# テンナンショウ属のアロザイム分化: (3) マムシグサ群(マムシグサ節)

J. Phytogeogr. & Taxon.
42 : 99-109, 1995

# Jin Murata* and Takayuki Kawahara**: Allozyme Differentiation in *Arisaema* (Araceae) (3) *Arisaema serratum* Group (Sect. *Pedatisecta*)

# 邑田　仁*・河原孝行**：テンナンショウ属のアロザイム分化（3）マムシグサ群（マムシグサ節）

**Abstract**

To provide a genetic background for the systematics of *Arisaema*, allozyme differentiation in *Arisaema* was studied. Eighteen populations of the *Arisaema serratum* group, including the *A. maximowiczii, A. yamtense, A. monophyllum* and *A. tosaense* groups, were examined together with one population each of *A. undulatifolium* and *A. nikoense*. Seventeen gene loci of 11 enzyme systems were used for analysis. It is remarkable that the genetic distances between the examined populations do not exceed the value normally obtained for conspecific populations (D=0.16). The populations in the *A. serratum* group were more closely clustered within D=0.10 in UPGMA topology. This may suggest that *A. serratum* group is at a primary stage of speciation. The results of this study support the taxonomic treatment of *A. serratum* by Ohashi and Murata (1980) where various populations were included in a single species when they were not morphologically distinct.

**Key Words**: allozyme, Araceae, *Arisaema*, systematics, taxonomy.

## Introduction

Most of the species of Japanese *Arisaema* belong to sect. *Pedatisecta* Schott ex Engler. In the sense of Murata (1991), section *Pedatisecta* is characterized by the distinctly stipitate spadix appendage and spilodistichous leaf arrangement. Apart from the stipitate nature of the spadix appendage, the shape of the spathe and spadix is so diversified in this section that they are not useful for phylogenetic consideration. Vegetative characters seem to be more conservative and useful for grouping. The relative length of pseudostem to petiole and development of the rachis between leaflets appear to correlate each other (Fig. 1). One extreme is found in *A. ringens* and *A. ternatipartitum* (Fig. 1A), which have three leaflets without a rachis. Another extreme is in *A. serratum* in the sense of Ohashi & Murata (1980) (Fig. 1F), which is defined as having a long pseudostem and pedate leaves with many leaflets and a well developed rachis between leaflets. Taking the number of the leaflets into consideration, distinction of *A. serratum* becomes clearer (Fig. 2). From this point of view, the *A. maximowiczii* (Serizawa 1980) (Fig. 1E), *A. yamatense* (Serizawa 1982) (Fig. 1E), *A. monophyllum* (Fig. 1D), and *A. tosaense* (Fig. 1C) groups are similar to *A. serratum* and included in the *A. serratum* group in a broad sense, although they are distinct in certain characteristics. Accordingly, the *A. serratum* group is circumscribed as in Table 1.

The most substantial discussion about the taxonomic problems of *Arisaema serratum* and its allied species was made by Ohashi & Murata (1980). Through a morphological comparison of 24 previously described species, they recognized a wide range of variation in diagnostic characters of these "species" and tentatively concluded that

*Botanical Gardens, Nikko, Faculty of Science, University of Tokyo, 1842 Hanaishi, Nikko 321-14, Japan. 〒321-14 栃木県日光市花石町 1842　東京大学理学部附属植物園日光分園

**Forestry and Forest Products Research Institute, Matsunosato 1, Kukizaki-cho, Ibaragi 305, Japan. 〒305 茨城県稲敷郡茎崎町松の里 1　森林総合研究所

