
Original article

Morphological and ecological diversification of *Conocephalum conicum* complex in Japan and Taiwan

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Abstract

Based on DNA haplotype and morphology analyses, 3 separate species of *Conocephalum conicum* s. lat. and *C. salebrosum* had been recognized in Japan and Taiwan by Akiyama and Odrzykoski (2020), and are described here. Morphological features and patterns of distributional areas for the 4 species, including 3 new taxa, *C. orientalis* H. Akiyama, *C. purpureorubrum* H. Akiyama, and *C. toyotae* H. Akiyama (formerly recognized as *C. conicum* J, F, and R types, respectively) as well as pan-boreal *C. salebrosum* are described in detail.

Key words: *Conocephalum orientalis*, *Conocephalum purpureorubrum*, *Conocephalum salebrosum*, *Conocephalum toyotae*, hepatics, taxonomy

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Introduction

The genus *Conocephalum* Hill (Marchantiidae) is a complex thalloid liverwort and a member of the Conocephalaceae (Grolle 1972). The genus was long considered to include three species, i.e., the European endemic *C. conicum* (L.) Dumort., pan-boreal *C. salebrosum* Szweyk., Buczk. & Odrzyk., and the East Asian endemic *C. japonicum* (Thunb.) Grolle. However, a number of molecular systematic studies have revealed the presence of additional cryptic species in the *C. conicum* complex (for example, Akiyama and Hiraoka, 1994a; Kim et al., 1996, 2001; Miwa et al., 2009) and in the *C. japonicum* complex (Miwa et al. 2003). More detailed history of the genus is provided by Akiyama and Odrzykoski (2020).

Akiyama and Odrzykoski (2020) examined the inter-relationships among the 6 cryptic “species” in the *C. conicum* complex and 3 of the *C. japonicum* complex in a world-wide study and they noted the following three points: 1) the *Conocephalum conicum*/*salebrosum* complex and *C. japonicum* complex should be classified in separate genera, the latter as

Sandea japonica Steph. ex Yoshin. as Grolle (1984) already suggested; 2) the *Conocephalum conicum*/*salebrosum* complex is confirmed to include no less than 6 species in the world; and 3) there are 4 species in the *C. conicum*/*salebrosum* complex distributed in Japan and Taiwan. These 4 species were previously known as J type, F type, R type (or Chemotype III in Toyota 2000) and *C. salebrosum*. Morphological differences among the 4 species were summarized by Akiyama and Odrzykoski (2020; Table 2).

The main purpose of this report is to describe these 4 species found in Japan and Taiwan and present their differences in morphology and distributional pattern. To investigate the distribution of each species, their identities were checked by morphology of living plants and by DNA sequences of *rps4* [the plastid *trnS-rps4* region, i.e., *rps4* plus the *trnS-rps4* intergenic spacer (IGS)] for all plants (ca. 450 samples) gathered by the author in Japan and Taiwan from March 2017 to September 2020 and members of the “Jagoke Expedition Team” (a total of 56 people from Japan and Taiwan). All specimens examined are deposited in the cryptogamic herbarium of the Museum of Nature

and Human Activities, Hyogo (HYO) and shown as “specimens examined” compiled in Appendix of this paper. Living plants and those fixed in 50 % ethanol were used to investigate morphological features as well as coloration, glossiness, and their odor caused by volatile compounds which can be observed only in fresh conditions.

In addition to the morphological features previously examined by Szweykowski et al. (2005), the following were also investigated in this study; 1) mucilage canals and mucilage cells examined with alcohol-soaked specimens (Plate 9, A–D), 2) epidermal structures of thalli (Plate 8), and 3) shapes of fertilized carpocephala in female plants (Plate 7). These features are reflected in the keys to the species below and in the descriptions of each species.

When describing *Conocephalum salebrosum*, Szweykowski et al. (2005) considered the following features as important to distinguish the species from the European endemic *C. conicum* s. str.; 1) basal structure of the air pore apparatus observed in vertical sections of female carpocephala, and 2) the numbers of cells in the unistratose portion of the thallus margins. However, these features were not stable within each species and thus cannot be used as distinguishing features for Asian species. Furthermore, it became clear that cell arrangement of ventral scale appendages were too variable in size and shape including their cell arrangement according to developmental stages and environmental conditions to be used to distinguish each species, though Akiyama and Hiraoka (1994a) treated them as effective to distinguish the Japanese three cryptic species.

I follow here Akiyama and Odrzykoski (2020) who treated *Conocephalum japonicum* as a member of a different genus *Sandea* Lindb. *Sandea* and *Conocephalum* can be distinguished as shown in the following keys. For more information on *Sandea*, which is not treated here, refer to Kitagawa (1982), Grolle (1984), Miwa et al. (2003, 2004), and Akiyama and Matsumoto (2021).

Taxonomical Treatment

Key to the genera of the Conocephalaceae

1. Winter annual (sometimes perennial in warmer and wetter condition). Plants small, rather densely branched, thallus 3–6 mm wide. Thallus apices freely branched in late autumn, bearing parenchymatous sub-rounded propagules. Air-chamber borders not deeply impressed. Thallus

without mucilage canals. Female carpocephala with sporophytes surrounded with entire appendages during autumn and winter. Spore mother cells linear.

..... *Sandea* (not treated in this paper)

1. Perennial. Plants medium to robust, rather remotely branched, thallus 1–2 cm wide. Thallus apices not freely branched but form winter buds in late autumn, which resume growth in the next spring. Air-chamber borders more or less deeply impressed (except *C. salebrosum*). Thallus with long mucilage canals (except *C. toyotae*). Propagules almost always absent, but round tubers, formed from underside of thallus rarely found in European and North American species. Female carpocephala with sporophytes surrounded with deeply cleft appendages during autumn and winter. Spore mother cells variable in shape such as tetrahedral, ellipsoid or globose, but not linear.

..... *Conocephalum*

Conocephalum Hill, Gen. Nat. Hist. ed. 2, 2: 118 (1773), *nom. conser.*

Type species: *Conocephalum conicum* (L.) Dumort. ≡ *Marchantia conica* L., Species Plantarum 2: 1138 (1753) ≡ *Hepatica conica* (L.) Adans. ex Lindb., Commentationes Botanicae 115 (1822).

Description: **Plants** perennial, vigorous, aromatic or sometimes odorless, often leathery with undulate margins in sunny places, sometimes becoming quite thin in shaded conditions, 7–25 mm wide and 50–200 mm long, sometimes wider and longer, yellowish green to blackish green, with purplish red color at margins and lower side of thalli; lower side of thalli often changing to reddish purple in late autumn and winter. **Thalli** thicker along the costa, becoming thin towards the margins, flat, margins sometimes gently depressed; surface coarsely and regularly areolate with elongated-hexagonal, lighter whitish green, impressed lines; **areole** (Fig. 1) smaller at margin and apex of thalli, larger at inner part except for 2–3 lines at central part; each areole with a central, pale, more or less elevated pore [= **areolae** (Fig. 1)]; composed of unistratose portion at extra margins with 1–5 cell-lines, where aerenchymatous layer absent. **Epidermis** with hyaline cells, smaller at margins and central part, lax between them. **Oil-cells** present, scattered on both surfaces and appendages of ventral scales, often surrounded by 7–8 wedge-shaped cells, smaller and rich in number at lower surface of thallus margins. **Pores** surrounded by 2–5 rings of cells, each ring

with 6–8, narrowly elongate or curved cells, bounded by thin secretion. **Aerenchyma** (spongy tissue) low, in one layer, with network of chlorophyll-rich filamentous cells; chlorophyllous filaments with 3–5 cells underlying the areolae; each filament ending in hyaline, conspicuously elongated beaked cells; often with mucilage cells at costal and marginal part of thalli. **Ventral tissue** solid, except for the presence of mucilage canals (slime canals) along costal thicker part; upper cells with vertical striae or pitted striations. **Rhizoids** more or less abundant on wings and costae, sometime few. **Ventral scales** 2-ranked, pale or light to deep purplish red, with basally constricted, sub-circular, dark purplish red appendages; a few oil cells present. **Asexual reproduction** quite rare (probably lacking for Asian plants), with ill-defined tubers formed at lower side of thalli in older portions.

Dioicous. **Male receptacles** terminal on thalli, formed much earlier than female ones mostly along with development of a new thalli from winter buds in early spring, often positioned on more or less upwardly aligned thalli and elevated by short petiolate branches; not stalked, round or ellipsoid in outlines, thick; upper surface roughened with somewhat elevated or conical openings of the antheridial chambers, from which sperm cells are discharged into the air in late spring; fallen-off from thalli by late summer. **Female receptacles**, remaining sessile, deeply inside the cavity at the terminus of thalli, becoming soon shrunk without successful fertilization; receptacles with fertilized embryos (sporophyte) in archegonia also remain sessile until spores mature in early spring, rapidly raised upwards by elongation of translucent fresh long stalks just before spore dispersal. **Stalks** 4–10 cm in length, colorless or slightly greenish, rarely slightly tinted red, translucent, smooth, with a single rhizoid furrow, and lacking an aerenchyma-chlorenchyma layer. **Heads of female receptacles (carpocephala)** conical, size and apex shape different among each species, very shallowly to hardly lobed, usually with 5–8 lobes, each bearing a single archegonium; lower part of areolae with much more compound structure compared to that of usual thalli. **Paleae** absent. **Involucres** membranous, tubular, undivided. **Pseudoperianth** absent.

Sporophytes with short foets and relatively massive setae; setae slightly elongating and capsules barely protuberant just before dehiscence. **Capsules** obovoid-ellipsoidal, cells of the unistratose wall with distinct annular thickenings; dehiscence via irregular

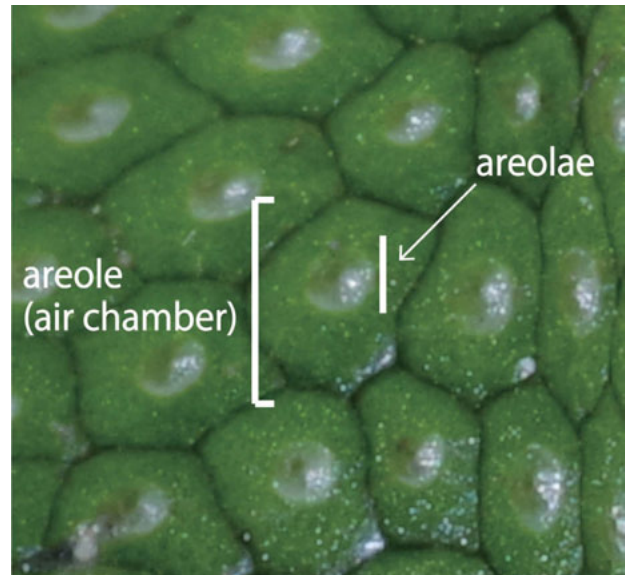


Figure 1. Areolae (air pore and surroundings) and areole (air chamber) in the upper surface of thallus.

clefts (often 8 in number) from the top to the base, but not extending to the middle of capsule. **Elaters** ca. 2–3 times greater in number than spores, quite variable in size and shape, often pointed at both ends, with 2–3 narrow spirals. **Spores** slightly irregular spherical to ovoid, 60–120 μm in longer diameter (just before dehiscence), thin-walled, delicately papillose on proximal (inner) surface, delicately papillose with scattered larger papillae on distal (outer) surface; spores chlorophyllous, precociously pluricellular, reaching maximum size just before dehiscence; fertility ranging from less than 40 % to almost 100 %; often varying in size and fertility even in a single species.

Note 1 (Dorsal grooves between air chambers). Degree of glossiness and thickness of outer cell-walls of upper epidermis of thalli vary among species and can be used to determine species identity. Although cell arrangement at the junction of air chamber walls to epidermis is not stable within each species, depth of grooves (deep or shallow) between air chambers are stable within a species. For example, as pointed out by Szweykowski et al. (2005), *C. conicum* s. str. has plane surfaces and *C. salebrosum* has more or less uneven surfaces (species epithet was named after this feature). The Asian *C. salebrosum*, however, has mostly plane surfaces (Plate 8, M–P) compared to deeply depressed grooves found in the other 3 species. Therefore, the plane surfaces can be one of the useful

features to distinguish Asian *C. salebrosum* from the FE type of *C. purpureorubrum*, both of which have similar plant appearance in northern Japan.

Note 2 (Air pore structure). Lower areolae structure in a female carpocephalum is more highly complexed than that observed in the surface of a vegetative thallus. Szweykowski et al. (2005) used it as one the useful features to distinguish *C. conicum* s. str. from *C. salebrosum* in Europe. For Asian plants, even including Asian plants of *C. salebrosum*, however, this feature is not stable within each species: both short and long types were found in all 4 species and the feature cannot reliably be used to distinguish the Asian species.

Szweykowski et al. (2005) also pointed out that epidermal cells of carpocephala are mostly bistratose in *C. conicum* s. str., while they are unistratose in *C. salebrosum*. In Asian plants, they are mostly bistratose in *C. salebrosum* and *C. toyotae*, 3–4-stratose and sometime more in *C. orientalis* and *C. purpureorubrum*.

Note 3 (Endosporic germination). Spores are slightly irregular spherical or ovoid in shape. Their size and shape changes during the process of endosporic germination, reaching 70–120 µm in longer diameter just before dehiscence. Fertility of spores varies among plants in each species (sometimes even among capsules of a single carpocephalum); for example, it is 40–100 % in *C. orientalis* with smaller sterile spores. Discharged spores contain a number of chloroplasts inside because of endosporic germination. They lose geminating ability within 30 days under room condition (Inoue 1966).

Note 4 (Male receptacles). Male plants of *Conocephalum* species produce receptacles near the tips of newly formed lobes in spring. The size of male receptacles are vary in size and shape even in the same population. Young, newly formed lobes are branched and both or one of lobe bears a single male receptacle at the tip. When the male receptacle is formed, growth of the lobe tentatively ceases and the lobe remains short, standing upwards with a short stipe which is almost entirely composed of a midrib of the usual thallus (Fig. 2-A). Since *Conocephalum* species (and *Sandea*) are known to explosively release microscopic water droplets containing sperm cells into the air (Shimamura et al., 2015), these upwardly oriented, short branches with male receptacles at the top may be an efficient platform to release sperm from a higher position above the soil surface.

Note 5 (Growing substrata). All species of

Conocephalum and *Sandea* mostly grow on soil with well-developed rhizoids elongating downwards and never attaching directly to the rock surface without a thin soil layer. The only exception is found with *C. salebrosum* elongating on calcareous walls. This requirement for an amount of soil as a growth substrate may be one of the reasons why *Conocephalum* species are not distributed at lower elevations in subtropical regions in Japan and Taiwan, where rocky substrates are almost devoid of soil cover due to the extent and speed of water flow during the rainy season.

Note 6 (Fungal infection). When plants of *Conocephalum* growing on the ground, irrespective of species, fungal mycelia almost always invade the parenchyma along the midribs. Such infected portions are recognized by the pale purplish red color contrasting from the surrounding uninfected colorless parts. The process of mycelial invasion was studied in detail by Carré and Harrison (1961) and Clee (1943).

Note 7 (Mucilage in thalli). Fresh plants, especially larger plants of *Conocephalum orientalis*, store a lot of mucilage within mucilage canals. They can be recognized as transparent and sticky liquid running down through the holes of the canals as seen in transverse sections of the thallus (Plate 9, H). It is a clear liquid when fresh, but turns opaque, whitish and rather solid when soaked in ethanol, thus making it easier to observe.

Both oil cells and mucilage cells are present in *Conocephalum* species. Inner contents of oil cells disintegrate when soaked in 50 % ethanol, while the contents of mucilage cells that are transparent in fresh conditions, as in the case of mucilage canals, becomes opaque and whitish and thus visible to the naked eye. Mucilage cells are solitary and slightly larger in size than surrounding cells. In contrast, oil cells in thalli (mostly at the upper and lower margins) and ventral scales are surrounded by a number of long rectangular cells arranged in a circle.

Conocephalum salebrosum, often growing in rather dry habitats, tends to have a greater number of mucilage canals and mucilage cells in thalli. In contrast, *C. toyotae*, which grows under snow cover during the winter season, lacks both mucilage canals and mucilage cells. These structures are expected to be closely related to desiccation tolerance.

According to Cavers (1904), Bolleter (1905), and Kobiyama and Crandall-Stotler (1999), mucilage canals originate from longitudinal connections of original unicellular mucilage cells. The relationships

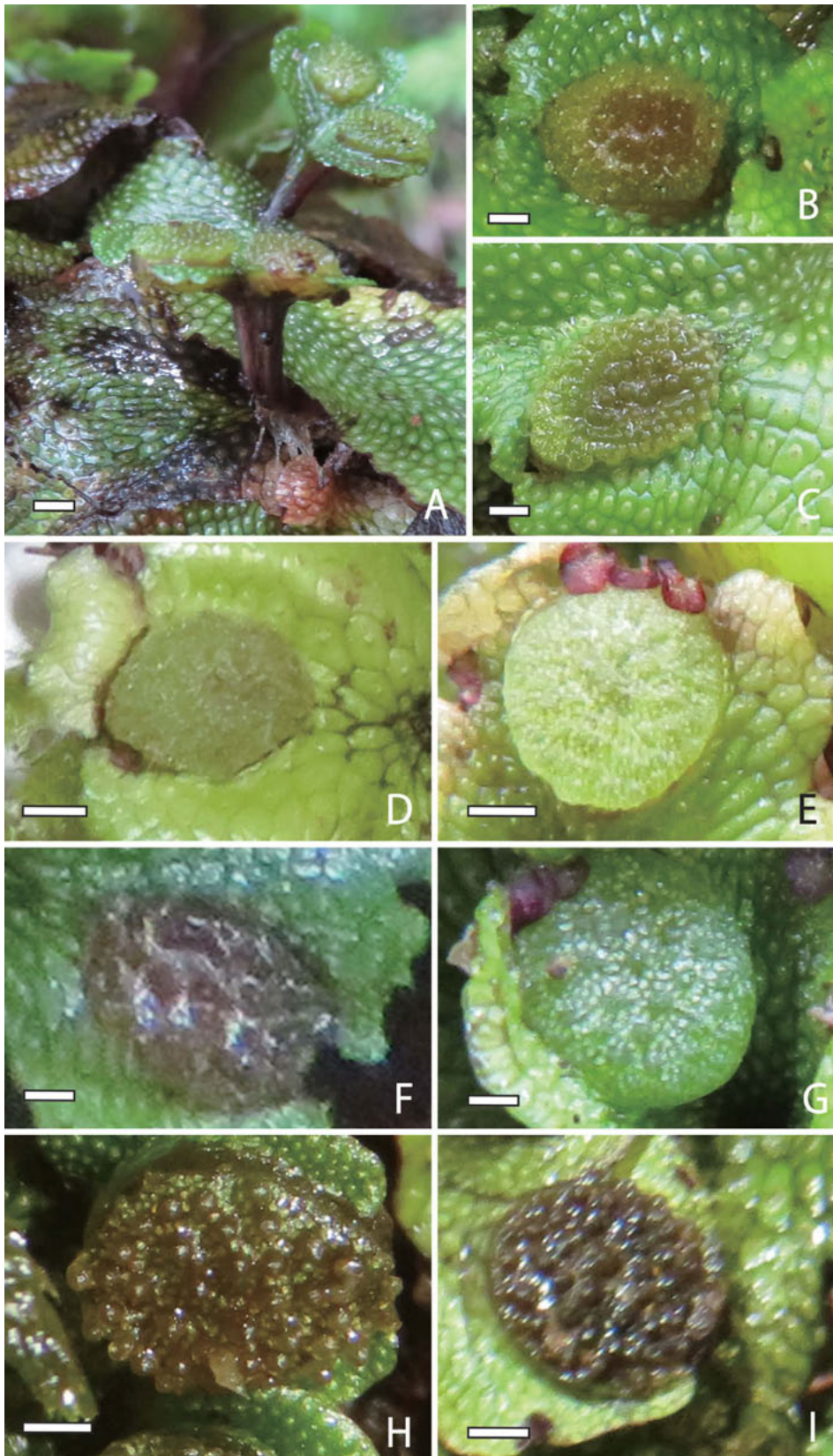


Figure 2. Male receptacles of the 4 species of *Conocephalum*. A–C: *C. orientalis*. D and E: *C. purpureorubrum*. F and G: *C. salebrosum*. H and I: *C. toyotae*. Scale bars = 2 mm for A, 1 mm for the others. A and C: Tsunokame, Hyogo Pref., 17 June 2017. B: Ashizuri, Kochi Pref., 2 April 2018. D: Umaji-mura, Kochi Pref., 3 May 2018. E: Totsugawa, Nara Pref., 24 May 2019. F: Taishaku-kyo, Hiroshima Pref., 10 July 2017. G: Atsunai, Hokkaido Pref., 28 April 2018. H: Yuzawa-cho, Niigata Pref., 22 June 2018. I: Nikko-shi, Tochigi, 14 July 2018.

between these mucilage cells along the costal region of thalli and those scattered all over the thalli remain unsolved.

Three species of the *Conocephalum conicum/salebrosum* complex, formerly known as J, F (or FS in Akiyama and Hiraoka 1994) and R types distributed in Japan and Taiwan, are described as new species based on morphological examination using a number of fresh samples as well as molecular phylogeny (Akiyama and Odrzykoski, 2020). Asian *Conocephalum salebrosum* [formerly known as T-type in Akiyama and Hiraoka (1994)] differs slightly from European *C. salebrosum* in the luster of the thalli, and shape of the apical end of the female carpocephala. According to Szweykowski et al. (2005), European endemic *Conocephalum conicum s. str.* is different from the Asian 4 species in totally flat outer epidermis of thallus; dorsal thallus surfaces of *C. conicum s. str.* are usually even, limits between particular air chambers are lying at same level as rest of epidermis, and highest cells of air chamber walls are usually not inserted into epidermal layer.

Keys to the 4 species of *Conocephalum* in Japan and Taiwan

1. Air chambers (areole) small, similar in size between those at the margins and the central costal parts (Fig. 3 G, H). Grooves between air chambers deeply impressed. Cells of upper epidermis of thalli large and with thin walls (Plate 8 Q–S). Mucilage canals absent along midrib of vegetative thalli (Plate 9 G), but present at upper portion of carpocephala. Mucilage cells absent. Carpocephala after fertilization helmet-shape with round apices (Plate 7 I, J). Living plants with distinctive odor of Matsutake mushrooms (Methyl cinnamate) even after long-term cultivation in a green house, but weakened or lost in late autumn or in artificial humid conditions such as in tightly sealed transparent plastic cups.
..... 4. *C. toyotae*
1. Air chambers (areole) becoming narrower and longer towards central costal portions (Fig. 3 A–F). Grooves between air chambers shallow (*C. salebrosum*) or deeply impressed (*C. orientalis* and *C. purpureorubrum*). Cells of upper epidermis of thalli rectangular in shape with thin (*C. salebrosum* and Western Japanese form of *C. purpureorubrum*) or thick walls (*C. orientalis* and Eastern Japanese form of *C. purpureorubrum*). Mucilage canals present along the midrib of thalli and carpocephala. Mucilage cells present (*C. salebrosum*) or often absent (*C. orientalis* and *C. purpureorubrum*). Carpocephala after fertilization conical, narrowly acute to obtuse, but not round. Plants with various kinds of scent, often fresh, earthy or slightly musty odor, sometime odorless, quite rarely with Matsutake mushroom odor in Eastern Japanese form of *C. purpureorubrum*. ... 2
2. Plants with distinctly shiny thalli, light green (Fig. 3 A), but often becoming yellowish when growing in shaded places (Fig. 3 B). Thalli wide, vigorous. Size of air chambers smaller at thallus margins, larger towards the center. Grooves between air chambers mostly deep. Areolae almost always occupying more than half of the width of air chambers. Outer epidermal cells with thick walls (Plate 8 A–D). 1. *C. orientalis*
2. Plants matt, yellowish green (Western Japanese form of *C. purpureorubrum* and *C. salebrosum*) or slightly shiny, blackish green (Eastern Japanese form of *C. purpureorubrum*). Air chambers mostly similar in size at margins and central parts. Grooves between air chambers deep (*C. purpureorubrum*) or shallow (*C. salebrosum*). Areolae occupying less than 1/3 of the width of air chambers. Outer epidermal cells with thin (Western Japanese form of *C. purpureorubrum* and *C. salebrosum*) or thick walls (Eastern Japanese form of *C. purpureorubrum*). 3
3. Plants often thick, becoming thin when growing in fully shaded conditions. Upper surface of thalli matt and yellowish green (Western Japanese form; Fig. 3 C) or slightly shiny and blackish green (Eastern Japanese form; Fig. 3 D); sometimes with a blackish central line on upper surface. Lower surface of thalli usually reddish purple even in summer seasons. Upper epidermal cells with thin (Western Japanese form; Plate 8 I–L) or thick walls (Eastern Japanese form; Plate 8 E–H). Grooves between air chambers deep (Plate 8 E–L). Mucilage canals well developed, but mucilage cells often absent. Rhizoids often dense, occurring throughout lower surfaces of thalli. Carpocephala after fertilization with round or slightly flat apices (Plate 7 A, B). Plants almost always with fresh, earthy odor, quite rarely with Matsutake mushroom odor in the Eastern Japanese form.
..... 2. *C. purpureorubrum*
3. Plants often thin; especially those growing directly

on surfaces of limestone cliffs becoming as thin as paper. Upper surface of thalli matt, yellowish green, almost lacking blackish lines in the center. Lower surface of thalli yellowish green (Plate 5 E, G), rarely becoming reddish orange at margins or whole surface (in Taiwanese plants; Plate 5 B). Upper epidermal cells with thin walls, becoming smaller towards the central parts (Plate 8 M–P). Grooves between air chambers shallow (Plate 8, M–P). Both mucilage canals and mucilage cells well developed. Rhizoids often few, only developing at central costal parts. Carpocephala after fertilization sharply pointed (in Japanese plants; Plate 7 C, D) or round (in Taiwanese and European plants). Plants usually with slightly musty odor or without odor when growing on drier substrata. Often found in limestone areas; restricted to rather damp and shaded places near the mouths of limestone caves in western Japan, where cool and wet air supplied throughout the year. 3. *C. salebrosum*

1. *Conocephalum orientalis* H. Akiyama, n. sp.

Figs. 2 (A–C), 3 (A, B), 4 (A–D), 5 (B, D), 7 (A, B), Plates 1 (A–L), 2 (A–J), 8 (A–D), 10 (A)

Protologue: Plants similar to *Conocephalum salebrosum*, but larger and wider, reaching 20 cm in length, 1–2 cm in width. Thalli distinctively shiny with thick walls of upper epidermal cells. Air pores circular to elliptical; areolae occupying no less than half of width of air chambers.

