

A REVISION OF THE GENUS CALYCVULARIA MITT.
(CALYCVULARIACEAE, MARCHANTIOPHYTA)

РЕВИЗИЯ РОДА CALYCVULARIA MITT.
(CALYCVULARIACEAE, MARCHANTIOPHYTA)

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Abstract

The genus *Calycularia* is revised worldwide. Descriptions, key for identification of species, differentiation from habitually similar species, distribution, ecology as well as illustrations and worldwide distribution map of *Calycularia* spp. are provided. *C. crispula* Mitt. is excluded from hepatic flora of Russia, Canada, Japan and Korea.

Резюме

Проведена ревизия рода *Calycularia*. Приводятся подробные описания видов, ключ для определения видов, отличия их от внешне похожих таксонов, распространение, экология, а также рисунки и карта ареалов видов. *C. crispula* Mitt. исключена из флоры печеночников России, Канады, Японии и Кореи.

KEYWORDS: *Calycularia*, liverworts, phytogeography, taxonomy

INTRODUCTION

Calycularia is an oligotypic genus the relationships of which remain ambiguous. The genus was placed in Pelliaceae H. Klinggr. (Evans, 1937), Dilaenaceae s. lat. (Schuster, 1964), Pallaviciniaceae Migula (Schljakov, 1976), Allisoniaceae (R.M.Schust. ex Grolle) Schljakov (Schuster & Inoue, 1975, Schuster, 1982). Recently based on molecular data it has been separated into the monotypic family Calyculariaceae (Crandal-Stotler et al., 2008). The genus includes two accepted species. The type species of the genus, *C. crispula* Mitt., was described by W. Mitten (1861) based on specimens collected by J.D. Hooker in Sikkim (Himalaya). This species is restricted to mountains of the tropics and subtropics. The second species of the genus, *C. laxa* Lindb. & Arnell was described from the Russian Arctic (Dudin-ka, Lower Enisei River) by S.O. Lindberg &

H.W. Arnell (1889) and subsequently found in the north and in the mountains of Siberia and the Far East of Russia (Konstantinova, Bakalin et al., 2009), as well as in Alaska (Steere & Inoue, 1978), with a single locality in Europe (Konstantinova & Lavrinenko, 2002). As was stressed earlier (Schuster & Konstantinova, 1996) separating *C. laxa* from *C. crispula* remains very problematical.

Both species of *Calycularia* were recorded for Russia (Konstantinova, Bakalin et al., 2009). We studied 137 specimens of *Calycularia* preserved in the herbaria of H (8 specimens), KPABG (65), LE (34), MO (10), UPS (3), VLA (17). In total 105 specimens labeled as *C. laxa* and 32 labeled as *C. crispula*, including type specimens of both species, were revised. As a result *C. crispula* is excluded from the hepatic flora of Russia, Canada, Japan and Korea, and the distribution of *C. laxa* is expanded.

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TAXONOMIC TREATMENT

Calycularia Mitt., Journ. L. Soc. 5(1):122. 1861. Type: *Calycularia crispula* Mitt. (l.c.).

Plants relatively large, 0.2-1.2 cm wide, 1-5 cm long, nearly flat or with strongly undulate or crispate margins, pale to yellowish or deep green often with secondary goldish, fuscous, reddish to purplish red or red-brown pigmentation. *Branching* terminal, less often ventral, simple or pseudo-dichotomously 1-2 times furcated. *Rhizoids* pale brown or fuscous, restricted to midrib, relatively dense and numerous, sometimes scarce. Apical portion of thallus emarginated or nearly obcordate, sometimes strongly recurved back to the dorsal surface. *Midrib* rather distinct, dorsally flat or concave, ventrally convex, 8-20 cells thick, rather abruptly or more or less gradually tapering into unistratose margin 3-50 cells wide. Epidermal cells on dorsal side obliquely oriented and gradually decreasing from midrib toward the thallus margin whereas on ventral side they are increasing from midrib toward the thallus margin. Cross section with one layer of dorsal epidermal cells smaller than medulla, ventral epidermis in 1-4 layers of small cells with relatively incrassate light purple or brownish walls, central strands lacking. Cells of median part of thallus usually freely mycorrhizal. Ventral scales more or less numerous, restricted to costal area and most abundant towards an apical notch, purplish red or sometimes colorless, straight or recurved to arcuate, 2-6(-8)-seriate at base, abruptly tapering into an uniseriate tip with marginal teeth or cilia. *Oil-bodies* minute 1.0-3.7 μm , homogenous or from 2-4(-5) granules, 12-58 per cell (fig. 1:16). Asexual reproduction lacking.

Dioicous. *Gametangia* dorsal at thallus. Male plants (fig. 2:2,3) usually smaller than female plants with dorsal scales mostly in several rows along midrib or (rarely) scattered over the entire apical portion of the thallus. *Androecia* subtended by unistratose bracts which are erect or concave, lamelliform, variable in shape and size, laciniate-dentate, each bract with 1-4 sessile globose antheridia, antheridial stalk multicellular. *Archegonia* aggregated in well-defined or diffuse clusters and surrounded by slender scales (or sometimes mixed with them). The archegonial scales yellowish red or colorless, erect, arcuate, or prostrate, similar in shape to ventral sca-

les, linear to lanceolate, with marginal teeth or cilia. *Pseudoperianth* purplish red to red-brown or colorless, large, up to 6 mm high and up to 5 mm wide, usually at apical part of the thallus or rarely medially, infundibuliform, bell-shaped or inflated-cylindrical, in cross section rounded, at base multistratose, 3-4 cells thick, near mouth one layered and plicate, pseudoperianth mouth with 3-4 massive laciniate or ciliate lobes. Cells of lobes (40-)50-60 μm wide, (50-)65-100 μm long. *Calyptra* large, pyriform, at bases more or less thick. *Capsules* brownish to blackish, broadly oval to globose, with 2-4-stratose wall with characteristic thickening bands in all strata, dehiscent by 4-7 irregular valves. *Seta* massive, up to 2.5 cm long and 0.5 mm thick, in cross section 7-22 cells in diameter. *Elaters* 2-4 spiral, 8-12 μm wide, 120-300 μm long, with spirals ca. 2 μm thick. *Spores* brownish black, 30-80 μm in diameter, oval to globose, with long conical or cylindrical echinate outgrowths.

Differentiation. *Calycularia* differs from most genera of the simple thalloid hepatics in having lamellate and usually purplish ventral scales which are 2-5(-6)-seriate to almost one half or more of their length with several teeth or cilia with slime papillae on margins. Only *Blasia* and *Cavicularia* have lamellate scales with dentate margins, but their shape is quite different and species of these genera have a very distinct appearance that differs from *Calycularia* in having 1) *Nostoc*-filled small blackish auricles ventrally, 2) stellate multicellular gemmae, 3) ellipsoidal smooth gemmae in flask-shaped receptacles (in *Blasia*), 4) vestigial central strand. The rest of simple thalloid species have uniseriate ventral (and rarely dorsal) hairs which are 2(-13) cells long, colourless or brownish, and have apical slime papillae only.

