov. Ilan: Piyanan Pass, 1600–1900 m, 16.1.1964, *S. Kurokawa 833*. Prov. Nantou: Chitou, 30.1.1964, *S. Kurokawa 1410a*. Prov. Taitung: Mt. Ali, 25.12.1925, *Y. Asahina F281b*. INDIA. Senchal, Darjeeling, c. 2400 m, 6.4.1960, *M. Togashi s.n.* MALAYSIA. Tanah Rata, Pahang, c. 1650 m, 2.3.1965, *M. E. Hale 29713*. THAILAND. Phu Kradung, 1200–1300 m, 26.2.1964, *S. Kurokawa 1943*. INDONESIA. Java, Mountain Garden of Tjibodas, c. 1400 m, 12–13.3.1964, *S. Kurokawa 2217*. Bali Island, Mt. Butur, 29.3.1973, *M. Togashi s.n.* NEW GUINEA. Eastern Highland District, Andandara logging area, 40 km S of Kainantu, c. 1600 m, 17.11.1965, *S. Kurokawa 6066*. PHILIPPINES. Remnants of mossy oak forest, c. 2000 m, Hill above barrio of Mt. Data, 7–8.1964, *M. E. Hale [26158] & J. Banaag*. AUSTRALIA. Queensland, Maiala National Park, Mt. Glorious, c. 700 m, 1.11.1965, *S. Kurokawa 5493*. New South Wales, *Casuarina* and *Melaleuca* thicket, E side of the road, 20 km N of Kempsey, Pacific Highway, c. 15 m, 29.10.1965, *S. Kurokawa 5231*.

Race 2. JAPAN. Honshu. Prov. Mikawa: Taguchi-machi, Kita-shitara-gun, 30.10.1965, *M. Togashi s.n.* Prov. Kii: Mt. Koya, 23.8.1952, *Y. Asahina 1525*. Prov. Aki: Matsunaga, Kochi-cho, Kamo-gun, c. 230 m, 25.11.1972, *H. Kashiwadani 10273*. Shikoku. Prov. Iyo: Ukena-mura, Kami-ukena-gun, 17.7.1950, *T. Kawasawa s.n.* (herb. *Y. Asahina 1521*).

### 39. *Usnea himantodes* Stirt., Scott. Natur. 7: 75, 1883.

Lectotype (*vide* Stevens 1999): Australia, New South Wales, Illawarra, 1882, *W. Kirton s.n.* (BM, not seen). Chemistry: usnic, norstictic, menegazziaic, stictic, constictic and cryptostictic acids (Stevens 1990).

*Usnea neoguineensis* Asahina, J. Jpn. Bot. 43: 496, 1968. Holotype: Papua New Guinea, Morobe District, Middle Creek logging area, Bulolo, ca. 850 m alt., 11–12.11.1965, *S. Kurokawa 5787* pr.p. (TNS!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

*Usnea neoguineensis* var. *gracilior* Asahina, J. Jpn. Bot. 43: 497, 1968. Holotype: Papua New Guinea, Eastern Highland District, Andandara logging area, 40 km S of Kainantu, ca. 1600 m alt., 17.11.1965, *S. Kurokawa 6061* (TNS!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

*Usnea shikokiana* Asahina, J. Jpn. Bot. 40: 172, 1965. Holotype: Japan, Shikoku, Prov. Tosa, Mt. Myojin-dake, Nagaoka-gun, 2.2.1962, *I. Yoshimura 3949* (TNS!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

Thallus fruticose, pendent, up to 100 cm long, grayish-green to yellowish-green when fresh, straw-yellow in herbarium specimens, pale to dark brown at the base; branching subisotomic-dichotomous; branches matt to glossy on the surface, without pseudocyphe-lae, with punctiform or irregular shaped maculae, ridged, uninflated, 0.5–1.6 mm in diam., tapering only near the apices, with many fibrils and lateral branches; lateral branches slightly broadened at the base; papillae hemispherical; soralia common, formed on lateral branches or the ridges of thicker branches, developed from the top of eroded papillae, discrete each other to form rounded in shape, smaller than branch diam., sessile to slightly stipitate, cortical margin not reflexed, convex at the top, very rarely with isidiomorphs,

lacking granular soredia. Cortex thin to moderate in thickness, 8.6–20% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina almost the same as medullary hyphae. Medulla dense, thin, 7.4–19% of the radius, lacking red pigment. Axis fistulose in well developed thalli, thick, 33–46% of the diameter, I – or very rarely faint blue. Apothecia not seen.

Chemistry. Usnic, norstictic, menegazziaic, stictic and constictic acids.

The distinguishing features of *U. himantodes* are (1) the pendent thallus with subisotomic-dichotomous branching, (2) the ridged branches, (3) the small rounded soralia on lateral branches and the ridges of thicker branches, and (4) the presence of stictic acid as a major substance.

Although *U. himantodes* has been considered to belong to subgenus *Usnea*, the fistulose axis in mature thalli suggests that this species should be transferred to subgenus *Eumitria*. In addition, molecular phylogenetic results of the related species, *U. pectinata*, suggest the taxonomic position of this group (Ohmura 2001).

*U. himantodes* resembles *U. pectinata* in having a pendent thallus, and the presence of stictic acid as a major substance. However, it can be distinguished from *U. pectinata* by the presence of ridged branches.

*U. himantodes* is widely distributed in tropical regions such as Australia, Philippines, East Africa and India (Stevens 1990). It is rarely found in Japan and Taiwan.

Representative specimens examined. JAPAN. Shikoku. Prov. Tosa: Nagasawa Water Fall, Higashi-tsunomura, Takaoka-gun, c. 600 m, 26.3.1983, *H. Kashiwadani 19842b*. TAIWAN. Prov. Nantou: Chito, 30.1.1964, *S. Kurokawa 1417*.

#### 40. *Usnea pectinata* Taylor, in Hook, London J. Bot. 6: 191, 1847.

Holotype: [Bangladesh], Sylhet, *Wallich s.n.* (FH!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

*Usnea hossei* Vain., Ann. Soc. Zool. Bot. Fenn. Vanamo 1: 34, 1921. Holotype: [Thailand], Siam, Dio Sutep, 1675 m alt., 1904, *C. C. Hosseus s.n.* (TUR-V 00475!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

*Usnea hossei* f. *subtrichodea* Asahina, Lich. Jap. 3: 54, 1956, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Settsu, Sengari, Dojo-mura, Arima-gun, 30.11.1952, *M. Togashi s.n.* (herb. *Y. Asahina 52113a*, TNS!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

*Usnea longissima* Ach. var. *misamisensis* Vain., Philipp. J. Sci. 4: 655, 1909, syn. nov. – *U. misamisensis* (Vain.) Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 418, 1938. Holotype: Philippines, Mindanao, Prov. Misamis, Mt. Malindang, 5.1906, *E. A. Mearns & W. T. Hutchinson 4807* (TUR-V 00599!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

Thallus fruticose, pendent, up to 50 cm long, grayish-green to yellowish-green when fresh, straw-yellow in herbarium specimens, dark brown at the base, with annular-cracks from the base to the apices; branching subisotomic-dichotomous; branches matt to glossy on the surface, without pseudocypbellae, with punctiform to irregular-shaped maculae on lateral branches, terete, uninflated, 0.26–0.53 mm in diam., gradually tapering except elongated terminal branches; elongated terminal branches corticate but often disjunctively annulated, with few to many fibrils and short lateral branches; lateral branches slightly broadened at the base; papillae absent; soralia rarely formed on lateral branches or thicker branches, developed from maculae or scars of detached fibrils or lateral branches, discrete,

punctiform, smaller than branch diam., sessile to slightly stipitate, cortical margin not reflexed, convex at the top, very rarely with isidiomorphs, lacking granular soredia. Cortex 10–19% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina almost the same as medullary hyphae. Medulla dense, thin, 6.6–15% of the radius, lacking red pigment. Axis solid, thick, 40–63% of the diameter, I- or very rarely faint blue. Apothecia not seen.

Chemistry. Usnic, norstictic, menegazzaic, stictic and constictic acids.

The distinguishing features of *U. pectinata* are (1) the pendent thallus with elongated terminal branches, (2) the dark brown base, (3) the punctiform maculae on lateral branches (Fig. 10B), (4) the *merrillii*-type plectenchymatous cortex, and (5) the presence of stictic acid as a major substance.

When Asahina (1956) described *U. hossei* f. *subtrichodea*, he did not cite a specimen in the protologue. However, he did show a photograph in the protologue. The specimen, labeled as Japan, Honshu, Prov. Settsu, Sengari, Dojo-mura, Arima-gun, 30.11.1952, *M. Togashi* s.n. (herb. *Y. Asahina* 52113a), is identical with it. Therefore, this specimen is designated here as the lectotype of *U. hossei* f. *subtrichodea*.

*U. pectinata* resembles *U. himantodes* in having a pendent thallus, and the presence of stictic acid as a major substance. This species can be distinguished from *U. himantodes* by the absence of ridged branches, but it is sometimes quite difficult to distinguish between *U. pectinata* and slender form of *U. himantodes*. Final taxonomic decision should be made when more material has been studied.