Type: JAPAN, Hyogo Pref., Yabu-shi, Oya-cho, Yokoiki valley, 30 Nov. 2020, *H. Akiyama 26465* (holotype in HYO; isotypes distributed as exiccatae “Bryophytes of Asia” from HIRO).

Previous names: *Conocephalum conicum* J-type (Odrzykoski et al., 1991; Akiyama and Hiraoka, 1994a, b; Akiyama et al., 1998; Kim et al., 1996, 2001; Miwa et al., 2005; Akiyama, 2006, 2014; Ludwiczuk et al., 2013; Miyatake et al., 2018; Akiyama and Odrzykoski, 2020). *Conocephalum conicum* Chemotype I and Chemotype II (Toyota et al. 1997; Toyota 2000).

Conocephalum orientalis was first recognized as a distinct “type” in the *C. conicum* complex by Odrzykoski and Szweykowski (1991) and then widely accepted by others (Akiyama and Hiraoka, 1994a; Kim et al., 1996, 2001; Miwa et al., 2010; Akiyama and Odrzykoski, 2020). For more details, see Akiyama and Odrzykoski (2020).

Japanese name: Oo-jiyagoke.

Etymology: Species epithet is selected because of its distribution areas in the Far East Asia.

Description: **Plants** perennial, vigorous, with refreshing forest scent, leathery, almost always shiny, 9–20 mm wide, to 20 cm long, usually green, yellowish green in shaded places; undersurface light green, becoming reddish purple towards late autumn. **Thalli** relatively thin, except along the costa, flat, margins plane or gently undulate; surfaces coarsely and regularly areolate with air chambers, with elongated-hexagonal, deeply impressed lines (grooves between air chambers); with 2–4 (–5) rows of unistratose portion at margins. **Areole** hexagonal, becoming smaller towards the margins, narrower and slightly longer along costa, with a pale, rather flatly elevated pore in the center. **Pores** mostly round, slightly elliptical along costa. **Areolae** occupying more than 1/2 of areole width. **Epidermal cells** hyaline, long rectangular in longitudinal section, with thick walls above. **Mucilage cells** of aerenchyma and ventral tissue often absent (74 out of 100 specimens examined lacking mucilage cells). **Rhizoids** abundant on wings and costae. **Ventral tissue** solid, except for the presence of 3–4 mucilage canals along costa, often with symbiotic fungi. **Ventral scales** in two rows, usually large, rarely small in size; appendages reniform to almost circular, margins entire or undulate, 0.25–0.48 × 0.4–0.90 mm. **Asexual reproduction** lacking.

Dioicous. **Female carpocephala** with fertilized sporophytes large, conical with obtuse and slightly round apices; with a number of short mucilage canals in aerenchyma; epidermis in 2–4 layers; with stalks reaching 9 cm in length when discharging spores, colorless. **Elaters** quite variable in size and shape, 150–350 μm in length, 12–38 μm in width. **Spores** 65–130 μm in longer diameter.

Habitat: *Conocephalum orientalis* has the largest plant bodies among all Japanese hepatics. In almost all cases, large *Conocephalum* plants that grow at streamside are this species. If thalli are shiny, the size of the air chambers increases toward the center of the thalli, and areolae are larger than 1/2 of the air chamber width, the plant can be definitely identified as *C. orientalis*. The species may become larger in size and forms quite large colonies in slightly shaded places, such as along streams and on seepage slopes of trail banks in forests.

Conocephalum orientalis almost always does not grow directly on rock surfaces without soil. However, there are exceptions; it can grow directly on surfaces

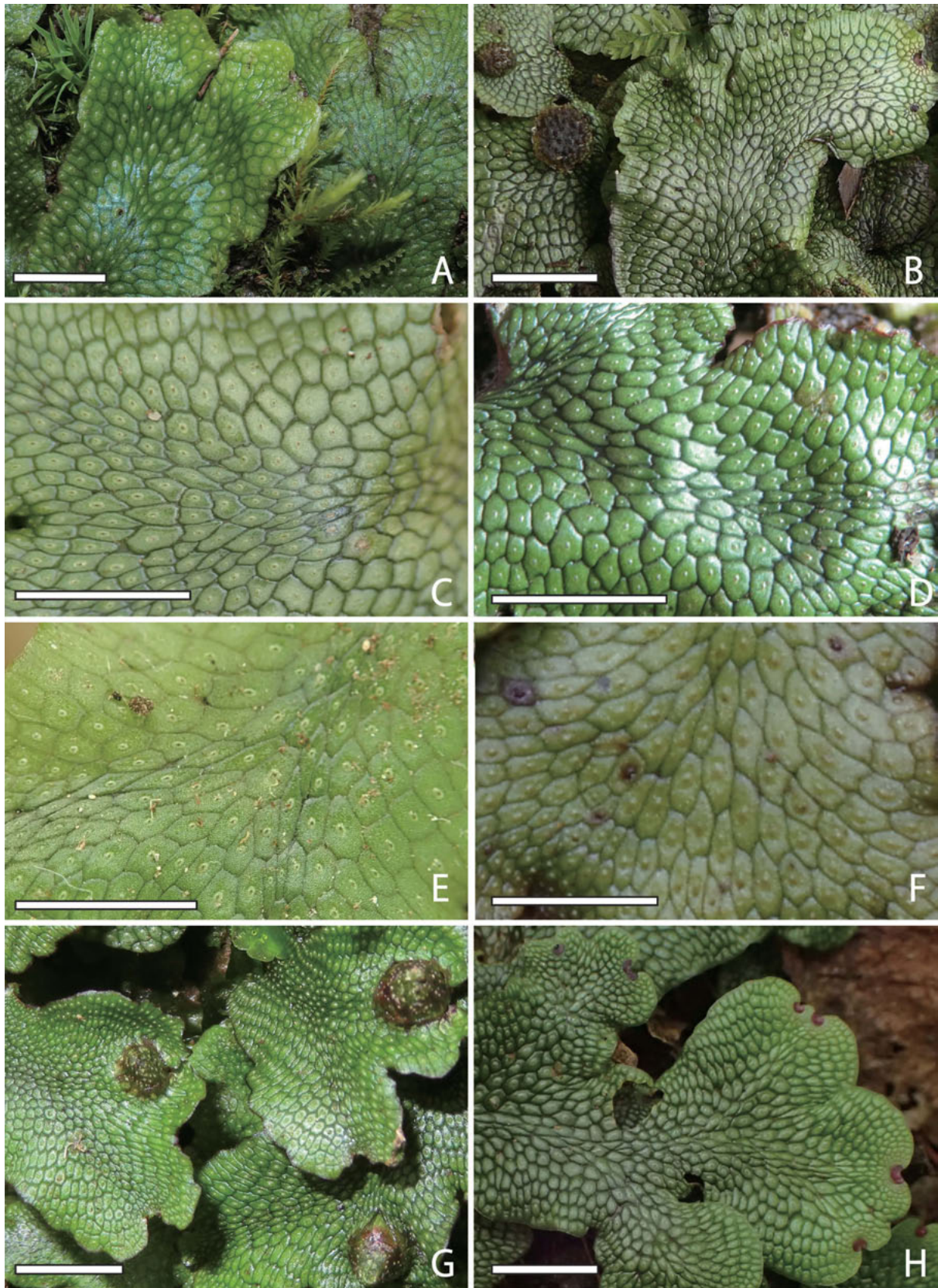


Figure 3. Comparison of areolae among the 4 species of the *Conocephalum conicum/salebrosum* complex. A: *C. orientalis*. B: *C. orientalis* (J3 type). C: *C. purpureorubrum* (FW form). D: *C. purpureorubrum* (FE form). E and F: *C. salebrosum*. G and H: *C. toyotae*. A: Hyogo Pref., Kami-cho, 26 Sept. 2018 (*Akiyama s.n.*). B: Aomori Pref., Hirosaki-shi, 22 Aug. 2017 (*Uchida s.n.*). C: Miyazaki Pref., Nichinan (*Akiyama 26705*). D: Tokyo Metro., Mt. Takao, 4 Dec. 2017 (*Akiyama 25268*). E: Fukuoka Pref., Hiraodai 29 Aug. 2019 (*Akiyama 26704*). F: Hiroshima Pref., Kami-Taishakukyo, 10 July 2017 (*Akiyama 25094*). G: Nagano Pref., Arimine, 30 Aug. 2018 (*Akiyama 25677*). H: Hokkaido Pref., Shari-cho, 8 Sept. 2018 (*Uchida 712*). Scale bars = 5 mm.

of large boulders in places where there is extreme amount of rainfall, such as Yakushima Island and the southern part of Miyazaki Prefecture.

Distribution: Japan [Hokkaido, Honshu, Shikoku, Kyushu, Ryukyu (Amami Isl., Tokunoshima Isl., Okinawa Isl. (only north of Nago-shi)], Taiwan. This is the most populous species among the 4 species of Asian *Conocephalum*, especially in Kinki and Chugoku Districts of Japan. Although previously known only from Japan, it was newly collected during the present surveys at two localities in the central Taiwan (Nantou Co., Xitou, and Yilan Co., Taipingshan). Horikawa (1934) previously reported *Conocephalum conicum* s. lat. from Iriomote Island (Hinai, Mt. Hatoma-mori; Okinawa Prefecture), but there has been no additional report from the island despite a number of subsequent intensive surveys (Isono et al., 1999, p. 100).

Specimens examined: See Appendix.

Note 1 (Mucilage in thallus). Plants grown in good moisture conditions become quite succulent. When such thalli are cut transversely, clear slimy contents (polysaccharides) can be observed flowing abundantly from the cross section of the mucilage canals (Plate 9, H).

Note 2 (Color of underside of thalli). In late autumn, the underside of thalli turn reddish purple and also winter buds are produced at the tip of thalli, which produce new shoots in the next spring. New shoots from winter buds become elongate and form conspicuous heart-shaped lobes. The base of these heart-shaped lobes is more or less colored pale reddish purple.

Note 3 (Variation in odor of plants). Fresh plants of *Conocephalum orientalis* have a strong refreshing odor that can be reminiscent of a deep forest. The composition of volatile components has been studied in detail by Asakawa et al. (1981), Toyota (2000), Miyatake et al. (2018) and others. *Conocephalum orientalis* with rigid and thick thalli in the coastal regions of southwestern Japan (recognized as J2 type in the present paper) was reported to produce large amounts of Methyl cinnamate (the main source of Matsutake odor of *C. toyotae*) when cultured in sealed plastic containers (Toyota et al., 1997; Toyota, 2000; Ab Ghahi et al., 2016; Miyatake et al., 2018).

Note 4 (Variation in plant appearance). The shape and color of thalli vary greatly according to the surrounding environments. When plants grow in darker places, for example, at the entrance of a cave, thalli become quite thin and yellowish in color and

such plants resemble *C. salebrosum*.

Plants with yellowish green color are sometimes found on roadside soils or beside streams in *Cryptomeria japonica* plantations. Ordinary green plants were also commonly present in the vicinity, and their DNA features (*rps4* or *trnH-psbA*) are not different (Akiyama and Odrzykoski 2020). Plants growing at higher altitudes in mountainous areas of central Honshu, Japan (for example, Jigokudani in the northern part of Mts. Yatsugatake, Nagano Prefecture) have very thin thalli and appeared similar to *Conocephalum salebrosum*, but their DNA feature is revealed to be the same of the typical *C. orientalis*.

In contrast, some individuals become hard and yellowish, probably due to tanning of the thalli surface when they formed population at places exposed to direct sunlight, such as concrete retaining walls along a sunlit roadways. In such plants, the ventral scales are dense, and their appendages are large and strongly colored reddish purple, which is reflected in the color of upper side of the thalli. Such plants may be mistaken for the Western Japanese form of *C. purpureorubrum*, but they can be distinguished as *C. orientalis* by noting the glossiness of the thallus surface, larger areolae comparing to air chamber size, and thick walls of the epidermal cells of the thalli.

The underside of the thalli varies in color with the seasons of the year. It is pale green from spring to autumn (with pale reddish purple at the basal part of the midrib), but the entire underside surface of thalli become reddish purple in late autumn and winter. Thus, it is not easy to distinguish *C. orientalis* from *C. purpureorubrum* by the color of underside of thalli alone at those seasons.

In subtropical regions such as the Satsuma Archipelago, Okinawa Archipelago, and Taiwan, the overwintering plants remain green on the underside of the thalli and continue growth even in winter and do not produce winter buds (Fig. 4, A, B).

Note 5 (Ecological form, J2 type). Along the Pacific coast from the Kinki District to the western Japan (see Appendix for distribution), when growing in sunny and dry conditions, the plants are very thick in texture with conspicuous wavy margins. Such an ecotype was first reported by Toyota et al. (1997) and referred to as "Chemotype II". This type is recognized as J2 type of *Conocephalum orientalis* in this paper.

Note 6 (Ecological form, J3 type). In Hokkaido and Tohoku Districts, as well as Ibaraki and Hyogo Prefectures (see Appendix for distribution), there are plants with broad and matt thalli of a blackish

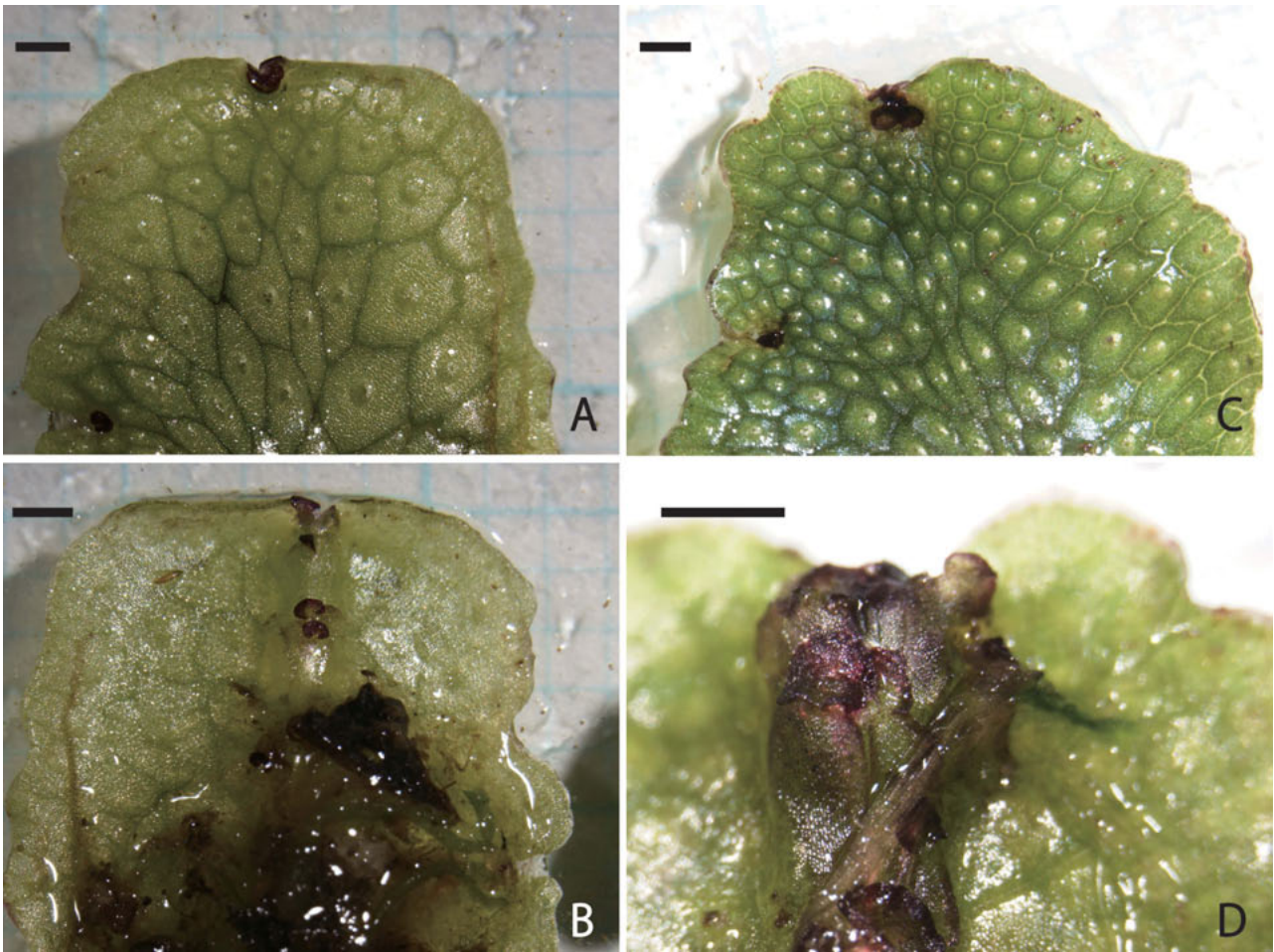


Figure 4. *Conocephalum orientalis*. Plants without winter buds (Tokunoshima Island, Akiyama 25908; A and B), and those with winter buds (Amami-Oshima Island, Arangachi Fall, Akiyama 24421; C and D). Scale bars = 1 mm.

yellow-green color. The grooves between air chambers (areolae) are wide and blackish-green in color. This form is tentatively named as “J3 type” hereafter. The J3 type is more common than the usual *Conocephalum orientalis* in the mountain areas in Hokkaido and the northern Tohoku District (Mr. Uchida, personal communication). Another good feature of the J3 type is the color of the underside of the wide thalli, which is tinged orange to reddish-purple even in summer (Plate 2, H–L).

The J3 type of *Conocephalum orientalis* is sometimes difficult to distinguish from the Eastern Japanese form of *C. purpureorubrum*, because they share a similar appearance, such as the matt and yellowish green color of the upper surface of the thallus, reddish purple color of the lower surface of the thalli even in summer, and thick walls of upper epidermal cells of the thalli. The larger areolae (1/2 or more of the width of the air chamber) compared to those of Eastern Japanese form *C. purpureorubrum* (less than 1/2) can be a useful feature to separate these

two species.

Note 7 (Ecological form, small plants). There are plants of *Conocephalum orientalis* with smaller thalli, which look similar to *C. toyotae*. They have much narrower areole (air chamber) than usual plants even at the central portions along the costa. Such plants have been found at lowlands, such as Nambu-cho, Yamanashi Prefecture, Kamigori-cho, Hyogo Prefecture, Yakushima Island and Tokunoshima Island, Kagoshima Prefecture, and Kunigami Village, Okinawa Prefecture. Especially in Yakushima Island, such smaller plants prevail along streams at lower elevations, and larger, normal plants are restricted to the higher elevations. Based on preliminary results using *psbA-trnH* sequences, there is a slight genetic differentiation between the two types.

Note 8 (Plants without winter buds). In Amami-Oshima and Tokunoshima Islands (Kagoshima Prefecture), a different type of plants is commonly found. One of the characteristic features of such plants is the absence of winter buds at the apical parts

of the thallus lobes, even in winter season (Fig. 4). Previous study based on allozymes (Isono et al., 1999) reported unique alleles from these local populations. Plants growing in subtropical regions, such as Ryukyu Archipelago and Taiwan, also do not produce winter buds and continue their growth even in winter. Their DNA markers (*rbcL* and *rps4*), however, do not differ from the typical ones.

Note 9 (*Conocephalum* used as human food materials). Some Japanese bryologists cook whole thallus of *Conocephalum orientalis* in heated oil and eat them as if they were potato chips. The unique aroma is extinguished by heating, and the taste is similar to that of dried seaweed laver, “nori”.

2. *Conocephalum purpureorubrum* H. Akiyama, n. sp.

Figs. 2 (D, E), 3 (C, D), 5 (A, D), 6 (A–D), Plates 3 (A–J), 4 (A–I), 8 (E–L), 10 (B)

Protologue: Upper surfaces of thalli matt and yellowish green, or slightly shiny and blackish green. Upper epidermal cells of thalli with thin or thick walls. Lower surface of thalli reddish purple even in summer, with dense rhizoids.

Type: JAPAN, Oita Prefecture, Saiki-shi, Honjyo, Inoue, 70 m elev., 34.943661° N, 131.743191° E, 13 March 2018, *H. Akiyama 25427* (holotype HYO, isotypes HIRO, NICH, TNS).

Previous names: *Conocephalum conicum* FS type (Akiyama and Hiraoka 1994a, b). *Conocephalum conicum* F type (Kim et al., 1996, 2001; Akiyama et al., 1998; Miwa et al., 2005; Akiyama, 2006, 2014; Ludwiczuk et al., 2013; Miyatake et al., 2018), *Conocephalum conicum* KYT and YFS types (Kim et al., 1996, 2001).

Japanese Name: Urabeni-jyagoke.

Etymology: Species epithet is descriptive of the reddish purple color of the lower surface of thalli even in summer season.

Description: **Plants** perennial, small to large, with slight forest scent, quite rarely with Matsutake mushroom scent, dull and yellowish green (Western Japanese form) or slightly shiny and blackish green (Eastern Japanese form), 6–16 mm wide, to 15 cm long; undersurface reddish purple even in summer seasons. **Thalli** relatively thin, except along the costa, flat, margins plane; surfaces coarsely and regularly areolate with air chambers, with deeply impressed lines of grooves between air chambers; mucilage canals well developed, 3–4 in numbers; with 2–3 (–4) rows of unistratose portion at thallus margins.

Areole hexagonal, becoming smaller towards the margins, narrower and slightly longer along costa, with a pale, more or less elevated pore in the center. **Pores** small, mostly round. **Areolae** small, occupying ca. 1/3 of the width of areole (air chamber) (Plate 3, I, J). **Epidermal cells** long rectangular in section, with upper cells with thin (Western Japanese form) or thick walls (Eastern Japanese form). **Mucilage cells** of aerenchyma and ventral tissue often present (20 lacking out of 43 specimens examined). **Rhizoids** abundant on wings and costae. **Ventral tissues** solid, except for the presence of 3–4 mucilage canals, often with symbiotic fungi. **Ventral scales** in two rows, usually large, rarely small in size; appendages reniform to almost circular, margins entire or undulate, 0.28–0.80 × 0.30–1.10 mm. **Asexual reproduction** lacking.

Dioicous. **Female carpocephala** with fertilized sporophytes medium in sizes, conical with obtuse apices (Plate 7, B); with a number of short mucilage canals in aerenchyma; epidermis in 1–2 (–3) layers (Western Japanese form) or (1–) 2–3 layers (Eastern Japanese form); with stalks 3–6 cm in length when discharging spores, colorless. **Elaters** variable in size and shape, 100–350 μm in length, 10–38 μm in width. **Spores** 70–110 μm in longer diameter.

Habitat: *Conocephalum purpureorubrum* can grow in drier habitats than *C. orientalis*, but tends to grow in more humid habitats when it grows with *C. salebrosum*. As for how these three species separate their microhabitats when they grow sympatrically, a case study at Mt. Takao (Tokyo Metro.) is useful (Akiyama and Hiraoka, 1994a).

Distribution: Southern China, South Korea, Taiwan, Japan (Honshu, Shikoku, Kyushu, Okinawa). The northern limit of *Conocephalum purpureorubrum* in Japan is the central part of Fukushima Prefecture in Honshu, and the southern limit is the northern part of Okinawa Island (Yasuda, Kunigami Village). It is almost absent from the Japan Sea side of Honshu (Hokuriku, Kinki and Chugoku Dist.).

Note 1 (Variation of plant appearance). When growing in a darker place such as along small streams in dense *Cryptomeria japonica* plantations [e.g., Aikawa, Tokushima Prefecture and Nagasaka, Nabari-shi, Mie Prefecture], thalli of *Conocephalum purpureorubrum* become smaller and thinner than usual, and it is rather difficult to distinguish it from poorly developed *C. salebrosum*.

Note 2 (Slower regrowth). Regrowth from winter buds in early spring of *Conocephalum*



Figure 5. Difference in plant appearance of the 4 species of *Conocephalum* in mixed populations. A: Western Japanese form of *C. purpureorubrum* (FW) and *C. salebrosum* (S), Mie Pref., Akame. B: *C. orientalis* (J) and *C. salebrosum* (S), Hiroshima Pref., Taishaku-kyo. C: *C. toyotae* (R) and *C. salebrosum* (S), Toyama Pref., Arimine. D: Western Japanese form of *C. purpureorubrum* (FW) and *C. orientalis* (J), Miyazaki Pref., Kobuse. Scale bar = 1 cm.

purpureorubrum occurs about half a month later than the other 3 species in central Japan. This difference is maintained even when plants are cultivated in the same environment, and thus some underlying genetic background is expected for such difference in the onset of growth.

Note 3 (Western and Eastern Japanese forms). Among the Japanese plants (including a few Taiwanese plants), for which I was able to observe by living conditions, there are two distinct forms in *Conocephalum purpureorubrum*: One is matt, yellowish green thalli of plants growing in the western part of Japan, and the other is slightly shiny, blackish green thalli of plants growing in the eastern part Japan. The Taiwanese plants are similar to the eastern Japanese form in their slightly shiny appearance.

Based on allozyme analyses, such a difference has already been noted in *Conocephalum purpureorubrum* (Akiyama and Hiraoka, 1994a). Kim et al. (1996)

further suggested that there was an additional form from the Yakiyama population (Fukuoka Pref., western Japan). However, I was unable to distinguish it from the usual Western Japanese form, even using highly variable *psbA-trnH* sequences.

All the studied samples of *Conocephalum purpureorubrum* form a single, well supported monophyletic clade in the analyses using *rbcL* and/or *rps4* sequences (Akiyama and Odrzykoski 2020). But, using the more variable *psbA-trnH* (including hyper repeated portions), two forms can be recognized. They are referred as the Western Japanese form (FW) and the Eastern Japanese form (FE) hereafter. These two forms also can be distinguished by their morphological features as described above and in the “Key to the two forms of *C. purpureorubrum*” below. Spore shape and size do not differ between them. Although *C. purpureorubrum* has been reported from a wide area of eastern Asia (Odrzykoski et al. 1991;

Miwa et al. 2009), I have not been able to study plants outside of Japan and Taiwan in this survey. Further study of the samples collected from all over its wide distributional range in East Asia is needed to fully understand the variability.

Key to the two forms of *C. purpureorubrum*

1. Thalli distinctly matt, yellowish green. Upper epidermal cells of thalli with thin walls. Distributed in western part of Japan (from western part of Aichi Pref. to north of Okinawa Island).
.....Western Japanese form (FW)
1. Thalli slightly shiny, blackish green. Upper epidermal cells of thalli with thick walls. Distributed in eastern Japan (from Fukushima Pref. to eastern part of Aichi Pref.) and Taiwan.
.....Eastern Japanese form (FE)

Western Japanese form (FW)

Figs. 3 (C), 5 (A, D), 6 (A, B), Plates 3 (A–J), 8 (I–L)

Japanese name: Saigoku-urabeni-jyagoke

Description: Thalli broad and rather thin, matt, yellowish green. Upper epidermis of thalli with thin walls. Underside of thalli not shiny. Underside of younger thalli mostly reddish purple in color, rarely green but soon turning into reddish purple in late summer.

