

Hybrids in the Fern Genus *Osmunda* (Osmundaceae)

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Abstract Four described putative hybrids in genus *Osmunda*, *O. intermedia* from Japan, *O. ruggerii* from eastern U.S.A., *O. nipponica* from central Japan, and *O. mildei* from southern China, are enumerated with notes on their hybridity. It is suggested that *Osmunda intermedia* is an intrasubgeneric hybrid (*O. japonica* of subgenus *Osmunda* × *O. lancea* of subgenus *Osmunda*), *O. ruggerii* is an intersubgeneric hybrid (*O. regalis* of subgenus *Osmunda* × *O. claytoniana* of subgenus *Claytosmunda*), *O. nipponica* is an intersubgeneric hybrid (*O. japonica* × *O. claytoniana* of subgenus *Claytosmunda*), and *O. midlei* is an intersubgeneric hybrid (*O. japonica* × *O. angustifolia* or *O. vachellii* of subgenus *Plenasium*). Among the four, *O. intermedia* is the most widely distributed and can reproduce in culture, suggesting that it can reproduce to some extent in nature.

Key words: Hybrid, *Osmunda intermedia*, *Osmunda mildei*, *Osmunda nipponica*, *Osmunda ruggerii*.

Introduction

The genus *Osmunda* has been classified in either the broad or narrow sense. In the previously most accepted and the most lumping classification, it was divided into three subgenera, *Osmunda*, *Osmundastrum* and *Plenasium* (Ching *et al.*, 1959; Kramer and Green, 1991; Whetstone and Atkinson, 1993; Iwatsuki, 1995). In the most splitting classification, *Osmunda s.l.* was recognized to comprise three genera, *Osmunda*, *Osmundastrum* and *Plenasium* (Tagawa, 1941, 1959; Bovrov, 1967). Recent molecular analyses demonstrated that *Osmunda cinnamomea* or *Osmundastrum cinnamomeum* is the less closely related to *Osmunda s.s.* even than genera *Leptopteris* and *Todea*, and *Osmunda claytoniana* or *Osmundastrum claytonianum* is sister to a clade of *Osmunda s.s.* and *Plenasium* (Yatabe *et al.*, 1999; Metzgar *et al.*, 2008). Recently, Yatabe *et al.* (2005) proposed a new subgenus *Claytosmunda* for *Osmunda claytoniana*. As a result, *Osmunda s.l.* is a paraphyletic group and the family Osmundaceae is classified into four genera and three subgenera, i.e., genus *Osmunda s. s.* with

three subgenera *Claytosmunda*, *Osmunda*, and *Plenasium*, genus *Leptopteris*, genus *Todea*, and genus *Osmundastrum* (see also Metzgar *et al.*, 2008).

Four putative hybrids are known in the genus *Osmunda s.l.* in eastern U.S.A. and eastern Asia and are intrasubgeneric (subgenus *Osmunda s.s.*) or intersubgeneric (subgenera *Osmunda* and *Plenasium*, and subgenera *Osmunda* and *Claytosmunda*). Yatabe *et al.* (1999) estimated that *Osmundastrum cinnamomeum* diverged from the rest 294 million years ago (MYA), a clade of *Leptopteris* and *Todea* diverged 210 or 206 MYA, and *Osmunda s.s.* diverged from *Plenasium* 150 MYA. If the estimation is reasonable, part of the hybrids are derived from parental species that diverged long time ago. The hybrids vary not only in the systematic and evolutionary backgrounds, but also in fertility. *Osmunda* × *intermedia* is somewhat fertile and the others are sterile. Those hybrids were described or analyzed in separate papers. In this paper the four hybrids are compared together.

