

Updates of Taxonomic Treatments for Ferns of Japan 1. *Botrychium*, *Osmolindsaea* and *Pteris*

Atsushi Ebihara^{1,*}, Narumi Nakato² and Sadamu Matsumoto¹

¹Department of Botany, National Museum of Nature and Science,
Amakubo 4-1-1, Tsukuba, Ibaraki 305-0005, Japan

²Narahashi 1-363, Higashiyamoto-shi, Tokyo 207-0031, Japan

*E-mail: ebihara@kahaku.go.jp

(Received 11 November 2014; accepted 24 December 2014)

Abstract Reflecting the results of recent studies on Japanese ferns, some new taxonomic treatments are proposed including three new hybrid taxa, *Botrychium* × *silvicola* (= *B. atrovirens* × *B. japonicum*), *Osmolindsaea* × *yakushimensis* (= *O. japonica* × *O. odorata*) and *Pteris* × *pseudosefuricola* (= *P. cretica* × *P. multifida*).

Key words: *Botrychium*, ferns, hybrids, Japan, *Osmolindsaea*, *Pteris*.

Japan is considered as one of the most advanced areas in studies of fern flora (e.g. Iwatsuki *et al.*, 1995), and even nowadays it has been updated continually by additions of new taxa, especially interspecific hybrids. We propose some new taxonomic treatments for the flora to fit the names to their biological entities inferred from morphological, cytological or molecular evidences.

1. A new hybrid combination for *Botrychium* (Ophioglossaceae)

Sceptridium japonicum (Prantl) Lyon var. *silvicola* Sahashi was originally described from Oshima Island (Sahashi, 1983a), Tokyo, Japan. The author, commenting that this taxon is a probable hybrid between *S. japonicum* and *S. atrovirens* (Sahashi) M.Kato from the viewpoint of its habitat and gross morphology, described it as a variety, not a hybrid probably because it produces normal tetrahedral spores (Sahashi, 1983b). Based on the results of our nuclear DNA analyses (A. Ebihara and Y. Watano, unpublished) that showed its genotype is a combination of unique alleles in *S. japonicum* and *S. atrovirens*, it is better to be treated as a hybrid taxon in accordance

with the presently accepted species concept that recognizes the two hexaploid parental lineages as independent species (Sahashi, 1979). At the moment, it is uncertain whether the spores are truly fertile or sterile but with normal external shape, and testing the viability of spores in the groups producing mycotrophic gametophytes is time-consuming (Whittier and Peterson, 1984; Takahashi and Imaichi, 2007), but, none the less it is worthwhile to clarify the grounds for apparent fertility of this 'hybrid' taxon, and also the boundary of species in predominantly inbreeding ferns (Watano and Sahashi, 1992).

Botrychium* × *silvicola (Sahashi) Ebihara, **stat. nov.**

— *Sceptridium japonicum* (Prantl) Lyon var. *silvicola* Sahashi, J. Jpn. Bot. 58: 241, Fig. 1B & Fig. 2, 1983. — *Botrychium japonicum* (Prantl) Underw. var. *silvicola* (Sahashi) M.Kato, Fl. Jap. 1: 26, 1995.

Jap. Name: Gojinka-hanawarabi.

Distribution: Tokyo Metropolis, Izu Islands.



Fig. 1. Holotype of *Osmolindsaea yakushimensis* Ebihara et Nakato (*N. Nakato 1018*, TNS [VS-469765], voucher of chromosome count $2n=235$, pentaploid). A: the whole sheet (scale bar=5 cm); B: fertile lamina (scale bar=1 cm).



Fig. 2. *Osmolindsaea* × *yakushimensis* in Yakushima Isl., growing on moist, stream-side rocks (photograph by T. Oka in April 2013).