Although *U. pectinata* has a solid axis and the general habit looks like *U. longissima*, this species is considered to belong to subgenus *Eumitria* for the following two reasons. *U. pectinata* itself does not have a fistulose axis, but the mature thallus of *U. himantodes* has a fistulose axis as reported by Asahina (1968c). In addition, a molecular phylogenetic result strongly suggests that a weaker relationship between *U. pectinata* and *U. longissima* and a closer relationship with *U. baileyi* (Ohmura 2001).

In Japan, *U. pectinata* is distributed in Honshu, Shikoku and Kyushu, where it grows on tree bark and commonly on rocks at elevations between 100 and 1000 m. In Taiwan, it is found at elevations between 1000 and 2000 m. This species shows the tropical element distribution pattern similar to *U. himantodes*.

Exsiccata examined. JAPAN. Honshu. Prov. Settsu: Sengari, Dohjo-mura, Arima-gun, on rocks, c. 200 m, 30.11.1952, *M. Togashi* s.n. (Y. Asahina: Lich. Jap. Exs., Fasc 4, 192; as *U. hossei* f. *subtrichodea*). TAIWAN. Prov. Chiayi, en route from Su-Su-Lu to Mt. Ali, 2000–2200 m, 7.1.1964, *S. Kurokawa* 673 (S. Kurokawa & H. Kashiwadani; Lich. Rar. Cri. Exs., 547; as *U. misamisensis*). THAILAND. Phu Kradung, 1200–1300 m, 25.2.1964, *S. Kurokawa* 1888 (S. Kurokawa & H. Kashiwadani; Lich. Rar. Cri. Exs., 347).

Representative specimens examined. JAPAN. Honshu. Prov. Kai: Oshino-mura, Minami-tsuru-gun, 28.4.1969, *M. Togashi* s.n. Prov. Mimasaka: Mt. Yahazu, Kamo-cho, Tomata-gun, c. 750 m, 23.11.1981, *C. Igi* 98. Shikoku. Prov. Awa: Amagoi Fall, Kamiyama-cho, Myozai-gun, c. 470 m, 30.12.1979, *T. Nakano* s.n. Prov. Iyo: Mt. Iwayaji, Kami-ukena-gun, c. 500 m, 21.10.1970, *H. Kashiwadani* 8533. Kyushu. Prov. Bungo: Kakizaka, Yabakei-machi, Shimoge-gun (33°27'N, 131°07'E), on rocks along Yamakuni River, c. 110 m, 3.3.1997, *Y. Ohmura* 2988. Prov. Hizen: Kurokami, Saga-gun, 31.8.1968, *M. Togashi* s.n. TAIWAN. Prov. Nantou: Keitau, 24.12.1933, *Y. Asahina* F-3324a. INDONESIA. Sumatra, Prov. Jambi, SW slope of Gunung (Mt.) Tujuh, Gunung Kerinci Seblat National Park, on tree in mossy forest, c. 2000 m, 27.11.1997, *M. Kato* s.n. (herb. *Y. Ohmura* 4373).

Subgenus *Dolichousnea* Y. Ohmura, subgen. nov.

Thallus pendulus, ramificatio isotomicus-dichotomus, annularis-pseudocyphellae praesens intra segmenta, axis I + coerulescens, hypothecium (70)–100–160–(200)  $\mu\text{m}$  crassae.

Type species: *Usnea longissima* Ach.

The subgenus *Dolichousnea* is separated from the subgenera *Usnea* and *Eumitria* by the presence of annular-pseudocyphellae and thicker hypothecium. So far only three species are known to belong to this subgenus.

Subgenus *Dolichousnea* can be treated as a genus rank, because it has an annular-pseudocyphella and a thicker hypothecium in apothecium. The presence or absence of pseudocyphellae, its morphology and the difference of morphological features in sexual organ have been considered as evolutionally significant features for Parmeliaceae (Hale 1981, Kurokawa 1994, Tehler 1996). But it is appropriate to treat the taxa belonging to subgenus *Dolichousnea* as a subgenus rank, because the taxa have the synapomorphies of the genus *Usnea*: the fruticose thallus, having a central cartilaginous axis throughout the thallus, and presence of usnic acid in the cortex.

41. *Usnea diffracta* Vain., Bot. Mag. Tokyo 35: 45, 1921.

Holotype: Japan, Hokkaido, Prov. Kushiro, on *Betula*, 19.8.1918, A. Yasuda 231 (TUR!). Chemistry: usnic, barbatic, diffractaic, baeomycesic and squamatic acids.

*Usnea diffracta* f. *huei* Asahina, Lich. Jap. 3: 69, 1956, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Kai, Lakeside of Yamanaka, Mt. Fuji, on *Picea polita*, 11.8.1952, M. Togashi s.n. (TNS!). Chemistry: usnic, barbatic, diffractaic, baeomycesic and squamatic acids.

*Usnea diffracta* f. *depauperata* Asahina, Lich. Jap. 3: 69, 1956, syn. nov. Isotype: Japan, Hokkaido, Rebunshiri, Faurie 9461 (KYO, not seen).

*Usnea diffracta* subsp. *subdiffracta* Asahina, Lich. Jap. 3: 70, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Kai, Mt. Fuji, T. Watanabe s.n. (TNS!). Chemistry: usnic and bourgeanic acids.

Thallus fruticose, pendent, up to 70 cm long, grayish-green to yellowish-green when fresh, straw-yellow in herbarium specimens, pale to dark brown at the base; branching isotomic-dichotomous; branches corticate, glossy on the surface, with annular-pseudocyphellae between segments and rarely with the punctiform maculae on the surface of lateral branches, terete, uninflated, 0.7–1.3 mm in diam., gradually tapering, with few lateral branches and few fibrils; lateral branches cylindrical at the base; papillae absent; soralia absent. Cortex thick, 5–15% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina almost the same as medullary hyphae. Medulla moderate in density, 15–33% of the radius, red pigment absent. Axis solid, 21–55% of the diameter, I + blue. Apothecia occasional, lateral on branches, up to 11.0 mm in diam., cup-shaped; thalloid exciple with many fibrils; disc epruinose, lacking white rim, pale yellow to brown; epihymenium 0–8.0  $\mu\text{m}$  thick; hymenium 50–70  $\mu\text{m}$  thick; hypothecium 70–145  $\mu\text{m}$  thick; spores 6.5–7.0  $\times$  3.5–4.5  $\mu\text{m}$  long.

Chemistry. Race 1, usnic, diffractaic, barbatic, baeomycesic, squamatic and bourgeanic acids ( $\pm$ ), and atranorin ( $\pm$ ); Race 2, usnic, diffractaic, barbatic, 4-*O*-demethylbarbatic, baeomycesic, squamatic and salazinic acids; Race 3, usnic, barbatic, 4-*O*-demethylbarbatic, baeomycesic and squamatic acids; Race 4, usnic and bourgeanic



acids.

*U. diffracta* is a distinctive species and it is readily distinguished from other *Usnea* species by (1) the pendent thallus with isotomic-dichotomous branching, lacking elongated filamentous terminal branches, (2) the uninflated branches, (3) the presence of annular-pseudocyphellae between segments, (4) the absence of soralia and papillae, and (5) the *merrillii*-type plectenchymatous cortex.

When Asahina (1956) described *U. diffracta* f. *huei*, he cited in the protologue two specimens collected from Japan (Hokkaido, Prov. Tokachi, Shimonozuka, and Honshu, Mt. Fuji, Yamanaka) in the protologue to show the ratio of cortex, medulla and axis. The latter specimen is housed in TNS and agrees with the protologue of this taxon. Thus, the specimen collected from Yamanaka is selected as the lectotype of *U. diffracta* f. *huei*.

Although Asahina (1956) separated *U. diffracta* f. *huei* from *U. diffracta* by its angular branches and transverse or oblique cracks on the thallus, these features are considered to belong the natural range of *U. diffracta*. Therefore, f. *huei* is treated as a synonym of *U. diffracta* in the present study.

Asahina (1956) reported *U. diffracta* f. *depauperata* which has fibrils growing from cracks between segments forming nesting appearance. However, the numbers of fibrils growing from cracks varies from a few to abundant; therefore, f. *depauperata* is treated as a synonym of *U. diffracta* in the present study.

Although Asahina (1956) separated *U. diffracta* subsp. *subdiffracta* from *U. diffracta* differing only in chemistry, no morphological and ecological differences were found between them. Therefore, *U. diffracta* subsp. *subdiffracta* is treated as a synonym of *U. diffracta*, which is treated as Race 3 in the present study.

Four chemical races were recognized from the present area. The most common race was the Race 1 (diffractaic acid, 87%); Race 2 (diffractaic and salazinic acids, 10%), Race 3 (barbatic acid, 2%) and Race 4 (bourgeanic acid only, 1%) were rarely found. As no morphological and ecological differences were found among them, chemical differences found in this species are considered to have no taxonomic value.

In Japan, *U. diffracta* is distributed from Hokkaido to Kyushu, where it grows on twigs or bark of coniferous trees such as *Abies*, *Picea* and *Tsuga*, or broadleaf trees such as *Betula*, *Fagus*, *Prunus* and *Tilia*. It rarely grows on rocks. It is found at elevations between 50 and 2500 m. *U. diffracta* is one of the commonest *Usnea* species in East Asia, and is known only from this region.

Exsiccata examined. Race 1. JAPAN. Hokkaido. Prov. Nemuro: Bettouga, on deciduous trees, c. 50 m, 1.9.1965, *S. Kurokawa 65747* (*S. Kurokawa* & *H. Kashiwadani*, *Lich. Rar. Cri. Exs.* 148).

