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Comprehensive analysis of relationships of the representatives of subfamily *Cryptogrammoideae* (Pteridaceae)

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Summary. This research is the first comprehensive analysis of the intrageneric relationships inside the subfamily *Cryptogrammoideae*: 14 taxa of *Coniogramme* and one species of *Cryptogramma* were involved additionally in the molecular phylogenetic studies based on *rbcL* gene of plastid DNA; spore morphology of 32 taxa of cryptogrammoid ferns, namely 22 taxa of *Coniogramme*, nine species of *Cryptogramma* and one species of *Llavea* were studied using scanning electronic microscopy (SEM); 31 taxon of *Cryptogrammoideae* were studied using herbarium data from Herbaria across Europe and Asia (P, PE, LE, VLA, ALTB, TK) according to global botanical and geographical zones. As a result of this comprehensive analysis, we established a deep divergence of *Coniogramme merillii* in *Coniogramme* superclade: this species is the sister lineage to the remainder of *Coniogramme*. We revealed also the separateness of *Co. suprapilosa* from *Co. rosthornii* and *Co. longissima*, *Co. africana* from *Co. lanceolata* and *Co. fraxinea*, *Co. robusta* from *Co. jinggangshanensis*, *Co. wilsonii* and *Co. japonica*. Among *Cryptogramma* species, the relationship of Far Eastern *Cr. gorovoi* with *Cr. crispa* from the Caucasus and the Turkish endemic *Cr. bithynica* but not with any Far Eastern species was revealed. Spores of *Coniogramme* are characterized by simple smooth, granulate and papillate macro-ornamentation, spores of *Cryptogramma* species have the more coarse colliculate or tuberculate macro-ornamentation. Peculiarities of macro-ornamentation allow us to define six spore types in cryptogrammoid ferns: four spore types in *Coniogramme* and two spore types in *Cryptogramma*; the same spore type we assigned for *Llavea cordifolia* and *Coniogramme suprapilosa*. In *Coniogramme*, the grouping of species attending the spore type does not agree with existing classification and phylogenetic hypotheses. Genetic separateness of *Co. suprapilosa* corresponds with its exceptional verrucate spore sculpture not found in other *Coniogramme* species. In *Cryptogramma*, the grouping on the spore types corresponds with other morphological characteristics, existing system and molecular phylogeny. Spore ornamentation has diagnostic value in the recognition of cryptogrammoid taxa at the generic and section (in *Cryptogramma*) level.

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Sino-Japanese and Sino-Himalaian regions of Eastern Asiatic Subkingdom are the centers of origin and diversity for subfamily *Cryptogrammoideae* and especially for the genus *Coniogramme*.

Комплексный анализ родства представителей подсемейства *Cryptogrammoideae* (Pteridaceae)

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Ключевые слова: морфология спор, папоротники, систематика, сканирующая электронная микроскопия (СЭМ), филогения, филогеография, *Coniogramme, Cryptogramma, Cryptogrammoideae*, *Llavea,* Pteridaceae.

Аннотация. Представлен первый комплексный анализ родственных отношений в подсемействе *Cryptogrammoideae*: 14 таксонов *Coniogramme* и один вид *Cryptogramma* были дополнительно привлечены к молекулярно-филогенетическим исследованиям на основе гена *rbcL* пластидной ДНК; с применением метода сканирующей электронной микроскопии (СЭМ) изучены споры 32 таксонов криптограммоидных папоротников, выявлено распространение 31 таксона *Cryptogrammoideae* в соответствии с глобальным ботанико-географическим районированием с использованием данных из Гербариев Европы и Азии (P, PE, LE, VLA, ALTB, TK). В результате установлена глубокая дивергенция *Coniogramme merillii* в суперкладе *Coniogramme*: этот вид является родственной линией остальной части рода; выявлена обособленность *Co. suprapilosa* от *Co. rosthornii* и *Co. longissima*, *Co. africana* от *Co. lanceolata* и *Co. fraxinea*, *Co. robusta* от *Co. jinggangshanensis*, *Co. wilsonii* и *Co. japonica*. Среди видов *Cryptogramma* выявлено родство дальневосточного *Cr. gorovoi* с кавказской и европейской *Cr. crispa* и турецким эндемиком *Cr. bithynica*, а не с каким-либо из дальневосточных видов. Споры *Coniogramme* характеризуются простой гладкой, зернистой и папиллятной макроскульптурой, споры видов *Cryptogramma* имеют более грубую колликулятную или бугорчатую макроскульптуру. Особенности макроскульптуры позволяют выделить шесть типов спор у криптограммоидных папоротников: четыре типа спор у *Coniogramme* и два у *Cryptogramma*; один и тот же тип спор выявлен у *Llavea cordifolia* и *Coniogramme suprapilosa*. Для рода *Coniogramme* группировка видов по типу спор не согласуется с существующей классификацией и филогенетическими гипотезами. Генетическая обособленность *Co. suprapilosa* соотносится с необнаруженной у других видов *Coniogramme* бородавчатой скульптурой спор. В роде *Cryptogramma* группировка видов по типу спор согласуется с морфологическим характеристиками, существующей системой и молекулярной филогенией. Скульптура спор имеет диагностическое значение при распознавании таксонов криптограммоидных папоротников на родовом и секционном (в роде *Cryptogramma*) уровне. Центрами происхождения и разнообразия подсемейства *Cryptogrammoideae*, особенно рода *Coniogramme*, являются китайско-японский и китайско-гималайский регионы Восточноазиатского подцарства.

Introduction

According to the modern system of the family Pteridaceae E. D. M. Kirchn, three genera – *Coniogramme* Fée, *Cryptogramma* R. Brown, and *Llavea* Lag. – belong to the subfamily *Cryptogrammoideae* S. Lindsay (Smith et al., 2006; Prado et al., 2007; Schuettpelz et al., 2007; Christenhusz et al., 2011; Zhang et al., 2013; PPG I, 2016). The separate family Cryptogrammaceae Pic. Serm. was proposed by R. E. G. Pichi-Sermolli (1963) who included three genera: *Cryptogramma*, *Llavea* and *Onychium* Kaulfuss. These representatives have similar morphological features of sporophytes, such as the structure of the terminal lobes of the fertile fronds, the presence of indusia, and partial to complete frond dimorphism. R. Ch. Ching (1940, 1978) did not accept Pichi-Sermolli's Cryptogrammaceae and put *Cryptogramma*, *Llavea*, and *Onychium* into the family Sinopteridaceae Koidzumi. R. M. Tryon and A. F. Tryon (1982) included these three genera as part of tribe *Cheilantheae* within the large family Pteridaceae. Later,

R. M. Tryon et al. (1990) transferred *Onychium* into the subfamily *Taenitidoideae* of Pteridaceae, whereas *Ctyptogramma* and *Llavea* remained in the subfamily *Cheilanthoideae*.

Molecular phylogenetic study based on the plastid DNA loci *rbcL*, *atpB*, and *atpA* confirmed indisputable relationship of three genera *Cryptogramma*, *Llavea*, and *Coniogramme* into the large family Pteridaceae, where the topology of "cryptogrammoid-clade" is well-supported and clade is monophyletic (Zhang et al., 2005; Schuettpelz et al., 2007; PPG I, 2016). A relationship between *Coniogramme*, *Cryptogramma,* and *Llavea* was never suggested based on morphology alone. This group is highly variable in morphology, and a clear morphological synapomorphy is lacking (Schuettpelz et al., 2007). Analysis of six-locus plastid dataset (*rbcL, rbcL–accD, rbcL–atpB, rps4–trnS, trnG–trnR*, and *trnP–petG*) demonstrated monophyly of *Coniogramme* and *Cryptogramma* within *Llavea*/*Coniogramme*/*Cryptogramma* clade; their relationship as sister taxa was not suggested until the advent of molecular research (Schuettpelz et al., 2007; Metzgar et al., 2013). According to a molecular study by J. S. Metzgar et al. (2013), *Coniogramme* and *Cryptogramma* are more closely related to each other than to *Llavea*, i. e. *Llavea* is sister to *Coniogramme* and *Cryptogramma* together.

Coniogramme is a largest genus in the subfamily, numbering from 20 (PPG I, 2016) or 25–30 (Zhang, Ranker, 2013) to 50 (Wang et al., 2020) species. This paleotropical genus is mainly distributed in the tropical and subtropical regions of Asia and extends to Africa and Malesia from Malaya and Sumatra east to New Guinea and in the Pacific to Samoa and Hawaiian Islands (Hieronymus, 1916; Tryon, Lugardon, 1991; Zhang, Ranker, 2013). A half of the representatives of the genus *Coniogramme* is endemic species. The genus is one of the most complex in the family Pteridaceae due to the high polymorphism of morphological features and hybridogenicity. The reason for a large number of synonyms among described taxa is the lack of clear diagnostic features for their identification. The most valuable diagnostic features are the shape of the frond lobes and their margins, the presence and type of hydathodes, the colour of the stipe and rachis (Zhang, Ranker, 2013). Recently a new feature was revealed for representatives from series *Coniogramme* – the number of annulus cells, which is stable at the species level and has great phylogenetic significance (Wang et al., 2020). Based on the morphology of sporophyte, the genus *Coniogramme* was divided into the section *Notogramme* (C. Presl) Ching ex K. H. Shing and section *Coniogramme* with series *Coniogramme* and *Serratae* Ching ex K. H. Shing (Shing, 1981). Twelve *Coniogramme* species were included in the phylogenetic reconstruction based on five chloroplast markers (*matK, psbA-trnH, rbcL, rps4-trnS, trnL-F*) by Wang et al. (2020). According to this study, *Coniogramme* ser. *Coniogramme* as formally distinguished by the morphology of pinnule margins is not a monophyletic group.

Among *Coniogramme* species, diploids (n = 30) *Coniogramme affinis* Hieron. and *Co. procera* Fée (Khullar et al., 1988; Kato et al., 1992), tetraploids (n = 60) *Co. africana* Hieron. and *Co. rosthorni* Hieron. (Löve et al., 1977) and hexaploid (n = 90) *Co. pilosa* Hieron. (Löve et al., 1977) were identified. Two ploidy levels (n = 30, 60) were indicated for *Co. fraxinea* (D. Don) Diels, *Co. japonica* (Thunb.) Diels, and *Co. intermedia* Hieron. (Kurita, 1972; Singh, Roy, 1988; Weng, Qiu, 1988; Kato et al., 1992).

The genus *Cryptogramma* includes about ten (Alverson, 1989a, b; Vaganov et al., 2010; Zhang, Ranker, 2013) extratropical species distributed mainly in the northern hemisphere, one species – *Cr. fumariifolia* (Phil. ex Baker) H. Christ – occurs in the south of South America (Raven, 1963; Alverson, 1989a; Zhang G. M., Zhang X. Ch., 2003; Metzgar et al., 2013). The genus includes two sections, *Cryptogramma* and *Homopteris* Rupr., sometimes considered as subgenera *Cryptogramma* and *Homopteris* (Rupr.) Tzvelev (Tzvelev, 1989; Shmakov, 2001). Species from the sect. *Cryptogramma* have erect rhizomes, fronds with a more coriaceous texture and generally prefer acidic, rocky habitats (Alverson, 1989a). *Cryptogramma stelleri* (S. G. Gmel.) Prantl, the only species of the sect. *Homopteris* (or subgen. *Homopteris*), has creeping rhizome, membraneous texture of fronds, and is often calciphilous (Hultén, Fries, 1986; Alverson, 1993). Based on molecular-phylogenetic studies, J. S. Metzgar et al. (2013, 2016) supported the recognition of nine taxa in *Cryptogramma* at the species level, as well as the monophyly of the two sections *Cryptogramma* and *Homopteris*.

The following chromosome counts are known for *Cryptogramma*: n = 30 (diploids) in *Cr. acrostichoides* R. Br., *Cr. brunoniana* Wall. ex Hook. et Grev., *Cr. cascadensis* Alverson, *Cr. stelleri* (Khullar et al., 1988; Alverson, 1989a; Gervais et al., 1999) and n = 60 (tetraploids) in *Cr. crispa* (L.) R. Br. and *Cr. sitchensis* (Rupr.) T. Moore (Alverson, 1989a; Pajarón et al., 1999).

Llavea is a monotypic American genus with a single species, *Llavea cordifolia* Lag., distributed in

the Central America from Mexico to Guatemala and Costa Rica (Palacios-Rios et al., 2017a). *Llavea cordifolia* is diploid with $n = 29$ (Knobloch, 1967).

Today, many studies have shown that characters of spore ornamentation, identified by scanning electron microscopy (SEM), are of diagnostic value and in most cases are congruent with the results of molecular phylogenetic studies (Gureyeva, Kuznetsov, 2015; Palacios-Rios et al., 2017b; Chao, Huang, 2018; Vaganov et al., 2020; Irfan et al., 2021; Vaganov, 2022). To date, there is some information on the spore morphology of *Cryptogramma, Coniogramme*, and *Llavea* species in the form of short descriptions of morphology and/or SEM-photographs (Tryon, Lugardon, 1991; Yu et al., 2001; Zhang G. M., Zhang X. Ch., 2003; Gureyeva et al., 2009; Vaganov et al., 2010, 2011; Vaganov, 2016).

Molecular phylogenetis study based on six plastid DNA regions (*rbcL, rbcL–accD, rbcL–atpB, rps4–trnS, trnG–trnR*, and *trnP–petG*) of nine species *Cryptogramma* was performed by J. S. Metzgar et al. (2013, 2016). This study supported the recognition of nine published *Cryptogramma* taxa at the species level, most species were found to be reciprocally monophyletic. Within *Coniogramme*, methods of molecular phylogenetic analysis based on five plastid DNA regions (*matK, psbA–trnH, rbcL, rps4–trnS*, and *trnL–F*) were applied for 11 species for species formally grouped into a series *Coniogramme* (Wang et al., 2020). This study has indicated that the present defined *Coniogramme* series *Coniogramme* is not a monophyletic group, and *C. merrillii* is a sister to the rest of *Coniogramme*.

The aim of presented work is an integrating study of the genera *Coniogramme*, *Cryptogramma*, and *Llavea* (*Cryptogrammoideae*, Pteridaceae) including molecular phylogenetic analysis, morphology of spores and phylogeography based on large number of taxa, including taxa that were not previously involved in the studies.

2. Material and methods

Information on the distribution of *Coniogramme*, *Cryptogramma*, and *Llavea* taxa was compiled from Herbaria across Europe and Asia (P, PE, LE, VLA, ALTB, and TK), as well as from Global Biodiversity Information Facility (GBIF, 2023) aggregated data of digitized herbarium specimen. Google Earth was used to clarify coordinates from the herbarium labels. The QGIS3.14 software was used to map the species distribution. In the botanical-geographical zoning of the Earth, we followed the global vegetation classification by R. V. Kamelin (2017).