Species of *Calycularia* are most likely to be mistaken for species of *Aneura*, *Pellia* or *Moerckia*. Apart from lamellate ventral scales *Calycularia* differs from *Aneura* in: 1) having purplish or brownish secondary pigmentation, never present in *Aneura*; 2) more or less well-defined midrib vs. lack of distinct midrib in *Aneura*; 3) thalli with more or less wide unistratose wings, never present in *Aneura*; 4) sex organs always dorsal on unmodified thalli whereas in *Aneura* the formation of sex organs is restricted to late-

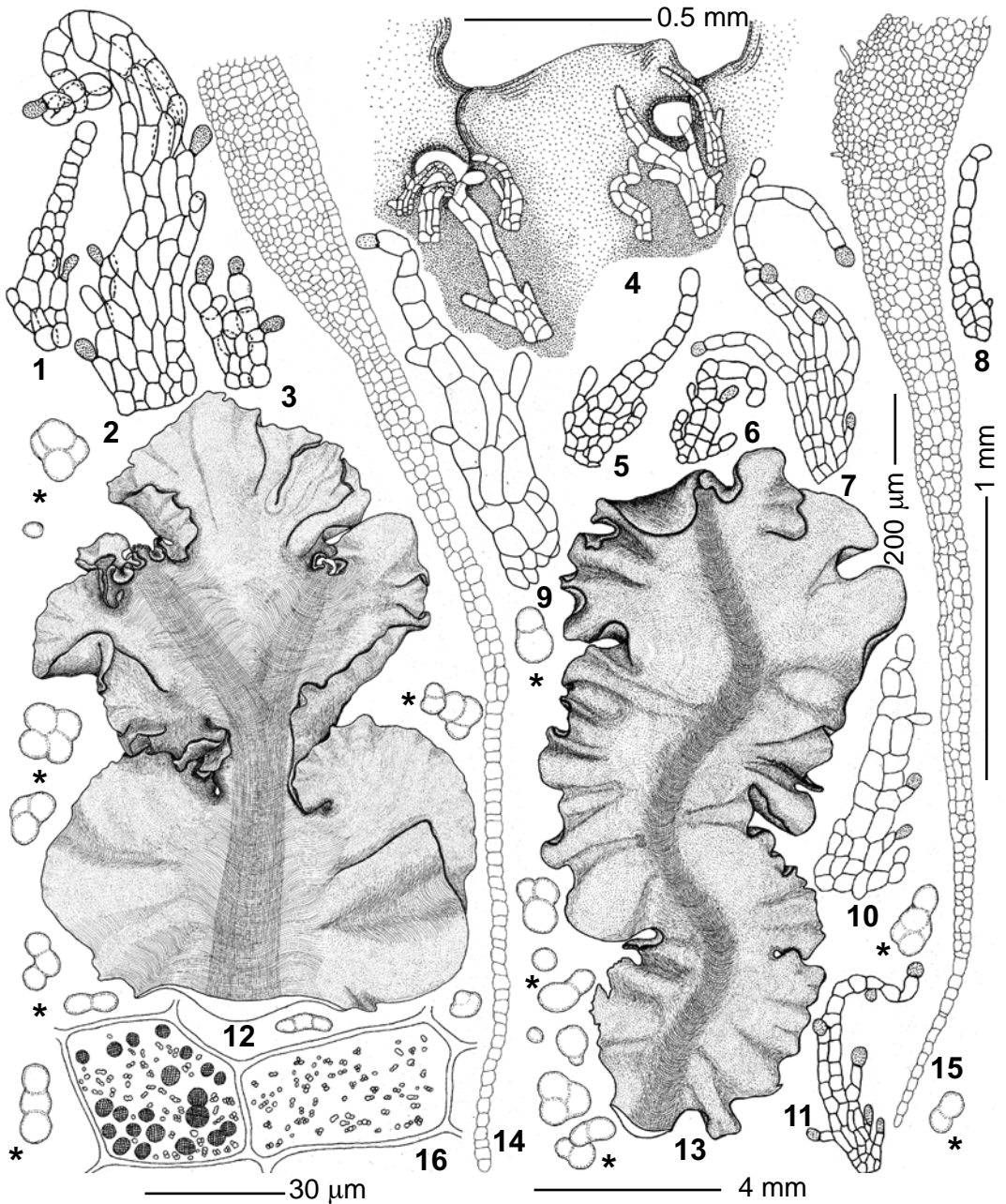


Fig. 1. *Calycularia crispula* (1-3, 12, 14): 1-3 – ventral scales; 12 – sterile plant; 14 – transverse section of thallus. *C. laxa* (4-11, 13, 15-16): 4 – ventral surface of thallus apex; 5-11 – ventral scales; 13 – sterile plant; 15 – transverse section of thallus; 16 – dorsal epidermal cells with chloroplasts (black) and oil-bodies (light) indicated. Enlarged oil-bodies are marked by asterisk. 2, 12 – from Sikkim *Hooker* # n.1679, LE; 1-3, 14 – from Taiwan *Inoue* # 3 Bryoph. selecta exsiccata, LE; 4 – from Alaska *Konstantinova* et al. # A114-1-92, KPABG; 5, 6, 8 – from Yamal *Potemkin*, LE; 7, 11, 15, 16 – from Primorskiy Territory *Mamontov* # 128-1-10, KPABG; 9, 10 – from South Korea *Bakalin* # *Kor-2-1-09*, KPABG. Scale bars: 4 mm for 12-13; 1 mm for 14-15; 0.5 mm for 4; 200 µm for 1-3, 5-11; 30 µm for 16.