Representative specimens examined. Race 1. JAPAN. Hokkaido. Prov. Ishikari: Ukushima Marsh, Kamikawa-cho, Kamikawa-gun (44°56'N, 142°58'E), on *Picea glehnii*, c. 900 m, 28.7.1997, *Y. Ohmura 3663*. Prov. Teshio: along small road 2.5 km from the coast, Toyotomi-cho, Teshio-gun (45°12'N, 141°36'E), on *Abies sachalinensis*, 10–20 m, 30.5.1995, *Y. Ohmura 1040*. Honshu. Prov. Mutsu: Ouse, 25.10.1933, *S. Murai s.n.* (herb. *Y. Asahina 2800*). Prov. Shimotsuke: Odashiro-gahara, Okunikko, Nikko-city, on deciduous tree, c. 1400 m, 26.11.1998, *M. Higuchi s.n.* (herb. *Y. Ohmura 4508*). Prov. Musashi: en route from Jyumonji Pass to Mt. Ohyama, Chichibu-gun (35°56'N, 138°44'E), on *Tsuga diversifolia*, 1980–2160 m, 9.12.1996, *Y. Ohmura 2889*. Prov. Etchu: Makawa, 22.7.1936, *Y. Asahina 2862*. Prov. Shinano: SE slope of Mt. Nyukasa, Fujimi-machi, Suwa-gun (35°53'N, 138°11'E), on *Abies* sp., 1830 m, 30.6.1997, *Y. Ohmura 3232*. Prov. Kai: Lakeside of Syojiko, 9.1952, *M. Togashi s.n.* (herb. *Y. Asahina 5209*). Prov. Suruga: 2-gome, Ohmiya-guchi, Mt. Fuji, 6.1933, *Y. Asahina*

3360a. Prov. Izu: Amagi, 4.9.1922, *Y. Asahina* 118. Prov. Mikawa: Iwagoya Park, 31.3.1960, *Y. Asahina*, *S. Kurokawa* & *M. Nuno* s.n. Prov. Hida: Ohshirakawa River, Ohno-gun, 6.8.1932, *M. Nishijima* s.n. (herb. *Y. Asahina* 2865). Prov. Mimasaka: Mt. Yahazu, Kamo-cho, Tomata-gun, c. 750 m, 23.11.1981, *C. Igi* 84. Prov. Suo: Mt. Jakuchi, Kuga-gun, on *Fagus crenata*, 1050–1200 m, 6.6.1967, *H. Kashiwadani* 3072. Shikoku. Prov. Awa: Mt. Kenzan, 20.8.1934, *F. Fujikawa* s.n. (herb. *Y. Asahina* 2872). Prov. Iyo: Mt. Nametoko-yama, Kita-uwa-gun, 28.4.1928, *M. Ogata* s.n. (herb. *Y. Asahina* 2879). Kyushu. Prov. Bungo: en route from Notohge Pass to Mt. Ichino-dake, Yamakuni-machi, Shimoge-gun, on rocks, 720–910 m, 10.10.1996, *H. Kashiwadani* [39974b] & *Y. Umezu*. Prov. Ohsumi: near Hananoego, Yakushima Island, c. 1500 m, 9.11.1962, *M. Togashi* s.n. TAIWAN. Prov. Chiayi: Nimandaira, Mt. Ali, 25.12.1925, *Y. Asahina* F-285. Prov. Ilan: Mt. Taiping, 31.7.1936, *S. Asahina* s.n. Prov. Taitung: Mt. Lachialachiaerh, c. 1800 m, 22.1.1965, *S. Kurokawa* 70269. CHINA. Between Ping Yung and Tai Suan, Southern Chekiang, c. 500–900 m, 16–25.7.1924, *R. C. Ching* 2158 pr.p. RUSSIA. Usriiskii kraï, Reka Muhen', ust'e Sadoma, Zabolochennii Laricetum, on *Betula japonica*, 18.12.1927, *V. M. Savich*' s.n. Saghalien, Mt. Suzuya, 19.7.1932, *Y. Asahina* s.n.

Race 2. JAPAN. Honshu. Prov. Rikuzen: Yuhama, Hanayama-mura, Kurihara-gun, 24.7.1932, *T. Kimura* s.n. Prov. Musashi: Magosou-dani, Nippara, Hikawa-cho, Nishi-tama-gun, c. 1500 m, 25.11.1969, *M. Togashi* s.n. Prov. Kaga: Mt. Hakusan, c. 1520 m, 2.6.1967, *H. Kashiwadani* 6853. Prov. Kai: Grand Forest of *Picea*, Lakeside of Yamanaka, Mt. Fuji, 16.8.1952, *Y. Asahina* s.n. Prov. Ohmi: 5-gome, Taiheiji-dani, Mt. Ibuki, 7.11.1961, *M. Togashi* s.n. Kyushu. Prov. Buzen: Mt. Hikosan, 18.11.1962, *S. Kurokawa* 62486. CHINA. Pref. Kanto: Konshun, 10.7.1943, *S. Asahina* s.n.

Race 3. JAPAN. Honshu. Prov. Inaba: Ohmura, Yazu-gun, 17.8.1950, *Y. Ikoma* s.n. (herb. *Y. Asahina* 2861). Shikoku. Prov. Tosa: Nagasawa Water Fall, Higashi-tsuno-mura, Takaoka-gun, c. 600 m, 26.3.1983, *H. Kashiwadani* 19843.

Race 4. Only the lectotype specimen of *U. diffracta* subsp. *subdiffracta*.

#### 42. *Usnea longissima* Ach., Lich. Univ., 626, 1810.

Holotype: Lusitania, ad ramos arborum, *Mosig* s.n. (H-ACH 1893!). Chemistry: usnic and diffractaic acids (annotated by P. M. Jørgensen in 1975).

*Usnea longissima* var. *robustior* Asahina, Lich. Jap. 3: 48, 1956, syn. nov. Lectotype (selected here): Japan, Hokkaido, Prov. Kushiro, Lakeside of Mashu, 28.6.1953, *Y. Asahina* s.n. (TNS!). Chemistry: usnic, barbatic and 4-*O*-demethylbarbatic acids.

*Usnea longissima* var. *vulgata* Asahina, Lich. Jap. 3: 46, 1956, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Etchu, Makawa, 23.7.1936, *Y. Asahina* 2412 (TNS!). Chemistry: usnic, barbatic and 4-*O*-demethylbarbatic acids.

*Usnea longissima* subsp. *ambigua* Asahina, Lich. Jap. 3: 48, 1956, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Kai, Yatsugatake Mts., 28.5.1926, *Y. Asahina* 2422 (TNS!). Chemistry: usnic, barbatic, diffractaic, 4-*O*-demethylbarbatic, baecomycesic and squamatic acids.

*Usnea longissima* subsp. *dubia* Asahina, in Hara, Fl. eastern Himalaya, 603, 1966, syn. nov. Lectotype (selected here): India, Darjeeling, Phalut-Sandakphu, 6.6.1960, *M. Togashi* s.n. (TNS!). Chemistry: usnic and unidentified fatty acids.

*Usnea longissima* subsp. *jesoensis* Asahina, Lich. Jap. 3: 48, 1956, syn. nov. Lectotype (selected here): Japan, Hokkaido, Prov. Kitami, Forestry Training Station of Hokkaido University, Oketo-mura, Tokoro-gun, 7.1923, collector unknown (herb. *Y. Asahina* 550, TNS!). Chemistry: usnic, evermic and lecanoric acids.

Thallus fruticose, pendent, up to several meters long, grayish-green to yellowish-green when fresh, straw-yellow in herbarium specimens, pale to dark brown at the base; branching isotomic-dichotomous; branches decorticate (very rarely corticate), matt on the surface, with annular-pseudocyphellae between segments and twisted maculae on the surface of lateral branches, lacking longitudinal furrow, terete, uninflated, 0.35–0.75 mm in diam., gradually tapering, elongated towards distal branches, with many short lateral branches; lateral branches broadened at the base; papillae absent; soralia occasionally

formed on lateral branches, developed from cortex or maculae,  $\pm$  discrete, punctiform or surrounding the branch, slightly stipitate, cortical margin not reflexed, convex at the top, occasionally with isidiomorphs, lacking granular soredia. Cortex 6.7–16% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina almost the same as medullary hyphae. Medulla dense, thin, 6.7–20% of the radius, lacking red pigment. Axis solid, thick, 37–69% of the diameter, I + blue. Apothecia rare, lateral on lateral branches, up to 11 mm in diam., flat to cup-shaped; thalloid exciple with many fibrils; disc pruinose, pale yellow, lacking white rim; epihymenium 8.0–16  $\mu\text{m}$  thick; hymenium 40–50  $\mu\text{m}$  thick; hypothecium 140–200  $\mu\text{m}$  thick; spores 7.0–8.0 $\times$ 3.5–4.8  $\mu\text{m}$  long.