Table 1

Studied taxa, herbarium number and place of storage of the examined specimens (an asterisks mark the taxa which spores were studied for the first time)

No.	Taxon	Country, herbarium number, and herbarium code
1	**Coniogramme affinis* (Wall.) Hieron.	China, Sichuan. Song Zipu. 01 VIII 1954. PE-00587617 (PE)
2	*Co. africana* Hieron.	Cameroon, Southwest region, J.-M. Onana. VII 2001. P00968223 (P)
3	**Co. caudiformis* Ching et K. H. Shing	China, Hunan. Xi Jian-Ming. 08 XI 2007. PE-01769269 (PE)
4	**Co. emeiensis* Ching et K. H. Shing	China, Hunan, Liu Bingrong, Yan Yuehong. 26 VI 2007. PE-01769317; China, Nanchuan, Li Guofeng, 30 VII 1957, PE-00598529; China, Guangxi, Qin Renchang, 13 VIII 1928, PE-00598215; China, Sichuan, Emai Shan, R.C. Ching, PE-00598262, type. (PE)
5	**Co. falcipinna* Ching et K. H. Shing	China, Sangzhi, Beijing Team, PE-01570623 (PE)
6	*Co. fraxinea* (Don) Diels	China, Kweichow, A. N. Steward, C. Y. Chiao, H. C. Cheo. 16 IX 1931 (LE); China, Yunnan, Sino-Soviet Mission, PE-00587823; China, Yunnan, Yunnan University, 12 X 1965, PE-00587775 (PE)
7	*Co. intermedia* Hieron. var. *intermedia*	China, Hunan, Liu Linhan. 25 X 1962. PE-00587987; China, Yunnan, Chung Ju-shi, 26 IX 1958 (LE); Japan, Kyushu, M. Kawabata, 26 VII 1963. PE-01715052; Japan, R. Itoo. PE-01715045; China, Yunnan, Wang Zhongren. 26 I 1978. PE-00598219; Japan, Shimonada-machi. Y. Miyoshi. 23 IX 1956. PE-01715073; China, Hubei. Wuhan University. 17 VIII 1951. PE-00587665; China, Sichuan. Xing Gongxia, Lang Kaiyong. 24 VIII 1963. PE-00598241 (PE)

Table 1 (continued)

No.	Taxon	Country, herbarium number, and herbarium code
8	**Co. intermedia* var. *glabra* Ching	China, Sichuan, Xing Gongxia, Lang Kaiyong. 19 VIII 1963. PE-00598501; China, Sichuan, Xing Gongxia, Lang Kaiyong. 16 VIII 1963. PE-00598493; China, Tibet, T. Naito et al. 14 V 1986. PE-00587774 (PE)
9	*Co. japonica* (Thunb.) Diels	Japan, Yokosuka. M. Le D` Sayatier. 1866. № 1572 (LE); China, Henan, Plant Resources Investigation Team. 09 VII 1984. PE-00598017; China, Jiangxi, Cheng Jingfu. 22 VI 1973. PE-00587754; China, Guangdong. Deng Liang. 01 IX 1958. PE-00587773; China, Anhui, M. B. Deng. 18 X 1996. PE-01644009; China, Hubei, Dai Lunying, Qian Chonghai. 19 X 1951. PE-00587832 (PE)
10	**Co. lanceolata* Ching	China, Yunnan, R. C. Ching, № 50448. 24 XI 1952. PE-00598191 (PE)
11	**Co. madagascariensis* C. Chr.	Madagaskar, Antsiranana, F. Rakotondrainibe. 3 XI 1994. P00006493 (P)
12	**Co. petelotii* Tardieu	China, Yunnan, T. T. Yu. 21 IX 1938. PE-00598322 (PE)
13	*Co. pilosa* Hieron.	U. S. A., A. A. Heller. IX 1895. P00518737 (P)
14	**Co. procera* (Wall.) Fée	China, Yunnan, K. M. Feng. PE-00598332 (PE)
15	**Co. pubescens* Hieron.	India, Simpla, Zhang Xianchun. 16 IX 2001. PE-01715075 (PE)
16	**Co. robusta* Christ var. *robusta*	China, Hunan, Beijing Team. 27 VIII 1988. PE-01557759; China, Hunan, Wu Shifu et al. 07 IX 1989. PE-00598372; China, Guizhou, Liu Zhengyu. 29 VII 1996. PE-00001394 (PE)
17	**Co. robusta* var. *splendens* Ching et K. H. Shing	China, Hunan, Zhou Joy, Ouyang Haibo, 22 VIII 2007. PE-01769305 (PE)
18	**Co. rosthorni* Hieron.	China, Taibai, Wang Fayan, Fu Kunjun, Huang Boxing, etc. 08 X 1955. PE-00598472 (PE)
19	**Co. rubicaulis* Ching	China, Guangxi. 17 IX 1989. PE-02019193 (PE)
20	**Co. serrulata* Fée	China, Yunnan. 09 V 1913. PE-01715042; China, Gongshan, Jin Xh., Wang L.S., Wang Q. et al. 20 VII 2013. PE-02004117 (PE)
21	**Co. suprapilosa* Ching	China, Sichuan, Kong Xianxu. 30 VII 1978. PE-00598461 (PE)
22	**Co. wilsonii* Hieron.	China, Wang Tso-Pin. PE-00598522; China, Henan. 1959. PE-00598513 (PE)
23	*Cryptogramma acrostichoides* R. Br.	U. S. A., Alaska, 29 VII 1990, S. Kharkevich (VLA); Russia, Kurile Islands, V. Yu. Barkalov. 14 XII 1985 (LE)
24	*Cr. brunoniana* Wall. ex Hook. et Grev.	China, Sikkim, J. J. (LE); China, Shaanxi, Girald, PE-00576078; China, Chongqing, Eighth Forest Manager Brigade. 25 VII 1958. PE-00576079 (PE)
25	*Cr. cascadensis* E.R. Alverson	U. S. A., California, A. A. Heller. 27 VII 1903 (LE); U. S. A., Geo. Hansen. 10 I 1894. P01270635 (P)
26	*Cr. crispa* (L.) R. Br.	Russia, Murmansk, M. Kachurin. VIII 1937. (LE); France, Valsenestre, R. Barbezat. 27 VIII 1939. P01572968 (P)
27	**Cr. fumariifolia* (Phil.) Christ	South America, P01323621 (P)
28	*Cr. gorovoii* Vaganov et Shmakov	Russia, Sakhalin, Pavlova and Pankov. 13VIII 1966. ALTB1010000027, typus (ALTB)
29	*Cr. raddeana* Fomin	Russia, Buryatia, Lake Baikal. Baikal ridge. T.V. Egorova and V. N. Siplivinsky, 1–3 VIII 1967 (LE)
30	*Cr. sitchensis* (Rupr.) T. Moore	Russia, Magadan, V. A. Golub. 08 XII 1933. No. 8 (LE); U. S. A., Alaska, C. Kharkevich. 22 VII 1990 (VLA)
31	*Cr. stelleri* (S.G. Gmel.) Prantl	Russia, Altai, A. Pyak. 25 VII 1990. TK-004507 (TK)
32	*Llavea cordifolia* Lag.	Mexico, Nuevo Leon, C. G. Pringle. 12 III 1906 (LE)

Morphology and morphometry of spores

Samples for studying spore morphology using scanning electron microscopy (SEM) were collected from herbarium specimens (P, PE, ALTB, LE, TK, and VLA), including type material of *Coniogramme emeiensis* Ching et K.H. Shing and *Cryptogramma gorovoii* Vaganov et Shmakov. Fifty-six samples comprising 32 taxa, including 22 taxa of *Coniogramme*, nine species of *Cryptogramma*, and one species of *Llavea* were analyzed (Table 1). Spores of 19 taxa were studied for the first time. Identification of species was confirmed by the first author (AVV).

Ultrastructure of spores was performed using SEM, only mature spores were used for observations. Spores were mounted on metal stubs with adhesive double-sided tape, covered with gold or gold/palladium mixture under vacuum, and examined with Mini-SEM SNE-4500M (SEC Co. Ltd, Korea) at Tomsk State University (Tomsk, Russia) and Hitachi S 3400 N (Hitachi Science Systems, Ltd, Japan) at the Institute for Water and Environmental Problems of Siberian Branch of Russian Academy of Science (Barnaul, Russia). Spore surfaces were scanned in a high vacuum at voltage of 25 or 30 kV, with 400× to 14000× magnification.

SEM-micrographs of spores in the polar (distal and proximal) and in equatorial positions were used for the description of the shape and ornamentation of spores. The shape of the distal and proximal parts of the spore as seen in the equatorial position we described using the terms of Nayar and Devi (1966). In terminology for the description of spore ornamentation, we followed basically Lellinger (2002). Here we used the following terms for description of ornamentation (sculpture) of spores in cryptogrammoid ferns:

– smooth: the surface is smooth without sculptural elements visible in SEM;

– granulate: the presence of minute, granule-like elements;

– papillate: the presence of minute densely spaced papillae;

– verrucate: the presence of elements that are slightly longer than wide, irregular in shape (wart-like), and have obtuse to round apex; verrucae are formed by inner massive consolidated layer of perispore;

– colliculate: the presence of elements that are contiguous, broadly attached, no higher than wide, and with an obtuse to round apex;

– tuberculate: the presence of tubercles that are as long as wide and have a rarely truncate or an obtuse to round apex.

SEM-micrographs of spores in distal, proximal and equatorial positions were used for the measurements using the software "Image J". A total of 1863 spore images were analyzed in detail. Equatorial diameter (ED) in polar view, length (LL) and width (LW) of laesura arms in proximal view were used as the main biometrical characters of spores. All measurements were taken on 25 spores from each species. Datasets were processed using the software Statistica 8.0 (2008, http://www.statsoft.com) with estimation of the mean (M) and standard error (SE). The minimum, mean, and maximum are given in micrometres.

Molecular phylogenetic analyses

Sequences for *rbcL* gene of plastid DNA were used for phylogenetic analyses. DNA was extracted from samples obtained from herbarium specimens representing 26 taxa, including 22 accessions of *Coniogramme*, 2 accessions of *Cryptogramma*, one accession of *Syngramma*, and one accession of *Taenitis* (Table 2). Herbarium material was obtained in Herbaria P, PE, and ALTB. Furthermore, 18 accessions of 14 *Coniogramme* taxa, 16 accessions of 10 *Cryptogramma* taxa, 1 accession of *Llavea,* 1 accession *Actiniopteris*, and 1 accession *Onychium* were downloaded from Genbank (NCBI, National Center for Biotechnology Information, https://www.ncbi.nlm.nih.gov/) (Table 2). Accessions of *Syngramma*, *Taenitis*, *Actiniopteris*, and *Onychium* were used as the outgroup.

DNA isolation was performed using a DiamondDNA Plant kit (ABT, Russia) according to the manufacturer's protocol. *RbcL* plastid DNA regions were amplified using the Biomaster HS-Taq PCR-Color (2×) (Biolabmix, Russia) with primers according to the Korall et al. (2006). PCR amplification was carried out according to the following parameters: initial denaturation for 5 min at 95 °C, followed by 35 amplification cycles: 30 s at 94 °C, 30 s at 52 °C, 90 s at 72 °C; postelongation for 7 min at 72 °C. PCR products was purified using MAXLIFE MagnetDNA kit (MVM-Diagnostic, Russia). Sanger sequencing was perfomed on an automatic sequencher ABI Prism 3130xl (Applied Biosystems, U. S. A.).

All sequences were aligned using ClustalX 2.1 (Larkin et al., 2007), and the resulting alignment was then refined manually in Geneious Prime 2022.2.2 (Biomaters Ltd., U. S. A.).

Sequence evolution models were evaluated using General Time-Reversible (GTR) with gamma distribution and invariant sites with the aid of jModelTest2 (Darriba et al., 2012). Bayesian analyses were conducted with MrBayes 3.2.6 with four Markov chains for 1 million generations, sampling trees every 250 generations with 250 000 burn-in length (Huelsenbeck, Ronquist, 2001).

Table 2

Sources of the material and GenBank accession numbers for *rbcL* sequences of the taxa under the study

No.	Taxon	*rbc*L GB Acc. NR / base pair	Author	Locality	Voucher
1	*Actiniopteris radiata* Link	AF336100 / 1325 bp	Gastony, Johnson (2001)	Olduvai Gorge, Tanzania	Gastony 12-97-102
2	*Coniogramme affinis*	OQ984939 / 1195 pb	Present study	China, Beside the Eagle Ditch in Yongxing Township. Baoxing County. Sichuan Province	PE00587617
3	*Co. affinis*	OQ984938 / 1195 pb	Present study	China, Shaanxi Province	PE00587604
4	*Co. africana*	OQ984934 / 1195 pb	Present study	Cameroon, Southwest region, Mt Kupe, Kupe Village	P00968223
5	*Co. caudiformis*	OQ984942 / 1195 pb	Present study	China. Hunan Province. Liuyang County Dawei Mountain Forest Farm	PE01769269 (type)
6	*Co. emeiensis*	MN867753 / 1254 bp	Wang et al. (2020)	Badong, Hubei	Yudong Wu 012
7	*Co. falcipinna*	OQ984944 / 1195 pb	Present study	China, Chekiang Province	PE00587754
8	*Co. fraxinea*	MN867752 / 1233 bp	Wang et al. (2020)	Cangyuan, Yunnan	Zhongyang Li PT-1049
9	*Co. fraxinea*	MN867750 / 1248 bp	Wang et al. (2020)	Menglian, Yunnan	Zhongyang Li PT-1073
10	*Co. fraxinea*	MN867764 / 1236 bp	Wang et al. (2020)	Ruili, Yunnan	Gangmin Zhang 1816-4
11	*Co. gigantea* Ching	MN867760 / 1227 bp	Wang et al. (2020)	China, Jinping, Yunnan Province	Junwen Zhao Z2018070805
12	*Co. gigantea*	MN867751 / 1236 bp	Wang et al. (2020)	Maguan, Yunnan	Zhongyang Li PT-1195 pb
13	*Co. intermedia* var. *glabra*	OQ984947 / 1195 pb	Present study	[from the label]	PE828500
14	*Co. intermedia* var. *Glabra*	OQ984946 / 1195 pb	Present study	China. Tibet Autonomous Region. Tongmai, Bomi County	PE00587774
15	*Co. intermedia* var. *intermedia*	OQ984945 / 1195 pb	Present study	[from the label]	PE00587667
16	*Co. intermedia* var. *intermedia*	OQ984948 / 1195 pb	Present study	China, Hunan Province	PE01769257
17	*Co. japonica*	AB574813 / 1205 bp	Ebihara et al. (2010)	–	–
18	*Co. japonica*	MN867756 / 1236 bp	Wang et al. (2020)	Hezhou, Guangxi	Rihong Jiang HZ058
19	*Co. japonica*	OQ984930 / 1195 pb	Present study	Japan, Izu peninsula, Shizuoka Prefecture, Kamo District, Nashimoto, river valley Kawazu, Fuji-Hakone-Izu National Park. 35°	ALTB1010004712

Table 2 (continued)

No.	Taxon	*rbc*L GB Acc. NR / base pair	Author	Locality	Voucher
20	*Co. jinggangshanensis* Ching et K. H. Shing	OQ984931 / 1195 pb	Present study	China, Jiangxi Province	PE01769311
21	*Co. jinggangshanensis*	OQ984932 / 1195 pb	Present study	[from the label]	PE00598511
22	*Co. lanceolata*	MN867741 / 1290 bp	Wang et al. (2020)	Yunxian, Yunnan	Caihong Wang 20181014-2-1
23	*Co. lanceolata*	MN867763 / 1236 bp	Wang et al. (2020)	Longling, Yunnan	Gangmin Zhang 1820-7
24	*Co. lanceolata*	MN867742 / 1293 bp	Wang et al. (2020)	Yunxian, Yunnan	Caihong Wang WZ2018072902-01
25	*Co. longissima* Ching et Kung	OQ984937 / 1195 pb	Present study	China, Hunan Province	PE01769246
26	*Co. maxima* Ching et K.H. Shing	OQ984943 / 1195 pb	Present study	China, Hunan Province	PE01769317
27	*Co. merrillii* Ching	MN867758 / 1005 bp	Wang et al. (2020)	China, Wuzhishan, Hainan Province	Wuzhishan Fern Survey 309
28	*Co. merrillii*	MN867744 / 846 bp	Wang et al. (2020)	China, Lingshui, Hainan Province	Shiyong Dong 544-1
29	*Co. petelotii*	MN867761 / 1236 bp	Wang et al. (2020)	Jinping, Yunnan	Junwen Zhao Z2018070806
30	*Co. procera*	MN867754 / 1233 bp	Wang et al. (2020)	China, Nujiang, Yunnan Province	Xianchun Zhang 6344
31	*Co. pubescens*	OQ984940 / 1195 pb	Present study	Yunnan, Shweli-Salwin divide, Coll. George Forrest № 24628	PE01715084
32	*Co. pubescens*	OQ984941 / 1195 pb	Present study	India. Simpla. Coll: Zhang Xianchun	PE01715075
33	*Co. robusta*	OQ984929 / 1195 pb	Present study	China. Hunan province. Tongdao Dong Autonomous County of Dupo Township	PE00598372
34	*Co. rosthornii*	MN867745 / 1194 bp	Wang et al. (2020)	China, Yangbi, Yunnan Province	Junwen Zhao ZY17082110
35	*Co. rosthornii*	OQ984936 / 1195 pb	Present study	China. Sichuan Province. Sanlanggang. Leibo County	PE00598461
36	*Co. rubicaulis*	MN867762 / 1233 bp	Wang et al. (2020)	China, Rongshui, Guangxi Province	Caihong Wang 1825-2-3
37	*Co. rubicaulis*	MN867755 / 1230 bp	Wang et al. (2020)	China, Xinyi, Guangdong Province	Yuehong Yan WYD573
38	*Co. sinensis* Ching	OQ984949 / 1195 pb	Present study	China, Hunan Province	PE00598327
39	*Co. sinensis*	OQ984950 / 1195 pb	Present study	Sichuan Province	PE01363233
40	*Co. suprapilosa*	OQ984935 / 1195 pb	Present study	China. Hubei Province	PE01363196
41	*Co. wilsonii*	OQ984933 / 1195 pb	Present study	China, Jiangxi Province	PE01769248
42	*Cryptogramma acrostichoides*	KC700093 / 1309 bp	Metzgar et al. (2013)	U. S. A., Alaska, Kodiak, near the transient boat harbor	Studebaker 09-473 (ALA)
43	*Cr. acrostichoides*	KC700102 / 1309 bp	Metzgar et al. (2013)	Russia, Kamchatka, north of Kamchatka peninsula, near Karaginskij	Chernyagina s. n. (ALA)

Table 2 (continued)