2. A new hybrid of *Osmolindsaea* (Lindsaeaceae)

Osmolindsaea odorata (Roxb.) Lehtonen et Christenh., the type species of the recently established genus *Osmolindsaea* (Lehtonen *et al.*, 2010) is distinct from *O. japonica* (Baker) Lehtonen et Christenh., a closely related taxon often placed at its varietal rank, in ploidy level — i.e. *O. odorata* is hexaploid ($n = 150$, Manickam and Irudayaraj, 1988; $n = 155$, Kurita, 1962) and *O. japonica* is tetraploid ($n = \text{ca. } 80$, Mitui, 1976; $n = \text{ca. } 75$, $2n = \text{ca. } 150$, Lin *et al.*, 1990). In Yakushima Isl. in southern Japan, where the two species sometimes grow nearby, morphologically intermediate forms are observed. The voucher specimen of pentaploid “*O. odorata*” by Nakato (1987) best matches the intermediate forms, and the ploidy level is intermediate accordingly. We concluded that this is an interspecific hybrid between *O. japonica* and *O. odorata*. The presence of this hybrid or intermediate form has been suggested several times (e.g. Nakaïke, 1982; Lehtonen *et al.*, 2013) but this is the first record with an obvious citation of specimens.

Osmolindsaea × *yakushimensis* Ebihara et Nakato, **hybr. nov.** (Figs. 1, 2)

Jap. Name: Koke-hongu-shida (first appeared

in Sugimoto [1966]).

Differs from *O. japonica* in its frequently interrupted sori, and from *O. odorata* in its smaller frond sizes and stream-side habitat. Produces irregular spores.

Typus: JAPAN. Kagoshima Pref., Yakushima Isl., Hanaage-gawa River. 1981-12-18. *N. Nakato 1018*, voucher of chromosome count $2n = 235$ (holo-TNS [VS-469765]).

Distribution: Japan (Yakushima Isl.) and possibly in Taiwan (Lehtonen *et al.*, 2013).

Habitat: On moist, stream-side rocks, not very close to the water surface as in *O. japonica*.

A pentaploid hybrid between *O. japonica* and *O. odorata*. Rhizomes short creeping, densely covered with brown scales, ca. 0.5 mm long, 1–4-cell wide at bases, bearing fronds at intervals of 0.5–1 cm. Stipes stramineous to purplish with darker bases, 2–4 cm long. Laminae lanceolate in outline, 5–10 × 1.2–2.0 cm, 1-pinnate. Lateral pinnae 12–17 pairs, shortly stalked, dimidiate, 0.6–1.0 × 0.3–0.5 cm at middle portion, often significantly shortened at basal parts. Sori marginal, interrupted, forming 2–6 oblong ones per pinna.

Note: The frond shape and size in general are similar to those of larger individuals of *O. japonica*, but the marginal sori are often interrupted as in *O. odorata*.

Additional specimens examined: Japan. Kagoshima Pref., Yakushima Isl., Nakase-gawa River. 1973-3-27. *H. Miyazaki s.n.* (TNS [VS-806058]).

3. Identity of ‘*Pteris* × *sefuricola*’ (Pteridaceae)

Though not yet published validly, the name ‘*Pteris* × *sefuricola* Sa. Kurata’ has been widely used as a name for the interspecific hybrid between *P. cretica* L. and *P. multifida* Poir. (e.g. Kurata and Nakaïke, 1994, 1997; Iwatsuki *et al.*, 1995). The plant was first noticed by Mr. S. Tsutsui at Kanayama, Sawara-machi, Fukuoka Prefecture located in the Sefuri Mountain Range, and was later recorded throughout the mainland Japan (Kurata, 1977). Its partly winged rachis is clearly intermediate between the two parental species, but a degree of infraspecific variation

has been known, including variation in the vein character of the sterile lamina (for example every vein reaches the margin in some individuals but veins terminating short of the margin are mixed in others) and the ratio of the production of normal spores (for example all spores are normal in some individuals but mostly abortive or irregular-shaped in others). Although Kurata (1977) denied correlation between the vein character and the ratio of normal spores, Yamazumi (1989) successfully grouped '*P. × sefuricola*' individuals collected in Minoh, Osaka Pref. into two types, namely, the "M-type" and the "C-type". The "M-type" had veins not reaching the margin and produced mostly irregular-shaped spores, while the "C-type" had veins reaching the margin and produced normal spores by apogamous reproduction. We also observed that all the specimens, whose veins were confirmed to reach the margin, produced only normal spores. These observations suggested that '*P. × sefuricola*' represents a mixture of two different biological entities rather than a complex with clinal variation. All known traits of the "M-type" are well explained by combining those of *P. cretica* and *P. multifida*; its tetraploidy probably originated from fertilization between a reduced diploid egg of sexual tetraploid *P. multifida* and an unreduced diploid sperm of apogamous diploid cytotype of *P. cretica*. Although both Kurata (1977) and Yamazumi (1989) hypothesized that the "C-type" is stabilized progenies of the "M-type", the "C-type", an apogamous diploid ($2n = 58$, Yamazumi [1989]), is not cytologically identical with the tetraploid "M-type" ($2n = 116$, Nakato, 1975; Matsumoto [1976]). Alternatively, a more natural hypothesis would be that the "C-type" is an extreme form of *P. cretica* with well developed wings of rachis. This hypothesis is supported by our molecular data, which showed that chloroplast *rbclA*-sequences (700 bp) of a "C-type" individual collected in Shirada, Higashiizu-cho, Shizuoka Pref. (TNS [VS-1225892]) is identical to two of those of *P. cretica* (AB697620, AB697621, Jaruwattanapan *et al.*, 2013). In other words, the maternal parent of the "C-type" is not *P. multifida* but