Chemistry. Race 1, usnic, barbatic, 4-*O*-demethylbarbatic ( $\pm$ ), squamatic ( $\pm$ ) and unidentified fatty acids ( $\pm$ ), and atranorin ( $\pm$ ); Race 2, usnic, diffractaic, barbatic ( $\pm$ ), 4-*O*-demethylbarbatic ( $\pm$ ), baeomycesic ( $\pm$ ), squamatic ( $\pm$ ) and unidentified fatty acids ( $\pm$ ), and atranorin ( $\pm$ ); Race 3, usnic, evernic, lecanoric and squamatic acids ( $\pm$ ), and atranorin ( $\pm$ ).

The distinguishing features of *U. longissima* are (1) the pendent thallus with isotomic-dichotomous branching, (2) the terete branches which are decorticate and elongated towards the apices, (3) the presence of annular-pseudocypellae between segments, (4) the absence of granular soredia, (5) the *merrillii*-type plectenchymatous cortex, and (6) the presence of barbatic, diffractaic or evernic acids as the major substance.

When Asahina (1956) described *U. longissima* var. *robustior*, he showed a photograph of its thallus in the protologue. The specimen, labeled as Japan, Hokkaido, Prov. Kushiro, Lakeside of Mashu, 28.6.1953, *Y. Asahina s.n.*, coincides with the photograph, and morphological and chemical features agree with the protologue. Therefore, this specimen is designated here as the lectotype of *U. longissima* var. *robustior*.

When Asahina (1956) described *U. longissima* var. *vulgata*, he did not cite any specimens in the protologue. The specimen, labeled as Japan, Honshu, Prov. Etchu, Makawa, 23.7.1936, *Y. Asahina 2412*, was apparently used for the description of the protologue, since the anatomical note in the packet coincides well with the protologue. The chemical features of this specimen are also identical with the protologue. Therefore, this specimen is designated as the lectotype of *U. longissima* var. *vulgata*.

When Asahina (1956) described *U. longissima* subsp. *ambigua*, he did not cite any specimens in the protologue. However, he mentioned that its distribution was Prov. Kai, Mt. Yatsugatake and Hokkaido. The authentic specimen, labeled as Japan, Honshu, Prov. Kai, Yatsugatake Mts., 28.5.1926, *Y. Asahina 2422* is not in conflict with the protologue morphologically as well as chemically. Therefore, this specimen is designated here as the lectotype of *U. longissima* subsp. *ambigua*.

When Asahina (1966) described *U. longissima* subsp. *dubia*, he selected a specimen labeled as "Phalut-Sandakphu on 5–6.6.1960, *M. Togashi s.n.*" as the type. According to the protologue, the specimen, however, was divided into two specimens; one was housed in TNS and the other in TI. At that time, he did not designate which specimen was the holotype or isotype. The specimen housed in TNS agrees well with the protologue morphologically as well as chemically. Therefore, this specimen is designated as the lectotype of *U. longissima* subsp. *dubia*.

When Asahina (1956) described *U. longissima* subsp. *jesoensis*, he did not cite any specimens in the protologue. In the packet of the specimen, labeled as Japan, Hokkaido, Prov. Kitami, Forestry Training Station of Hokkaido University, Oketo-mura, Tokoro-gun, 7.1923, collector unknown (herb. *Y. Asahina* 550), there is a handwritten note by Asahina in Japanese as “evernic acid was first detected from this specimen which was morphologically identical with *U. longissima*”. This specimen was apparently used for making the protologue; it is not in conflict with the protologue morphologically and chemically. Therefore, this specimen is designated here as the lectotype.

Three chemical races were recognized in the present area. The commonest race was Race 1 (barbatic acid, 53%); Race 2 (diffractaic acid, 30%) and Race 3 (evernic acid, 17%) were occasionally found. Race 1 and Race 2 are chemically close each other, because barbatic and diffractaic acids belong to the same chemical group ( $\beta$ -orcinol depside). However, Race 3 is distantly related to Race 1 and Race 2 biosynthetically, because evernic acid belong to the other chemical group (orcinol depside). No morphological and ecological differences were found among all three races. Therefore, they are treated under a single species. It should be noted that another chemical race (usnic and unidentified fatty acids only) has been known in eastern Himalaya (Asahina 1966).

Asahina (1956, 1966) reported six subspecies differing only in chemistry for *U. longissima*: (1) subsp. *longissima* containing barbatic acid, (2) subsp. *ambigua* Asahina containing diffractaic acid, (3) subsp. *jesoensis* Asahina containing evernic acid, (4) subsp. *sensibilis* Asahina containing salazinic acid, (5) subsp. *persensibilis* Asahina containing fumarprotocetraric acid, and (6) subsp. *dubia* Asahina containing unidentified fatty acids. However, subsp. *sensibilis* and subsp. *persensibilis* belong to *U. trichodeoides* (see note under that species). Other subspecies are treated as synonyms of *U. longissima*.

*U. longissima* resembles *U. trichodeoides* in having an isotomic-dichotomous branching thallus with elongated terminal branches. However, it can be distinguished from the latter by the terete branches at elongated parts when mature and the presence of depsides such as barbatic, diffractaic and evernic acids.

In Japan, *U. longissima* is distributed in Hokkaido, Honshu and Shikoku, where it grows on bark of coniferous trees such as *Abies*, *Larix* and *Picea*, or broadleaf trees such as *Betula*, *Salix* and *Quercus* at elevations between 150 and 2300 m (at lower elevation in Hokkaido, and higher elevation in Honshu and Shikoku). In Taiwan, it is found at elevations between 1500 and 3000 m. *U. longissima*, one of the commonest species in the genus *Usnea*, is widely distributed in boreal regions of Asia, Europe, Russia and North America (Motyka 1936–38).

Representative specimens examined. Race 1. JAPAN. Hokkaido. Prov. Kitami: Tokusyoppe, Furu-ume, Bihoro-cho, Abashiri-gun, on *Abies sachalinensis*, c. 330 m, 2.9.1996, *Y. Ohmura* 2686. Prov. Nemuro: along the trail from Rausu Hot Spring to the top of Mt. Rausu, Rausu-cho, Menashi-gun (44°02'N, 145°09'E), on *Abies sachalinensis*, 370–460 m, 27.8.1996, *Y. Ohmura* 2533. Prov. Tokachi: around camp site of Seinen-no-ie at the lakeside of Lake Onneto, Ashoro-cho, Ashoro-gun (43°23'N, 143°59'E), on *Fraxinus mandshurica* var. *japonica*, 650 m, 7.9.1995, *Y. Ohmura* 1760. Honshu. Prov. Rikuchu: Mt. Hayachine, 25.7.1928, *G. Toba* s.n. (herb. *Y. Asahina* 2406). Prov. Iwashiro: Toriko-daira, Mt. Higashi-azuma, c. 1600 m, *H. Kashiwadani* 15408. Prov. Shimotsuke: Lakeside of Kirikomi, 3.5.1931, *Y. Asahina* 2410. Prov. Kozuke: Mt. Shibutsu, 16.7.1950, *Y. Asahina* 2407. Prov. Musashi: Mt. Ryogami, 22.8.1942, *K. Hisauchi* s.n. (herb. *Y. Asahina* 2420). Prov. Sagami: Mt. Hiru-

ga-dake, Tanzawa Mts., 3.1.1957, *M. Togashi s.n.* Prov. Shinano: en route from Azusayama to Jyumonji Pass, Minami-saku-gun (35°56'N, 138°44'E), on *Betula ermanii*, 1860–2030 m, 9.12.1996, *Y. Ohmura 2881*; en route from Gyozya-goya to Minoto-sanso, Yatsugatake Mts., Chino-city, on twigs of *Abies veitchii*, elevation 2000–2300 m, 29.8.1997, *Y. Ohmura 3808*. Prov. Kai: Okuniwa, NW slope of Mt. Fuji, Minami-tsuru-gun, on twig of *Tsuga diversifolia*, c. 2300 m, 9.5.1998, *Y. Ohmura 4416*. Prov. Suruga: Subashiri-guchi, Mt. Fuji, 16.7.1952, *Y. Asahina [52716] & M. Togashi*. Prov. Yamato: Mt. Sanjohgatake, Ohmine Mts., 10.6.1952, *M. Togashi s.n.* Prov. Kii: Mt. Koya, 10.10.1926, *Y. Numajiri s.n.* (herb. *Y. Asahina 2405*). Prov. Inaba: Mt. Hyonosen, 27.7.1930, *K. Yasuda s.n.* Shikoku. Prov. Iyo: Iwayaji Temple, Kami-ukena-gun, 28.11.1965, *M. Togashi s.n.* Prov. Tosa: Isa, Hata-gun, 25.8.1931, *F. Fujikawa s.n.* (herb. *Y. Asahina 2416*). TAIWAN. Mt. Nan-Fu-Ta-San, 1500–2400 m, 19.1.1964, *S. Kurokawa 950*. Prov. Taichung Hsien: en route from Ssu-yuan to To-chia-tun Shan, Mt. Nanhuta Shan, Hoping, 1900–2250 m, 9.11.1989, *H. Kashiwadani 35877*. CHINA. Yunnan, Zhongdian-xian, en route from Zhongdian to Baishuidai, on *Larix sp.*, 3500 m, 19.9.1994, *H. Harada [14899] & L.-S. Wang*. KOREA. Pref. Kankyo-Nando, Mt. Hakuto-san, 28.7.1940, *F. Azuma s.n.* RUSSIA. Kurile, Etorofu Island, Shana, 8.1938, *T. Takemoto & Tsunematsu s.n.*; Saghalien, Takinosawa, 30.7.1932, *Y. Asahina s.n.* INDIA. Phalut, Darjeeling, c. 3000 m, 9.5.1960, *M. Togashi s.n.* Sikkim, Olothang-Jongri, 3900 m, 23.5.1960, *M. Togashi s.n.* BHUTAN. Gusa (2600)–Pari La (3550)–Chamsa (3500), 14.5.1967, *H. Hara et al. s.n.* NEPAL. Kathomandu, en route from Lukhla to Namche-bazar, c. 3500 m, 5.5.1973, *T. Oda s.n.*; E. Nepal, below Siling Tzokupa to Siling Tzokupa, 3400 m, 21.11.1963, *M. Togashi s.n.*

