Original article

Systematic study of *Aptychella robusta s. lat.* in East and Southeast Asia (Pylaisiadelphaceae, Musci)

Hiroyuki Akiyama [1)], James R. Shevock [2)], Mitsu Matsumoto [3)], Nobuaki Hayashida [4)], Thien Tam Luong [5),6)], Narin Printarakul [7)] and Kuei-Yu Yao [8)]

[1)] *Museum of Nature and Human Activities, Hyogo, Yayoigaoka-6, Sanda-shi, Hyogo 669-1546, Japan*

[2)] *California Academy of Sciences, 55 Music Concourse Drive, Golden Gate Park, San Francisco, CA 94118, U.S.A.*

[3)] *Hattori Botanical Laboratory/ Miyazaki Plant Study Group, Obi, Nichinan-shi, Miyazaki 889-2535, Japan*

[4)] *Yamakara-Yakushima, Anbo, Yakushima-cho, Kagoshima 891-4311, Japan*

[5)] *Department of Ecology - Evolutionary Biology, Faculty of Biology - Biotechnology, University of Science - Vietnam National University Ho Chi Minh City, 227 Nguyen Van Cu, District 5, Ho Chi Minh City, Vietnam*

[6)] *Biodiversity Unit, University of Turku, FI-20014, Turku, Finland*

[7)] *Department of Biology, Chiang Mai University, 239, Huay Kaew Road, Muang District, Chiang Mai 50200, Thailand*

[8)] *Endemic Species Research Institute, Taiwan, 552005 No. 1 Mingsheng East Road, Jiji Township, Nantou County, Taiwan*

Abstract

Phylogenetic relationships among the members of the epiphytic moss, *Aptychella robusta s. lat.* (Pylaisiadelphaceae), mainly from East and Southeast Asia, were examined using chloroplast DNA (*rbc*L, *rps*4, and *trn*L-F) sequences as well as morphological features based on detailed examination of type and authentic specimens. Present analysis revealed unexpected species diversity in the group formerly recognized as *A. robusta s. lat.* and *A. planula*, and total 12 species were recognized here including 6 new species in the group; they are *A. formosana* H.Akiyama, Shevock & K.-Y.Yao **sp. nov.**, *A. minutissima* H.Akiyama, Shevock & M.Matsumoto **sp. nov.**, *A. muelleri* Dixon, *A. perdecurrens* (Dixon) T.J.Kop., *A. planula* (Mitt.) M.Fleisch., *A. robusta* (Broth.) M.Fleisch. *s. str.*, *A. rubiginosa* H.Akiyama, N.Printarakul & N.Hayashida **sp. nov.**, *A. subdelicata* Broth., *A. triangularis* H.Akiyama & Shevock **sp. nov.**, *A. viridis* H.Akiyama **sp. nov.**, *A. yakumontana* H.Akiyama & N.Hayashida **sp. nov.**, and *A. yuennanensis* Broth. Some of the species previously recognized as synonyms of *A. robusta* or *A. planula* by Tan & Buck (1989), Tan (1991), and Tan & Jia (1999) are treated as separate species here; they are *A. subdelicata*, *A. muelleri*, and *A. yuennanensis*.

Key words: *Aptychella,* cryptic species, Pylaisiadelphaceae*, rbc*L*, rps*4*,* taxonomy*, trn*L-F.

(Received: 24 June, 2022 / Accepted: 7 October, 2022 / Published: 10 March, 2023)

INTRODUCTION

Aptychella (Broth.) Herzog is a genus in the family Pylaisiadelphaceae (Goffinet et al. 2009, Akiyama et al. 2015, Akiyama 2017a, 2019) or Sematophyllaceae *s. lat.* (Han & Jia 2021). Distinctive morphological characteristics of the genus are turf-forming thin populations, densely and pinnately branched prostrate primary stems, and ascending lateral secondary stems, from which a few, long and gemmiferous secondary stems are differentiated. The upper part of this gemmiferous stems become thicker with bundles of filamentous propagules in leaf axils, while the uppermost part of the stems are suddenly narrowed with much smaller reduced leaves. As a result, apical part of each gemmiferous secondary stems looks distinctly caudate. In addition, leaf margins are widely or narrowly recurved, alars of leaves are well differentiated with quadrate to long rectangular cells with more or less decurrent bases to stems at both sides. Filamentous propagules are composed of single row of smooth, rectangular, thin-walled cells. In addition, peristomes are in two rows: each exostome tooth is with a tendency to be depressed in the middle and sometimes perforate. Endostome segments are filamentous with low basal membranes, and cilia are absent.

A total of 34 species have been described in the genus to date (Tropicos, 2021), but a number of species were moved to other genera (Appendix 2). In recent years, several species have been added to the genus: they are *A. imbricata* (H.Akiyama, Ying Chang & B.C.Tan) H.Akiyama (originally as *Clastobryopsis imbricata* H.Akiyama, Ying Chang & B.C.Tan) from northern Thailand, *A. touwii* H. Akiyama from central part of New Guinea, *A. hawaiica* H.Akiyama & Shevock from Hawaiian Islands, and *A. linii* H.Akiyama from northern Taiwan (Akiyama 2016, 2019, Akiyama & Shevock 2019, Akiyama et al. 2010). On the other hand, *A. chilensis* Herzog known from southern Chile was proposed to classify as *Ombronesus chilensis* (Herzog) Frank Müll. & H.Akiyama in the Ptychomniaceae (Müller & Akiyama 2016). As a result, a total of 14 species are currently recognized in the genus (Appendix 2). As for phylogenetic relationship of *Aptychella* to the other members the Pylaisiadelphaceae, Akiyama (2019) suggested *Aptychella* to be closely related to a monotypic genus *Microgammiella* H.Akiyama, which is distributed in Myanmar, Vietnam and Taiwan.

Species diversity in the genus *Aptychella* is centered in East and Southeast Asia, and 10 of the 14 species had been reported from this region. In addition, five species, such as *A. brevinervis* (M.Fleisch.) M.Fleisch., *A. robusta* (Broth.) M.Fleisch., *A. clemensiae* E.B.Bartram, *A. perdecurrens* (Dixon) T.J.Kop., and *A. touwii* H.Akiyama, have been reported from New Guinea, which is another center of species diversity of the genus. Although two or three species are known from Central and South America, genetic diversity was revealed to be quite low in spite of morphological differences among plants from geographically separate localities, and probably they might be grouped into a single variable species, *A. proligera* (Broth.) Herzog *s. lat.* (Akiyama et al. 2015).

Two types of exostome teeth have been recognized in *Aptychella*. One is with open pores or depressions along the median lines, while the other is without such structure. According to this difference, the genus was once treated as separate two genera: *Aptychella* Herzog (1916) [Type species: *A. proligera* (Broth.) Herzog] without perforate teeth, and *Clastobryopsis* M.Fleisch. (1923) [Type species: *C. planula* (Mitt.) M.Fleisch.] with perforate ones. The Asian species were treated as *Clastobryopsis* M. Fleisch., while the Central and South American species as *Aptychella* (e.g. Tan & Buck 1989: 308-310). However, based on molecular phylogenetic analysis, Akiyama et al. (2015) proposed that the two genera should be merged into a single genus, *Aptychella*.

Species of *Aptychella* are all similar in gametophytic morphology, making it difficult to know species identities only based on morphological features, and this is one of the reasons why species classification of the genus has long been confusing. It has been pointed out that there are two groups within *Aptychella* species: they are (1) *A. brevinervis* group with well-developed single (sometimes forked above) costae, and (2) *A. robusta* group with indistinct or short and double costae (Akiyama et al. 2015). Species diversity of the former group has been largely resolved by molecular phylogenetic analysis; it includes *A. brevinervis*, *A. pseudobrevinervis* H.Akiyama, *A. oblongifolia* H.Akiyama, and *A. proligera* in addition to *A. touwii* that no fresh sample was available (Akiyama et al. 2015). On the other hand, the latter group remained ambiguous for their species diversity mainly because of sample deficiency for molecular analyses at that time and thus it was suggested that the latter group contain at least two subclades (Akiyama et al. 2015). However, it was left unclear whether these two subclades corresponding to *A. robusta* and *A. planula* (Tan 1991, Tan & Buck 1989, Tan & Jia 1999).

The main objective of this study is to determine species

diversity of *Aptychella robusta s. lat.* For this reason, we collected a number of plant samples previously recognized as *A. robusta* and *A. planula* with short and double costae from wide geographical areas and conducted molecular phylogenetic analyses. We also did morphological studies using specimens borrowed from a number of herbaria to determine morphological variation in each species as well as type specimens to determine the scientific names to be used.

MATERIALS AND METHODS

Examination of herbarium specimens

A number of herbarium specimens including types, which were used to fix nomenclatural issues, were examined on loans from the following herbaria, BM, CAS, FH, H, HIRO, HSNU, HYO, KUN, KYO, L, MO, NICH, NY, OSA, PC, PE, PHH, SING, TAIE, TNS and UC.

Taxon sampling for molecular analyses

Most of the examined samples for DNA sequence analyses were extracted directly from plants newly collected by the authors or recently collected herbarium specimens. Field studies were carried out at Doi Inthanon National Park in Thailand, Bidoup-Nui Ba National Park and Tam Dao National Park in Vietnam, Cameron Highland, Genting Highland and Mt. Kinabalu in Malaysia, Mt. Victoria in Myanmar, Gaoligonshan National Park and Laojunshan Mts in China, Syuejin and Dasyueshan Nature Reserves, Mt. Beidawuk, Sun-Link-Sea and Mandarin Duck Lake in Taiwan, as well as several localities in southwestern Japan with permissions for collections.

In this study, we used 46 samples from the *A. robusta s. lat.* + *A. planula* group collected from Japan, Taiwan, Myanmar, Vietnam, Thailand, China, and Philippines. In additions, the following species were included from previous works; single sample of *A. linii* H.Akiyama and *A. hawaiica* H.Akiyama & Shevock, respectively, two samples of *A. imbricata* H.Akiyama et al., nine samples of *A. brevinervis* (M.Fleisch.) M.Fleisch., three samples of *A. oblongifolia* H.Akiyama, four samples of *A. proligera* (Broth.) Herzog, and four samples of *A. pseudobrevinervis* H.Akiyama. As a result, we were able to include nine species out of 11, which were previously recognized by Tan (1991), Tan & Jia (1999), Akiyama et al. (2010), and Akiyama & Shevock (2019) (See Appendix 1).

Although *Aptychella touwii*, *A. robusta*, *A. perdecurrens*, *A. clemensiae* (≡ *A. brevinervis*), and *A. brevinervis* have been reported from New Guinea, another center of the species diversity of *Aptychella* (Akiyama 2016, Tan et al. 2011), we were not able to obtain DNA samples from these sources and unfortunately could not examine the specimens cited by them. Of these, *A. perdecurrens*, for which we were able to examine the holotype specimen, was treated here only based on morphological features.

We added two samples of *Microgammiella flagelliformis* H.Akiyama, and single sample of *Pylaisiadelpha tristoviridis* (Broth.) Afonia, H.Tsubota & Ignatova, single sample of *Isopterygium propaguliferum* Toyama, and single sample of *Yakushimabryum subintegrum* (Tixier) H.Akiyama from the Pylaisiadelphaceae in the present analysis, all of which were shown to be closely related to *Aptychella* by previous studies. *Brachythecium plumosum* (Hedw.) Shimp. is used as an outgroup as suggested by Akiyama et al. (2015) and Akiyama (2017a, 2019).

A total of 76 samples (six genera and 13 species) were included in the present molecular phylogenetic analyses. Voucher information for the newly registered accessions in DDBJ are provided in Appendix 1.

DNA extraction, amplification, and sequencing

DNA extraction and amplification followed the same methods described in Akiyama *et al*. (2015) and Akiyama (2017a). Nucleotide sequences were newly obtained from 40 samples for this study, including 120 nucleotide sequences (Appendix 1). Sequenced regions are: (1) the plastid *trn*S-*rps*4 region [i.e., *rps*4 plus the *trn*S–*rps*4 intergenic spacer (IGS), hereafter *rps*4], (2), the plastid *trn*L-F region, including the *trn*L_{UAA} group I intron and the *trn*L-F IGS (hereafter *trn*L-F), and (3) the ribulose 1,5-bisphosphate carboxylase/oxygenase large subunit (hereafter *rbc*L).

We used MUSCLE (Edgar 2004) to manually align the final consensus sequences, together with previously published sequences obtained from NCBI via an internet web browser implemented in MEGA 7.0.21 (Kumar *et al*. 2016).

Phylogenetic analyses

Preliminary analyses using *rps*4, *trn*L-F, and *rbc*L (substitution model: TN93+G+I) data sets separately yielded no conflicting branches with high bootstrap support or posterior probabilities and thus combined data sets of all three sequences were used for further analyses. There was no ambiguity in the alignment except for

hyper variable sites of *trn*L-F, which were deleted and not used in the analyses.

We performed Maximum Likelihood (ML) and Maximum Parsimony (MP) analyses using MEGA 7.0.21 (Kumar *et al.* 2016) with the option of partial deletion (PD; site coverage cutoff 95%) for missing data, and Bayesian Inference (BI) using MrBayes ver. 3.2.2 (Ronquist & Huelsenbeck 2003). For MP analyses, we used default settings with TBR branch-swapping with 1000 random addition replicates. We used TN93+G+I model (Tamura 1992) in the ML analysis, which were determined as an optimal model according to the Akaike's Information Criterion (AIC: Akaike 1973) as implemented in MEGA 7.0.21. We did non-parametric bootstrapping analyses for ML and MP analyses. This was performed with 500 pseudo-replicates with simple taxon additions in both ML and MP analyses. For BI analysis, we used T93N+G+I model with 10,000,000 generations; trees were sampled every 1,000 generations. The first 12,500 trees were removed for the burn-in phase. Bayesian posterior probability was calculated as node support values. We used Fig Tree ver. 1.4.3 (Rambaut 2016) as a tree editing program.

RESULTS AND DISCUSSION

We got a single most parsimonious tree for MP analysis with 729 steps in tree length (CI = 0.484346, RI = 0.859719). Bootstrap values of ML (BSML) and MP (BSMP) analyses and posterior probabilities of BI analysis (PPBI) are shown on each node in this order (Fig. 1).

As for the position of *A linii*, *A. hawaiica*, and *A. imbricata*, however, there was inconsistency in the results based on 1) MP and ML and 2) BI method, but these differences were supported by neither high bootstrapping values nor high probabilities, and thus we showed the final result of the present analyses by the ML tree (Fig. 1). In the following part, we only refer clades with high supporting values by all of the three analyses.

Monophyly of Aptychella

All the members of *Aptychella robusta s. lat.* and the monocostate species were resolved into a single clade with high supporting values. The result suggests that all *Aptychella* samples analyzed form a single clade with high supporting values (BSML/ BSMP/ PPBI = 94/95/1.0; Fig. 1, thick black arrow). This agree with the result of Akiyama et al. (2015), which revealed that the genus was monophyletic.

Among the species included in the analysis, systematic position of 1) *Aptychella imbricata* and 2) *A. linii* + *A. hawaiica* remained ambiguous. On the other hand, two clades with high supporting values were recognized for all the other species except for "*A. yakumontana*" (Fig. 1). One of them includes all species with a long, single costae (*A. brevinervis*, *A. oblongifolia*, *A. proligera* and *A. pseudobrevinervis*) with high supporting value (100/100/1.0). This clade was already pointed out by Akiyama et al. (2015), and it is again supported here by larger scale analysis. In addition, systematic position of *A. proligera* (the sole member of the genus in the New World) is again revealed as it falls within the same clade with the Asian species, which suggests populations in the New World had been originated by ancient long distance distribution. The other clade was recognized with rather high supporting value (66/87/0.92) and it includes 10 subclades of species with short and double costae, each of them with moderate to high supporting values (ranging from 92/75/0.79 for "*A. minutissima*" to 100/100/1.0 for "*A. rubiginosa*" and "*A. muelleri*") except the subclade of "*A. triangularis*" with a single sample. They are detailed in the next section. The subclade of "*A. yakumontana*" (100/100/1.0) was not resolved its relationship to the others and its phylogenetic position remained ambiguous.

Species diversity found within the 'Aptychella robusta s. lat.'

Akiyama et al. (2015) analyzed 11 samples of *A. robusta s. lat.* and noted that there were at least two subgroups in the group. In the present analysis with more samples, a total of 11 clades were resolved among 46 samples of the groups.

Checking morphological features of the samples belonging to these 11 clades as well as other herbarium specimens listed below, we found that plant of each clade can be characterized by shared morphological features (Figs. 4–13). We also examined the type specimens of formerly described species under *Aptychella* or related genera, and concluded that each clade should be recognized as a separate species; five of them can be attributed to the previously describe species, such as *A. muelleri*, *A. planula*, *A. robusta*, *A. subdelicata* and *A. yuennanensis*, even though the latter two were once treated as synonyms of *A. robusta.* Meanwhile, the other six should be treated as new species of *Aptychella.* Our results can be summarized as follows:

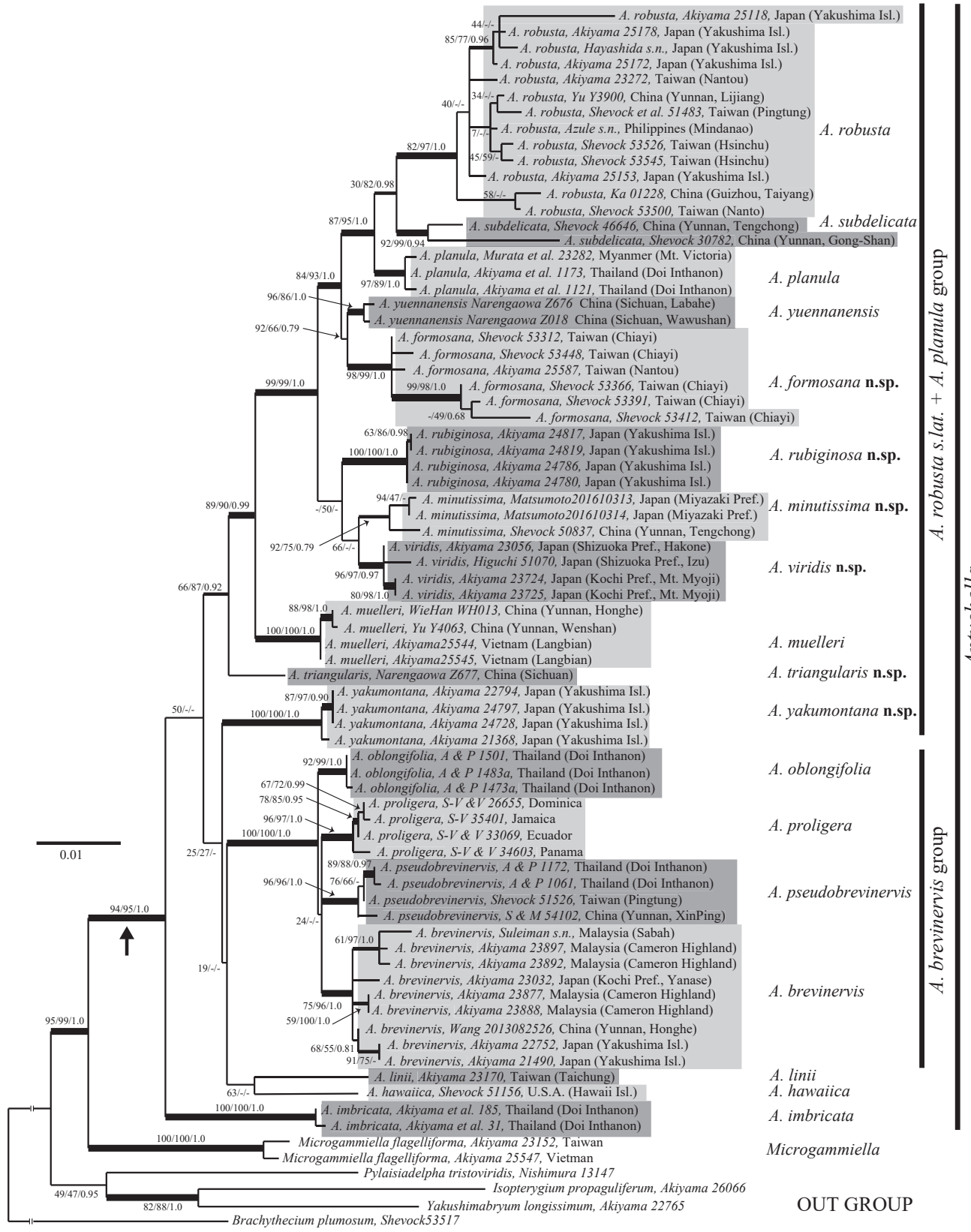

Figure 1. Phylogenetic tree of *Aptychella* based on ML analysis. Bootstrapping values of ML analysis (BSML), those of MP analysis (BSMP) and Bayesian posterior probabilities (PPBI) are indicated beside each branch in order of BSML/ BSMP/ PPBI. All *Aptychella* samples analyzed form a single clade with high supporting values (thick black arrow). Thick lines; BSMP≧70, BSML≧70 and PPBI≧0.95. Median lines; two of three values meet BSMP≧70, BSML≧70 or BIPP≧0.95. Thin lines; others.

1. The clade with a single sample ("*A. triangularis*" in Fig. 1) was found to be the outermost to the others except for "*A. yakumontana*". Another specimen belonging to this clade was confirmed by morphological examination.

2. Three samples of *Aptychella planula* (Figs. 6–7) and 13 samples of *A. robusta* (Fig. 8) form separate, well-supported two clades (97/89/1.0 and 82/97/1.0, respectively). The two species differ especially in the shape of alar region and degree of recurved leaf margins, and furthermore, as pointed out by Tan & Jia (1999), there is a difference in distribution pattern: *A. planula* distributed in the Himalayas, while *A. robusta* in the warm temperate zones of East and Southeast Asia.

3. Total of four samples of "*Aptychella yakumontana*" (Fig. 12) form a separate well-supported clade (100/100/1.0) outside those consisting of samples with short and double costae. Its phylogenetic relationship to the other members were not resolved and thus needs future re-examination. Morphologically, plants of "*A. yakumontana*" look most similar to those of *A. robusta*, but "*A. yakumontana*" can be distinguished by its narrower leaves. Both species often grow sympatrically on Yakushima Island (southwestern Japan), but *A. robusta* seems to prefer brighter sites according to our field observation.