P. cretica.

Keys to the plants formerly identified as 'P. × sefuricola'

1a. Veins of sterile fronds usually not reaching cartilaginous margins. Spores mostly irregular, sometimes almost normal

..... *P. × pseudosefuricola*

1b. Veins of sterile fronds always reaching cartilaginous margins. Spores normal

..... *P. cretica* (a winged form) [Figs. 3, 5a]

Pteris × pseudosefuricola Ebihara, Nakato et S. Matsumoto, **hybr. nov. (Figs. 4, 5b)**

— *Pteris × sefuricola* Sa. Kurata, nom. nud., p.p.

Jap. Name: Ai-inomotoso.

Differs from *Pteris cretica* in having veins not reaching cartilaginous margins in sterile lamina.

Typus: JAPAN. Tokyo Metropolis, Shinagawa-ku, near the Embassy of Burma, early September, 1970. *S. Matsumoto 2326* (holo-TNS [VS-1220664]).

Plants originated from hybridization between *P. cretica* and *P. multifida*. Rhizomes short creeping or ascending, bearing linear, brown scales, up to 5 mm long. Fronds more or less dimorphic. Stipes stramineous, sometimes brownish, 10–70 cm long in fertile ones, 10–55 cm long in sterile ones, bearing sparse hairs. Fertile laminae ovate to lanceolate in outline, 15–45 × 10–40 cm, 1-pinnate, papyraceous, pale green, terminal pinnae 10–40 × 0.6–1.5 cm, lateral pinnae 2–5 pairs, lowest ones often bilobed, 7–30 × 1.7–2.2 cm, segments 0.5–1.4 cm wide, base of the first (uppermost) pair of lateral pinnae decurrent toward rachis at least halfway to the second lateral pinnae, base of the second pair of lateral pinnae decurrent toward rachis slightly, lower pinnae short-stalked, margins dentate at sterile parts. Sterile laminae ovate in outline, slightly smaller than fertile ones, 10–40 × 6–30 cm, 1-pinnate, terminal pinna 6–30 × 1.0–2.3 cm, lateral pinnae 1–5 pairs, lowest ones often bilobed, 6–23 × 2–14 cm, segments 0.9–2.0 cm wide, base of the first (uppermost) pair of lateral pinnae decurrent toward rachis at least halfway to the second lat-



Fig. 3. A winged form of *Pteris cretica*, a duplicate of the original collection, to which '*P. × sefuricola* Sa. Kurata' was given (S. Tsutsui 779, TNS [VS-1161733]).



Fig. 4. Holotype of *Pteris* × *pseudosefuricola* Ebihara, Nakato et S. Matsumoto (*S. Matsumoto* 2326, TNS [VS-1220664]).