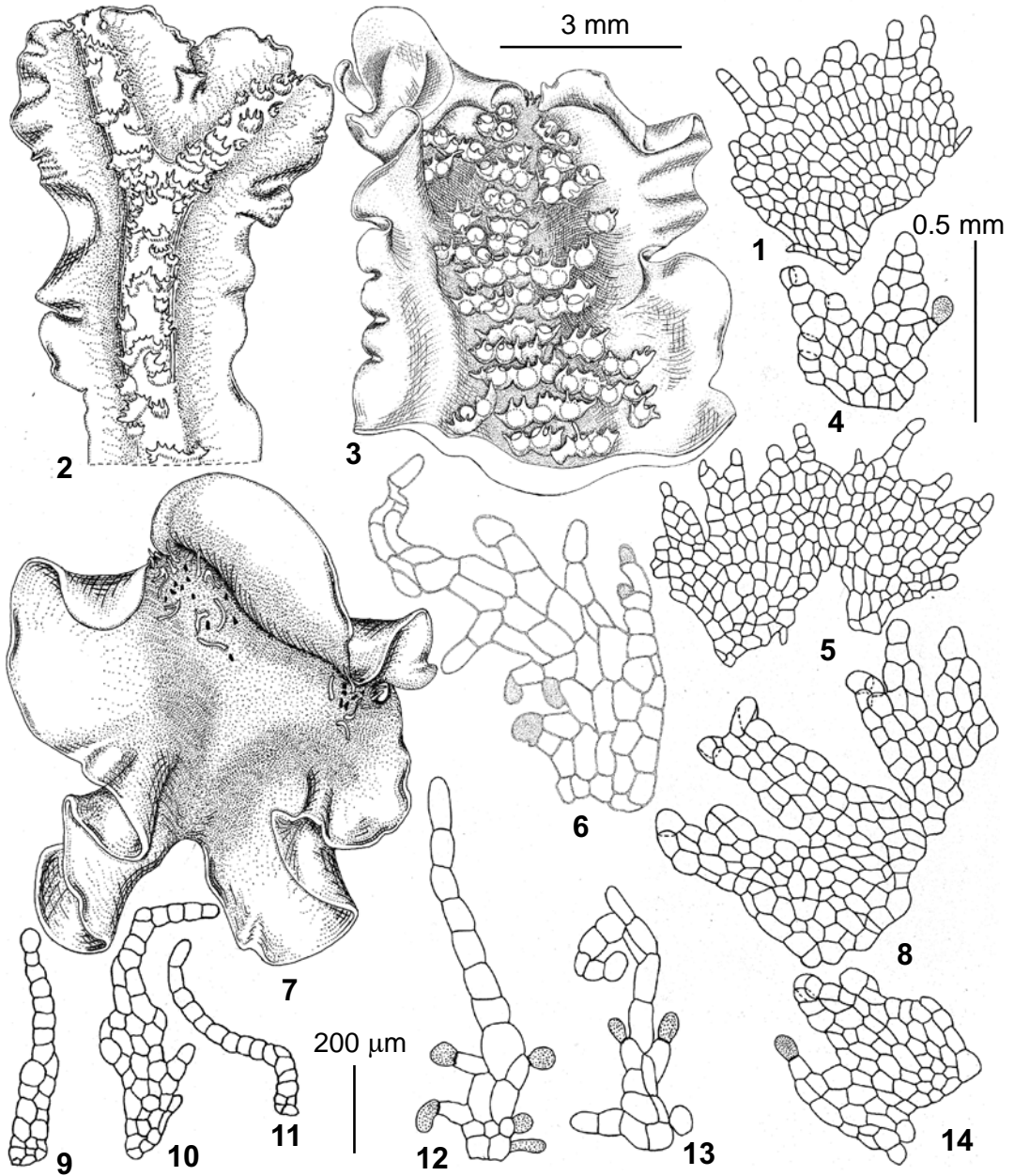


Fig. 2. *Calycularia laxa* (1-3, 5-7, 9-13): 1, 5 – male scales; 2-3 – male plants; 7 – female plant with archegonia (black) indicated; 6, 9-13 – female scales. *C. crispula*: 4, 8, 14 – male scales. 1, 3, 5 – from Arkhangelsk Province Lavrinenko # G100258, KPABG; 2 – from Alaska Konstantinova et al. # A114-1-92, KPABG; 4, 8, 14 – from Taiwan Inoue # 3 Bryoph. selecta exsiccata, LE; 7, 9-11 – from Yamal Potemkin, LE; 6, 12-13 – from South Korea Bakalin # Kor-2-1-09, KPABG. Scale bars: 3 mm for 2-3, 7; 0.5 mm for 1, 4, 5, 8, 14; 200 μm for 6, 9-13.

ral extremely short reproductive branches. *Pellia* is easily distinguished from *Calycularia* by the absence of dorsal scales in male and female plants. Antheridia in *Pellia* are usually solitary in cavities marked as small dorsal reddish brown

protuberance with a central elevated ostiole. *Hattorianthus*, *Pallavicinia* and *Moerckia flotoviana* differs from *Calycularia* in: 1) having central strands; 2) cylindrical to ovoid capsule vs. spherical in *Calycularia*; 3) capsule wall layers lack-

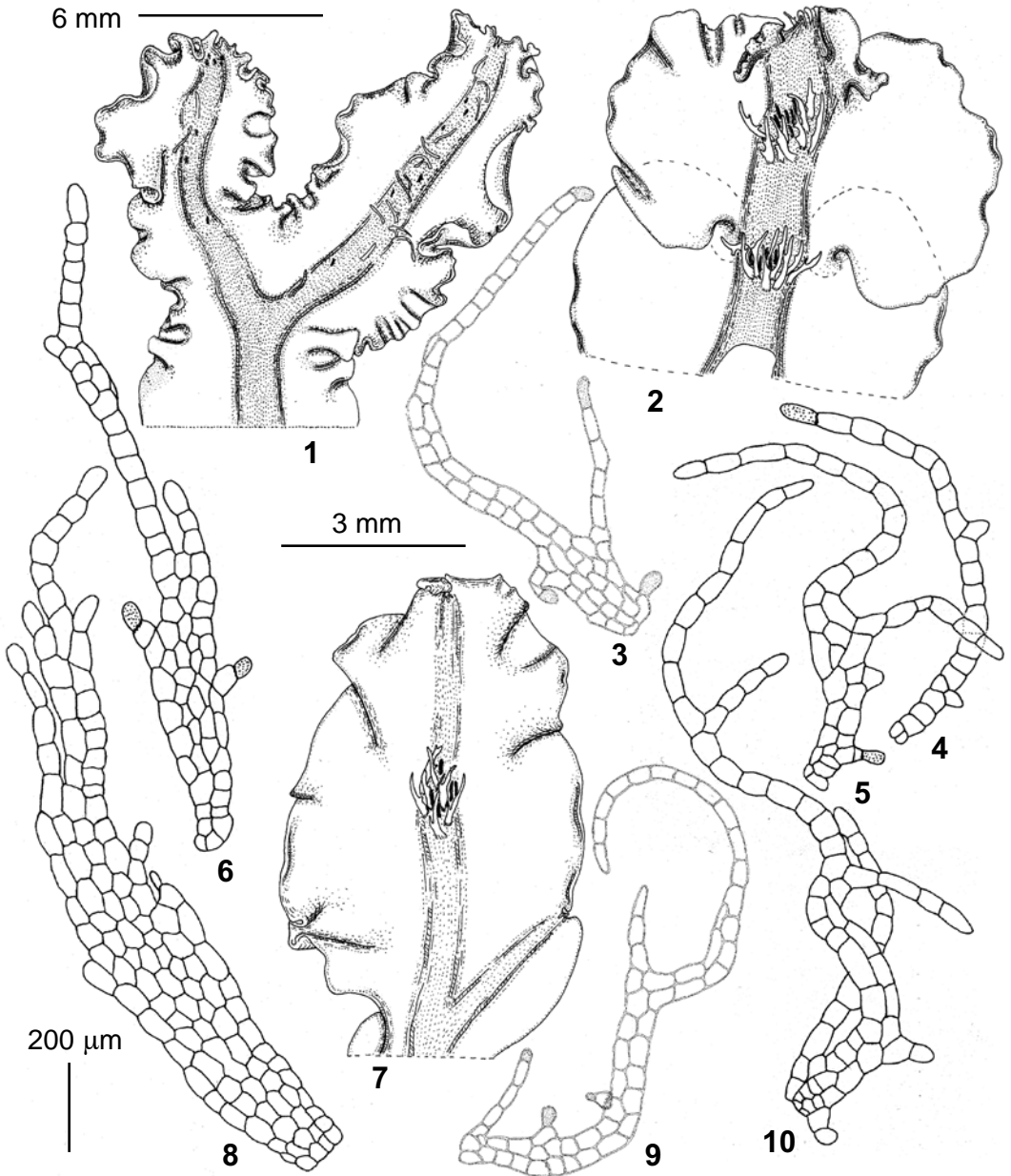


Fig. 3. *Calycularia laxa* (1, 3-10): 1, 7 – female plants with archegonia (black) indicated; 3-6, 8-10 – female scales. *C. crispula*: 2 – female plant with archegonia (black) indicated. 1, 4, 5, 10 – from Primorskiy Territory Mamontov # 128-1-10, KPABG; 2 – from Sikkim Hooker # n.1679, LE; 3, 9 – from Buryatia Konstantinova # 13-4-01, KPABG; 6-8 – from Japan Inoue # 485 Ser. 10 Hepaticae japonicae, LE. Scale bars: 6 mm for 1; 3 mm for 2, 7; 200 μ m for 3-6, 8-10.

ing bandlike stiffening thickenings whereas in *Calycularia* all wall layers have conspicuous semi-annular or spiral bands; 4) spores that never have conical or cylindrical echinate projections. In addition *Hattorianthus erimonus* has a thallus that is diagnostically erect or ascending from slender,

stipelike bases, and *Moerckia flotoviana* is a fragrant species, which has a strong and disagreeable smell (like in *Lophocolea heterophylla*) both in live and herbarium material, whereas *Calycularia* has cedar-oil like smell which is distinct after moistening of dried specimens.