4. Six samples of "*Aptychella formosana*" (Fig. 4) form a well-supported clade (98/99/1.0) and three of them also form highly supported subclade (99/98/1.0). There is no morphological differences among these six samples as well as other specimens listed in the following taxonomic treatment.

5. Four samples of "*Aptychella rubiginosa*" (Fig. 9) form a well-supported clade (100/100/1.0). Plants of this clade are characterized by 1) gemmiferous caudate secondary stems with lateral long branches, 2) stems in reddish brown color, and 3) absence of turf-forming secondary stems.

6. Four samples of "*Aptychella viridis*" (Fig. 11), which were collected in Japan and formerly recognized as *A. robusta*, were found to form a well-supported clade (96/97/0.97). This clade is distant from those of the true *A. robusta.* In addition, plants of *A. robusta* show different morphological features from those of "*A. viridis*".

7. There is a moderately supported (92/75/0.79) clade of "*Aptychella minutissima*" (Fig. 5) comprising single sample from China (Yunnan Province) and two samples from Japan (Miyazaki Prefecture). Their very narrow and small leaves are good morphological features of this species.

8. Two samples of *Aptychella subdelicata* and two samples of *A. yuennanensis* (Fig. 13) form two well-supported clades (92/94/0.94 and 96/86/1.0, respectively). Although, the former species once treated as a synonym of *A. planula* (Tan 1991) or as a synonym of *A. planula* var. *delicata* (M.Fleisch.) B.C.Tan & Y.Jia (Tan & Jia 1999), and the latter as a synonym of *A. robusta* (Tan 1991, Tan & Jia 1999), our present results on both molecular phylogenetic and morphological analyses support to treat them as two separate species.

Yakushima Island (Kagoshima Pref., Japan) is geographically very small (ca. 504.88 km²). We intensively collected samples from the island and found that those samples were able to be divided into three well-supported clades (*Aptychella robusta s. str.*, "*A. rubiginosa*", and "*A. yakumontana*"; Fig. 1). Since there is another species, *A. brevinervis* with single long costa, four species were confirmed in total from this small island, which suggest this island as one of the diversity centers of the genus.

Unfortunately, *Aptychella perdecurrens*, which has been reported from Papua New Guinea, could not be included in the present molecular phylogenetic analysis. This species differs significantly from other members of the genus in the absence of secondary stem differentiation into gemmiferous caudate (GCS) and turf-forming ones (TFS), total absence of filamentous propagules, and isomorphic shape and size in laminal cells (Tan et al. 2011). Furthermore, leaves of secondary stems are narrowly triangular and shorter (less than 1.4 mm in length) compared to other *Aptychella* species (Fig. 13). These features suggest that its remote generic affinity to *Aptychella*.

The clades that were found to be monophyletic in the present molecular phylogenic analyses described above were also can be characterized by shared morphological features. Therefore, we conclude that they should be treated as independent separate species. As a result, if including ambiguous *A. perdecurrens*, the total number of species in the clade of *Aptychella robusta s. lat.* with short and double costae reaches 11, and each of them can be distinguished as shown in the following keys.

TAXONOMIC TREATMENTS

Genus *Aptychella* (Broth.) Herzog, Bibliotheca Botanica 87: 157 (1916) (Pylaisiadelphaceae).

Basionym: *Rhaphidostegium* sect. *Aptychella* Broth., Nat. Pflanzenfam. I (3): 1115 (1908). Type species: *Rhaphidostegium proligerum* Broth., lectotype selected by Herzog (1916).

= *Aptchella* Herzog & E.B.Bartram, Bernice P. Bishop Mus. Bull. 101: 227 (1933), invalid, orthographic variant.

= *Clastobryopsis* M.Fleisch., Musci Buitenzorg 4: 1179 (1923). Type species: *Clastobryopsis planula* (Mitt.) M.Fleisch., *fide* Akiyama et al. (2015).

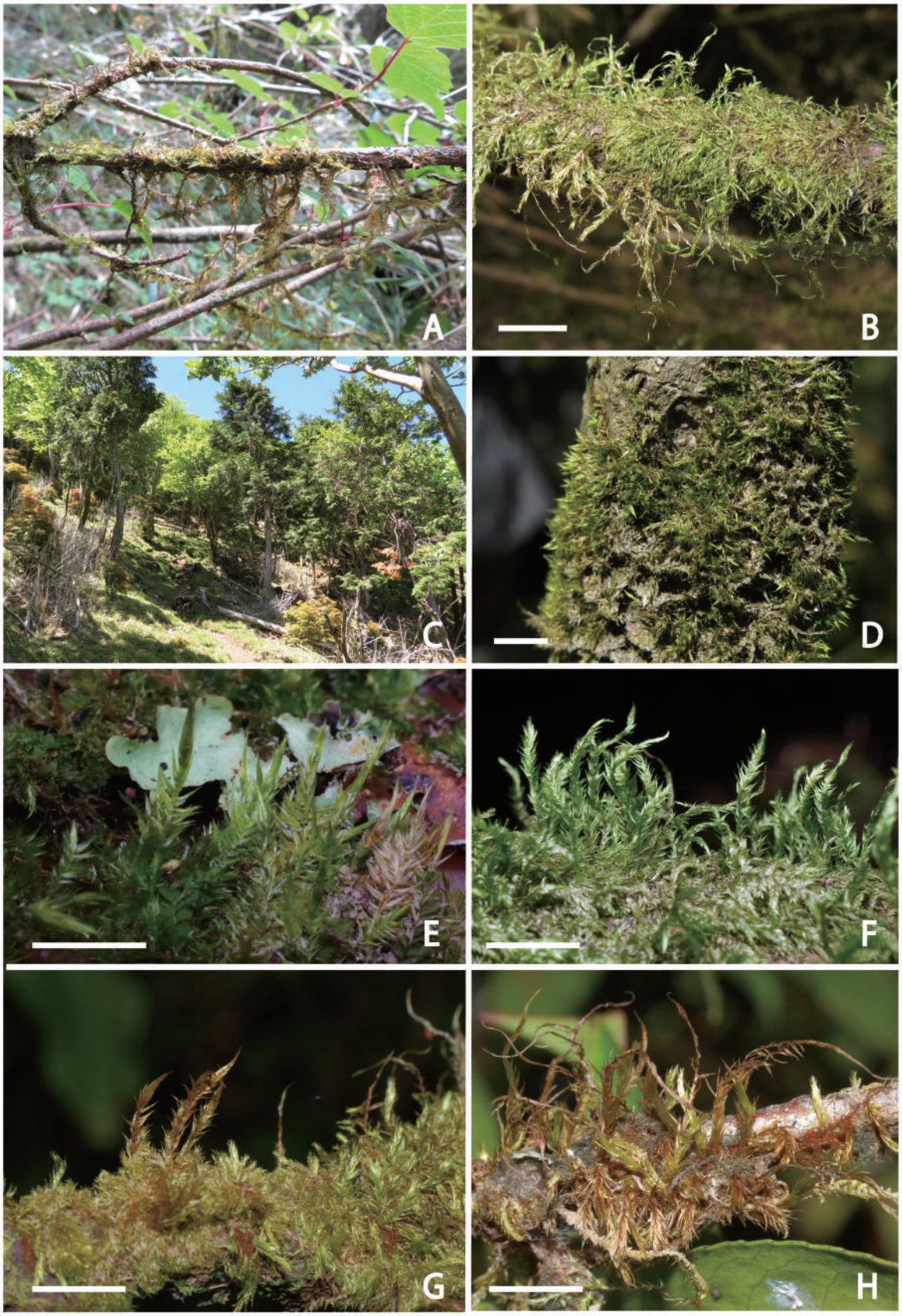

Figure 2 . Plants and habitats of *Aptychella* in Japan and Taiwan (1).

A and B: *A. formosana* (Taiwan, Nantou Co., Mt. Hehuanshan, type locality) . C and D: *A. minutissima* (Japan, Miyazaki Pref. Mt. Ichifusa). E and F: *A. robusta* (E: Taiwan, Taichung City, Dasyueshan. F: Japan, Kagoshima Pref., Yakushima Isl.). G and H: *A. planula* (Thailand, Chiang Mai, Doi Inthanon). Scales = 1 cm.

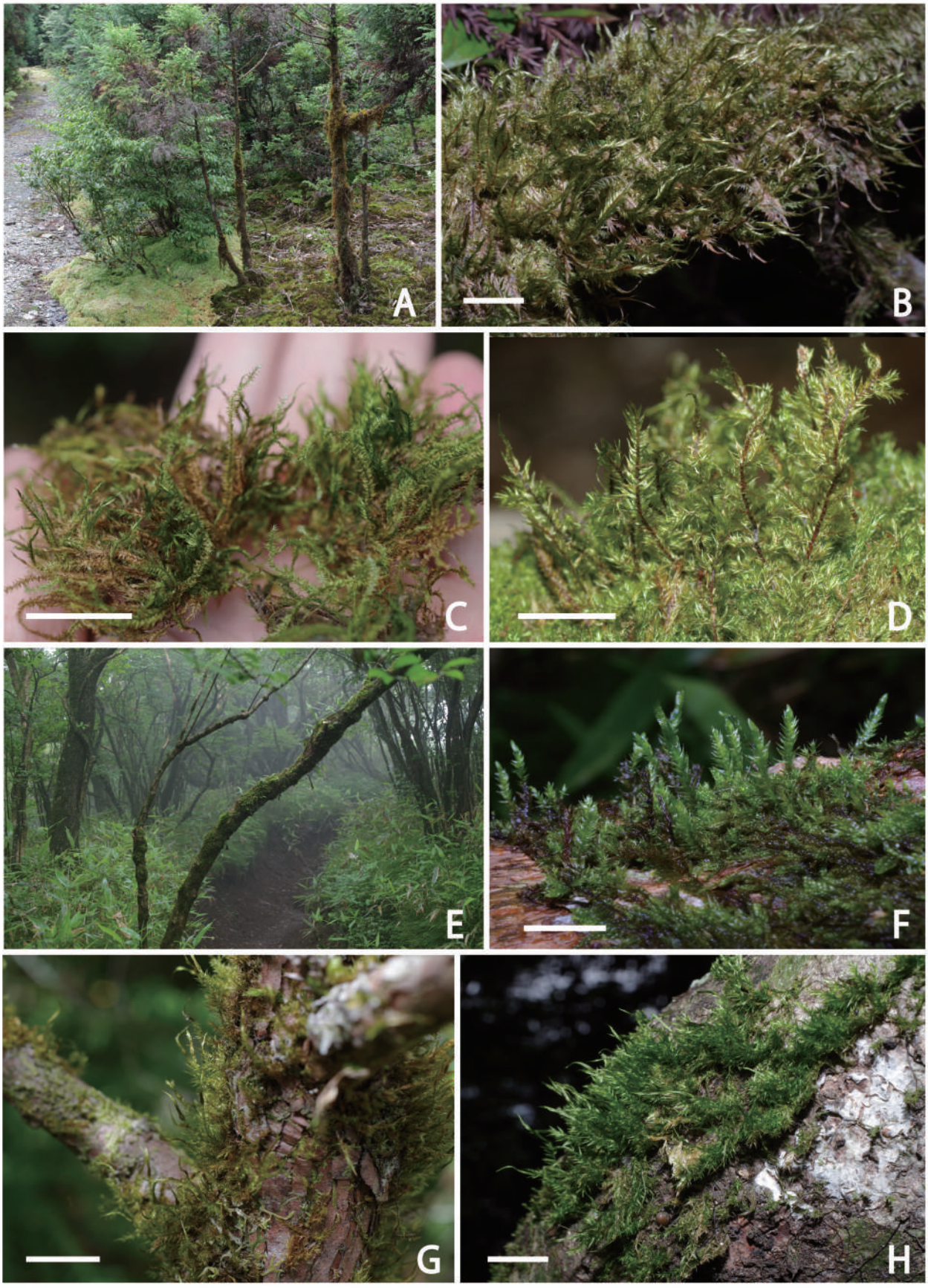

Figure 3 . Plants and habitats of *Aptychella* in Japan and Taiwan (2).

A–D: *A. rubiginosa* (Japan, Kagoshima Pref., Yakushima Isl., type locality). E and F: *A. viridis* (Japan, Kanagawa Pref., Hakone). G and H: *A. yakumontana* (Japan, Kagoshima Pref., Yakushima Isl.). Scales = 1 cm.

All *Aptychella* species are epiphytic, preferring slightly brighter sites such as forest margins and seem to prefer small diameter twigs and branches for growing substrates. Plants have a remarkable appearance that makes it easy to distinguish the genus from other related genera even with the naked eye in the field. Soloniferous primary stems (SPS; for example, Fig. 4B) are short in length, creeping on substrates, and densely pinnately branched with numerous, ascending secondary stems. Most of lateral secondary stems are short, simple or sparsely branched, and forming lawn-like turf (turfforming secondary stems: TFS, for example Fig. 4B). On the other hand, there are also much fewer, long, ascending, and prominently caudate secondary stems (gemmiferous caudate secondary stems: GCS, for example Fig. 4B), which bear bundle of filamentous propagules in leaf axils just below the tips. The uppermost parts of GCS bear much smaller leaves and become prominently caudate. Leaves of GCS and TFS differ not only in size and shape, but in alar morphology. Alars of GCS leaves are composed of quadrate to short rectangular cells arranged in a scalariform manner. In many species, alars of TFS are less differentiated. Therefore, one should take care to examine well-developed leaves from the middle parts of GCS to know the identity of the plant being examined. In many species, leaf bases are more or less decurrent to stems, but it varies widely among leaves even on a single stem. In addition, some species, such as *A. planula*, has leaves without prominent decurrence. Peristome teeth are of the *Neckera* type, and the smooth or slightly papillose outer surfaces of exostome teeth sometimes have a longitudinal row of small pores in the center (Fig. 7). The most closely related genus is *Microgammiella* H.Akiyama (Akiyama 2019).

In the present study, a total of 18 species of *Aptychella* are recognized according to molecular phylogenetic analyses as well as morphological examination of a number of herbarium specimens including types. As a result, if adding two species and one variety that were not included in the present analyses (*A. perdecurrens, A. proligera* var. *chlorophyllosa,* and *A. touwii*), the total number of species in *Aptychella* becomes 20 species and one variety (Appendix 2). These species can be distinguished in the following key:

Key to the species of *Aptychella*

[Species treated in detail are indicated with numerical numbers before their scientific names.]

1. Plants totally pendulous, gemmiferous caudate secondary stems (GCS) absent. Filamentous asexual propagules unknown. (Endemic to Papua New Guinea) .....4. *A. perdecurrens*
1. Plants sometimes with pendulous parts, but ascending GCS always differentiated. Filamentous propagules present. 2
2. Leaves of GCS deeply carinate, with sharp and prominent 1(–3) spines on back of the basal part of keels. (Endemic to Northern Thailand). ..... *A. imbricata* (Akiyama et al. 2010)
2. Leaves of GCS concave or flat, but never carinate, without spines on back. 3
3. Leaves of both turf-forming secondary stems (TFS) and GCS with single and long costae (sometime forked above), often extending middle of leaf length. 4
3. Leaves of both TFS and GCS with indistinct or short and double costae. 8
4. Plants restricted to Central America and northern South America. ..... *A. proligera* (Akiyama et al. 2015)
4. Plants distributed in East and Southeast Asia and Hawaii. 5
5. Leaves of GCS usually 3–4 mm in length; alar cells long-rectangular, well-pitted. Endemic to highlands of New Guinea. ..... *A. touwii* (Akiyama 2016)
5. Leaves of GCS less than 2.5 mm in length; alar cells short-rectangular to quadrate, not or slightly pitted. Plants widely distributed in East and Southeast Asia. 6
6. Plants large; leaves of median parts of GCS reaching 2.5 mm in length, concave, plicate; alar cells greenish but soon turning reddish brown, more or less inflated, never decurrent to stems. Widely distributed in East and Southeast Asia. ..... *A. brevinervis* (Akiyama 2014)
6. Plants small; leaves of median parts of GCS usually less than 2.0 mm in length, plane; alar cells greenish, not inflated, plane, decurrent to stems. Known from Thailand, China, Taiwan, and Philippines. 7
7. Leaves of GCS deltoid; margins strongly recurved especially at basal part; alar cells not reaching the costa, widely decurrent to stems. Known from Thailand, China, and Taiwan. ..... *A. pseudobrevinervis* (Akiyama 2014)
7. Leaves of GCS oblong-lanceolate; margins not or scarcely recurved; alar cells reaching to the costa, narrowly decurrent to stems. Known from north Thailand, China, Taiwan and Philippines.

..... *A. oblongifolia* (Akiyama 2014)

8. Plants very small. GCS short and upright, not caudate at apices, shorter than 7 mm in length. Endemic to central Taiwan.
..... *A. linii* (Akiyama & Shevock 2019)

8. Plants medium to large. GCS long and variable in shape, caudate at apex, mostly longer than 10 mm in length. Widely distributed in East and Southeast Asia. 9

9. Leaves of GCS triangular, widest at base. 10

9. Leaves of GCS variable, more or less narrowed at base. 11

10. TFS few and not forming turf. Leaves of TFS ovate below, 0.5–0.9 mm in length. Known from southwestern China. ..... 9. *A. triangularis*

10. TFS numerous and forming thin turf. Leaves of TFS narrowly to linear lanceolate, 0.8–1.0 mm in length. Known from central Taiwan. ..... 1. *A. formosana*

11. Leaves of GCS, linear-lanceolate, margins usually plane. 12

11. Leaves of GCS, ovate lanceolate, margins more or less recurved. 14

12. Leaves of GCS less than 1.4 mm in length; margins plane or weakly recurved. ..... 2. *A. minutissima*

12. Leaves of GCS longer than 1.6 mm in length; margins narrowly but distinctly recurved except for uppermost part. 13

13. Leaves of GCS with well developed decurrence at bases. ..... 8. *A. subdelicata*

13. Leaves of GCS without long decurrence at bases.
..... 12. *A. yuennanensis*

14. GCS branched, with several long lateral stems; stems reddish brown in color. Alar cells of both GCS and TFS leaves large, long rectangular (similar to those of *Brotherella* spp.). ..... 7. *A. rubiginosa*

14. GCS usually not branched, sometimes with short side branches; stems green or pale reddish brown in color. Alar cells of GCS short rectangular, arranged in scalariform manner. 15

15. Leaves of GCS widely ovate, becoming much narrower at bases. ..... 3. *A. muelleri*

15. Leaves of GCS ovate to lanceolate, not becoming much narrower at bases. 16

16. Margins of GCS leaves mostly plane, partially narrowly recurved, entire or with weak serration; alars rarely decurrent to stems. Himalayan element.
..... 5. *A. planula*

16. Margins of GCS leaves distinctly recurved except leaf apices, serrulate especially at upper portions. Distributed in warm temperate region in East and Southeast Asia. 17

17. Apices of GCS leaves gradually acute to narrowly acuminate. Alars of TFS leaves weakly developed, with 3–4 quadrate cells. Endemic to Japan.
..... 10. *A. viridis*

17. Apices of GCS leaves narrowly acuminate. Alars of TFS leaves usually well developed with more than ten quadrate cells (sometimes weakly developed with several quadrate cells). 18

18. Leaves of GCS linear lanceolate; apices never channeled. Endemic to Japan (Yakushima Isl.).
..... 11. *A. yakumontana*

18. Leaves of GCS ovate to narrowly ovate; apices often channeled. 19

19. Endemic to the Hawaiian Islands.
..... *A. hawaiica* (Akiyama & Shevock 2019)

19. Widely distributed in East and Southeast Asia.
..... 6. *A. robusta*

1. Aptychella formosana H.Akiyama, Shevock & K.-Y. Yao, ***sp. nov.*** (Figs. 2A–B and 4)

Diagnosis: Similar to *Aptychella robusta*, but plants smaller, leaves of gemmiferous caudate secondary stems much broader at base, with low serration, and leaves of turf-forming secondary stems narrow-lanceolate.

Type: Taiwan, Nantou Co., Ren'ai Township, Mt. Hehuanshan, behind the High Altitude Experimental Station of Endemic Species Research Institute, ca. 3000 m elev., 24.1614° N, 121.2868° E, 31 May 2018, *H.Akiyama 25584* (holotype HYO, isotypes CAS, TAIE).