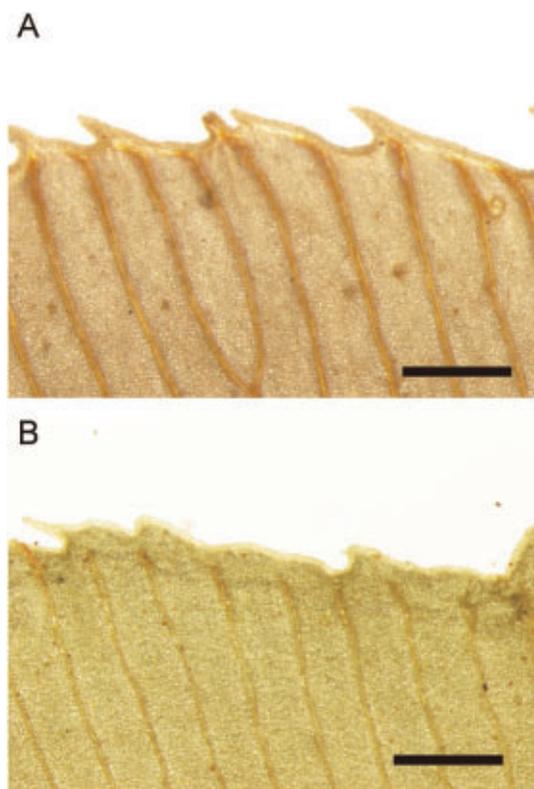


Fig. 5. Veins at the margins in sterile fronds. A: a winged form of *Pteris cretica* (S. Tsutsui 779, TNS [VS-1161733]) with veins reaching cartilaginous margins; B: *Pteris* × *pseudosefuricola* (S. Matsumoto 2326, TNS [VS-1220664]) with veins terminating short of cartilaginous margins. Scale bar = 1 mm.

eral pinna, lower pinnae short-stalked, margins dentate and cartilaginous, veins often terminating short of the cartilaginous margins. Sori elongate along margins of pinnae, covered by false indusia.

Note: We examined a duplicate specimen of the original material of '*Pteris* × *sefuricola*' (Kurata, 1977) kindly provided by Mr. S. Tsutsui, and confirmed that its veins reach the margins: i.e. it is a winged form of *P. cretica*. We then explored additional specimens from Sefuri Mountains where the original material was collected. As a result, we found out that all the collections obtained from the area as '*Pteris* × *sefuricola*' were actually *P. cretica*. This

observation indicates that it is difficult to validate the name '*Pteris* × *sefuricola*' for the hybrid taxon — '*P.* × *sefuricola*' is not present in the Sefuri Mountains. Here, we provide a new epithet for the hybrid to avoid etymological confusion.

Both triploid (Nakato and Hyodo, 2011) and tetraploid cytotypes (Nakato, 1975; Matsumoto, 1976) are known, and the former is known only from Ehime Prefecture (Nakato and Hyodo, 2011). Molecular analyses by Jaruwattanaphan *et al.* (2013) suggested that the tetraploid cytotype originated from hybridization between *P. cretica* and *P. multifida*, but the origin of triploid has been unresolved. The tetraploid can produce normal shape spores only at a low ratio (ca. 5%), but the normal spore germinates, and the resultant gametophyte can form sporophyte by apogamy (Nakato, 1975). While the triploid produced normal spores at a higher ratio (ca. 90%) (Nakato and Hyodo, 2011).

Additional specimens examined. JAPAN. Gunma Pref. Tano-gun, Yoshii-machi, Shio-Higashiya, 1980-12-28, *T. Waku 10513* (TNS [VS-1192025]). Saitama Pref. Chichibu-gun, Minano-machi, Kanazawa, 1983-10-31, *T. Iwata 2376* (TNS [VS-932216]). Tokyo Metropolis. Ome-shi, Sawai, 1973-9-?, *N. Nakato s.n.* (TNS [VS-328656], voucher of Fig. 1 of Nakato [1975], TNS [VS-328658], voucher of Fig. 3 of Nakato [1975]), 1973-3-10, *N. Nakato s.n.* (TNS [VS-328663], 'sample no. 5', TNS [VS-328864] 'sample no. 6', voucher of Nakato [1975]); Shizuoka Pref. Numazu-shi, Washizu-san, cultivated stock of Tsukuba Botanical Garden [TBG79443], *S. Matsumoto 70-8-1* (TNS [VS-1179254] tetraploid, voucher of Jaruwattanaphan *et al.*, 2013). Shizuoka Pref. Numazu-shi, Washizu-san, cultivated stock of Tsukuba Botanical Garden [TBG126793], *T. Hosokura SM990731-30* (TNS [VS-1179256], tetraploid, voucher of Jaruwattanaphan *et al.*, 2013); Kamo-gun, Kawazu-cho, Nashimoto, cultivated stock of Tsukuba Botanical Garden [TBG126794], *T. Hosokura SM990731-31* (TNS [VS-1179255], tetraploid, voucher of Jaruwattanaphan *et al.*, 2013). Aichi