Habitat: The Western Japanese form of *Conocephalum purpureorubrum* usually grows on soil away from streams. It sometimes grows mixed with *C. orientalis* (e.g. Akame Gorge, Nara Prefecture; Obtuse Waterfall, Miyazaki Prefecture; Todoroki Waterfalls, Tokushima Prefecture), but the latter can be distinguished by the distinctive luster of the thalli with green color and larger size of female receptacles, if they are present.

Distribution: Japan; Honshu (from western Aichi Pref. to Yamaguchi Pref.), Shikoku, Kyushu, and northern Okinawa Island (Yanbaru, mountain areas of Kunigami District).

Specimens examined: See Appendix.

Note 1 (Black strands on dorsal surface of thalli). Blackish green strands are sometimes present in the middle of the dorsal surface of plants because of the deep reddish purple color at the center of the underside and ventral scales. The plant illustrated by Akiyama (2014; Fig. 4, erroneously treated as “*Conocephalum salebrosum*” there) is a good example.

Note 2 (Difference from *Conocephalum orientalis*

J3 type). Western Japanese form rarely looks similar to the J3 type of *C. orientalis* (Fig. 2 B, C). Smaller size of areolae (air pores and surrounding transparent part) and thin walls of upper epidermal cells of thalli in the Western Japanese form can be used to separate these two species.

Eastern Japanese form (FE)

Figs. 3 (D), 6 (C, D), Plates 4 (A–I), 8 (E–H)

Japanese name: Azuma-urabeni-jyagoke

Description: Plants about as wide as those of *Conocephalum orientalis*, but somewhat thinner; surfaces of thalli slightly shiny and blackish green. Upper epidermis of thalli with thick walls. Grooves between air chambers are rather wide and deeply depressed. Underside of thalli reddish purple throughout the year, and the grooves between air chambers appearing darker in color when viewed from the surface.

Habitat: Though sometimes growing along streams, it usually forms population on soil of valley slopes far from the water.

Distribution: Japan; Honshu (from central part of Fukushima Prefecture to the eastern part of Aichi Prefecture). Taiwan.

Specimens examined: See Appendix.

Note 1 (Variation of plant color). Plants of the Eastern Japanese form of *Conocephalum purpureorubrum* rarely become more or less matt and yellowish green, as in the Western Japanese form when growing in drier habitats.

Note 2 (Color of grooves). Deep and blackish grooves between air chambers are not found in the Japanese *C. salebrosum*, and this feature is thus useful to distinguish the two species in the Kanto District, where both species often grow in close proximity.

3. *Conocephalum salebrosum* Szweyk., Buczk. & Odrzyk., Pl. Syst. Evol. 253: 146 (2005).

Figs. 2 (F, G), 3 (E, F), 5 (A, C), Plates 5 (A–K), 8 (M–P), 11 (A)

Type: POLAND, Western Carpathians, Tatry Mountains, Kościeliska Valley, Wąwóz Kraków gully; on moist humus covering shady calcareous rocks, alt. 1050 m; 26 April 2002, coll. K. Buczkowska and A. Baczkiewicz s.n. (holotype POZW, not seen).

Previous names: *Conocephalum conicum* S type (Szweykowski et al., 1981; Odrzykoski and Szweykowski, 1991; Akiyama et al., 1998; Kim et al., 2001; Miwa et al., 2005), *Conocephalum conicum* T type (Akiyama and Hiraoka, 1994a, b; Kim et al.,

2001).

Japanese name: Takao-jiyagoke.

Etymology: Species epithet “*salebrosum*” is derived from the uneven surface of the upper epidermis of thalli, comparing to those with quite flat surface of *C. conicum* s. str. (formerly known as L type) in Europe (Szweykowski et al., 2005).

Description (Mainly based on Japanese and Taiwanese plants): **Plants** perennial, small to medium, matt, pale yellowish green, often becoming much smaller and thinner when growing on limestone walls or shaded calcicolous soil; dorsal blackish lines along costa absent; ventral surfaces pale green, rarely slightly shiny and tinged with reddish purple when growing at higher elevations in Taiwan; with slightly musty scent, often odorless when growing on drier substrates. **Thalli** 6–15 mm wide, to 10 cm length, thin, flat, margins plane; surfaces coarsely and regularly areolate with air chambers, with shallow grooves; mucilage canals well developed, more than 3

in number; with 2–3 (–4) rows of unistratose portion at thallus margins. **Areole** not becoming smaller towards the thallus margin. **Pores** small, mostly round. **Areolae** small, occupying 1/3 of areole width. **Epidermal cells** rectangular, with thin upper walls, becoming smaller towards the central portion along costae. **Mucilage cells** of aerenchyma and ventral tissue almost always present, even in older portion of thalli (present in 42 of 44 samples examined). **Ventral tissues** solid, except for the presence of 3–5 mucilage canals along costa, often with symbiotic fungi. **Rhizoids** often few, mostly restricted to central portion along costae. **Ventral scales** in two rows mostly small in size; appendages small, rarely large, almost circular to reniform, margins entire or undulate, 0.25–0.60 × 0.35–1.10 mm. **Asexual reproduction** lacking in Japan.

Dioicous. **Female carpocephala** with fertilized sporophytes medium in size with a number of short mucilage canals in aerenchyma; sharply pointed



Figure 6. Western Japanese form (Miyazaki Pref., Hinokage-cho, Matsumoto s.n.: A and B) and Eastern Japanese form (Gunma Pref., Naganohara-machi, Nakazawa 3398; C and D) of *Conocephalum purpureorubrum*. Scale bars = 1 cm.

(Plate 7, D) for Japanese plants but with obtuse tops in Taiwanese plants (refer Note 3 below); epidermis in 1–2 layers; with stalks 3–4 cm in length when discharging spores, colorless. **Elaters** mostly short and thick, 85–250 µm in length, 10–45 µm in width. **Spores** smaller in size than the other three species of *Conocephalum* in Japan, 60–100 µm in longer diameter.

Habitat: *Conocephalum salebrosum* is distributed nationwide except for Kagoshima and Okinawa Pref., but in western Japan it is almost always restricted to limestone areas, especially around cave entrances where cool and moist air regularly blows from the caves throughout the year. This may have something to do with the fact that *C. salebrosum* is distributed mainly at higher elevations and higher latitudes in the world.

Both mucilage canals along costal regions and mucilage cells in wings are much more developed and more numerous than the other 3 species in Japan. Since *Conocephalum salebrosum* often grows at basal parts of vertical limestone cliffs, the presence of such structures containing a lot of mucilage may contribute to desiccation resistance in such dry habitats.

Distribution: Pan-boreal, widely distributed at higher latitudes in the northern hemisphere. In Japan, *C. salebrosum* has been found from Rishiri Island, Hokkaido Prefecture to Hitoyoshi City, Kumamoto Prefecture. Among our collections in East Asia, it has been collected from higher elevations; for example above 2000 m in elev. in central Taiwan and Yunnan, China.

Szweykowski et al. (2005) cited a number of specimens of *Conocephalum salebrosum* from Asia, including Japan. Their identification was, however, based on morphology. Judging from a re-examination of the specimens they cited, their identification is often erroneous because the differences between 1) *C. salebrosum* and 2) *C. orientalis* or *O. purpureorubrum* were not clearly recognized at that time.

Specimens examined: See Appendix.

Note 1 (Comparison between European and Asian populations). In Europe, where *Conocephalum salebrosum* was first recognized as S (smaller) type of *C. conicum s. lat.*, plants that were narrower, less shiny, and had more uneven surfaces of thalli than *C. conicum s. str.* [= L (larger) type] were thought to be characteristic of *C. salebrosum*.

Plants of *Conocephalum salebrosum* from Japan and Taiwan and those from other parts of Europe, America, and Asia share the same DNA sequences

and cannot be distinguished (Akiyama and Odrzykoski 2020), but the extent of morphological differentiation among them has not been examined sufficiently. For example, the shapes of fertilized female carpocephala were different between Japanese plants and the others, as described above. Since *C. salebrosum* is a pan-boreal, globally distributed species of the northern hemisphere, it is expected to have a high degree of genetic and morphological diversity within its distribution areas. Plants identified as *C. salebrosum* (for example, Iqbal et al. 2011) in some local monographs of northern India suggest that probably there is another taxon with different morphological features.

The lower structure of the air pores on the female carpocephala is used as one of the features to distinguish *C. conicum s. str.* from *C. salebrosum* (Szweykowski et al., 2005). However, though this structure is very difficult to observe, as far as I have been able to confirm, it is not stable even within a species among the 4 Japanese species (Akiyama and Odrzykoski, 2020).

Note 2 (Variation in thickness of thallus). Especially when growing on vertical limestone cliffs, thalli of *Conocephalum salebrosum* often become very thin, like a paper. Similarly, in damp and dark conditions (e.g., a little inside the entrance to a limestone cave), thalli also become smaller and thinner. Good examples are populations under the Onbashi of the Taishakukyo ravine (Hiroshima Prefecture), the Ubusune-no-hokora, Hiraodai Plateau (Fukuoka Prefecture) in Japan.

Note 3 (Sharp apices of female carpocephala). Female carpocephala are rare in this species; so far, they have been found at Gokoku Shrine, Ibaraki Pref., Mt. Takao, Tokyo Metro., Arimine Lake, Toyama Pref., Ina-shi and Mt. Nyugasa, Nagano Pref., and Taishakukyo, Hiroshima Pref. in Japan. Sharply pointed apices of developed carpocephala are unique among *Conocephalum* species, which are bluntly round in *C. orientalis*, helmet-shaped in *C. toyotae*, and narrowly round with slightly flattened tips in *C. purpureorubrum*. Therefore, carpocephala shape can be used as one of the good features to distinguish *C. salebrosum* from the other 3 species, even if they are rarely produced.

Unfortunately, Szweykowski et al. (2005), who studied the morphology of the European *C. salebrosum* in detail, gave no description relating to the shape of female carpocephala. Examining the photographs of living plants and dried herbarium

specimens, they are blunt-headed, and none of them have sharply pointed apices as in the Japanese plants. A single specimen of *C. salebrosum* from Ren'ai township, Mt. Hehuanshan, Taiwan (*H. Akiyama 25616*; HYO) had blunt apices on its carpocephala.

Note 4 (Resemblance to *Wiesnerella* in sterile condition). Sterile plants of *Conocephalum salebrosum* without male or female sexual organs can easily be mistaken for *Wiesnerella denudata* (Mitt.) Steph. in the field. However, they can be distinguished by the difference in glossiness of thallus surface, difference in the shape and color of ventral scales (especially in the appendages). In addition, they have a different scent of thalli when crushed between fingers.

4. *Conocephalum toyotae* H. Akiyama, n. sp.

Figs. 2 (H, I), 3 (G, H), 5 (C), 7 (A, B), Plates 6 (A–J), 8 (Q–S), 11 (B).

Protologue: Air chambers almost similar in size all over the thallus. Upper epidermal cells large in thickness in cross sections with thin outer walls. Mucilage canals absent and almost always no mucilage cells developed. Female carpocephala with fertilized sporophytes helmet-shaped, with round apices.

TYPE: JAPAN, Hyogo Pref., Yabu-shi, Oya-cho, Yokoiki valley, 700 m elev., 35.325840° N, 134.544164° E, 30 March, 2021, *H. Akiyama 26610* (holotype in HYO, isotypes distributed as exiccatae “Bryophytes of Asia” from HIRO)

Previous names: *Conocephalum conicum* R type (Miwa et al., 2010; Miyatake et al., 2018; Akiyama and Odrzykoski, 2020). *Conocephalum conicum* Chemotype III (Toyota et al., 1997; Toyota, 2000; Kim et al., 2001).

Japanese name: Matsutake-jyagoke

Etymology: Species epithet honors Prof. Dr. Masao Toyota, who first recognized and reported the plants with strong scent of methyl cinnamate contents. Saito (1998) proposed a new name, *Conocephalum fragrans*, but it is a *nomen nudum*, lacking description.

Description: **Plants** with distinct scent of methyl cinnamate (odor of Matsutake mushroom), which can be easily lost when dried; slightly shiny, blackish green; underside of thalli usually not becoming reddish purple except for over-winter portions. **Thalli** 8–15 mm wide, to 10 cm length, thin except along costa, flat, margins plane; surfaces coarsely and regularly areolate with air chambers, with deep grooves (Fig. 3, G–H, Plate 8, Q–S); with 1–2 (–3)

rows of unistratose portion at margins. **Areole** (air chamber) small but not becoming narrower and longer at central parts along costae, thus giving a unique appearance of uniform areole size throughout the thalli; with deep grooves between air chambers. **Areolae** large, mostly occupying 1/2 of width of areole. **Epidermal cells** short rectangular, more or less bulging, thick in cross section, with thin upper walls. **Mucilage cells** of aerenchyma and ventral tissue almost always absent (present in a single specimen out of 30 examined). **Ventral tissues** solid, without mucilage canals. **Rhizoids** dense and abundant on wings and costa of ventral surface. **Ventral scales** arranged in two rows, often small, sometimes large in size; appendages reniform to almost circular, margins entire or undulate, 0.27–0.80 × 0.36–0.80 mm. **Asexual reproduction** lacking.

Dioicous. **Female carpocephala** with fertilized sporophytes helmet-shaped with round apices; with a few, short mucilage canals in aerenchyma; epidermis in 2 (–3) layers; with stalks 3–6 cm in length when discharging spores, slightly greenish. **Elaters** variable in size and shape, 100–300 μm in length, 8–30 μm in width. **Spores** 70–120 μm in longer diameter.

Habitat: *Conocephalum toyotae* often grows in disturbed habitats, such as close to human settlements and roadside banks at forest edges. Though it can form pure colonies, it often grows as small patches within large populations of *C. orientalis*.

Distribution: USSR (Sakhalin; Miwa et al. 2014 as R type), Japan (Hokkaido, Honshu, Shikoku). Probably widely distributed in Far East Asia, especially at higher latitudes.

Specimens examined: See Appendix.

Note 1 (Scent of Matsutake mushroom). *Conocephalum toyotae* has a strong odor of Matsutake mushroom (mainly caused by methyl cinnamate), and this is one of the most characteristic features of the species, and with a fresh plant in your hands, it will not be mistaken for any of the other 3 Japanese species. If it does not smell so much, especially in autumn and winter, check the distinct scent by rubbing a small amount of thalli between your fingers.

Conocephalum conicum A type (including C type) and *C. salebrosum* from North America (Odrzykoski and Szweykowski, 1991; Akiyama and Odrzykoski, 2020) have a large amount of methyl cinnamate as a volatile component and have been reported to have a strong scent of Matsutake mushroom, as in the case of *C. toyotae* (Ludwiczuk et al. 2013). Unfortunately, I did not have a chance to examine living fresh plants

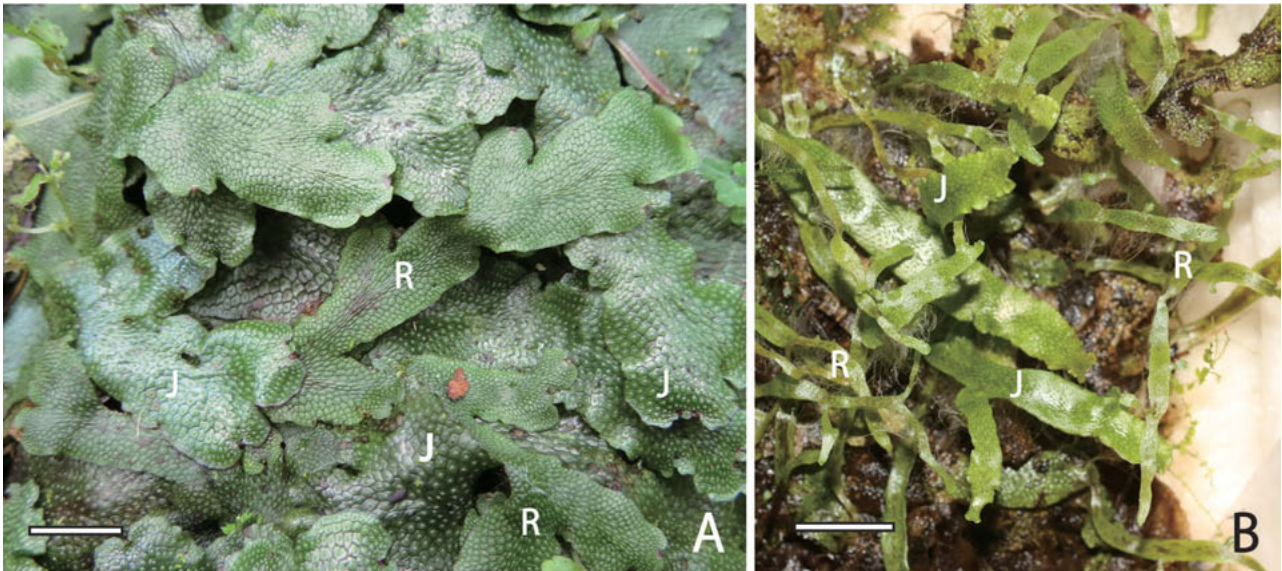


Figure 7. Mixed population (Tokushima Pref., Katsuura-machi) of *Conocephalum toyotae* (R) with *C. orientalis* (J). A: Mixed plants in the field (17 Nov. 2018). B: Spindly growth of both *C. toyotae* (R) and *C. orientalis* grown in a sealed plastic cup cultivated over three months. Note that *C. toyotae* has much narrower spindly shoots than *C. orientalis*. Scale bars = 1 cm.

of the A type, so I cannot confirm whether they have a similar smell of *T. toyotae* or not. Molecular phylogenetic analysis indicates that *C. conicum* A type and *C. toyotae* are not closely related to each other (Akiyama and Odrzykoski, 2020).

Note 2 (Variation in plant appearance). Thalli of *Conocephalum toyotae* are blackish green in color and somewhat shiny. They are narrower than those of *C. orientalis*, which often form mixed populations with *C. toyotae*. The underside of the thalli of *C. toyotae* is green to reddish purple, but becomes deep reddish purple in late autumn and winter. Air chambers are almost all the same size and do not become larger towards the central parts along costae. Since areolae occupy more than 1/2 the width of the air chambers in *C. toyotae*, it gives the appearance that white areolae are distributed densely throughout the thallus surfaces in this species. Both male and female plants seem to be abundant in Japan, and female carpocephala with fertilized sporophytes are often encountered.

Conocephalum toyotae is rather stenotypic and shows little variation in morphological features comparing to the other 3 Japanese species. Genetic differentiation is also the least among the 4 species in Japan (Akiyama and Odrzykoski, 2020).

Note 3 (Absence of mucilage canals). Mucilage canals, which are well developed in the other 3 species of *Conocephalum* in Japan, are not differentiated at all in *C. toyotae*. Fungi that coexist within the thalli of *C. conicum/salebrosus* complex tend to settle

in the mucilage canals and their surrounding cells, suggesting that *C. toyotae* might have a different life strategy in terms of symbiosis to the other 3 species.

Note 4 (Distribution pattern). *Conocephalum toyotae* was first reported from trailsides banks in moist and shaded *Cryptomeria japonica* plantation in a deep ravine in Tokushima Prefecture, Shikoku District (Toyota et al., 1997; Toyota, 2000). The present study reveals, however, it is mainly distributed on the Japan Sea side of Honshu District (from Niigata Prefecture to Shimane Prefecture) and sporadically in Shikoku District (Plate 11, B), a distribution pattern similar to that of the moss *Hypnum cupressiforme* Hedw. (Ando 1987). Such a distribution pattern is believed to be correlated to the Japan Sea climate (Suzuki 1962). Judging from the larger epidermal cells with thin outer walls as well as the absence of mucilage canals and mucilage cells in aerenchyma and ventral tissues, *C. toyotae* may be vulnerable to drought. This may be a reason why *C. toyotae* is restricted to areas with the Japan Sea climate is developed, where snow-cover during winter aids survival of the species.

Note 5 (Succulent shoots). When a sample of a mixed population of *Conocephalum toyotae* and *C. orientalis* is grown in the same over-humid environment (e.g., in a sealed plastic case), *C. orientalis* produces wide, ribbon-like long succulent shoots (Maybrook, 1914), while they are quite narrow in *C. toyotae* (Fig. 7, B). This difference is probably due to the different size of the meristematic cells at

the tip of their thalli. It was reported that the volatile components change drastically in such succulent plants in artificial conditions and no longer methyl cinnamate is produced in *C. toyotae* (Ab Ghahi et al., 2016; Miyatake et al., 2018).

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Appendix. Examined specimens of 4 species of the *Conocephalum conicum/salebrosus* complex in Japan and Taiwan. All specimens are deposited at the cryptogamic herbarium of Museum of Nature and Human Activities, Hyogo (HYO). Identities of all specimens are confirmed by molecular marker (*rps4* or *psbA-trnH* of chloroplast genome) and/or morphological observation of living plants including specific scent caused by volatile components.

***Conocephalum orientalis* H. Akiyama**

JAPAN.

Hokkaido Pref.: Rishirifuji-cho, Oniwaki, Mt. Rishiri, 600–650 m elev., 45.165644° N, 141.256836° E, 8 Sept. 2018, *A. Uchida 20180046 (711)*; Kuromatsunai-cho, Utasai Forest Park, 50 m elev., 42.652778° N, 140.310278° E, 16 Sept. 2018, *Y. Oppata 3702*; Urahoro-cho, Atsunai, 80–110 m elev., 42.899850° N, 143.781506° E, 28 April 2018, *A. Uchida 20180008 (695)*; *ibid.*, Higashiyama-cho, 30–40 m elev., 42.80896° N, 143.67161° E, 28 April 2018, *A. Uchida 2018004 (688)*; *ibid.*, Rushin, 210–290 m elev., 43.000753° N, 143.680878° E, *A. Uchida 2018007 (693)*; Shintotsukawa-cho, 120–130 m elev., 43.536733° N, 141.787661° E, 21 July 2019, *A. Uchida 20190009*; Uryu-cho, 610–630 m elev., 43.871111° N, 141.636389° E, 22 July 2019, *A. Uchida 20190043 (759)*; Shiraoi-cho, Takeura, 37 m elev., 42.5036° N, 141.2315° E, 9 Apr. 2021, *K. Izumida 065*; Tomakomai-shi, Midorigaoka park, 222 m elev., 42.660278° N, 141.590833° E, 23 Apr. 2020, *K. Izumida 025 and 026*.

Aomori Pref.: Hirosaki-shi, Sakamoto, Mt. Kudoji, 40.531154° N, 140.423577° E, 450–550 m elev., 20 Aug. 2017, *A. Uchida 20170029 (Hirosaki-2)*; *ibid.*, Osuke, 40.566583° N, 140.339556° E, 125–175 m elev., 22 Aug. 2017, *A. Uchida 20170032 (Hirosaki-5)*; *ibid.*, Hirosaki Park, 38 m elev., 40.6097° N, 140.4646° E, 11 Sept. 2018, *M. Sawada 20180911-1*; Kuroishi-shi, *M. Uzawa 4124*; Towada-shi, Tsutanomori, 470 m elev., 40.595967° N, 140.952766° E, 29 Aug. 2014, *H. Akiyama 23836*; *ibid.*, 40.595278° N, 140.952500° E, 1 June 2018, *T. Kano 5918*; *ibid.*, Okuse, 40.589444° N, 140.958611° E, 1 June 2018, *T. Saeki 4503*; *ibid.*, Tsuta-onsen, 480 m elev., 19 Oct. 2018, *T. Yamaguchi 39375*; Aomori-shi, Mt. Chobosan, 28 Oct. 2017, *A. Washimi s.n.*; Fukaura-machi, Osedo, 118 m elev., 40.733° N, 140.083° E, 29 April 2018, *M. Sawada 20180429-1*; Sai-mura, Nuidoshiyama, 579 m elev., 41.323293° N, 140.846722° E, 21 Sept. 2018, *M. Sawada 20180921*; Mutsu-shi, Ohminato, Suigenchi Park, 42 m elev., 41.2579° N, 141.1401° E, 22 May 2018, *M. Sawada 20180524-1*.

Iwate Pref.: Ichinoseki-shi, Higashiyama-machi, Matukawa, Takinosawa, 38.978833°N, 141.238444°E, 1 Oct. 2019, *M. Uzawa 5203*.

Miyagi Pref.: Sendai-shi, Aoba-ku, Kamiaiko, 250 m elev., 38.273397° N, 140.692930° E, 15 Nov. 2019, *H. Ikeda 702*; *ibid.*, Taihaku-ku, Moniwa, Sahoyamanishi, 63 m elev.,

38.2379° N, 140.8169° E, 17 Aug. 2019, *Y. Utsumi 190817-1*, 2 and 3.

Akita Pref.: Oga-shi, Kitaurashinzan Mizukuizawa, 160 m elev., 39.9294° N, 139.7670° E, 30 Sept. 2019, *Y. Asakawa s.n.*; *ibid.*, Kitaura, 250 m elev., 39.9272° N, 139.7530° E, 24 Oct. 2019, *H. Ikeda 700*; Noshiro-shi, Hutatsui-machi, Tashiro, 170 m elev., 40.081372° N, 140.251783° E, 22 Oct. 2019, *H. Ikeda 699*; Yurihonjyo-shi, Chokai-machi, Sarukura, 39.176553° N, 140.160683° E, 4 Oct. 2018, *A. Tanaka 20181104-1*; Nikaho-shi, Sakigata-machi, in front of a visitor center, on the way to Shishigahana moor, 4 May, 2019, *H. Fujii s.n.*; Higashinaruse-mura, Iwaigawa, Kakkyogawa National Forest, Tensho Fall, 440 m elev., 39.1790° N, 140.7528° E, 18 Aug. 2020, *S. Sato, S.S.TSF 3*; Yuzawa-shi, Koyasukyo, 269 m elev., 39.009722° N, 140.661111° E, 04 July 2020, *M. Chishiki s.n.*

Yamagata Pref.: Oe-machi, Aterasawa, Hashigami, 195 m elev., 38.3871° N, 140.2114° E, 16 Aug. 2019, *H. Fujii 20190816A, B and C*; Yonezawa-shi, Shirabu-onsen, 1130 m elev., 37.77144° N, 140.132267° E, 23 Sept. 2019, *H. Shirasaki 26636*.