Race 2. JAPAN. Hokkaido. Prov. Kitami: en route from Rishiri-hokuroku camp site 2.5 km S of Sakae-machi to Mt. Pon-yama, Oshidomari, Rishiri-fuji-cho, Rishiri-gun, Rishiri Island (45°13'N, 141°13'E), on *Abies sachalinensis*, 140–360 m, 1.6.1995, *Y. Ohmura 1091*. Prov. Ishikari: Ukishima Marsh, Kamikawa-cho, Kamikawa-gun (44°56'N, 142°58'E), on twigs of *Picea glehnii*, c. 900 m, 28.7.1997, *Y. Ohmura 3664*. Honshu. Prov. Shimotsuke: c. 1 km W of Meotobuchi Hot Spring, Kuriyama-mura, Shiyoa-gun, on branches of *Rhododendron sp.* growing on cliff along stream, c. 1200 m, 23.11.1999, *H. Kashiwadani 42187*. Prov. Shinano: Mt. Tateshina, 1300 m, 30.5.1967, *M. Togashi s.n.* (herb. *Y. Asahina 67530*). Prov. Kai: Mt. Shichimen-zan, 8.1922, *Y. Asahina 112a*. Prov. Suruga: Subashiri-guchi, Mt. Fuji, 3.5.1963, *F. Fujikawa s.n.* TAIWAN. Mt. Nan-Fu-Ta-San, on twigs of *Osmanthus bioritsuensis*, 2400–2600 m, 20.1.1964, *S. Kurokawa 1056*. Prov. Taichung Hsien, en route from Ssu-yuan to To-chia-tun Shan, Mt. Nanhuta Shan, Hoping, 2500 m, 10.11.1989, *H. Kashiwadani 36003*. CHINA. Pref. Kanto, Konshun, 10.7.1943, *S. Asahina s.n.* (herb. *Y. Asahina 43710*). KOREA. Kankyo-hokudo, Mt. Manto-san, 3.10.1939, *Y. Kimura s.n.* (herb. *Y. Asahina 39109*). INDIA. Darjeeling, Phalut, 3500 m, 9.5.1960, *M. Togashi s.n.*; Sikkim, Gamotang, c. 3900 m, 29.5.1960, *M. Togashi s.n.* NEPAL. Khumbu, Hinku Valley, near Kote (27°40'N, 86°48'E), on *Pinus sp.*, c. 3500 m, 18.3.1999, *A. Shimizu s.n.* (herb. *Y. Ohmura 4505*).

Race 3. JAPAN. Hokkaido. Prov. Kitami: Tokusyoppe, Furu-ume, Abashiri-cho, Abashiri-gun, on *Abies sachalinensis*, c. 330 m, 2.9.1996, *Y. Ohmura 2685*. Prov. Kushiro: around Hyotan-numa, Akari-cho, Akan-gun (43°25'N, 144°11'E), on *Acer mono* var. *glabrum*, c. 440 m, 10.9.1995, *Y. Ohmura [2059] & H. Kashiwadani*. Honshu. Prov. Shimotsuke: Mt. Nikko, collector unknown. Prov. Shinano: SE slope of Mt. Nyukasa, Fujimimachi, Suwa-gun (35°53'N, 138°11'E), on *Larix kaempferi*, 1830 m, 30.6.1997, *Y. Ohmura 3239*. Prov. Kai: Mt. Shichimen-zan, 8.1922, *Y. Asahina 112a*. TAIWAN. Prov. Taichung Hsien: en route from Ssu-yuan to To-chia-tun Shan, Mt. Nanhuta Shan, Hoping, 2700–2950 m, 11.11.1989, *H. Kashiwadani 36135*. KOREA. Kankyo, 1934, *To s.n.* RUSSIA. Saghalien, Takigozawa, 31.7.1932, *Y. Asahina 2503*. INDIA. Phalut-Sandarakhpu, Darjeeling, 6.6.1960, *M. Togashi s.n.* NEPAL. Gola-Zongi, Walungchun, 11.11.1963, *M. Togashi s.n.* BHUTAN. Shodu to Barshong, 3500–3800 m, 24.5.1967, *H. Hara et al. s.n.*

#### 43. *Usnea trichodeoides* Vain., Ann. Acad. Sci. Fenn., Ser. A, 6(7): 8, 1915.

Lectotype (selected by Swinscow & Krog 1978): [South Africa], Cap b. Spei, *Persoon 27* pr.p. (H-ACH 1882!). Chemistry: usnic and protocetraric acids (Swinscow & Krog 1978).

*Usnea longissima* Ach. var. *hokkaidensis* Räsänen, J. Jpn. Bot. 16: 86, 1940, syn. nov. Holotype: Japan, Hokkaido, Tomuraushi, corticola, 1935, *M. Sato s.n.* (H?, not seen). Chemistry: not examined by TLC [KOH + yellow turning to red (Räsänen 1940): probably salazinic acid].

*Usnea longissima* subsp. *persensibilis* Asahina, Lich. Jap. 3: 49, 1956, syn. nov. Holotype: Japan, Honshu, Prov. Shinano, Mountainside of Mt. Norikura, 7.8.1952, *Y. Asahina 5287* (TNS!). Chemistry: usnic acid, atranorin

and US4.

*Usnea longissima* subsp. *sensibilis* Asahina, Lich. Jap. 3: 49, 1956, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Shinano, Mountainside of Mt. Norikura, 7.8.1952, *Y. Asahina s.n.* (TNS!). Chemistry: usnic and salazinic acids.

*Usnea longissima* subsp. *sensibilis* f. *tingens* Asahina, Lich. Jap. 3: 49, 1956 (misprint); J. Jpn. Bot. 42: 293, 1967, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Shinano, Mountainside of Mt. Norikura, 7.8.1952, *Y. Asahina s.n.* (TNS!). Chemistry: usnic and salazinic acids, and atranorin.

*Usnea montis-fuji* Motyka, Lich. Gen. *Usnea* Stud. Monogr. Pars Syst. 2: 420, 1938, syn. nov. Isotype: Japan, Honshu, Prov. Suruga, Mt. Fuji, 1925, *Y. Asahina s.n.* (TNS!). Chemistry: usnic, protocetraric and salazinic acids.

*Usnea montis-fuji* f. *cinerea* Asahina, Lich. Jap. 3: 51, 1956, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Kai, Yoshida-guchi, 1-gome, Mt. Fuji, 10.8.1952, *M. Togashi s.n.* (TNS!). Chemistry: usnic, protocetraric and salazinic acids, and atranorin.

*Usnea pseudomontis-fuji* Asahina, Lich. Jap. 3: 51, 1956, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Suruga, Subashiri-guchi, 1-gome, Mt. Fuji, 5.7.1931, *Y. Asahina 201* (TNS!). Chemistry: usnic, fumarprotocetraric and succinprotocetraric acids, atranorin, and US3.

Thallus fruticose, pendent, up to several meters long, grayish-green to yellowish-green when fresh, straw-yellow in herbarium specimens, pale to dark brown at the base; branching isotomic-dichotomous; branches areolately corticate when mature, matt on the surface, with annular-pseudocyphellae between segments and twisted maculae on the surface of lateral branches, with longitudinal furrow, terete to distinctly flat, uninflated, 0.3–0.9 mm in diam., gradually tapering, elongated towards distal branches, with many short lateral branches; lateral branches slightly broadened at the base; papillae absent; soralia often formed on lateral branches, developed from cortex or maculae,  $\pm$  discrete, punctiform to rounded or surrounding the branch, slightly stipitate, cortical margin not reflexed, convex at the top, often with isidiomorphs, lacking granular soredia. Cortex thick, 2.1–21% of the radius, *merrillii*-type plectenchymatous; hyphae pachydermatous, lacking red pigment, lumina almost the same as medullary hyphae. Medulla dense, thin, 4.0–20% of the radius, lacking red pigment. Axis solid, thick, 37–85% of the diameter, I + dirty blue. Apothecia rare, lateral on lateral branches, up to 4.0 mm in diam., flat to cup-shaped; thaloid exciple with many fibrils; disc epruinose, brown, lacking white rim; epihymenium 0–4.0  $\mu$ m thick; hymenium 60–84  $\mu$ m thick; hypothecium 100–140  $\mu$ m thick; spores 5.2–7.2  $\times$  4.0–4.8  $\mu$ m long.

Chemistry. Race 1, usnic, salazinic, protocetraric ( $\pm$ ) and constictic acids ( $\pm$ ), and atranorin ( $\pm$ ); Race 2, usnic, fumarprotocetraric and succinprotocetraric acids ( $\pm$ ), US3 ( $\pm$ ), and atranorin ( $\pm$ ); Race 3, usnic acid, atranorin, and US4.