Pref. Chita-gun, Minamichita-cho, Ohi, 1986-2-16, *K. Inukai 7603* (TNS [VS-944208]); Hazu-gun, Isshiki-cho, Tsuigome, 1990-10-25, *K. Inukai 10620* (TNS [VS-944209]); Toyohashi-shi, Ishimaki-san, 1977-12-10, *T. Waku 8175* (TNS [VS-1192026]). Mie Pref. Inabe-gun, Fujiwara-cho, Nishinojiri, foot of Mt. Fujiwara-dake, alt. 150 m, 1985-6-22, *F. Miyamoto s.n.* (TNS [VS-808092]); Hokusei-cho, Tashida Valley, 1976-12-11, *T. Waku 5654* (TNS [VS-1192027]); Suzuka-gun, Seki-cho, Kabuto Pass — Fudo-taki Fall, 1975-11-9, *H. Miyazaki 4204* (TNS [VS-808113]); Owase-shi, Mikisato, Yasogawa, 1988-3-6, *K. Ohora 18686* (TNS [VS-9508457]); Kitamuro-gun, Kii-nagashima-cho, Ohara, Mukai, 1991-3-7, *Y. Higuchi s.n.* (TNS [VS-944214]). Osaka Pref. Minoh-shi, Minoh Park, 1976-10-17, *T. Oka s.n.* (TNS [VS-1102029]). Wakayama Pref. Higashimuro-gun, Kumanogawa-cho, Shiko-dani, alt. 150 m, 1991-11-24, *K. Seto 37615* (TNS [VS-723612]). Okayama Pref. Kibi-gun, Showa-cho, Yandani, 1977-2-12, *T. Nakaike s.n.* (TNS [VS-944227]). Yamaguchi Pref. Saba-gun, Tokuji-cho, under Sabagawa Dam, 1992-8-17, *A. Minami 82764* (TNS [VS-944164]); Iwakuni-shi, Akadani, 1992-3-2, *A. Minami s.n.* (TNS [VS-944173]). Ehime Pref. Shikokuchuo-shi, Doi-cho, Ohkawa, 2003-4-12, *S. Hyodo 10711* (TNS [VS-1192023]); Kita-gun, Uchiko-cho, Ikazaki, Fukuoka, 2009-2-23, *S. Hyodo 13721* (TNS [VS-1138395], $2n = 87$, triploid, voucher of Nakato and Hyodo [2011]), Shukuma, 1978-11-5, *S. Hyodo 9* (TNS [VS-378871]); Iyo-shi, Futami-cho, Kaminada, Ohe, 2008-12-14, *S. Hyodo 13483* (TNS [VS-1192020]); Niihama-shi, Hagyu, 2009-12-11, *S. Hyodo 14021* (TNS [VS-1192021]); Seiyo-shi, Mikame-cho, Minae, 2012-2-12, *S. Hyodo 15699* (TNS [VS-1192022]). Fukuoka Pref. Tagawa-gun, Kawara-machi, Seto, alt. 60 m, 1970-12-29, *S. Tsutsui 7429* (TNS [VS-1192024]). Kumamoto Pref. Aso-gun, Choyomura, Kawayo, alt. 300 m, cultivated stock of Tsukuba Botanical Garden [TBG133346], *S. Matsumoto 01-023* (TNS [VS-1179257], tetraploid, voucher of Jaruwattanaphan *et al.*, 2013); Kuma-gun, Itsuki-mura, 1974-2-9, *N. Sahashi*

s.n. (TNS [VS-366901]).