No.	Taxon	*rbc*L GB Acc. NR / base pair	Author	Locality	Voucher
44	*Cr. bithynica* S. Jess	KT000629 / 1309 bp	Metzgar et al. (2016)	Turkey, Uludağ, silicate scree slope on NNE side of mountain	Jessen SJ-3820 (ALA)
45	*Cr. brunoniana*	KC700082 / 1309 bp	Metzgar et al. (2013)	China, Xizang (Tibet) Province, Baxoi Xian, Anjiu La (pass), N of Rawu (Raog)	Boufford 29733 (GH)
46	*Cr. brunoniana*	KC700081 / 1309 bp	Metzgar et al. (2013)	Taiwan, NanTou County, Mt. ShihMen	Kuo 455 (TAIF)
47	*Cr. cascadensis*	KC700086 / 1291 bp	Metzgar et al. (2013)	U. S. A., Oregon, Deschutes / Linn County boundary, McKenzie Pass	Alverson s.n. (ALA)
48	*Cr. cascadensis*	KC700087 / 1294 bp	Metzgar et al. (2013)	U. S. A., Washington, King County, Source Lake Lookout Trail, above Source Lake	Zika 25404 (ALA)
49	*Cr. crispa*	KT000630 / 1309 bp	Metzgar et al. (2016)	Russia, Dombai, North Caucasus	Jessen SJ-3099 (ALA)
50	*Cr. crispa*	KC700089 /	Metzgar et al. (2013)	Spain: Madrid Province, Sierra de Guadarrama, Siete Picos	Pajarón s.n. (ALA)
51	*Cr. fumariifolia*	KC700079 / 1309 bp	Metzgar et al. (2013)	Chile, Provincia de Ñuble, Comuna de Pinto, Shangri-La	Larraín 34009 (ALA, CONC)
52	*Cr. gorovoii*	OQ984927 / 1195 pb	Present study	Russia, Sakhalin isl., Makarov district, north of the villages Zaozernoe, Southern slope of Mount Ostrovskaya, along the river Ugledarka, 48°24'N, 142°40'E	Vaganov, Salokhin (2239-1_SSBG)
53	*Cr. gorovoii*	OQ984928 / 1195 pb	Present study	Russia, Sakhalin isl., Makarov district, north of the villages Zaozernoe, Southern slope of Mount Ostrovskaya, along the river Ugledarka, 48°24'N, 142°40'E	Vaganov, Salokhin (2239-2_SSBG)
54	*Cr. raddeana*	KC700084 / 1309 bp	Metzgar et al. (2013)	Russia, Republic of Buryatia, Severo-Muisky range, Samokuya	Naumov 1989 (NS)
55	*Cr. raddeana*	KC700085 / 1309 bp	Metzgar et al. (2013)	Russia, Khabarovsky krai, 30 km north of Sofiysk	Netchaev s.n. (NS)
56	*Cr. sitchensis*	KC700103 / 1309 bp	Metzgar et al. (2013)	U. S. A., Alaska, between Portage and Whittier, Bering Glacier	Metzgar 248 (ALA)
57	*Cr. sitchensis*	KC700106 / 1309 bp	Metzgar et al. (2013)	U. S. A., Alaska, Palmer, Hatcher Pass	Metzgar 249 (ALA)
58	*Cr. stelleri*	KC700076 / 1309 bp	Metzgar et al. (2013)	Taiwan: NanTou County, Hohuan Shelter	Kuo 492 (TAIF)
59	*Cr. stelleri*	KC700077 / 1309 bp	Metzgar et al. (2013)	U. S. A., Alaska: Alexander Archipelago: Prince of Wales Island	Johnson 20104 (ALA)
60	*Llavea cordifolia*	KC700108 / 1309 bp	Metzgar et al. (2013)	Mexico: Hidalgo: Municipio Nicolas Flores. On road to Nicolas. Flores from Cardonal	Rothfels 3025 (ALA, DUKE, MEXU)
61	*Onychium japonicum* (Thunb.) Kunze	KU744808 / 1246 bp	Zumkeller et al. (2016)	Plant material was obtained from the Botanic Garden Bonn	Botanic garden accession numbers «xx-0-BONN-26126»
62	*Syngramma borneensis* (Hook.) J. Sm.	OQ98492 / 1195 pb	Present study	Mimika Regency, PT-Freeport Indonesia Concession Area: Tributary of the Marao river. 4°	PE01578069
63	*Taenitis pinnata* (J. Sm.) Holttum	OQ984925 / 1195 pb	Present study	About 2 km NNE of Julatten, north Queensland. 16°	PE01966567

Phylogeography

Phylogeography of taxa was reconstructed using Mesquite software (Maddison W., Maddison D., 2018). Selected characters were optimized onto the tree set obtained from the maximum likelihood (ML) analysis of *rbcL* including one exemplar for each species. Jukes-Cantor distance models of DNA evolution were used with the choice of the single Linkage clustering method (with maxtrees set to 10,000). For the table with standard categorical data in Mesquite, we used three characters designating floristic kingdom, subkingdom and region. Characters were treated as unordered, categorical variables and mapped onto the phylogenetic trees obtained from the *rbcL* dataset to infer patterns of evolution.

3. Results

3.1. Phylogeographic analysis

The analysis of the generalized material using a global vegetation classification by R. V. Kamelin (2017) showed that the distribution of *Coniogramme*, *Cryptogramme*, and *Llavea* is limited to three floristic kingdoms, including nine subkingdoms and 17 regions of the Old and New World (Fig. 1). Most of the studied species (24 out of 40) are located in the largest floristic Kingdom on the Earth – the Holarctic Kingdom, nine taxa occur in both, Holarctic and Paleotropical Kingdoms, five species are distributed in Paleotropical Kingdom only, one species grow in Neotropical Kingdom and one species – in both, Holarctic and Neotropical Kingdoms.

All taxa of *Coniogramme* are distributed in the Old World, among them, 16 taxa are distributed in east part of Holarctis, five taxa – in both, east Holarctis and Paleotropis, and five species grow in Paleotropis. The most species occur in East Asia in Sino-Japanese Region; some of them distributed westward to Sino-Himalaian (*Co. emeiensis*, *Co. falcipina*, *Co. intermedia* var. *glabra*, *Co. robusta* (including variations), *Co. rosthornii*, *Co. suprapilosa*) and Indian (*Co. affinis*, *Co. lanceolata*) Regions and eastward to Indochinese and Malesian Regions (*Co. petelotii, Co. procera, Co. pubescens*), the most widespread are *Co. fraxinea* and *Co. intermedia* var. *intermedia.* The narrow geographic range within the single floristic region is characteristic for *Co. caudiformis* and *Co. longissima* (Sino-Himalaian Region), *Co. japonica, Co. jinggangshanensis* and *Co. rubicaulis* (Sino-Japanese Region) and *Co. pilosa* (Hawaian Region). Only two species occur outside of East Asia and the Pacific Islands: *Co. africana* (African Subkingdom, Guineo-Congolian and Zambezian Regions) and *Co. madagascariensis* (Madagascar Subkingdom, Madagascar Region).

The genus *Cryptogramma* is distributed mainly in extratropical Holarctis of the Old and New World, the only species – *Cr. fumariifolia* is an endemic growing in Neotropis in the mountain of Andian Region with temperate climate. The most widespread is *Cr. stelleri* and *Cr. acrostichoides*, which occur in three subkingdoms of Holarctis.

The geographic range of the single species of *Llavea* lies in Holarctis of New World (Pacific-American Region) and Neotropis (Carribean Region).

3.2. Phylogenetic analysis of the *rbcL* dataset

The dataset for 40 species was comprised. The aligned data matrix for the protein-coding *rbcL* locus was 1195 bp in length, where "n" we used to denote empty values. The BI tree shows a similar topology with the ML tree. The posterior probability values are shown at the nodes (Fig. 2). Our results showed that all genera *Coniogramme*, *Cryptogramma*, and *Llavea* formed the separate clades. The assertion was confirmed that *Llavea* is sister to *Coniogramme* and *Cryptogramma* together. The genera *Coniogramme* and *Cryptogramma* are reciprocally monophyletic, and their representatives are united by absolute relationship (PP = 1.0).

Inside *Coniogramme* superclade, *Co. merrillii* is sister to the rest taxa and its topology is strongly supported (PP = 1.00). The rest *Coniogramme* taxa are grouped into two strongly supported (PP = 1.0) unequal clades, which we named *Coniogramme*-I-clade including 20 taxa, and *Coniogramme*-II-clade including 4 species. The *Coniogramme*-I-clade dichotomizes into the subclades of the first order (PP = 0.99) including 13 and 7 taxa respectively. The first subclade uniting 13 taxa is divided into the next two unequal subclades of the second order. First of them is divided (PP = 0.62) into two parts, one of which (PP = 0.9) remains unresolved and is characterized by the unspecific set of eight taxa, another part includes two species that are strongly supported (PP = 1.0) as monophyletic lineages – *Co. affinis* and *Co. pubescens*. The second subclade of the second order (PP = 1.0) includes three species, among them, *Co. suprapilosa* is sister to *Co. rosthornii* and *Co. longissima* together, and the only accession of *Co. longissima* nested with one of accessions of *Co. rosthornii.*

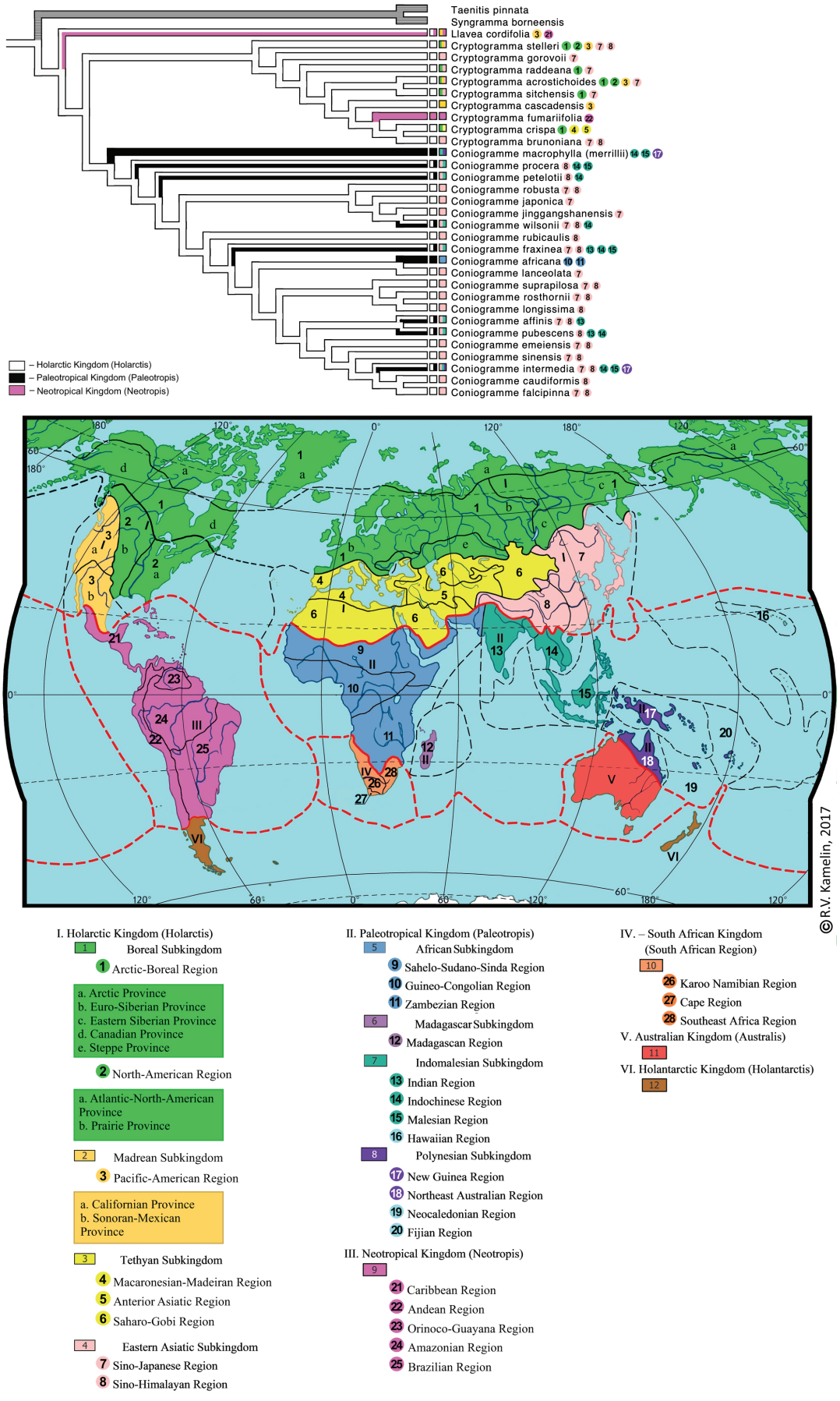

Fig. 1. Distribution of *Coniogramme*, *Cryptogramme*, and *Llavea* taxa among global floristic regions. Phylogeography of the genera is shown using Mesquite.

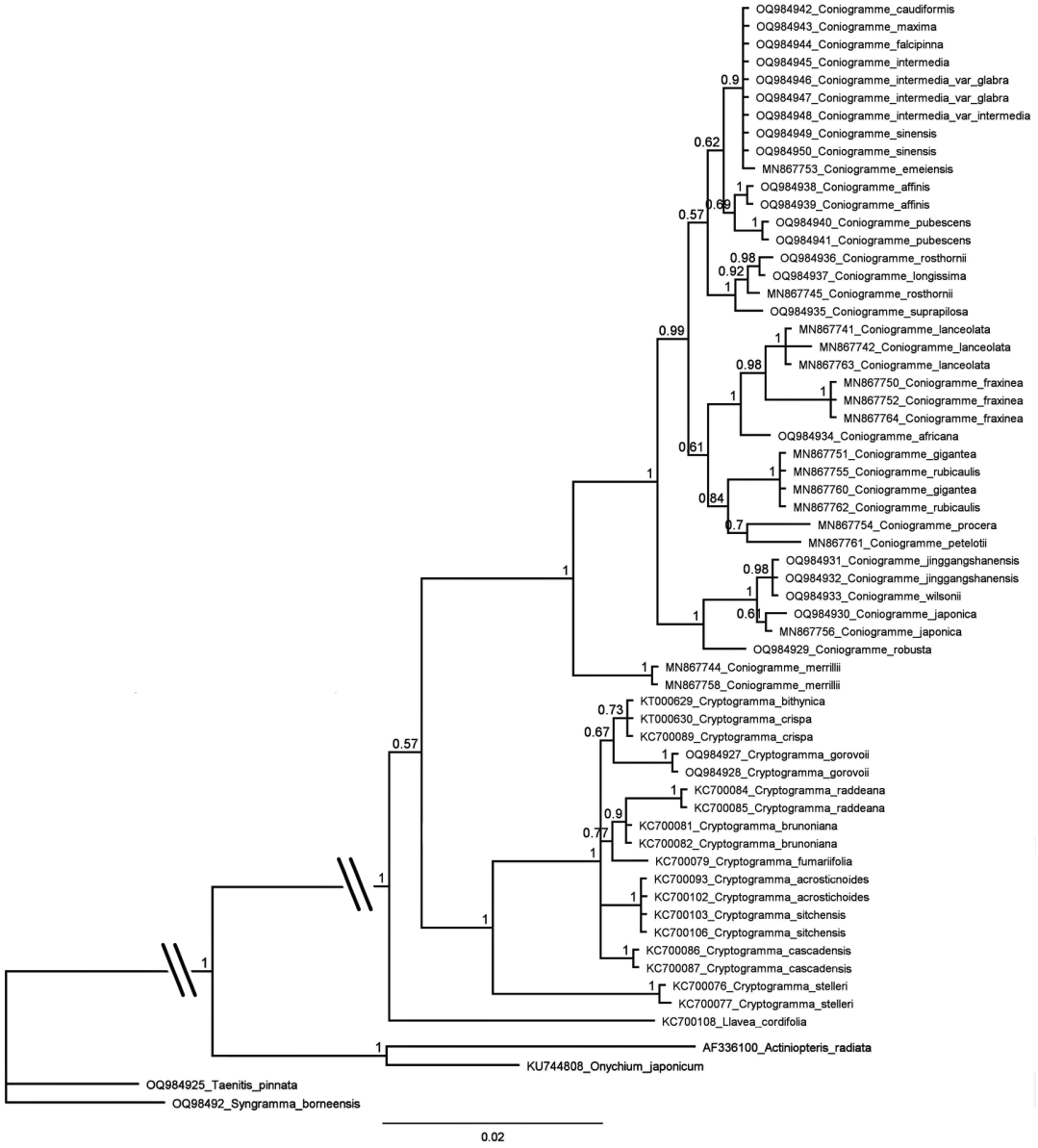

Fig. 2. The majority rule consensus topology resulting from the Bayesian / Markov Chain Monte Carlo analysis of the *rbcL* dataset. Branch length corresponds to the estimated number of substitutions. Values above branches correspond to the bootstrap values.

The second first order subclade of *Coniogramme*-I clade includes seven species, that are united into two moderately supported (PP = 0.61) subclades of the second order. First of them includes three well-supported lineages corresponding to three species from which *Co. africana* is sister to *Co. lanceolata* and *Co. fraxinea* together, and accessions of the two last species are characterized by their genetic homogeneity in *rbcL* gene. Another second order subclade includes two lineages: moderately supported (PP = 0.7) lineage with *Co. procera* and *Co. petelotii* and strongly supported one (PP = 1.0) with *Co. gigantea* and *Co. rubicaulis* that appear to be identical in *rbcL* gene.

The *Coniogramme*-II-clade unites four species (PP = 1.0). Two lineages correspond with two species – *Co. robusta* and *Co. japonica*, besides *Co. robusta* is sister to the rest species of this clade. The third unresolved lineage includes two accessions of *Co. jinggangshanensis* Ching et K.H. Shing and single accession of *Co. wilsonii*.