KEY FOR IDENTIFICATION OF SPECIES OF
CALYCULARIA

1. The margin of the thallus is wavy but not to the extent of forming lobe-like structures. The costal region is not distinctly separated from the remaining part of the thallus and gradually tapers into a 2-1 cell thick part. Lobes of the pseudoperianth mouth lacinate-ciliate with cilia 7-13 cells long and uniseriate almost from the base. Seta 15-22 cells in diameter. Spores with projections mostly conical, needle-like, at apex acuminate or weakly rounded *C. laxa*
- Plants nearly flat, thallus deeply divided towards midrib on lobe-like structures. The costal region is relatively distinctly separated and more or less abruptly tapers into a 1-2 cell thick "wing". Lobes of the pseudoperianth mouth lacinate with lacinia biseriate (or more) almost to the apex, or rarely with uniseriate teeth 1-2 cells long. Seta 7-10 cells in diameter. Spores with projections cylindrical, truncate or emarginated at apex *C. crispula*

Calycularia crispula Mitt., J. Linn. Soc., Bot. 5(1): 122. 1861. — *C. birmensis* Steph. Bull. Herb. Boissier 16: 4. 1900 = (Spec. Hepat. 1: 359). — *C. compacta* Kashyap, Liverworts of the Western Himalayas and the Panjab plain 2: 105. 1932. — *C. formosana* Horik., J. Sci. Hiroshima Univ., Series B, Division 2 (Botany) 2: 137. 1934. — *C. golae* Gerola, Lavori di Botanica. Torino 12: 473. 1947.

Illustrations: Figs. 1-6; Kashyap, 1932 (plate XXVII); Pande & Udar, 1956 (p. 333, 335, 337, 339, 341); Renzaglia, 1982 (p. 84, 85). — Map: Schuster, 1983 (p. 506, fig. 11:4).

Plants 0.5-0.7 cm wide, 1-3 cm long, prostrate, nearly flat, thallus deeply divided towards midrib on lobe-like structures (fig. 1:12, 3:2, 4:1), pale to yellowish green, simple or 1-2 times furcated, often with ventral shoots arising from the midrib that probably serve as organs of vegetative propagation. *Rhizoids* yellowish or colorless, numerous. The costal region is relatively distinctly separated, more or less abruptly tapering into a 1-2 cell thick "wing". Midrib in cross section 8-20 cells high, unistratose margin 20-40(-50) cell rows wide. Inner cells of the midrib (21-)30-52 μm wide, (16-)26-52 μm high, (52-)80-160 μm

long, in transverse section rounded-hexagonal, in longitudinal section rectangular. Cells of ventral epidermis of the midrib (13-)20-40 μm wide, (10-)23-34 high, (28-)30-40 μm long, weakly differ from inner cells. Cells of ventral epidermis of the wings (26-)34-60 μm wide, (13-)23-30 high, (40-)50-80 μm long. Dorsal cells above midrib 16-26 μm wide, 20-36 high, 40-80 μm long. Dorsal cells along midrib 30-60 μm wide, 34-44 high, (39-)50-90 μm long. Dorsal cells of wings (30-)50-60 μm wide, 29-47 high, (44-)50-70 μm long. Cells of unistratose margins (26-)36-52 μm wide, 36-55 high, (39-)52-88 μm long. *Ventral scales* hyaline, purplish or purplish red, straight or recurved, 300-1500 μm long, 80-230 μm wide, at base 2-5(-6) cells wide, gradually or abruptly tapering to a long uniseriate tip, with a marginal cilia or slime papillae (fig. 1:1-3). Cells of ventral scales 26-50(-57) μm wide and (50-)55-90(-140) μm long. Oil-bodies 1.5-4.9 μm , 6-34 per cell.

Dioicous. *Archegonia* in numerous dense clusters, protected by prostrate scales. *Archegonial scales* colourless, inserted posteriorly and laterally to archegonia and united at the base into a half ring, 170-250 μm wide, 800-1600 μm long, 2(-3-6) seriate to almost 2/3-3/4 of their length and with 2-7(-9) teeth not more than 2-3 cells long, or with slime papillae only (fig. 4:3-7). Cells of archegonial scales 31-50 μm wide, 50-120(-156) μm long. *Pseudoperianth* colourless, lobes of the mouth with spiral curved acuminate or T-like laciniae (fig. 4:11). Cells of laciniae (34-)42-65 μm wide and (57-)70-96(-117) μm long. The *capsule wall* 2-4 layered – often on one valve. The epidermal cells large, hyaline, in longitudinal section 15-25 μm high, 33-67 μm long, in transverse section 31-46 μm wide, with transverse semiannular thickenings. Inner layers with cells much smaller, 9-16 μm high, 40-78 μm long, in transverse section 11-27 μm wide, with semiannular and spiral thickenings. *Seta* 7-10 cells in diameter. *Spores* oval to globose, 35-45(-60) μm (measured with outgrowths), with a long cylindrical outgrowths, which are truncate or emarginated at apex (fig. 5:4-7), see as well Singh & Singh, 2010a).

Variation and differentiation. *C. crispula* is most likely to be mistaken for *C. laxa*. In addition to characters given in the key it differs in 1) the width of unistratose wing of the thallus that