Description: Plants shiny green in color with a brownish tint when old. Primary stems substrate, densely pinnately branched, with a tendency to droop from the substrate, forming a dense turf with short, secondary stems (TFS) less than 4 mm in length. A few gemmiferous secondary stems (GCS) ascending, 5–7 mm in length, caudate at tips. Filamentous propagules ca. 0.5 mm in length, with a row of smooth cells. Leaves of GCS gradually narrowing and acuminate from broadly ovate base, 1.2–1.5 mm in length, distinctly decurrent to stems; costae short and double; margins minutely serrate above, nearly entire below, often narrowly recurved all around; laminal cells linear 80–100 μm in length, smooth; alars well developed with thin-walled, quadrate to long rectangular cells. Leaves of TFS narrowly lanceolate to linearly lanceolate, 0.8–1.0 mm in length, slightly concave, with narrowly pointed tips, not decurrent to stems; margins

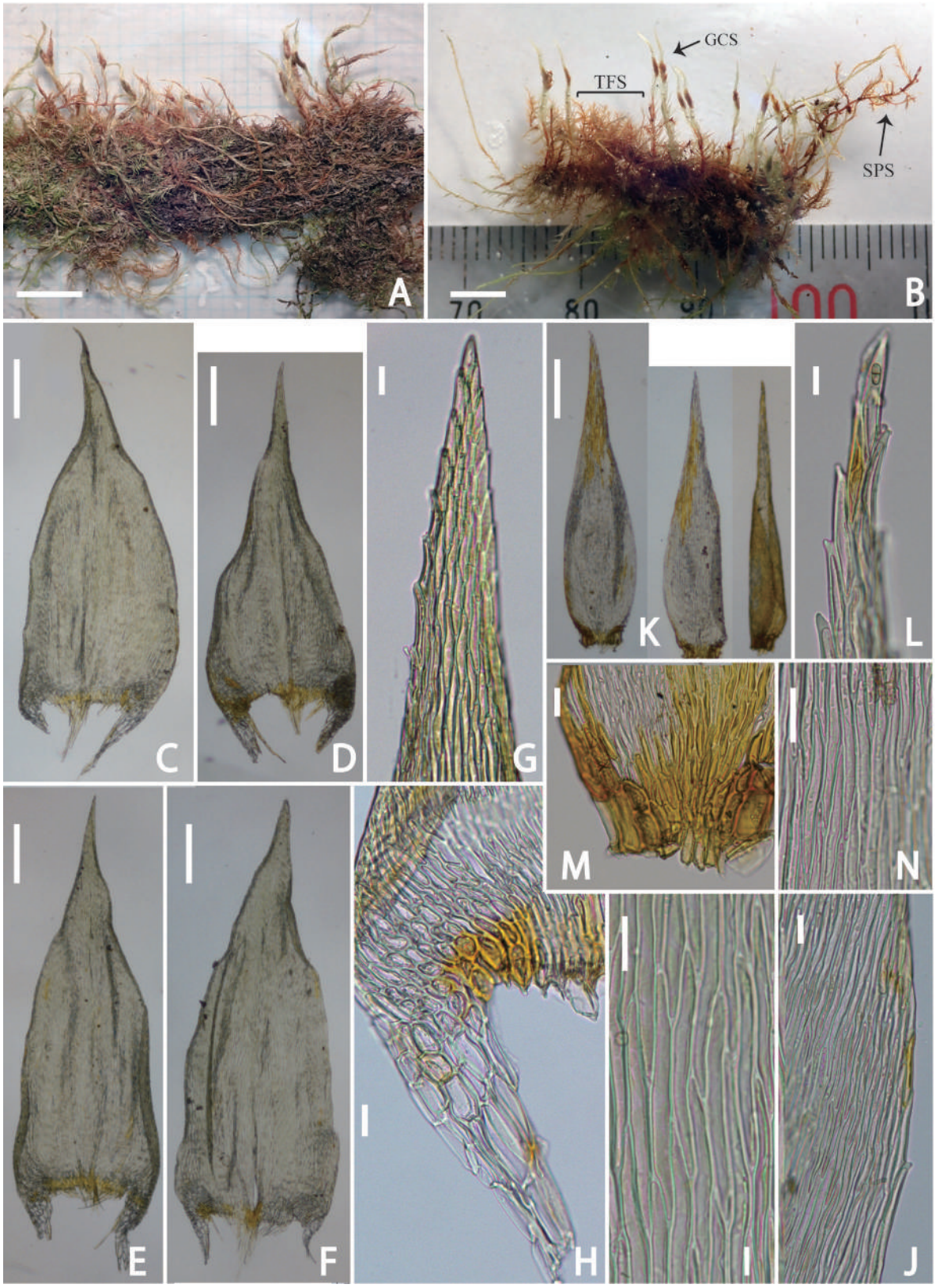

Figure 4. *Aptychella formosana.* All taken from the holotype (*H.Akiyama 25584*).

A: Plant (dry). B: Plant (wet). C–J: Leaves of gemmiferous caudate secondary stems. K–N: Leaves of turf-forming secondary stems. G and L: Leaf apices. H and M: Alars. I and N: median laminal cells. J: Upper margins. GCS: Gemmiferous caudate secondary stems. TFS: Turf-forming secondary stems. SPS: Stoloniferous primary stem.

Scales: A and B = 5 mm; C–F and K = 0.2 mm; H–J and L–N = 20 μm.

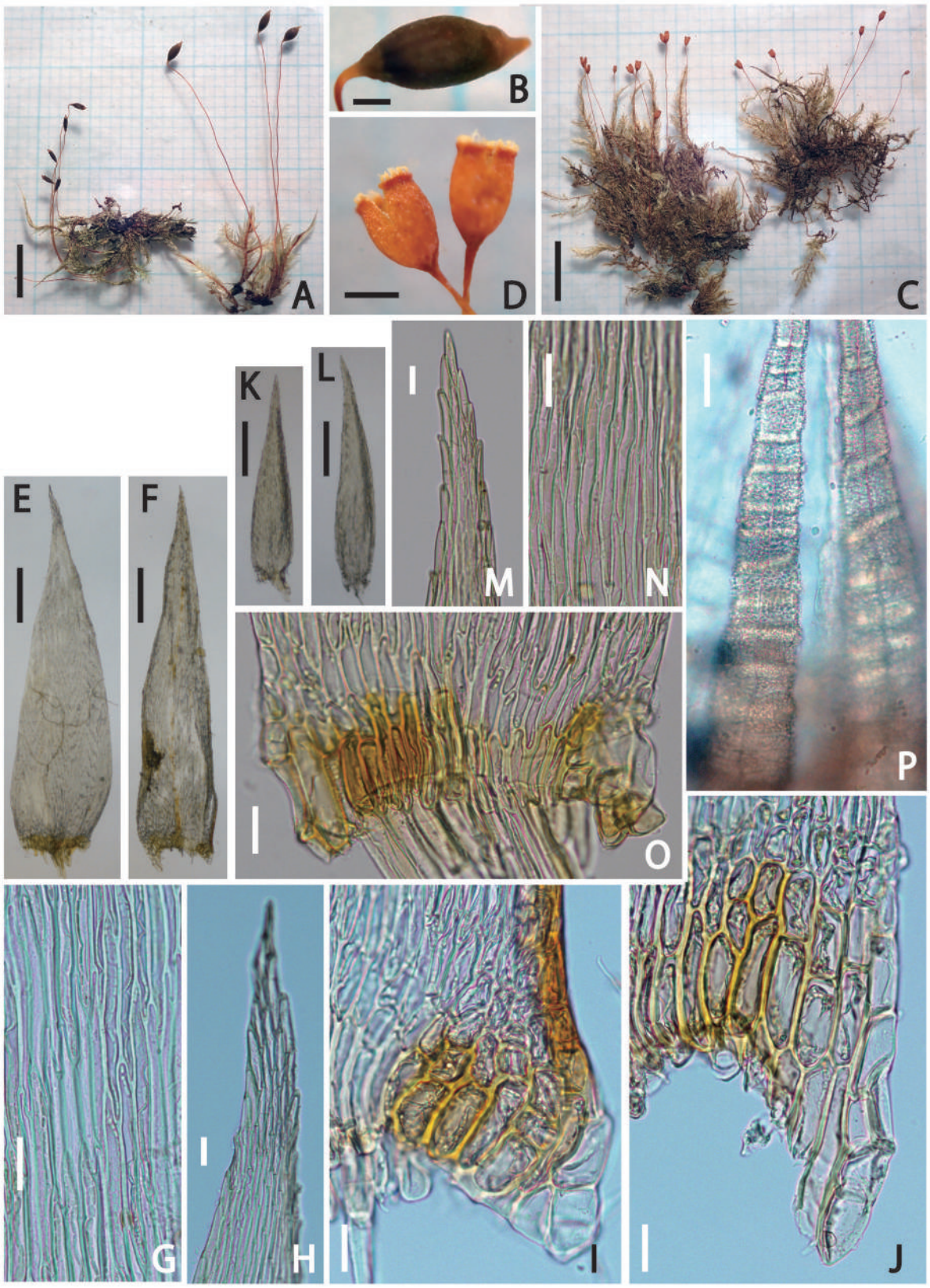

Figure 5. *Aptychella minutissima.* All taken from the holotype except for C and D (*J.R.Shevock et al. 46425*).
A and C: Plants (dry) with sporophytes. B and D: Close-up of sporophytes. E and F: Leaves of gemmiferous caudate secondary stems. K–O: Leaves of turf-forming secondary stems. H and M: Leaf apices. G and N: Median laminal cells. I, J and O: Alars. P: Outer surface of peristome teeth without perforation. Scales: A and C = 5 mm; B and D = 0.5 mm; E, F, K, L = 0.2 mm; others = 20 μm.

minutely serrate above, entire below, plane or narrowly recurved; laminal cells linear, 60–80 μm in length, smooth, plane or slightly prorate; alar cells quadrate to rectangular, colored in pale reddish brown, slightly thick-walled. Sexual organs and sporophytes unknown.

Habitat: Growing on small shrub trunks and branches, often hanging from shrub branches, at wind-blown places in higher altitudes.

Distribution: Endemic to subalpine regions of the central Taiwan.

Distinguishing features: 1) plants similar to those of *Aptychella robusta* in general appearance, especially in the wide and prominent decurrent bases of GCS leaves, 2) broadly ovate GCS leaves, 3) narrowly recurved and only weakly serrulate leaf margins, and 4) very short and double costae.

Other specimens examined. TAIWAN: Chiayi Co., along the 2.2 km trail from Paiyun Lodge to West Yushan Peak about 0.2 km above the lodge, 23°28'00.7" N, 120°56'53.6" E, 3465 m elev., 25 Oct 2018 *J.R.Shevock et al. 53366* (CAS, HYO, TAIE); ibid., 3460 m elev., *Shevock et al. 53391* (CAS, HYO, TAIE); ibid., 3402 m elev., *J.R.Shevock 53412* (CAS, HYO, TAIE); ibid., 3170 m elev., 23 Oct 2018, *J.R.Shevock et al. 53312* (CAS, HYO, TAIE); ibid., 3000 m elev., *Shevock et al. 53434* (CAS, HYO, TAIE); ibid., 2820 m elev., *J.R.Shevock et al. 53448* (CAS, HYO, TAIE). Nantou Co., Ren'ai Township,, Mt. Hehuanshan, behind the High Altitude Experimental Station of Endemic Species Research Institute, ca. 3000 m elev., 24.1614° N, 121.2868° E, 31 May 2018, *H.Akiyama 25583* and *25585* (both HYO). Hualien Co., Mt. Hohuan-shan, en route from Tayuling to Konankuan, 2900 m elev., 28 Aug 1998, *H.Akiyama et al. 200-b* (HYO).

2. *Aptychella minutissima* H.Akiyama, Shevock & M. Matsumoto, ***sp. nov.*** (Figs. 2C–D and 5)

Diagnosis: Similar to *Aptychella robusta*, but plants much smaller in size. Gemmiferous caudate secondary stems (GCS) weakly developed from turf-forming secondary stems (TFS). Leaves of GCS with hardly recurved margins; costae short and double, often indistinct. Leaves of TFS slightly ligulate above, with weakly differentiated alars. Peristome teeth without pores.

Type: China, Yunnan Prov., Jin-Ping Co., along road to radar installation facility off of highway from Fenshuiling Pass. 22°51'46.0" N, 103°13'38.0" E., 1975 m elev., 8 Sep 2017 *J.R.Shevock & L.Zhang 50837* (holotype CAS, isotypes HYO, KUN; intermingled with *Aptychella oblongifolia*).

Description: Plant small, less than 1 cm in height. Primary stems short, pinnately branched. GCS less than 8 mm in length, not strongly differentiated from TFS. Leaves of GCS narrowly lanceolate from narrow ovate base, more or less decurrent at base, gradually narrowed into apices, 1.4–1.7 mm in length, 0.3–0.4 mm in width, plane or weakly concave; margins entire but minutely crenulate above, almost plane, rarely narrowly recurved only at basal parts; costae short and double, often indistinct; alars weakly to moderately differentiated with somewhat inflating, rectangular, thin-walled cells. Leaves of TFS lanceolate, acute to acuminate, 0.5–0.9 mm in length, plane or slightly concave, margins narrowly recurved or plane, minutely serrate above, almost entire below; alars with several enlarged cells arranged in a single row at base. Dioicous? Perigonia not observed. Perichaetia at basal parts of ascending stems. Perichaetial leaves narrowly lanceolate from ovate base, reaching 1.5 mm in length, ecostate, margins plane. Postfertilized perichaetial leaves not so differing from surrounding leaves. Seta 20–25 mm in length, yellowish brown, smooth, loosely twisted from lower left to upper right. Capsule horizontal to inclined, or upright, ovoid to long ovoid, smooth, 1.5–2.0 mm in length, 0.5–0.6 mm in width; operculum 0.4 mm in length, short rostrate. Annulus absent. Exothecial cells hexagonal, evenly thick-walled, not collenchymatous. Stomata absent. Peristome double, pale yellow. Exostome teeth narrowly lanceolate, ca. 350 μm in length, 50 μm in width at base, pale yellow, not perforate, minutely papillose throughout. Endostome with low basal membranes, ca. to 40 μm in height; segments linear, to 250 μm in length, densely and minutely papillose throughout. Spore small, 10–15 μm in diameter, trilete, distorted spherical, smooth.

Habitat: Growing on branches of small shrubs and bamboo grass at rather open places in montane forests.

Distribution: Thailand, China and Japan.

Distinguishing features: 1) short and lanceolate GCS leaves, 2) narrowly ligulate apices of TFS leaves, 3) often indistinct costae and hardly curved margins both in GCS and TFS leaves, and 4) weak differentiation of alars both in GCS and TFS leaves.

Other specimens examined. THAILAND: Chiang Mai, Doi Inthanon National Park, Ang Ka trail, 18°31' N, 98°24' E, 2500 m elev., 11 Mar 2011, *H.Akiyama & N.Printarakul 1507* and *1508* (both HYO); ibid., 18°34' 08" N, 98°29'05" E, 2300 m elev., 15 Jan 2011, *H.Akiyama*

et al. 1052 & 1208 (both HYO). **CHINA:** Yunnan Prov., Teng-Chong Co., Western slope of the Gaoligonshan, 25°34'01.6" N, 98°11'48.7" E, 2685 m elev., 25 Apr 2015, *J.R.Shevock, W.-Z.Ma & Y.-L.Yao 46425* (CAS, HYO, KUN; with sporophyte); ditto, Zhao-Tong Dist., Chongjsiung around Niu-chang-bau, 2100 m elev., 17 Jul 1992, *H.Akiyama 10345-b* (HYO). **JAPAN:** Miyazaki Pref., Nishimera-mura, Mt. Ichifusa, 1540 m elev., 31 Oct 2016, *M.Matsumoto 20161031-3 & 20161031-4* (HYO); ibid., 1540 m elev., 21 May 2019, *H.Akiyama 26005 & 26007* (both HYO).

Note. Japanese and Chinese plants differ in leaf shape and leaves of Japanese plants are narrower in width. Sporophytes also shows variation within Chinese plants; they are also found from another Chinese specimen (*Shevock et al. 46425*), but are different from those of the type in the following features; setae are 8 mm in length, and capsules are upright, shortly ovoid, 0.6–1.0 mm in length (Fig. 5C–D).

In Japan, *Aptychella minutissima* grows sympatrically (but not intermingled) with *A. viridis*. The sole population of this species in Japan is now under severe damage because of heavy browsing damage to plants caused by deer and its future survival is uncertain.

3. *Aptychella muelleri* Dixon, Annales Bryologici 6: 32 (1933). (Fig. 13B–D)

≡ *Clastobryopsis muelleri* (Dixon) Tixier, Rev. Bryol. Lichénol. 43: 413 (1977). Type: Sikkim, *Kurz 213b*, as *Urophila aurea* Müll.Hal., *ms. in* Herb. Hampe; Herb. Mus. Brit. (holotype BM).

Synonym: *Clastobryum caudiforme* Dixon. Type: India, *Griffith 183*, ex hb. Mitten 183 (holotype BM!), **syn. nov.**

Description: Primary stems densely or sparsely, pinnately branched. Gemmiferous caudate secondary stems (GCS) 1–2 cm in length, indistinctly differentiated from shorter turf-forming secondary stems (TFS). Filamentous propagules 1.5–2.1 mm in length, composed of rectangular smooth cells. Leaves of GCS broadly to narrowly ovate, slightly concave, becoming narrower at base, acute or gradually narrowed into slender apices, more or less decurrent to stems, 1.4–2.1 mm in length, 0.5–0.7 mm in width, plane or weakly concave; laminal cells narrowly lanceolate, 70–100 μm in length, smooth; margins entire, minutely crenulate above, almost plane, rarely narrowly recurved only at basal parts; costa short and double, often indistinct; alars highly differentiated with somewhat bulging, rectangular, thin-walled cells. Leaves of TFS similar to those of GCS in shape but shorter in length, plane or slightly concave; margins, almost entire; alars with several enlarged cells arranged in a single row at base. Dioicous? Perichaetia on primary stems. Seta ca. 1.0–1.2 cm in length, smooth. Capsules ovoid, to 2 mm in length, smooth; exothecial cells hexagonal, evenly thick-walled; stomata absent. Peristome double, Exostome teeth pale yellow, linear lanceolate, 350–380 μm in height, finely papillose, with small pores in the central line. Endostome segments filamentous, ca. 350 μm in length, finely papillose; basal membrane almost absent.

Previous illustration: Gangulee (1980, drawn from the type in BM), Printarakul et al. (2013; Fig. 4 as *Clastobryopsis muelleri*).

Habitat: Growing on branches of small shrubs in montane forests.

Distribution: India (Sikkim), Thailand, Vietnam, and China.

Distinguishing features: 1) plants similar to those of *Aptychella planula*, with weak differentiation between gemmiferous caudate secondary stems and turf-forming secondary stems, 2) broadly ovate leaves with narrowed bases, and 3) entire and plane leaf margins.

Other specimens examined. THAILAND: Chiang Mai, Doi Inthanon, 2550 m elev., 4 Mar 2008, *H.Akiyama et al. 21542* (HYO). **VIETNAM:** Lam Dong Prov., Bidoup-Nui Ba National Park, hiking trail to the summit of Mt. Langbian, 1900 m elev., 29 Apr 2018, *H.Akiyama 25544 & 25545* (both HYO); ibid., hiking trail toward Langbian Peak, 12°01'26" N, 108°25'59" E, 1910–1920 m elev., 13 Feb 2015, *B.H.Duong & T.T.Luong LB01309* (PHH). **CHINA:** Yunnan Prov., Honghe Co., Jinping, Zhemi, Liangzizhai, Xilong Mountain Natural Reserve, 22°41'53.53" N, 102°48'47.68" E, 1635 m elev., 24 Nov 2015, *W.Han 013* (PE); ibid., Wenshan Co., Maguan, Dulong, Laojunshan Mts., 22°56'34.47"–36.73" N, 104°33'27.15"–46.78" E, 2079–2276 m elev., 30 Oct 2016, *Y.Ning-Ning Y4063* (PE).

4. *Aptychella perdecurrens* (Dixon) T.J.Kop., Acta Bryolichenologica Asiatica 7: 69 (2017). (Fig. 13E)

Basionym: *Clastobryum perdecurrens* Dixon, J. Bot. 80: 30. (1942) ≡ *Clastobryopsis perdecurrens* (Dixon) B.C.Tan, J. Hattori Bot. Lab. 70: 92 (1991). Type: Papua New Guinea, Owen Stanley Range, above the Gap, circa 2450 m, 16 Dec 1935, *C.E.Carr 13826* (holotype BM!, isotype FH!, NY, MO).

Description: Primary stems prostrate on substrate, sparsely pinnately branched. Secondary stems long pendent, reaching 10 cm in length, with short side branches. Gemmiferous caudate secondary stems (GCS) not differentiated. Asexual propagules absent. Leaves of secondary stems narrowly triangular to linear lanceolate, acuminate to long acuminate, less than 1.4 mm in length, plane or slightly concave; margins flat, slightly recurved below, entire below, weakly toothed above, slightly decurrent; alar cells few, quadrate and rectangular, thick-walled, in well-defined colored cluster. Medial laminal cells narrowly elongate to linear, 50–75 μm in length, thin-walled. Autoicous? Perigonial leaves broadly ovate, acute, strongly concave, slightly toothed near apex. Perichaetial leaves ovate to broadly ovate lanceolate, gradually long acuminate, serrulate near apex; alars not differentiation. Setae 15–20 mm in length, distally papillose. Capsules ovoid, erect. ca. 1 mm in length; annulus absent; exothecial cells quadrate to rectangular and oblong, unevenly thick-walled, not collenchymatous. Opercula rostrate. Peristome double. Exostome teeth erect when wet, not well-developed, narrow, papillose, median lines distinct, with a few seemingly "perforated spots" along the midline on some teeth. Endostome segments filamentous, finely papillose. Spores greenish in color, 8–12 μm in diameter, papillose. [Descriptions above, especially sporophytic features, are mostly following Tan et al. (2011)].

Previous illustration: None. An image of the holotype specimen is available at website of BM. The image of a specimen of TROPICOS shows the distinctive long and drooping shoots.

Habitat: Epiphyte on twigs, bush, or branches of trees in primeval montane rainforests at 2100–3300 m elev. according to Tan et al. (2011).

Distribution: Endemic to Papua New Guinea.

Distinguishing features: 1) long pendent, sparsely branched plants as in the case of Meteoriaceous species, 2) no differentiation between gemmiferous caudate secondary stems and turf-forming secondary ones, 3) total absence of filamentous propagules, 4) shorter and narrower leaves comparing to other members of *Aptychella* (Fig. 13E), 5) very short and double costae, 6) narrow alar regions with 2–3 rows of quadrate cells arranged in scalariform manner, 7) autoicous sexuality (according to Tan et al. 2011), 8) peristome teeth with a few seemingly “perforated spots” along the midline on some (Tan et al. 2011).

Other specimen examined. None. A number of specimens were reported from Huon Peninsula, PNG (Tan et al. 2011), but we did not have an opportunity to examine them.

Note. Plants are slender, with “long, pendent secondary stems and branches with lax foliation, much like members of the family Meteoriaceae” (Tan et al. 1991). Long pendent shoots are sometimes encountered in other species of *Aptychella*, such as *A. brevinervis* in Cameron Highland, Malaysia and *A. formosana* in Taiwan. Other members of the Pylaisiadelphaceae, such as *Yakushimabryum subintegrum* also often have long pendent shoots. This feature gives a different appearance of this species from the other members of *Aptychella*. On the other hand, 1) rather large, decurrent, orange-purple, opaque alars of leaves and 2) perforation or thin-walled areas along the median lines of exostome teeth (Tan 1991) suggest its relationship to the genus (Tan 1991). However, the most important feature of *A. perdecurrens* is the total absence of gemmiferous caudate secondary stems as well as filamentous propagules. Thus we consider that the generic affinity of this species should be re-examined with additional molecular analysis with fresh materials. Autoicous sexuality of *A. perdecurrens* might also suggest its remote affinity to the genus.