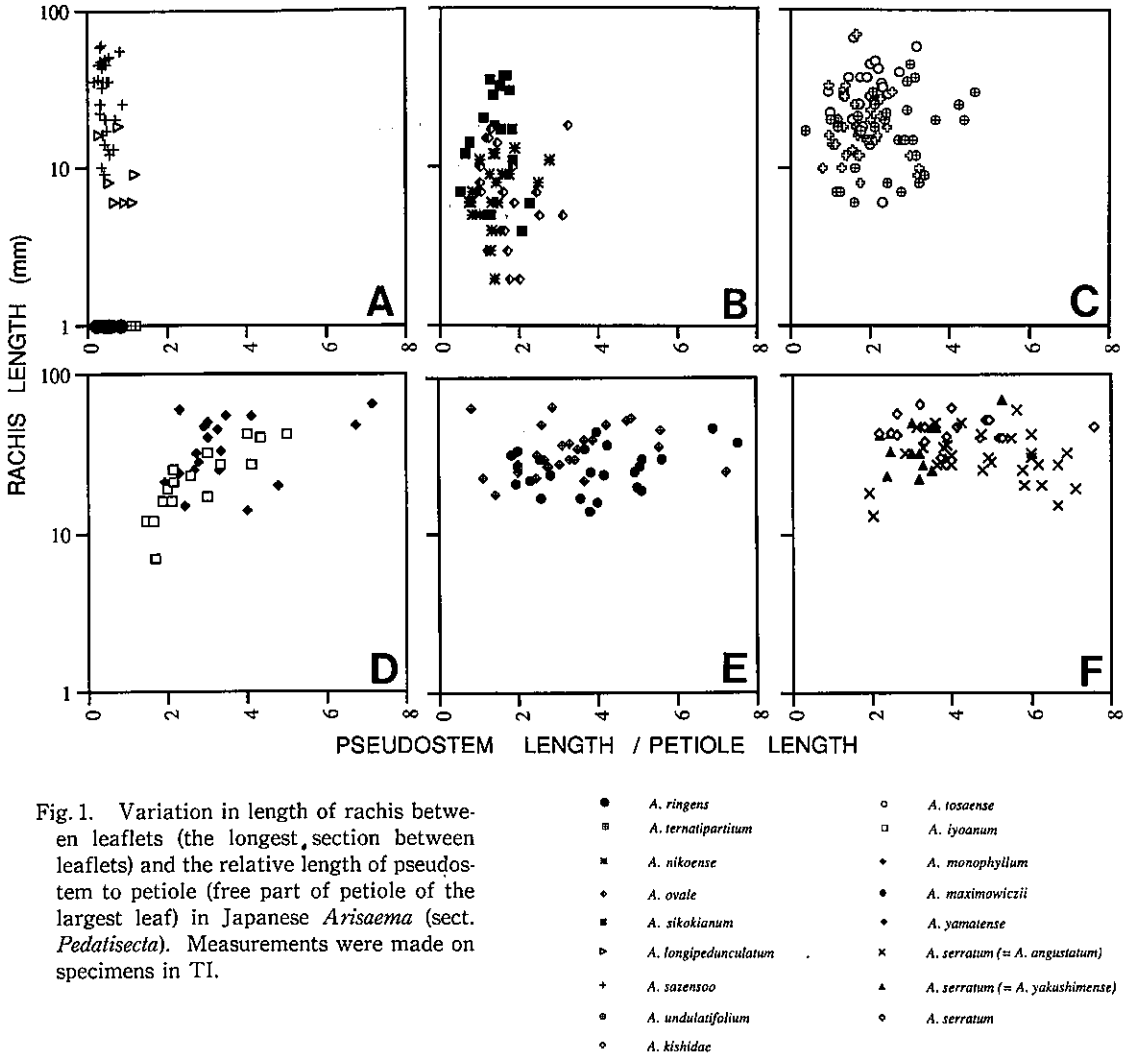


Fig. 1. Variation in length of rachis between leaflets (the longest section between leaflets) and the relative length of pseudostem to petiole (free part of petiole of the largest leaf) in Japanese *Arisaema* (sect. *Pedatisecta*). Measurements were made on specimens in TI.

they were conspecific.

The *A. maximowiczii* group includes *A. maximowiczii* (Fig. 4A) and *A. unzense* and is characterized by the elongate apex of the spathe blade and very slender spadix appendage.

The *A. yamatense* group includes *A. yamatense* (Figs. 3, 4B) and *A. abei* and characterized by the densely papillate spathe blade and/or spadix appendage somewhat deformed apically.