The distinguishing features of *U. trichodeoides* are (1) the pendent thallus with isotomic-dichotomous branching, (2) the elongated branches which are flat and areolately corticate when well developed, (3) the presence of annular-pseudocyphellae between segments, (4) the *merrillii*-type plectenchymatous cortex, and (5) the presence of depsidones such as salazinic or fumarprotocetraric acids as the major substance.

When Asahina (1956) described *U. longissima* subsp. *persensibilis*, he did not cite any specimens in the protologue. However, according to the protologue, this taxon has only been collected from Mt. Norikura. Only one specimen, labeled as Japan, Honshu, Prov. Shinano, Mountainside of Mt. Norikura, 7.8.1952, *Y. Asahina 5287*, is located in TNS, which is not in conflict with the locality and date, and the morphological features of this

specimen agree with the protologue. Although the occurrence of fumarprotocetraric acid is mentioned in the protologue, US4 (unidentified substance; lower than the spot of fumarprotocetraric acid on TLC plate) was detected from this specimen instead of fumarprotocetraric acid by TLC. US4 is considered as a chemically close substance with fumarprotocetraric, protocetraric or succinprotocetraric acids, judging from the spot color on TLC plate after heating with 10% H<sub>2</sub>SO<sub>4</sub>. The identification of fumarprotocetraric acid in the protologue is considered to be erroneous, since it was detected by microchemical test and paper chromatography. Thus, the specimen can be accepted as the holotype of *U. longissima* subsp. *persensibilis*.

When Asahina (1956) described *U. longissima* subsp. *sensibilis*, he did not cite any specimen in the protologue. The authentic specimen, labeled as Japan, Honshu, Prov. Shinano, Mountainside of Mt. Norikura, 7.8.1952, *Y. Asahina s.n.*, is not in conflict with the protologue morphologically and chemically. Therefore, this specimen is designated as the holotype of *U. longissima* subsp. *sensibilis*.

When Asahina (1956) described *U. longissima* subsp. *sensibilis* f. *tingens*, he did not cite any specimen in the protologue. The authentic specimen, labeled as Japan, Honshu, Prov. Shinano, Mountainside of Mt. Norikura, 7.8.1952, *Y. Asahina s.n.*, is not in conflict with the protologue morphologically and chemically. Therefore, this specimen is designated as the holotype of *U. longissima* subsp. *sensibilis* f. *tingens*.

When Asahina (1956) described *U. montis-fuji* f. *cinerea*, he showed a photograph of the thallus in the protologue. The authentic specimen, labeled as Japan, Honshu, Prov. Kai, Yoshida-guchi, 1-gome, Mt. Fuji, 10.8.1952, *M. Togashi s.n.*, is identical with the photograph, and agrees well with the protologue morphologically as well as chemically. Therefore, this specimen is designated as the lectotype of *U. montis-fuji* f. *cinerea*.

When Asahina (1956) described *U. pseudomontis-fuji*, he did not designate the type specimen in the protologue. However, he showed a photograph of thallus in the protologue. The authentic specimen, labeled as Japan, Honshu, Prov. Suruga, Subashiri-guchi, 1-gome, Mt. Fuji, 5.7.1931, *Y. Asahina 201*, is identical with the photograph. In addition, this specimen is marked as "Typus" on the label, and agrees well with the protologue morphologically and chemically. Therefore, this specimen is designated as the lectotype of *U. pseudomontis-fuji*.

Three chemical races were recognized in the present area. The commonest race was Race 1 (salazinic acid, 61%). Race 2 (fumarprotocetraric acid, 38%) was also commonly found. But Race 3 has only been collected once. No morphological and ecological differences were found among them. Therefore, they are treated as chemical races of *U. trichodeoides* in the present study.

*U. trichodeoides* resembles *U. hesperina*, *U. longissima* and *U. pectinata*. However, it can be distinguished from them by the flat branches when well developed. The slender form of *U. trichodeoides* can be distinguished from *U. longissima* and *U. pectinata* by the presence of salazinic and protocetraric acids, or US4, and from *U. hesperina* by the decorticate or areolately cracked cortex on the elongated branches.

In Japan, *U. trichodeoides* is distributed in Hokkaido, Honshu and Shikoku, where it grows on bark of coniferous trees such as *Abies*, *Larix*, *Picea* and *Pinus*, or broadleaf trees

such as *Betula*, *Fagus* and *Salix* at elevations between 50 and 2500 m (at low elevation in Hokkaido, and higher elevation in Honshu and Shikoku). In Taiwan, it grows on tree bark such as *Ilex* and *Salix* at elevations between 1800 and 3600 m. *U. trichodeoides* is widely distributed in boreal to temperate regions of Asia, Australia, Europe and East Africa (Asahina 1956, Awasthi 1986, Stevens 1999, Swinscow & Krog 1978).

Representative specimens examined. Race 1. JAPAN. Hokkaido. Prov. Kitami: en route from Rishiri-hokuroku camp site 2.5 km S of Sakae-machi to Himenuma Pond, Oshidomari, Rishirifuji-cho, Rishiri-gun, Rishiri Island (45°13'N, 141°14'E), on *Abies sachalinensis*, 140–360 m, 1.6.1995, *Y. Ohmura 1074*. Prov. Kushiro: along Route 44, Akkeshi-cho, Akkeshi-gun, on *Abies sachalinensis*, c. 100 m, 2.9.1996, *Y. Ohmura 2728*. Prov. Tokachi: along the trail from Tomuraushi Hot Spring to the top of Mt. Tomuraushi, Daisetsu Mts., Shintoku-cho, Kamikawa-gun (43°28'N, 142°52'E), on *Betula* sp., 680–1000 m, 22.7.1997, *Y. Ohmura 3499*. Honshu. Prov. Iwashiro: Ichinoki-mura, Yama-gun, on *Fagus crenata*, 9.7.1949, *M. Omura s.n.* (herb. *Y. Asahina 207*). Prov. Shimotsuke: Yumoto, Nikko, 20.9.1952, *Y. Asahina 5292*. Prov. Musashi: Karisaka Pass, Chichibu-gun, c. 1400 m, 23.5.1970, *M. Togashi & S. Kurokawa s.n.* Prov. Shinano: around Oh-ahara Marsh, Hase-mura, Kami-ina-gun (35°53'N, 138°11'E), on *Larix kaempferi*, 1820 m, 30.6.1997, *Y. Ohmura 3246*. Prov. Kai: Hirano, Lakeside of Yamanaka, Minami-tsuru-gun, c. 980 m, 24.7.1957, *S. Kurokawa 57081*; Lake side of Yamanaka, Mt. Fuji, 6.6.1956, *M. Togashi s.n.* (herb. *Y. Asahina 195*); Goten-niwa, Mt. Fuji, 970 m, 26.5.1963, *S. Kurokawa 63024*. Prov. Suruga: Lakeside of Syojiko, Mt. Fuji, 9.1952, *M. Togashi s.n.* Prov. Kii: Mt. Koya, 18.6.1926, *Y. Numaziri s.n.* Shikoku. Prov. Awa: Mt. Kenzan, 20.8.1934, *F. Fujikawa s.n.* (herb. *Y. Asahina 2003*). TAIWAN. Mt. Shi-San, Mt. Shin-Kao-San, 3300–3600 m, 3.1.1964, *S. Kurokawa 451*. Prov. Taichung Hsien: en route from Ssu-yuan to To-chia-tun Shan, Mt. Nanhuta Shan, Hoping, on *Salix* sp., 2400–2800 m, 10.11.1989, *H. Kashiwadani 35751*. KOREA. Pref. Kankyo-Nando, Mt. Hakuto-san, 17.9.1942, *Y. Kobayasi s.n.* INDIA. Darjeeling, Rimbick, 2200 m, 6.5.1960, *M. Togashi s.n.* NEPAL. E. Nepal, Birwa-Yektin, 2200 m, 28.11.1963, *M. Togashi s.n.*

Race 2. JAPAN. Hokkaido. Prov. Kushiro: along Route 44, Akkeshi-cho, Akkeshi-gun, on *Abies sachalinensis*, c. 100 m, 2.9.1996, *Y. Ohmura 2766*. Honshu. Prov. Mutsu: Mt. Nuido-iwa, Shimokita-gun, Summit area, on twigs, c. 620 m, 17.5.1994, *H. Kashiwadani 37928*. Prov. Musashi: Magosou-dani, Nippara, Hikawa-machi, c. 1500 m, 25.11.1969, *M. Togashi s.n.* Prov. Shinano: around Oh-ahara Marsh, Hase-mura, Kami-ina-gun (35°53'N, 138°11'E), on *Larix kaempferi*, 1820 m, 30.6.1997, *Y. Ohmura 3249*; Daimon Pass, Ikenotaira, 22.5.1959, *Y. Asahina [59225]*, *S. Kurokawa & M. Nuno*. Prov. Suruga: Lakeside of Shoji, Mt. Fuji, 9.1952, *M. Togashi s.n.* TAIWAN. Prov. Taichung Hsien: en route from Ssu-yuan to To-chia-tun Shan, Mt. Nanhuta Shan, Hoping, c. 2500 m, 10.11.1989, *H. Kashiwadani 36005*. INDIA. Phalut, Darjeeling, 9.5.1960, *M. Togashi s.n.* NEPAL. E. Nepal, below Silin Tzokupa, 3200 m, 21.11.1963, *M. Togashi s.n.*

Race 3. JAPAN. Honshu. Prov. Shinano: Mountainside of Mt. Norikura, 8.8.1952, *M. Togashi s.n.* (herb. *Y. Asahina 5287a*).