Tan (1993) reported *Aptychella perdecurrens* from Borneo Island, Malaysia, based on a specimen (*Tan 89-303*, SING!) collected in the vicinity of Paka Cave (ca. 3000 m elev.) of Mt. Kinabalu. It is true that the plant resembles *A. perdecurrens* in the slender and long pendent shoots and differentiation of alars with cells arranged in slightly scalariform manner. However, the most-basal row of alar cells are much larger than the others and deeply colored, leaf bases are scarcely decurrent, and leaf margins are plane or slightly incurved, which clearly suggest its close affinity not to *Aptychella* but with the genus *Mastopoma*. Therefore, report of *A. perdecurrens* from Mt. Kinabalu should be excluded because of a misidentification.

5. *Aptychella planula* (Mitt.) M.Fleisch., Die Musci der Flora von Buitenzorg 4: 1671 (1923). (Figs. 2G–H, 6, and 7).

Basionym: *Stereodon planulus* Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1: 111 (1859) ≡ *Symphyodon planulus* (Mitt.) A.Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 296 (1878) ≡ *Clastobryopsis planula* (Mitt.) M.Fleisch., Musci Buitenzorg 4: 1180 (1923) ≡ *Clastobryum planulum* (Mitt.) Brühl, Rec. Bot. Surv. India 13(1): 127 (1931). Type: In Himalayae orient. reg.

temp., *J.D.Hooker 764* (syntype NY); In mont. Khasia. reg. temp., *J.D.Hooker & T.Thomson 753b* (isosyntype BM). Note: The latter isosyntype specimen, judging from the photograph presented by the web site of Natural History Museum, does not belong to *Aptychella* but resembles *Erythrodontium julaceum* because of tightly imbricate leaf arrangement in stems and branches as already indicated on an annotation label attached to the specimen sheet.

Aptychella borii Dixon, J. Bombay Nat. Hist. Soc. 39: 790 (1937). Type: Pulebudze, Naga Hills, 1850 m, 8 Aug 1935, *Dr. N.L.Bor 293d* (holotype BM), *fide* Tan & Jia (1999).

Symphyodon delicatus Broth. ex M.Fleisch., Musci Buitenzorg 4: 1180 (1923), *invalid, cited as synonym ≡ *Clastobryopsis delicata* M.Fleisch., Musci Buitenzorg 4: 1180 (1923) ≡ *Aptychella delicata* (M.Fleisch.) M.Fleisch., Musci Buitenzorg 4: 1671 (1923) ≡ *Clastobryum delicatum* (M.Fleisch.) Broth. & Dixon, Ann. Bryol. 6: 34 (1933) ≡ *Clastobryopsis planula* var. *delicata* (M.Fleisch.) B.C.Tan & Y.Jia, J. Hattori Bot. Lab. 86: 14 (1999). Type: Sikkim-Himalaya, prope Kurseong, Sepoydura Forest, 6000 ft., rarus! 17 Aug 1899, leg. *Dpcorn & Scuaur s.n.* (holotype H!; as *Symphyodon delicatus* on label; no. 2315 of Bryotheca E. Levier).

Clastobryum subplanulum Broth. ex Dixon, Ann. Bryol. 6: 33 (1933). Type: NW Himalayas, Thihri Garhwal, Kidarkanta, Jun 1904, *Bahadru s.n.*, ex Bryotheca Levier 6230 (isotype H-BR!), *fide* Tan & Jia (1999) as *Clastobryopsis planula* var. *delicata*.

Description: Plants rather shiny, yellowish green in color. Primary stems prostrate on substrata, densely branched. Gemmiferous caudate secondary stems (GCS) and turf-forming secondary stems (TFS) clearly differentiated. GCS to 2 cm in length, more or less complanately foliated, with long slender and caudate tips. Filamentous propagules abundant, smooth, 0.36–0.56 mm in length. Leaves of GCS 1.4–2.0 mm long, ovate-lanceolate, acuminate, slightly concave; margins plane all around, rarely narrowly recurved below, entire or minutely crenulate; costae short and double, often indistinct; laminal cell narrowly elongate, 30–60 μm in length, smooth, plane; alars differentiated with quadrate to short rectangular cells, usually not inflated, usually not decurrent to stems, rarely slightly decurrent. Leaves of TFS 1.1–1.2 mm in length, ovate, acuminate; costa indistinct or very short and double; margins almost entire; alars slightly differentiated with several quadrate cells, not decurrent to stems. Calyptra cucullate, naked, to 1 mm in length. Perichaetia on primary stems. Perichaetial leaves narrowly lanceolate, acuminate, ecostate. Setae 8–15 mm in length, smooth, reddish brown in color. Capsules subglobose to shortly ovoid, upright or slightly inclined, 0.8–1.4 mm in length, smooth; annuli absent; exothecial cells quadrate to hexagonal, evenly thick-walled, not collenchymatous; stomata few, 1–2 in number at capsule base. Opercula inclined, shortly rostrate, ca. 0.5 mm in length. Peristome double. Exostome teeth pale yellow, lanceolate, to minutely papillose, to 120 μm in length, with row of pores along central lines. Endostome segment filamentous, ca. 120 μm in length with low basal membrane; cilia none. Spores spherical, minutely papillose, 20–25 μm in diameter. [See also Gangulee (1980: 1833), Tan & Jia (1999: 12) and Jia et al. (2005) as *Clastobryopsis planula*.]

Previous illustration: Gangulee (1980) as *Clastobryopsis planula* based on a specimen collected in Sikkim (Kurz 2429).

Habitat: Growing on tree trunks and horizontally spreading branches of short shrubs in sparse montane thickets, preferring rather sunny spots.

Distribution: Nepal, Bhutan, Eastern India, Thailand and China (Jia et al. 2005). Tan (1991: 93) wrote that "*Clastobryopsis planula* shows a wide distribution along the Himalayan ranges extending into the Yunnan highlands of China".

Distinguishing features: 1) rather small plant size comparing to closely related *Aptychella robusta*, 2) gemmiferous caudate secondary stems well differentiated, ca. 1.5 cm in length, more or less complanately foliated, 3) forming small but dense turf-like population, 4) narrow and scarcely decurrent alars and more or less plane and indistinctly crenulate margins of GCS leaves, 5) weak differentiation of alars of TFS leaves, and 6) presence of a row of small pores along the central lines in exostome teeth (Figs. 7C & D).

Representative specimens examined. NEPAL: Junbesi, *M.Higuchi 18040* (TNS). **MYANMAR:** Chin State, Mt. Victoria, in the vicinity of Kanpetlet, 21°13' N, 93°58' E, 2460 m elev., 12 Mar 2002, *J.Murata et al. 23282-a & 23282-c* (both HYO); ibid., 2820 m elev., 9 Mar 2002, *J.Murata et al. 22344* (HYO). **THAILAND:** Chiang Mai, Doi Inthanon National Park, 15 ha permanent plot near Check Point 2, 1700 m elev., 14 Jan 2010, *H.Akiyama et al. 1121* (HYO); ibid., 18°34'08" N, 98°29'05" E, ca. 2300 m elev., 15 Jan 2010, *H.Akiyama et al. 1173* (HYO).

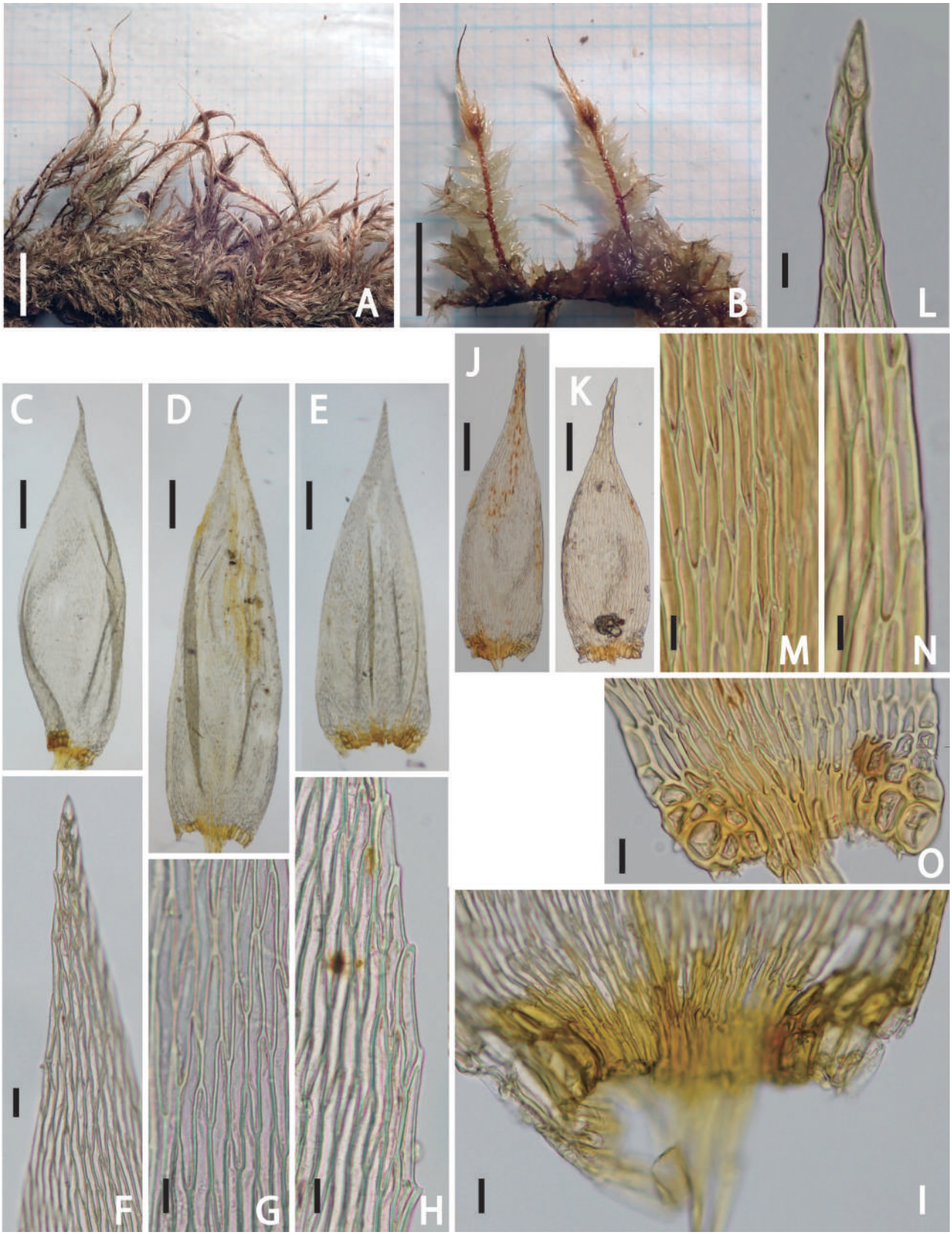

Figure 6. *Aptychella planula*. A–I: *H.Akiyama et al. 151*. J–O: *M.Higuchi 18040.*

A: Plant (dry). B: Close-up of gemmiferous caudate secondary stems (wet). C–I: Leaves of gemmiferous caudate secondary stems. J–O: Leaves of turf-forming secondary stems. F and L: Leaf apices. G and M: median laminal cells. H and N: Upper leaf margins. I and O: Alars. Scales: A and B = 5 mm; C–E, J and K = 0.2 mm; Others = 20 µm.

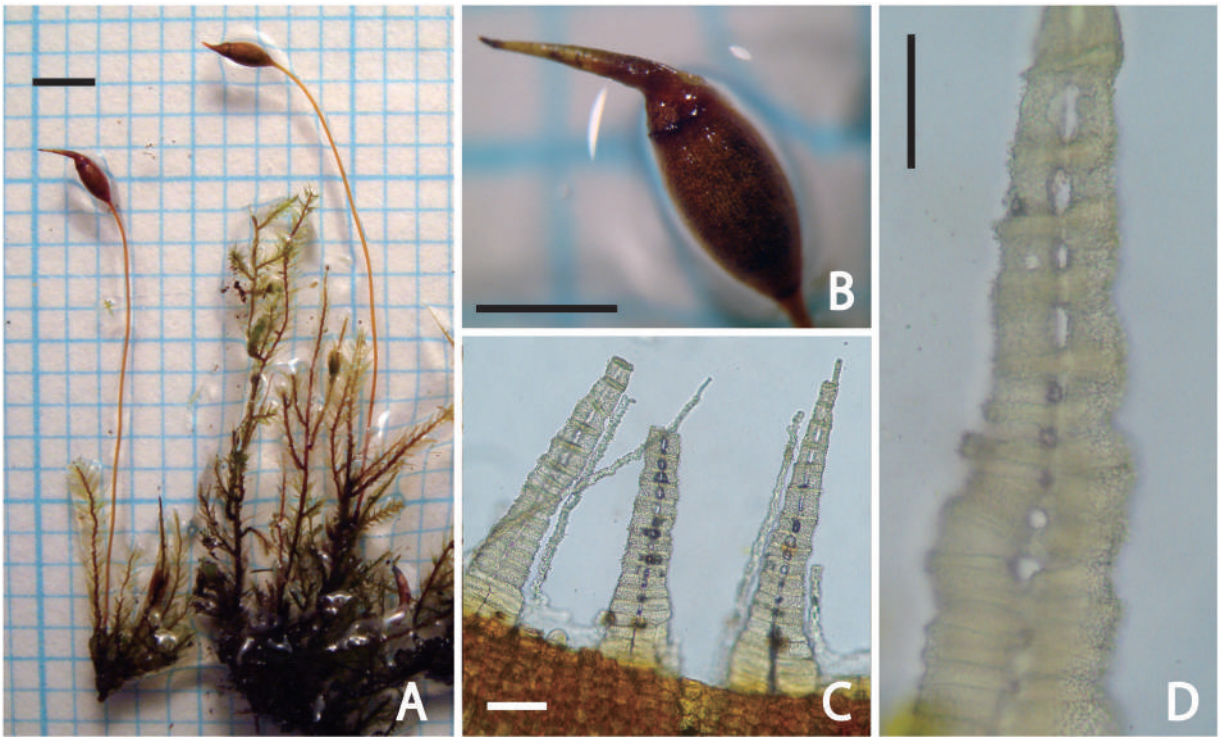

Figure 7. Sporophytes of *Aptychella planula*. All from *H.Akiyama et al. 1348*.
A: Wet plant with sporophytes. B: Close-up of theca with rostrate operculum covered by a cucullate and naked calyptra. C: Peristome with lanceolate exostome teeth and filamentous endostome segments. D: Close-up of exostome tooth with distinct perforation along the central line. Scales: A = 2 mm. B = 1 mm. C and D = 20 μm.

Note. Since we did not examine type materials of *Aptychella planula*, we tentatively follow the concept presented by Tan (1991) and Jia et al. (2005). According to them, *A. planula* can be well circumscribed by subplicate and scarcely decurrent leaves with almost plane margins and weak serration near the apices. On the other hand, closely related *A. robusta* has non-plicate and broadly decurrent leaves with conspicuously recurved, markedly toothed margins. In addition, *A. planula* differs from *A. robusta* in smaller plant size, weak recurved leaf margins and plane leaf apices especially in GCS leaves. They also differ in distributional patterns; *A. planula* has been known from Himalaya regions, while *A. robusta* has been known from warm temperate regions of Southeast and Far East Asia.

Tixier (1977) treated *Aptychella planula* as a synonym of *A. robusta*. However, Tan & Buck (1989), Tan (1991), and Tan & Jia (1999) did not accept this synonymy, and it is also followed here because these two species can be distinguished in morphologies and distribution areas as Tan & Jia (1999) well pointed out.

Tan & Buck (1989) pointed out that there was a vertical chain of small pore-like perforation at the center of exostome teeth of *Aptychella planula*. We confirm such structures in some specimens of the species collected in northern Thailand (Fig. 7). While, Dixon (1933) wrote about the peristome feature based on the isotype specimen of *Clastobryum delicatum* as follows; "peristomii omnino fere laevibus, pellucidis. Seta ad 1–1.25 cm. longa, pertenuis, flexuosa. Endostomium?". Tan & Jia (1999) treated *A. delicata* as a variety under *C. planula* and made a new combination as *C. planula* var. *delicata* (M.Fleisch.) B.C.Tan & Y.Jia because of the difference in their peristome structure. However, we tentatively follow Tan (1991) who treated *A. delicata* as a synonym of *A. planula*.

Nematode galls are found at apices of turf-forming secondary stems from one of the specimens of *Aptychella planula* collected at Doi Inthanon, northern Thailand (*H.Akiyama & N.Printarakul 1525*, HYO; Akiyama unpublished).

6. *Aptychella robusta* (Broth.) M.Fleisch., Die Musci der Flora von Buitenzorg 4: 1671 (1923). (Figs. 2E–F and 8)

Basionym: *Clastobryum robustum* Broth., Philippine J. Sci. sect. C, Bot. 5: 155 (1910) ≡ *Clastobryopsis robusta* (Broth.) M.Fleisch., Musci Buitenzorg 4: 1181 (1923). Type: Philippines, Luzon, Province of Benguet, Mount Pulog, Bur. Sci. 8912, *McGregor s.n.* (holotype H!).

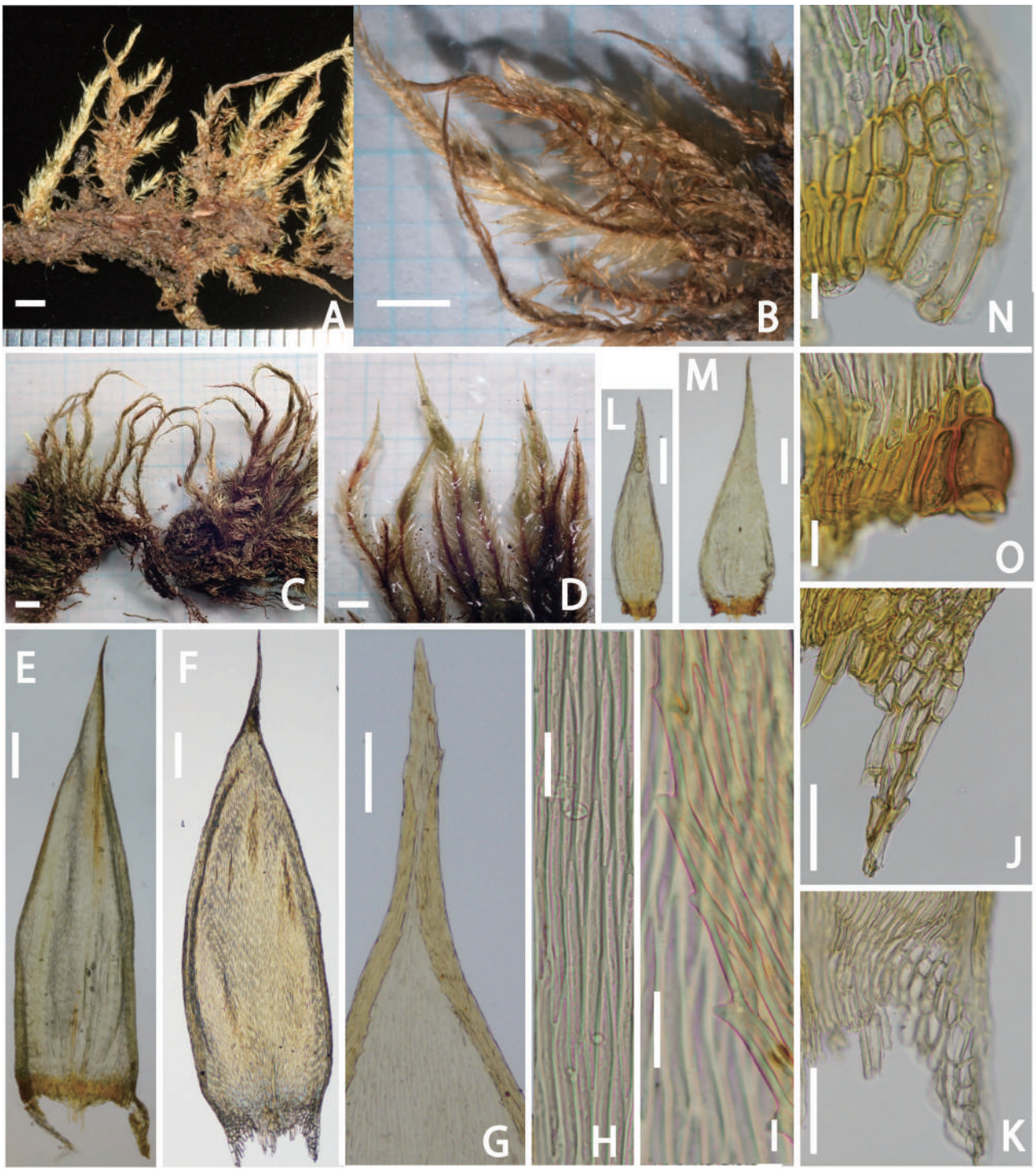

Figure 8. *Aptychella robusta.* C, D, M and N from *J.R.Shevock et al. 51483*, L and O from *H.Akiyama 25118*, and others from the holotype. A, B and C: Plants (dry). D: Plant (wet). E–K: Leaves of gemmiferous caudate secondary stems. L–O: Leaves of turf-forming secondary stems. E–F: Leaves with distinct revolution at margins. G: Grooved leaf apex. H: Median laminal cells. I: Upper leaf margin with sharp serration. J, K, N and O: Alars. Scales: A–D = 2 mm. E, F, L and M = 0.2 mm. G, J and K = 0.1 mm. H, I, N and O = 20 μm.

Synonyms: *Clastobryopsis heteroclada* M.Fleisch., Musci Buitenzorg 4: 1181 (1923) ≡ *Aptychella heteroclada* (M.Fleisch.) M.Fleisch., Musci Buitenzorg 4: 1671 (1923). Type: Indonesia, West Java, Gepfel des Pangerango, 3000 m, *M.Fleischer s.n.* (syntype FH); am Gedeh um Kandang Badak, 2500 m, *M.Fleischer s.n.* (syntype FH!), *fide* Tan & Buck (1989), Tan & Jia (1999).