Fukushima Pref.: Koriyama-shi, Konan-cho, Hamaji, 624 m elev., 37.440266° N, 140.185729° E, 20 Sept. 2018, *N. Morita 6*; Tamura-shi, Tokiwamachi, Wasezawa, Mt. Otakineyama, 800 m elev., 37.356667° N, 140.685556° E, 25 Oct. 2020, *S. Nemoto 1028*.

Ibaraki Pref.: Bando-shi, *M. Uzawa 4144*; Kitaibaragi-shi, Hanakawa-cho, Hanazono Shrine, 410 m elev., 36.860525° N, 140.628152° E, 9 March 2019, *H. Akiyama 25951*; Sakuragawa-shi, Motoki, Amabiki Shrine, 190 m elev., 36.3307° N, 140.1216° E, 10 March 2019, *H. Akiyama 25974*; Kuji-gun, Taishi-cho, Sanuki, Hatuhara river, 36.843333°N, 140.264167°E, 28 Sept. 2019, *M. Uzawa 5198*;

Tochigi Pref.: Sano-shi, Akiyama-cho, 360 m elev., 36.5472° N, 139.5074° E, 24 March 2018, *H. Ikeda 648*; Nikko-shi, Sannai, 17 May 2018, *Y. Ohshima s.n.*; Kanuma-shi, Iriawano, Ozaku, 36.5870426° N, 139.5719909° E, 12 May 2018, *Y. Ohshima s.n.*

Gunma Pref.: Naganohara-machi, Kitakaruizawa, 1070 m elev., 36.273597° N, 138.361791° E, 29 April 2018, *K. Nakazawa 1132*; Nakanoyjo-machi, Iriyama, 1520 m elev., 36.7144° N, 138.6390° E, 23 April 2018, *K. Nakazawa 1127*.

Tokyo Metro.: Minato-ku, Arisugawanomiya Memorial

Park, 21 Dec. 2017, *S. Suzuki s.n.*; *ibid.*, Takao-cho, Mt. Takao, 6th trail, 380–490 m elev., 35.6250° N, 139.2450° E, 4 Dec. 2017, *H. Akiyama 25268* and *25279*; Uratako-cho, 4 Dec. 2017, *H. Akiyama 25289*; Hachijyo-shi, Isl. Hachijyo, Mt. Mihara, 680 m elev., 16 May 2013, *H. Akiyama s.n.*; *ibid.*, Mitsune, 300 m elev., 33.10092° N, 139.81438° E, 2 Jan. 2018, *H. Ikeda 626* and *629*; *ibid.*, Miyake Isl., 55 m elev., 34.11466° N, 139.4983° E, 29 Dec. 2017, *H. Ikeda 618*.

Chiba Pref.: Chiba-shi, Otaki-machi, Otaki Prefectural Park, 45–140 m elev., 35.2832° N, 140.2325° E, 6 March 2019, *H. Akiyama 25945*, *25946*, *25947* and *25948*; *ibid.*, Wakaba-ku, Noro, Izumi Nature Park, 30 m elev., 35.5803° N, 140.2242° E, 10 March 2019, *H. Akiyama 25975*.

Kanagawa Pref.: Yokosuka-shi, Umahori-machi, Natural Education Garden, 35.257222°N, 139.717222°E, 28 July 2017, *M. Uzawa 4216*; Zama-shi, Iriya, 26 Nov. 2017, *A. Washimi s.n.*; *ibid.*, Sagamigahara, 35.5053° N, 139.4299° E, 21 Jan. 2018, *A. Washim180121-1*; Yamakita-machi, Kurokura forest road, 29 Nov. 2017, *H. Suzuki 171129-A01h*; Hatano-shi, Nishiyama forest road, Kansuke bridge, 29 Nov. 2017, *H. Suzuki 171129-E09h*; Fujisawa-shi, Enoshima, 35.2995° N, 139.4806° E, 14 Jan. 2018, *A. Washimi 20180114-1*.

Yamanashi Pref.: Hayakawa-cho, Akazawa, 452 m elev., 35.402953° N, 138.373904°E, 6 May, *H. Ikeda 651*; Minamikoma-gun, Nanbu-cho, 900 m elev., 35.210561° N, 138.426463° E, 6 Nov. 2019, *H. Ikeda 701*.

Shizuoka Pref.: Shizuoka-shi, Suruga-ku, Yahatayama Park, 48 m elev., 34.970699° N, 138.402160° E, 21 Jan. 2018, *T. Kawakami s.n.*

Nagano Pref.: Karuizawa-cho, Nagakura, Shiraitonotaki trail, 26 Nov. 2017, *A. Yoshida 46*; Chino-shi, Mugikusa-pass, ca. 2100 m elev., Jigokutani, 30 June 2018, *M. Shimadate s.n.*; Kiso-machi, Kaidakougen, Nishino, 1128 m elev., 35.928172° N, 137.581123° E, 30 Aug. 2018, *H. Akiyama 25697*; Nagiso-machi, Oshide, 623 m elev., 35.56237° N, 137.61724° E, 30 Aug. 2018, *H. Akiyama 25702*; Iida-shi, Iida Pass, 1220 m elev., 35.55606° N, 137.73500° E, 30 Aug. 2018, *H. Akiyama 25709*; Toyone-mura, Sakauba, 890 m elev., 35.186686° N, 137.675099° E, 31 Aug. 2018, *H. Akiyama 25722*; Anan-cho, Shinno, 715 m elev., 35.280175° N, 137.770557° E, 31 Aug. 2018, *H. Akiyama 25719* and *25720*.

Niigata Pref.: Sado-shi, Mt. Ooji, 575 m elev., 37.959444° N, 138.483333° E, 22 Oct. 2017, *M. Uzawa 4325*; Yahikomura, Yahiko Shrine, 60 m elev., 37.706419° N, 138.825120° E, 7 Jan. 2018, *H. Shirasaki 25201*; Gosen-shi, Goyagawa, 50 m elev., 37.705452° N, 139.226432° E, 22 April 2018, *H. Shirasaki 25212*; Yuzawa-cho, Mt. Naeba, 959 m elev., 36.88859° N, 138.744256° E, 17 June 2018, *H. Shirasaki 25260*; Itoigawa-shi, Kajiyama, entrance of the trail to Mt. Komagatake, 300 m elev., 36.926111° N, 137.970833° E, 15 July 2018, *H. Shirasaki 25278*; Murakami-shi, Takane,

Suzugataki, 340 m elev., 38.342500° N, 139.667500° E, 9 Sept. 2018, *H. Shirasaki 25385*; *ibid.*, Kitaohdaira, Ishiguroike, 240 m elev., 38.308333° N, 139.605556° E, 8 Sept. 2018, *H. Shirasaki 25372*; Iwafune-gun, Sekikawamura, Oishi, Higashimatagawa, 250 m elev., 38.030088° N, 139.577744° E, 25 May 2019, *H. Shirasaki 26472*.

Toyama Pref.: Tateyama-cho, Tateyama, Takimidai, 1250 m elev., 36.5783° N, 137.4936° E, 30 Oct. 2019, *N. Sakai s.n.*; Toyama-shi, Arimine, Oritate, 1360 m elev., 36.48253° N, 137.47467° E, 29 Aug. 2018, *H. Akiyama 2567*; Nanto-shi, Narude, 376 m elev., 36.35203° N, 136.87193° E, 27 Aug. 2018, *H. Akiyama 25668* (intermingled with *C. orientalis*).

Ishikawa Pref.: Hakusan-shi, Shiramine, around the entrance of Tani tunnel, 230 m elev., 36.08928° N, 136.52916° E, 27 Aug. 2018, *H. Akiyama 25659*; *ibid.*, Aratani, 690 m elev., 36.14514° N, 136.5893° E, 27 Aug. 2018, *H. Akiyama 25660*; *ibid.*, Chugu, backyard of Exhibition Center building, 600 m elev., 36.261304° N, 136.76056° E, 27 Aug. 2018, *H. Akiyama 25662*.

Fukui Pref.: Eiheiji-cho, Ichinono, 36.051474° N, 136.328904° E, 9 June 2018, *Y. Oishi 20180609-1*; Katsuyama-shi, Muraoka-cho, Tochikamidani, 230 m elev., 36.08928° N, 136.52916° E, 27 Aug. 2018, *H. Akiyama 25659*.

Gifu Pref.: Hida-shi, Kamioka-cho, Iwatani, 880 m elev., 36.39347° N, 137.38170° E, 29 Aug. 2018, *H. Akiyama 25688*; Takayama-shi, Asahi-machi, Suzuran Park, 720 m elev., 36.08960° N, 137.32796° E, 30 Aug. 2018, *H. Akiyama 25693*; *ibid.*, Manyu, 745 m elev., 36.08839° N, 137.35355° E, 30 Aug. 2018, *H. Akiyama 25695*; Ibigawa-cho, Sakauchi-Kawakami, 470 m elev., 35.602567° N, 136.338744° E, 30 Jan. 2020, *Y. Kasai 8147*; Yamagata-shi, Kanzaki, Natusakataniguchi, 210 m elev., 35.637505° N, 136.704276° E, 30 Jan. 2020, *Y. Kasai 8149*; Yoro-cho, Takahayashi 1298-2, 27 July 2018, *A. Yoshida 57*.

Aichi Pref.: Seto-shi, Iwama-machi, *A. Sakuragi 148*; Toei-cho, Nakashidara, 360 m elev., 34.095293° N, 137.673064° E, 31 Aug. 2018, *H. Akiyama 25725*; Shidara-cho, Tashiro, 390m elev., 35.063869° N, 137.610102° E, 31 Aug. 2018, *H. Akiyama 25727*; Shinshiro-shi, Hotokezaka-toge Pass, 517 m elev., 35.046727° N, 137.582414° E, 31 Aug. 2018, *H. Akiyama 25728*; *ibid.*, Kadotani, Hirasawa, 200 m elev., 34.972289° N, 137.566290° E, 31 Aug. 2018, *H. Akiyama 25729*; *ibid.*, Horaiji-san, at the entrance of Akibamichi trail, 230 m elev., 34.972253° N, 137.579848° E, 31 Aug. 2018, *H. Akiyama 25730*; *ibid.*, Kawai, Chichiwa valley, 379 m elev., 35.025278° N, 137.662778° E, 2 April 2020, *M. Chishiki 6183*; Seto-shi, Yoshino-cho, Kaishonomori Park, Aug. 2018, *F. Noda s.n.*

Mie Pref.: Matsusaka-shi, Iitaka-cho, Hachisu, Miyanotani valley, 450–600 m elev., 34.340278° N, 136.146111° E., 18

May 2017, *H. Akiyama 24974*; *ibid.*, Nonoguchi, 160 m elev., 6 June 2018, *N. Morita s.n.*; *ibid.*, Sakanai-cho, 205 m elev., 34.536074° N, 136.430977° E, 3 Oct. 2019, *N. Morita 7*; Nabari-shi, Nagaki, 14 June 2017, *H. Akiyama s.n.*; Shima-shi, Isobe-cho, Erihara (Amano-iwato), 100 m elev., 34.407883° N, 136.763456° E, 20 Dec. 2015, *H. Akiyama 24319*; *ibid.*, Akame-cho, Akame-keikoku valley, 300 m elev., 34.563333° N, 136.085556° E, *H. Akiyama 24882*; *ibid.*, Nagasaka, 235 m elev., 35.5849° N, 136.0843° E, 26 Nov. 2017, *H. Akiyama 25261*; Tsu-shi, Ichishi-cho, Haze, 34.627069° N, 136.383303° E, 16 Nov. 2017, *E. Tamura 4443*; *ibid.*, 34.629869° N, 136.382717° E, *E. Tamura 4448*; Iga-shi, Suwa, 7 April 2019, *Y. Ohshima s.n.*; *ibid.*, Yubune, 220 m elev., 34.846793° N, 136.176685° E, 29 Oct. 2018, *N. Morita s.n.*; Inabe-shi, Fujiwara-cho, Oogaito, Mt. Fujiwara, 287 m elev., 35.1674° N, 136.4639° E, 3 April 2018, *M. Chishiki 5843*; *ibid.*, Mt. Oike, 712m elev., 35.1886° N, 136.4239° E, 4 April 2018, *M. Chishiki 5845* (intermingled with *C. toyotae*); Higashiomi-shi, Ohwada-cho, 411 m elev., 35.103333° N, 136.400555° E, 5 April 2018, *M. Chishiki 5847*; Kameyama-shi, Atimoto-cho, 8 May 2018, *Y. Ohshima s.n.*; Kihoku-cho, Soga, Fudodani valley, 390 m elev., 34.1282618° N, 136.1446538° E, 18 July 2018, *N. Morita 20180718-1*; *ibid.*, Miura, 55 m elev., 34.157504° N, 136.266475° E, 22 Oct. 2018, *N. Morita s.n.*; Kuwana-shi, Tado-machi, Tado, 35.134583° N, 136.613472° E, 5 Nov. 2018, *T. Fukuda s.n.*; Minami-Ise-machi, Higashimiya, 35 m elev., 34.266921° N, 136.549475° E, 11 Sept. 2019, *N. Morita s.n.*; Kumano-cho, Kushiya-cho, 23 m elev., 33.864785° N, 136.066457° E, 30 Oct. 2018, *Y. Ohshima 20181030-1*; Owase-shi, Sugari-machi, Niu, 90 m elev., 14 July 2019, *H. Doei 25181*.

Shiga Pref.: Maibara-shi, Kaminyu, Samegai-valley, 200 m elev., 35.2953° N, 136.3422° E, 8 July 2017, *H. Akiyama 25072* and *25073*; *ibid.*, Kotsuhara, Oku-Ibuki, 510 m elev., 35.503333° N, 136.375000° E, 8 July 2017, *H. Akiyama 25083*; *ibid.*, Azusakawachi, upper reach of Azusagawa, 215 m elev., 35.316667° N, 136.378056° E, 14 Nov. 2018, *Y. Kasai 6704*; Takashima-shi, Kutsuki-Murai, Yokotani valley, 215 m elev., 35.308889° N, 135.892222° E, 23 Nov. 2017, *Y. Kasai 5357*; *ibid.*, Katsuno, 95 m elev., 35.291667° N, 136.006389° E, Nov. 2017, *Y. Kasai 5360* and *5361*; Ohtsu-shi, Sakamoto, Hiyoshi Shrine, Nishihongu-Higashihongu, 160 m elev., 6 Jan. 2018, *K. Nakazato 103, 104* and *106*;

Kyoto Pref.: Kyoto-shi, Sakyo-ku, Hounenin temple, 95 m elev., 35.022778° N, 135.797222° E, 18 June 2017, *H. Akiyama s.n.*; *ibid.*, Nishikyoku, Arashiyama, Genrokuzan-cho, *T. Saeki 4343*; *ibid.*, Saiho-ji temple, 8 Feb. 2019, *H. Akiyama s.n.*; Nantan-shi, Miyama-cho, Ashu, 412 m elev., 35.320000° N, 135.720278° E, 30 Oct. 2018, *M. Chishiki 5865*.

Osaka Pref.: Osaka-shi, Nishi-ku, Utsubo Park, 23 June

2011, *H. Akiyama s.n.*; *ibid.*, Chuo-ku, Osaka Chamber of Commerce and Industry, 5 m elev., 34.6841° N, 135.5113° E, 5 Feb. 2018, *K. Nakasato 00108*; Kawachinagano-shi, Kagata, 505 m elev., 34.22° N, 135.33° E, 4 March 2018, *S. Sakiyama 2018030412*; Takatsuki-shi, Nakahata, 383 m elev., 34.9611° N, 135.6075° E, 14 March 2018, *K. Nakasato 00109*; Shimamoto-cho, Honmachi, 94 m elev., 34.8833° N, 135.6500° E, 29 March 2018, *H. Tsuji 425*.

Nara Pref.: Kawakami-mura, Koudako, 350 m elev., 34.287299° N, 135.989392° E, 16 Jan. 2018, *M. Kimura 8423, 8424* and *8425*; *ibid.*, Ikari, 780 m elev., 34.34073° N, 136.00950° E, 18 Jan. 2018, *M. Kimura 8427*; *ibid.*, Ootenjyo Waterfall, 1040 m elev., 34.285377° N, 135.923082° E, 28 May, 2018, *M. Kimura 8470*; Tenkawa-mura, Dorogawa, in the vicinity of Godaimatu limestone cave, 900 m elev., 34.2651° N, 135.8950° E, 20 Oct. 2019, *T. Saeki 5210*; Kashiba-shi, Mt. Futakami, 95–230 m elev., 34.534444–5461° N, 135.675556–6819° E, 7 Jan. 2018, *T. Kano 5802, 5804, 5806, 5808* and *5809*; Totsukawa-mura, Tamakigawa, Tamaki Shrine, 1000 m elev., 33.926654° N, 135.829232° E, 16 May 2019, *M. Kimura 8585*.

Wakayama Pref.: Wakayama-shi, Tomoga-shima Isl., 28 m elev., 34.2828° N, 135.0047° E, 28 Oct. 2020, *H. Doei 26148*; Tanabe-shi, Gomanodanzan Forest Park, ca. 1100 m elev., 15 July 2018, *H. Doei 24698* and *24699*; *ibid.*, Ryujinmura, Omatagawa, Kamise, 450 m elev., 16 July 2018, *H. Doei 24723*; *ibid.*, Hongu-cho, upper reach of Ohto river, Nakagoya-dani, 380 m elev., *H. Doei 24807*; Katuragi-cho, Hanazono, Yanase, 650 m elev., 15 July 2018, *H. Doei 24700*; Susami-cho, Hirose-dani, Kotonotaki forest road, 200 m elev., 5 Aug. 2018, *H. Doei 24750, 24764* and *24774*; Shingu-shi, Kumanogawa-cho, Unehata, upper reach of Wadagawa river, 250 m elev., 2 Aug. 2018, *H. Doei 24740* and *24743*; *ibid.*, Kamatsuka, Seikantoro, 180 m elev., *H. Doei 24885*; *ibid.*, 180 m elev., 18 Aug. 2018, *H. Doei 24875*; Kushimoto-cho, Sabe, 5 m elev., 33.551553° N, 135.863800° E, 24 Nov. 2018, *Y. Kasai 6704*; Nachikatsuura-cho, Nagai, 14 m elev., 33.598928° N, 135.873671° E, 24 Nov. 2018, *Y. Kasai 6712*; Tomogashima 28 Dec. 2020, *H. Doei 26148* (small type).

Hyogo Pref.: Kawanishi-shi, Hitokura Park, 232 m elev., 34.9180° N, 135.4197° E, 1 July 2017, *H. Akiyama s.n.*; Kami-cho, Muraoka, Uwano-kogen, 600 m elev., 35.429598° N, 134.583142° E, 26 Sept. 2018, *H. Akiyama s.n.*; Aogaki-cho, *H. Akiyama s.n.*; Sanda-shi, Aimoto, 10 June 2017, *H. Akiyama s.n.*; Tanba-shi, Kasuga-cho, Tari, Higaoku valley, 160 m elev., 35.182222° N, 135.149722° E, 14 May 2017, *H. Akiyama 24972*; Tatsuno-shi, Shingu-cho, Tsunokame, 34.937246° N, 134.451306° E, 8 Sept. 2020, *H. Akiyama 26392* (distributed as *exicatae* from HIRO); Kamigori-cho, Koto, 34.922994° N, 134.449417° E, 8 Sept. 2020, *H. Akiyama 26400* (small type); Kobe-shi, Suma-ku, Yokoo,

Tsubakiyama Park, 150 m elev., 34.665417° N, 135.113417° E, 3 Jan. 2018, *K. Nakasato 00103*; Shinonsen-cho, Hanasaka, 35.6187° N, 134.4461° E, 21 June 2018, *M. Michimori s.n.*; Yabu-shi, summit of Mt. Hyonosen, 1490 m elev., 35.3546° N, 134.5138° E, 9 Oct. 2018, *H. Akiyama 25772* (intermingled with *Sandea japonica*); *ibid.*, Ohya-cho, Yokoiki-keikoku valley, 980 m elev., 35.3409° N, 134.5276° E, 9 Oct. 2018, *H. Akiyama 25797*; Kinosaki-cho, Ueyama, 10 Apr. 2021, *T. Suzuki s.n.*

Tottori Pref.: Hino-gun, Kofu-cho, Ebi, 175 m elev., 35.285959° N, 133.492384° E, 20 March 2018, *A. Kato s.n.*; *ibid.*, Mitsukue, 600 m elev., 35.28° N, 133.49° E, 25 March 2018, *A. Kato s.n.*; *ibid.*, 17 Oct. 2019, *T. Kano 646*; *ibid.*, Miyaichi, 438 m elev., 35.293735° N, 133.534924° E, 26 Aug. 2019, *H. Akiyama 26065*; Tottori-shi, Aoya-cho, Hatsushoji, 96 m elev., 35.475070° N, 133.983014° E, 7 Jan. 2018, *A. Yoshida 51* and *52*; *ibid.*, Uemachi, Ouchidani Park, 20 m elev., 35.5007° N, 134.2485° E, 30 July 2018, *A. Yoshida 54*; Saji-cho, Ohi, 133 m elev., 35.3382° N, 134.1531° E, 26 Aug. 2019, *H. Akiyama 26096*; Kurayoshi-shi, Sekikane-cho, Inubasari pass, 517 m elev., 35.3193° N, 133.7207° E, 26 Aug. 2019, *H. Akiyama 26090*; Nichinan-cho, Yato, beneath Dainyu pass, 400 m elev., 35.1635° N, 133.2530° E, 26 Aug. 2019, *H. Akiyama 26092*; Misasa-cho, Kijiyama, 394 m elev., 35.3153° N, 133.8778° E, 26 Aug. 2019, *H. Akiyama 26094*.

Shimane Pref.: Ota-shi, Sanbe-cho, Tane, foot of Mt. Sanbe, 230 m elev., 34.1767° N, 134.6000° E, 15 April 2018, *T. Yamaguchi 39109*; *ibid.*, Ikeda, foot of Mt. Sanbe, 610 m elev., 34.1505° N, 132.6283° E, 15 April 2018, *T. Yamaguchi 39100*; Hamada-shi, Misumi-cho, Shimokoraiguchi, 116 m elev., 34.735624° N, 134.006663° E, 22 Feb. 2019, *M. Ohta s.n.*; Oki-gun, Okinoshima-cho, Saigo, 215 m elev., 36.263333° N, 133.296667° E, 16 June 2018, *T. Tango 01419*; Okuizumo-cho, Takezaki, 520 m elev., 35.1969° N, 133.1710° E, 26 Aug. 2019, *H. Akiyama 26093*; Izumo-shi, Sada-cho, Ichikubota, 97-104 m elev., 35.245189° N, 132.689659° E, 27 Aug. 2019, *H. Akiyama 26097* and *26098*; *ibid.*, Sada-cho, Ichikubota, 97 m elev., 35.2427° N, 132.6799° E, 27 Aug. 2019, *H. Akiyama 26098*; Iinan-cho, Shitumi, 365 m elev., 35.1288° N, 132.6813° E, 27 Aug. 2019, *H. Akiyama 26099*; *ibid.*, Tsunoi, 574 m elev., 35.141938° N, 132.64041° E, 27 Aug. 2019, *H. Akiyama 26100*; Gotsu-shi, Sakurae-cho, en route to Kan'non Fall, 63 m elev., 34.947790° N, 132.449343° E, 27 Aug. 2019, *H. Akiyama 26101* and *26102*.

Okayama Pref.: Okayama-city, Kita-ku, Korakuen, Okayama Korakuen Garden 34.668806° N, 133.935457° E, *E. Tamura 4462*; Kita-ku, Shinjyo-shimo, 8 m elev., 34.673817° N, 133.810307° E, 21 Feb. 2018, *N. Nishihara s.n.*; Niimi-shi, Hongo, 34.941111° N, 133.418333° E, 10 July 2017, *H. Akiyama 25101*; Wake-cho, Taga, Nature Conservation Center, 203 m elev., 34.851667° N, 134.054167° E, 25 March 2018,

M. Chishiki 5840 and *5841*; Maniwa-shi, Kanba, Kanba Waterfall, 345 m elev., 35.115000° N, 133.680556° E, 21 Sept. 2018, *M. Chishiki 5867*; Kagamino-cho, Okutsu-Kawanishi, 340 m elev., 35.2142° N, 133.9117° E, 9 March 2020, *M. Chishiki 5921*; Maniwa-shi, Kanba, Kanbanotaki waterfall, 345–377 m elev., 35.115000-116111° N, 133.679167-680556° E, 21 Sept. 2018, *M. Chishiki 5866* and *5867*; *ibid.*, Hiruzenbessho, 522 m elev., 35.292856° N, 133.778445° E, 26 Aug. 2019, *H. Akiyama 26091*; Kagamino-cho, east of Nigyo-toge Pass, 670 m elev., 35.309278° N, 133.948211° E, 26 Aug. 2019, *H. Akiyama 26088*.

Hiroshima Pref.: Hatsukaichi-shi, Miyajima Isl., en route from Tatara to Okunoin temple, 250 m elev., 34.2772° N, 132.3092° E, 9 April 2018, *S. Uchida s.n.*; Shobara-shi, Tojo-cho, Kami-Taishakukyo, 410 m elev., 34.865278° N, 133.206389° E, 10 July 2017, *H. Akiyama 25096*; *ibid.*, 14 March 2018, *H. Akiyama 25439*; *ibid.*, Saiiki-cho, Hirako, 450 m elev., 34.9025° N, 133.1306° E, 17 June 2018, *T. Yamaguchi 39111*.

Yamaguchi Pref.: Mine-shi, Taishodo limestone cave, 160 m elev., 34.2771° N, 131.3187° E, 8 Dec. 2017, *M. Hayashi 25598*; *ibid.*, Syuho-cho, Akiyoshi, Syuhodo Cave, 80 m elev., 34.2253° N, 131.3050° E, 25 Oct. 2018, *M. Hayashi 27162*; Yamaguchi-shi, Ato, Izumonaka, Chomon-kyo valley, 169 m elev., 34.3195° N, 131.5660° E, 16 Dec. 2017, *M. Hayashi 26190*; *ibid.*, Tada, 10 m elev., 34.279833° N, 132.173250° E, 18 March 2018, *T. Yamaguchi 39103*; *ibid.*, Atotokusashita, 286 m elev., 34.3742° N, 131.6890° E, 27 Aug. 2019, *H. Akiyama 26103*; Hagi-shi, Fukue, *M. Hayashi 26366*; Syunan-shi, Miyanosita, Takatobara-hachiman Shrine, 27 m elev., 34.0852° N, 131.7159° E, 4 Feb. 2018, *M. Hayashi 25671*; Nagato-shi, Shibuki, 230 m elev., 34.290680° N, 131.185459° E, 31 Aug. 2019, *N. Morita s.n.*;

Tokushima Pref.: Katsuura-cho, Tanano, Tachikawa Valley, 120–390 m elev., 24 June 2017, *H. Akiyama 25058*, *25059* and *25060*; *ibid.*, Mamidani, 410 m elev., 33.870222° N, 134.453972° E, 24 June 2017, *H. Akiyama 25062* and *25063*; *ibid.*, 410 m elev., *H. Akiyama 25254*; Kamikatsu-cho, Shokuta, 290 m elev., 33.873611° N, 134.415000° E, 24 June 2017, *H. Akiyama 25064*, *25065* and *25068*; Miyoshi-shi, Higashiiya, Sugeoi, in the vicinity of Nishijima cable station, 1717 m elev., 33.85944° N, 134.093056° E, 7 Oct. 2019, *M. Chishiki s.n.*; Mima-gun, Tsurugi-machi, Ichiu, 31 March 2018, *Y. Asakawa s.n.*; *ibid.*, Sadamitsu, 183 m elev., 33.982222° N, 134.076944° E, 06 Oct. 2019, *M. Chishiki s.n.*; Kaiyo-cho, Aikawa, 65 m elev., 33.646111° N, 134.275833° E, 25 March 2017, *H. Akiyama 24916*.