The *A. monophyllum* and *A. tosaense* groups are defined here for the first time. The *A. monophyllum* group consists of *A. monophyllum* and *A. iyoanum* (Fig. 4D) and usually has a single foliage leaf and a deltoid or deltoid-ovate spathe blade. The *A. tosaense* group consists of *A. tosaense* (Fig. 4C) and *A. kishidae* and has a spathe with a distinctly elongate tip.

In this study, the allozyme differentiation between various populations of the *A. serratum* group and *A. nikoense* Nakai and *A. undulatifolium* Nakai was examined. *Arisaema nikoense* (Fig. 1B) is very distinct from *A. serratum* group by the leaves with 5(-7) leaflets, shorter pseudostem and the inflorescence opening much earlier than the leaves. *Arisaema undulatifolium* (Fig. 1C) appears intermediate between the *A. serratum* group and *A. nikoense* but is distinct in the more numerous ovules per ovary than in other species (Murata 1986).

## Materials and Methods

Sample populations and voucher specimens are listed in Table 2. The populations examined named as *serratum* (1)-(12) are attributable to the

Table 1. Circumscription of *Arisaema serratum* group in broad sense based on morphology. Species in parenthesis are indistinguishable from the adjacent species above

| Species | name of examined populations attributable to the "species" |
|---|---|
| ***Arisaema serratum*** in the sense of Ohashi & Murata (1980) | |
| *A. angustatum* Fr. et Sav. (Fig. 4H) | *serratum* (12) |
| *A. hatijoense* Nakai | *serratum* (10), (11) |
| *A. japonicum* Blume (Fig. 4F)<br>(*A. koshikiense* Nakai, *A. pseudojaponicum* Nakai,<br>*A. yakusimense* Nakai, ?*A. amplissimum* Bl.) | *serratum* (9) |
| *A. longilaminum* Nakai (Fig. 4G)<br>(*A. sinanoense* Nakai) | *serratum* (1), (3) |
| *A. mayebarae* Nakai | *serratum* (13) |
| *A. peninsulae* Nakai<br>(*A. boreale* Nakai, *A. proliferum* Nakai,<br>*A. speirophyllum* Nakai) | *serratum* (4) |
| *A. planilaminum* J.Murata | |
| *A. serratum* (Thunb.) Schott<br>(*A. capitellatum* Nakai, *A. niveum* Nakai,<br>? *A. hakonecola* Nakai, ? *A. koidzumianum* Kitam.) | *serratum* (2), (7), (8) |
| *A. solenochlamys* F. Maekawa | *serratum* (6) |
| *A. suwoense* Nakai | |
| *A. takedae* Makino (Fig. 4E)<br>(*A. izuense* Nakai) | *serratum* (5) |
| **Group of *A. maximowiczii*** (Serizawa 1982) | |
| *A. maximowiczii* (Engl.) Nakai (Fig. 4A)<br>ssp. *maximowiczii*<br>ssp. *tashiroi* (Kitam.) Serizawa | *maximowiczii* (1), (2) |
| *A. unzense* Serizawa | |
| **Group of *A. yamatense*** (Serizawa 1980) | |
| *A. yamatense* (Nakai) Nakai<br>var. *yamatense* (Fig. 3)<br>var. *sugimotoi* (Nakai) Ohashi et J.Murata (Fig. 4B) | *yamatense* |
| *A. abei* Serizawa | |
| **Group of *A. monophyllum*** | |
| *A. monophyllum* Nakai | |
| *A. iyoanum* Makino (Fig. 4D) | *iyoanum* |
| **Group of *A. tosaense*** | |
| *A. tosaense* Makino (Fig. 4C) | *tosaense* |
| *A. kishidae* Makino | |