Description: Plants light green to yellowish green, forming turf on substrata. Primary stems prostrate on substrate, densely branched. Gemmiferous caudate secondary stems (GCS) well differentiated, to 1.5–2.0 cm in length, slender and with caudate tips curved when dry, straight when moist, sparsely branched at base. Turf-forming secondary stems (TFS) mostly less than 0.5 cm in length, crowded, with short branches. Filamentous propagules numerous with rectangular smooth cells, ca. 0.6 mm in length. Leaves of GCS narrowly ovate, gradually acuminate into narrow apices, 1.6–2.2 mm in length, slightly concave, deeply involute and becoming canaliculate at apices (Fig. 8G), distinctly decurrent to stems at bases; margins more or less recurved all around, distinctly serrulate above; costae short and double; laminal cells linear, smooth, 60–100 μm in length; alars well differentiated with quadrate to rectangular cells arranged in scalariform manner. Leave of TFS similar in shape, much smaller, 0.8–1.2 mm in length; costae very short and double, often indistinct; margins narrowly recurved, serrulate above, alar regions small, with quadrate to rectangular cells, sometimes with a few inflate, reddish brown cells arranged in a single row. Sporophytes not observed. Also see Fleischer (1923: 1181, as *Clastobryopsis heteroclada*), Bartram (1939: 313), Noguchi et al. (1994: 1084), Tan & Jia (1999: 15, as *C. robusta*) Jia et al. (2005: 26, as *C. robusta*), and Tan et al. (2011: 13, as *C. robusta*).

Previous illustration: Fleischer (1923; as *Clastobryopsis heteroclada*), Bartram (1939; fig. 398), Noguchi et al. [1994; Figure 477a, but also see Akiyama (2017b)], Jia et al. (2005).

Habitat: Growing on stems, laterally or upwardly extending branches of small shrubs and short trees at rather open, windy places in montane forests. In Yakushima Island, this species forms dense population on branches of short shrubs at sunny places along a road.

Distribution: Widely distributed in Southeast and East Asia. Tan et al. (2011) reported this species from Papua New Guinea, but we did not have a chance to examine the voucher specimens.

Distinguishing features: 1) well differentiated and long GCS, 2) clear difference in shape and size between leaves of GCS and TFS, 3) narrowly acuminate and distinctly involute leaf apices, 4) distinctly serrate upper leaf margins, 5) long decurrent alars of GCS leaves, and 6) alars of smaller TFS leaves often with a single row of inflated and colored cells at base as in the case of Sematophyllaceous species.

Representative specimens examined. CHINA: Yunnan Prov., Wenshan Co., Maguan, Dulong, Laojunshan Mts., 22°56'31.65" N, 104°32'34.39" E, 1966 m elev., 28 Oct 2016, *Y.Ying-Ying 3900* (PE); ibid., Teng-Chong Co., Western slope of the Gaoligonshan. Guyong Forest Farm, Lunma He Field Station, 25°29'47.0" N, 98°19'34.7" E, 2980 m elev., 29 Apr 2015, *J.R.Shevock et al.* 46510 (CAS, KUN). Guizhou Prov., summit of Sun Mountain, 1500 m elev., 13 May 2003, *Ka 01228* (PE). **JAPAN:** Kagoshima Pref., Yaku-cho, Yakushima Isl., in the vicinity of the entrance of Yodogawa trail, 30.301427° N, 130.531043° E, 1300 m elev., 30 Aug 2017, *H.Akiyama 25118* (HYO); ibid., between the entrance of Yodogawa trail and Yodogawa lodge, 30.3006° N, 130.5352° E, 1350–1410 m elev., 1 Sep 2017, *H.Akiyama 25183, 25172* and *25178* (all HYO); ibid., 30°18'12" N, 30°32'00" E, 1300 m elev., 28 Aug 2016, *N.Hayashida s.n.* (HYO). **TAIWAN:** Pintung Co., Beidawu Mountain National Trail, along the trail above the junction with the trail to Kuaigu Inn at 4 km trail marker, 22°36'51.0" N, 120°44'32.0" E, 2250 m elev., 27 Apr 2018, *J.R.Shevock et al. 51483* (CAS, HYO, TAIE); Taichung City, Heping Dist., Dasyueshan National Forest Recreation Area, along a trail between Police Station to Small Sacred Tree, 24°15'26"N, 121°00'32"E, 2200 m elev., 10 Oct 2013, *H.Akiyama 23272* (HYO); Nantou Co., Sun-Link-Sea Forest Recreation Area, along a Yueling Trail from the Nature Education Center toward Chinglong Waterfall, 23°38'16.0" N, 120°47'16.7" E, 1650 m elev., 28 Oct 2018, *J.R.Shevock et al. 53500* (CAS, HYO, TAIE). Hsinchu Co., Yuanyang Lake Natural Reserve, slope above Mandarin Duck Lake, 24°34'39.5" N, 121°24'29.7" E, 1680 m elev., 30 Oct 2018, *J.R.Shevock et al. 53526* and *53545* (both CAS, HYO, TAIE). **PHILIPPINES:** Mindanao, Mt. Kitanglad, 9 Sep 2007, *Azuelo et al. s.n.* (HYO, UC).

Note. Close resemblance in outer morphologies between *Aptychella robusta* and *A. planula* was already pointed out in details by previous authors (Tan & Buck 1989, Tan 1991, Tan & Jia 1999). According to them, well-developed leaf alars with long decurrence to stems of *A. robusta* is a good feature to distinguish it from *A. planula*. In addition, *A.*

robusta is distributed in Southeast and southern part of East Asia, while *A. planula* restricted to the Himalayan regions. Although Tixier (1977) treated *Clastobryopsis heteroclada* as a synonym of, not *A. robusta*, but *A. planula*, it is not followed here. According to our observation, deep canaliculate leaf apices in GCS leaves and distinct recurved margins with distinct serration are also good features to separate them. A number of specimens were reported from China (Jia et al. 2005: 25) by the name of *Clastobryopsis planula* and *C. robusta* (Jia et al. 2005), but their identity need critical re-examination because of high species diversity found in *A. robusta s. lat*.

Aptychella robusta (as *Clastobryopsis robusta*) was once reported from the Hawaiian Islands (Staples et al. 2004, Hoe 1973 and others) based on misidentification of *Aptychella hawaiica*, which was recently described as new species by Akiyama & Shevock (2019).

Zanten (1964) reported *Aptychella robusta* from New Guinea and stated that "the stems are sometimes up to 10 cm long". In addition, *A. robusta* was also reported from Huon Peninsula, Papua New Guinea as *Clastobryopsis robusta* (Tan et al. 2011) and they listed a total 13 specimens. We did not have an opportunity to examine these specimens and thus re-examination of New Guinean specimens of *A. robusta* are highly needed to confirm their identity. Considering high species diversity in the genus in SE and East Asia found in *A. robusta s. lat.*, they may represent different taxa.

Tixier (1977) treated *Aptychella robusta* as a synonym of *A. proligera*, but it is not supported by molecular and morphological attributes, and therefore, we do not follow his treatment.

Aptychella robusta has been reported from disjunctive localities in southwestern Japan. They are treated here as new taxa (*A. minutissima*, *A. rubiginosa*, *A. viridis* and *A. yakumontana*) except the true *A. robusta* collected in Yakushima Island. As a result, total four species of *Aptychella*, such as *A. brevinervis*, *A. robusta*, *A. rubiginosa* and *A. yakumontana*, have been documented for Yakushima Island, Japan. They are differentiated by habitat preference; *A. brevinervis* and *A. rubiginosa* often grow at rather sunny and open, windy places at forest edges, while *A. robusta* and *A. yakumontana* prefer a little darker places in sparse mixed forests. In addition, the latter two have similar plant appearance and thus it is often difficult to distinguish them in the field. Narrower GCS leaves and well differentiated alar regions of TFS leaves of *A. yakumontana* can be used to separate them under a microscope observation.

There are two specimens listed below that have a typical *Aptychella robusta* morphology but have shorter (less than 0.3 mm in length) filamentous propagules with short, rather thick-walled cells. Unfortunately, we were not able to add them into our molecular phylogenetic analysis, and thus cannot confirm their identity. In the Pylaisiadelphaceae, similar case of infrageneric variation in propagule morphology has been reported in the genus *Yakushimabryum* (Akiyama 2017a).

Specimens examined. **CHINA:** Sichuan Prov., Ya'an City, Tianquan Co., River Labahe Natural Reserve, along the Guanfanggou Valley, 30°09'42"–10'33" N, 102°28'33" –27'51" E, 1876–2617 m elev., 26 Jun 2015, *Narengaowa Z597* (PE); ibid., O'mei-shan city, O'mei-shan, summit area, 29°40' N, 103°20' E, 2900 m elev., 1 Jul 1992, *H.Akiyama 10147* (HYO, SING).

Aptychella heteroclada was described by Fleischer (1923) and he offered a good illustration of the species. We examined the type specimen kept at Farlow Herbarium (FH) and found that it includes plants showing long, drooping secondary stems. The tendency to droop in secondary stems is common in *Aptychella* (e.g., *A. formosana* and *A. brevinervis*), and we consider it is appropriate to treat such plants with long pendent secondary stems as mere intraspecific variation of *A. robusta.* (In addition, such plants are often confused with smaller *Acroporium* species that have similar drooping secondary stems). The following specimen is a good example [INDONESIA, West Java, am Gede, 2000 m, 14 Jul 1898, *M.Fleischer s.n.* (FH; stored as *Clastobryum heteroclada* M.Fleisch.)].

7. ***Aptychella rubiginosa*** H.Akiyama, N.Printarakul & N.Hayashida, ***sp. nov.*** (Figs. 3A-D and 9)

Diagnosis: Similar to *Aptychella robusta*, but gemmiferous caudate secondary stems (GCS) reaching 3 cm in length, with lateral long branches, stems markedly colored in reddish brown, and alars with large, inflated reddish brown cells arranged in 1–2 rows at bases.

Type: Japan, Kagoshima Pref., Kumage-gun, Yaku-cho, Yakushima Isl., Arakawa forest road, in the vicinity of the entrance of Yodogawa trail, 30.30745° N, 130.54008° E, 1230 m elev., 5 Mar 2013, *H.Akiyama 22760* (holotype HYO, isotypes CAS, NICH).

Description: Plants rough in texture, more or less shiny, yellowish green in color. Primary stems densely and pinnately branched. GCS well differentiated, reaching 3 cm in length, with several long lateral branches at

bases; stems colored in reddish brown. Turf-forming secondary stems (TFS) sparse. Filamentous propagules numerous, with smooth rectangular cells. Leaves of GCS 1.4–1.8 mm long, lanceolate to narrowly ovate below, gradually narrowed into somewhat ligulate apices; costae short and double; margins recurved less than 1/2 of leaf length, plane and minutely serrulate above; median laminal cells linear, smooth, 60–80 μm in length; alars well developed but hardly decurrent, with colored reddish brown, thick-walled fusiform to long rectangular cells arranged in 1–2 rows at base, and several smaller quadrate to rectangular cells above. Leaves of TFS lanceolate, 1.0–1.2 mm in length, often concave; costae indistinct or very short and double; margins plane or narrowly recurved below, distinctly serrulate above; median laminar cells similar to those of GCS leaves; alars well developed with inflate, colored cells arranged in 1–2 rows, just similar to those of GCS leaves. Dioicous. Perichaetia born on the basal to middle parts of ascending GCS. Perichaetial leaves ca. 1 mm in length, with narrow base, narrowly acuminate; ecostate; margins plane, serrulate. Perichaetia with 6–8 archegonia, paraphyses absent. Sporophytes not observed.

Habitat: On shrub branches at rather open and windy places in montane forests. Often intermingled with *Aptychella brevinervis* in Japan.

Distribution: Thailand, China and Japan.

Distinguishing features: 1) long and basally branched GCS reaching 3 cm in length, 2) reddish brown color of stems, 3) well marked alars with inflated and colored cells arranged in 1–2 rows at bases.

Other specimens examined. THAILAND: Chiang Mai, Doi Inthanon, Ank Ka trail, 2500 m elev., 2011 Mar 11, *H.Akiyama & N.Printarakul 1500* (HYO); ibid., 2280 m elev., 20 Jan 2010, *H.Akiyama et al. 1348* (HYO). **CHINA**: Yunnan Prov., Zhao-tong Dist., Cheng-siung around Niu-chang-bau, 2100 m elev., 17 Jul 1992, *H.Akiyama 10345-a* (HYO). **JAPAN:** Kagoshima Pref., Kumage-gun, Yaku-cho, Yakushima Isl., side branch of Arakawa forest road, 30.30745° N, 130.54008° E, 1230 m elev., 5 Mar 2013, *H.Akiyama 24746* (HYO; same locality of the type); ibid., in the vicinity of the entrance of Yodogawa trail, 30.2964° N, 130.5706° E, 1150 m elev., 1 Sep 2016, *H.Akiyama 24780* and *24786* (both HYO); ibid., 30.8028° N, 130.5525° E, 1170 m elev., 1 Sep 2016, *H.Akiyama 24817* and *24819* (both HYO); ibid., in the vicinity of Yodogawa lodge, 30.3005° N, 130.5241° E, 1380 m elev., 1 Sep 2017, *H.Akiyama 25185, 15190, 25191* and *25193* (all HYO).

Note. In Yakushima Island, southwestern Japan, there are a total of three species of *Aptychella* that have short and double costae; they are *A. rubiginosa*, *A. robusta* and *A. yakumontana*. The latter two grow in rather dimly lit places of montane forests, while *A. rubiginosa* grows densely on the branches of shrubs along forest roads in open and sunny places where the view of the sky is not influenced by tall trees. It can be easily identified in the field by noting the difference in such habitat characteristics as well as remarkably larger size of gemmiferous caudate secondary stems of *A. rubiginosa*.

8. *Aptychella subdelicata* Broth., Symbolae Sinicae 4: 117 (1929). (Fig. 13A)

Type: China, Northwestern Yunnan, *Handel-Mazzetti 9095* (holotype H-BR!).

Description: Plants small, forming a thin turf on substrata. Primary stems shortly prostrate on substrata, pinnately branched. Gemmiferous caudate secondary stems (GCS) to 1.5–2 cm in length, sparsely branched. Turf-forming secondary stems (TFS) short, to 1 cm in length, pinnately branched. Filamentous propagules numerous, to 0.6 mm in length, with rectangular, smooth cells. Leaves of GCS patent, narrowly lanceolate, long acuminate, often involute above, reaching 1.4 mm in length, narrowly decurrent to stems at bases; costae short and double; margins narrowly but distinctly recurved except apices; laminal cells linear, 70–80 μm in length, smooth; costae short and double; alars differentiated, often with a number of quadrate cells arranged in a scalariform manner, sometime with inflated colored rectangular cells arranged in two rows with much smaller quadrate cells above. Leaves of TFS similar to those of GCS in shape but smaller and with less differentiated alars. Dioecious? Perichaetial leaves lanceolate, acuminate; costae indistinct. Setae ca. 1 cm in length, smooth, pale reddish brown in color. Capsules ovoid. [Sporophytic features are after Dixon (1933), Brotherus (1929), and Gangulee (1980)].

Previous illustration: Gangulee (1980; Fig. 931).

Habitat: Growing on stems and branches of shrubs in filtered light, dense mixed hardwood forests.

Distribution: China.

Distinguishing features: 1) narrowly lanceolate, short GCS leaves reaching to 1.4 mm in length, 2) weak but distinct recurved leaf margins, and 3) long decurrence at leaf bases.

Other specimens examined. CHINA: Guangxi Prov.,

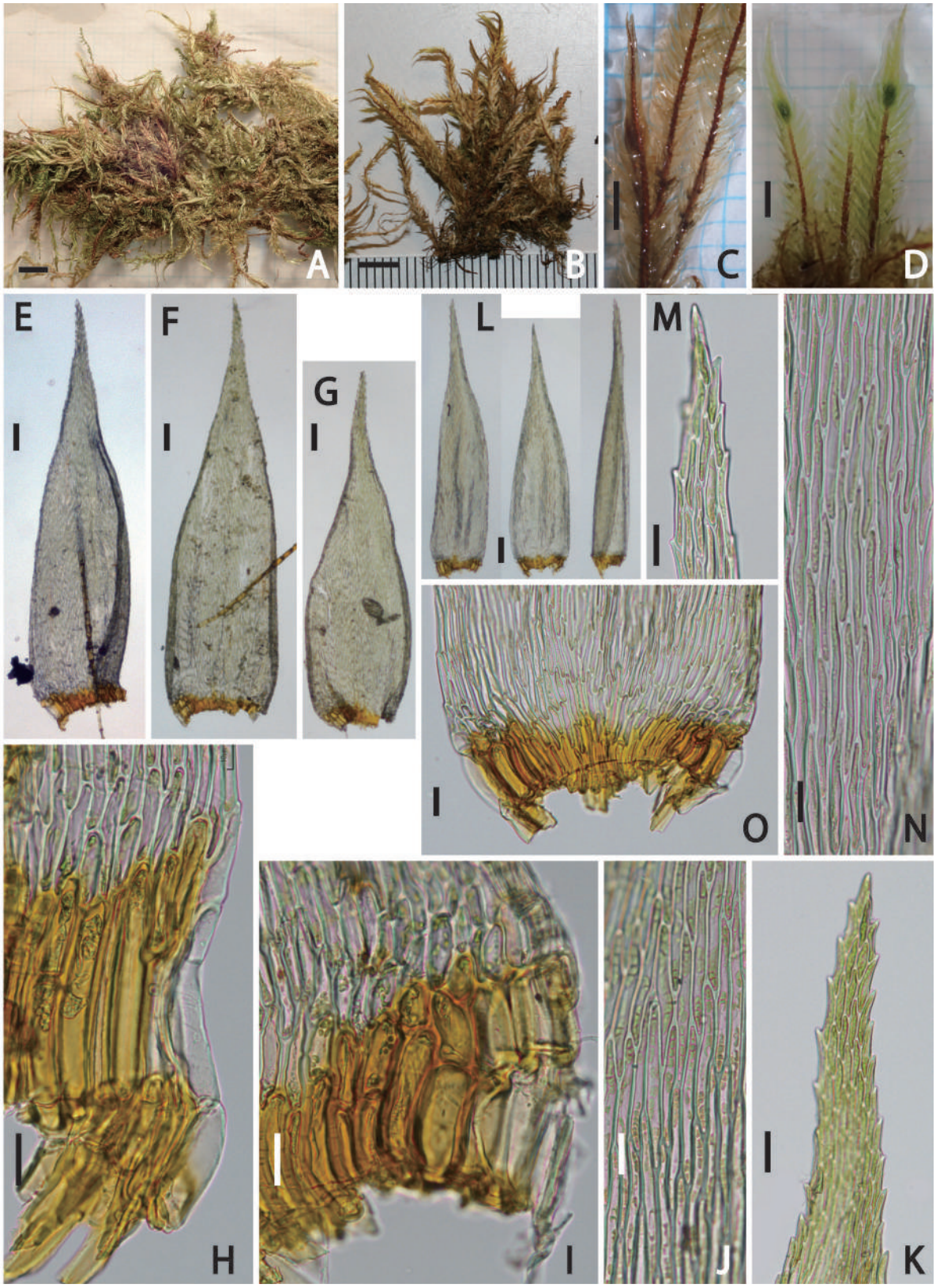

Figure 9. *Aptychella rubiginosa.* All from the holotype.

A and B: Plants (dry). C: Close-up of branching gemmiferous caudate secondary stems (wet) with perichaetia at basal portion. D: Upper part of gemmiferous caudate secondary stems. E–K: Leaves of gemmiferous caudate secondary stems. L–O: Leaves of turf-forming secondary stems. H, I and O: Alars. K and M: Leaf apices. J and N: Median laminal cells. Scales: A and B = 5 mm. C and D = 2 mm. E–G, L and M = 100 μm. O, M and N = 20 μm.

Long Sheng, 1500 m elev., 15 Aug 1964, *Wu 538* (MO). Yunnan Prov., Meng Hai, 1350 m elev., 21°50'00" N, 101°50'00" E, 1 Mar 1957, *W.-X.Xu 6289* (MO): Yunnan Prov., Gong-shan Co., Cikai Xiang, 26 Sep 2007, *J.R.Shevock et al. 30782* (CAS, E, HYO, KUN, MO); ibid., Teng-Chong Co., Western slope of the Gaoligongshan, 2.6 km above Danzha Forestry Farm Headquarters, 2685 m elev., 25°34'01.6" N, 98°11'48.7" E, 25 Apr 2015, *J.R.Shevock et al. 46424* (CAS, KUN): ibid., headwaters of the Lingjiatang River, Mingguang Forestry Farm, 25°44'09.7" N, 98°29'15.6" E, 2350 m elev., 6 May 2015, *J.R.Shevock et al. 46646* (CAS, KUN).

Note. Tixier (1977) treated *Aptychella handelii* Broth. as a synonym of *A. subdelicata.* The isotype specimen deposited in H-BR (China, Northwestern Yunnan, *Handel-Mazzetti 9367*), however, includes only a scanty amount of poorly developed shoots. Judging from the shape of alar cells of the leaves, it does not belong to the Pylaisiadelphaceae, but to some species of the Hypnaceae. We would like to propose to treat *A. handelii* as ***nom. dub.,*** though we were not able to locate the holotype. Tixier (1977) also treated *Clastobryum excavatum* Broth. as synonyms of *A. subdelicata*, which is not followed here.

Tixier (1977) regarded *Aptychella subdelicata* as a distinct species in the genus. On the other hand, Tan (1991) treated this species as a synonym of *Aptychella planula*. Later, Tan & Jia (1999: 14) proposed to treat *A. delicata* as a variety of *A. planula* and wrote that "The type of *Aptychella subdelicata* Broth. from Yunnan is the only Chinese specimen of *Clastobryopsis planula* var. *delicata* that we saw. *Clastobryopsis planula* var. *delicata* is also known from Sikkim and India (Gangulee 1980)." We do not follow their idea and treat *A. subdelicata* as a distinct species based on the present molecular analysis. This species, however, is quite similar to *A. robusta*, for example in leaf shape, distinctly recurved leaf margins and alar shape, and it is not easy to separate *A. subdelicata* and *A. robusta* only by morphological features.