The *Cryptogramma* superclade includes two strongly supported (PP = 1.0) clades corresponded to two sections (subgenera): *Cryptogramma* including the most of species and *Homopteris* including a single species *Cr. stelleri*. Plastid *rbcL* gene has not resolved the *Cryptogramma*-clade, it includes four groups as equal, one of which includes accessions

of a single species – *Cr. cascadensis*, other groups include different species. The first group includes two lineage: strongly supported monophyletic *Cr. gorovoii* and moderately supported lineage including *Cr. bithynica* S. Jess. and *Cr. crispa*. In the second group, *Cr. fumariifolia* supported on the specific level, accessions of the *Cr. raddeana* formed the strongly supported monophyletic lineage within *Cr. brunoniana*. Finally, the third group is unresolved and includes all accessions of *Cr. acrostichoides* and *Cr. sitchensis* as equal.

3.3. Spore morphology and morphometry

Spores of all examined species of *Coniogramme*, *Cryptogramma*, and *Llavea* are trilete and tetrahedral or tetrahedral-globose in shape. In equatorial position, the distal part is convex to hemispherical, proximal part is flat, convex or conical. In polar position, spores are triangular, roundish-triangular or triangular-roundish in outline with straight, concave or convex sides and rounded corners. Macro-ornamentation of the spores of *Coniogramme* is not well defined, mostly the same on proximal and distal part of spore. Macro-ornamentation of the spores of *Cryptogramma* is more coarse and slightly different on proximal and distal part. Micro-ornamentation of the spore surfaces is presented by granular deposits in varying density. Three laesura arms form a clearly visible commissure without commissural flange. Laesura arms are mostly straight, long, reaching the spore corners, or short with length from ⅓ to ¾ of radius of the spore as seen in proximal-polar position. The main characters of spores of all examined taxa are shown in detail in figures 3–10 and described in the Table 3.

Based on definition of macro-ornamentation, we recognise six spore types in cryptogrammoid ferns. The first four types of ornamentation – smooth, granulate, papillate, and verrucate – are formed by perispore, exospore is smooth (types I–IV); these type are different to each other in the presence / absence and the size of the prominent elements of sculpture. The next two types of ornamentation – colliculate and tuberculate – are characterized by more coarse sculpture elements formed by thick exospore, the thin perispore conforms to exospore (types V–VI).

Type I – Proximal and distal faces smooth, without any sculpture. This type includes two narrowly endemic species of *Coniogramme* – *Co. madagascariensis* (Madagascar, Reunion) and *Co. rubicaulis* (Guangxi, China) (Fig. 3). Spore surface without or with sparse granular deposits. Both species are characterized by the flat proximal and convex distal part of spore. Laesura arms are reaching spore corners, very prominent in spores of *Co. madagascariensis* (Fig. 3; Table 3).

Type II – Proximal and distal faces with granulate ornamentation. This type is the largest and contains 13 taxa of *Coniogramme* including two varieties of *Co. intermedia* and two varieties *Co. robusta* (Figs 3–6, Table 3). Spores of *Co. serrulata* (Blume) Fée are characterized by smooth proximal and granulate distal face (Fig. 6). Spore surface mostly with solitary or sparse granular deposits. The shape of the proximal part of spores is mostly flat or flat to convex, two taxa have spores with conical proximal part – *Co. intermedia* var. *glabra* and *Co. pilosa*; the distal part is hemispherical (Figs 4, 5; Table 3). Laesura arms are mostly reaching of spore corners, in *Co. fraxinea* they are of a half the radius of spore. Laesura arms are prominent in *Co. falcipinna*, *Co. intermedia* var. *glabra*, *Co. pilosa*, and *Co. serrulata*. Spores of most species of this type are depressed between laesura arms; spores of *Co. fraxinea, Co. pilosa*, *Co. procera*, *Co. pubescens*, and *Co. robusta* (both varieties) are unusual depressed what could be due to the incompletely developed wall in the spores (Figs 4–6).

Type III – Proximal and distal faces with papillate ornamentation. This type includes five *Coniogramme* species: Southeast Asian *Co. affinis*, Far-Eastern *Co. japonica*, and Southasian *Co. rosthorni*, *Co. wilsonii*, and *Co. petelotii* (Figs 6, 7). Granular deposits on spore surfaces are absent or solitary; spores of *Co. petelotii* covered by dense granular deposits, especially on the distal surface. The shape of the proximal part of spores is different, from flat in *Co. japonica* to conical in *Co. affinis* and *Co. rosthorni*; the distal part is hemispherical in all species of the type III. The laesura arms are different in length relatively spore radius in different species, very prominent in *Co. affinis* and *Co. japonica*, obscured by sculpture in *Co. rosthorni* (Figs 6, 7; Table 3).

Type IV – Proximal and distal faces with verrucate ornamentation. This type includes two species of two genera – *Coniogramme suprapilosa* and *Llavea cordifolia* with the spore ornamentation formed of verrucae varied in shape and size, more prominent in distal face. Spore surface without granular deposits in *Co. suprapilosa* and with sparse deposits in *L. cordifolia*. Proximal and distal parts of spores are different in shape. Spores of *Co. suprapilosa* are unusual depressed in proximal part between laesura arms. Laesura arms are prominent in *Co. suprapilosa* and quite obscured by sculpture in *L. cordifolia* (Fig. 8; Table 3).

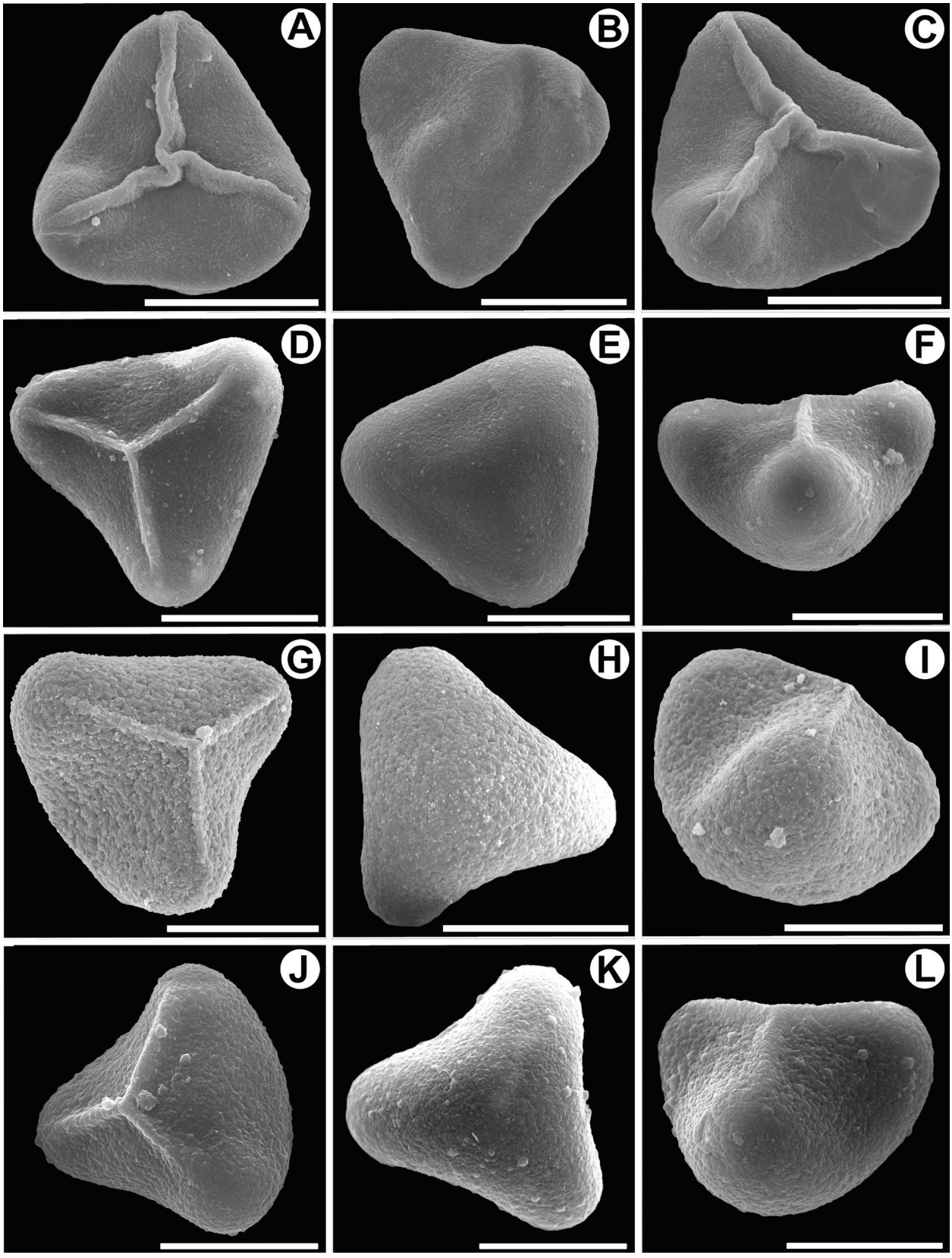

Fig. 3. SEM micrographs of the spore type I: *Coniogramm madagascariensis* (**A–C**) and *Co. rubicaulis* (**D–F**), proximal and distal faces are smooth. SEM micrographs of the spore type II: *Co. africana* (**G–I**) and *Co. caudiformis* (**J–L**), proximal and distal faces are granulate. Spores in proximal view (A, C, D, G, J), spores in distal view (B, E, H, K), spores in equatorial view (F, I, L). Very prominent laesura arms (D, F). Scale bars: 20 μm.

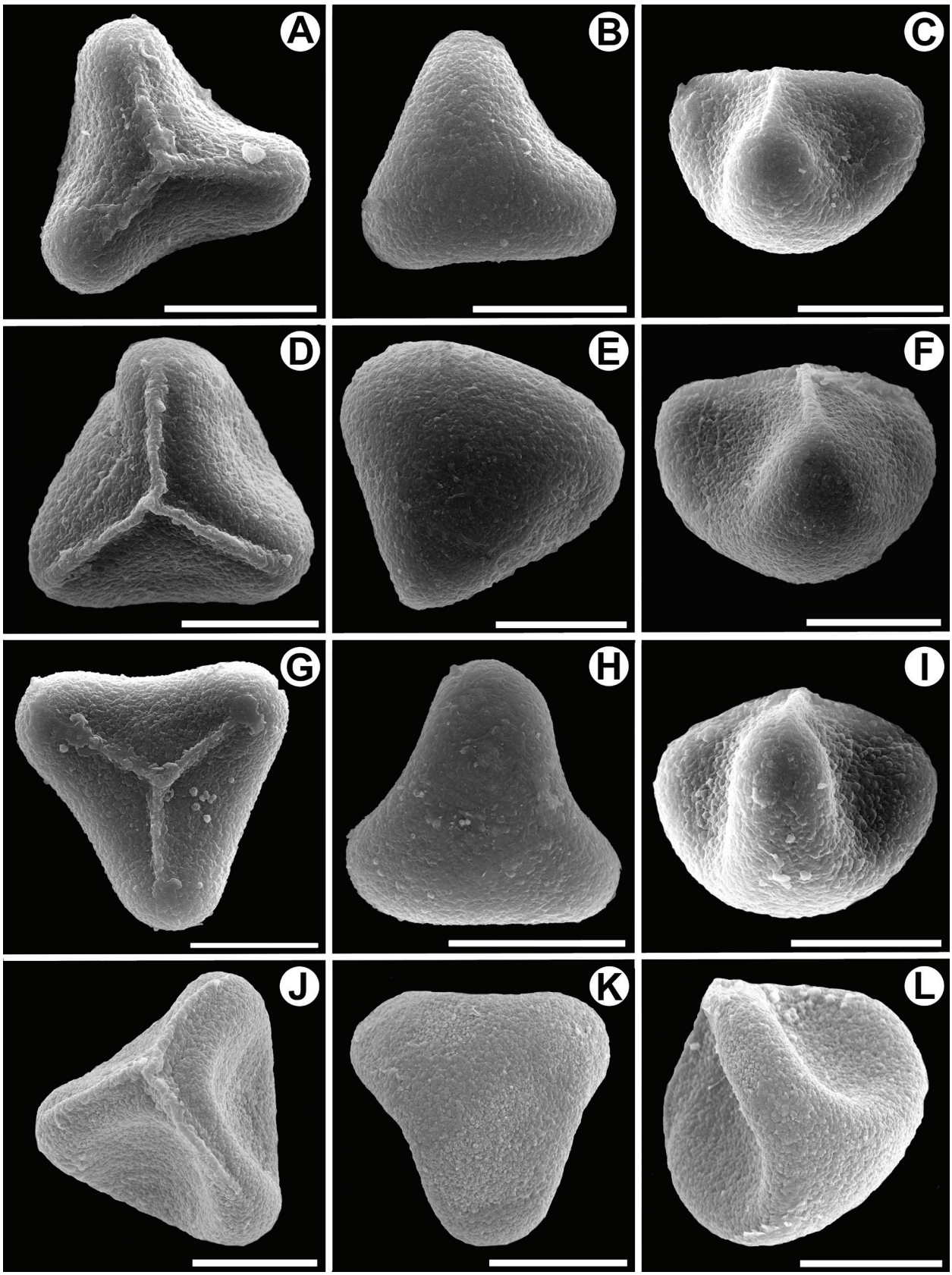

Fig. 4. SEM-micrographs of the spore type II: *Coniogramme emeiensis* (**A–C**), *Co. falcipinna* (**D–F**), *Co. fraxinea* (**G–I**), *Co. pilosa* (**J–L**), proximal and distal faces are granulate. Spores in proximal view (A, D, G, J), spores in distal view (B, E, H, K), spores in equatorial view (C, F, I, L). Deeply depressed areas between laesura arms (I, J, L). Scale bars: 20 μm.

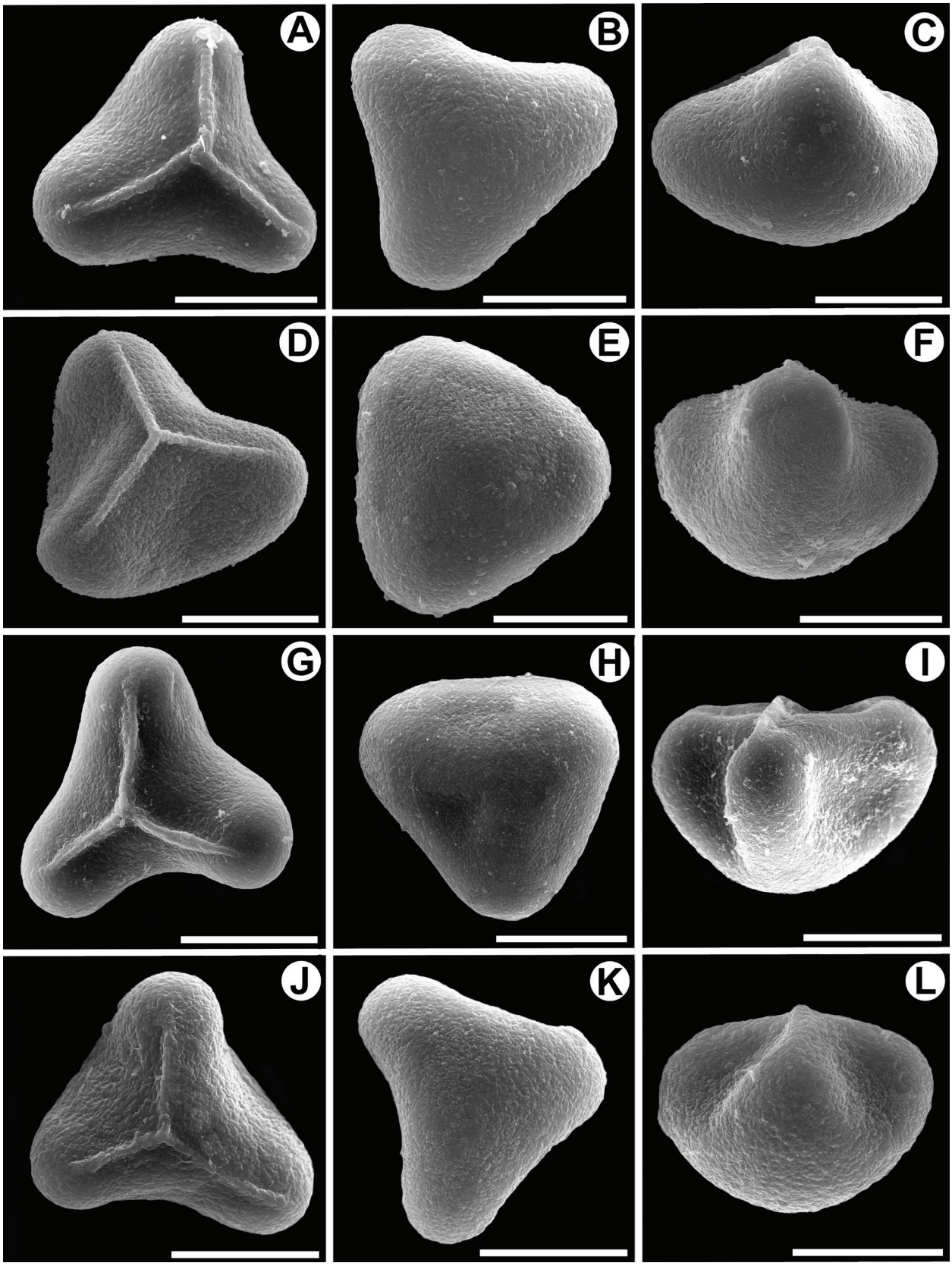

Fig. 5. SEM-micrographs of the spore type II: *Coniogramme intermedia* var. *glabra* (**A–C**), *Co. intermedia* var. *intermedia* (**D–F**), *Co. procera* (**G–I**), *Co. pubescens* (**J–L**), proximal and distal faces are granulate. Spores in proximal view (A, D, G, J), spores in distal view (B, E, H, K), spores in equatorial view (C, F, I, L). Deeply depressed areas between laesura arms (F, I). Scale bars: 20 μm.