Kochi Pref.: Agawa-gun, Niyodogawa-cho, Nakatsu-keikoku, 3 Nov. 2019, *S. Suzuki s.n.*; Agawa-gun, Ino-cho, Kase, 33.7793° N, 133.3070° E, 27 March 2018, *T. Yamaguchi 39105*; *ibid.*, Kuwase, entrance of the trail to Mt. Kanpuzan,

1208 m elev., 33.7989° N, 133.2653° E, 24 Sept. 2018, *M. Chishiki* 5859; *ibid.*, Mt. Kanpuzan, 1130 m elev., 33.79953° N, 133.26631° E, 28 Oct. 2018, *K. Iwata* 4503; (intermingled with *C. purpureorubum* western type); Tosashimizu-shi, Ashizurimisaki, 90 m elev., 37.7308° N, 133.0131° E, 29 March 2018, *T. Yamaguchi* 39107 and 39150; Umaji-mura, Yanase, 457–568 m elev., 33.655278° N, 134.081389° E, 24 April 2018, *M. Chishiki* 5850-A, 5850-B and 5851; Aki-shi, Furui, 159 m elev., 33.933056° N, 133.981389° E, 24 April 2018, *M. Chishiki* *s.n.*; Okawa-mura, Takano, 349 m elev., 33.790000° N, 133.422222° E, 25 Sept. 2018, *M. Chishiki* 5860 and 5861.

Kagawa Pref.: Man'no-cho, Katsuura, 430 m alt., 34.096444° N, 134.001944° E, 9 Feb. 2020, *M. Saji* 2872 and 2873; *ibid.*, Shioiri, Noguchi Dam, 6 Feb. 2020, *M. Saji* 2875; Mitoyo-shi, Saita-cho, Saitanaka, 34.097° N, 133.770° E, 9 Feb. 2020, *M. Saji* 2874.

Ehime Pref.: Saijyo-shi, Nishinokawa, 440 m elev., 33.80143° N, 133.15485° E, 15 Jan. 2018, *K. Iwata* 3753; *ibid.*, Nakaoku, 195 m elev., 33.8647° N, 133.1786° E, 15 Jan. 2018, *K. Iwata* 3752; Yawatahama-shi, Yashiro, 35 m elev., 33.442688° N, 132.428329° E, 3 April 2018, *K. Iwata* 4100; Ohsu-shi, Hijikawa-cho, Ohtani, Mt. Gozaisho, 560 m elev., 33.43639° N, 132.63692° E, 3 April 2018, *K. Iwata* 4104; Ino-cho, Kuwase, Mt. Kanpuzan, 1130 m elev., 33.79953° N, 133.26631° E, 28 Oct. 2018, *K. Iwata* 4503; Uchiko-cho, Nakagawa, Odamiyama Valley, 800 m elev., 33.5312° N, 132.8940° E, 22 March 2019, *K. Iwata* 4767.

Fukuoka Pref.: Iizuka-shi, Yakiyama, Yakiyama Camping Site, 180 m elev., 33.650355° N, 130.597744° E, 11 March 2018, *H. Akiyama* 25390; Kawara-machi, Saido-sho, Gotokugoe-Pass, 260 m elev., 33.693209° N, 130.839314° E, 12 March 2018, *H. Akiyama* 25400; Fukuoka-shi, Mt. Seburi, 857 m elev., 33.434861° N, 130.360528° E, 10 Oct. 2018, *A. Tanaka* 20181010-2; *ibid.*, Higashi-ku, Shimohara, Mt. Tachibana, 33.677206° N, 130.464767° E, 2 Nov. 2018, *A. Tanaka* 20181102; Kitakyushu-shi, Kokuraminami-ku, Hiraodai, Senbutsudo Cave, 300 m elev., 33.7543° N, 130.9047° E, 12 March 2018, *H. Akiyama* 25402; Itoshima-shi, Northeastern slope of Mt. Ihara, Mizunashi Valley, 530–650 m elev., 33.4820° N, 130.2618° E, 20 March 2020, *H. Akiyama* 26328; Dazaifu-shi, Uchiyama, Mt. Homansan, 632 m elev., 33.536111° N, 130.566389° E, 28 Sept. 2020, *M. Chishiki* *s.n.*

Saga Pref.: Tosu-shi, Tateishi-cho, Ochouzu camping site, 33.384047° N, 130.456036° E, 27 Nov. 2017, *T. Ohya* 430; Saga-shi, Fujimi-cho, Kamikumagawa, 33.361796° N, 130.219398° E, 25 Nov. 2017, *T. Ohya* 431; Takeo-shi, Yamauchi-cho, Miyano, 33.2226614° N, 129.915337° E, 29 Nov. 2017, *T. Ohya* 432; Kashima-shi, Yamaura, 460 m elev., 32.9978° N, 130.0617° E, 25 Jan. 2020, *T. Ohya* 460; Tara-

cho, Tara, Mt. Tara, 893 m elev., 32.975000° N, 130.091111° E, 8 Oct. 2020, *M. Chishiki* *s.n.*

Nagasaki Pref.: Nagasaki-shi, Kounoura, Kitaoonakao-machi, Nagasaki Prefectural Forest, 31 Aug. 2019, *M. Matsumoto* *s.n.*; Ohmura-shi, Kamisuwa, Yamada Fall, 32.923889° N, 129.979444° E, 17 May 2018, *A. Tanaka* *s.n.*; *ibid.*, Kuroki-cho, entrance of Mt. Kyogatake, 314 m elev., 32.977500° N, 130.057500° E, Oct. 2020, *M. Chishiki* *s.n.*; *ibid.*, Mt. Taradake, 779 m elev., 32.973333° N, 130.083056° E, 8 Oct. 2020, *M. Chishiki* *s.n.*; Kamigoto-cho, Tainouragou, 18 m elev., 32.945833° N, 129.101944° E, 19 Oct. 2020, *M. Chishiki* *s.n.*; *ibid.*, Arakawagou (San'noyama shrine), 421 m elev., 32.32933056° N, 129.053056° E, 20 Oct. 2020, *M. Chishiki* *s.n.*; Tsushima-shi, Mitushima-cho, Sumo, 351 m elev., 34.26366611° N, 129.251666° E, 1 Oct. 2020, *M. Chishiki* *s.n.*; *ibid.*, Kamiagata-cho, Sago, Mt. Mitake, 456 m elev., 2 Oct. 2020, *M. Chishiki* *s.n.*

Oita Pref.: Anshin'in-machi, Ukenokuchi, Iwaya, 245 m elev., 33.3809807° N, 131.3595792° E, 12 March 2018, *H. Akiyama* 25406; Yufuin-machi, Tsukahara, in the vicinity of Yufuin Parking Area, 620 m elev., 33.308891° N, 131.403855° E, 12 March 2018, *H. Akiyama* 25414 and 25415; Saiki-shi, Honjyo, Onagara, in the vicinity of Onagara Limestone Cave, 40 m elev., 32.948952° N, 131.756136° E, 13 March 2018, *H. Akiyama* 25425; Usuki-shi, Nodzu, Iwaya, 125 m elev., 32.996332° N, 131.706531° E, 13 March 2018, *H. Akiyama* 25428; Bungoohno-shi, Mie-machi, Asase, Sugao-Sekibutu, 80 m elev., 33.0245° N, 131.6162° E, 23 Oct. 2019, *N. Nishihira* 5210.

Miyazaki Pref.: Nichinan-shi, Obi, Obi castle, *M. Uzawa* 4064; *ibid.*, Inohae, *M. Uzawa* 4069; *ibid.*, Sakatani, Taneda, 34 m elev., 31.6128° N, 131.3270° E, 2 Sept. 2017, *H. Akiyama* 25203 and 25205; *ibid.*, Kusuhara, Ioshi Shrine, 38 m elev., 31.6241° N, 131.3467° E, 2 Sept. 2017, *H. Akiyama* 25206; *ibid.*, Sakatani, Kobuse-no-taki Fall, 140 m elev., 31.6373° N, 131.2464° E, 2 Sept. 2017, *H. Akiyama* 25197, 25198 and 25200; Gokase-cho, foot of Mt. Shiraiwa, 1470 m elev., 1 Nov. 2017, *M. Matsumoto* *s.n.*; Nobeoka-shi, 600 m elev., 2 Nov. 2017, *M. Matsumoto* *s.n.*; Ebino-shi, Ohkoubira, 32.067526° N, 130.913792° E, 4 Feb. 2018, *M. Matsumoto* 180204-1; Tsuno-cho, Kawakita, Osuzu Valley, parking lot, 400 m elev., 32.2855° N, 131.4661° E, 22 May 2019, *H. Akiyama* 26014.

Kumamoto Pref.: Minamioguni-machi, Manganji, 560 m elev., 33.084917° N, 131.104434° E, 13 March 2018, *H. Akiyama* 25434; Hitoyoshi-shi, Shikame-taki Waterfall, 260 m elev., 32.1937° N, 130.6945° E, 25 July 2018, *M. Matsumoto* 20180725-3.

Kagoshima Pref.: Yakushima-cho, Yakushima Isl., side branch of Anbo road, between Kigensugi and Kawakamisugi, 1260 m elev., 30.303724° N, 130.542297° E, 31 Aug. 2016, *H.*

Akiyama 24743; *ibid.*, Hanaage river, 126 m elev., 30.291321° N, 130.627913° E, 31 Aug. 2016, *H. Akiyama s.n.* (small type); *ibid.*, Nakama, 88 m elev., 30.259044° N, 130.445875° E, 11 March 2018, *N. Hayashida 714*; *ibid.*, Nakama forest road, 223 m elev., 11 March 2018, *N. Hayashida 715*; Amami-oshima Isl., Uken-son, Arangachi, Arangachi-Fall, 30 m elev., 28.270611° N, 129.323583° E, 14 Jan. 2016, *H. Akiyama 24421*; *ibid.*, Yamato-son, foot of Mt. Yuwan, Materia-Fall, 180 m elev., 28.316694° N, 129.351222° E, 13 Jan. 2016, *H. Akiyama 24402*; Tokunoshima Isl., Tokunoshima-cho, Kamezu, 80 m elev., 27.746718° N, 128.998488° E, 17 Jan. 2019, *H. Akiyama 25906*; *ibid.*, Amagi-cho, Nishiakkona, 110 m elev., 27.767520° N, 128.95081° E, 17 Jan. 2019, *H. Akiyama 25907*; *ibid.* western foot of Mt. Inokawa, 137-155 m elev., 27.777149° N, 128.951944° E, 17 Jan. 2018, *H. Akiyama 25908* and *25909*; *ibid.*, Isen-cho, Kojima, 135 m elev., 27.742416° N, 128.921666° E, 17 Jan. 2019, *H. Akiyama 25910*.

Okinawa Pref.: Kunigami-son, Hiji, between entrance gate to Hijiohtaki Fall, 20 m elev., 26.7172° N, 128.1832° E, 7 Feb. 2018, *H. Akiyama 25372* and *25373*; *ibid.*, Aha, Tanagagumui-waterfall, 59 m elev., 26.724722° N, 128.286667° E, 21 March 2018, *M. Chishiki 5839*; Ogimi-son, Ada, just above the Ingah Bridge, 70 m elev., 26.7621° N, 128.3037° E, 7 Feb. 2018, *H. Akiyama 25375*; Ogimi-son, Tsuha, between entrance to Tahtaki Fall, 40 m elev., 26.6325° N, 128.0933° E, 6 Feb. 2018, *H. Akiyama 25347* and *25349*.

TAIWAN.

Nantou Co.: Lugu township, Xitou Forest Recreation Area, 1200–1300 m elev., 23.6709° N, 120.7975° E, 2 June 2018, *H. Akiyama 25644*, *25652* and *25656*.

Chiayi Co.: Alishan, Shih Meng Gu, 1463 m elev., 23.562778° N, 120.774722° E, May 2018, *K.-Y. Yao 7655*.

Yilan Co.: Datong Township, Taiping Mountain Forest Resort, 1 April 2019, *H. Fujii s.n.*

***C. orientalis* J2 type**

JAPAN.

Mie Pref.: Komono-cho, summit area of Mt. Gozaisho, Choyodai Park, 1200 m elev., 35.0204° N, 136.4191° E, 21 May 2017, *N. Morita s.n.*

Nara Pref.: Totsukawa-mura, Tamakigawa, Tamaki Shrine, 1000 m elev., 33.926654° N, 135.829232° E, 16 May 2019, *M. Kimura 8585*.

Tokushima Pref.: Anan-shi, around Hanasaka, 70 m elev., 33.858056° N, 134.591111° E, 25 March 2017, *H. Akiyama 24892*; Hiwasa-cho, around Okugata, 10 m elev., 33.724167° N, 134.511111° E, 25 March 2017, *H. Akiyama 24893*; Tokushima-shi, Yamashiro, Nishihama, Tokushima Bunri University, 34.0534° N, 134.5574° E, 8 March 2018, *H. Akiyama 25379* (transplanted population).

***C. orientalis* J3 type**

JAPAN.

Hokkaido Pref.: Shari-cho, Raiun, 55–65 m elev., 43.833056° N, 144.642694° E, 13 July 2017, *A. Uchida 20170007* (Hokkaido-4); *ibid.*, Fuji, Mt. Shari, 310–320 m elev., 43.804694° N, 144.768389° E, 30 July 2017, *A. Uchida 20170017* (Hokkaido-8); Kamikawa-cho, Soun-kyo, 650–750 m elev., 43.721639° N, 142.956250° E, 4 Aug. 2017, *A. Uchida 20170024* (Hokkaido-12); Kamishihoro-cho, Nukapira nature trail, 536 m elev., 43.367092° N, 143.189809° E, *Y. Oppata 3611*; Sapporo-shi, Minamiku, Ishiyama Park, 1 Aug. 2019, *T. Saeki 5160*; Tomakomai-shi, Tarumae, foot of Mt. Tarumae, Shindomon, 385 m elev., 42.673056° N, 141.433889° E, 29 April 2020, *K. Izumida TRM-020*.

Aomori Pref.: Hirosaki-shi, Osuke, 125–175 m elev.,

40.566750° N, 140.339583° E, 22 Aug. 2017, *A. Uchida 20170030* (Hirosaki-3); Hirosaki-shi, Nishimeya-mura, Tshiro, Chichibogataki Fall, 114 m elev., 40.569444° N, 140.295278° E, 5 July 2020, *M. Chishiki s.n.*; Fukaura-machi, Iwasaki, 133 m elev., 40.5826° N, 139.9887° E, 25 Aug. 2019, *M. Sawada 20190825-1*; Towada-shi, Takada, Mts. Hakkouda, Tsuta-onsen, 520 m elev., 40.598889° N, 140.950278° E, 18 Oct. 2018, *T. Yamaguchi 39374*; *ibid.*, Oirase-keikoku valley, 252 m elev., 40.5500° N, 140.9833° E, 22 Oct. 2018, *M. Sawada 20181022-2*; Aomori-shi, Uchimannpe, Mt. Chyobo, 43 m elev., 40.907513° N, 140.597084° E, 17 April 2018, *M. Sawada 20180417-2*.

Iwate Pref.: Hanamaki-shi, Osako-machi, Foot of Mt. Hayachine, en route from Odagoke to Kawaranobou, 1128 m

elev., 39.540556° N, 141.48500° E, 19 Aug. 2019, *M. Uzawa 5140*; *ibid.*, 1100 m elev., 39.540000° N, 141.482222° E, 19 Aug. 2019, *M. Uzawa 5141*.

Akita Pref.: Happou-cho, Minehama, Mizusawa, Mizusawa Dam, 220 m, 40.3616° N, 140.0976° E., 20 Oct. 2018, *M. Takaoka s.n.*; Higashinaruse-mura, Iwaigawa, Kakkyogawa National Forest, Tensho Fall, 440 m elev., 39.1790° N, 140.7528° E, 18 Aug. 2020, *S. Sato TSF 3R*.

Fukushima Pref.: Hinoemata-mura, Mt. Hiuchigatake, Bunazawa Fall, 1246 m elev., 36.983611° N, 139.33333° E, 23 Aug. 2019, *S. Nemoto 965*.

Niigata Pref.: Yuzawa-cho, Mt. Naeba, Kagura-mitsumata ski resort, 959 m elev., 36.8886° N, 138.7543° E, 17 June 2018, *H. Shirasaki 25620*.

Ibaraki Pref.: Kuji-gun, Taishi-cho, Sanuki, Hatuhara river, 36.843333° N, 140.264167° E, 28 Sept. 2019, *M. Uzawa 5197*.

Hyogo Pref.: Yabu-shi, Mt. Hyonosen, at the base of Koshiki-iwa, 1420 m elev., 35.3550° N, 134.5116° E, 9 Oct. 2018, *H. Akiyama 25776* and *25780*; *ibid.*, Yokoike Valley, 770 m elev., 30 Nov. 2020, *H. Akiyama 26468*.

Conocephalum purpureorubrum H. Akiyama **Eastern Japanese form (FE)**

JAPAN.

Fukushima Pref.: Iwaki-shi, Ogawa-machi, Natuigawa valley, 210 m elev., 37.189444° N, 140.802500° E, 9 Sept. 2019, *S. Nemoto 20190909*.

Gunma Pref.: Naganohara-machi, Kawarayu, 510 m elev., 36.325406° N, 138.416271° E, 21 Nov. 2018, *K. Nakazawa 7398*; *ibid.*, 25 Nov. 2017, *A. Yoshida 42*; Fujioka-shi, Shimohino, Kuroishi, 270 m elev., 36.203717° N, 138.987592° E, 31 Dec. 2017, *M. Kimura 8420*; Tano-gun, Ueno-mura, Narahara, near the Oinuana Limestone Cave, 770 m elev., 36.078083° N, 138.737861° E, 30 Dec. 2017, *M. Kimura 8416*.

Tochigi Pref.: Nikko-shi, Sannai, 36.76° N, 139.60° E, 27 April 2018, *Y. Ohshima s.n.*; *ibid.*, Chugu Shrine, 1387 m elev., 36.722680° N, 139.492362° E, 14 June 2018, *Y. Ohshima s.n.*; Tochigi-shi, Izuru-cho, Mangannji, 340 m elev., 36.4667° N, 139.5833° E, 11 May 2018, *T. Saeki 4463*.

Ibaraki Pref.: Hitachiohta-shi, Mt. Nishikanasa, 36.651922° N, 140.450608° E, 28 July 2017, *M. Uzawa 4246* and *4247*; Hanakawa-cho, Hanazono Shrine, 450 m elev., 36.860000° N, 140.629167° E, 3 Nov. 2017, *M. Uzawa 4350*; *ibid.*, 36.861944° N, 140.626389° E, 19 Nov. 2017, *M. Uzawa 4375* (with strong smell of Matsutake mushroom flavor); *ibid.*, precinct of Hanazono Shrine, 433 m elev., 36.861163° N, 140.625939° E, 9 March 2019, *H. Akiyama 25949* and *25953*; Kuji-gun, Daigo-machi, Sanuki, Hatsuhara river, 36.8422° N, 140.2669° E, 28 Sept. 2019, *M. Uzawa 5197* and *5198*.

Chiba Pref.: Ichihara-shi, Yoro-keikoku, 1993, *H. Akiyama s.n.* (see Akiyama and Hiraoka 1994); Kyonan-machi, Motona, at the foot of Mt. Nokogiri, 27 m elev., 35.152905° N, 139.831570° E, 9 Oct. 2018, *T. Furuki 25043*; Isumi-gun, Otaki-machi, Otaki Prefectural Park, 80–140 m elev., 35.28° N, 140.23° E, 6 March 2019, *H. Akiyama 25944* and *25947*.

Tokyo Metro.: Hachioji-shi, Mt. Takao, 6th trail, 380–490 m elev., 35.6250° N, 139.2450° E, 4 Dec. 2017, *H. Akiyama*

25272, *25275* and *25281*; *ibid.*, 3th trail, 550 m elev., 35.6250° N, 139°2447° E, 4 Dec. 2017, *H. Akiyama 25283*; *ibid.*, Hikage-zawa, 300 m elev., 35.6329° N, 139.2432° E, 4 Dec. 2017, *H. Akiyama 25286*; Okutama-cho, Nippara, in the vicinity of Limestone Cave, 630 m elev., 35.8520° N, 139.0405° E, 5 Dec. 2017, *H. Akiyama 25293*; *ibid.*, Higashi-Nippara, 615 m elev., 35.8471° N, 139.0388° E, 5 Dec. 2017, *H. Akiyama 25295*; *ibid.*, Nippara, Kurawasa, 510 m elev., 35.8428° N, 139.0625° E, 5 Dec. 2017, *H. Akiyama 25301*; Fuchu-shi, Musashidai, Musashidai Park, 65 m elev., 35.6885° N, 139.4611° E, 11 Jan. 2018, *A. Yoshida 53*; Machida-shi, Hramachida, 35.547728° N, 139.449807° E, 28 Jan. 2018, *A. Washimi 180128*; Oshima-mura, Izu-Oshima Isl., Senzufudo, 34.780777° N, 139.419139° E, 16 Jan. 2020, *K. Yanagiba s.n.*; Miyake-mura, Miyake Isl., 55 m elev., 34.11466° N, 139.4983° E, 29 Dec. 2017, *H. Ikeda 630*.

Kanagawa Pref.: Yamakita-cho, Nakagawa, at the entrance of Youkizawa, 540 m elev., 35.4720° N, 139.0630° E, Nov. 2017, *H. Suzuki 171129-C05h*; Hakone-cho, Motohakone, foot of Mt. Komagatake, 1993, *H. Akiyama s.n.* (see Akiyama and Hiraoka 1994); *ibid.*, Bougasawa, 1993, *H. Akiyama s.n.* (see Akiyama and Hiraoka 1994).

Nagano Pref.: Matsukawa-cho, Ikuta, 35.598827° N, 137.981398° E, 17 Dec. 2017, *M. Ohta 2017121701*; Inashi, Ina, foot of Mt. Chausu, 1357 m elev., 35.825031° N, 137.854775° E, 1 July 2018, *Y. Oishi 20180701-2*; Kiso-machi, Mitake, 812 m elev., 35.83676° N, 137.63362° E, 30 Aug. 2018, *H. Akiyama 25700* and *25701*; Nagiso-machi, Oshide, 623 m elev., 35.56237° N, 137.61724° E, 30 Aug. 2018, *H. Akiyama 25703*; Iida-shi, Iida Pass, 1220 m elev., 35.55606° N, 137.73500° E, 30 Aug. 2018, *H. Akiyama 25710*; Toyone-mura, Sakauba, 890 m elev., 35.186686° N, 137.675099° E, 31 Aug. 2018, *H. Akiyama 25723*.

Yamanashi Pref.: Hayakawa-cho, Amehata, 35.455733° N, 138.291530° E, 5 May 2018, *H. Ikeda 650*.

Shizuoka Pref.: Kawanehon-cho, Kurishiro, 35.182667° N, 138.159583° E, 22 Dec. 2017, *M. Ohta 2017122203*.

Aichi Pref.: Okazaki-shi, Ishihara-machi, Kuragari Valley, 452 m elev., 34.920278° N, 137.407778° E, 4 April 2020, *M. Chishiki 6184*; Toyone, Sakauba, 890 m elev., 35.186686° N,

137.675099° E, 31 Aug. 2018, *H. Akiyama 25723*.

TAIWAN.

Nantou Co.: Lugu township, Xitou Forest Recreation Area, 1200–1300 m elev., 23.6709° N, 120.7975° E, 2 June 2018, *H. Akiyama 25642, 25644 and 25655*.

***Conocephalum purpureorubrum* H. Akiyama Western Japanese form (FW)**

JAPAN.

Toyama Pref.: Tateyama-machi, Ashikuraji, Buna-saka National Forest, Hachiro-zaka, 1060 m elev., 36.576821° N, 137.517083° E, *M. Michimori 20180830-3*.

Gifu Pref.: Ibigawa-cho, Kasugakawai (NE part of Mt. Ibuki), 1032 m elev., 35.423611° N, 136.433333° E, 3 Aug. 2018, *M. Chishiki 5852*; Yamagata-shi, Kanzaki, Iodo, Shiraiwa valley, 325 m elev., 35.662962° N, 136.713374° E, 30 Jan. 2020, *Y. Kasai 8150*.

Mie Pref.: Nabari-shi, Akame, Senjyutaki Fall, 355 m elev., 34.461080° N, 136.089106° E, 31 March 2018, *H. Akiyama 25533*; Kihoku-cho, Soga, Fudodani valley, 466 m elev., 34.1246613° N, 136.1369683° E, 18 July 2018, *N. Morita 20180718-2*.

Kyoto Pref.: Kyoto-shi, Nishikyo-ku, Arashiyama, Genrokuzan-cho, 57 m elev., 35.0136° N, 135.6696° E, *H. Akiyama 25805* (intermingled with *C. salebrosum*).

Nara Pref.: Kawakami-mura, Ikari, 815 m elev., 34.342745° N, 136.010077° E, 18 Jan. 2018, *M. Kimura 8426*; *ibid.*, Otenjyo Waterfall, 1040 m elev., 34.285377° N, 135.923082° E, 28 May, 2018, *M. Kimura 8469*; Totsukawamura, Tamakigawa, Mt. Tamaki-san, 1050 m elev., 33.926303° N, 135.831571° E, 16 May 2019, *M. Kimura 8586*; *ibid.*, Uchihara, in the vicinity of Sasanotaki Waterfall, 480 m elev., 34.0611° N, 135.8579° E, 5 May 2019, *T. Saeki 5039*.