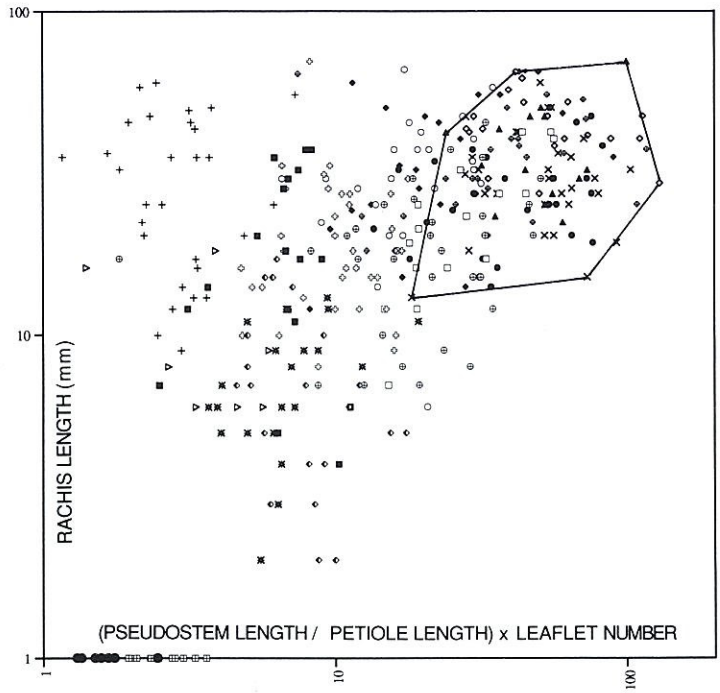


Fig. 2. Variation in length of rachis between leaflets and the value [(length of pseudostem / length of petiole) × leaflet number] in Japanese *Arisaema* (sect. *Pedatisecta*). The range of *A. serratum* is outlined. Symbols correspond to Fig. 1. Measurements were made on specimens in TI.

Fig. 3. *Arisaema yamatense*, a species of the *A. yamatense* group (Serizawa 1982), which is included in the *A. serratum* group. Plants of the *A. serratum* group commonly have a long pseudostem and pedate leaves with many leaflets and a well developed rachis between the leaflets.

following "species" on the bases of morphology: (1) *longilaminum*, (2) *serratum* in the strict sense, (3) *longilaminum*, (4) *peninsulae*, (5) *takedae*, (6) *solenochlamys*, (7) *serratum* in the strict sense, (8) *serratum* in the strict sense, (9) *japonicum*, (10) *hatijyoense*, (11) *hatijyoense*, (12) *angustatum*, (13) *mayebarae*. The diagnostic characters of these morphological entities (species) are summarized in Ohashi & Murata (1980). Chromosome numbers were previously determined for all of the populations examined and found to be diploid [2n=28, except in *serratum* (10) and (11) from Hachijyo Is. which have 2n=26 chromosomes]. Voucher specimens are preserved in the Herbarium, University of Tokyo (TI).

Horizontal satrch gel electrophoresis was conducted with 11 different enzyme systems; alcohol dehydrogenase (ADH), adenirate kinase (AK), diaphorase (DIA), glutamate dehydrogenase (GDH), malate dehydrogenase (MDH), mannose phosphate isomerase (MPI), phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), shikimate dehydrogenase (SDH), superoxide dismutase (SOD) and triose phosphate isomerase (TPI). AK, DIA, MPI and SOD were resolved using a Tris

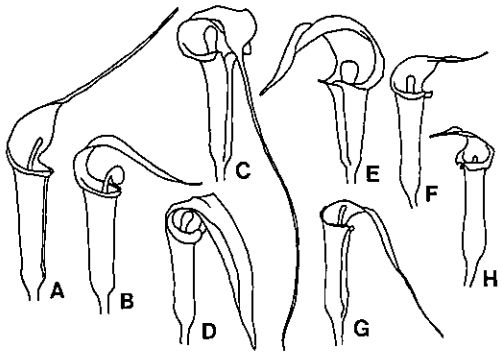


Fig. 4. Spathe and spadix morphology in the *Arisaema serratum* group. A: *A. maximowiczii*, B: *A. yamatense* ssp. *sugimotoi*. C: *A. tosaense*. D: *A. iyoanum*. E: *serratum* (=*A. takedae*). F: *A. serratum* (=*A. japonicum*). G: *A. serratum* (=*A. longilaminum*). H: *A. serratum* (=*A. angustatum*).