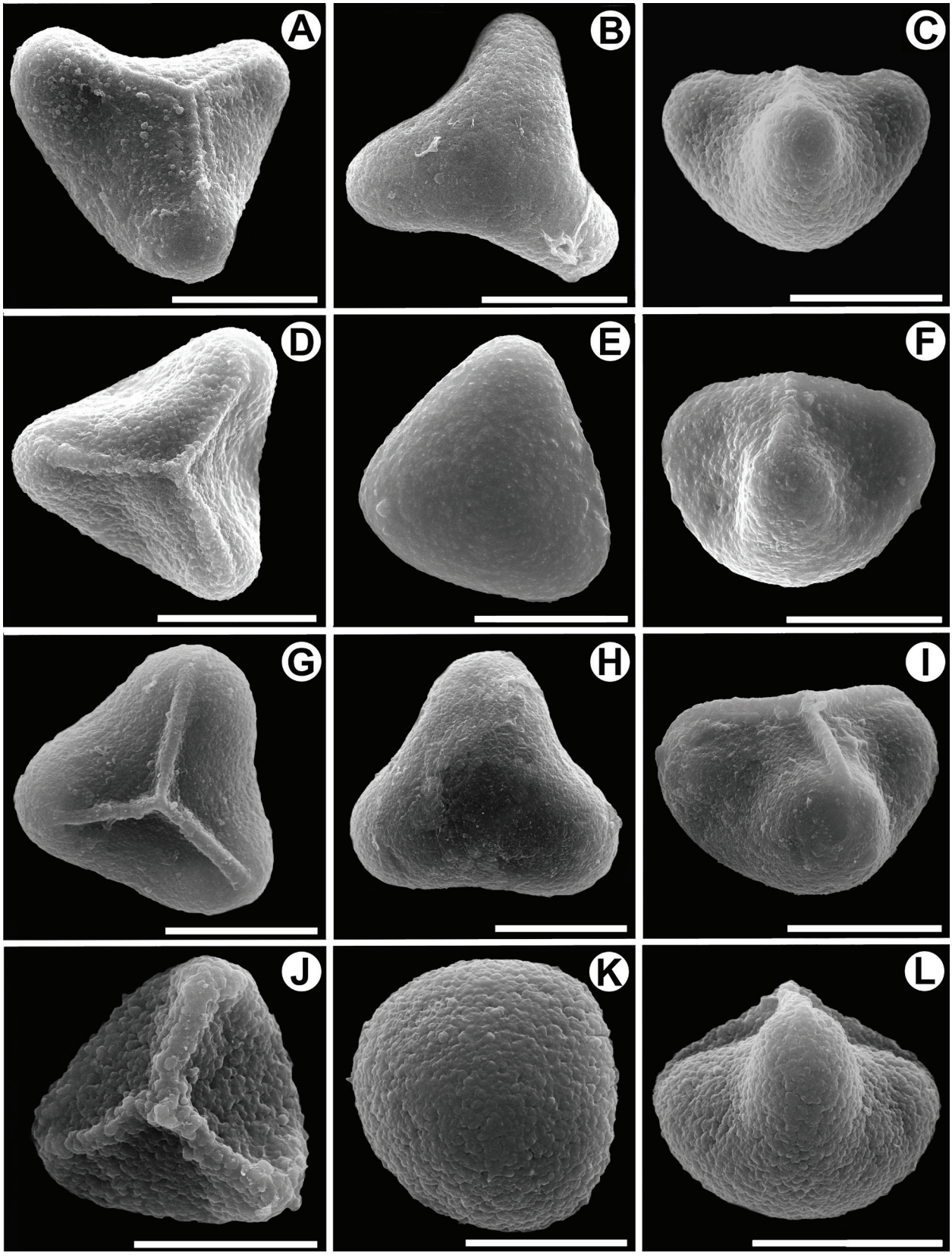

Fig. 6. SEM-micrographs of the spore type II: *Coniogramme robusta* var. *robusta* (**A–C**), *Co. robusta* var. *splendens* (**D–F**), *Co. serrulata* (**G–I**) proximal and distal faces are granulate. SEM-micrographs of the spore type III: *Co. affinis* (**J–L**), proximal and distal faces are papillate. Spores in proximal view (A, D, G, J), spores in distal view (B, E, H, K), spores in equatorial view (C, F, I, L). Prominent thin (G) and very prominent thick (J) laesura arms. Scale bars: 20 μm.

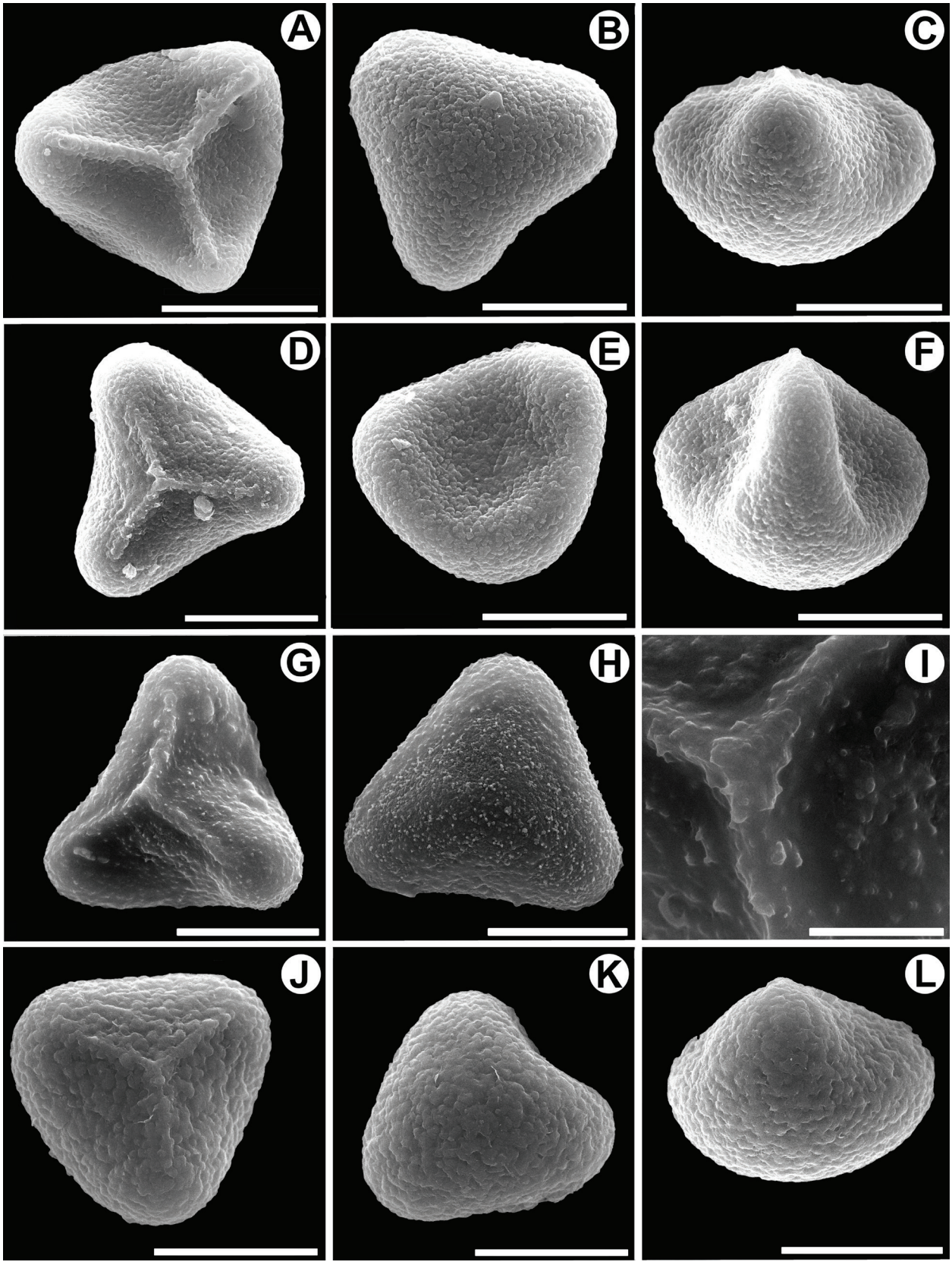

Fig. 7. SEM-micrographs of the spore type III: *Coniogramme japonica* (**A–C**), *Co. lanceolata* (**D–F**), *Co. petelotii* (**G–I**), *Co. rosthorni* (**J–L**), proximal and distal faces are papillate. Spores in proximal view (A, D, G, J), spores in distal view (B, E, H, K), spores in equatorial view (C, F, L), fragment of proximal side of spore and laesura arms (I). Dense granulate deposits on surfaces (G, H). Scale bars: 20 μm (A–H, J–L), 5 μm (I).

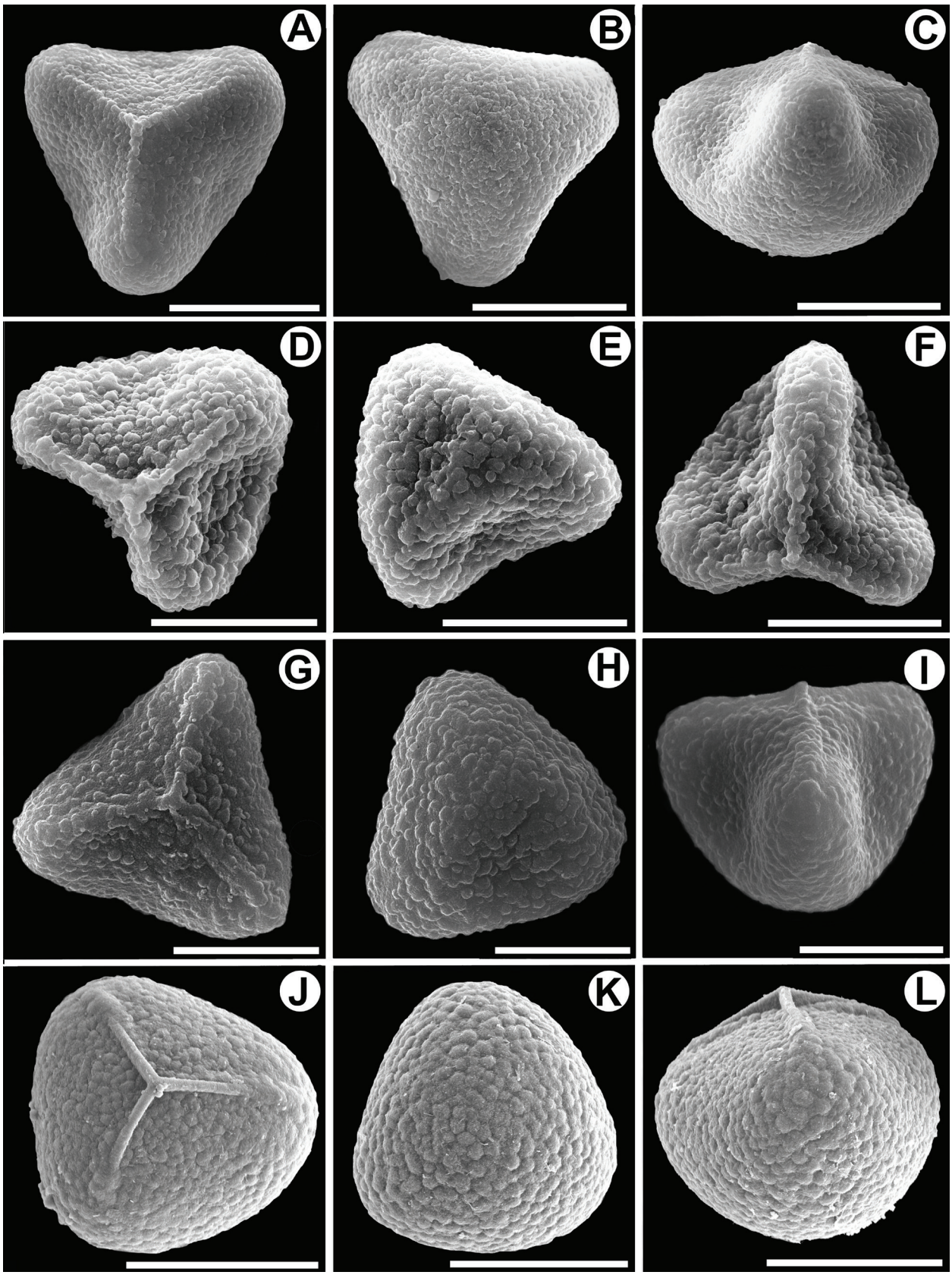

Fig. 8. SEM-micrographs of the spore type III: *Coniogramme wilsonii* (**A–C**). SEM-micrographs of the spore type IV: *Co. suprapilosa* (**D–F**), *Llavea cordifolia* (**G–I**), proximal and distal faces are verrucate. SEM-micrographs of the spore type V: *Cryptogramma fumariifolia* (**J–L**). Spores in proximal view (A, D, G, J), spores in distal view (B, E, H, K), spores in equatorial view (C, I, L), spore in equatorial-proximal view (F). The deeply depressed areas between laesura arms (F), prominent laesura arms with sculptural elements on sides (D, G), short laesura arms partly obscured by sculpture (J). Scale bars: 20 μm (A–L).

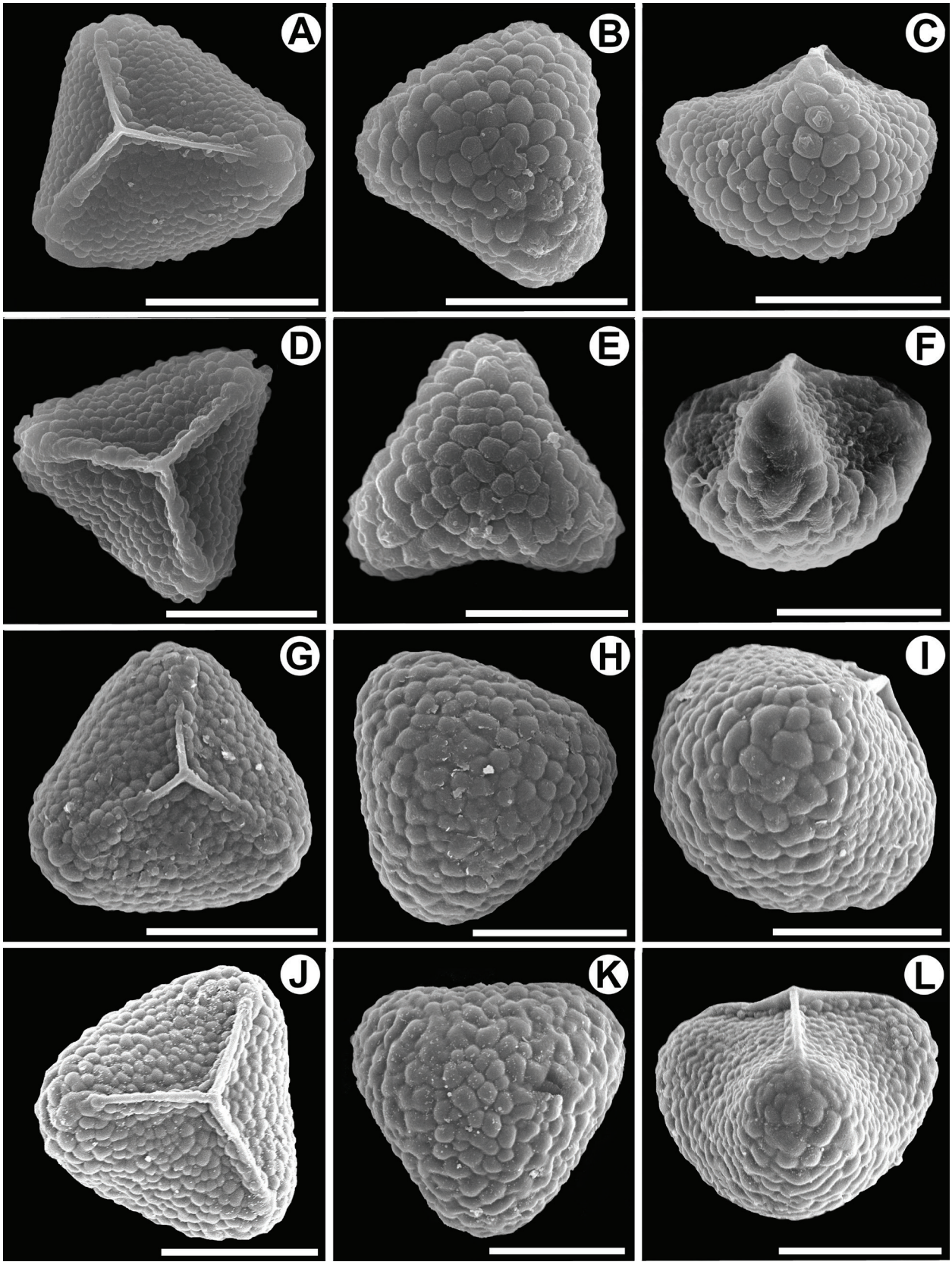

Fig. 9. SEM-micrographs of the spore type V: *Cryptogramma acrostichoides* (**A–C**), proximal and distal faces are colliculate *Cr. brunoniana* (**D–F**), *Cr. cascadensis* (**G–I**), *Cr. crispa* (**J–L**), proximal and distal faces are colliculate. Spores in proximal view (A, D, G, J), spores in distal view (B, E, H, K), spores in equatorial view (C, F, I), spore in equatorial-proximal view (L). Prominent laesura arms with sculptural elements on sides (A, D, J), short laesura arms partly obscured by sculpture (G). Scale bars: 20 μm (D–F), 30 μm (G–L), 40 μm (A–C).