Enumeration of hybrids

Osmunda* × *intermedia (Honda) Sugim., *Shokubutu Kensakushi* 1: 9. 1951; *Key Herb. Pl. Jap. Pterid.* 114. 1966; Nakaike, *Enum. Pterid. Jap.* 6. 1975; *New Fl. Jap. Pterid. Rev. & enlarged ed.* 88, f. 88. 1992; K. Iwats., *Fl. Jap.* 33. 1995—*O. japonica* var. *intermedia* Honda, *Bot. Mag. (Tokyo)* 44: 409. 1930—*O. lancea* Thunb. var. *lancea* f. *intermedia* (Honda) Tagawa, *Acta Phytotax. Geobot.* 15: 96. 1953; *Col. Ill. Jap. Pterid.* 35, 237. 1959. Type. *Honda s.n.*, anno. 1930 (TI !), Hikawa, Musashi (Tokyo metropolitan), Japan. [Fig. 1]

Osmunda lancea var. *latipinnula* Tagawa, *J. Jap. Bot.* 22: 160. 1948; *Col. Ill. Jap. Pterid.* 35, 237. 1959. Type. *Tagawa 2338* (KYO !), Nachi, Wakayama Pref.

Distribution. Japan (Honshu, Shikoku, Kyushu).

Cytology. $n=22$ (22II [36.6%], 21II+2I [3.2%], 1IV+20II [31.0%], 1IV+19II+2I [2.4%], 2IV+18II [15.9%], 2IV+17II+2I [1.3%], other pairings [9.6%]) (Shimura and Matsumoto, 1977). $n=22$ (Kurita, 1963). $2n=44$ (Tatuno and Yoshida, 1966).

Notes. This is an intrasubgeneric hybrid *Osmunda japonica* × *O. lancea*, which is supported morphologically (Tagawa, 1959; Iwatsuki, 1995) and karyologically (Tatuno and Yoshida, 1966). *Osmunda japonica* is distributed in eastern Asia extending west to the western Himalaya and south to northern Vietnam, while *O. lancea* is endemic to Japan and is a rheophyte growing in stream banks and bed rocks (Watano, 1986; Kato, 2007). *Osmunda* × *intermedia* occurs lo-



Fig. 1. *Osmunda* × *intermedia* in Hanno, Japan.

cally abundantly in and above stream banks but does not invade forest edges where *O. japonica* grows (Shimura, 1964). In an experimental condition, spores of the hybrid germinated and grew into gametophytes with both archegonia and antheridia or one of them. Several sporophytes arise from gametophytes, indicating that the hybrid can reproduce via spores in culture condition (Shimura, 1972). Young sporophytes occur in nature (Kato, Yatabe-Kakugawa and Tsutsumi, unpublished data). Thus, *Osmunda* × *intermedia* is the only hybrid that is partially reproducible among the four *Osmunda* hybrids: sporophylls are not rare in nature, though not typically normal (Shimura, 1964, 1972; Kato, Yatabe-Kakugawa and Tsutsumi, unpublished observations). It may be due to its intrasubgeneric hybridity involving the closely related parental species and the frequent occurrence of normal and subnormal meiosis (Shimura and Matsumoto, 1977).

Morphologically, *Osmunda* × *intermedia* is intermediate particularly in that the pinnule has an unequal base, i.e., a cuneate acroscopic base and a round or widely cuneate basiscopic base. The pinnule-base trait is ecologically significant for rheophytes with the pinnule-base suffered from water-current pressure while plants are submerged in turbulent currents (van Steenis, 1981; Imaichi and Kato, 1992). It may result in the ecological intermediacy noted above.

As pointed out by Tagawa (1953), *Osmunda* × *intermedia* is variable. It includes plants close to *O. lancea*, which were called *O. lancea* var. *lancea* f. *intermedia* (Honda) Tagawa, and those somewhat close to *O. japonica*, which were called *O. lancea* var. *latipinnula* Tagawa. Our field observations (Kato, Yatabe-Kakugawa and Tsutsumi, unpublished) reveal a considerable variation of *O. intermedia*, although not supporting Tagawa's taxonomy. This variation may be caused by phenotype segregation of F₂ or later progeny, multiple origins, and/or back-crosses.

Osmunda* × *ruggii R. M. Tryon, Amer. Fern J. **30**: 65. 1940; Whetstone et Atkinson, Fl. N. Amer. **2**: 109. 1993. Type. *Rugg* s.n. (GH, not

seen), Grafton Co., New Hampshire, USA.

[Fig. 2]

Distribution. Eastern U.S.A. (Connecticut, Virginia).