4. On the type material of *Pteris semipinnata* L.

The name *Pteris semipinnata* L. was described from China and has been usually applied to a plant species widely distributed in Asian tropics. Its closely related species, *P. dispar* Kunze was later described from a material collected in Japan, and is generally recognized as an East Asian plant ranging from Japan to China. This latter species differs from *P. semipinnata* in that the segments are narrower and the veins reach the margin (tip of teeth) of the frond in its sterile part. Kuo (1985) synonymized *P. dispar* under *P. semipinnata* after examining the type material of *P. semipinnata* in LINN (an image available at <http://linnean-online.org/12507/>), and accepted the name *P. dimidiata* Willd. for the plant formerly called '*P. semipinnata*'. However, his treatment has been followed by only a small number of subsequent Taiwanese publications, and the traditional treatment has been maintained in most of the recent flora of East Asia (e.g. Japan [Iwatsuki *et al.*, 1995], China [Zhang *et al.*, 2013] and Taiwan [Knapp, 2011]). Fraser-Jenkins (2008) also advocated the traditional treatment based on his identification: the type sheet of *P. semipinnata* was considered a mixture of two species, namely '*P. semipinnata*' in the traditional sense (the right-handed frond) and '*P. dispar*' in the traditional sense (the left-handed frond). The basis of his identification of the left-handed frond as '*P. dispar*' was its developed acroscopic lobes. However, the degree of acroscopic lobe development is variable in '*P. dispar*' (Nakato, 2012) and two fronds of the type sheet undoubtedly fall into the range of '*P. dispar*'. This justifies Kuo (1985)'s opinion and therefore we can no longer apply the name *P. semipinnata* in the traditional sense, and *P. semipinnata* should be used as the correct name for the plant formerly called '*P. dispar*'. On the other hand, the suggestion by Fraser-Jenkins (2008) that "Kuo overlooked the earlier name *Pteris alata* Lam., which also applies to *P. semipinnata*" is also justified and here we accept

Pteris alata Lam. as the correct name for '*P. semipinnata*' in the traditional sense instead of *P. dimidiata*.

Pteris alata Lam., Tabl. Encycl. t. 869, 1799.

Pteris dimidiata Willd., Sp. Pl. 5: 381, 1810.

Pteris semipinnata auct. non L.

Jap. Name. O-amakusa-shida

Distribution. Throughout E Asia, SE Asia and S Asia.

Pteris semipinnata L., Sp. Pl. 2: 1076, 1753.

Pteris dispar Kunze, Bot. Zeit. 6: 539, 1848.

Jap. Name. Amakusa-shida

Distribution. Japan, Korea, China and Taiwan.

Acknowledgments

We are grateful to S. Tsutsui for providing specimens of '*Pteris* × *sefuricola*' and T. Oka for providing a photograph of *Osmolindsaea* × *yakushimensis*. This study was partly supported by JSPS KAKENHI (Grant no. 24770083 to A.E.).