Table 2. A list of populations examined

| Population name | Number of samples | Locality (voucher specimen) |
|---|---|---|
| *iyoanum* | 34 | Ehime Pref., Omogo-mura (Murata, May 23, 1990) |
| *maximowiczii* (1) | 19 | Kumamoto Pref., Tomochi-machi (Murata, May 9, 1990) |
| *maximowiczii* (2) | 19 | Ooita Pref., Beppu-shi (Ohno, Jun. 17, 1990) |
| *nikoense* | 40 | Tochigi Pref., Nikko-shi, Yumoto (Murata, July 5, 1991) |
| *serratum* (1) | 10 | Nara Pref., Yoshino-gun, (Murata, June 26, 1991) |
| *serratum* (2) | 30 | Ooita Pref., Hayami-gun, Toyooka (Ohno, Jun. 17, 1990) |
| *serratum* (3) | 30 | Nagano Pref., Agatsuma-gun, Karuizawa machi (Murata, July 3, 1990) |
| *serratum* (4) | 30 | Nagano Pref., Agatsuma-gun, Karuizawa-machi (Murata, July 3, 1990) |
| *serratum* (5) | 30 | Nagano Pref., Agatsuma-gun, Karuizawa-machi (Murata, July 3, 1990) |
| *serratum* (6) | 25 | Nagano Pref., Agatsuma-gun, Karuizawa-machi (Murata, July 3, 1990) |
| *serratum* (7) | 30 | Chiba Pref., Chiba-shi, Nakano-cho (Kawahara, Apr. 24, 1990) |
| *serratum* (8) | 30 | Tochigi Pref., Botanical Gardens, Nikko, University of Tokyo (Murata, May 25, 1990) |
| *serratum* (9) | 30 | Kagoshima Pref., Ooguchi-shi (Murata May 9, 1990) |
| *serratum* (10) | 30 | Tokyo Pref., Hachijo Is. (Kawahara, Apr. 12, 1990 ) |
| *serratum* (11) | 30 | Tokyo Pref., Hachijo Is. (Kawahara, Apr. 12, 1990 ) |
| *serratum* (12) | 30 | Shizuoka Pref., Mt. Amagisan (Murata, May 15, 1990) |
| *serratum* (13) | 30 | Kumamoto Pref., Tomochi-machi (Murata, May 9, 1990) |
| *tosaense* | 40 | Ehime Pref., Ozu-shi. (Ohno July 12, 1991) |
| *undulatifolium* | 25 | Chiba Pref., Awa-gun, Maruyama-machi (Murata, May 4, 1990) |
| *yamatense* | 26 | Nara Pref., Yoshino-gun (Murata, July 4, 1990) |

citrate gel buffer system (0.042M Tris, 0.007M citric acid, 0.004M LiOH, 0.0025M bolic asid, pH7. 6) and an electrode buffer consisting of lithium -borate (0.039M LiOH, 0.263M boric acid) (Soltis *et al*. 1983). For the electrophoresis of other enzyme systems, the procedure used by Murata and Kawahara (1994) and Murata *et al*. (1994) was applied. The gel staining schedule of Wendel and Weeden (1989) was used with slight modification.

The proportion of polymorphic loci (P), alleric diversity (A) and gene diversity (H) for each population were calculated usisng Nei's statistics on gene diversity (1973). Standard genetic distance (D) were calculated usisng Nei's method (Nei 1972). The genetic distance matrix was used to construct phenograms by the unweighted pair

-group method using arithmatic averages (UPGMA: Sneath and Sokal 1973) and by the neighbour-joining method (Saitou & Nei 1987).

## Results and Discussion

A total of 17 loci, *Pgi, Pgm, Adh, Ak, Dia-1, Dia-2, Gdh, Mdh-1, Mdh-2, Mdh-3, Mpi, Sdh, Sod-1, Sod-2, Tpi-1, Tpi-2* and *Tpi-3* were used for genetic analysis. Table 3 shows the frequencies of alleles at the 17 loci in the populations examined. *Ak, Mdh-2, Sod-1* and *Sod-2* were fixed for the same allele in all plants examined. *Adh-d, Dia-1b, Dia-2b, Gdh-d, Pgm -c, Tpi-1c* and *Tpi-2a* were found to be major in all populations examined. *Adh-a* was also found in all populations but at low frequencies. No other alleles were found in all populations. The population of *iyoanum* have a fixed unique allele *Mdh-3 a*. The populations *serratum* (12) and *nikoense* have rare unique alleles *Sdh-a* and *Sdh -c*, respectively. The populations of *serratum* (10) and (11) share unique alleles *Pgi-c* and *h*. Other populations generally share major alleles but differ in the frequencies of the alleles.