### Key to species of the genus *Usnea* in Japan and Taiwan

- 1a. Thallus reddish; red pigment present in cortex . . . . . 2
- 1b. Thallus greenish-gray or yellowish-green; red pigment absent in cortex. . . . . 4
  - 2a. Red pigment present also in medulla just below the cortex; branches inflated; soralia concave at the top. . . . . (14) *U. dorogawensis* Asahina
  - 2b. Red pigment absent in medulla; branches uninflated; soralia convex at the top . . . . . 3
- 3a. Soralia present on fibrils; soralia on thicker branches are developed from the scars of detached fibrils or lateral branches; terminal and subterminal branches elongated; fibrils abundant on branches . . . . . (33) *U. rubrotincta* Stirt.
- 3b. Soralia absent or very rare on fibrils; soralia on thicker branches are developed from the top of eroded papillae; terminal and subterminal branches not elongated; fibrils sparse on branches. . . . . (32) *U. rubicunda* Stirt.
  - 4a. Red pigment present in medulla . . . . . 5
  - 4b. Red pigment absent in medulla . . . . . 7



- 5a. Axis fistulose ..... (38) *U. baileyi* (Stirt.) Zahlbr.
- 5b. Axis solid ..... 6
- 6a. Soralia rounded and becoming larger than branch diam.; red pigment present near the cortex, strawberry pink; diffractaic and/or barbatic acids present, murolic acid complex absent. .... (10) *U. ceratina* Ach.
- 6b. Soralia irregular in shape and smaller than branch diam.; red pigment present near the axis, reddish brown; diffractaic and barbatic acids absent, murolic acid complex present ..... (25) *U. mutabilis* Stirt.
- 7a. Cortex fragile, elongated branches decorticate or areolately corticate. .... 8
- 7b. Cortex stable, consistent on the branches ..... 10
- 8a. Thallus with dark brown base; annular-pseudocypbellae absent; stictic acid present; saxicolous or corticolous. .... (40) *U. pectinata* Taylor
- 8b. Thallus with concolorous or pale base; annular-pseudocypbellae present; stictic acid absent; corticolous ..... 9
- 9a. Branches flattened in well developed thallus, with longitudinal-furrows on the surface; areolately corticate on elongated terminal branches; salazinic or fumarprotocetraric acids, or US4 present. .... (43) *U. trichodeoides* Vain.
- 9b. Branches terete, without longitudinal-furrows on the surface; decorticate on elongated terminal branches; diffractaic, barbatic or evernic acids present ..... (42) *U. longissima* Ach.
- 10a. Branches ridged ..... 11
- 10b. Branches terete ..... 12
- 11a. Elongated branches broken into alate plates, distinctly ridged; caperatic acid present, stictic acid absent. .... (8) *U. angulata* Ach.
- 11b. Elongated branches never broken into alate plates, slightly ridged; caperatic acid absent, stictic acid present. .... (39) *U. himantodes* Stirt.
- 12a. Thallus pendent ..... 13
- 12b. Thallus erect to subpendent. .... 19
- 13a. Papillae common, verrucose or cylindrical; cortex *florida*-type plectenchymatous ..... (1) *U. filipendula* Stirt.
- 13b. Papillae rare or absent, hemispherical; cortex *merrillii*-type plectenchymatous ..... 14
- 14a. Branches inflated, constricted between segments; medulla lax ..... 15
- 14b. Branches uninflated, not constricted between segments; medulla dense. .... 16
- 15a. Pseudocypbellae present on the surface of branches; soralia and isidiomorphs absent ..... (20) *U. himalayana* C.Bab.
- 15b. Pseudocypbellae absent on the surface of branches; soralia and isidiomorphs present ..... (26) *U. nidifica* Taylor
- 16a. Annular-pseudocypbellae present between segments of branches; thicker branches flattened at the ramification; diffractaic and/or barbatic acids present. .... (41) *U. diffracta* Vain.
- 16b. Annular-pseudocypbellae absent between segments of branches; thicker branches always terete at the ramification; diffractaic and barbatic acids absent ..... 17
- 17a. Globose shaped secondary cortex developed on exposed axis; axis cribrous; salazinic acid present. .... (24) *U. merrillii* Motyka
- 17b. Globose shaped secondary cortex not developed on exposed axis; axis solid; salazinic acid absent ..... 18
- 18a. Maculae present on the surface of branches; thamnolic acid absent; distributed in tem-

- perate to subtropical regions . . . . . (19) *U. hesperina* Motyka
- 18b. Maculae absent on the surface of branches; thamnolic acid present; endemic to Yakushima Island . . . . . (37) *U. yakushimensis* Asahina
- 19a. Thallus with jet black base . . . . . 20
- 19b. Thallus with pale to dark brown base; cortex not *florida*-type plectenchymatous . . . . . 25
- 20a. Thallus inflated, cortex *ceratina*-type plectenchymatous . . . . (15) *U. fragilesceus* Lyngé
- 20b. Thallus uninflated, cortex *florida*-type plectenchymatous . . . . . 21
- 21a. Soralia present; usually sterile . . . . . 22
- 21b. Soralia absent; usually well fertile . . . . . (2) *U. florida* (L.) F. H. Wigg.
- 22a. Soralia convex at the top . . . . . (5) *U. subfloridana* Stirt.
- 22b. Soralia concave at the top . . . . . 23
- 23a. Soralia deeply excavating nearly into central axis; isidiomorphs absent; zeorin present . . . . . (3) *U. fulvoreaegens* (Räsänen) Räsänen
- 23b. Soralia slightly excavating and never reaching to central axis; isidiomorphs present at least in juvenile stages of soralia; zeorin absent . . . . . 24
- 24a. Soralia discrete, rounded; norstictic acid present . . . . . (4) *U. glabrescens* (Nyl.) Vain.
- 24b. Soralia confluent, elliptic; norstictic acid absent . . . . . (6) *U. wasmuthii* Räsänen
- 25a. Soralia present . . . . . 26
- 25b. Soralia absent; usually highly fertile . . . . . 38
- 26a. Thallus inflated . . . . . 27
- 26b. Thallus uninflated . . . . . 36
- 27a. Perforations present on thicker branches . . . . . (9) *U. bismolliuscula* Zahlbr.
- 27b. Perforations absent on thicker branches . . . . . 28
- 28a. Soralia concave at the top . . . . . (17) *U. glabrata* (Ach.) Vain.
- 28b. Soralia convex at the top . . . . . 29
- 29a. Soralia developed from scars of detached fibrils . . . . . 30
- 29b. Soralia developed from cortex, cracks or top of eroded papillae . . . . . 32
- 30a. Soralia punctiform, discrete from each other . . . . . 31
- 30b. Soralia irregular in shape, confluent with each other . . . . . (12) *U. dasaea* Stirt.
- 31a. Lateral branches constricted at the base; constictic acid present . . . . . (36) *U. subintumescens* Asahina
- 31b. Lateral branches broadened at the base; constictic acid absent . . . (21) *U. intumescens* Asahina
- 32a. Soralia rounded . . . . . 33
- 32b. Soralia irregular in shape . . . . . 35
- 33a. Thallus simple; thamnolic acid present . . . . . (22) *U. koyana* Asahina
- 33b. Thallus with many lateral branches; thamnolic acid absent . . . . . 34
- 34a. Cortex *ceratina*-type plectenchyma; unknown substances (US1 and US) present . . . . . (18) *U. hakonensis* Asahina
- 34b. Cortex *merrillii*-type plectenchyma; unknown substances (US1 and US2) absent . . . . . (11) *U. confusa* Asahina
- 35a. Papillae present; soralia developed from the tops of eroded papillae . . . . . (31) *U. pygmoidea* (Asahina) Y. Ohmura
- 35b. Papillae absent; soralia developed from cracks of cortex . . . . . (26) *U. nidifica* Taylor
- 36a. Soralia rounded, distinctly stipitate . . . . . (27) *U. nipparensis* Asahina
- 36b. Soralia punctiform, sessile to slightly stipitate . . . . . 37
- 37a. Base of thallus distinctly annularly cracked; cortex *merrillii*-type plectenchyma; salazinic acid

- present . . . . . (29) *U. pangiana* Stirt.
- 37b. Base of thallus continuous or irregularly cracked; cortex *ceratina*-type plectenchyma; stictic acid present . . . . . (7) *U. aciculifera* Vain.
- 38a. Branches inflated . . . . . 39
- 38b. Branches uninflated . . . . . 43
- 39a. Fibrils crisp . . . . . (23) *U. masudana* Asahina
- 39b. Fibrils straight . . . . . 40
- 40a. Apothecia cup-shaped . . . . . (16) *U. fuscorubens* Motyka
- 40b. Apothecia flat or sinuose . . . . . 41
- 41a. Apothecia sinuose; disc with white rim; thalloid exciple with few fibrils . . . . . (30) *U. pseudogatai* Asahina
- 41b. Apothecia flat; disc lacking white rim; thalloid exciple with many fibrils . . . . . 42
- 42a. Fibrils on apothecia broadened at the base . . . . . (34) *U. shimadai* Asahina
- 42b. Fibrils on apothecia cylindrical, never broadened at the base . . . . . (28) *U. orientalis* Motyka
- 43a. Annular cracks distinct especially near the base of thallus; apothecial disc with white rim; barbatic acid present . . . . . (13) *U. dendritica* Stirt.
- 43b. Annular cracks absent or very rare near the base of thallus; apothecial disc lacking white rim; caperatic acid present . . . . . (35) *U. sinensis* Motyka

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## INDEX

Accepted taxa from Japan and Taiwan are in Roman type; taxa that are synonyms are in italics.