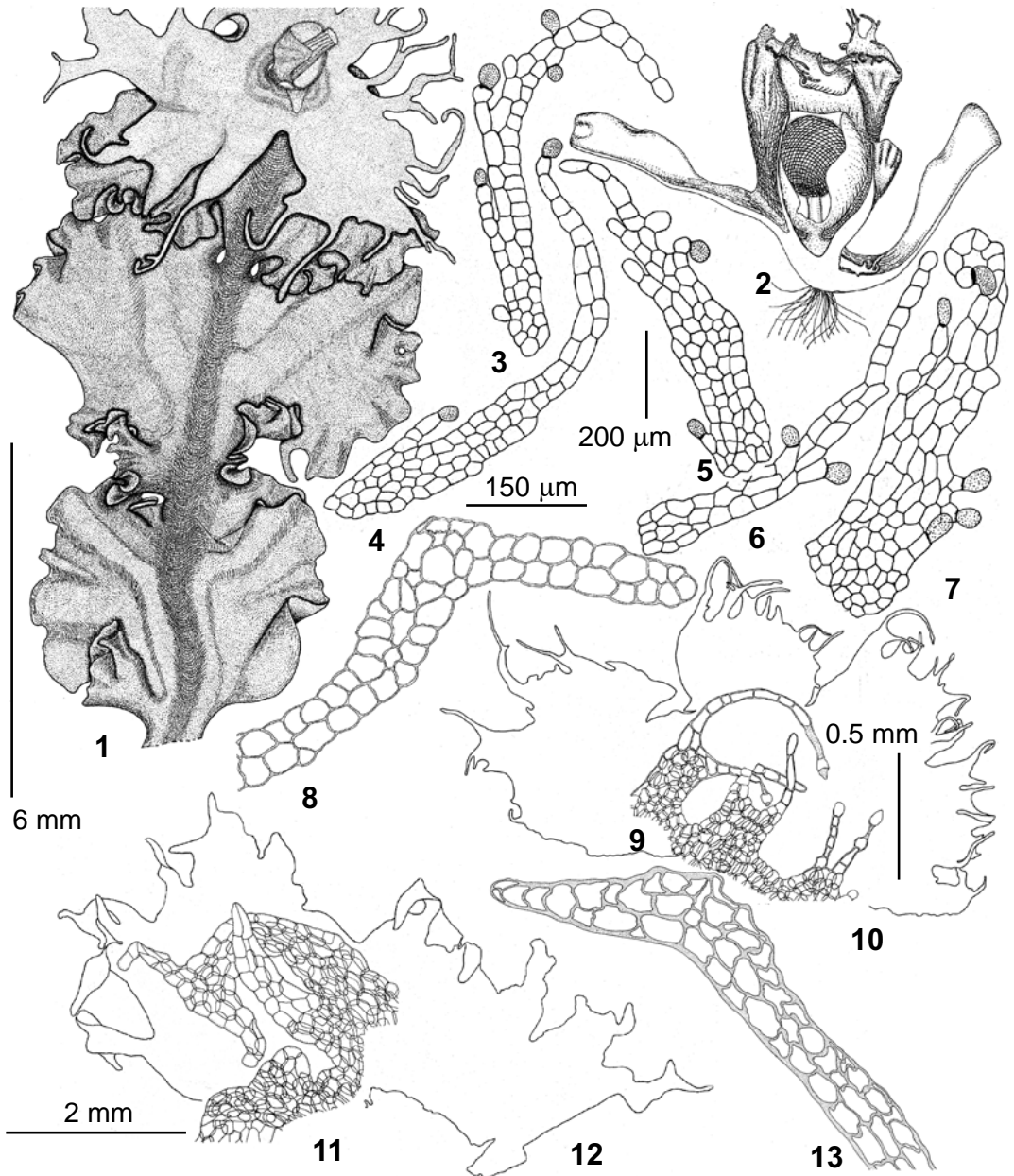


Fig. 4. *C. crispula* (1, 3-8, 11, 12): 1 – female plant; 3-7 – female scales; 8 – transverse section of pseudoperianth base (1/3 of height); 11 – part of pseudoperianth mouth; 12 – pseudoperianth. *C. laxa* (2, 9-10, 13): 2 – cross section of female plant with pseudoperianth, calyptra and capsule indicated; 9 – part of pseudoperianth mouth; 10 – pseudoperianth; 13 – transverse section of pseudoperianth base (1/3 of height). 1, 6-8, 11-12 – from Sikkim *Hooker* # n.1679, LE; 3-5 – from Taiwan *Inoue* # 3 *Bryoph. selecta exsiccata*, LE; 2, 9, 10, 13 – from Kamchatka *Bakalin* # K-3-3a-04, KPABG. Scale bars: 6 mm for 1-2; 2 mm for 10, 12; 0.5 mm for 9, 11; 200 µm for 3-7; 150 µm for 8, 13.

is usually 20-40(-50) cells wide whereas in *C. laxa* it rarely exceeds 20 (30) cells, 2) presence of ventral branching, never seen in *C. laxa*, 3) archegonia associated in numerous (to 6 per thal-

lus) dense clusters protected by prostrate scales united at the base into a half ring whereas in *C. laxa* archegonia mixed with slender scales forming 1-2 diffuse clusters along the midrib and, 4)

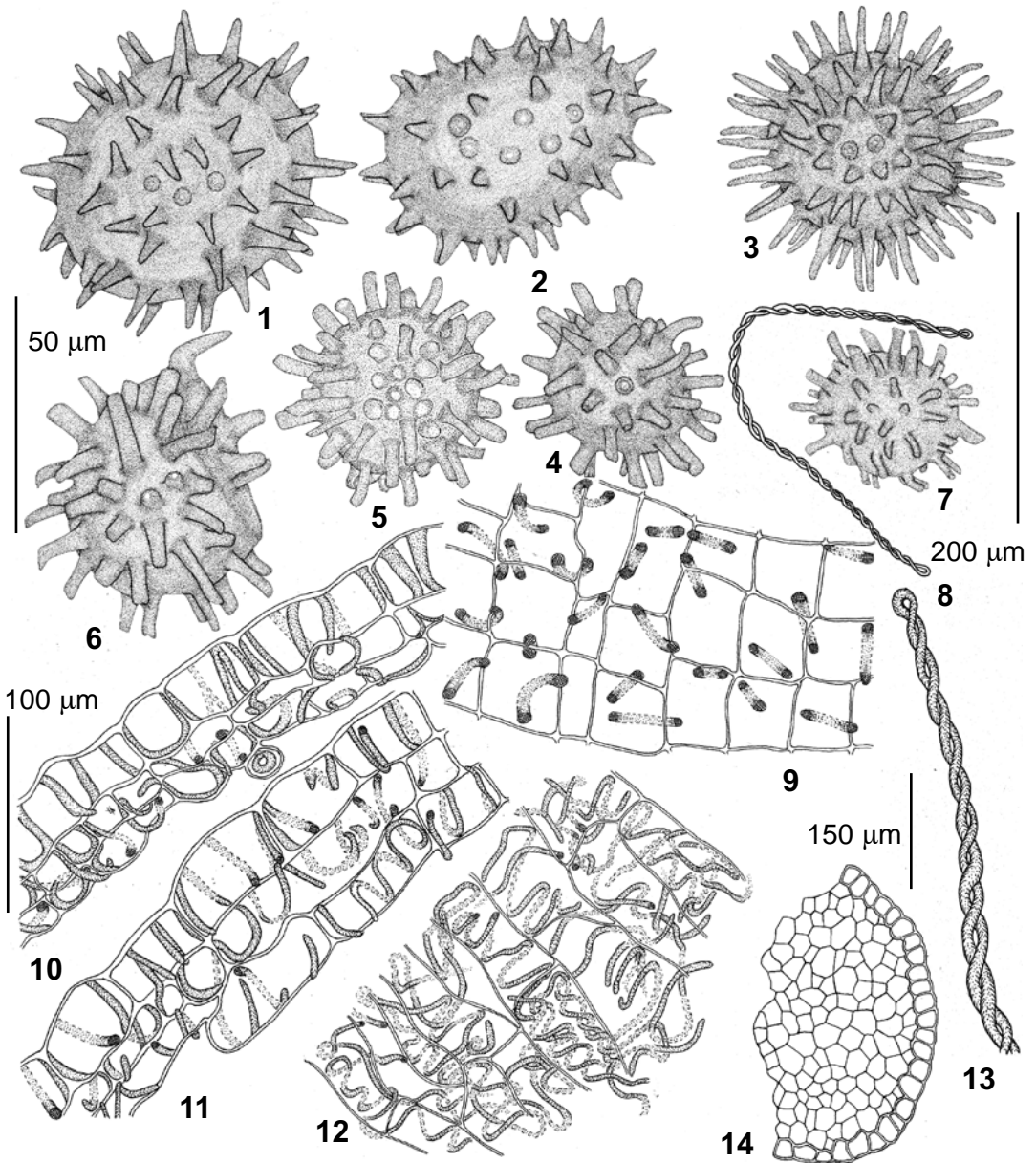


Fig. 5. *Calycularia laxa* (1-3, 8-14): 1-3 spores; 8, 13 – elaters; 9 – external surface of capsule wall; 10 – transverse section of capsule wall; 11 – longitudinal section of capsule wall; 12 – inner surface of capsule wall; 14 – seta cross section. *C. crispula*: 4-7 – spores. 1, 2, 10-12, 14 – from Kamchatka *Bakalin* # K-3-3a-04, KPABG; 3, 8, 13 – from Alaska *Potemkin* # 9209604, LE; 4, 7 – from Taiwan *Inoue* # 3 *Bryoph. selecta exsiccata*, LE; 5, 6 – from Sikkim *Hooker* # n.1679, LE. Scale bars: 200 µm for 8; 150 µm for 14; 100 µm for 9-12+; 50 µm for 1-7.

usually more lamellate 2-6(-8) seriate to almost 2/3–3/4 of their length archegonial scales vs. threadlike to linear and uniseriate to more than one half of their length in *C. laxa*, 5) usually lacking secondary pigmentation (excluding ventral scales and ventral side of midrib) whereas *C.*

laxa often has distinctly reddish coloration of dorsal side of thallus.

Ecology. *C. crispula* is a mountain species restricted to rather high altitudes from 1300 m alt. in Taiwan to 2700 m alt. in Africa and 3500 m alt. in Himalaya. It occurs on decaying logs,

tree boles, moist soil, in deep crevices and on shaded humus covered cliffs in river valleys, temperate evergreen forest zone in pure dense patches or mixed with *Aneura pinguis*, *Conocephalum conicum*, *Dumortiera hirsuta*, *Bazzania* spp., *Plagiochila* spp., *Riccardia* spp. According to Long & Grolle (1990) the species grows in Bhutan “on trees, stumps, logs, mossy boulders, rocks and on soil in cool broad-leaved, evergreen oak and mixed *Abies/Tsuga/Rhododendron* forests”.