Wakayama Pref.: Tanabe-shi, Gomanodanzan Forest Park, ca. 1100 m elev., 15 July 2018, *H. Doei 24688, 24693 and 24696*; *ibid.*, Ryujin-mura, 270 m elev., 16 July 2018, *H. Doei 24724*; Susami-cho, Hirose-dani, Kotonotaki forest road, 200 m elev., 5 Aug. 2018, *H. Doei 24762*; Shingu-shi, Kumanogawa-cho, Kamatuka, Seikantoro, 110 m elev., 18 Aug. 2018, *H. Doei 24874*.

Tokushima Pref.: Kaiyo-cho, Aikawa, *H. Akiyama 24895, 24896 and 24915*; *ibid.*, Todoroki Falls, *H. Akiyama 24949*; Katsura-cho, Tanano, Mamidani, 410 m elev., 33.870222° N, 134.453972° E, 24 June 2017, *H. Akiyama 25061*; Kamikatsu-cho, *H. Akiyama 25067 and 25069*; Mima-shi, Koyadaira, 1359 m elev., 33.8827° N, 134.2055° E, 24 July 2018, *M. Saji 1538 and 1539*.

Kochi Pref.: Umaji-mura, Yanase, 568 m elev., 24 April

2018, *M. Chishiki 5850-B*; Ino-cho, Wakinoyama, 1340 m elev., 33.753889° N, 133.365556° E, 27 Sept. 2018, *M. Chishiki 5862 and 5863*; *ibid.*, Kuwase, Mt. Kanpu-zan, 1130 m elev., 33.79953° N, 133.26631° E, 28 Oct. 2018, *K. Iwata 4502*.

Ehime Pref.: Saijyo-shi, Oonaru, 195 m elev., 33.8647° N, 133.1786° E, 15 Jan. 2018, *K. Iwata 3752*; Kumakogen-cho, Nishitani, 1117 m elev., 33.477500° N, 132.979167° E, 12 Sept. 2018, *M. Chishiki 5855*; Uchiko-cho, Nakagawa, Odamiyama Valley, 800 m elev., 33.5312° N, 132.8940° E, 22 March 2019, *K. Iwata 4768*.

Fukuoka Pref.: Iizuka-shi, Yakiyama, Yakiyama Camping Site, 180 m elev., 33.650355° N, 130.597744° E, 11 March 2018, *H. Akiyama 25383, 25386 and 25395*; Kitakyushu-shi, KokuraMinami, Hiraodai, at the entrance of Senbutu limestone cave, 290 m elev., 33.7543° N, 130.9047° E, 12 March 2018, *H. Akiyama 25404*; *ibid.*, Ubusune-no-hokora, 33.75089° N, 130.8941° E, 29 Aug. 2019, *H. Akiyama 26705 and 26706*; Fukuoka-shi, Mt. Seburi, 955 m elev., 33.437678° N, 130.365909° E, 10 Oct. 2018, *A. Tanaka 20181010-1*; *ibid.*, 658 m elev., 33.441389° N, 130.356111° E, 5 Oct. 2020, *M. Chishiki s.n.*; Itoshima-shi, Northeastern slope of Mt. Ihara, Mizunashi Valley, 530–650 m elev., 33.4820° N, 130.2618° E, 20 March 2020, *H. Akiyama 26329*; *ibid.*, north slope of Mt. Raizan, Seiga-no-taki Fall, 510 m elev., 33.4864° N, 130.8605° E, 20 March 2020, *H. Akiyama 26349*; Asakura-shi, Mt. Kosho-san, 539 m elev., 33.481389° N, 130.720278° E, 28 Oct. 2020, *M. Chishiki s.n.* (growing side-by-side with *C. salebrosum*).

Oita Pref.: Yufu-shi, Yufu-shi, Haginokusakawa, 33.308889° N, 131.211389° E, 18 March 2017, *M. Uzawa 4060*; Yufuin-machi, Tsukahara, in the vicinity of Yufuin Parking Area, 620 m elev., 33.308891° N, 131.403855° E, 12 March 2018, *H. Akiyama 25413*; Anshin'in-machi, Ukenokuchi, Iwaya, 245 m elev., 33.3809807° N, 131.3595792° E, 12 March 2018, *H. Akiyama 25407 and 25408*; Saiki-shi, Honjyo, Inoue, 70 m elev., 34.943661° N, 131.743191° E, 13 March 2018, *H. Akiyama 25427*; Takeda-shi, Kujyu-machi, Kujyu, 625 m elev., 33.029781° N, 131.282634° E, 13 March 2018, *H. Akiyama 25433*.

Kumamoto Pref.: Kumamoto Pref., Minamioguni-machi, Manganji, 560 m elev., 33.084917° N, 131.104434° E, 13 March 2018, *H. Akiyama 25435*.

Miyazaki Pref.: Nichinan-shi, Kobuse Falls, 140 m elev., 31.6373° N, 131.2464° E, 2 Sept. 2017, *H. Akiyama 25195* and *25196*; *ibid.*, Sakatani, Taneda, 120 m elev., 31.6372° N, 131.2526° E, 2 Sept. 2017, *H. Akiyama 25202*; Hinokage-cho, Ishigaki-no-mura, 250 m elev., 32.6982° N, 131.4033° E, 3 Nov. 2018, *M. Matsumoto s.n.*; Tsuno-cho, Kawakita, Osuzu Valley, parking lot, 400 m elev., 32.2855° N, 131.4661° E, 22

May 2019, *H. Akiyama 26013*.

Kagoshima Pref.: Kimotsuki-gun, Kanoya-shi, Kamitakakuma-cho, en route from Green Lodge to entrance of the trail to Mt. Oonogawa-dake, 170 m elev., 15 July 2014, *H. Akiyama 23819*; Kimotsuki-gun, Kimotuchi-cho, Mt. Hoyoshi, 650 m elev., 31.2500° N, 130.9667° E, 14 July 2014, *H. Akiyama 23810*.

Okinawa Pref.: Ogimi-son, Ada, just above the Ingah Bridge, 70 m elev., 26.7621° N, 128.3037° E, 7 Feb. 2018, *H. Akiyama 25376*.

Conocephalum salebrosus Szweyk., Buczk. & Odrzyk.

JAPAN.

Hokkaido Pref.: Rishiri Isl., Rishirifuji-cho, Oshidomari, 1530 m elev., *K. Kawai 15671*; *ibid.*, Oniwaki, Mt. Rishiri, 620–680 m elev., 45.164928° N, 141.256047° E, Sept. 2018, *A. Uchida 20180047 (712)*; Shari-cho, Raiun, 55–65 m elev., 43.83322° N, 144.642528° E, 13 July 2017, *A. Uchida 20170006* (Hokkaido-3); *ibid.*, Minehama, 190–200 m elev., 43.900333° N, 144.813583° E, 27 July 2017, *A. Uchida 20170015* (Hokkaido-6); *ibid.*, Fuji, Mt. Shari, 240–250 m elev., 43.808444° N, 144.779361° E, 30 July 2017, *A. Uchida 20170016* (Hokkaido-7); Kitami-shi, Midorigaoka-4, Midorigaoka Park, 200–250 m elev., 43.826694° N, 143.866944° E, 24 July 2017, *A. Uchida 20170010*; Sapporo-shi, Mt. Teine, in the vicinity of Nunojikinotaki Fall, 500 m elev., 43.0644° N, 141.1921° E, 1 Aug. 2019, *T. Furuki 25429*; *ibid.*, Mt. Soranuma, 470 m elev., 12 Aug. 2018, *T. Saeki 4673*; Urahoro-cho, Higashiyama-cho, 30–40 m elev., 42.808958° N, 143.671614° E, 28 April 2018, *A. Uchida 20180003 (686)*; *ibid.*, Atsunai, 80–110 m elev., 42.899642° N, 143.781294° E, 28 April, 2018, *A. Uchida 20180009 (697)*; Kamishihoro-cho, Shimizudani, 357 m elev., 43.309319° N, 143.314489° E, 9 May 2018, *Y. Oppata 3615*.

Aomori Pref.: Hirosaki-shi, Osuke, 40.566500° N, 140.339528° E, 125–175 m elev., 22 Aug. 2017, *Uchida 20170031* (Hirosaki-4); *ibid.*, Hirosaki Park, 38 m elev., 40.6097° N, 140.4646° E, 11 Sept. 2018, *M. Sawada 20180911-2*; Towada-shi, Takada, Mts. Hakkoda, Tsuta-onsen, 480 m elev., 40.596389° N, 140.954167° E, 18 Oct. 2018, *T. Yamaguchi 39375*; Higashitori-mura, Shitsukari, Kuwahatayama, 202 m elev., 41.3833° N, 141.4500° E, 6 Nov. 2018, *M. Sawada 20181106-1, 2* and *3*; Fukaura-machi, Iwasaki, 133 m elev., 40.5826° N, 139.9887° E, 25 Aug. 2019, *M. Sawada 20190825-2*; Sai-mura, Mt. Muidoushi, 579 m elev., 41.3167° N, 140.8500° E, 21 Sept. 2018, *M. Sawada 20180921*.

Iwate Pref.: Ichinohe-machi, Nesori, Kawamukai, 240 m elev., 40.1907° N, 141.3356° E, 18 March 2021, *S. Sato 2021310-1*; *ibid.*, Torikoe Shrine, 150 m elev., 40.2376° N, 141.2815° E, 18 March 2021, *S. Sato 2021318-5*.

Miyagi Pref.: Shitikashuku-machi, Watarase Wind Hole, Aug. 1993, *H. Akiyama s.n.* (see Akiama and Hiraoka 1994).

Yamagata Pref.: Yonezawa-shi, Shirabu-onsen spa, 1130 m elev., 37.77144° N, 140.132267° E, 23 Sept. 2019, *H. Shirasaki 26635*.

Tochigi Pref.: Sano-shi, Akiyama-cho, 365 m elev., 36.547275° N, 139.507441° E, 24 March 2018, *H. Ikeda 647*; Kanuma-shi, Iriawano, 950 m elev., 36.618400° N, 139.532290° E, 4 June 2018, *Y. Ohshima s.n.*; Sano-shi, Akiyama-cho, 365 m elev., 36.547275° N, 139.507441° E, 24 March 2018, *H. Ikeda 647*; Tochigi-shi, Izuru-cho, in the vicinity of Manganji temple, 340 m elev., 36.4789° N, 139.5859° E, 11 May 2018, *T. Saeki 4463*.

Gunma Pref.: Tsumagoi-mura, Oomae, Hosohara, 26 Nov. 2017, *A. Yoshida 43*; Higashi-Agatsuma-machi, Iwai, 347 m elev., 36.53° N, 138.84° E, 1 Dec. 2017, *K. Nakazawa 1004*; *ibid.*, Koizumi, 412 m elev., *K. Nakazawa 1022*; Ueno-ura, Narahara, 700 m elev., 36.081833° N, 138.737639° E, 30 Dec. 2017, *M. Kimura 8417*; Kannna-machi, Kagahara, 435 m elev., 36.090556° N, 138.82741° E, 30 Dec. 2017, *M. Kimura 8419*; *ibid.*, 500 m elev., 36.072139° N, 138.829222° E, 30 Dec. 2017, *M. Kimura 8418*; Fujioka-shi, Shimohino, Kuroishi, 290 m elev., 36.203200° N, 138.987319° E, 31 Dec. 2017, *M. Kimura 8421*.

Ibaraki Pref.: Kitaibaragi-shi, Hanakawa-cho, Hanazono Shrine, 410 m elev., 36.860525° N, 140.628152° E, 9 March 2019, *H. Akiyama 25950*; *ibid.*, Okubo-cho, Okubo Window hole, 125 m elev., 36.5643° N, 140.6087° E, 9 March 2019, *H. Akiyama 25961* and *25965*; *ibid.*, 11 Dec. 2018, *M. Uzawa 4771*.

Saitama Pref.: Chichibu-shi, Otaki, Jyumonji-toge Pass,

1970 m elev., 35.9434° N, 138.7343° E, Sept. 2018, *T. Furuki 25098*; *ibid.*, en route from Mitsumineguchi to Suba, 350 m elev., 35.954394° N, 138.966105° E, 7 March 2019, *H. Akiyama 25940*.

Tokyo Metr.: Hachiouji-shi, Takao-cho, Mt. Takao, 6th trail, 4 Dec. 2017, *H. Akiyama 25274*; *ibid.*, Hikage-zawa, 4 Dec. 2017, *H. Akiyama 25285*; Uratakao-cho, 4 Dec. 2017, *H. Akiyama 25290*; Okutama-cho, Nippara, in the vicinity of Limestone Cave, 630 m elev., 35.8520° N, 139.0405° E, 5 Dec. 2017, *H. Akiyama 25291* and *25292*; *ibid.*, Higashinippara, 615 m elev., 35.8471° N, 139.0388° E, 5 Dec. 2017, *H. Akiyama 25296*, *25297* and *25298*; *ibid.*, Nippara, Kurasawa, 510 m elev., 35.8428° N, 139.0625° E, 5 Dec. 2017, *H. Akiyama 25302*.

Yamanashi Pref.: Hokuto-shi, Kiyosato, 1360 m elev., 35.930000° N, 138.433889° E, 3 June 2018, *H. Ishiko 180603*.

Shizuoka Pref.: Kawanehon-cho, Kurishiro, 35.182750° N, 138.153000° E, 22 Dec. 2017, *M. Ohta 2017122201*.

Nagano Pref.: Karuizawa-cho, Nagakura, Shiraitonotaki trail, 26 Nov. 2017, *A. Yoshida 44*; Matsukawa-cho, Ikuta, 35.588015° N, 137.975924° E, 17 Dec. 2017, *M. Ohta 2017121702*; Chino-shi, Toyotaira, upper reach of Shibukawa-onsen Spur, 1650 m elev., 36.0367° N, 138.3050° E, 28 June 2019, *T. Furuki 25367*; *ibid.*, Meiji-onsen Spur, 9 Sept. 2018, *M. Michimori 201809091*; Ina-shi, Ina, foot of Mt. Chausu, 1373 m elev., 35.825031° N, 137.854775° E, 1 July 2018, *Y. Oishi 20180701-1*; Kiso-machi, Mitake, 885 m elev., 35.86417° N, 137.59931° E, 30 Aug. 2018, *H. Akiyama 25698*; *ibid.*, 812 m elev., 35.83676° N, 137.63362° E, 30 Aug. 2018, *H. Akiyama 25699*; Nagiso-machi, Ohira Pass, 1350 m elev., 35.55293° N, 137.69433° E, 30 Aug. 2018, *H. Akiyama 25706*; Iida-shi, Iida Pass, 1220 m elev., 35.55606° N, 137.73500° E, 30 Aug. 2018, *H. Akiyama 25707*; Fujimi-cho, foot of Mt. Nyugasa, 1640 m elev., 35.899722° N, 138.188611° E, 30 Aug. 2018, *T. Fukuda s.n.*; Ueda-shi, backyard of Ryukoin Temple, 585 m elev., 36.3386° N, 138.1917° E, 18 June 2019, *M. Uzawa 5012*; Matsumoto-shi, Azumi, Sawando, Sawando Bridge, 1020 m elev., 36.162778° N, 137.660000° E, 19 Sept. 2019, *M. Uzawa 5194*.

Niigata Pref.: Murakami-shi, Takane, Suzugataki, 340 m elev., 38.342500° N, 139.667500° E, 9 Sept. 2018, *H. Shirasaki 25383*.

Toyama Pref.: Toyama-shi, Arimine, Oritate, 1130 m elev., 36.48883° N, 137.46329° E, 29 Aug. 2018, *H. Akiyama 25676*; *ibid.*, 1360 m elev., 36.48274° N, 137.47443° E, 29 Aug. 2018, *H. Akiyama 25679*.

Gifu Pref.: Gero-shi, Kosaka-cho, Nigorigo-onsen, 1747 m elev., 35.923278° N, 137.447778° E, 31 July 2018, *M. Chishiki 5851*; Yamagata-shi, Taguri, 154 m elev., 35.599967° N, 136.746410° E, 23 March 2021, *H. Akiyama 26562*.

Mie Pref.: Matsusaka-shi, Iitaka-cho, Hachisu, Miyanotani

valley, 450-600 m elev., 34.340278° N, 136.146111° E., 18 May 2017, *H. Akiyama 24973*; Nabari-shi, Akame-shijyuhachi-taki valley, beside the Senjyutak fall, 377 m elev., 34.5609° N, 136.0891° E, 27 May 2019, *H. Akiyama 26043*; *ibid.*, in the vicinity of Ryugatubo, 384 m elev., 34.5603° N, 136.0900° E, 27 May 2019, *H. Akiyama 26044*.

Shiga Pref.: Maibara-shi, Mt. Ibuki, 600m NEE from summit car park, 1166 m elev., 35.425681° N, 136.416271° E, 16 Sept. 2019, *Y. Kasai 7607*.

Kyoto Pref.: Kyoto-shi, Nishikyo-ku, Arashiyama, Genrokuzan-cho, *T. Saeki 4342*; *ibid.*, *H. Akiyama 25807*; Kyotanba-cho, Shizushi Limestone Cave, 380 m elev., 10 Sept. 2011, *H. Akiyama 21981*.

Nara Pref.: Tenkawa-mura, Dorogawa, in the vicinity of Godaimatu limestone cave, 900 m elev., 34.2651° N, 135.8950° E, 20 Oct. 2019, *T. Saeki 5209*.

Hyogo Pref.: Yabu-shi, Oya-cho, Yokoiki Valley, 770 m elev., 35.3072° N, 134.5218° E, 30 Nov. 2020, *H. Akiyama 26470*; *ibid.*, 30 March 2021, *H. Akiyama 26617*.

Okayama Pref.: Niimi-shi, Ikura, Ikura limestone Cave, 140 m elev., 34.930000° N, 133.523056° E, 10 July 2017, *H. Akiyama 25103*; *ibid.*, Rasyomon, Sept. 2019, *A. Kato s.n.* (photos); Hisaka Limestone Cave, Aug. 2019, *H. Akiyama s.n.*

Hiroshima Pref.: Shobara-shi, Tojo-cho, Kami-Taishakukyo, ca. 410 m elev., 34.867500° N, 133.207222° E, 10 July, 2017, *H. Akiyama 25094*, *25097*, *25098*, *25099* and *25100*; *ibid.*, 14 March 2018, *H. Akiyama 25437* and *25438*.

Yamaguchi Pref.: Mine-shi, Taishodo limestone cave, 160 m elev., 34.2771° N, 131.3187° E, 8 Dec. 2017, *M. Hayashi 25598*.

Tokushima Pref.: Miyoshi-shi, Higashiiyadani, Mt. Tsurugij, 1780 m elev., 33.856944° N, 134.092500° E, 17 July 2018, *M. Saji 1529*; *ibid.*, 1750 m elev., 33.857222° N, 134.091667° E, 17 July 2018, *M. Saji 1530*; Kamikatsu-cho, Masaki, Jiganji temple, 33.941725° N, 134.427392° E, 7 April, 2020, *M. Saji 2998*.

Ehime Pref.: Toon-shi, Kamibayashi Forest Park, in the vicinity of a wind-hole, 980 m elev., 33.72278° N, 132.88535° E, 18 Oct. 2018, *K. Iwata 4467*, *4468* and *4469*.

Fukuoka Pref.: Kitakyusyu-shi, Kokuraminami-ku, Hiraodai, Ubusune-no-hokora, 33.75089° N, 130.8941° E, 24 March 2018, *K. Honda s.n.*; *ibid.*, 390 m elev., 29 Aug. 2019, *H. Akiyama 26704* and *26706*; Kama-shi, Mt. Kosho-san, Okunoin, at the base of limestone cliff, 840 m alt., 33.4839° N, 130.7252° E, 9 Nov. 2020, *T. Ohya 601*; *ibid.*, 539 m elev., 33.481389° N, 130.720278° E, 28 Oct. 2020, *M. Chishiki s.n.*

Kumamoto Pref.: Yamae-mura, Man'e, 750 m elev., 25 July 2018, *M. Matsumoto s.n.*

TAIWAN.

Nantou Co.: Ren'ai township, Mt. Hehuanshan, behind the High altitude experimental branch, 3000 m elev., 24.1617° N,

121.2869° E, 31 May 2018, *H. Akiyama 25580*; *ibid.*, along Renhe Road, in the vicinity of Ren'ai, 2340 m elev., 24.10° N, 121.20° E, 1 June 2018, *H. Akiyama 25611* and *25612*;

ibid., in the vicinity of Ren'ai, Rueiyan River Major Wildlife Habitat, 2200 m elev., 24.1042° N, 121.1973° E, 1 June 2018, *H. Akiyama 25613, 25614, 25615* and *25616*.

***Conocephalum toyotae* H. Akiyama**

JAPAN.

Hokkaido Pref.: Rishiri Isl., Rishirifuji-cho, Oniwaki, Mt. Rishiri, 700–720 m elev., 45.168789° N, 141.251500° E, 8 Sept. 2018, *A. Uchida 20180051 (713)*; *ibid.*, Oshidomari, Himenuma, 130 m elev., 45.226108° N, 141.247228° E, 27 June 2018, *K. Kawai 15682*; Nakagawa-cho, 30–50 m elev., 44.800178° N, 142.077539° E, 10 Sept. 2018, *A. Uchida 20180058 (716)*; Shari-cho, Honmachi, 5–15 m elev., 43.913667° N, 144.670222° E, 07 July 2017, *A. Uchida 20170004* (Hokkaido-1); *ibid.*, Raiun, 60–65 m elev., 43.835222° N, 144.643000° E, 12 July, 2017, *A. Uchida 2017005* (Hokkaido-2); Kamikawa-cho, Aizan-kei, 1040–1060 m elev., 43.717528° N, 142.818083° E, 2 Aug. 2017, *A. Uchida 20170020* (Hokkaido-9); *ibid.*, Soun-kyo, 750–850 m elev., 43.720278° N, 142.960306° E, 4 Aug. 2017, *A. Uchida 20170023* (Hokkaido-11); Kamishihoro-cho, 309 m elev., 43.250351° N, 143.353432° E, 9 May 2018, *Y. Oppata 3610*; Sapporo-shi, Mt. Soranuma, 470 m elev., 12 Aug. 2018, *T. Saeki 4672*; *ibid.*, Minami-ku, Tokiwa-Nijyo, Sapporo Art Park, 20 Aug. 2018, *T. Saeki 4675* and *4676*; Makkari-mura, Yashiro, Yoteizan Nature Park, 18 Aug. 2018, *T. Saeki 4674*; Kuromatsunai-cho, Kuromatsunai, in the vicinity of *Fagus crenata* Center, 95 m elev., 42.651111° N, 140.306389° E, 16 Sept. 2018, *Y. Oppata Yo-3707*; Otaru-shi, Nagahashi, Naebo Park, 80 m elev., 43.26° N, 140.98° E, 30 July 2019, *T. Saeki 5159*.

Aomori Pref.: Hirosaki-shi, Hyakuzawa, 135–145 m elev., 40.649806° N, 140.371194° E, 19 Aug. 2017, *A. Uchida s.n.* (Hirosaki-1); Towada-shi, Takada, Mts. Hakkoda, Tsuta-onsen, 480 m elev., 40.596389° N, 140.954167° E, 18 Oct. 2018, *T. Yamaguchi 39376*; *ibid.*, 470 m elev., 40.596389° N, 140.953056° E, 31 May 2018, *T. Saeki 4501* and *4502*; *ibid.*, Oirase-keikoku valley, Sept. 2018, *E. Tamagawa s.n.*; *ibid.*, 250 m elev., 22 Oct. 2018, *M. Sawada 20181022-1*; Aomori-shi, Shinjyou-hiraoka, Morinohiroba Park, 50 m elev., 40.7997° N, 140.6715° E, May 2018, *M. Sawada 20180506*.

Akita Pref.: Higashinaruse-mura, Iwaigawa, Kakkyogawa National Forest, Tensho Fall, 440 m elev., 39.1790° N, 140.7528° E, 18 Aug. 2020, *S. Sato TSF 1*.

Yamagata Pref.: Nishimurayama-gun, Nishikawa-machi, Iwanezawa, 420 m elev., 38.456988° N, 140.100939° E, 11 Dec. 2019, *M. Kimura 8626*; Sagae-shi, Jionji, Jionji temple,

165 m elev., 38.410174° N, 140.249627° E, 11 Dec. 2019, *M. Kimura 8629*.

Iwate Pref.: Ichinohe-machi, Nesori, Kawamukai, 240 m elev., 40.1907° N, 141.3956° E, 18 March 2021, *S. Sato 2021318-3*.

Miyagi Pref.: Kurihara-shi, Hanayama, Kusakizawa Kadoma, 240 m elev., 38.786886° N, 140.788652° E, 19 Sept. 2019, *N. Morita 5*.

Fukushima Pref.: Hinoemata-mura, Mt. Hiuchi, Oze, Dangoya-saka, 1584 m elev., 36.9357° N, 139.2746° E, 31 Aug. 2019, *S. Nemoto 974*.

Tochigi Pref.: Nikko-shi, Yumoto, 1566 m elev., 36.804526° N, 139.412878° E, 14 June 2018, *Y. Ohshima s.n.*

Gunma Pref.: Tone-gun, Minakami-machi, Mt. Omine, Minamigatani moor, 1050 m elev., 36.7353° N, 138.9207° E, 12 Oct. 2020, *K. Nakazawa 8131*.

Nagano Pref.: Kisofukushima-shi, Kaidakogen, Shimonohara, 1200 m elev., 35.967° N, 137.550° E, 2 Oct. 2016, *H. Akiyama 24820*; *ibid.*, Nishisatoko, 1270 m elev., 35.97106° N, 137.54943° E, 30 Aug. 2018, *H. Akiyama 25696*; Iida-shi, Iida Pass, 1220 m elev., 35.55606° N, 137.73500° E, 30 Aug. 2018, *H. Akiyama 25708*; Shimojyo-mura, Yohi, 560 m elev., 35.372963° N, 137.791048° E, 31 Aug. 2018, *H. Akiyama 25717*; Anan-cho, Shinno, 890 m elev., 35.243581° N, 137.762288° E, 31 Aug. 2018, *H. Akiyama 25721*; Karuizawa-machi, Nagakura, Shiraitonotaki-fall trail, 1260 m elev., 36.4099° N, 138.5942° E, 26 Nov. 2017, *A. Yoshida 44* and *45*; Ueda-shi, Bessho Spur, Bessho-Hizawa Wind Hole, 820 m elev., 36.3338° N, 138.1487° E, 18 June 2019, *M. Uzawa, Y. Degawa and T. Hosono 5025*.