According to Tixier (1977), the type specimen of *Aptychella subdelicata* bears peristomate capsule, which we were not able to confirm. Tixier (1977) wrote that "Seta ca. 1.3 cm. Capsules 2 mm in length. Peristome double. Exostome teeth ca. 300 μm in height. Endostome segments filamentous, of same height, split at top; basal membrane almost absent".

9. *Aptychella triangularis* H.Akiyama & Shevock, ***sp. nov.*** (Fig. 10)

Diagnosis: Similar to *Aptychella robusta*, but leaves of gemmiferous caudate secondary stems (GCS) short triangular to widely ovate with distinct decurrence at bases and rather long costae.

Type: China, Sichuan Prov., Tianquan Co., Ya'an, River Labahe Natural Reserve, along the wooden trestle of scenic spot, 30°10'55"–11'37" N, 102°25'03"–25'48" E, 2288–2569 m elev., 27 Jun 2015, *Narengaowa Z677* (holotype PE).

Description: Plants epiphytic, forming a dense turf. Primary stems prostrate, pinnately branched, reddish brown to pale brown in color. GCS well differentiated, sparsely branched at base, simple above, to 2.4 cm in length. Turf-forming secondary stems (TFS) sparsely or densely pinnately branched, to 0.5 cm in length. Filamentous propagules numerous, to 1.1 mm in length, with rectangular smooth cells. Leaves of GCS triangular to widely ovate, narrowly acuminate, widely decurrent to stems at bases; margins narrowly recurved except near apices and basal portion, entire to weakly crenulate above, entire below; costae double, reaching to 1/3 of leaf length; laminal cells linear, thin-walled, plane, 50–70 μm in length; alars well differentiated with pale green to pale reddish brown, thin-walled, quadrate to short rectangular cells arranged in a scalariform manner. Leaves of TFS much smaller than those of GCS, ovate, acuminate to narrowly acuminate, slightly concave, 0.5–0.9 mm in length, hardly decurrent to stems at bases; costae indistinct; margins mostly plane, sharply serrate above; alars weakly differentiated, with several thick-walled, reddish brown, quadrate to rectangular cells. Sexual organs and sporophytes unknown.

Habitat: Growing on rotten wood in upper montane evergreen broad-leaved forests.

Distribution: China.

Distinguishing features: 1) short triangular to widely ovate GCS leaves, 2) wide and distinct decurrence at bases of GCS leaves with quadrate to short rectangular, thin-walled cells arranged in a scalariform manner, 3) long (to 1/3 of leaf length) and double costae of GCS leaves, 4) smaller TFS leaves with sharply serrate upper margins.

Other specimen examined. CHINA: Yunnan Prov., Fenshuiling Nat. Nature Reserve, 2411 m, 25 Aug 2013, *J.Wang et al. 20130825-26* (HSNU; intermingled with small amount of *Aptychella brevinervis*).

Note. Our present molecular analysis suggests that *Aptychella triangularis* becomes a sister to all other clades

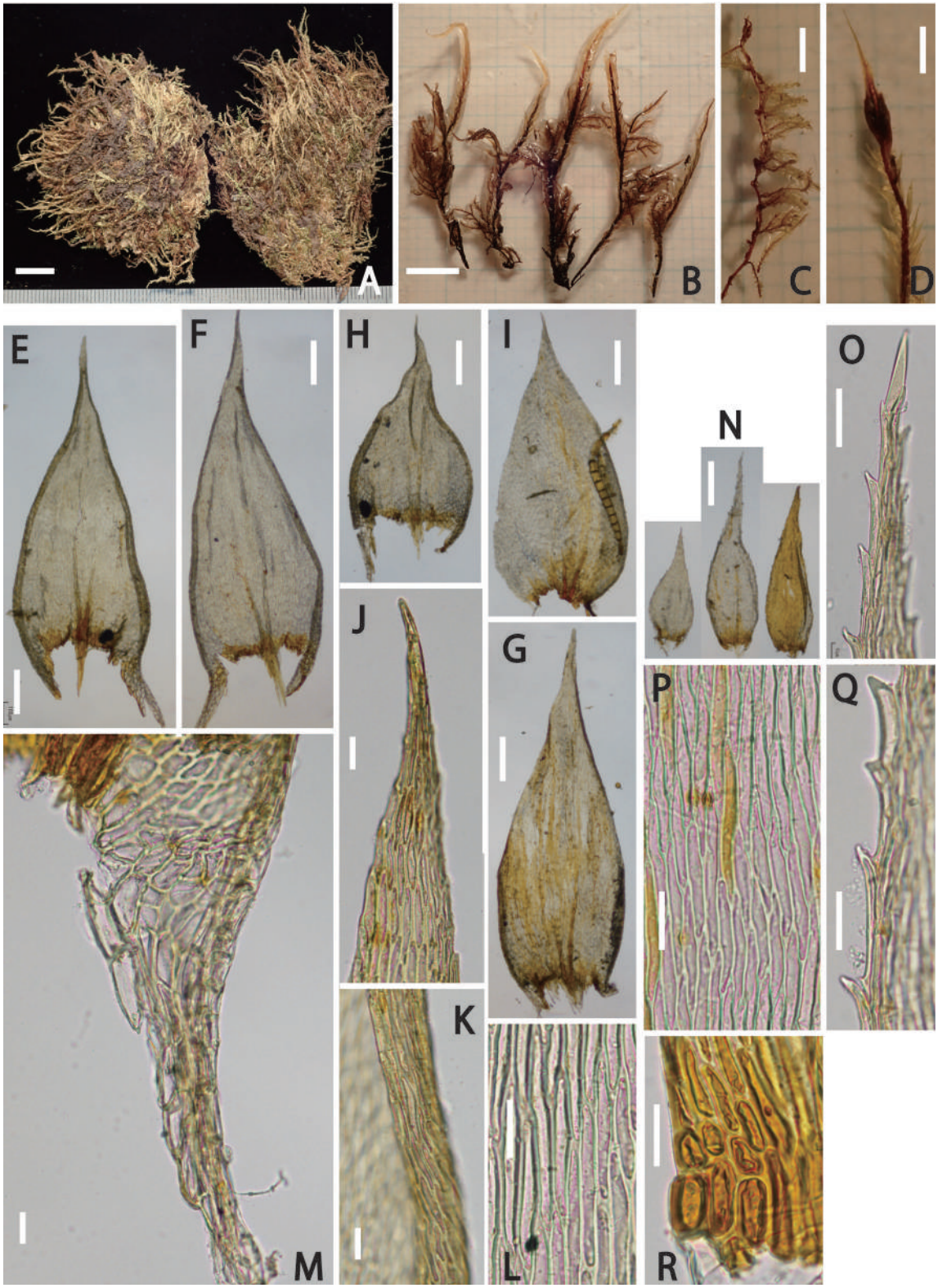

Figure 10. *Aptychella triangularis*. All from the holotype.

A: Plants (dry). B: Gemmiferous caudate secondary stems (wet). C: Pinnately branched stoloniferous primary stem and short turf-forming secondary stems (wet). D: Upper part of gemmiferous caudate secondary stems (wet). E–G and J–M: Leaves of upper part of gemmiferous caudate secondary stems. H and I: Leaves of lower part of gemmiferous caudate secondary stems. N–R: Leaves of turf-forming secondary stems. J and O: Leaf apices. K and Q: Upper leaf margin. L and P: Median laminal cells. M and R: Alars. Scales: A and B = 5 mm. C and D = 2 mm. E–I, N and O = 0.2 mm. J–M and O–R = 20 μm.

of *A. robusta s. lat.* (except *A. yakumontana*). This species mostly resembles to *A. formosana*, newly described species from Taiwan, in triangular to wide ovate leaf shape of gemmiferous caudate secondary stems with wide decurrent bases. However, the latter differs not only in distribution area but also in the shorter costae.

10. *Aptychella viridis* H.Akiyama, ***sp. nov.*** (Figs. 3E–F and 11)

Diagnosis: Closely related to *Aptychella robusta*, but leaves of gemmiferous caudate secondary stems (GCS) shorter 1.2–1.6 mm in length, less sharply acuminate, with shorter median laminal cells, crenulate and plane upper margins, and less developed alar regions.

Type: Japan, Kochi Pref., Kamiuke-gun, Kumakougen-cho, summit area of Mt. Myojin, 33.575° N, 133.048° E, ca. 1500 m elev., 3 Jun 2014, *H.Akiyama 23724* (holotype HYO, isotypes CAS, NICH).

Description: Plants vividly green in fresh condition, becoming pale brownish green when old, forming thin turfs on substrata. Primary stems stoloniferous, densely branched. GCS clearly differentiated, mostly simple, to 2.5 cm in length. Turf-forming secondary stems (TFS) 0.5–1.2 cm in length, sparsely branched. Filamentous propagules numerous, ca. 0.5 mm in length, with rectangular smooth cells. Leaves of GCS ovate-lanceolate, usually long acuminate, sometimes acute, 1.2–1.6 mm in length, slightly concave, often shallowly plicate; costae short and double, often indistinct, but sometimes reaching 1/4 in leaf length; margins narrowly recurved, often more or less canaliculated near apices, crenulate above, entire below; median laminal cells linear, more or less thick-walled, 60–80 μm in length; alars well differentiated, with quadrate to rectangular, more or less inflated, thin-walled cells, in pale reddish brown color, narrowly decurrent to stems. Leaves of TFS similar in shape to those of GCS, but much smaller, 0.6–0.9 mm in length, usually deeply involute above; alars weakly differentiated with less than ten quadrate to rectangular cells, weakly colored in pale reddish brown, not decurrent to stems. Sexual organs and sporophytes unknown.

Habitat: It often grows on the branches and trunks of small shrubs in sparse and windswept montane forests, or on thin branches in dense short shrubs in grassland at upper elevations. Arikawa et al. (2006a) reported *Aptychella viridis* as *A. robusta* from Kanagawa Prefecture, Japan and pointed out that “The fact that this species is found only on ridges that are exposed to winds blowing across the ocean from the south is interesting because it suggests how this species invaded and established itself ".

Distribution: Endemic to central and southwestern Japan.

Distinguishing features: 1) young plants in vivid green color, 2) short GCS leaves ranging from 1.2–1.6 mm in length, 3) distinctly recurved leaf margins with weak crenulation above, and 4) usually deeply involute, small TFS leaves, with weak differentiation of alars.

Other specimens examined. JAPAN: Kanagawa Pref., Hakone, en route from Komagatake to Owakudan via Kamiyama, 3 Aug 1980, *Z.Iwatsuki 8524 & 8536* (NICH); ibid. Mt. Komagatake, 35.2325° N, 139.0189° E, 1400 m elev., 28 Nov 1992, *H.Akiyama s.n.* (HYO); ibid., en route from Mt. Komagatake to saddle of a hill at 1240 m elev., 1240–1320 m elev., 18 Jul 2013, *H.Akiyama 23056* (HYO). Shizuoka Pref., Izu-shi, Mt. Amagi, south of Hacchoike Pond, Aosuzudai, 34°50'29" N, 138°57'58" E, 1210 m elev., Nov 29 2012, *M.Higuchi 51070* (TNS). Kochi Pref., Kamiuke-gun, Kumakougen-cho, summit area of east slope of Mt. Myojin, 33.5756° N, 133.0481° E, 1480 m elev., 17 Jul 1992, *H.Deguchi 21503* (HYO, KOCH, NICH); ibid., Mt. Myojin, 33.575° N, 133.048° E, ca. 1500 m elev., 3 Jun 2014, *H.Akiyama 23725, 23726, 23727, 23728,* and *23735* (all HYO). Ehime Pref., Kamiukena-gun, Yanadani-mura, Tengu-kogen plateau, 33.4794° N, 133.0099° E, 1300–1480 m elev., 23–24 Aug 1978, *Z.Iwatsuki & H.Kiguchi 5336* (NICH). Miyazaki Pref., Mt. Osuzu, 1200–1400 m elev., Nov 1950, *Y.Kuwahara 638 & 639* (NICH); Nishimera-mura, Mt. Ichifusa, 32.3075° N, 131.1053° E, 1540 m elev., 31 Oct 2016, *M.Matsumoto 20161031-1* and *20161031-2* (both HYO); ibid., ca. 9th station to the top of Mt. Ichifusa, 21 May 2019, *H.Akiyama & M.Matsumoto 26004, 26005, 26006-a, 26007* and *26010* (all HYO).

Note. Plants collected widely from Japan (from central Honshu to southern Kyushu, excluding Yakushima Island) have been identified previously as *Aptychella robusta*, but they are in fact *A. viridis* except those reported from Mt. Ichifusa, Miyazaki Pref. Vividly green color of young plants are distinctive in *A. viridis*. However, when becoming older or growing at windy and sunny places, plant color becomes more brownish yellow.

According to our field observations, *Aptychella viridis* and *A. minutissima* were found coexisting (but not forming mixed population) in the same location of Mt. Ichifusa at sunny gap along a trail in a sparse shrubby thicket accompanied with dense bamboo grasses. It is the sole locality of *A. minutissima* in Japan, and trunks of bamboo

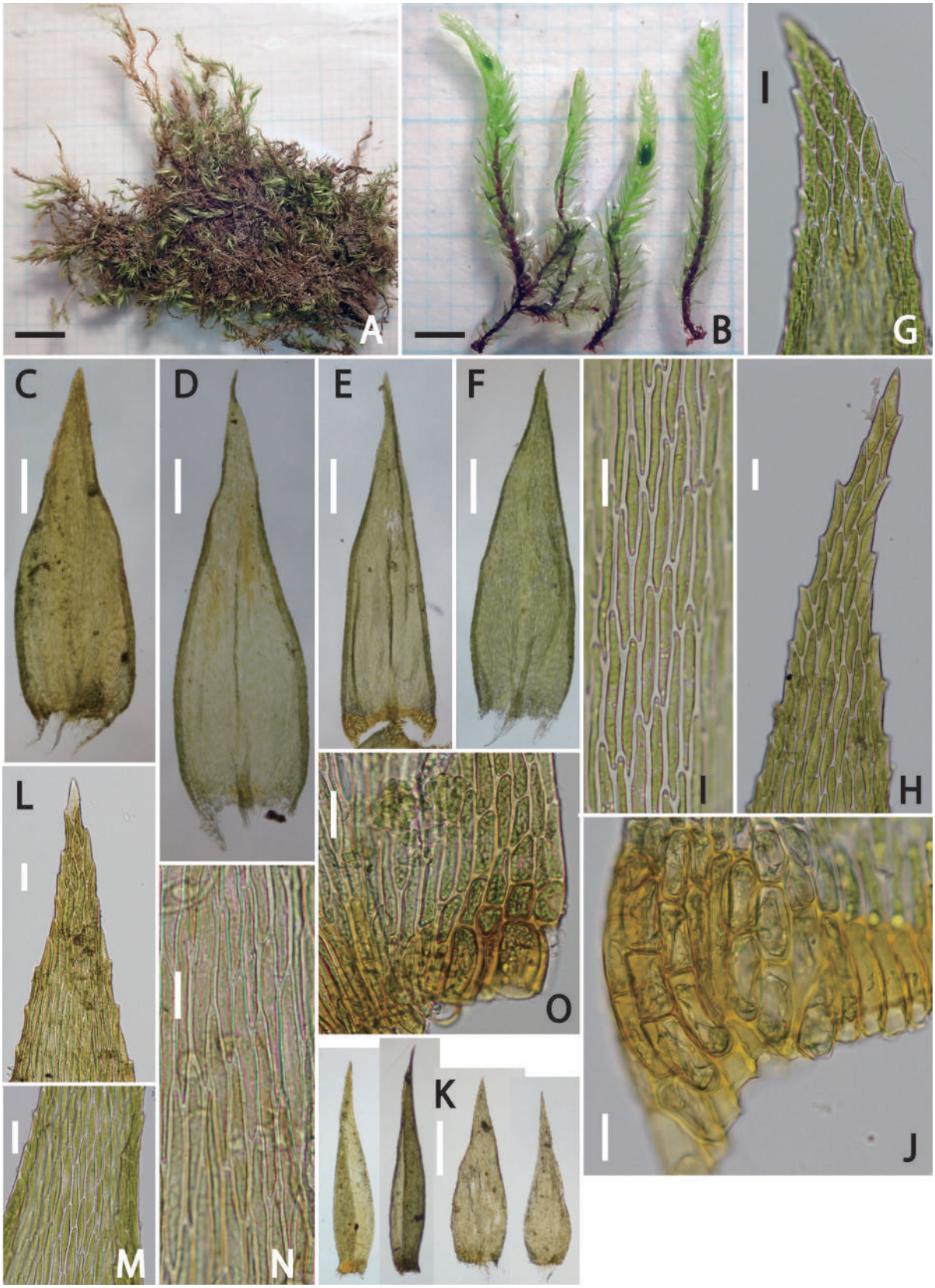

Figure 11. *Aptychella viridis.* F and G from *H.Akiyama s.n.* (28 Nov 1992) and the others from the holotype.
A: Plants (dry). B: Gemmiferous caudate stems (wet). C–J: Leaves of gemmiferous caudate stems. K–O: Leaves of turf-forming stems. G, H and L: Leaf apices. M: Upper leaf with deeply involute margins. N and I: Median laminal cells. J and O: Alars. Scales: A = 5 mm. B = 2 mm. C–F and K = 0.2 mm. G–J and L–O = 20 μm.

grasses on which they grow are suffered severe browsing pressure by Japanese deer, and the future survival of the population is highly doubtful.

11. *Aptychella yakumontana* H.Akiyama & N.Hayashida, ***sp. nov.*** (Figs. 3G–H and 12)

Diagnosis: Similar to *Aptychella robusta*, but leaves of gemmiferous caudate secondary stems (GCS) linear lanceolate, apices gradually narrowed, with weak serration at margins and very short or indistinct double costae.

Type: Japan, Kagoshima Prefecture, Yaku-cho, Yakushima Island, side branch of Anbo road, between Kigensugi and Kawakamisugi, 30°18'13" N, 130°32'32" E, 1260 m elev., 31 Aug 2016, *H.Akiyama 24728* (holotype HYO, isotypes CAS, NICH).

Description: Plant forming small patches, green in color. Primary stems prostrate on substrata, pinnately branched. GCS distinctly differentiated, reaching 2.0 cm in length, simple, sometimes tips becoming long and flexuose. Turf-forming secondary stems (TFS) less than 1 cm in length, teretely foliated, sparsely branched. Filamentous propagules numerous, to 1 mm in length, with rectangular and smooth cells. Leaves of GCS obliquely spreading both in dry and wet conditions, tightly appressed above the gemmiferous portions, narrowly lanceolate, gradually narrowed into long acuminate 2.0–2.4 mm in length, less than 0.5 mm in width, more or less narrowed at base, slightly plicate and weakly concave; costae indistinct to very short and double; margins narrowly recurved throughout, often canaliculated below apices, crenulate to weakly serrulate above, entire below; median laminal cells linear, smooth, thin-walled, 60–100 μm in length; alars well differentiated, with slightly inflated, thin-walled, quadrate to rectangular cells arranged in a scalariform manner, long decurrence to stems. Leaves of TFS similar to GCS leaves but shorter, 0.6–1.2 mm in length; margins narrowly recurved below, minutely serrulate above; costae very short and double, often indistinct; laminal cells similar to GCS leaves; alars narrowly differentiated, with inflated, thin-walled quadrate to rectangular cells, not decurrent to stems. Sexual organs and sporophytes are unknown.

Habitat: Growing at rather shaded places in montane mixed forests. Often intermingled with *Aptychella brevinervis*, *A. robusta*, and *Yakushimabryum subintegrum*. Based on field observations on Yakushima Island, where *A. yakumontana* and *A. robusta* grow sympatrically, the former tends to occur in slightly darker places in montane forests.

Distribution: Endemic to Japan (Yakushima Island).

Distinguishing features: 1) green color of plants in fresh conditions, 2) simple GCS reaching 1.6 cm in length and clearly differentiated from TFS, 3) narrowly lanceolate and more or less plicate GCS leaves with long acuminate apices with margins narrowly but distinctly recurved almost to apices, 4) very short, double, often indistinct costae of GCS leaves, 5) long decurrent bases to stems of GCS leaves, and 6) TFS leaves similar in shape to those of GCS, but shorter, 0.6–1.2 mm in length.

Other specimens examined. JAPAN: Kagoshima Pref., Yaku-cho, Yakushima Isl., between Shikanosawa lodge and upper place of Hanayama trail, 1610 m elev., 22 Sep 2007, *H.Akiyama 21368* (HYO); ibid., side branch of Arakawa road, 30.304745° N, 130.54008° E, 1230 m elev., 5 May 2013, *H.Akiyama 22756* and *22749* (both HYO); ibid., 30°18'13" N, 130°32'32" E, 1260 m elev., 31 Aug 2016, *H.Akiyama 24724* and *24794* (both HYO); ibid., along a Anbo Road, in the vicinity of the entrance of Yodogawa trail, 30°17'55" N, 130°31'59" E, 1340 m elev., 1 Sep 2016, *H.Akiyama 24797* and *24804* (both HYO); ibid., between the entrance of Yodogawa-hodo trail and Yodogawa lodge, 30.3001° N, 130.5275° E, 1410 m elev., 1 Sep 2017, *H.Akiyama 25173* and *25182* (both HYO).

Note. *Aptychella yakumontana* is very similar to *A. robusta* in morphological features and often it is difficult to distinguish them in the field, but molecular phylogenetic analyses suggest its remote relationship to the other members of *A. robusta s. lat.*

12. *Aptychella yuennanensis* Broth., Symbolae Sinicae 4: 117 (1929). (Fig. 13F–G)

Type: China, Yunnan bor.-occid.: Prope fines Tibeto-Birmanicas inter fluvios Lu-djiang (Salween) et Djiou-djiang (Irrawadi orient. super.), 27°58' N, in regione frigide temperata, ca. 3000 m, 9 VII 1916, *Handel-Mazzetti 9440* (lectotype, H-BR!), lectotype selected by Tan & Buck (1989: 310).