Distribution. Asia: China (this study), India, Nepal (Kashyap, 1932; Pande & Udar, 1956; Singh, Singh & Dey, 2008; Singh & Singh, 2010b), Bhutan (Long & Grolle, 1990), Myanmar, Thailand (Schuster, 1983), Taiwan (Piippo, 1990), East Africa: Ethiopia, Tanzania, Zambia, Malawi (Jones, 1985; Wigginton & Grolle, 1996), North America: Mexico (Grolle, 1980), Costa Rica (Dauphin, 2005). The species was recorded for Japan (Inoue, 1976), Korea (Choi, 2009) and Canada (Davison and Smith, 1992) but was excluded from the floras of these countries during this study.

Selected specimens examined. TAIWAN. Ali Mt., Chia-Yi-Hsien, 28.X.1966 H. Inoue # 3 Bryoph. selecta exsiccata (LE). CHINA. Yunnan, Longyang Qu, 31.X.2003 D.G. Long # 32862 (MO). THAILAND. Payap, Doi (Mt.) Inthanon, 19.XII.1965 A. Touw # 106293 (MO). INDIA. Sikkim, J.D.Hooker # n.1679 (lectotypus LE, isolectotypus H-SOL). Khasia: Grif-fith (paratypus H-SOL). NEPAL. East Nepal, 25.VI.1972. Z.Iwatsuki, #1635 (H). TANZANIA. Southern Highlands: Kipengere Range, Mt. Ishinga, 26.V.1987 S.T. Iversen, E. Persson, B. Peterson & T.Pocs # 87146 B (H). MALAWI: Mulanje Mt., 24.VI.1991 B.J.O. 'Shea # M 7416a (MO).

Calycularia laxa Lindb. & Arnell, Kongl. Sv. Vet. Akad. Handlingar. 23(5): 68. 1889.

Illustrations: Figs. 1-6; Schljakov, 1976 (p. 45); Inoue, 1976 (p. 106, 107, 108, 109, as *C. crispula*); Steere & Inoue, 1978 (p. 335); Davison & Smith, 1992 (p. 267, as *C. crispula*). – Map: Schuster, 1983 (p. 506, fig. 11:3); Schuster & Konstantinova, 1996 (p. 29, fig. 1).

Plants 0.3-1.2 cm wide, 1-5 cm long, prostrate, nearly flat or with strongly undulate margins (fig. 1:13), never forming lobe-like structures, yellowish or deep green to reddish and purplish red and red-brown, simple or 1-2 times furcated, never with ventral branches. *Rhizoids*

yellowish or colorless, scarce on sterile thalli, and often dense and numerous in plants with mature perianths. Midrib in cross section 8-20 cells high, unistratose margin 3-20(-30) cell rows (fig. 1:15). Inner cells of the midrib (28-)40-60(-70) μm wide, (30-)40-50(-65) μm high, (80-)130-190 (260 in plants from Japan) μm long, in transverse section rounded-hexagonal, in longitudinal section rectangular. Cells of ventral epidermis of the midrib (17-)26-40(-44) μm wide, (13-)20-34 high, (44-)60-80 μm long. Cells of ventral epidermis of the wings (28-)50-70(-80) μm wide, (20-)30-40 μm high, (65-)90-160 μm long. Dorsal cells above the midrib 28-50 μm wide, 26-40 high, (70-)130-170 μm long. Dorsal cells near midrib 26-70 μm wide, 26-45 μm high, (60-)100-130 μm long. Dorsal cells of wings (26-)50-70 (-80) μm wide, 30-50 μm high, (50-)90-156 μm long. Cells of unistratose margins (30-)40-60 (-65) μm wide, 30-52 μm high, (40-)50-80 μm long. *Ventral scales* purplish red or sometimes colorless, straight or recurved (73-)250-1000 μm long and 60-200 μm wide, at base 2-3(-5) cells wide, gradually or abruptly tapering to a uniseriate tip to 8 cells long with a marginal teeth or cilia ending by apical slime papillae (fig. 1:5-8,10,11). Cells of ventral scales (16-)26-60(-90) μm wide and (16-)30-90(-180) μm long. *Oil-bodies* 1.0-3.7 μm , 12-58 per cell (fig. 1:16). In spite of the fact that the species was described as “inodora” (Lindberg & Arnell, 1889), most specimens have a distinct smell after moistening.

Dioicous. Male plants with dorsal scales in several rows along midrib or scattered over all the apical portion of the thallus (fig. 2:2-3). *Archegonial scales* yellowish to purplish red or colourless, erect, arcuate, or prostrate, threadlike to linear, 2-3(-4-6) cells at base, 80-180 μm wide, 370-1370(-1400) μm long, uniseriate to more than one half of their length (7-15 cells long), or almost from the base, with one or two cilia up to 5 cells long and with 2-3 slime papillae. Cells of archegonial scales (20-)30-60(-90) μm wide and (36-)40-90(-130) μm long. *Pseudoperianth* colourless to yellowish or purplish red, often with purplish red to red-brown lacinate-ciliate mouth, cilia uniseriate almost from the base, 3-14 cells long, their cells (31-)40-50 μm wide and (30-)40-65(-80) μm long (fig. 4:9,10). The *capsule wall* 2-4 layered – often on one valve. The epi-

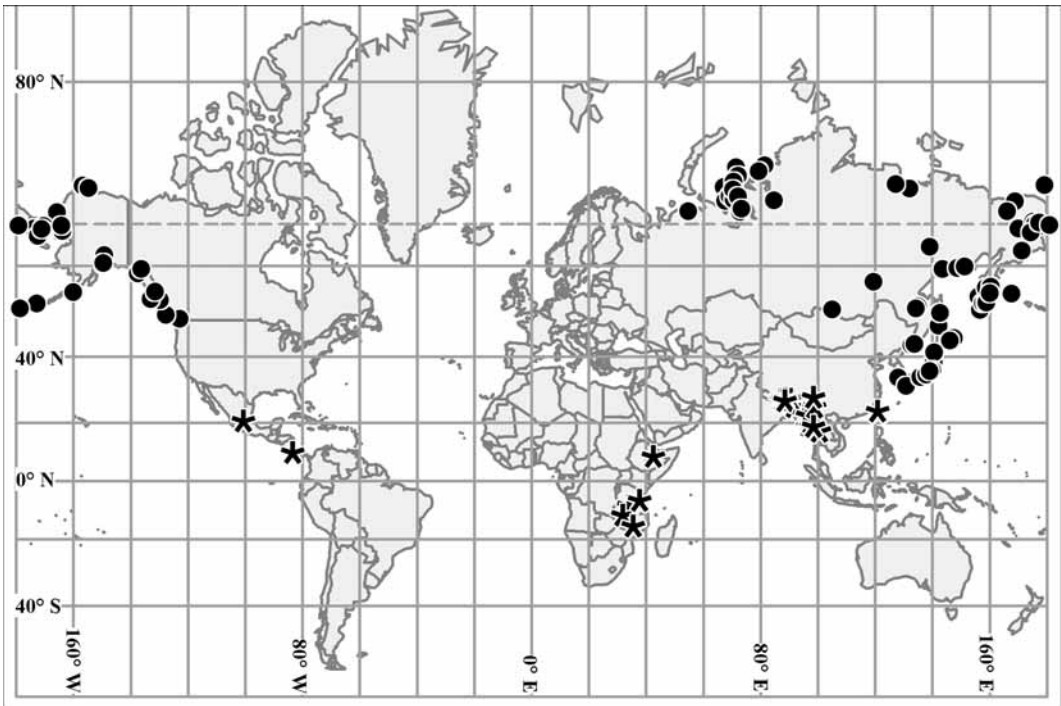


Fig. 6. World distribution of *Calycularia* species: circle – *C. laxa* Lindb. & Arnell; asterisk – *C. crispula* Mitt.

dermal cells large, in longitudinal section 30–37 μm high, 30–67 μm long, in transverse section 25–45 μm wide. Cells of inner layers much elongate, 12–28 μm high, 80–110 μm long, in transverse section 18–50 μm wide. *Seta* 15–22 cells in diameter. *Spores* (33–)40–60(–80) μm , oval to globose with a conical, needle-like or (very rarely) nearly cylindrical projections which are mostly acuminate or weakly rounded.