Gene diversity statistics (Table 4) for each population were calculated from the values in Table 3. In most cases the values are comparable to the average for monocotyledons (P=40.3, A=1.66, H=0.144: Hamrick and Godt 1979). It is notable that the sample proportion of polymorphic loci (P) is low in *serratum* (1), (11) and *yamatense*; gene diversity (H) is low in *serratum* (1), (9), (10), *A. tosaense*, and especially lower in *serratum* (11).

A phenogram by the UPGMA method (Fig. 5) and by the neighbour-joining method (Fig. 6) based on Nei's (1972) genetic distance values (Table 5) were calculated using the allelic frequencies shown in Table 3. It is remarkable that the average genetic distances between examined populations do not exceed the value normally obtained for conspecific populations (D=0.16: Crawford 1983; Thorpe 1982). The average genetic distance is largest between nikoense population and others (D=0.15), and *undulatifolium* (D=0.11) follows. Compared to the values between different species in sect. *Clavata* and sect. *Tortuosa* (D=0.35 - 1.51; Murata & Kawahara 1994) and in sect. *Fimbriata* (D=0.29 - 0.53; Murata *et al.* 1994), these values are much smaller. This suggests that genetic differentiation is generally small in sect. *Pedatisecta* even between morphologically distinct species.

Of the other populations more closely related to each other, *serratum* (12), *iyoanum*, a cluster consisting of *serratum* (10) and (11), *maximowiczii* (1), *tosaense* and a cluster consisting of *serratum* (9) and (13) are rather isolated. The remaining populations, most of which are included in *A. serratum*, form a large terminal cluster within D=0.016.

The population, *serratum* (12), morphologically attributable to *A. angustatum*, is isolated mainly because of the unique allele *Sdh-a* but this may not be characteristic of this "species" but a local mutation. The populations, *serratum* (10) and (11), are attributable to *A. hatijoense*. This "species" is morphologically not distinct but is endemic to Hachijo Is. and has an aneuploid chromosome number of 2n=26. It is therefore considered to be isolated geographically and cytologically from other populations which have 2n=28 chromosomes. *Arisaema hatijoense* may be characterized by a pair of unique alleles *Pgi-c* and *h*. It is reasonable that the morphologically distinct species, *A. iyoanum, A. maximowiczii* and *A. tosaense*, are rather isolated. *Arisaema maximowiczii* (1) is isolated not because of unique alleles but because of differences in the frequency of alleles while *maximowiczii* (2) is included in the terminal cluster with various populations of *A. serratum*. Notwithstanding its morphological distinction, *A. yamatense* is also included within the terminal cluster. *Serratum* (9) and (13) are attributable to *A. japonicum* and *A. mayebarae*, respectively, and commonly characterized by the inflorescence opening earlier than the leaves.

Consequently, the *A. serratum* group, which has various local populations that are morphologically different but not well differentiated genetically, appears to show a primary stage of speciation as was revealed for some species on oceanic islands (summarized in Crawford et al. 1987; Crawford 1989) and also for the continental genus *Heuchera* (Soltis 1985). The time course of this kind of speciation is suggested to be as short as 5000 to 20000 years (Lowrey and Crawford 1985; Crawford *et. al.* 1985, Stutz 1978). If this time course