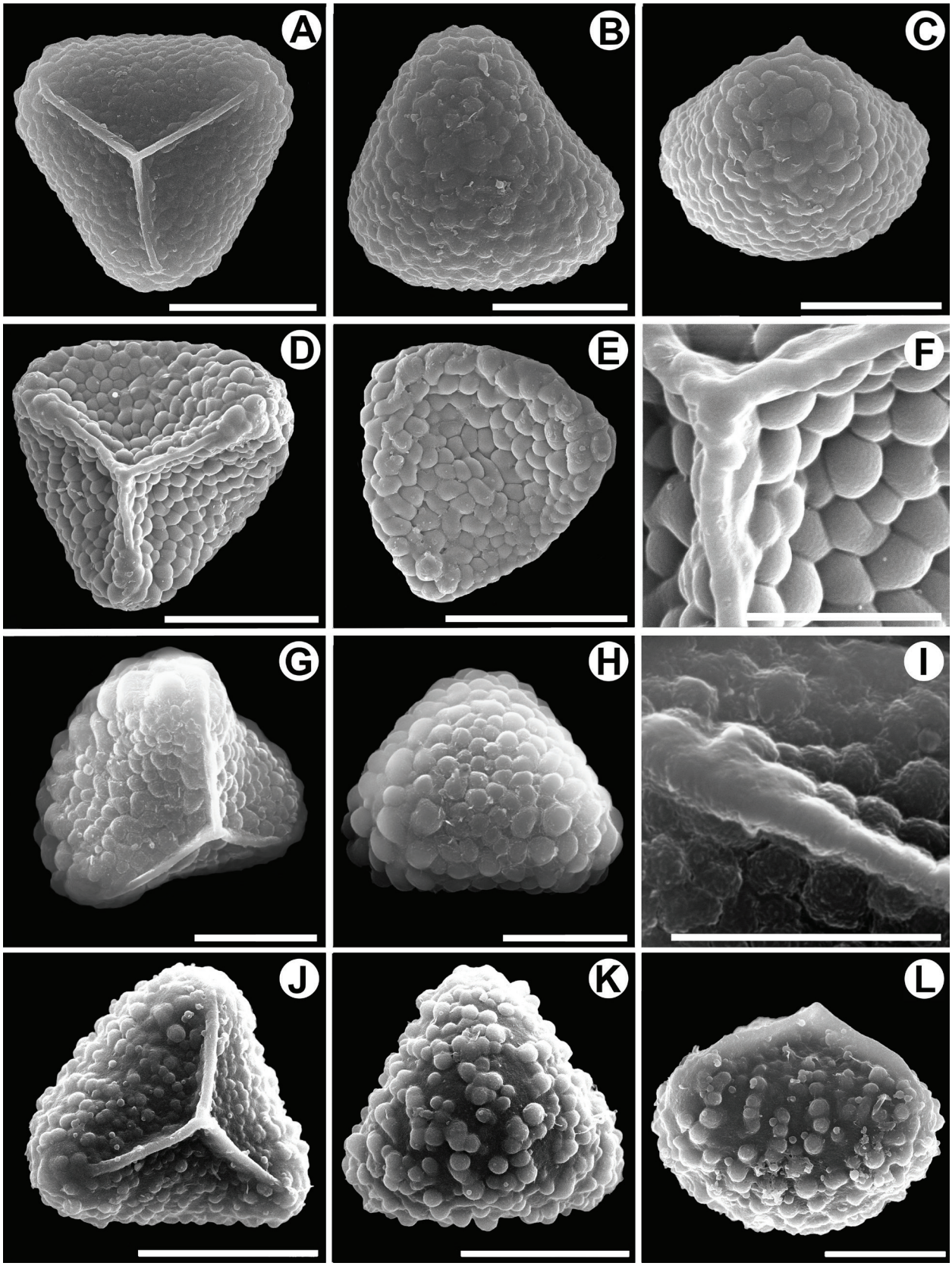

Fig. 10. SEM-micrographs of the spore type V: *Cryptogramma sitchensis* (**A–C**), *Cr. gorovoii* (**D–F**), *Cr. raddeana* (**G–I**), proximal and distal faces are colliculate. SEM-micrographs of the spore type VI: *Cr. stelleri* (**J–L**), proximal and distal faces are tuberculate, tubercle are irregular. Spores in proximal view (A, D, J), spores in distal view (B, E, H, K), spores in equatorial view (C, L), fragment of proximal side of spore and laesura arms (F, I). Prominent laesura arms with sculptural elements on sides (D, J), extremely prominent laesura arms (L). Scale bars: 10 μm (F, I), 20 μm (G, H, L), 30 μm (A, D, J, K), 40 μm (B, C, E).

Table 3

Type and morphology of the spores of *Coniogramme*, *Cryptogramma*, and *Llavea*

Spore type	Taxon	Shape of spore parts in equatorial position		Spore outline in polar position		Ornamentation		Laesura arms	Granular deposits
		Proximal	Distal	Proximal	Distal	Proximal face	Distal face		
I	*Coniogramme madagascariensis*	flat	convex	roundish-triangular	roundish-triangular	smooth	smooth	sinuous, prominent, reaching spore corners	absent
I	*Co. rubicaulis*	flat	convex	triangular	roundish-triangular	smooth	smooth	straight, reaching spore corners	sparse
II	*Co. africana*	flat to convex	hemispherical	triangular	triangular	granulate	granulate	straight, ¾ of radius	solitary
II	*Co. caudiformis*	flat	hemispherical	triangular	triangular	granulate	granulate	straight, ¾ of radius	solitary
II	*Co. emeiensis*	flat	hemispherical	triangular	triangular	granulate	granulate	straight, ¾ of radius	solitary
II	*Co. falcipinna*	flat	hemispherical	roundish-triangular	triangular-roundish	granulate	granulate	straight, prominent, reaching spore corners	sparse on distal side
II	*Co. fraxinea*	convex to flat	hemispherical	triangular	triangular	granulate	granulate	straight, ½ of radius	sparse
II	*Co. intermedia* var. *glabra*	conical	hemispherical	triangular	triangular	granulate	granulate	straight, prominent, reaching spore corners	solitary
II	*Co. intermedia* var. *intermedia*	convex	hemispherical	triangular	roundish-triangular	granulate	granulate	straight, reaching spore corners	sparse
II	*Co. pilosa*	conical	hemispherical	triangular	triangular	granulate	granulate	straight, prominent, reaching spore corners	sparse
II	*Co. procera*	flat	hemispherical	triangular	roundish-triangular	granulate	granulate	straight, prominent, reaching spore corners	sparse to abundant
II	*Co. pubescens*	convex	hemispherical	triangular	triangular	granulate	granulate	straight, ¾ of radius	absent
II	*Co. robusta* var. *robusta*	flat	hemispherical	triangular	triangular	granulate	granulate	straight, ½ of radius	sparse
II	*Co. robusta* var. *splendens*	flat to convex	hemispherical	triangular	roundish-triangular	granulate	granulate	straight, reaching spore corners	solitary
II	*Co. serrulata*	flat	hemispherical	triangular	triangular	smooth to granulate	smooth to granulate	straight, prominent, reaching spore corners	sparse
III	*Co. affinis*	conical	hemispherical	roundish-triangular	nearly roundish	papillate	papillate	straight, prominent, reaching spore corners	solitary

Table 3 (continued)

Spore type	Taxon	Shape of spore parts in equatorial position		Spore outline in polar position		Ornamentation		Laesura arms	Granular deposits
		Proximal	Distal	Proximal	Distal	Proximal face	Distal face		
III	*Co. japonica*	flat	hemispherical	roundish-triangular	triangular	papillate	papillate	straight, prominent, reaching spore corners	absent
III	*Co. lanceolata*	conical	hemispherical	roundish-triangular	triangular-roundish	papillate	papillate	straight, ⅔ of radius	absent
III	*Co. petelotii*	convex	convex to hemispherical	triangular	roundish-triangular	papillate	papillate	straight, ¾ of radius	abundant
III	*Co. rosthorni*	conical	hemispherical	triangular-roundish	roundish-triangular	papillate	papillate	straight, ½ of radius, obscured by sculpture	absent
III	*Co. wilsonii*	convex	hemispherical	triangular	triangular	papillate	papillate	straight, ¾ of radius	solitary
IV	*Co. suprapilosa*	convex	subconical	triangular	triangular	verrucate	verrucate	straight, prominent, reaching spore corners	absent
IV	*Llavea cordifolia*	flat	hemispherical	triangular	triangular	verrucate	verrucate	obscured by sculpture	sparse
V	*Cryptogramma acrostichoides*	convex	hemispherical	triangular	triangular	low-colliculate	colliculate	straight, prominent, reaching spore corners, with colliculae on both sides of laesura arms	solitary
V	*Cr. brunoniana*	convex	hemispherical	triangular	triangular	low-colliculate	colliculate	straight, prominent, reaching spore corners, with colliculae on both sides of laesura arms	sparse
V	*Cr. cascadensis*	convex	hemispherical	roundish-triangular	roundish-triangular	low-colliculate	colliculate	straight, ⅓ of radius, partly obscured by sculpture	sparse
V	*Cr. crispa*	convex	hemispherical	roundish-triangular	roundish-triangular	low-colliculate	colliculate	straight, prominent, reaching spore corners, with colliculae on both sides of laesura arms	sparse
V	*Cr. fumariifolia*	convex	hemispherical	triangular-roundish	triangular-roundish	low-colliculate	low-colliculate	straight, prominent, ½ of radius	sparse
V	*Cr. gorovoii*	convex	hemispherical	roundish-triangular	roundish-triangular	colliculate	colliculate	straight, prominent, ¾ of radius, with colliculae on both sides of laesura arms	solitary

Table 3 (continued)

Spore type	Taxon	Shape of spore parts in equatorial position		Spore outline in polar position		Ornamentation		Laesura arms	Granular deposits
		Proximal	Distal	Proximal	Distal	Proximal face	Distal face		
V	*Cr. raddeana*	convex	hemispherical	roundish-triangular	roundish-triangular	colliculate	colliculate	straight, prominent, reaching spore corners	sparse
V	*Cr. sitchensis*	convex to conical	hemispherical	roundish-triangular	roundish-triangular	low-colliculate	colliculate	straight, prominent, reaching spore corners	sparse
VI	*Cr. stelleri*	conical	hemispherical	triangular-roundish	triangular-roundish	tuberculate	tuberculate	straight, prominent, ¾ of radius, with irregular tubercle on both sides of laesura arms	sparse

Type V – Proximal and distal faces with colliculate ornamentation. This type is characteristic for spores of eight *Cryptogramma* species (Table 3). In the spores of *Cr. Fumariifolia*, colliculae are dense spaced, minute, almost the same size on the both proximal and distal faces (Fig. 8). In spores of *Cr. acrostichoides, Cr. brunoniana, Cr. cascadensis*, *Cr. crispa,* and *Cr. sitchensis*, colliculae are dense arranged, contiguous, different in size: colliculae on the proximal face are clearly smaller of those on the distal one (Figs 8, 9). In spores of *Cr. gorovoii* and *Cr. raddeana* colliculae are densely spaced, contiguous, slightly different in size: colliculae on proximal face are slightly smaller of those in distal one (Fig. 10). The proximal part of spores is convex, the distal part is hemispherical. Laesura arms reach spore corners in the most species of this type, two species have relatively short laesura arms, reaching ½ of radius in spores of *Cr. fumariifolia* and ⅓ of radius in *Cr. cascadensis*, the rest parts of laesura arms are obscured by sculpture. The salient feature of *Cryptogramma* spores is the presence of sculptural elements on the sides of prominent laesura arms (*Cr. acrostichoides*, *Cr. brunoniana*, *Cr. crispa*, *Cr. gorovoii*) (Figs 8–10; Table 3).

Type VI – Proximal and distal faces with tuberculate ornamentation. Tubercles irregularly spaced at some distance from each other, different in size: the tubercles on the proximal side are smaller than the tubercles on the distal one. This spore type has been observed only in *Cryptogramma stelleri*. The proximal part of spore is conical, the distal part is hemispherical. The laesura arms are extremely prominent, up to 4.2 μm, covered by tubercles irregular in shape and size (Fig. 10; Table 3).

Equatorial diameter (ED) was a parameter that was determined to characterize the spore size. By this parameter, spores of cryptogrammoid ferns vary from 24 to 57 μm on average. *Cryptogramma* species have larger spores than *Coniogramme* and *Llavea* species: ED in *Cryptogramma* spores varies from 36 to 62 μm (42–57 μm on average), spores of *Coniogramme* taxa vary from 23 to 42 μm (24–38 μm on average), and spores of *Llavea* vary from 34 to 41 μm (37.5 μm on average) (Table 4). Among *Coniogramme*, the largest spores are characteristic for *Co. falcipinna* (mean 38 μm), the smallest spores – for *Co. rosthorni* (about 24 μm on average). Among *Cryptogramma* species, the largest spores are characteristic for *Cr. Acrostichoides* (about 57 μm on average), *Cr. cascadensis* and *Cr. raddeana* have the smallest spores (42 μm on average). Noteworthy is that spores of two varieties of *Coniogramme*

intermedia and *Co. robusta* are different in size. The differences in size between spores of *Co. intermedia* var. *intermedia* and *Co. intermedia* var. *glabra* (37.8 and 30.6 μm on average respectively) are more significant than those between *Co. robusta* var. *robusta* and *Co. robusta* var. *splendens* (28.7 and 30.7 μm on average respectively) (Table 4). The spore size does not correlate with spore types: within the same spore type, spores of different size are found.

Among the *Coniogramme* species, *Co. falcipinna* has the longest laesura arms, *Co. rosthorni* and *Co. suprapilosa* – the shortest, and *Co. suprapilosa* the thickest laesura arms. Among *Cryptogramma* species, *Cr. gorovoii* has the longest and thickest laesura arms, and *Cr. cascadensis* and *Cr. raddeana* – the shortest ones. Relatively long and thick laesura arms are characteristic for the *Llavea cordifolia* spores (Table 4).