- Eumitria baileyi* Stirt. 75  
 –*formosa* Stirt. 75  
 –*implicita* Stirt. 75  
*Lichen comosus* Ach. 29  
 –*floridus* L. 26  
*Usnea aciculifera* Vain. 33  
 – f. *abbreviata* Asahina 33  
 – *alisani* Asahina 72  
 – f. *condensata* Asahina 72  
 – *angulata* Ach. 34  
 – *asahinai* Motyka 34  
 – *baileyi* (Stirt.) Zahlbr. 75  
 – var. *eizanensis* (Asahina) Asahina 75  
 – var. *yokawensis* (Asahina) Asahina 75  
 – subsp. *septentrionalis* Asahina 75  
 – f. *creberrima* (Asahina) Asahina 75  
 – f. *subcreberrima* (Asahina) Asahina 75  
 – *barbata* (L.) F. H. Wigg. var. *dasyopoga* Ach. 25  
 – var. *dasyopoga* Röhl. 25  
 – var. *glabrescens* Nyl. 28  
 – *bismolliuscula* Zahlbr. 35  
 – f. *subramulifera* Asahina 35  
 – f. *turgescens* Asahina 36  
 – subsp. *pseudomolliuscula* Asahina 36  
 – *capilliformis* Asahina 51  
 – *ceratina* Ach. 38  
 – *ceratinella* Vain. 69  
 – *cineraria* Motyka 62  
 – *comosa* (Ach.) Vain. 29  
 – subsp. *colorans* Asahina 29  
 – subsp. *melanopoda* Asahina 31  
 – subsp. *praetervisa* Asahina 29  
 – *confusa* Asahina 40  
 – subsp. *kitamiensis* (Asahina) Asahina 42  
 – subsp. *pygmoidea* Asahina 65  
 – subsp. *rubroreagens* Asahina 40  
 – subsp. *subconfusa* Asahina 41  
 – *creberrima* Vain. 75  
 – var. *fistulescens* Asahina 38  
 – var. *simplicior* Asahina 38  
 – *cribrosa* Asahina 56  
 – *croceorubescens* Vain. 62  
 – f. *tenuiramea* Asahina 57  
 – *dasaea* Stirt. 41  
 – *dasyopoga* Röhl. 25  
 – *dendritica* Stirt. 44  
 – *dichotoma* Fr. 52  
 – *diffracta* Vain. 80  
 – f. *depauperata* Asahina 80  
 – f. *huei* Asahina 80  
 – subsp. *subdiffracta* Asahina 80  
 – *dorogawensis* Asahina 45  
 – *eizanensis* Asahina 75  
 – *filipendula* Stirt. 25  
 – *flexilis* Stirt. 52  
 – *florida* (L.) F. H. Wigg. 26  
 – var. *comosa* (Ach.) Biroli 29  
 – var. *mollis* Vain. 46  
 – *formosa* (Stirt.) Zahlbr. 75  
 – *fragilescens* Lyng. 46  
 – var. *mollis* (Vain.) P. Clerc 46  
 – *fulvoreaegens* (Räsänen) Räsänen 26  
 – *fuscorubens* Motyka 48  
 – *galbinifera* Asahina 41  
 – f. *subfibrillosa* Asahina 41  
 – *glabrata* (Ach.) Vain. 49  
 – subsp. *pseudoglabrata* Asahina 49  
 – *glabrescens* (Nyl.) Vain. 28  
 – var. *fulvoreaegens* Räsänen 26  
 – subsp. *asiatica* Asahina 31  
 – subsp. *pseudocolorans* Asahina 31  
 – *hakonensis* Asahina 50  
 – f. *inactiva* Asahina 50  
 – *hesperina* Motyka 51  
 – *himalayana* C. Bab. 52  
 – f. *major* Asahina 52  
 – *himantodes* Stirt. 77  
 – *hondoensis* Asahina 62  
 – subsp. *inflatula* Asahina 62  
 – f. *fujisanensis* Asahina 62  
 – subsp. *lacunosula* Asahina 62  
 – *hossei* Vain. 78  
 – f. *subtrichodea* Asahina 78  
 – *implicita* (Stirt.) Zahlbr. 75  
 – var. *yokawensis* Asahina 75  
 – f. *creberrima* Asahina 75

- f. *subcreberrima* Asahina 75  
 - *intumescens* Asahina 54  
 -- f. *condensata* Asahina 54  
 - *japonica* Vain. 58  
 - *japonica* var. *boninensis* Asahina 58  
 - *kinkiensis* Asahina 41  
 -- f. *gracilior* Asahina 41  
 - *koyana* Asahina 55  
 - *kurokawae* Asahina 58  
 - *kushiroensis* Asahina 58  
 -- subsp. *subasiriensis* Asahina 65  
 - *kyotoensis* Asahina 42  
 - *leucopilodea* Nyl. 36  
 - *longissima* Ach. 82  
 -- var. *hokkaidensis* Räsänen 85  
 -- var. *misamisensis* Vain. 78  
 -- var. *robustior* Asahina 82  
 -- var. *vulgata* Asahina 82  
 -- subsp. *ambigua* Asahina 82  
 -- subsp. *dubia* Asahina 82  
 -- subsp. *jesoensis* Asahina 82  
 -- subsp. *persensibilis* Asahina 85  
 -- subsp. *sensibilis* Asahina 86  
 --- f. *tingens* Asahina 86  
 - *malacea* Zahlbr. 46  
 - *masudana* Asahina 55  
 - *merrillii* Motyka 56  
 - *misamisensis* (Vain.) Motyka 78  
 - *mollis* Stirt. 46  
 - *molliuscula* Vain. 35  
 - *montis-fuji* Motyka 86  
 -- f. *cinerea* Asahina 86  
 - *mutabilis* Stirt. 57  
 - *neoguineensis* Asahina 77  
 -- var. *gracilior* Asahina 77  
 - *nidifica* Taylor 58  
 - *nidularis* Asahina 58  
 -- var. *subnuda* Asahina 59  
 - *nipparensis* Asahina 60  
 -- f. *reagens* Asahina 60  
 - *ogatai* Asahina 44  
 - *orientalis* Motyka 61  
 -- f. *esorediosa* Asahina 61  
 - *pangiana* Stirt. 62  
 -- subsp. *hondoensis* (Asahina) Asahina 62  
 - *pectinata* Taylor 78  
 - *pensylvanica* Motyka 67  
 - *plicata* (L.) F. H. Wigg. var. *comosa* (Ach.) Ach. 29  
 -- var. *dasyypoga* Ach. 25  
 -- var. *glabrata* Ach. 49  
 - *pseudintumescens* Asahina 54  
 - *pseudogatai* Asahina 64  
 - *pseudomontis-fuji* Asahina 86  
 - *pseudorientalis* Asahina 48  
 - *pseudorubescens* Asahina 69  
 -- var. *anaemica* Asahina 69  
 - *pseudorubicunda* Asahina 67  
 - *pygmea* Motyka 36  
 - *pygmea* Asahina 65  
 -- subsp. *kitamiensis* Asahina 42  
 - *pygmoidea* (Asahina) Y. Ohmura 65  
 - *roseola* Vain. 38  
 -- subsp. *pseudoroseola* Asahina 38  
 - *rubescens* Stirt. 69  
 -- var. *anaemica* Asahina 70  
 -- var. *areolata* Motyka 70  
 -- var. *rubrotincta* (Stirt.) Motyka 69  
 -- subsp. *aberrans* Asahina 70  
 - *rubicunda* Stirt. 67  
 -- var. *ceratinella* (Vain.) Motyka 69  
 -- var. *spilota* (Stirt.) G. N. Stevens 70  
 -- subsp. *aberrans* Asahina 67  
 - *rubrotincta* Stirt. 69  
 - *shikokiana* Asahina 77  
 - *shimadai* Asahina 72  
 - *sinensis* Motyka 72  
 - *societatis* Vain. 59  
 - *spilota* Stirt. 70  
 - *spinigera* Asahina 42  
 -- f. *subnuda* Asahina 42  
 - *straminea* Müll. Arg. 59  
 - *subflexilis* Stirt. 53  
 - *subfloridana* Stirt. 29  
 -- subsp. *praetervisa* (Asahina) P. Clerc 29  
 - *subintumescens* Asahina 73  
 -- f. *olivaceoviridis* Asahina 73  
 - *subroseola* Asahina 38  
 - *sulcata* Motyka 34  
 - *torquescens* Stirt. 34  
 -- var. *asahinai* (Motyka) Asahina 34  
 - *trichodeoides* Vain. 85  
 - *undulata* Stirt. 42  
 - *wasmuthii* Räsänen 31  
 - *yakushimensis* Asahina 74