Cytology. $2n=44$ (all univalents) (Wagner *et al.*, 1978).

Notes. This is an intersubgeneric sterile hybrid *Osmunda regalis* of subgenus *Osmunda* × *O. claytoniana* of subgenus *Claytosmunda*, supported by morphology, cytology, chemotaxonomy, and allozyme polymorphism (Tryon, 1940; Wagner *et al.*, 1978; Whetstone and Atkinson, 1993; Li and Haufler, 1994). The hybrid grows together with the parents (Wagner *et al.*, 1978). One of two populations is extirpated and the existing other is estimated to be more than 1100 years old (Whetstone and Atkinson, 1993).

Wagner *et al.* (1978) described that the hybrid is sterile in nature, but transplants produced fertile pinnae with reduced laminae and produced aborted spores, but chromosomes at meiosis were all univalents.

Osmunda* × *nipponica Makino, Bot. Mag. (Tokyo) **26**: 385. 1912; C. Chr., Ind. Fil. Suppl. **2**: 24. 1917; Nakai, Bot. Mag. (Tokyo) **41**: 681. 1927; Tagawa, Col. Ill. Jap. Pterid. **34**, 237. 1959; H. Ito, J. Jap. Bot. **39**: 248. 1964; Sugim., Keys Herb. Pl. Jap. Pterid. **115**. 1966; Nakaike, Enum. Pterid. Jap. **6**. 1975; New Fl. Jap. Pterid. Rev. & enlarged ed. **88**, f. 88. 1992. Type. *F. Uhara* s.n. Aug. 1909 (MAK!), Mt. Akagi, Gunma Prefecture, Japan. [Fig. 3]

Distribution. Central Honshu, Japan (single and type locality, Mt. Akagi, Gunma Pref.)

Cytology. Unknown.

Notes. Little information is available for the hybridity of this fern. It looks like *O. ×ruggii* (Figs. 3, 4). A single specimen has been collected due to rarity and reproductive traits are unknown. It is similar to *O. japonica*, but the frond is less finely dissected with the pinnules hardly free from the costa, and the pinnae and pinnules are shorter. In these characters *Osmunda* × *nipponica* is also similar to *O. claytoniana* and *Osmundastrum cinnamomeum*. Ito (1964) suggested



Fig. 2. *Osmunda* × *ruggii* in Virginia, USA, provided by F. Wagner.

that this is an intersubgeneric hybrid *Osmunda japonica* of subgenus *Osmunda* × *O. claytoniana* of subgenus *Claytosmunda*. Sugimoto (1979) suggested that it is *O. japonica* × *Osmundastrum cinnamomeum* (*O. cinnamomea*), indicating a possibility that it is an intergeneric hybrid. It is reported that the putative hybrid grows together with the putative parents in the locality. Reproductive traits are unknown, but the sterile type specimen and extremely rarity may suggest that it is an intergeneric or intersubgeneric sterile hybrid.

Osmunda* × *mildei C. Chr., Ind. Fil. 474. 1906; Edie, Ferns Hong Kong 25, 59, f. 14. 1978; Wu, Fl. Guangdong 7: 38. 2006 — *O. bipinnata* Hook., Fil. Exot. t. 9, 1857, non L. 1753. Type. *Harland* (K?), Hong Kong. [Fig. 4]

Distribution. Hong Kong, Guangdong (Shenzhen), Jiangxi (Mt. Qiyun).

Cytology. $2n=44$ ($2sm+6st+33t+3T$) (He *et al.*, 2006), $n=44$ (usually univalents) (Zhang *et*

al., 2008).

Notes. This hybrid is characterized by the bipinnatifid leaf with round pinna-segments and lower fertile pinnae. This leaf morphology is reminiscent of *Osmunda* subgenera *Osmunda* and *Plenasium*, and less likely of subgenus *Claytosmunda* and genus *Osmundastrum*. In a karyological analysis, He *et al.* (2006) reported that *Osmunda mildei* has a karyotype of $2n=2sm+6st+33t+3T$, and, based on the karyological and morphological data, suggested that it is a hybrid of *O. japonica* with $2n=2sm+8st+32t(2SAT)+2T$ and *O. angustifolia* with $2n=2sm+4st+34t+2T$. *Osmunda angustifolia* is a rheophyte growing on stream banks or stream bed rocks and occurs in Hong Kong and Guangzhou (Guangdong).