Variation. *C. laxa* is quite variable with regards to size and coloration of both thalli and scales, as well as size of cells and the appearance of thalli. Plants from the tundra zone are usually smaller (rarely exceeding 6 mm width and 15 mm length) than those from the mountains of South Siberia, the southern part of Far East of Russia, south Alaska and British Columbia that run up 12 mm wide and 5 cm long. The size of thalli often correlates with the size of ventral and archegonial scales. Ventral scales are usually not more than 250–375 μm long and 80 μm wide in plants from the tundra (but in single specimens from Yamal to 600 μm long), whereas in southern plants they can reach 625–750 μm length and 130 μm width.

Variation of archegonial scales. Archegonial scales are much smaller in northern plants (375–750 μm long), whereas in the southern populations they can run up to 1375 μm long. They are usually threadlike, linear and uniseriate to more than one half of their length but in some plants from Yamal as well as from Japan and Korea they are (2-)3-4(-6) seriate to almost 2/3 of their length, moreover plants from Japan and Korea have very large cells of archegonial scales (to 65 μm wide and to 180 μm long) that is characteristic for *C. crispula*. Sometimes single 3-4 seriate to almost 2/3 of their length archegonial scales mixed with that are threadlike and becoming uniseriate for much of their length even in one plant as in specimens from Yamal (fig. 2:10). In general, threadlike and uniseriate to more than one half of their length, appendages are more characteristic for *C. laxa* whereas more lamellate (2-)3-4(-6) seriate to almost 2/3 of their length shoots corresponds with *C. crispula*.

Variation in distribution of antheridia. Dorsal scales of male plants are mostly concentrated in several rows along the midrib but sometimes in small arctic plants with relatively wide thalli they

can be scattered over the entire apical portion of the thallus. Steere & Inoue (1978) considered the position of antheridia an important taxonomical feature and mainly based on that Davison & Smith (1992) referred specimens from South Alaska and British Columbia to *C. crispula*.

Variation in pigmentation of plants. Most studied plants from the tundra show more or less clear secondary pigmentation. On exposed sites the species may be conspicuously purple-reddish or green with fuscous, reddish to purplish red or red-brown colored margins and (if present) pseudoperianth and its mouth especially. However plants from shaded depressions may have no trace of secondary pigmentation. The majority of the studied specimens from the southern mountains are deep green with sometimes purplish colored margins.

Differentiation. *C. laxa* is most likely to be mistaken for *C. crispula*, the separation of these two taxa was discussed above. Sterile thalli of *C. laxa* are more likely to be confused with *Moerckia* or *Pellia*. They differ from both in having multicellular and usually purplish ventral scales which are 2(or more)-seriate to almost one half of their length with several teeth or cilia at margins, vs. uniseriate colourless or brownish ventral (and rarely dorsal) hairs in *Moerckia* or *Pellia*.

Ecology. The species grows at low elevations in the Yamal Peninsula, the valley of the Lena River and some other tundra regions, but in the mountains of South Siberia it reaches up to 1700 m alt., and in Primorsky Territory to 1500 m alt. In the tundra zone it occurs in moist habitats in river and lake valleys where it grows on damp sandy soil, peat and humus covered rocks along banks of streams, in dried river beds, in depressions between peat hillocks, in crevices of cliffs, among boulders in rock fields. It has also been collected on spots of bare soil in different types of tundra, on nival slopes, among boulders in rocky lichen tundra and on bare soil in sedge-lichen tundra, occasionally in sedge-moss bogs. In mountains at the southern limit of their distribution the species is restricted to valleys of rivers where it is found on wet, often moss covered, cliffs and rocks along streams in deep humid ravines, near waterfalls, on fine-grained and sandy soil or peat between rocks, in shaded crevices on wet cliffs, at the bottom of cliffs and rock out-

crops, both in subalpine and forest zones including broadleaved forests, mixed and coniferous forests. Here it grows with other hepatics of such habitats. The species usually forms mats or grows as single plants among bryophytes, mixed more often with *Diplophyllum taxifolium*, *D. albicans*, *Macrodiplphyllum microdontum*, *M. plicatum*, *Cephalozia bicuspidata*, *Tritomaria quinquedentata*, *Calypogeia integrastipula*, etc. In the tundra zone it is also associated with *Sphenolobus minutus*, *Blepharostoma trichophyllum* var. *brevirete*, *Cephalozia pleniciceps*, *Cephalozia grimsulana*, *Gymnomitrium corallioides*, *Lophozia ventricosa* var. *longiflora*, *Ptilidium ciliare*, *Scapania curta*, *S. scandica*, rarely with *Lophozia silvicoloides* (Kamchatka Peninsula) or *Macrodiplphyllum imbricatum*, *Cephalozia pachycaulis* (Alaska), *Pleurocladula albescens*, *Anthelia juratzkana*, *Marsupella commutata*, *Nardia geoscyphus*, *Schistochilopsis opacifolia*, etc.

Distribution. Arctomontane species with Asian – western North American distribution and a single locality in east European Arctic, that presumably represents post-glacial invasion (Konstantinova & Lavrinenko, 2002). In Siberia it is more or less widespread in arctic and subarctic tundras of the Yamal Peninsula (Potemkin, 1993) and Chukotka (Afonina & Duda, 1993), known from several localities in the Taimyr Peninsula (Schuster & Konstantinova, 1996) and north of the Republic of Sakha (Sofronova, 2005), southwards to mountains of the southern part of East Siberia (Bakalin, 2004), South Siberia (Kazanovsky & Potemkin, 1995; Konstantinova, 2004, as *C. crispula*), Amur Province, Kuril Islands, Primorskiy Territory (Konstantinova, Bakalin & al., 2009, as *C. crispula*) and Korea (Choi, 2009, as *C. crispula*), eastwards to Magadan Province, Khabarovsk Territories, Kamchatka Peninsula (Bakalin, 2010) and Japan (Inoue, 1976, as *C. crispula*). Recently it was found that the species is not very rare in Kamchatka Peninsula (Bakalin, 2009, 2010), in the mountains of South Siberia (our unpublished data) as well as in Primorskiy Territories, Sakhalin and Kuril Islands (Bakalin, 2010, as *C. crispula*). In North America the species was recorded from arctic Alaska (Steere & Inoue, 1978), south Alaska and Canada (Davison & Smith, 1992 and Schofield et al., 2004 as *C. crispula*). It was collected by the senior author during the field trip

organized by Dr. D. Horton in South Alaska (Kenai and Talkeetna mountains). Several specimens from the Seward Peninsula (arctic Alaska) collected by Dr. A.D. Potemkin (LE, unpublished) should be added to these reports. For sure the species is much more widespread in the north of Siberia, Far East of Russia and arctic Alaska as well as in the mountains of South Siberia, Far East of Russia and the west coast of North America.

Selected specimens examined. USA. Alaska: Shumagin Islands, Simeonof Island, 25.VII.1996 *W.B. Schofield* # 108120 (MO); Pribilof Islands, St. Paul Island, 12.VII.1997 *W.B. Schofield* with *S. Talbot* & *S. Looman Talbot* # 106293 (MO). Seward Peninsula, Killeak Lakes, 26.VII.1992 *Potemkin* # 9206904 (LE). Kenai Mts., ca. 1000 m alt., 1.VII.1992 *Konstantinova* with *D. Horton*, *R.M. Schuster* & *T.O'Brien* # A58-92, A70-92 (KPABG). Talkeetna Mts., Fern Mine Stream valley, Fairangel Creek, 1150 m. alt., 7.VII.1992 *Konstantinova* with *D. Horton*, *R.M. Schuster* & *T. O'Brien* # A114-1-92 (KPABG).