Niigata Pref.: Yuzawa-cho, Mt. Naeba, 959 m elev., 36.88859° N, 138.754256° E, 17 June 2018, *H. Shirasaki 25259*; Itoigawa-shi, Kajiyama, Mt. Nokogiri, 1180 m elev., 36.921389° N, 137.968333° E, 15 July 2018, *H. Shirasaki 25292*; Myoko-shi, Ikenotaira, Imoriike pond, 740 m elev., 36.866111° N, 138.177023° E, 19 Oct. 2019, *H. Shirasaki 26686* (intermingled with *C. orientalis*); Uonuma-shi, Ozegahara, in the vicinity of Toden lodge, 1390 m elev., 39.944721° N, 139.242525° E, 12 July 2020, *M. Uzawa 5550*.

Toyama Pref.: Toyama-shi, Nakachiyama, 337 m elev., 36.57113° N, 137.37194° E, 29 Aug. 2018, *H. Akiyama 25672*; *ibid.*, Arimine, 905–1100 m elev., 36.51058–36.41950°

N, 137.43948–137.4499° E, 29 Aug. 2018, *H. Akiyama* 25673, 25674, 25475, 25680, 25681, 25682, 25683 and 25684; *ibid.*, Oritate, 1130 m elev., 36.48883° N, 137.46329° E, 29 Aug. 2018, *H. Akiyama* 25677; Tateyama-machi, Ashikuraji, between Hyakken-Nameri and Ryujitaki fall, 740 m elev., 36.570058° N, 137.446152° E, 30 Aug. 2018, *M. Michimori* 20180830-1 and 2.

Ishikawa Pref.: Hakusan-shi, Chugu, backyard of Exhibition Center building, 600 m elev., 36.261304° N, 136.76056° E, 27 Aug. 2018, *H. Akiyama* 25663.

Gifu Pref.: Hida-shi, Kamioka-cho, Iwaitani, 880 m elev., 36.39347° N, 137.38170° E, 29 Aug. 2018, *H. Akiyama* 25687; *ibid.*, Wasafu, Yamanomura camping site, 980 m elev., 36.40038° N, 137.39699° E, 29 Aug. 2018, *H. Akiyama* 25689; Gujyo-shi, Meiho, Hatasa, 800 m elev., 35.858220° N, 137.070470° E, 24 March 2021, *H. Akiyama* 26589.

Aichi Pref.: Toyone-mura, Sakauba, 890 m elev., 35.186686° N, 137.675099° E, 31 Aug. 2018, *H. Akiyama* 25724.

Mie Pref.: Inabe-shi, Fujiwara-cho, Oogaito, Mt. Oike, 712 m elev., 35.1886° N, 136.4239° E, 4 April 2018, *M. Chishiki* 5845 (intermingled with *C. orientalis*); Matsusaka-shi, Sakanai-cho, en route to Sakanai Fudo Shrine, 205 m elev., 34.526074° N, 136.430977° E, 03 Oct. 2019, *N. Morita* 7 (intermingled with *C. orientalis*); *ibid.*, 240 m elev., 34.526396° N, 136.431006° E, 14 March 2021, *N. Morita s.n.*

Kyoto Pref.: Kyoto-shi, Sakyo-ku, Kurama-Kibune-cho, 340 m elev., 35.128611° N, 135.765278° E, 13 Dec. 2017, *T. Saeki* 4345; Nantan-shi, Miyama-cho, Ashu, 412 m elev., 35.320000° N, 135.720278° E, 30 Oct. 2018, *M. Chishiki* 5864.

Nara Pref.: Uda-shi, Haibara, Nizaka, Fukatani-Ryuchin

valley, 320 m elev., 34.54888° N, 136.0111° E, 18 April 2019, *T. Saeki* 4985; Yoshino-gun, Kawakami-mura, Ikari, 770 m elev., 33.340324° N, 136.009267° E, 17 Jan. 2020, *M. Kimura* 8634.

Hyogo Pref.: *ibid.*, Ohya-cho, Yokoiki-keikoku valley, 980 m elev., 35.3409° N, 134.5276° E, 9 Oct. 2018, *H. Akiyama* 25796 (intermingled with *C. orientalis*); *ibid.*, 30 Nov. 2020, *H. Akiyama* 26466; *ibid.*, 30 March 2021, *H. Akiyama* 26611; Shinonsen-cho, Kishida, upper reach of Kishiada river, Kiritaki-keikoku, 450 m elev., 35.4652° N, 134.4689° E, 29 Nov. 2018, *H. Akiyama* 25822 and 25823.

Okayama Pref.: Kagamino-cho, Kamisaibara, 915 m elev., 35.344722° N, 133.998333° E, 26 Nov. 2019, *M. Chishiki* 5821.

Tottori Pref.: Aoya-cho, Tawaradani, Fudotaki Fall, 83 m elev., 35.476667° N, 133.969444° E, 30 Oct. 2019, *M. Chishiki s.n.*; Kofu-cho, Mitsukue, 600 m elev., 25 Aug. 2018, *A. Kato s.n.*; Saji-cho, Tatsumi-toge pass, 746 m elev., 35.315265 N, 134.002508 E, 26 Aug. 2019, *H. Akiyama* 26087.

Tokushima Pref.: Katsuura-machi, Tanano, Mamidani, 410 m elev., 33.870000° N, 134.455556° E, 26 Nov. 2016, *M. Toyota s.n.* (intermingled with *C. orientalis*); *ibid.*, 19 Nov. 2017, *H. Akiyama* 25254 (intermingled with *C. orientalis*); Anan-shi, Mizui-cho, Wakasugidani, 190 m elev., 33.894167° N, 134.522222° E, 24 Dec. 2018, *M. Saji* 1891.

Ehime Pref.: Saijyo-shi, Fujinoishi, Mt. Kanpuzan, 1547 m elev., 33.808333° N, 133.257500° E, 24 Sept. 2018, *M. Chishiki* 5858; *ibid.*, 1550 m elev., 33.80757° N, 133.26030° E, 28 Oct. 2018, *K. Iwata* 4495; Kita-gun, Uchiko-cho, Nakagawa, Odamiyama-keikoku, 800 m elev., 33.53120° N, 132.89399° E, 22 March 2019, *K. Iwata* 4769.

Legends for Plates.

Plate 1. *Conocephalum orientalis* (1).

A: Young female plants. B: Ditto, underside. C: Ditto. Note that thallus of last growing season changed color into deep reddish purple on undersides. D: Young male plants. E: New male receptacles are often born on a short petiolate branch, which can raise them into higher position. F: Old male plants (male receptacles already dropped-off). G: Newly produced thalli are sometime tinged reddish purple even in spring and summer seasons. H: Plants under diffused light often produce thin thalli, which resemble those of *C. salebrosum*. I: Comparison of thin thallus (left) and normal thallus (right) of *C. orientalis*. J: Female receptacle (carpocephalum) with fertilized sporophytes inside. K: Carpocephala on the top of elongated stalks. L: Plants from Taiwan with reddish purple color on ventral surface. A–E: Hyogo Pref., Tatsuno-shi, 8 June 2018. F: Tokyo Metr. Mt. Takao, 4 Dec. 2017. G: Ditto., 22 June 2017 (photo taken by Ms. S. Suzuki). H: Mie Pref., Nabari-shi, 26 Nov. 2017. I: Hyogo Pref., Kamigori-cho, 8 Sept. 2020. J: Tokyo Metr. Mt. Takao, 4 Dec. 2017. K: Mie Pref., Nabari-shi, 31 March 2018. L: Taiwan, Chito, 7 June 2018, *Akiyama 25656*. Scale bars = 5 mm.

Plate 2. *Conocephalum orientalis* (2). Variation in thallus appearance including J2 and J3 types.

A: Morphological variation within a single population. B: Plants can grow directly on boulder in southwestern Japan, where rain falls heavily. C and D: Color variation within a single locality. Plants with yellowish color tend to grow at more sunny places. E and F: J2 type of *C. orientalis*, with wavy thallus margins. G–L: J3 types of *C. orientalis* with reddish purple color on ventral surface of thallus. Note that dorsal grooves between air chambers more or less distinctly blackish reddish purple in color. A: Mie Pref., Nabari-shi, 14 June 2016. B: Miyazaki Pref., Nichinan-shi, 2 Sept. 2017. C and D: Aomori Pref., Towada-shi, Tsuta-spur (*C: Yamaguchi 39375*. D: *Yamaguchi 39374*). E and F: Tokushima Pref., Tokushima-shi, 10 March 2018 (*Akiyama 25379*). G and H: Hokkaido Pref., Shari-cho, 13 July 2017 (*Uchida s.n.*). I and J: Aomori Pref., Hirosaki-shi, 5 July 2020 (*Chishiki s.n.*). K and L: Hyogo Pref., Mt. Hyonoson, 9 Oct. 2018 (*Akiyama 25776*). Scale bars = 5 mm.

Plate 3. *Conocephalum purpureorubrum* (1) Western Japanese form (FW).

A and C: Dorsal surfaces of thalli. B and D: Ventral surfaces of thalli, totally or partially tinged reddish purple. E and F: Thalli not tinged reddish purple except for midrib and ventral scales. G and H: Carpocephala with matured sporophytes. I and J: Variation in appearance of dorsal surfaces of thalli within a single population. A and B: Mie Pref., Nabari-shi, 28 May 2019 (*Akiyama 26043*). C and D: Taiwan, Nantou Co. Xitou, 7 June 2018 (*Akiyama 25655*). E and F: Tokushima Pref., Kamikatsu-cho, 24 June 2017 (*Akiyama 25067*). G: Oita Pref., Saeki-shi, 13 March 2018. H: Oita Pref., Yufuin-machi, 12 March 2018. I and J: Fukuoka Pref., 29 Aug. 2019 (*Akiyama 26705*). Scale bars = 5 mm.

Plate 4. *Conocephalum purpureorubrum* (2) Eastern Japanese form (FE).

A–I: Variation of dorsal and ventral surfaces of thalli. A–C: Chiba Pref., Kyonan-machi, 9 Oct. 2018 (*Furuki 25043*). D: Toyama Pref., Tateyama-cho, 30 Aug. 2018 (*Michimori s.n.*). E: Tochigi Pref., Nikko-shi, 27 Apr. 2018 (*Ohshima s.n.*). F and G: Tokyo Metro., Mt. Takao, 4 Dec. 2017 (*Akiyama 25283*). H: Tokyo Metro., Okutama-cho, 5 Dec. 2017 (*Akiyama 25301*). I: Nagano Pref., Kiso-machi, 30 Aug. 2018 (*Akiyama 25700*). Scale bars = 5 mm.

Plate 5. *Conocephalum salebrosum*.

A: Dorsal surfaces of thalli. B: Dorsal and ventral surfaces of thalli. C: Plants on boulder covered with thin soil at Mt. Takao (Lower right: *C. orientalis* directly growing on soil). D: Ditto. Close-up of dry thalli. E: Plants growing on limestone boulder with very thin thallus. F: Plants growing on limestone cliff. G: Ditto. Close-up of both surfaces of thalli. H: Thallus with immature female carpocephalum. I: Plants growing on moist limestone wall. J: Ditto. Close-up of thalli. K: Plants at shaded, moist place becoming small in size. A: Tokushima Pref., Mt. Tsurugi, 17 July 2018 (*Saji 1529*). B: A: Taiwan, Taichung, 7 June 2018 (*Akiyama 25613*). C and D: Tokyo Metro., Mt. Takao, 4 Dec. 2017. E: Hokkaido Pref., Mt. Soranuma, 12 Aug. 2018 (*Saeki 4673*). F and G: Fukuoka Pref., Hiraodai, 30 Aug. 2019. H: Nagano Pref., Mts. Yatsugatake, 28 June 2019 (*Furuki 25367*). I–K: Tokyo Metro., Nippara, 5 Dec. 2017. Scale bars = 5 mm.

Plate 6. *Conocephalum toyotae*.

A and B: Typical habitat along a trail in *Cryptomeria japonica* plantation along a small and deep ravine. C: Suburban road-side habitat, mixed with *C. orientalis*. D: Female plant with a carpocephalum with fertilized sporophytes inside. E: Ditto. F: Ventral surfaces of female plants with carpocephala. G: Dorsal and ventral surfaces of thalli. H: Dorsal surface of thalli. I: Plants with poorly developed air chambers, showing reddish color of ventral tissues. J: Female plants with slightly developed carpocephala within cavities at the top of thalli. A, B and H: Tokushima Pref., Katsuura-machi, 19 Nov. 2017. C: Toyama Pref., Toyama-shi, 19 Aug. 2018. D–F: Toyama Pref., Tateyama-cho, 30 Aug. 2018 (*Akiyama 25673*). G: Hokkaido Pref., Sapporo-shi, 12 Aug. 2018 (*Saeki 4672*). H: Nagano Pref., Kaidakogen, 30 Aug. 2018 (*Akiyama 25696*). J: Nagano Pref., Iida-shi, 30 Aug. 2018 (*Akiyama 25708*). Scale bars = 5 mm.

Plate 7. Sporophytes and carpocephala with fertilized sporophytes of the 4 species of Japanese *Conocephalum*.

A and B; *C. purpureorubrum*. C and D; *C. salebrosum*. E and F; *C. orientalis*. G and H: Sporophytes and carpocephala bearing mature sporophytes for *C. purpureorubrum* (above), *C. salebrosum* (middle), and *C. orientalis* (below). I and J: *C. toyotae*. A: Tokyo Metro., Takao-san, 4 Dec. 2018. B, G (above) and H (above): Oita Pref., Saiki-shi, 13 March 2018. C, D, G (middle), and

H (middle): Hiroshima Pref., Taishaku-kyo, 14 March 2018. E, F, G (below) and H (below): Tokyo Metro, Takao-san, 4 Dec. 2018. I: Toyama Pref., Arimine, 29 Aug. 2018. J: Toyama Pref., Tateyama-cho, 11 June 2020. Scale bars = 2 mm.

Plate 8. Transverse sections of epidermis of *Conocephalum* species.

Note that (1) thick walls in *C. orientalis* and FE-form of *C. purpureorubum*, which cause their shiny appearance, and (2) scarcely furrowed grooves between air chambers in *C. salebrosum*. A, C, E, G, I, K, M, O and Q are from costal regions, and the others from wings. A–D: *C. orientalis* (A and B: Akiyama 25068. C and D: Ikeda 702). E–H: *C. purpureorubum* (FE-form. E and F: Akiyama 25944. G and H: Akiyama 25272). I–L: *C. purpureorubum* (FW-form. I and J: Akiyama 26103. K and L: Akiyama 25196). M–P: *C. salebrosum* (M and N: Akiyama 25615. O and P: Akiyama 25438). Q–S: *C. toyotae* (Q: Toyota 20161126. S: Morita s.n.). Scale bar = 25 μ m.

Plate 9. Mucilage canals and mucilage cells.

A–C and E: *Conocephalum salebrosum*. D and F: *C. purpureorubrum*. G: *C. toyotae*. H: *C. orientalis*. All samples except for H were soaked in 50 % methanol. A and B: Mucilage canals running along midribs and mucilage cells scattered over wings. (Hokkaido Pref., Shari-cho, Uchida s.n.). C: Ditto. (Yamagata Pref., Yonezawa-shi, Shirasaki 26635). D: Short mucilage canals and mucilage cells in aerenchyma just under a surface of carpocephalum (Miyazaki-shi, Nichinan, Matsumoto 20191212). E–G: Transverse sections of thalli showing cross-sections of mucilage canals. Note that *C. toyotae* lacks mucilage canals. H: Leak of transparent mucilage from cross-sections of mucilage canals. Scale bars = 5 mm (A and D); 1 mm (B and D); 200 μ m (E–G); 20 μ m (H).

Plate 10. Distribution maps (1).

A: *Conocephalum orientalis* (blank circle). B: *C. purpureorubum* (green square; including both Western and Eastern Japanese forms).

Plate 11. Distribution maps (2).

A: *Conocephalum salebrosum* (red square). B: *C. toyotae* (black star).



Plate 1. *Conocephalum orientalis* (1).



Plate 2. *Conocephalum orientalis* (2).



Plate 3. *Conocephalum purpureorubrum* Western Japanese form (FW).

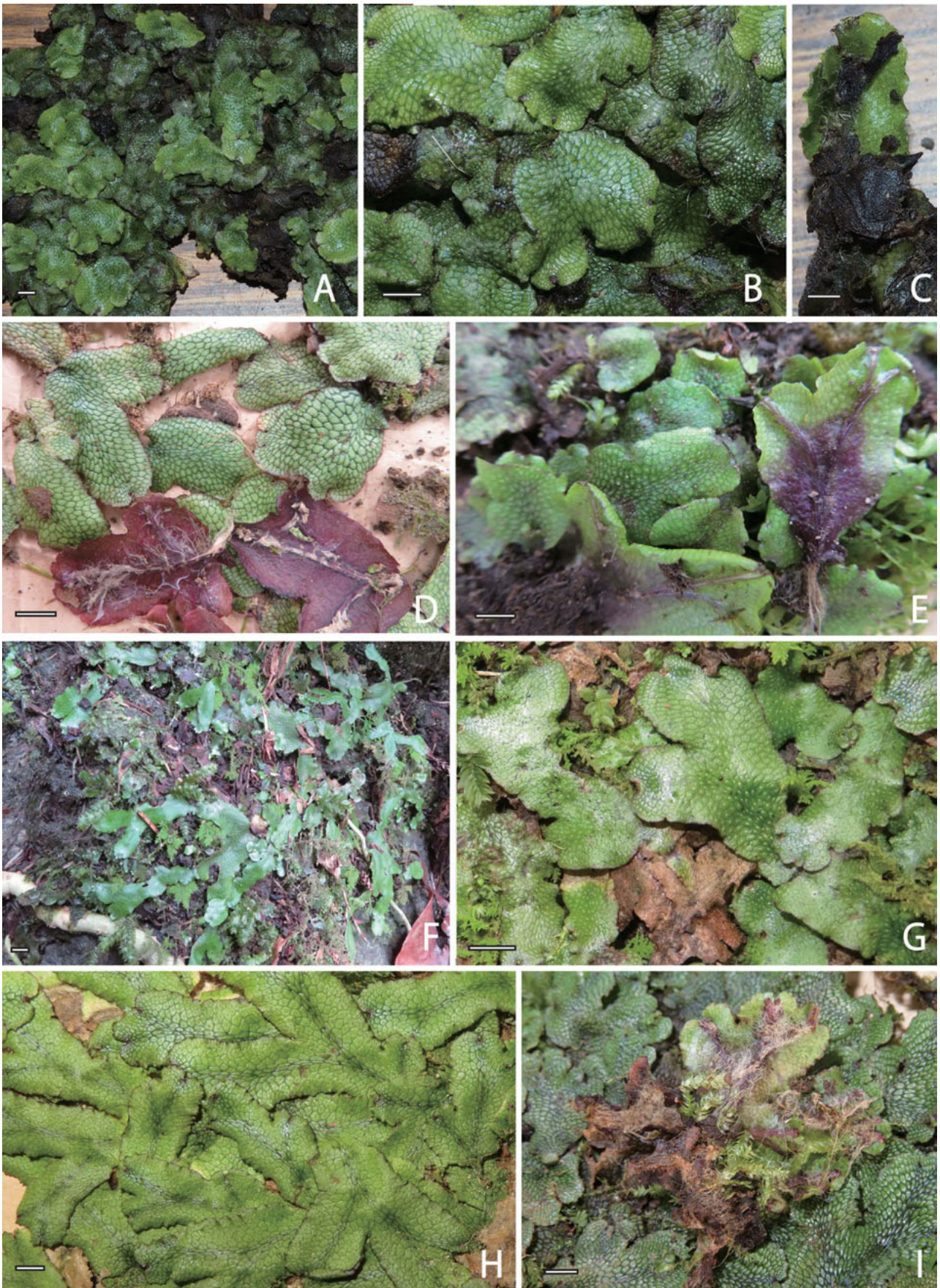


Plate 4. *Conocephalum purpureorubrum* Eastern Japanese form (FE).

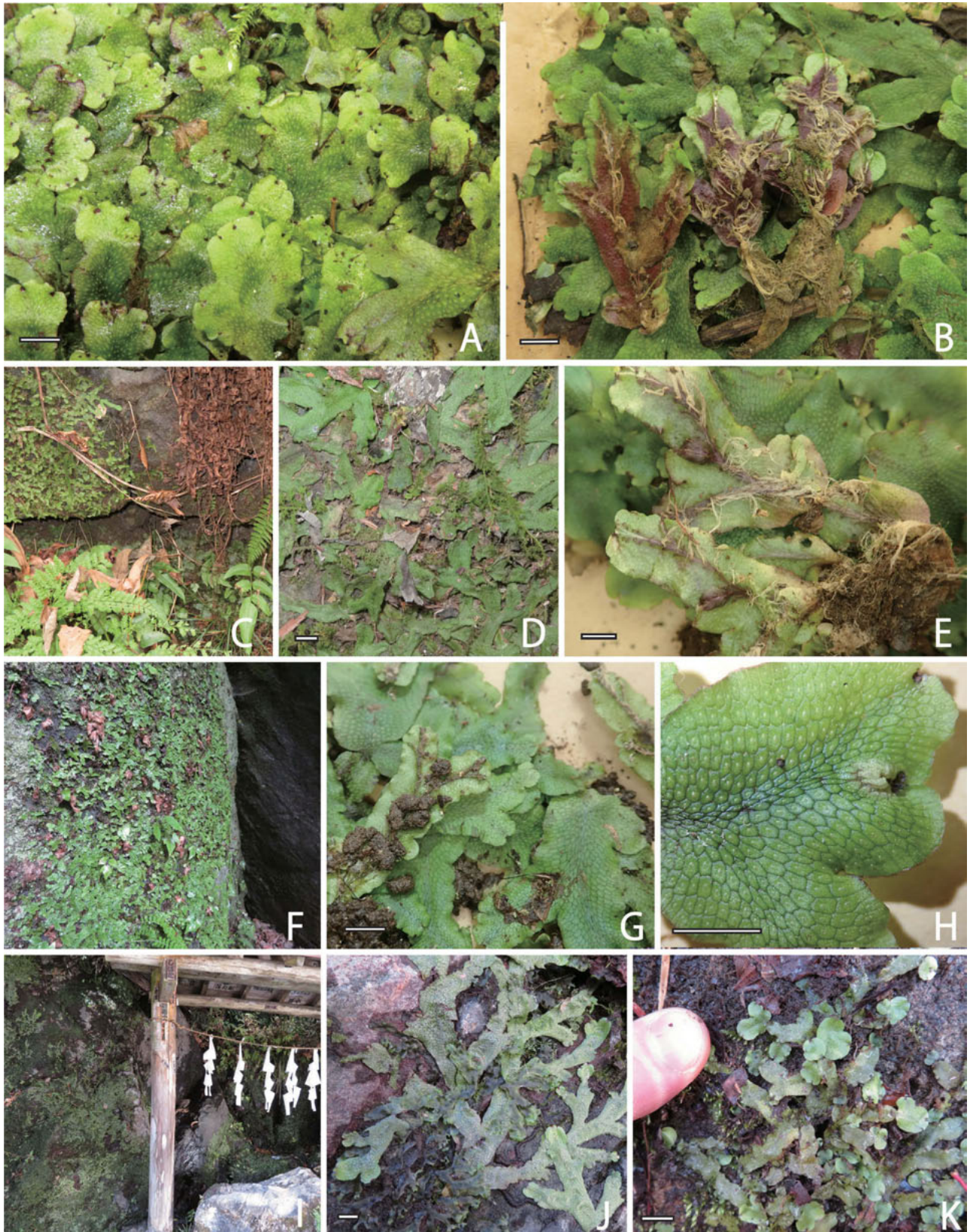


Plate 5. *Conocephalum salebrosum*.

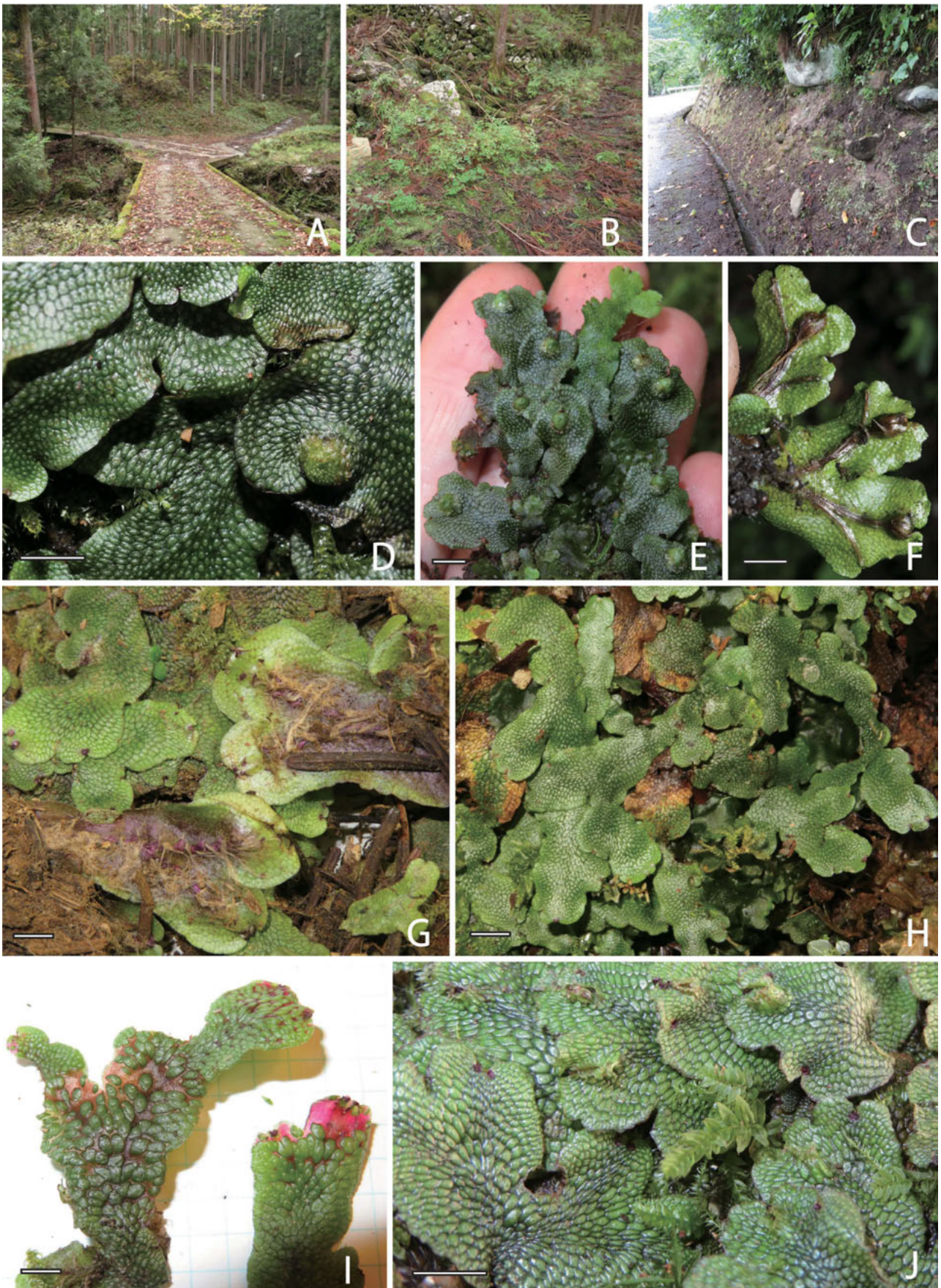


Plate 6. *Conocephalum toyotae*.