Later, Zhang *et al.* (2008) described the absence of chromosome pairings at meiosis, which is abnormal, and resulting abortive spores in *O. mildei* and suggested that it is a sterile F_1 hybrid between *O. japonica* and *O. vachellii*, because *O. vachellii* occurs in the localities of *O. mildei*, but



Fig. 3. Holotype of *Osmunda* × *nipponica* (MAK) collected from Mt. Akagi, Japan.



Fig. 4. *Osmunda* × *mildei* in Shengzheng, China, photo image taken at Shenzhen FairyLake Botanical Garden with permission of S.-Z. Zhang.

O. angustifolia does not occur in some of the localities. Gou *et al.* (2008) also proposed this parentage from DNA sequence data. If *O. mildei* is a hybrid, *O. japonica* × either *O. angustifolia* or *O. vachellii*, it is an intersubgeneric sterile hybrid between subgenera *Osmunda* and *Plenasium*. Less than 10 individuals are known in a few localities, but *O. mildei* can propagate in experimental conditions (S.-Z. Zhang, personal commun.). It is uncertain whether it propagates in nature.

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References

- Bovrov, A. E. 1967. The family Osmundaceae (R. Br.) Kaulf.: its taxonomy and geography. *Botanicheskii Zhurnal* **52**: 1600–1610 (in Russian).
- Ching, R.-C., Fu, S.-H., Wang, C.-H. and Shing, G.-H. 1959. Osmundaceae. *Flora Reipublicae Popularis Sinicae* **2**: 77–85.
- Edie, H. H. 1978. Ferns of Hong Kong. Hong Kong Uni-