RUSSIA. Arkhangelsk Province: Bolshezemel'skaya Tundra, 19.VII.00 *O.V. Lavrinenko* # G100258 (KPABG). Tyumen Province: Yamal Peninsula, Mys Kamenny Settlement, 24.VI.1988 *Potemkin* (LE). Krasnoyarsk Territory: Taymyr Peninsula, Bol'shoy Arcticheskij Reserve, valley of Medusa River, 11.VII.2001 *Varlygina* # G102142 (KPABG); Dickson Distr., Sibiryakova Island, 10.VII.1989 *A. Kozhevnikova* # G109859 (KPABG). *Enisey River, Dudinka Settlement, 2.VIII.1876 Arnell* # 78 (holotypus, H-SOL 2122001). Republic of Sakha (Yakutiya): Nizhne-Kolymskiy Distr., 17.VIII.1972 *Stepanova* # 1/122 (LE). Republic of Buryatia: Khamar-Daban Range, Middle of Levaya Anosovka River, 4.VIII.2001 *Konstantinova* # 13-4-01 (KPABG); idem, valley of Pereemnaya River, Chyerno Lake, 9.VIII.2001 *Konstantinova* # 60-2-01 (KPABG). Zabaikalskiy Territory: Udokan Range, Kiryalta Lake, 1340 m alt., 4.VII.2000 *Bakalin* # 4-47-00 (KPABG). Chukotskiy Autonomous District: Ayon Island, Ryveem River, 24.VII.1983 *Afonina* (LE); Anadyr River basin, upper Tanyurer and Golubaya Rivers, 18.VII.1981 *Afonina* (LE); Cross Bay, Egvekinot Village, 17.VII.1974 *Afonina* # G108540 (KPABG); Iony Lake, 5.VII.1974 *Afonina* (LE); Kamchatskaya Province: South Kamchatka, Topolevyyi Range, 300 m alt., 4.VIII.2001 *Bakalin* # 73-1-01 (KPABG). Central Kamchatka, Bystrinskiy Distr., Esso Village surroundings, 9.IX.2003 *Bakalin* # K-106-5-03 (KPABG); East Kamchatka, Rakovaya Mt., 500 m alt., 19.VI.2004 *Bakalin* # K-20-19-04 (KPABG); idem, 23.V.2004 *Bakalin* # K-3-3a-04 (KPABG). Commander Islands, Medniy Island, Gladkovskaya Bay, 5.VII.2007 *Bakalin* # K-67-5-04 (KPABG). Sakhalinskaya Province: Kunashir Island, Tyatya volcano, 1200 m alt., Krutoj Stream, 14.IX.2007 *Bakalin* # K-58-3a-06 (VLA); Shiko-

tan Island, Notoro Mt., 200 m alt., 25.VIII.2007 *Bakalin* # K-41-30-07 (VLA); Iturup Island, Bigatyr Range, Stokap volcano, 400 m alt., 13.VIII.2007 *Bakalin* # K-24-6-07 (VLA). Khabarovsk Territory: Verkhneburenskiy Distr., Dusse Alin Range, 1550 m alt., 11.VIII.1997 *M.S. Ignatov* # MI-1043-97 (KPABG). Okhotsk Distr., Lanzhinsky Mts., Malta Mt., 485 m alt., 20.VII.2008 *Bakalin* # P-24-4-08 (VLA); East end of Lanzhinsky Mts., 200 m alt., 27.VII.2008 *Bakalin* # P-45-12-08 (VLA). Primorskiy Territory: Shkotovsky Distr., Livadijskiy Range, Pidan Mt., valley of Oyry Stream, 1300 m alt., 10.X.2005 *Bakalin* # P-74-63-05 (VLA). Lazovsky Distr., Alekseevsky Range, Olkhovaya Mt., 1500 m alt., 3.X.2006 *Bakalin* # P-65-29-06 (VLA); Benevskiye waterfalls, 500 m alt., 6.X.2006 *Bakalin* # P-68-16-06 (VLA); idem, 7.09.2010 *Mamontov* # 128-1-10 (KPABG).

SOUTH KOREA. Deokgyu-san: Deokgyu National Park, 26.VI.2008 *Bakalin* # Kor-11-2-08 (VLA). Kyong Nam: Chiri Mt. National Park, 13.VI.2009 *Bakalin* # Kor-2-1-09 (VLA); idem, 14.VI.2009 *Bakalin* # Kor-5-7-09 (VLA); idem, 14.VI.2009 *Bakalin* # Kor-5-12-09 (VLA). JAPAN. Saitama Pref.: Chichibu Mts., Ochigava valley, 800 m alt., 3.XI.1957 *Inoue* # 485 Ser. 10 (1958) *Hepaticae japonicae* (LE).

CONCLUSION

As has been stressed before (Steere & Inoue, 1978; Schuster & Konstantinova, 1996), the separation of *C. laxa* and *C. crispula*, remains very problematical. We found that the main diagnostic features described by Lindberg & Arnell (1889) and Steere & Inoue (1978) are unreliable. In particular, unistratose thallus wings in *C. laxa* vary from 3 to 20 or even 30 cell rows (in some specimens from Chukotka, Alaska and Khamar-Daban) that fit well within the limit of variation of *C. crispula*. Antheridia in *C. laxa* are often confined to the costal region, which is characteristic of *C. crispula*. Very variable and as a result not appropriate for distinguishing of species are the shape and size of archegonial and ventral scales. However *C. laxa* shows some features that are more or less constant and distinguishes it from *C. crispula*. We believe that the best diagnostic features are the sculpture of spores, the character of the pseudo-perianth mouth and (less distinct) the shape of the thallus, branching patterns and location of archegonia. The problem is that male and female plants occur quite often whereas sporophytes are very rare. Based on combinations of characters specimens from Southern Siberia (Konstantinova, 2004), Far East of Russia (Bakalin, 2007a,b; Bakalin et al.,

2009; Konstantinova et al., 2003) and Canada (Davison & Smith, 1992, according to description and drawings, specimens were not seen) that were identified earlier as *C. crispula* are referred to *C. laxa*. Especially troublesome are specimens from Japan (Inoue, 1976) and Korea. These plants are very large, have usually wide uniseriate wings ca. 30 cells wide, often have no trace of secondary pigmentation and in plants from Japan archeogonial scales are (2-)3-6 seriate to almost 2/3 of their length and have quite large cells to 65 µm wide and 130 µm long. It corresponds with *C. crispula*. On the other hand, the thalli in studied specimens from Japan are not divided in leave-like structures, and only lateral branches are present, that is characteristic for *C. laxa*. Sporophytes were not found in studied specimens from Japan but on the drawings of Japanese specimens in Inoue (1976) the sculpture of spores is quite similar to that of *C. laxa*. It convinced us that the specimens from Japan should be referred to this species.

Calycularia laxa and *C. crispula* differ in their distribution (see map). The latter species has disjunctive, relictual areal restricted to tropical mountains, whereas the former is a species of northern and temperate mountains and tundra zone. *C. crispula* is probably an ancient species and *C. laxa* is its tertiary derivate that was preserved in some refuges (like Beringia, some places in Khamar-Daban etc.) and more or less successfully distributed in postglacial time. Unfortunately only a limited number of specimens of *C. crispula* were available for this study. So the variability of this taxon is still much less known than that of *C. laxa*. Future study of variability of both species including molecular study is needed to resolve remaining taxonomical problems.

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