Description: Plants small. Primary stems prostrate, pinnately branched. Gemmiferous caudate secondary stems (GCS) differentiated, to 1.5 cm in length, mostly simple. Turf-forming secondary stems (TFS) dense, to 8 mm in length, sparsely pinnate branched. Filamentous propagules to 9 mm in length, with rectangular smooth cells. Leaves of GCS narrowly lanceolate, gradually narrowed into long attenuate apices, sometimes narrowly ligulate above, to 2.1 mm long, weakly concave, usually scarcely

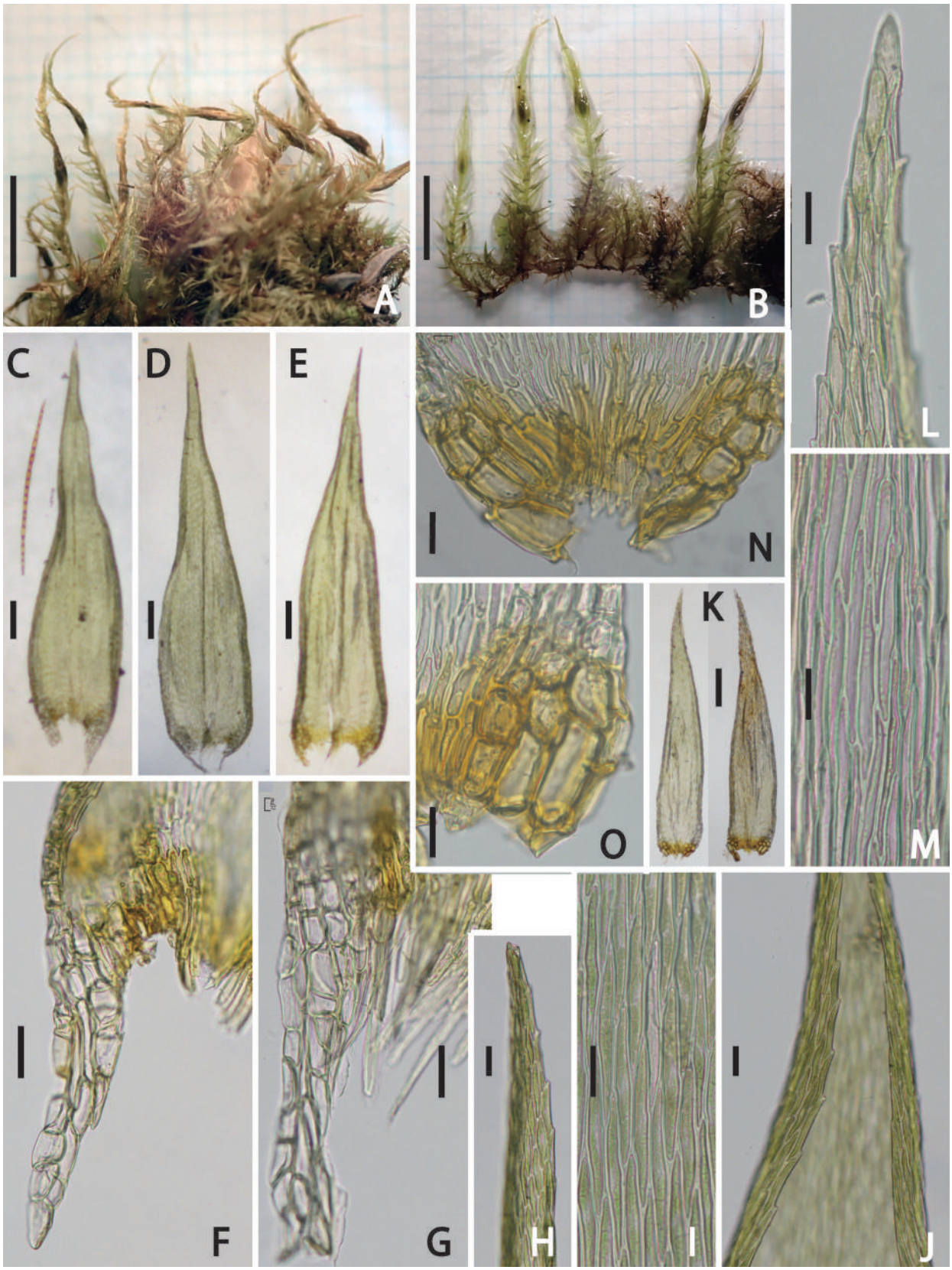

Figure 12. *Aptychella yakumontana*. All from the holotype.

A: Plant (dry). B: Plant (wet). C–J: Leaves of gemmiferous caudate secondary stems. K–O: Leaves of turf-forming secondary stems. F, G, N and O: Alars. H and L: Leaf apices. I and M: Median laminal cells. J: Upper leaf with deeply involute margins. Scales: A and B = 5 mm. C–E and K = 0.2 mm. F–J and L–O = 20 μm.

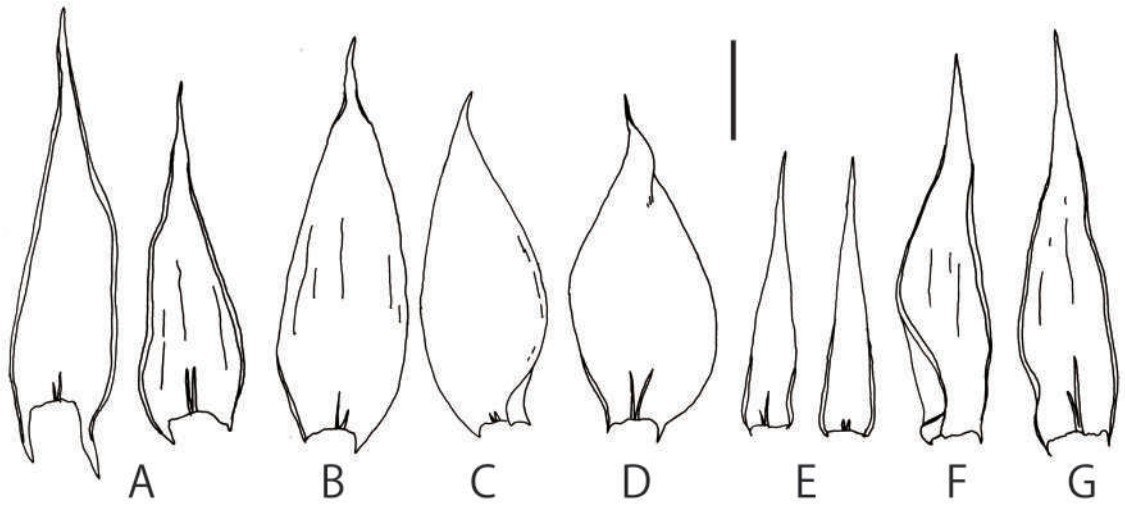

Figure 13. Leaves of *Aptychella* spp.

A: Leaves of gemmiferous caudate secondary stems of *A. subdelicata* (holotype). B–D: Ditto, *A. muelleri* (B: *Ning-Ning 4063*. C: *H.Akiyama 25544.* D: holotype of *Clastobryum caudiforme*). E: Leaves of pendent secondary stems of *A. perdecurrens* (holotype; note that no gemmiferous caudate secondary stems was reported for this species). F and G: Leaves of gemmiferous caudate secondary stems of *A. yuennanensis* (F: lectotype. G: *Narengaowa Z018*). Scale = 0.5 mm.

decurrent to stems at bases, rarely narrowly decurrent; margins narrowly recurved except for apices, almost entire or weakly crenulate above; costae short and double; median laminal cells 60–80 μm in length; alars well developed with quadrate to rectangular cells, in reddish brown or colorless, arranged in a scalariform manner. Leaves of TFS similar to those of GCS but smaller, ca. to 1.4 mm in length. Perichaetia on primary stems. Inner perichaetial leaves long lanceolate; margins distinctly toothed at apices; scarcely but rarely slightly decurrent at bases. Seta ca. 8 mm in length, smooth, reddish brown in color. Capsules oblong-ovate, erect, to 1.5 mm in length, shortly rostrate, with obliquely conical opercula. Peristome double. Spores brownish brown, smooth, 15–18 μm in diameter. [Saprophytic features are mostly adopted from Brotherus (1929)].

Previous illustration: None.

Habitat: On tree trunks (e.g. *Rhododendron*) and rotten wood at the edge of upper montane forests.

Distribution: China.

Distinguishing features: 1) alar structures similar to those of *Aptychella robusta*, 2) linear lanceolate, weakly concave leaves of gemmiferous caudate secondary stems (GCS), with narrowly acuminate apices, 3) weakly crenulate, narrowly recurved margins of GCS leaves except for apices, and 4) scarcely decurrent bases (rarely distinct) of GCS leaves.

Other specimens examined. CHINA: Sichuan Prov., Tianquan Co., Ya'an city, River Labahe Natural Reserve, along the wooden trestle of scenic spot, 30°10'55"–11'37" N, 102°25'03"–25'48" E, 2288–2569 m elev., 27 Jun 2015, *Narengaowa Z676* (PE); ibid., Hongya Co., Meishan city, Mountain Wawu Natural Reserve, along the stairs and on the top of Mountain Wawu, 29°39'27" N, 101°57'01" E, 2625 m elev., 23 May 2015, *Narengaowa Z018* (PE); Yunnan, bor.-occid., in regione frigide temperata jugi Schōndsula. inter fluvios Landsang-djiang (Mekong) et Lu-djiang (Salween), 28°04' N, ad margines silvarum bambusetorumsque, 3600–3950 m elev., 23 Sep 1915, *Handel-Mazzetti 8363* (H; one of the former syntypes).

Note. Tixier (1977), Tan & Buck (1991) and Tan & Jia (1999) proposed to treat *Aptychella yuennanensis* as a synonym of *A. planula* (or *A. delicata*) without supporting evidence. It is true that both species share scarcely decurrent leaf bases, but examining the lectotype of *A. yunnanensis*, we propose to treat them as separate species because *A. yuennanensis* has narrower and shorter leaves comparing to *A. planula*. Our molecular phylogenetic analysis also suggests this treatment; the clade of *A. yuennanensis* becomes sister to that of *A. formosana*, both of which share the narrowly lanceolate GCS leaves.

There is a specimen collected in China (Guangxi Prov., Long Sheng, Huaping Forestry Area, south slope of Mt. Hongmaojai, Aug 1964, *Wu 1168b*, MO) identified as *Aptychella yuennanensis*, but we did not examine its identity.

Species not treated

1. *Aptychella linearifolia* Herzog, Bibliotheca Botanica 88: 24 (1920).

Type: Bolivia, An Baumrinde im Bergwald von Ineacorral, ca. 2200 m, *Herzog 5343* (syntype JE, not seen); im Nebelwald ueber Comarapa, ca. 2600 m, *Herzog 3944* (syntype JE, not seen); hierher gehoert auch *Herzog 4349* (syntype JE, not seen).

Note. This species was originally described based on three specimens collected in Bolivia and we examined none of them. Judging from the original description, it does not seem to differ much from the typical *Aptychella proligera*.

2. *Aptychella proligera* var. *chlorophyllosa* Herzog, Bibliotheca Botanica 88: 25 (1920).

≡ *A. chlorophyllosa* (Herzog) Tixier, Rev. Bryol. Lichénol. 43: 421 (1977). Type: Bolivia, Im Coranital auf Baumaesten, *Herzog 3416* (holotype JE, not seen).

Note. According to the description given by Herzog (1920), var. *chlorophyllosa* differs from the type variety in much larger group of alar cells, which are quite chlorophyll-rich and sharply differentiated from the usually heavily brown laminal cells. Brood bodies were not developed.

Tixier (1977: 221) treated *Aptychella chlorophyllosa* as a distinct species. However, considering the extensive morphological variation previously reported in *A. proligera s. lat.* (Akiyama et al. 2015), it might be better to treat var. *chlorophyllosa* as a synonym of *A. proligera* itself.

Additional localities of the previously reported species

1. ***Aptychella oblongifolia*** H.Akiyama, Bryological Research 11: 75 (2014).

Specimen examined. **PHILIPPINES:** Luzon, Mt. Pulog, 16°36' N, 120°54' E, 2600–2700 m elev., 3 Feb 1968, *M. Jacob B182* (L). **CHINA:** Yunnan Prov., Jin-Ping Co., along road to radar installation facility off of highway from Fenshuiling Pass. 22°51'46.0" N, 103° 13'38.0" E, 1975 m elev., 8 Sep 2017, *J.R.Shevock & L.Zhang 50837* (CAS, KUN, intermingled with *A. minutissima*); ibid., Wenshan, Maguan, Dulong, Laojunshan Mts., 22°56'31.65" N, 104°32'34.39" E, 1966 m elev., 28 Oct 2016, *Y.Nign-Nign Y3899* (PE). **TAIWAN:** Hsinchu Co., Yuanyang Lake Natural Reserve, along trail in vicinity of the entrance gate of reserve, slope above Mandarin Duck Lake, 24°34'30.2" N, 121°24'42.8" E, 1700 m elev., 30 Oct 2018, *J.R.Shevock et al. 53517* (CAS, HYO, TAIE).

2. ***Aptychella pseudobrevinervis*** H.Akiyama, Bryological Research 11: 71 (2014).

Specimen examined. **CHINA:** Yunnan Prov., Xin-Ping Co., Mountain Ranges of the Cinping Region, Gasa Zhen, Ailao Mountains, Jinshin Pass, 23°56'40.7" N, 101°29'47.0" E, 2465 m elev., 23 Apr 2019, *J.R.Shevock & Y.Manontov 54102* (CAS, HYO). **TAIWAN:** Pingtung Co., Beidawu Mountain National Trail, along the trail above the junction with the trail to Kuaigu Inn at the 5.5 km trail marker post, 22°36'53.3" N, 120°44'52.4" E, 2550 m elev., 27 Apr 2018, *J.R.Shevock et al. 51526* (CAS, HYO, TAIE).

Acknowledgments

We thank the late Dr. B. C. Tan, Dr. Y. Jia, Dr. T. Arikawa, Dr. M. Suleiman, Dr. M. Higuchi, Dr. H. Deguchi, Dr. K. Santanachote, Dr. K.-T. Yong, Dr. S.-H. Lin, Dr. B.-C. Ho. and Dr. J.-D. Yang for their valuable advice and kind help in the field surveys. We are much in debt to the curators of BM, CAS, FH, H, HIRO, HSNU, HYO, KOCH, KUN, KYO, L, MO, NICH, NY, OSA, PC, PE, PHH, SING, TAIE, TNS and UC for kind loans of valuable specimens including types. We also thank to Dr. X.-L. He and Dr. T. Koponen for their information about the Papua New Guinean *Aptychella* specimens deposited in H. We owe very much to the Office of the National Research Council of Thailand (NRCT) for permission of field research in Doi Inthanon National Park, the Director board of Bidoup-Nui Ba National Park for the collecting permit, the authorities concerned in Japan for allowance for collections within National Parks (Hakone and Yakushima Island). This study was financially supported by JSPS KAKENHI no. 24570108 and no. 16K07488 to H. Akiyama, no. 24255007 to Dr. M. Kanzaki (Kyoto University), no. 13375003 to Dr. J. Murata (the University of Tokyo), and the Environment Research and Technology Development Fund to Dr. T. Yahara (Kyushu University).

References

Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov, B. N. and Caski, F. (eds.), *Proceedings of the 2nd International Symposium on Information Theory*. Akadimiai Kiado, Budapest: 267–281.

Akiyama, H. (2014) Newly found sporophytes and male plants of *Yakushimabryum longissimum* (Pylaisiadelphaceae, Musci) and a significant extension of its distribution. *Bryological Research,* **11**, 63–69.

Akiyama, H. (2016) *Aptychella touwii* (Pylaisiadelphaceae, Musci) sp. nov., from New Guinea with singly costate leaves. *Bryological Research*, **11**, 167–171.

Akiyama, H. (2017a) Systematic study of the *Yakushimabryum* and related genera in the Pylaisiadelphaceae (Bryophyta). *Acta Phytotaxonomica et Geobotanica*, **63**, 145–174.

Akiyama, H. (2017b) Taxonomical and ecological notes on Asian bryophytes, 32. A note on the illustration of *Aptychella robusta* (Broth.) M. Fleisch. in Noguchi *et al.* (1994). *Bryological Research* **11**, 234–236. [In Japanese]

Akiyama, H. (2019) Phylogenetic re-examination of the "*Gammiella ceylonensis*" complex reveals three new genera in the Pylaisiadelphaceae (Bryophyta). *Bryophyte Diversity and Evolution* **141**, 35–64.

Akiyama, H., Chang, Y. and Tan, B. C. (2010) *Clastobryopsis imbricata* (Pylaisiadelphaceae) sp. nov. from Doi Inthanon, northern Thailand. *Bryologist*, **113**, 752–759.

Akiyama, H., Schäfer-Verwimp, A., Printarakul, N., Suleiman, M., Tan, B. C., Goffinet, B., Yong, K. T., and Müller, F. (2015) Phylogenetic study of the genus *Aptychella* (Pylaisiadelphaceae, Musci). *Bryologist*, **118**, 273–283.

Akiyama, H. and Shevock, J. R. (2019) Two new species of *Aptychella* (Pylaisiadelphaceae, Musci) from Hawaiian Island and Taiwan. *Bryological Research*, **11**, 337–345.

Allen, B. H. (2018) Moss flora of Central America, part 4. Abroniaceae-Polytrichaceae. *Monographs in Systematic Botany from the Missouri Botanical Garden* **132**, 1–830.

Arikawa, T. (2004) A taxonomic study of the genus *Pylaisia* (Hypnaceae, Musci). *Journal of the Hattori Botanical Laboratory*, **95**, 71–154.

Arikawa, T., Kiguchi, H., Sugimura, K., Hiraoka, T. and Hiraoka, S. (2006a) *Clastobryopsis robusta* in Kanagawa Prefecture, Japan. *Bryological Research*, **9**, 60–61. [In Japanese]

Arikawa, T., Tsubota, H. and Higuchi, M. (2006b) A reappraisal of *Pylaisiopsis* (Sematophyllaceae). *Bryologist* **109**, 381–390.

Bartram, E. B. (1939) Mosses of the Philippines. *Philippine Journal of Science,* **68**, 1–437.

Brotherus V. F. (1929) Musci. pp. 1–147. In Handel-Mazzetti H. (ed.), *Symbolae Sinicae 4*, Verlag von Julius Springer, Wien.

Buck, W. R. (1998) Pleurocarpous mosses of the West Indies. *Memoirs of the New York Botanical Garden*, **82**, 1–400.

Churchill, S. P. and Linares Castillo, E. L. (1995) Prodromus bryologiae Novo-Granatensis: introducción a la flora de musgos de Colombia, parte 2. Grimmiaceae a Trachypodaceae. *Biblioteca José Jerónimo Triana*, **12**, 455–924.

Dixon, H. N. (1933) New species of Clastobryeae from Indo-Malaya. *Annales Bryologici*, **6**, 31–37.

Edgar, R. C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, **32**, 1792–1797.

Fleischer, M. (1923) *Die Musci der Flora von Buitenzorg 4*. pp. (i–xxxi) + pp. 1105–1729. Brill, Leiden.

Gangulee, H. C. (1980) *Mosses E. India* fasc. 8 (Hypnobryales-Hypnineae: Floristic trends: Index: Errata): pp. (xlv–liii) + 1753–2145. Privately published, Calcutta.

Goffinet, B., Buck, W. R. and Shaw, A. J. (2009) Morphology, anatomy, and classification of the Bryophytes. pp. 55–138. In B. Goffinet & A. J. Shaw (eds.), *Bryophyte Biology*, 2nd ed. Cambridge Univ. Press, Cambridge.

Han, J. and Jia, Y. (2021) Phylogeny and classification of the Sematophyllaceae *s.l.* (Hypnales, Bryophyta). *Journal of Systematics and Evolution*, **59**, 524–540.

Herzog, T. (1916). Die bryophyten meiner zweiten Reise durch Bolivia. *Bibliotheca Botanica*, **87**, 1–168, pl. 1–4.

Herzog, T. (1920). Die Bryophyten meiner zweiten Reise durch Bolivia. *Bibliotheca Botanica*, **88**, 1–31.

Hoe, W. J. (1973) Additional new and noteworthy records for Hawaiian mosses-2. *Bryologist,* **76**, 296–298.

Jia, Y., Wu P.-C. and Tan, B. C. (2005) Sematophyllaceae. In: He S. and Jia Y. (eds.). *Moss Flora of China*, vol. 8, pp. 3–79. Missouri Botanical Garden Press, St. Louis.

Kumar, S., Stecher, G. and Tamura, K. (2016) MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, **33**, 1870–1874.

Müller, F. and Akiyama, H. (2016) *Aptychella chilensis* belongs to the Ptychomniaceae and not Pylaisiadelphaceae based on DNA and morphological analyses. *Cryptogamie, Bryologie*, **37**, 251–258.

Noguchi, A., Iwatsuki, Z. and Yamaguchi, T. (1994) *Illustrated moss flora of Japan*, part 5. Hattori Botanical Laboratory, Nichinan.

Printarakul, N., Tan, B. C., Santanachote, K and Akiyama, H. (2013) New and noteworthy records of mosses from Doi (Mt.) Inthanon, Chiang Mai, Chom Tong District, northern Thailand. *Polish Botanical Journal*, **58**, 245–257.

Rambaut, A. (2016) Fig Tree: Tree Figure Drawing Tool, v.1.4.3. http://tree.bio.ed.ac.uk/software/figtree/

Ronquist, F. and Huelsenbeck, J. P. (2003) MRBAYES 3: Bayesian

phylogenetic inference under mixed models. *Bioinformatics*, **19**, 1572–1574.

Staples, G. W., Imada, C. T., Hoe, W. J. and Smith, C. W. (2004) A revised checklist of Hawaiian mosses. *Tropical Bryology*, **25**, 35–69.

Tamura, K. (1992) Estimation of the number of nucleotide substitutions when there are strong transition-transversion and G+C- content biases. *Molecular Biology and Evolution*, **9**, 678–687.

Tan, B. C. (1990) Six new taxa of Malesian mosses. *Bryologist*, **93**, 429–437.

Tan, B. C. (1991) Miscellaneous notes on Asiatic mosses, especially Malesian Sematophyllaceae (Musci) and others. *Journal of the Hattori Botanical Laboratory*, **70**, 91–106.

Tan, B. C. (1993) Noteworthy range extension of Malesian mosses. *Journal of the Hattori Botanical Laboratory*, **74**, 227–233.

Tan, B. C. (2000). Additions to the moss floras of Mt. Wilhelm Nature Reserve and Mt. Gahavisuka Provincial Park, Papua New Guinea. *Journal of the Hattori Botanical Laboratory*, **89**, 173–196.