Table 4

The main biometric characters of the spores of *Coniogramme*, *Cryptogramma*, and *Llavea*, Min (Mean ± SE), Max (ED – equatorial diameter, LL – length of laesura arms, LW – width of laesura arms, SE – standard error of the mean)

Spore type	Taxon	ED, μm	LL, μm	LW, μm
I	*Coniogramme madagascariensis*	24.9(26.3 ± 0.98)28.2	14.7(15.2 ± 0.27)15.6	1.5(2.0 ± 0.12)2.3
I	*Co. rubicaulis*	33.2(33.6 ± 0.35)34.3	14.9(17.0 ± 1.03)18.1	1.1(1.3 ± 0.11)1.5
II	*Co. africana*	27.9(29.2 ± 0.70)30.3	14.5(15.6 ± 0.77)17.0	1.8(2.0 ± 0.12)2.2
II	*Co. caudiformis*	29.9(32.5 ± 1.34)36.3	12.5(12.9 ± 0.37)13.6	1.1(1.4 ± 0.18)1.7
II	*Co. emeiensis*	29.5(31.2 ± 0.44)32.6	9.1(11.1 ± 0.89)14.7	0.7(1.2 ± 0.20)1.9
II	*Co. falcipinna*	36.2(38.0 ± 0.88)39.0	17.6(18.4 ± 0.77)19.9	1.4(1.5 ± 0.09)1.7
II	*Co. fraxinea*	34.8(35.9 ± 0.56)36.7	12.6(13.8 ± 0.59)14.5	1.7(1.9 ± 0.12)2.1
II	*Co. intermedia* var. *glabra*	27.5(30.6 ± 1.20)33.9	10.0(13.4 ± 1.15)18.2	1.3(1.8 ± 0.14)2.2
II	*Co. intermedia* var. *intermedia*	32.0(37.8 ± 1.64)41.9	12.6(15.6 ± 0.80)17.9	0.9(1.5 ± 0.18)2.1
II	*Co. pilosa*	30.2(31.9 ± 0.84)32.9	16.7(18.9 ± 1.36)21.4	1.2(1.8 ± 0.43)2.6
II	*Co. procera*	36.8(37.0 ± 0.20)37.4	14.3(14.7 ± 0.22)15.0	0.9(1.3 ± 0.26)1.8
II	*Co. pubescens*	34.2(34.9 ± 0.47)35.8	12.2(14.9 ± 0.48)17.3	1.4(1.5 ± 0.30)1.8
II	*Co. robusta var. robusta*	28.1(28.7 ± 0.28)29.0	10.8(11.1 ± 0.22)11.5	1.4(1.4 ± 0.01)1.4
II	*Co. robusta var. splendens*	29.4(30.7 ± 0.78)32.1	15.0(15.6 ± 0.27)16.3	1.4(1.8 ± 0.38)2.6
II	*Co. serrulata*	28.8(31.6 ± 1.42)33.4	13.2(14.3 ± 0.95)16.2	1.4(1.9 ± 0.27)2.3
III	*Co. affinis*	27.6(28.4 ± 0.49)29.2	11.9(13.8 ± 1.02)15.4	2.5(2.8 ± 0.17)3.1
III	*Co. japonica*	31.5(34.1 ± 0.85)36.8	12.5(15.3 ± 0.70)17.4	1.7(2.2 ± 0.13)2.6
III	*Co. lanceolata*	30.0(33.6 ± 1.15)37.0	12.4(13.4 ± 0.67)14.7	0.6(0.9 ± 0.09)1.2
III	*Co. petelotii*	27.1(30.8 ± 0.99)34.7	14.2(15.8 ± 0.58)18.0	0.8(1.2 ± 0.10)1.6
III	*Co. rosthorni*	23.4(23.8 ± 0.45)25.6	6.6(10.2 ± 0.80)11.9	0.8 (1.2 ± 0.08)1.4
III	*Co. wilsonii*	27.5(30.0 ± 1.27)31.7	12.5(13.6 ± 0.82)15.2	0.8(1.1 ± 0.20)1.5
IV	*Co. suprapilosa*	29.4(30.0 ± 0.28)30.3	9.4(10.0 ± 0.32)10.5	2.5(4.3 ± 1.20)7.1
IV	*Llavea cordifolia*	33.8(37.5 ± 0.85)41.1	17.2(19.4 ± 0.65)21.5	1.9(2.7 ± 0.03)3.5
V	*Cryptogramma acrostichoides*	48.9(56.8 ± 0.77)62.3	17.3(23.5 ± 0.38)26.0	1.5(1.9 ± 0.08)3.1
V	*Cr. brunoniana*	37.9(48.4 ± 0.68)52.3	17.8(23.0 ± 0.38)25.4	1.6(2.3 ± 0.15)3.6
V	*Cr. cascadensis*	35.8(42.6 ± 0.63)45.5	9.9(17.6 ± 0.53)19.7	0.8(1.1 ± 0.05)1.6
V	*Cr. crispa*	42.7(47.2 ± 0.46)50.2	19.0(20.6 ± 0.27)22.6	1.5(1.7 ± 0.08)2.0
V	*Cr. fumariifolia*	42.2(45.0 ± 1.10)49.1	16.1(18.6 ± 0.50)21.3	1.7(2.1 ± 0.23)2.5
V	*Cr. gorovoii*	41.2(52.7 ± 1.00)58.0	18.7(25.7 ± 0.70)32.0	1.5(2.8 ± 0.11)3.4
V	*Cr. raddeana*	40.9(43.0 ± 0.40)45.7	15.6(17.9 ± 0.35)20.0	1.3(1.6 ± 0.04)1.8
V	*Cr. sitchensis*	48.7(52.0 ± 0.55)55.9	22.0(24.2 ± 0.26)27.4	1.1(1.9 ± 0.07)2.3
VI	*Cr. stelleri*	40.5(47.1 ± 0.8)50.4	16.5(19.8 ± 0.7)24.0	1.4(1.8 ± 0.1)2.1

Discussion

The previous molecular phylogenetic reconstruction of the family Pteridaceae showed the earlier differentiation of the cryptogrammoid ferns from the rest Pteridaceae: cryptogrammoid clade comprised three genera is sister to the remainder of the Pteridaceae (Schuettpelz et al.,

2007). Our results confirmed previous hypotheses of relationship between *Coniogramme*, *Cryptogramma*, and *Llavea*, monophyly each of them and the earlier differentiation of *Llavea* from the remainder cryptogrammoid: *Llavea* is sister to *Coniogramme* and *Cryptogramma* together, it means that *Coniogramme* and *Cryptogramma* are more closely related than each of these genera with *Llavea* (Zhang et al., 2005; Schuettpelz et al., 2007; Metzgar et al., 2013; Wang et al., 2020). Molecular-phylogenetic study of all three genera of the cryptogrammoid ferns was revealed (Metzgar et al., 2013).

South-East Asia is the center of species richness of the cryptogrammoid ferns: six of nine species of *Cryptogramma* and 24 of 40 species of *Coniogramme* involved in our phylogeographic analysis occur in Eastern-Asiatic Subkingdom (Sino-Japanese and Sino-Himalayan Regions) of Holarctis. From here, species can spread westward through Sino-Himalayan and Indian Regions and Southern Arabia to African continent, southward to Indomalesian Subkingdom, northward to Eastern-Siberian and Arctic provinces and further to the west through boreal regions of Eurasia and to the east to the Pacific part of the North American continent. *Llavea* is the earliest diverging member of cryptogrammoid, which spread to Pacific part of North American continent perhaps in Cretacious, when Laurasia was divided from the Atlantic side into the North American and Eurasian continents, and from another, Pacific side, these continents were united (Ushakov, Yasamanov, 1984). Further in isolation, *Llavea cordifolia* was formed as the separate species and genus in the south of the Pacific-American Region.

***Coniogramme* phylogeny**

Our phylogenetic reconstruction based on *rbcL* gene confirmed that the genus *Coniogramme* is monophyletic, but the sections *Coniogramme* and *Notogramme* as well as *Co*. ser. *Coniogramme* and *Co*. ser. *Serratae* Ching ex K. H. Shing separated on the base of character of pinnule margins are not monophyletic.

Coniogramme merrillii

Co. merrillii was described in 1927 by E.D. Merrill as a var. *coriacea* Merr. belonging to *Co. fraxinea* and further redescribed by Ching (1930) as a distinct species *Co. merrillii*. Zhang et al. (2015) in their revision of *Coniogramme* from Hainan province (China) detected that the type specimen of *Co. merrillii* is identical to South East Asian *Co. macrophylla* and *Co. merrillii* should be treated as synonym of *Co. macrophylla* (Blume) Hieron. Based on plastid DNA analysis, Wang et al. (2020) established that *Co. merrillii* (accession from Hainan) is sister to the rest representatives of *Coniogramme*. They established also that both specimen of *Co. merrillii* from Hainan and *Co. macrophylla* from Java (Indonesia) have the closer number of sporangium annulus cells (17–19 and 16–18 respectively) and accepted the taxonomic treatment of Zhang et al. (2015) about synonymisation of *Co. merrillii* to *Co. macrophylla*. C. Fraser-Jenkins et al. (2015, 2017) considered *Co. merrillii* is the poorly developed plants of *Co. fraxinea* and the name *Co. merrillii* should be reduced as a synonym of *Co. fraxinea*. Our study confirmed that *rbcL* gene separated *Co. merrillii* from other members of *Coniogramme* and *Co. merrillii* should not be considered as the member of the type section and type series *Coniogramme*. The genetic apartness of *Co. merrillii* is combined with three morphological characters having diagnostic value: free veins, undulate lamina margins, and extending of hydathodes to lamina margins. But because we have not accession of *Co. macrophylla* from its geographic range out of Hainan, we can not confirmed the synonymisation of *Co. merrillii* to *Co. macrophylla*. And certainly we agree with Wang et al. (2020) that *Co. merrillii* should not be a synonym of *Co. fraxinea*.

***Coniogramme*-I clade**

The large *Coniogramme*-I clade includes 20 taxa formally belonged to the sect. *Coniogramme*. The clade is divided into two unequal subclades. First of them includes 13 species and is divided into the next two subclades: the one of eight taxa (six species + two varieties of *Co. intermedia*), which remained unresolved (*intermedia*-subclade), and the second well resolved subclade of two species – *Co. affinis* and *Co. pubescens* (*affinis-pubescens*-subclade).

Intermedia-subclade includes taxa formally belonged to ser. *Serratae* of sect. *Coniogramme*. Plastid DNA gene *rbcL* has not resolved this subclade that may be due to two reasons – genetic proximity and insufficiency of using one marker *rbcL* for distinction of the species. According to threatment in the "Flora of China" (Zhang, Ranker, 2013), *Co. caudiformis*, *Co. falcipinna*, *Co. sinensis, Co. emeiensis* are the distinct species, endemic for the different part of China, whereas *Co. maxima* described by Ching and Shing (1981) as the distinct species close to *Co. intermedia* is reduced as the synonym to *Co. intermedia* var. *intermedia*. All members of *intermedia*-subclade are close morphologically. The following

morphological characters are typical for *intermedia*-subclade: lamina 1- or 2-pinnate, lowermost pinnae simple pinnules or pinnate, never 2-pinnate, pinnule margins are serrate, pinnules abaxially are not papillose, hydathodes extending to tooth base or slightly into teeth. *Coniogramme emeiensis* and *Co. falcipinna* are distinguished by the shape of pinnules and extending of hydathodes; *Co. sinensis* and *Co. caudiformis* are distinguished by the color of the stipe and rachis. All species of the *intermedia*-subclade involved in spore analysis have spores of the II type with granulate ornamentation. The largest spores are characteristic for *Co. falcipinna* and *Co. intermedia* var. *intermedia* (ED in average is 38.0 and 37.8 μm respectively). Two varieties of *Co. intermedia* have spores different in size.

Coniogramme intermedia (including var. *intermedia* and var. *glabra*) is the most widespread species from the *intermedia*-subclade. Its geographic range covers the East and Southeast Asia and extends westward to Central Asia (Nepal, Pakistan, North India) and eastward to Indonesia (Fig. 11). Distribution of the all species of this subclade does not go beyond the range of *Co. intermedia*. Thus, the taxa of this subclade are very close to each other both morphologically and genetically and require further molecular phylogenetic study using of more of plastid and nuclear DNA loci, especially for endemic species.

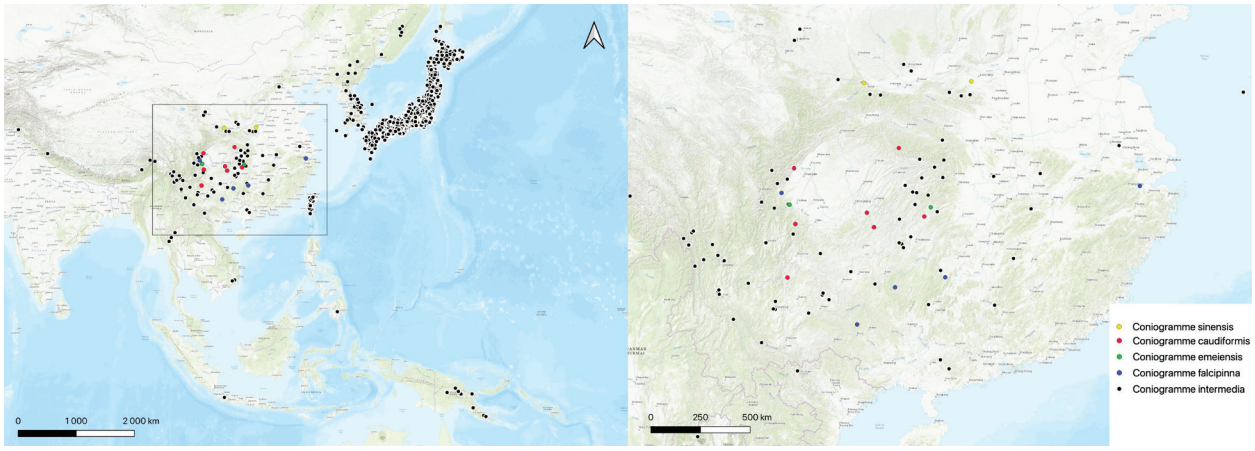

Fig. 11. Distribution of *Coniogramme intermedia, Co. sinensis, Co. caudiformis*, *Co. emeiensis*, and *Co. falcipinna*

***Affinis-pubescens*-subclade** is moderately supported in *rbcL* phylogeny and contains strongly supported lineage corresponded with two species – *Co. affinis* and *Co. pubescens*. These species are well distinguished by dividing of lamina: 3-pinnate with 2-pinnate lowermost pinnae in *Co. affinis* vs 1-pinnate with simple or pinnate lowermost pinnae in *Co. pubescens* (Zhang, Ranker, 2013). We indicated also the differences in ornamentation and size of spores: papillate ornamentation and small size is characteristic for *Co. affinis*, granulate ornamentation and larger size – for *Co. pubescens*. Both species occur in China, India, Myanmar, and Nepal, *Co. affinis* is more widely distributed in China than *Co. pubescens*.

Well-supported ***suprapilosa*-subclade** includes three species, from which *Co. suprapilosa* differs in *rbcL* gene from *Co. rosthornii* and *Co. longissima*. *Coniogramme suprapilosa* and *Co. rosthornii* occur in South and Central China, and *Co. rosthornii* is distributed wider than *Co. suprapilosa*. These species are distinguished by abaxially papillose pinnules and 2-pinnate lamina in *Co. rosthornii* and not papillose pinnules and 3-pinnate lamina in *Co. suprapilosa*. Furthermore, among *Coniogramme* species, *Co. suprapilosa* has the most different spores with verrucate ornamentation, which we considered to IV spore type, while *Co. rosthornii* has more simple papillate ornamentation of spores. Third species *Co. longissima* was described from Sichuan and Hubei as the separate species close to *Co. maxima* Ching et K. H. Shing (Shing, 1981). Zhang and Ranker (2013) considered it as synonym of *Co. emeiensis*. In our *rbcL* phylogeny, accession of *Co. longissima* from Hunan (China) is united with one accession of *Co. rosthornii* from Sichuan in the same lineage, the second accession of *Co. rosthornii* is in another lineage of the same subclade, while accession of *Co. emeiensis* is nested in the unresolved *intermedia*-subclade. According to our *rbcL* analysis, *Co. longissima* is closer to *Co. rosthornii* than *Co. emeiensis*. Thus, we refrain from synonymizing *Co. longissima* and *Co. emeiensis*

until data on other DNA regions and spore studies become available.

Another part of dichotomy of the *Coniogramme*-I clade includes two subclades named *africana*-subclade and *petelotii*-subclade. All these species belong to sect. *Coniogramme* ser. *Coniogramme* having entire margins of pinnules and free venation.

***Africana*-subclade** includes *Co. africana*, *Co. lanceolata*, and *Co. fraxinea*, whose accessions are resolved in *rbcL* phylogeny as monophyletic, and *Co. africana* is sister to *Co. lanceolata* and *Co. fraxinea* together. *Coniogramme africana* is the only species from African continent presented in our phylogenetic analysis, which has been never involved in any molecular analyses. Topology of *Co. africana* in the phylogramm confirms its separateness from other species of these subclade. *Coniogramme lanceolata* and *Co. fraxinea* are closer to each other than to *Co. africana*. *Coniogramme lanceolata* was described as a distinct species based on the shape of pinnae and position of the hydathodes (Shing, 1981). Later, Lu (2001), Fraser-Jenkins (2008), Fraser-Jenkins et al. (2017) reduced it to the synonym of *Co. fraxinea*. Zhang and Ranker (2013) treated *Co. lanceolata* as the synonym of *Co. merrillii*. In 2015, Zhang et al. reduced it to *Co. macrophylla* together with *Co. merrillii*. In the phylogenetic study by Wang et al. (2020), *Co. merrillii* is sister to the rest species of *Coniogramme*, whereas *Co. lanceolata* is closely related to *Co. fraxinea*. Both *Co. lanceolata* and *Co. fraxinea* have short hairs on the abaxial side of frond, and the same number of sporangium annulus cells, indicating that these two species are closely related, but differs by the localization of hydatodes (Wang et al., 2020).

Our phylogenetic reconstruction fully confirms this conclusion and shows that *Co. lanceolata* and *Co. fraxinea* are closely related to each other, and each of them is closer to *Co. africana,* the only *Coniogramme* species occurred in African continent, than to Hainan endemic *Co. merrillii* or Asian *Co. macrophylla*. Morphology of spores does not correspond with *rbcL* phylogeny: spores of *Co. africana* and *Co. fraxinea* have granulate ornamentation (II type), whereas spores of *Co. lanceolata* are papillate (III-type), but spores of all three species are different in the laesura length relative to spore radius. Spores of all these species are clearly depressed in proximal part between laesura arms. We accepted *Co. africana, Co. fraxinea*, and *Co. lanceolata* as the distinct species.

The next subclade named ***petelotii-gigantea*-subclade** includes four species formed two lineages: *Co. gigantea* + *Co. rubicaulis* and *Co. procera* + *Co. petelotii*. First of them includes four accessions which are not resolved by *rbcL*, the second one includes two close species.