Table 3. Allele frequencies at 17 loci in the populations examined

| Gene | Allele | *A. serratum* (1) | (2) | (3) | (4) | (5) | (6) | (7) | (8) | (9) | (10) | (11) | (12) | (13) | *A. yamatense* | *A. maximowiczii* (1) | (2) | *A. tosaense* | *A. iyoanum* | *A. undulatifolium* | *A. nikoense* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pgi-2 | a | | 0.03 | | | | | | | | | | | | | | | | | | |
| | b | | | 0.02 | | | 0.02 | | | 0.07 | | | | 0.02 | | | | | 0.06 | 0.04 | |
| | c | | | | | | | | | | 0.62 | 0.83 | | | | | | | | | |
| | d | | | 0.10 | 0.02 | 0.05 | | | 0.02 | | | | | | | | 0.03 | | 0.15 | | |
| | e | 0.55 | 0.43 | 0.21 | 0.25 | 0.47 | 0.10 | 0.30 | 0.22 | 0.02 | | | 0.18 | 0.02 | 0.23 | 0.66 | 0.50 | 0.04 | 0.13 | 0.20 | 0.21 |
| | f | 0.05 | | | | | | | | 0.02 | | 0.02 | | | | | | | | | |
| | g | 0.40 | 0.53 | 0.65 | 0.67 | 0.48 | 0.84 | 0.70 | 0.75 | 0.83 | | | 0.72 | 0.87 | 0.71 | 0.34 | 0.47 | 0.95 | 0.59 | 0.72 | 0.63 |
| | h | | | | | | | | | | 0.38 | 0.15 | | | | | | | | | |
| | i | | | | | | | | | | | | 0.02 | | | | | | | | |
| | j | | | 0.02 | 0.07 | | 0.04 | | 0.02 | 0.07 | | | 0.02 | 0.10 | 0.02 | | | | 0.07 | | 0.16 |
| | k | | | | | | | | | | | | 0.02 | | | | | | | 0.04 | |
| | l | | | | | | | | | | | | | | | | | 0.01 | | | |
| Gdh | a | | 0.17 | | | | | | | | | | 0.10 | | | | | 0.05 | 0.01 | | |
| | b | 0.50 | 0.38 | 0.35 | 0.42 | 0.46 | 0.52 | 0.37 | 0.25 | 0.08 | 0.17 | | 0.40 | 0.05 | 0.44 | 0.34 | 0.26 | 0.83 | 0.38 | | 0.08 |
| | c | | | | | | | | | | | | | | | | | | | | |
| | d | 0.40 | 0.60 | 0.43 | 0.56 | 0.46 | 0.48 | 0.60 | 0.71 | 0.87 | 0.80 | 1.00 | 0.48 | 0.90 | 0.52 | 0.61 | 0.63 | 0.18 | 0.60 | 0.96 | 0.89 |
| | e | 0.10 | | 0.23 | 0.02 | 0.08 | | 0.03 | 0.03 | 0.05 | 0.03 | | 0.02 | 0.05 | 0.04 | 0.05 | 0.10 | 0.03 | | 0.04 | 0.04 |
| Pgm-1 | a | 0.05 | | 0.08 | 0.07 | 0.05 | 0.04 | 0.08 | 0.07 | | | 0.05 | | 0.05 | 0.06 | | | | 0.04 | | 0.15 |
| | b | | | | | | | | | | | | 0.02 | | 0.02 | | | | 0.01 | 0.02 | |
| | c | 0.90 | 0.97 | 0.89 | 0.91 | 0.93 | 0.96 | 0.92 | 0.92 | 0.98 | 1.00 | 0.92 | 0.93 | 0.95 | 0.92 | 0.97 | 1.00 | 0.90 | 0.94 | 0.54 | 0.76 |
| | d | 0.05 | 0.03 | 0.03 | 0.02 | 0.17 | | | 0.02 | 0.02 | | 0.03 | 0.03 | | | 0.03 | | 0.05 | | 0.44 | 0.09 |
| | e | | | | | | | | | | | | 0.02 | | | | | | | | |
| Adh | a | 0.05 | 0.04 | 0.13 | 0.06 | 0.08 | 0.06 | 0.05 | 0.13 | 0.05 | 0.08 | 0.18 | 0.33 | 0.18 | 0.24 | 0.21 | 0.16 | 0.18 | 0.32 | 0.69 | 0.18 |
| | b | | | | | | | | | 0.03 | | | | | 0.02 | | | | | | |
| | c | | | 0.17 | 0.02 | 0.05 | 0.06 | | | | | | 0.03 | | | | | | | | |