Tan, B. C. and Buck, W. R. (1989) A synoptic review of Philippine Sematophyllaceae with emphasis on Clastobryoideae and Heterophylloideae. *Journal of the Hattori Botanical Laboratory*, **66**, 307–320.

Tan, B. C. and Iwatsuki, Z. (1993) A checklist of Indochinese mosses. *Journal of the Hattori Botanical Laboratory*, **74**, 325–405.

Tan, B. C. and Jia, Y. (1999) A preliminary revision of Chinese Sematophyllaceae. *Journal of the Hattori Botanical Laboratory*, **86**, 1–70.

Tan, B. C., Koponen, T. and Norris, D. H. (2011) Bryophyte flora of the Huon Peninsular, Papua New Guinea. LXX. Sematophyllaceae (Musci) 2. *Brotherella, Clastobryum, Clastobryopsis, Heterophyllium, Isocladiella, Isocladiellopsis, Meiotheciella, Meiothecium, Papillidiopsis, Rhaphidostichum* and *Wijkia*. *Acta Bryolichenologica Asiatica*, **4**, 3–58.

Tan, B. C., Koponen, T. and Norris, D. H. (2017) Bryophyte flora of the Huon Peninsula, Papua New Guinea. LXXVII. Sematophyllaceae (Musci) 3. *Macrohymenium*, *Mastopoma*, *Rhaphidorrhynchium*, *Sematophyllum*, *Trismegistia* and *Warburgiella*, with a key to the genera and a checklist of the taxa. *Acta Bryolichenologica Asiatica*, **7**, 3–70.

Tixier, P. (1977) Clastobryoïdées et taxa apparentés. *Revue Bryologique et Lichénologique*, **43**, 397–464.

Tropicos (2021). Tropicos.org. Missouri Botanical Garden, St. Louis, MO. Website www.tropicos.org [accessed 17 Aug 2022].

Zanten, B. O. van. (1964) Scientific results of the Netherlands New Guinea Expedition 1959: mosses of the Star Mountains Expedition. *Nova Guinea, n.s.,* **10**, 263–368.

Appendix 1. The total 76 samples used in the analyses and their accession numbers (in order of *rps*4, *trn*L-F, and *rbc*L). Samples with new accessions are indicated with an asterisk (*) before species names and with voucher information in brackets.

Genus ***Aptychella***

A. brevinervis (*Akiyama 21490*), LC059865, LC059909, ---

A. brevinervis (*Akiyama 22752*), AB938185, LC059910, LC059955

A. brevinervis (*Akiyama 23032*), LC059866, LC059911, LC059953

A. brevinervis (*Akiyama 23877*), LC059867, LC059912, LC059893

A. brevinervis (*Akiyama 23888*), LC059868, LC059913, LC059956

A. brevinervis (*Akiyama 23892*), LC059869, LC059914, LC059957

A. brevinervis (*Akiyama 23897*), LC059870, LC059915, LC059958

A. brevinervis (*Suleiman s.n.*), AB971898, LC059916, LC059959

A. brevinervis (*Wang 201382526*), LC389289, LC389293, LC389285

**A. formosana* (Taiwan, Chiayi, *Shevock et al. 53312*), LC720071, LC720031, LC719990

**A. formosana* (Taiwan, Chiayi, *Shevock et al. 53448*), LC720072, LC720032, LC719991

**A. formosana* (Taiwan, Chiayi, *Shevock et al. 53366*), LC720070, LC720030, LC719989

**A. formosana* (Taiwan, Chiayi, *Shevock et al. 53391*), LC720069, LC720029, LC719988

**A. formosana* (Taiwan, Chiayi, *Shevock et al. 53412*), LC720068, LC720028, LC719987

**A. formosana* (Taiwan, Chiayi, *Akiyama 25587*), LC720073, LC720033, LC719992

A. hawaiica (*Shevock et al. 51156*), LC389290, LC389294, LC389286

A. imbricata (*Akiyama et al. 185*), LC059871, LC059918, ---

A. imbricata (*Akiyama et al. 31*), AB971899, LC059917, GU560188

A. linii (*Akiyama 23170*), LC389291, LC389295, LC389287

**A. minutissima* (Japan, Miyazaki Pref., Mt. Ichifusa, *Matsumoto 201610313*), LC720074, LC720034, LC719993

**A. minutissima* (Japan, Miyazaki Pref., Mt. Ichifusa, *Matsumoto 201610314*), LC720075, LC720035, LC719994

**A. minutissima* (China, Yunnan Prov., *Shevock & Zhang 50837*), LC720076, LC720036, LC719995

**A. muelleri* (China, Yunan Prov., Honghe, *Wie Han WH013*), LC720077, LC720037, LC719996

**A. muelleri* (China, Yunnan Prov., Wenshan, *Yu Y4063*), LC720078, LC720038, LC719997

**A. muelleri* (Vietnam, Langbian, *Akiyama 25544*), LC720079, LC720039, LC719998

**A. muelleri* (Vietnam, Langbian, *Akiyama 25545*), LC720080, LC720040, LC719999

A. oblongifolia (*Akiyama & Printarakul 1473a*), LC059872, LC059919, LC059961

A. oblongifolia (*Akiyama & Printarakul 1483a*), LC059873, LC059920, LC059962

A. oblongifolia (*Akiyama & Printarakul 1501*), LC059874, LC059921, LC059963

**A. planula* (Myanmar, Mt. Victoria, *Murata et al. 23282*), LC720081, LC720041, LC720000

**A. planula* (Thailand, Doi Inthanon, *Akiyama et al. 1173*), LC720082, LC720042, LC720001

**A. planula* (Thailand, Doi Inthanon, *Akiyama et al. 1121*), LC720083, LC720043, LC720002

A. proligera (*Verwimp 26655*), LC059857, LC059926, LC059966

A. proligera (*Verwimp 33069*), LC059860, LC059929, LC059969

A. proligera (*Verwimp 34603*), LC059862, LC059930, LC059970

A. proligera (*Verwimp 35401*), LC059861, LC059931, LC059971

A. pseudobrevinervis (*Akiyama & Printarakul 1061*), LC059875, LC059935, LC059972

A. pseudobrevinervis (*Akiyama & Printarakul 1172*), LC059876, LC059936, LC059973

**A. pseudobrevinervis* (Taiwan, Pingtung Co., *Shevock et al. 51526*), LC720084, LC720044, LC720003

**A. pseudobrevinervis* (China, Yunnan Prov., *Shevock & Manontov 54102*), LC720085, LC720045, LC720004

A. robusta (*Akiyama 23272*), AB971901, LC059943, LC059980

**A. robusta* (Taiwan, Pingtung Co., *Shevock et al. 51483*), LC720092, LC720052, LC720012

**A. robusta* (Taiwan, Hsinchu Co., *Shevock et al. 53526*), LC720093, LC720053, LC720013

**A. robusta* (Taiwan, Hsinchu Co., *Shevock et al. 53545*), LC720095, LC720055, LC720015

**A. robusta* (Taiwan, Nanto Co., *Shevock et al. 53500*), LC720094, LC720054, LC720014

A. robusta (*Azule s.n.*), LC389292, LC389296, LC389288

**A. robusta* (Japan, Kagoshima Pref., Yakushima Isl., *Hayashida s.n.*), LC720086, LC720046, LC720005

**A. robusta* (Japan, Kagoshima Pref., Yakushima Isl., *Akiyama 25118*), LC720087, LC720047, LC720006

**A. robusta* (Japan, Kagoshima Pref., Yakushima Isl., *Akiyama 25178*), LC720090, LC720050, LC720009

**A. robusta* (Japan, Kagoshima Pref., Yakushima Isl., *Akiyama 25172*), LC720089, LC720049, LC720008

**A. robusta* (China, Yunnan Prov. Lijiang, *Yu Y3900*), ---, LC720051, LC720010

**A. robusta* (Japan, Kagoshima Pref., Yakushima Isl., *Akiyama 25153*), LC720088, LC720048, LC720007

**A. robusta* (China, Guizhou Prov., Taiyang, *Ka 01228*), LC720091, ---, LC720011

**A. rubiginosa* (Japan, Kagoshima Pref., Yakushima Isl., *Akiyama*

24780), LC720096, LC720056, LC720016

**A. rubiginosa* (Japan, Kagoshima Pref., Yakushima Isl., *Akiyama 24786*), LC720097, LC720057, LC720017

**A. rubiginosa* (Japan, Kagoshima Pref., Yakushima Isl., *Akiyama 24817*), LC720098, LC720058, LC720018

**A. rubiginosa* (Japan, Kagoshima Pref., Yakushima Isl., *Akiyama 24819*), LC720099, LC720059, LC720019

**A. subdelicata* (China, Yunnan Prov., Teng-chong, *Shevock et al. 46646*), LC720100, LC720060, LC720020

**A. subdelicata* (China, Yunnan Prov., Gong-Shan, *Shevock et al. 30782*), LC720101, LC720061, LC720021

**A. triangularis* (China, Sichuan, Tianquan, *Narengaowa Z677*), LC720102, LC720062, LC720022

A. viridis (*Akiyama 23056*), LC059882, LC059942, LC059979 (deposited as *A. robusta*)

A. viridis (*Higuchi51070*), AB971902, LC059945, LC059983 (deposited as *A. robusta*)

A. viridis (*Akiyama 23724*), LC059883, LC059938, LC059981 (deposited as *A. robusta*)

A. viridis (*Akiyama 23725*), LC059884, LC059944, LC059982 (deposited as *A. robusta*)

A. yakumontana (*Akiyama 21368*), LC059877, LC059937, LC059974 (deposited as *A. robusta*)

A. yakumontana (*Akiyama 22749*), LC059879, LC059940, LC059976 (deposited as *A. robusta*)

**A. yakumontana* (Japan, Kagoshima Pref. Yakushima Isl., *Akiyama 24728*), LC720103, LC720063, LC720023

**A. yakumontana* (Japan, Kagoshima Pref. Yakushima Isl., *Akiyama 24797*), LC720104, LC720064, LC720024

**A. yunnanensis* (China, Sichuan Prov., Labahe, *Narengaowa Z676*), LC720105, LC720065, LC720025

**A. yunnanensis* (China, Sichuan Prov., Wawushan, *Narengaowa Z018*), LC720106, LC720066, LC720026

Genus ***Microgammiella***

M. flagelliformis (*Akiyama 25547*), LC493893, LC493873, LC493853

M. flagelliformis (*Akiyama 23152*), LC493894, LC493872, LC493852

Genus **Isopterygium**

I. propaguliferum (*Akiyama 26066*), LC059889, LC059951, LC059990

Genus ***Pylaisiadelpha***

P. tristoviridis (*Nishimura 13147*), LC059888, LC059949, LC059988

Genus ***Yakushimabryum***

Y. subintegrum (as *Y. longissimum*, *Akiyama 22765*), LC059891, LC059952, LC059991

Outgroup

**Brachythecium plumosum* (Shevock et al. 53517), LC720107, LC720067, LC720027

Appendix 2. List of species once regarded as members of *Aptychella* and related genera. All species are arranged in alphabetical order. Accepted names are shown in bold and synonyms in italic with reference.

Acanthocladium Mitt.

A. clarkii Dixon

→ **Aptychella brevinervis**, *fide* Tan et al. (2011).

Aptychella (Broth.) Herzog

A. americana (Cardot) Broth.

→ **A. proligera**, *fide* Churchill & Linares (1995).

A. borii Dixon

→ **A. planula**, *fide* Tan & Jia (1999).

A. brevinervis (M.Fleisch.) M.Fleisch.

A. caudata Herzog

→ **A. proligera**, *fide* Tixier (1977), Buck (1998), Allen (2018).

A. chilensis Herzog

→ **Ombronesus chilensis**, *fide* Müller & Akiyama (2016).

A. chlorophyllosa (Herzog) Tixier

→ **A. proligera** var. **chlorophyllosa**, *fide* Herzog (1920).

A. clemensiae E.B.Bartram

→ **A. brevinervis**, *fide* Tan (2000) and Tan et al. (2011) as *Clastobryopsis brevinervis*; Akiyama (2016).

A. colombica R.S.Williams

→ **A. proligera**, *fide* Churchill & Linares (1995), Allen (2018).

A. delicata (M.Fleisch.) M.Fleisch.

→ **A. planula**, *fide* Tan (1991), this study.

→ *A. planula* var. *delicata*, *fide* Tan & Jia (1999)

A. formosana H.Akiyama, Shevock & K.-Y.Yao, **sp. nov.**

A. glabrifolia (Broth. & Watts) Broth.

→ **Clastobryum caudatum**, *fide* Tixier (1977).

A. glomeratopropagulifera (Toyama) Seki

→ *Gammiella tonkinensis*, *fide* Tan (1990).

→ **Yakushimabryum tonkinensis**, *fide* Akiyama (2017a).

A. handelii Broth.

→ ***nom. dub.***, this study.

A. hawaiica H.Akiyama & Shevock

A. heteroclada (M.Fleisch.) M.Fleisch.

→ **Aptychella robusta**, *fide* Tan & Buck (1989), Tan & Jia (1999).

A. imbricata (H.Akiyama, Y.Chang & B.C.Tan) H.Akiyama

A. linearifolia Herzog

?→ **A. proligera**, this study.

A. linii H.Akiyama

A. minutissima H.Akiyama, Shevock & M.Matsumoto, **sp. nov.**

A. muelleri Dixon

A. oblongifolia H.Akiyama

A. perdecurrens (Dixon) T.J.Kop.

Note: As for the generic affinity of this species, see the notes under the species in this study.

A. planula (Mitt.) M.Fleisch.

A. planula var. *delicata* (M.Fleisch.) B.C.Tan & Y.Jia

→ **A. planula**, fide Tan (1990), this study.

A. proligera (Broth.) Herzog

A. proligera (Broth.) Herzog var. **chlorophyllosa** Herzog

A. pseudobrevinervis H.Akiyama

A. robusta (Broth.) M.Fleisch.

A. rubiginosa H.Akiyama, N.Printarakul & N.Hayashida, **sp. nov.**

A. scalaris (Müll.Hal.) M.Fleisch.

→ **Clastobryum scalare**, *fide* Tixier (1977).

A. serrulata (Cardot & P. de la Varde) Broth.

→ **Bonnosukea serrulata**, *fid*e Akiyama (2019).

A. speciosa (Mitt.) Tixier

→ **Pylaisia speciosa** (Mitt.) A.Jaeger, *fide* Arikawa et al. (2006b).

A. subdelicata Broth.

A. subintegra Tixier

→ **Yakushimabryum subintegrum**, *fide* Akiyama (2017a).

A. tamdaoensis Tixier

→ **Yakushimabryum subintegrum,** *fide* Akiyama (2017a).

A. tenuiramea (Mitt.) Tixier

→ **Brotherella** sp., *fide* Tan (1990), Arikawa (2004).

A. tonkinensis (Broth. & Paris) Broth.

→ **Yakushimabryum tonkinense**, *fide* Akiyama (2017a).

A. touwii H.Akiyama

A. triangularis H.Akiyama & Shevock, **sp. nov.**

A. *viridis* H.Akiyama

A. yakumontana H.Akiyama, **sp. nov.**

A. yuennanensis Broth.

Bonnosukea H.Akiyama

B. serrulata (Cardot & P. de la Varde) H.Akiyama.

Clastobryopsis M.Fleisch.

→ **Aptychella**, *fide* Akiyama et al. (2015).

C. brevinervis M.Fleisch.

→ **Aptychella brevinervis**, *fide* Fleischer (1923).

C. delicata M.Fleisch.

→ *Aptychella delicata*, *fide* Fleischer (1923).

→ **Aptychella planula**, fide Tan (1990), this study.

C. heteroclada M.Fleisch.

→ **Aptychella robusta**, *fide* Tan & Buck (1989), Tan & Jia (1999) as *Clastobryopsis robusta*.

C. imbricata H.Akiyama, Ying Chang & B.C.Tan

→ **Aptychella imbricata**, *fide* Akiyama et al. (2015).

C. muelleri (Dixon) Tixier

→ **Aptychella muelleri**, this report.

C. perdecurrens (Dixon) B.C.Tan
→ **Aptychella perdecurrens**, *fide* Tan et al. (2017).
C. planula (Mitt.) M.Fleisch.
→ ***A*ptychella planula**, *fide* Fleischer (1923).
C. proligera (Broth.) M.Fleisch.
→ **Aptychella proligera**, *fide* Herzog (1916).
C. robusta (Broth.) M.Fleisch.
→ **Aptychella robusta**, *fide* Fleischer (1923).

Clastobryum Dozy & Molk.
C. americanum Cardot
→ **Aptychella proligera**, *fide* Churchill & Linares (1995).
C. capillaceum (Griff.) Broth.
→ **Pylaisiadelpha capillacea**, *fide* Tan & Jia (1999).
C. carinatum Dixon
→ **Aptychella brevinervis**, *fide* Tan (1991).
C. caudiforme Dixon
→ *Clastobryopsis planula*, *fide* Tan (1991).
→ **Aptychella muelleri**, this study.
C. delicatum (M.Fleisch.) Broth. ex Dixon
→ *Clastobryopsis planula*, *fide* Tan (1991).
→ *Clastobryopsis planula* var. *delicata*, *fide* Tan & Jia (1999).
→ **Aptychella planula**, *fide* Tan (1990), this report.
C. excavatum Broth.
→ ***nom. dubia***, this study.
C. glomeratopropaguliferum Toyama
→ **Yakushimabryum tonkinense,** *fide* Akiyama (2017a).
C. perdecurrens Dixon
→ **Aptychella perdecurrens**, *fide* Tan et al. (2017).
C. planulum (Mitt.) Brühl
→ **Aptychella planula**, *fide* Fleischer (1923).
C. robustum Broth.
→ *Aptychella robusta*, *fide* Fleischer (1923).
C. subplanulum Broth. ex Dixon
→ **Aptychella planula**, *fide* Tan (1991) as *Clastobryopsis planula*.

Myurium Schimp.
M. foxworthyi (Broth.) Broth.
→ **Aptychella robusta**, *fide* Tan & Iwatsuki (1993).

Ombronesus N.E.Bell, N.Pedersen & A.E.Newton.
O. chilensis (Herzog) Frank Müll. & H.Akiyama
O. stuvensis N.E.Bell, N.Pedersen & A.E.Newton
→ **Ombronesus chilensis**, *fide* Müller & Akiyama (2016).

Rhaphidostegium (Schimp.) De Not.
R. proligerum Broth.
→ ***A*ptychella proligera**, *fide* Herzog (1916).

Sematophyllum Mitt.
S. proligerum (Broth.) Broth.
→ **Aptychella proligera**, *fide* Fleischer (1923).

Stereodon (Brid.) Brid.
S. planulus Mitt.
→ **Aptychella planula**, *fide* Fleischer (1923).

Symphyodon Mont.
S. planulus (Mitt.) A.Jaeger
→ **Aptychella planula**, *fide* Fleischer (1923: 1671).

Wijkia H.A.Crum
W. clarkii (Dixon) H.A.Crum
→ **Aptychella brevinervis**, *fide* Tan et al. (2011).

Yakushimabryum H.Akiyama, Y. Chang, T.Yamag. & B.C.Tan.
Y. subintegrum (Tixier) H.Akiyama
Y. tonkinense (Broth. & Paris) H.Akiyama

原著論文

東アジアおよび東南アジア産オオタマコモチイトゴケ（広義）の分類学的研究（コモチイトゴケ科，蘚類）

秋山弘之[1]・James R. SHEVOCK[2]・松本美津[3]・林田信史[4]・
Thien Tam LUONG[5), 6)]・Narin PRINTARAKUL[7]・姚　奎宇[8]

東アジア・東南アジアを中心とした着生蘚類 *Aptychella robusta s. lat.*の系統関係を、葉緑体 DNA（*rbc*L, *rps*4, *trn*L-F）の塩基配列と、各国の主な標本庫から借用したタイプを含む標本を用いた形態的特徴の調査によって検討した．その結果、従来 *A. robusta s.lat.*と *A. planula*として認識されていたグループ内に予想外の種の多様性が見出され、結果として *A. formosana* H.Akiyama, Shevock & K.-Y.Yao **sp. nov.**, *A. minutissima* H.Akiyama, Shevock & M.Matsumoto **sp. nov.**, *A. muelleri* Dixon, *A. perdecurrens* (Dixon) T.J.Kop., *A. planula* (Mitt.) M.Fleisch., *A. robusta* (Broth.) M.Fleisch. *s. str.*, *A. rubiginosa* H.Akiyama, N.Printarakul & N.Hayashida **sp. nov.**, *A. subdelicata* Broth., *A. triangularis* H.Akiyama & Shevock **sp. nov.**, *A. viridis* H.Akiyama **sp. nov.**, *A. yakumontana* H.Akiyama & N.Hayashida **sp. nov.**, そして *A. yuennanensis* Broth. の 12 種を認識することができた．またこれまで *A. robusta* あるいは *A. planula* の異名とされていた種のうち, *A. subdelicata*, *A. muelleri*, *A. yuennanensis* については別種として扱うことを提唱した．

(2022 年 6 月 24 日受付, 2022 年 10 月 7 日受理, 2023 年 3 月 10 日発行)

[1] 兵庫県立人と自然の博物館 〒669-1546 兵庫県三田市弥生が丘 6 丁目

[2] California Academy of Sciences, 55 Music Concourse Drive, Golden Gate Park, San Francisco, CA 94118, U.S.A.

[3] 服部植物研究所／宮崎植物研究会 〒889-2535 宮崎県日南市飫肥

[4] Yamakara 屋久島 〒891-4322 鹿児島県屋久島町安房

[5] Department of Ecology - Evolutionary Biology, Faculty of Biology - Biotechnology, University of Science - Vietnam National University Ho Chi Minh City, 227 Nguyen Van Cu, District 5, Ho Chi Minh City, Vietnam

[6] Biodiversity Unit, University of Turku, FI-20014, Turku, Finland

[7] Department of Biology, Chiang Mai University, 239, Huay Kaew Road, Muang District, Chiang Mai 50200, Thailand

[8] Endemic Species Research Institute, Taiwan, 552005 No. 1 Mingsheng East Road, Jiji Township, Nantou County, Taiwan