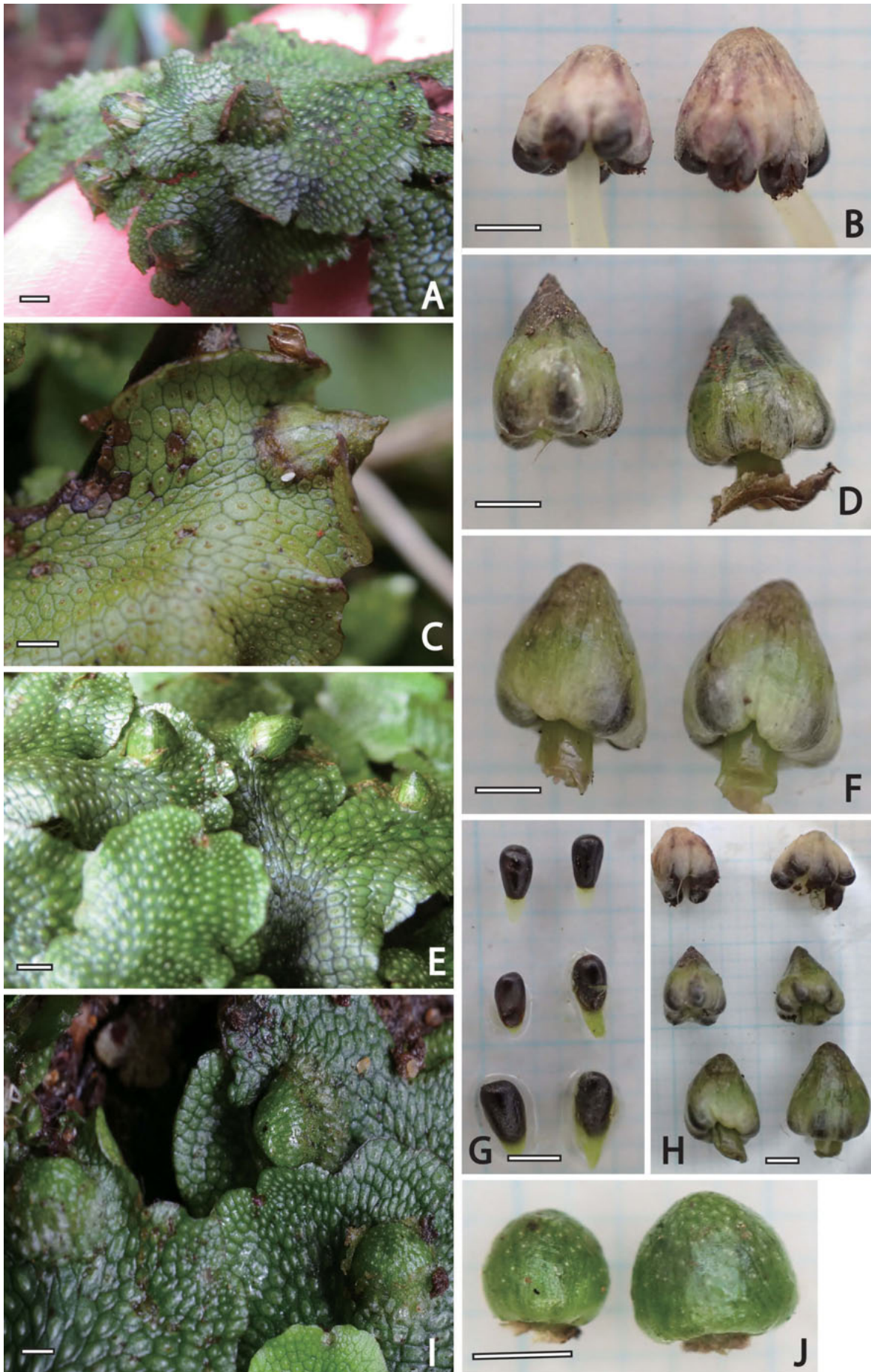


Plate 7. Sporophytes and carpocephala.

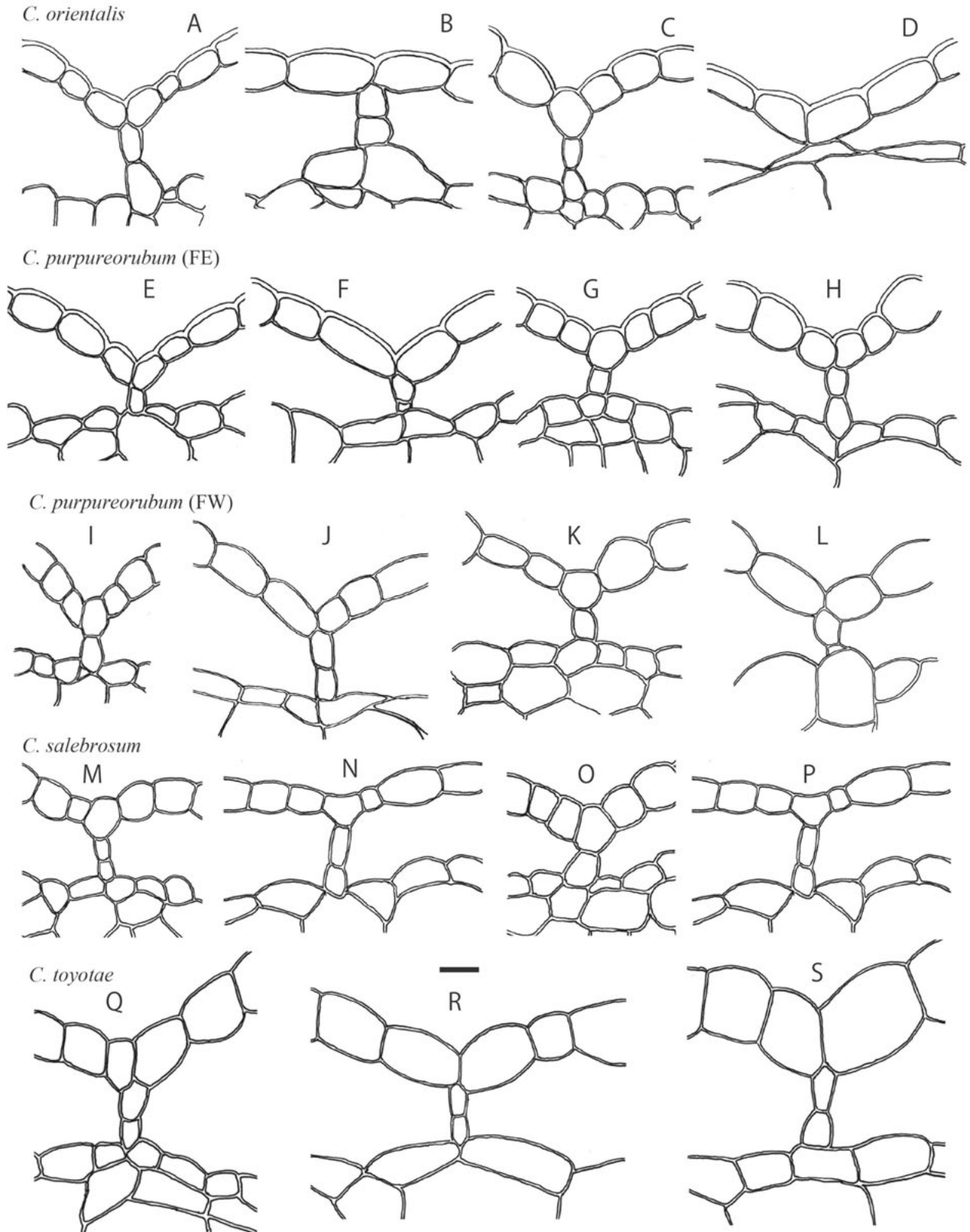


Plate 8. Transverse sections of epidermis.

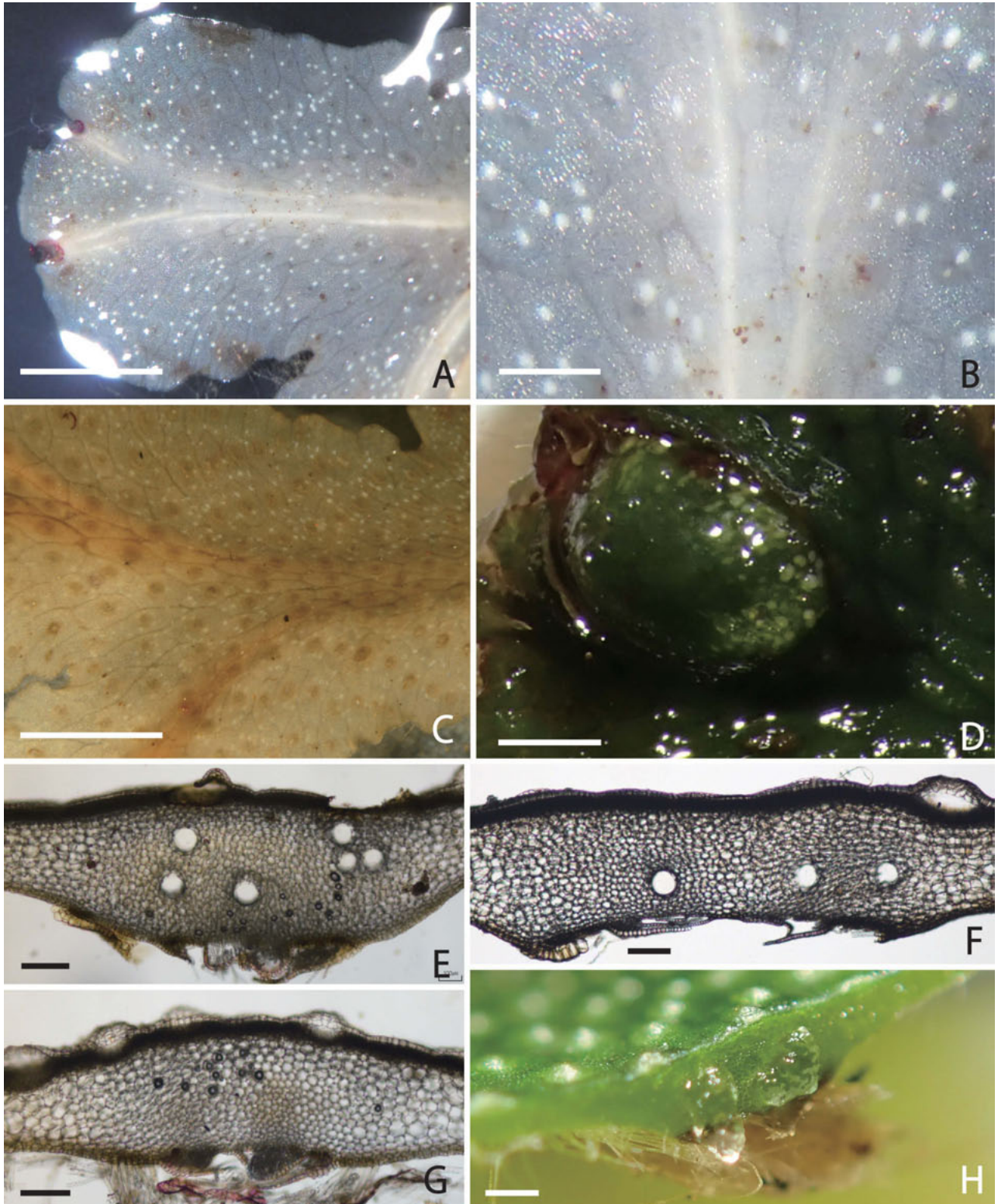


Plate 9. Mucilage canals and mucilage cells.

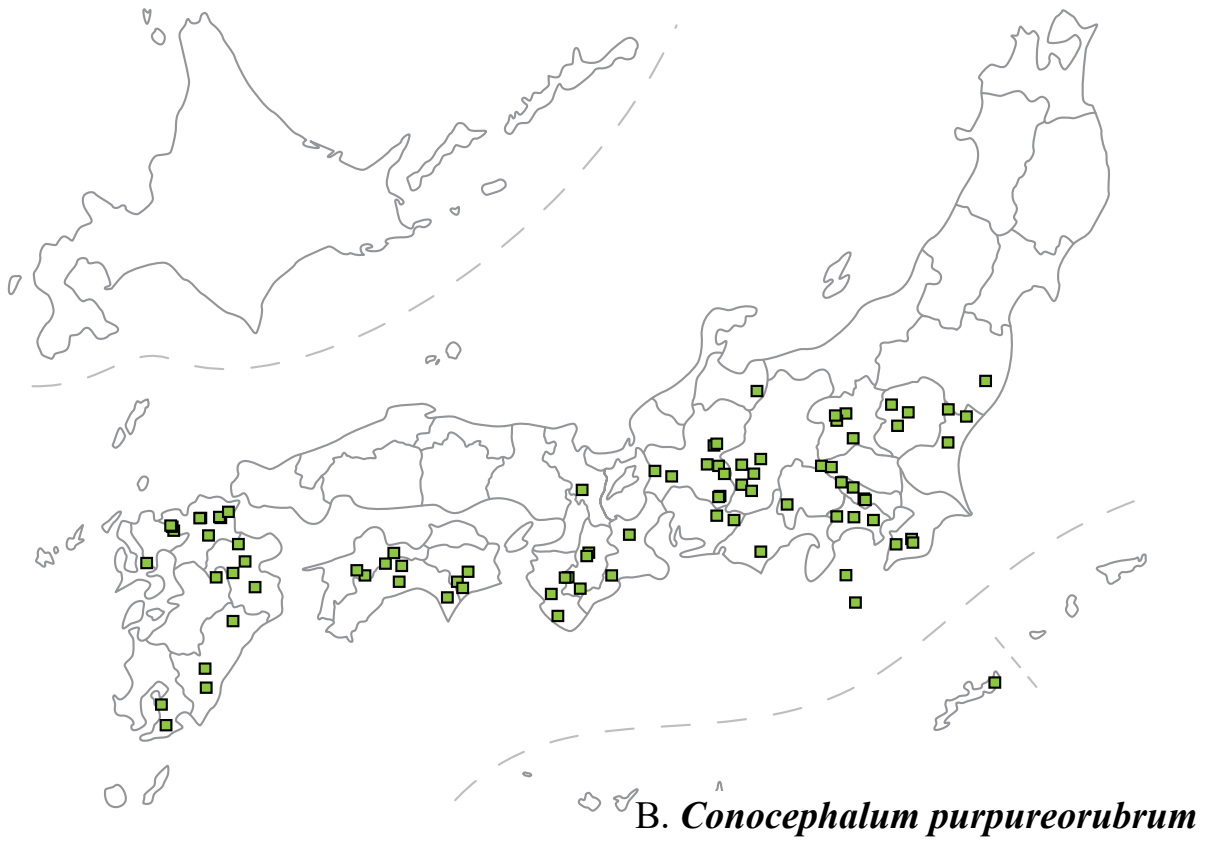
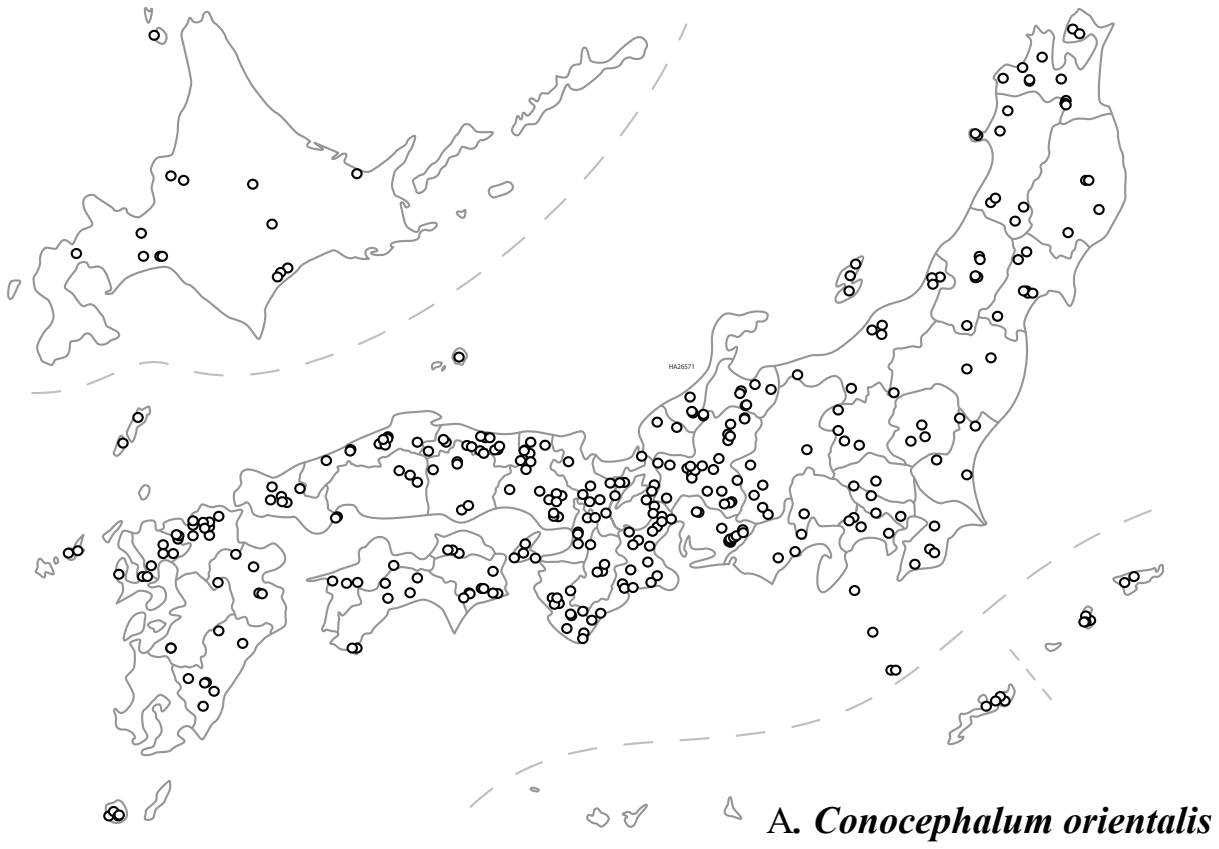


Plate 10. Distribution maps (1).

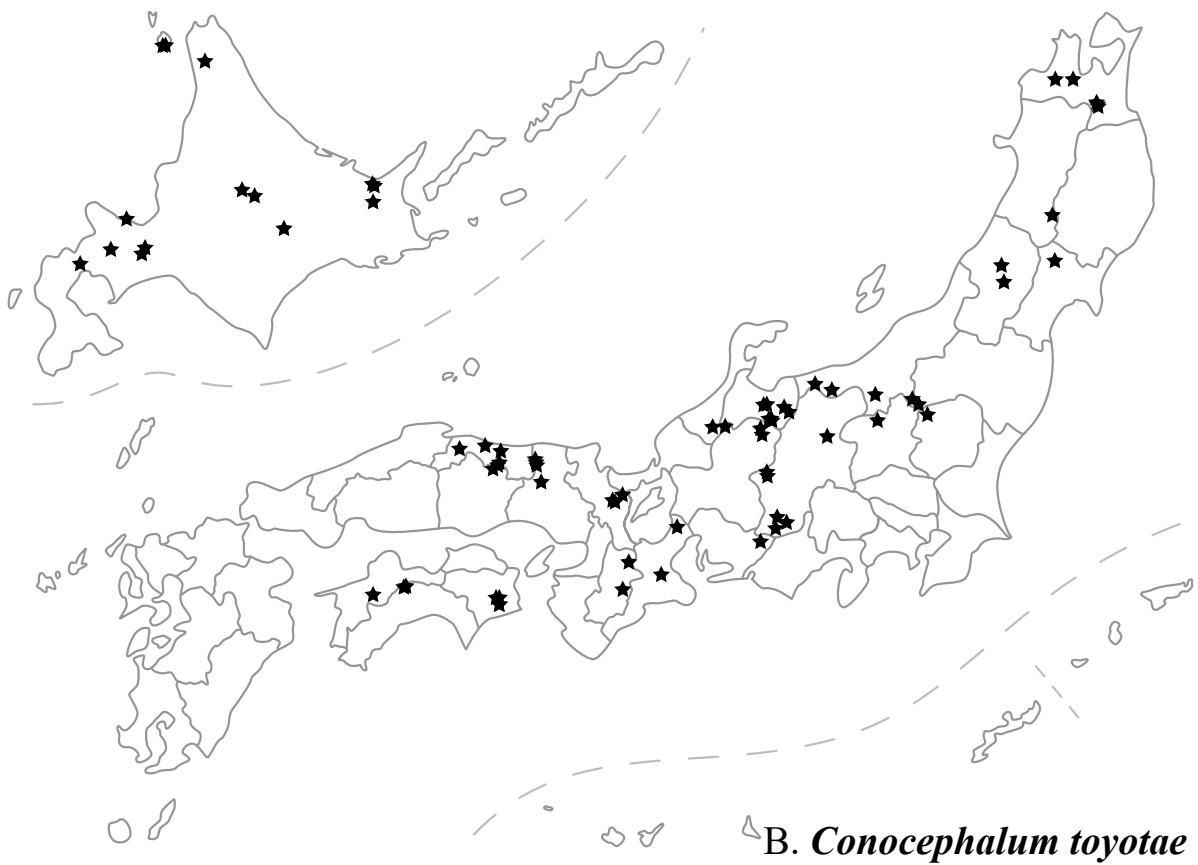
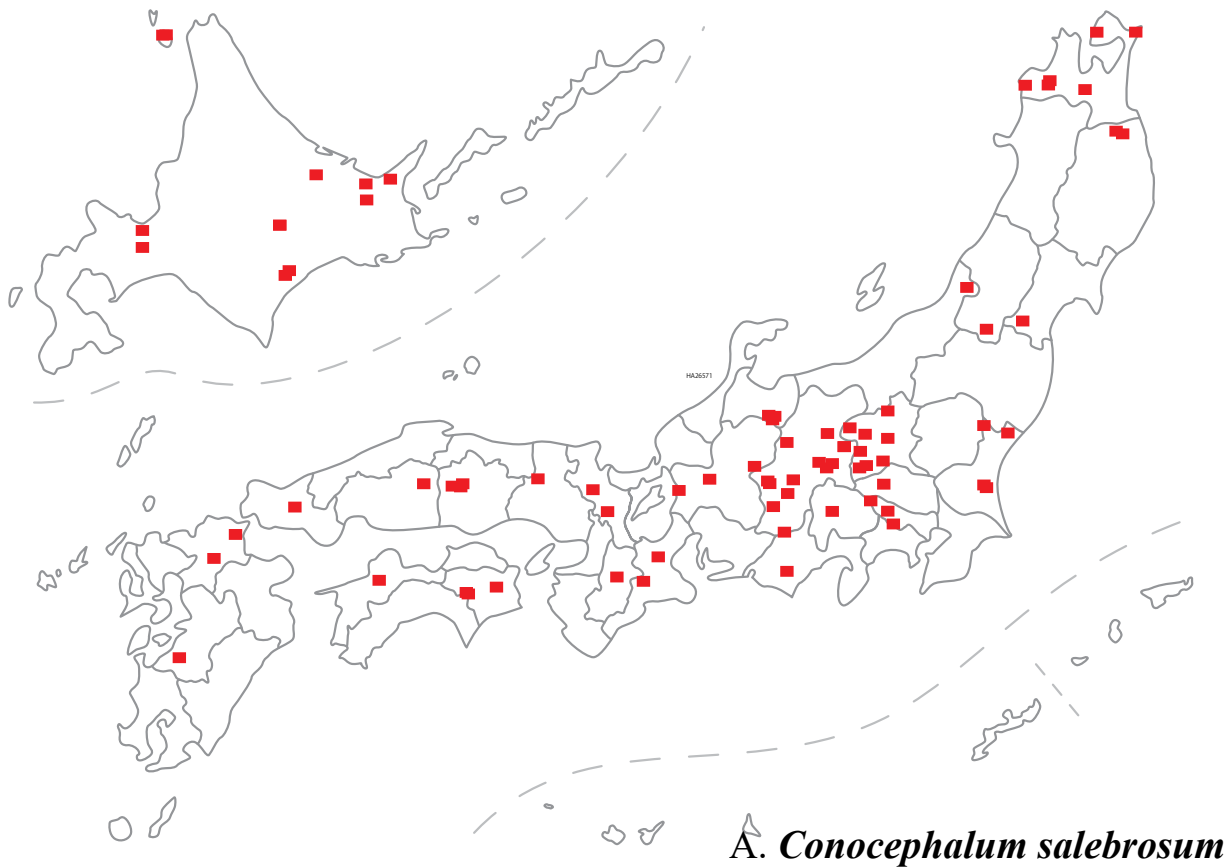


Plate 11. Distribution maps (2).

日本・台湾産ジャゴケ複合種における形態と生態の多様性

秋山 弘之¹⁾

形態の比較ならびに分子系統解析により、ジャゴケ属 *Conocephalum* とヒメジャゴケ属 *Sandea* は、それぞれ世界に 6 種と 3 種を持つ独立の属であることが示された (Akiyama and Odrzykoski 2020)。このうちジャゴケ属については日本には 4 種、台湾には 3 種が分布する。本論文ではこの成果ならびにジャゴケ探検隊のメンバーによって日本全国各地ならび台湾から得られた生植物を用いた形態と分布についての詳細な検討に基づき、これまで和名だけが与えられていた日本と台湾に分布するジャゴケ属植物 3 種のそれぞれを、オオジャゴケ *C. orientalis* H. Akiyama, ウラベニジャゴケ *C. purpureorubrum* H. Akiyama, そしてマツタケジャゴケ *C. toyotae* H. Akiyama を新種として記載した。また北半球冷温帯に広く分布するタカオジャゴケ *C. salebrosum* についても、日本・台湾産標本に基づいてヨーロッパ産植物との違いを比較検討して記載を与えた。

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