Coniogramme gigantea and *Co. rubicaulis* were described by Ching (in Shing, 1981) as distinct species, from which *Co. rubicaulis* is related to *Co. fraxinea* and *Co*. *gigantea* is related to *Co. rubicaulis*. Both species occur in China, *Co. rubicaulis* is regarded as endemic to Guangxi, *Co. gigantea* – as endemic to Yunnan (Shing, 1981; Zhang, Ranker, 2013). They differ from each other by colour of petioles and rachis and have the same number of sporangium annulus cells (Wang et al., 2020). We had not spores of *Co. gigantea* for SEM analysis and did not find any information about their ornamentation. Spores of *Co*. *rubicaulis* have no ornamentation and are smooth. Zhang and Ranker (2013) reduced *Co. gigantea* to a synonym of *Co. fraxinea*. Phylogenetic analysis using *rbcL*, as well as combine analysis with using five plastid DNA markers (Wang et al., 2020) shows that *Co. gigantea* is closely related to *Co. rubicaulis, Co. petelotii*, and *Co. procera* but distant to *Co. fraxinea*.

Coniogramme petelotii was considered as a synonym of *Co. fraxinea* (Fraser-Jenkins, 2008; Fraser-Jenkins et al., 2015, 2017), but other taxonomists regarded it as a distinct species (Shing, 1981; Lu, 2001; Zhang, Ranker, 2013). In our *rbcL*-phylogram, as well as combine phylogram by Wang et al. (2020), *Coniogramme petelotii* and *Co. procera* are clustered together that indicates their close relationship, while *Co. fraxinea* is distant from they both. *Coniogramme petelotii* is similar to *Co. fraxinea* in the number of sporangium annulus cells (Wang et al., 2020) but slightly different from it in ornamentation of spores: granulate in *Co. fraxinea* (II type) and papillate in *Co. petelotii* (III type). Yunnan endemic *Coniogramme petelotii* and more widespread *Co. procera* (China (Taiwan, Xizang, Yunnan), Bhutan, India, Myanmar, Nepal, Thailand, Vietnam) are different from each other by dividing of lamina, shape and spreading of hydatodes, character of pinnula margins (Zhang, Ranker, 2013) and ornamentation of spores. Morphological and phylogenetic analyses support these species as distinct but close related.

***Coniogramme*-II clade**

The clade united the species belonging to sect. *Notogramme*, which includes species having veins anastomosing to form at least some areoles on each side of midrib. In the *rbcL* phylogeny this clade is highly supported (PP = 1.0) and includes *Co. japonica* subclade and *Co. robusta* sister to it. Lineage of

Co. japonica including two accessions from China and Japan is moderately supported, but the topology of *Co. japonica* in the distinct lineage corresponds with unique for this species characters – veins anastomosing regularly to form 1 or 2 (to 3) continuous rows of areoles on each side of midrib. Plastid locus *rbcL* has not resolved another lineage including two accessions of *Co. jinggangshanensis* and one accession of *Co. wilsonii* (all accessions from China). This indicates that these two species are close genetically as well as morphologically: in *Co. wilsonii*, veins form a discontinuous row of areoles on each side of midrib and stipe is straw-colored, in *Co. jinggangshanensis*, veins form only 1 or 2 areoles on each side of midrib and stipe is chestnut-colored. Two species of the *Coniogramme*-II clade – *Co. japonica* and *Co. wilsonii* – have spores with papillate ornamentation. Topology of *Co. robusta* indicates its more genetic closeness with *Co. jinggangshanensis*, *Co. wilsonii*, and *Co. japonica* than with any of the other *Coniogramme* species. Morphologically, *Co. robusta* belongs to sect. *Coniogramme* ser. *Coniogramme* including species with free venation of lamina. Spores of *Co. robusta* have granulate ornamentation instead the papillate ornamentation of spores in *Co. wilsonii* and *Co. japonica*.

***Cryptogramma* phylogeny**

Phylogenetic reconstruction based on *rbcL* gene of plastid DNA showed the same result with the reconstruction based on six plastid DNA markers (Metzgar et al., 2013, 2016): the genus, as well as the sections (or subgenera) *Cryptogramma* and *Homopteris* within the genus are monophyletic. All included in our phylogenetic analysis accessions of all species are clustered into two clades related with the sections *Cryptogramma* and *Homopteris*.

Plastid gene *rbcL* has not resolved the section *Cryptogramma*, all accessions clustered in four subclades with uncertain topology. In this study we include *Cr. gorovoii* described from Sakhalin Island (Vaganov, Shmakov, 2007), that was not assessed in previous studies due to a lack of suitable material (Metzgar et al., 2013, 2016). In our phylogenetic studies we received the results similar to them in the studies by J. S. Metzgar et al. (2013, 2016): we recognized all taxa of the genus *Cryptogramma* included in the dataset as the distinct species. Surprisingly, Far Eastern *Cr. gorovoi* being involved in the *rbcL* analysis clustered with *Cr. crispa* (accessions from the Caucasus and Spain) and the Turkish octoploid *Cr. bithynica* but not with East Asian representatives of *Cryptogramma*. *RbcL* analysis has included *Cr. fumariifolia* in the same clade with two East Asian species *Cr. raddeana* and *Cr. brunnoniana*, that demonstrates their relativeness and perhaps indicates the migration of an ancestor of *Cr. fumariifolia* from East Asia to South America in Cretaceous but not from North to South America after the Pliocene glaciation. Metzgar et al. (2013) considered *Cr. fumariifolia* as the earliest diverging member of the section *Cryptogramma* lineage. Topology of *Cr. raddeana* and *Cr. brunnoniana* accessions indicates the close relationship between these species.

***Llavea* phylogeny**

Our study based on *rbcL* gene analysis confirmed the results of previous molecular phylogenetic studies (Metzgar et al., 2013, 2016; Wang et al., 2020): the single member of the genus *Llavea*, mainly the Central American species *L. cordifolia*, is the earliest diverging member of the subfamily *Cryptogrammoideae* sister to *Coniogramme* and *Cryptogramma* together. *Coniogramme* and *Cryptogramma* are more closely related to each other than each of these genera with *Llavea*.

Spores of 32 species of three genera of cryptogrammoid ferns (*Coniogramme*, *Cryptogramma*, and *Llavea*) have been characterized in detail. The spores of cryptogrammoid ferns do not have the cingulum and commissural flanges characteristic of other groups of ferns of the family Pteridaceae (Palacios-Rios et al., 2017b; Vaganov et al., 2018, 2020, 2021; Chen et al., 2022). In general, the simplicity in ornamentation (smooth, granulate, and papillate) is characteristic for the spores of the most *Coniogramme* species, except *Co. suprapilosa*. More coarse ornamentation of spores differs *Llavea* (verrucate) and *Cryptogramma* (colliculate and tuberculate). Peculiarities of macro-ornamentation allows us to define six spore types: four spore types in *Coniogramme* (I–IV), two spore types in *Cryptogramma* (V and VI) and one spore type in *Llavea* (IV).

General morphology, ornamentation and size of spores studied here correspond with the same features previously published for these genera (Nayar, Devi, 1966, 1967; Tryon, Lugardon, 1991; Zhang G. M., Zhang X. Ch., 2003).

Nayar and Devi (1966) gave the descriptions of spores of four species using the light microscopy: *Coniogramme africana, Co. fraxinea, Co. intermedia*, and *Co. javanica* Fée, and characterized spore ornamentation of the first two species as slightly granulose. Four *Coniogramme* species (*Co. japo-*

nica, *Co. macrophylla, Co. africana*, and *Co. pilosa*) were examined and illustrated by Tryon and Lugardon (1991). According to their SEM-micrographs, spores of *Co. japonica*, *Co. africana*, and *Co. pilosa* have the same ornamentation as the spores of the same species studied by us. Tryon and Lugardon (1991) identified spore ornamentation of *Co. japonica*, *Co. africana*, and *Co. pilosa* as papillate, while we identify it for *Co. japonica* as papillate, for *Co. africana* and *Co. pilosa* as granulate. Our dividing of *Coniogramme* based on spore types does not correspond with the existing classification of this genus based on the character of pinnule margins: sect. *Coniogramme* with ser. *Coniogramme* and ser. *Serratae* Ching and sect. *Notogramme*. Ser. *Coniogramme* includes species having spores of three spore types: I (*Co. rubicaulis*), II (*Co. fraxinea*) and III (*Co. petelotii*); ser. *Serratae* includes the species having spores of II (*Co. intermedia*, *Co. procera*) and III (*Co. rosthorni*) spore types. Section *Notogramme* includes species with III spore type (*Co. japonica*). Among *Coniogramme* species presented in our study, *Co. suprapilosa* has the most different spores with verrucate ornamentation, which we considered to IV spore type. In this character, *Co. suprapilosa* is closer to *Llavea cordifolia* than to other members of the genus *Coniogramme*.

The SEM-micrographs of *Cr. stelleri* and *Cr. crispa* s. l. from different part of their geographic range presented by Tryon and Lugardon (1991) are very similar with ours, but they have described such ornamentation as verrucate. Nayar and Devi (1967) mentioned and illustrated spores of *Cr. crispa* s. l. by LM, described ornamentation as densely subverrucate-areolate with usually circular in outline verrucae, smaller around the laesura. SEM-micrographs of spores of five taxa of *Cryptogramma* (*Cr. brunoniana*, *Cr. emeiensis*, *Cr. shensiensis* Ching, *Cr. brunoniana* var. *sinensis* (Christ) G. M. Zhang, and *Cr. stelleri*) presented in the work of G. M. Zhang and X. Ch. Zhang (2003), show a significant similarity in ornamentation with those in our study for the same species.

According to our study, all species of the sect. *Cryptogramma* have spores of V type. Among them, spores of *Cr. fumariifolia* are most distinguished from spores of other species with this spore type by low and quite uniform colliculae on the both part of spore. Among other species, the greatest similarity in ornamentation is noted between *Cr. acrostichoides, Cr. brunoniana, Cr. cascadensis*, *Cr. crispa,* and *Cr. sitchensis* and between *Cr. raddeana* and *Cr. gorovoii*. *Cryptogramma sitchensis*, which is the allotetraploid with progenitors *Cr. acrostichoides* and *Cr. raddeana* (Metzgar et al., 2013) has spores more similar with those of *Cr. acrostichoides* than with *Cr. raddeana*. The only member of the sect. *Homopteris*, *Cr. stelleri*, has spores that we assigned to the type VI. Thus, our grouping of *Cryptogramma* spores into two spore type is consistent with existing classification: all analysed species belonging to the sect. *Cryptogramma* have spores of V type with colliculate ornamentation, the single species of the sect. *Homopteris* has spores of VI type with tuberculate ornamentation.

Llavea cordifolia spores we assigned to the IV type with verrucate ornamentation. Tryon and Lugardon (1991) determined ornamentation of spores of this species as irregularly tuberculate to papillate and emphasized that the tuberculate to papillate contour is formed by perispore, not the exospore as in other spores in the Pteridaceae. According to our study of spores, *Llavea* is more similar to *Coniogramme* than to *Cryptogramma*, because the sculpture elements of ornamentation are formed by perispore in *Llavea* and *Coniogramme*, not by exospore as in *Cryptogramma.* The spores of *Llavea cordifolia* are especially similar in ornamentation with spores of *Coniogramme suprapilosa.*

Spore size based on equatorial diameter of all three genera ranges on average between 23 and 62 μm, which corresponds to the medium-sized spores characteristic of most species of homosporous ferns (Tryon, Lugardon, 1991). We did not found in literature data on the spore size for the most species of *Coniogramme* and *Cryptogramma*. Tryon and Lugardon (1991) mentioned about range of spore size for *Coniogramme* 30–50 μm (based on six species), for *Cryptogramma* – 43–57 μm (based on two species), for *Llavea cordifolia* – 32–42 μm. Nayar and Devi (1966) indicated range 24–30 × 40–42 μm for *Coniogramme* spores (based on four species) and size 42 × 56 μm for *Cryptogramma crispa*. Our range of this parameter based on measurements of spores of 21 *Coniogramme* species is shifted towards smaller values (25–42 μm) in compare with Tryon and Lugardon's data and corresponds with the range indicated by Nayar and Devi (1966). Spore size of *Cryptogramma* based on 9 species is characterized by the larger range – 38–62 μm in compare with Tryon and Lugardon's data. For *Llavea cordifolia*, we found the same range of spore size – 34–41 μm. The very similar in ornamentation, spores of *Llavea cordifolia* and *Coniogramme suprapilosa* are significantly different in size: 33.8–41.1 μm and 29.4–30.3 μm respectively.

Spore size may be related to ploidy level. A positive correlation between spore size and ploidy level was earlier observed in *Adiantum* L. and *Polystichum* Roth (Barrington et al., 1986), *Gymnocarpium* Newman (Sorsa, 1980; Pryer et al., 1983), *Cystopteris* Bernh. (Blasdell, 1963), but other authors observed no size differences between spores of the different ploidy levels, particularly between tetraploid and diploid species (Britton, 1968). In our study, spore size does not correspond with ploidy level in the species for which it is known. The difference in spore size between two diploids *Coniogramme affinis* and *Co. procera* is greater (ED = 28 and 37 μm on average respectively) than between each of them and the hexaploid *Co. pilosa* (ED = 32 μm on average); tetraploids *Co. africana* and *Co. rosthorni* have spores close in size or smaller (ED = 29 and 24 μm on average respectively) than mentioned diploids and hexaploid. The spores of autotetraploid *Cr. crispa* have the close size (ED = 47 μm on average) with spores of diploids *Cr. brunoniana*, *Cr. cascadensis, Cr. Raddeana*, and *Cr. stelleri* (ED = 48, 43, 43, and 47 μm on average respectively), but they are smaller than spores of diploid *Cr. acrostichoides* (ED = 57 μm on average). Spores of allotetraploid *Cr. sitchensis* (n = 60, ED = 52 μm on average) are intermediate in size between those of the parent species *Cr. acrostichoides* (n = 30, ED = 57 μm on average) and *Cr. raddeana* (n = 30, ED = 43.0 μm on average). Two chromosome counts are indicated for *Co. intermedia* (n = 30 and n = 60). Perhaps, different chromosome counts belong to different varieties especially since their spores are distinguished in size: spores in var. *glabra* (ED = 31 μm on average) are smaller than those in var. *intermedia* (ED = 38 μm).

Conclusion

In this study, phylogenetic reconstruction, spore morphology, and phylogeography for most taxa of the "cryptogrammoid clade" of the large family Pteridaceae were combined. A compehensive analysis of the data on phylogeny and spore morphology revealed correspondence of general character of spore ornamentation to each genus. The *Coniogramme* representatives produce spores with simple ornamentation – smooth, granulate, and papillate, ornamentation of spores of *Cryptogramma* and *Llavea* is more coarse – verrucate, colliculate, and tuberculate.

Phylogenetic reconstruction based on *rbsL* gene of plastid DNA sequencing of 24 taxa of *Coniogramme*, ten species of *Cryptogramma*, and one species of *Llavea* confirmed the previous conclusion about monophylly of each genus and close relationship between *Coniogramme* and *Cryptogramma* than between each of them and *Llavea*.

We established a deep divergence of *Coniogramme merillii* in the *Coniogramme* superclade: this species is the sister lineage to the remainder of *Coniogramme.* We revealed also the separateness of *Co. suprapilosa* from *Co. rosthornii* and *Co. longissima*, *Co. africana* from *Co. lanceolata* and *Co. fraxinea*, and *Co. robusta* from *Co. jinggangshanensis*, *Co. wilsonii*, and *Co. japonica*. We do not support synonymisation *Co. longissima* and *Co. emeiensis*, *Co. lanceolata* and *Co. merrillii, Co. gigantea* and *Co. fraxinea, Co. petelotii* and *Co. fraxinea.* We can not confirmed the synonymisation of *Co. merrillii* with *Co. macrophylla* until we have not accession of *Co. macrophylla* from different parts of its range. Genetic separateness of *Co. suprapilosa* corresponds with exceptional ornamentation of its spores. Among *Cryptogramma* species, the more closeness of Far Eastern *Cr. gorovoi* with *Cr. crispa* from Spain and the Caucasus and the Turkish *Cr. bithynica* but not with any Far Eastern species is unexpected.

In *Coniogramme*, the grouping of species attending the spore type does not agree with existing classification and phylogenetic hypotheses. In *Cryptogramma*, the grouping on the spore types corresponds with other morphological characteristics, existing classifications and molecular phylogeny.

Spore ornamentation has diagnostic value in the recognition of the cryptogrammoid taxa at the generic and section (in *Cryptogramma*) levels. The presented set of spore features could be used also for diagnostic of the species as the additional morphological characters, so it could be considered in the future taxonomical reviews and in the development of a classification system of the cryptogrammoid ferns, especially for *Coniogramme*.

East Asia (Sino-Japanese and Sino-Himalaian Regions) is the center of origin and diversity for the subfamily *Cryptogrammoideae* and especially for the genus *Coniogramme*.

Further research on the "cryptogrammoid clade" of Pteridaceae should be emphasized on detection of relativeness inside *Coniogramme*, especially inside the *Co. intermedia*-subclade including several close species.

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