- versity Press, Hong Kong.
- Gou, C.-Y., Zhang, S.-Z. and Gen, S.-L. 2008. Phylogenetic position and genetic relationship of *Osmunda mildei* (Osmundaceae); evidence from *rbcL* gene and *trnL-trnF* region. *Acta Botanica Boreali-Occidentalia Sinica* **28**: 2178–2183.
- He, Z.-C., Li, Y., Yan, B., Zheng, M. and Zhang S.-Z. 2006. Karyotype analysis of five species in *Osmunda* (Osmundaceae). *Acta Phytotaxonomica Sinica* **44**: 617–626.
- Hewitson, W. H. 1962. Comparative morphology of the Osmundaceae. *Annals of Missouri Botanical Garden* **49**: 57–93.
- Imaichi, R. and Kato, M. 1992. Comparative leaf development of *Osmunda lancea* and *O. japonica* (Osmundaceae): heterochronic origin of rheophytic stenophylly. *Botanical Magazine (Tokyo)* **105**: 199–213.
- Ito, H. 1964. Type specimens of ferns in Makino Herbarium. *Journal of Japanese Botany* **39**: 247–249.
- Iwatsuki, K. 1995. Osmundaceae. In: K. Iwatsuki *et al.* (eds.), *Flora of Japan*. Vol. 1. Pteridophyta and Gymnospermae, pp. 31–33. Kodansha, Tokyo.
- Kato, M. 2007. Distribution of Osmundaceae. *Bulletin of National Museum of Nature and Science, Series B (Botany)* **33**: 81–90.
- Kato, M., Darnaedi, D. and Iwatsuki, K. 1991. Fern rheophytes of Borneo. *Journal of Faculty of Science, University of Tokyo, Section III (Botany)* **15**: 91–110.
- Kramer, K. U. and Green, P. S. (eds.) 1990. Pteridophytes and Gymnosperms. In: Kubitzki, K. (ed.), *The Families and Genera of Vascular Plants*, Vol. 1. Springer-Verlag, Berlin.
- Kurita, S. 1963. Cytotaxonomical studies on some leptosporangiate ferns. *Journal of College of Arts and Science, Chiba University* **4**: 43–52, with 3 plates.
- Li, J.-W. and Hauffler, C. H. 1994. Phylogeny, biogeography, and population biology of *Osmunda* species: insights from isozymes. *American Fern Journal* **84**: 105–114.
- Makino, T. 1912. Observations on the flora of Japan. *Botanical Magazine (Tokyo)* **26**: 384–399.
- Metzgar, J. S., Skog, J. E., Zimmer, E. A. and Pryer, K. M. 2008. The paraphyly of *Osmunda* is confirmed by phylogenetic analyses of seven plastid loci. *Systematic Botany* **33**: 31–36.
- Nakai, T. 1927. Notes on Japanese ferns VI. Osmundaceae, Schizaeaceae & Gleicheniaceae. *Botanical Magazine (Tokyo)* **41**: 673–696.
- Shimura, Y. 1964. Ecological study of *Osmunda lancea* Thunb. var. *latipinnula* Tagawa at the southern foot of Mt. Fuji, Japan. *Japanese Journal of Ecology* **14**: 147–153.
- Shimura, Y. 1972. Study of reproduction of *Osmunda × intermedia* Sugimoto. *Journal of Geobotany* **20**: 38–42.
- Shimura, Y. and Matsumoto, S. 1977. On the chromosomal association in meiosis of *Osmunda × intermedia*. *Journal of Japanese Botany* **52**: 377–378.
- Sugimoto, J. 1979. Keys to Herbaceous Plants of Japan. III. Pteridophyta. Revised and enlarged ed. Inoue Book Company, Tokyo.
- Tagawa, M. 1941. Osmundaceae of Formosa. *Journal of Japanese Botany* **17**: 692–703.
- Tagawa, M. 1948. Fern miscellany (1). *Journal of Japanese Botany* **22**: 160–165.
- Tagawa, M. 1953. On *Osmunda lancea*, *O. japonica* var. *intermedia* and *O. lancea* var. *latipinnula*. *Acta Phytotaxonomica et Geobotanica* **15**: 96.
- Tagawa, M. 1959. Coloured Illustrations of the Japanese Pteridophyta. Hoikusha, Osaka.
- Tatuno, S. and Yoshida, H. 1966. Kalyologische Untersuchungen über Osmundaceae I. Chromosomen der Gattung *Osmunda* aus Japan. *Botanical Magazine (Tokyo)* **79**: 244–252.
- Tryon, R. M. Jr. 1940. An *Osmunda* hybrid. *American Fern Journal* **30**: 65–68.
- van Steenis, C. G. G. J. 1981. Rheophytes of the World. Sijthoff and Noordhoff, Alphen aan den Rijn.
- Wagner, W. H. Jr., Wagner, F. S., Miller, C. N. Jr. and Wagner, D. H. 1978. New observations on the royal fern hybrid *Osmunda × ruggii*. *Rhodora* **80**: 92–106.
- Watano, Y. 1986. Genetic life history of the homosporous fern *Osmunda lancea* Thunb. In: Iwatsuki, K., Raven, P. H. and Bock, W. J. (eds.), *Modern Aspects of Species*, pp. 211–219. University of Tokyo Press, Tokyo.
- Whetstone, R. D. and Atkinson, T. A. 1993. Osmundaceae Berchtold et J. Presl. In: *Flora of North America* Editorial Committee (ed.), *Flora of North America*. Vol. 2. Pteridophytes and Gymnosperms, pp. 107–109. Oxford University Press, New York.
- Yatabe, Y., Murakami, N. and Iwatsuki, K. 2005. *Claytosmunda*; a new subgenus of *Osmunda* (Osmundaceae). *Acta Phytotaxonomica et Geobotanica* **56**: 127–128.
- Yatabe, Y., Nishida, H. and Murakami, N. 1999. Phylogeny of Osmundaceae inferred from *rbcL* nucleotide sequences and comparison to the fossil evidence. *Journal of Plant Research* **112**: 397–404.
- Zhang, S.-Z., He, Z.-C., Fan, C.-R. and Yan, B. 2008. A cytogenetic study of five species in the genus *Osmunda*. *Journal of Systematics and Evolution* **46**: 490–498.