References

- Fraser-Jenkins, C. R. 2008. Taxonomic Revision of Three Hundred Indian Subcontinental Pteridophytes with a Revised Census-List. 686 pp. Bishen Singh Mahendra Pal Singh, Dehra Dun.
- Iwatsuki, K., Yamazaki, T., Boufford, D. E. and Ohba, H. 1995. Flora of Japan, Vol. I, Pteridophyta and Gymnospermae. 302 pp. Kodansha, Tokyo.
- Jaruwattanaphan, T., Matsumoto, S. and Watano, Y. 2013. Reconstructing hybrid speciation events in the *Pteris cretica* group (Pteridaceae) in Japan and adjacent regions. Systematic Botany 38: 15–27.
- Knapp, R. 2011. Ferns and Fern Allies of Taiwan. 1054 pp. KBCC Press, Taipei.
- Kuo, C.-M. 1985. Taxonomy and phytogeography of Taiwanese pteridophytes. Taiwania 30: 5–99.
- Kurata, S. 1977. 25 new ferns (3). Journal of Nippon Fernist Club 2(30): 510–512 (in Japanese).
- Kurata, S. and Nakaike, T. 1994. Illustrations of Pteridophytes of Japan. Volume 7. 412 pp. The University of Tokyo Press, Tokyo.
- Kurata, S. and Nakaike, T. 1997. Illustrations of Pteridophytes of Japan. Volume 8. 476 pp. The University of Tokyo Press, Tokyo.
- Kurita, S. 1962. Chromosome numbers of some Japanese ferns (III). Journal of College of Arts and Sciences, Chiba University 3: 463–468.
- Lehtonen, S., Tuomisto, H., Rouhan, G. and Christenhusz, M. J. M. 2010. Phylogenetics and classification of the pantropical fern family Lindsaeaceae. Botanical Journal of the Linnean Society 163: 305–359.
- Lehtonen, S., Tuomisto, H., Rouhan, G. and Christenhusz, M. J. M. 2013. Taxonomic revision of the fern genus *Osmolindsaea* (Lindsaeaceae). Systematic Botany 38: 887–900.
- Lin, S.-J., Kato, M. and Iwatsuki, K. 1990. Sporogenesis, reproductive mode, and cytotaxonomy of some species of *Sphenomeris*, *Lindsaea*, and *Tapeinidium* (Lindsaeaceae). American Fern Journal 80: 97–109.
- Manickam, V. S. and Irudayaraj, V. 1988. Cytology of ferns of the Western Ghats (South India). 51 pp. Today and Tomorrow's Printers & Publishers, New Delhi.
- Matsumoto, S. 1976. Cytogenetic studies on relatives of *Pteris cretica* and *P. multifida*. Bulletin of Japan Pteridological Society 46: 2–3 (in Japanese).
- Mitui, K. 1976. Chromosome numbers of some ferns in the Ryukyu Islands. Journal of Japanese Botany 51: 33–41.
- Nakaike, T. 1982. New Flora of Japan. Pteridophyta. 810 pp. Shibundo, Tokyo (in Japanese).
- Nakato, N. 1975. A cytological study on an intermediate form between *Pteris multifida* and *P. cretica*. Journal of Japanese Botany 50: 119–125 (in Japanese, with English summary).
- Nakato, N. 1987. Notes on chromosomes of Japanese pteridophytes (1). Journal of Japanese Botany 62: 261–267.
- Nakato, N. 2012. An abnormal diploid plant of *Pteris dispar* (Pteridaceae) showing irregular spore formation. Journal of Phytogeography and Taxonomy 60: 39–42 (in Japanese, with English summary).
- Nakato, N. and Hyodo, S. 2011. The origin of triploid *Pteris* × *sefuricola* (Pteridaceae) from Ehime Prefecture, Japan. Journal of Phytogeography and Taxonomy 58: 115–121 (in Japanese, with English summary).
- Sahashi, N. 1979. Morphological and taxonomical studies on Ophioglossales in Japan and the adjacent regions (3). Identity of *Sceptridium* Lyon in the Izu Islands. Journal of Japanese Botany 54: 241–281.
- Sahashi, N. 1983a. Morphological and taxonomical studies on Ophioglossales in Japan and the adjacent regions (8). New taxa of *Sceptridium* in Isl. Oshima, the Izu Islands. Journal of Japanese Botany 58: 240–247.
- Sahashi, N. 1983b. Morphological and taxonomical studies on Ophioglossales in Japan and the adjacent regions (9). Additional notes on *Sceptridium* in Isl. Oshima, the Izu Islands. Journal of Japanese Botany 58: 338–344.

- Sugimoto, J. 1966. Keys to Herbaceous Plants of Japan III. Pteridophyta. 460 pp. Rokugatsusha, Tokyo (in Japanese).
- Takahashi, N. and Imaichi, R. 2007. Developmental morphology of young gametophytes of *Botrychium microphyllum* in axenic culture. *Journal of Japan Women's University, Faculty of Science* 15: 45–49.
- Watano, Y. and Sahashi, N. 1992. Predominant inbreeding and its genetic consequences in a homosporous fern genus, *Sceptridium* (Ophioglossaceae). *Systematic Botany* 17: 486–502.
- Whittier, P. and Peterson, R. L. 1984. Gametophytes of *Botrychium lunarioides* and their mucilage-coated rhizoids. *Canadian Journal of Botany* 62: 2854–2860.
- Yamazumi, I. 1989. About *Pteris* × *sefuricola*. *Kinki Shokubutsu Dokokai Kaiho* 47: 1–2 (in Japanese).
- Zhang, G. M., Liao, W. B., Ding, M. Y., Lin, Y. X., Wu, Z. H., Zhang, X. C., Dong, S. Y., Prado, J., Gilbert, M. G., Yatskievych, G., Ranker, T. A., Hooper, E. A., Alverson, E. R., Metzgar, J. S., Funston, A. M., Masuyama, S. and Kato, M. 2013. Pteridaceae. In Wu, Z. Y., Raven, P. H. and Hong, D. Y. (eds.) *Flora of China*, Vol. 2–3 (Pteridophytes), pp. 169–256. Science Press, Beijing and Missouri Botanical Garden Press, St. Louis.