| | d | 0.80 | 0.90 | 0.70 | 0.92 | 0.87 | 0.88 | 0.95 | 0.87 | 0.92 | 0.91 | 0.82 | 0.63 | 0.82 | 0.74 | 0.53 | 0.79 | 0.83 | 0.66 | 0.31 | 0.83 |
| | e | | 0.06 | | | | | | | | | | | | | 0.26 | 0.05 | | | | |
| | f | 0.15 | | | | | | | | | | | | | | | | | 0.01 | | |
| Dia-1 | a | | 0.02 | 0.02 | | | | | | 0.02 | | | | | | | | | | | |
| | b | 1.00 | 0.98 | 0.78 | 0.90 | 0.98 | 0.92 | 0.65 | 0.82 | 0.98 | 0.97 | 1.00 | 0.91 | 0.95 | 0.94 | 1.00 | 1.00 | 0.95 | 0.91 | 0.98 | 0.95 |
| | c | | | 0.20 | 0.10 | 0.02 | 0.08 | 0.35 | 0.18 | | 0.03 | | 0.08 | 0.05 | 0.06 | | | 0.05 | 0.09 | 0.02 | 0.05 |
| Dia-2 | a | | | 0.02 | | | | | | 0.13 | | | | | | | | | | 0.02 | 0.21 |
| | b | 1.00 | 1.00 | 0.98 | 1.00 | 1.00 | 1.00 | 1.00 | 0.91 | 0.87 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.98 | 0.79 |
| | c | | | | | | | | 0.07 | | | | | | | | | | | | |
| | d | | | | | | | | 0.02 | | | | | | | | | | | | |
| Mdh-1 | a | | 0.16 | 0.10 | 0.42 | 0.30 | 0.06 | 0.15 | 0.12 | 0.05 | | | 0.08 | 0.20 | 0.23 | 0.05 | | 0.04 | 0.06 | 0.08 | |
| | b | | | | | | | | | | | | | | 0.02 | | | | | | |
| | c | 1.00 | 0.84 | 0.90 | 0.58 | 0.70 | 0.94 | 0.85 | 0.88 | 0.95 | 1.00 | 1.00 | 0.92 | 0.80 | 0.75 | 0.95 | 1.00 | 0.96 | 0.94 | 0.92 | 1.00 |
| Mdh-2 | | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| Mdh-3 | a | | | | | | | | | | | | | | | | | | 1.00 | | |
| | b | 1.00 | 1.00 | 0.98 | 1.00 | 0.83 | 0.94 | 0.97 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.97 | 1.00 | 1.00 | 1.00 | 1.00 | | 1.00 | 0.96 |
| | c | | | 0.02 | | 0.15 | 0.06 | 0.03 | | | | | | 0.03 | | | | | | | 0.04 |
| | d | | | | | 0.02 | | | | | | | | | | | | | | | |
| Tpi-1 | a | | 0.02 | | | 0.05 | | | | | | | | 0.12 | | | 0.05 | | | | 0.33 |
| | b | | | | | | | | | | 0.02 | | | | | | | | | | |
| | c | 1.00 | 0.98 | 1.00 | 1.00 | 0.95 | 1.00 | 0.92 | 0.93 | 1.00 | 0.98 | 1.00 | 0.85 | 0.88 | 1.00 | 0.97 | 0.95 | 1.00 | 1.00 | 1.00 | 0.65 |
| | d | | | | | | | 0.08 | 0.07 | | | | 0.15 | | | 0.03 | | | | | 0.02 |
| Tpi-2 | a | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.98 | 0.98 | 1.00 | 1.00 | 1.00 | 0.99 | 1.00 | 1.00 | 0.96 |
| | b | | | | | | | | | | | | 0.02 | 0.02 | | | | 0.01 | | | 0.04 |
| Tpi-3 | a | | 0.02 | 0.03 | | 0.15 | 0.06 | | | 0.15 | 0.32 | 0.20 | 0.17 | 0.13 | 0.04 | 0.03 | 0.05 | 0.04 | 0.03 | 0.86 | 0.02 |
| | b | 1.00 | 0.98 | 0.97 | 1.00 | 0.85 | 0.94 | 1.00 | 1.00 | 0.85 | 0.68 | 0.80 | 0.83 | 0.87 | 0.96 | 0.97 | 0.95 | 0.96 | 0.97 | 0.14 | 0.95 |
| | c | | | | | | | | | | | | | | | | | | | | 0.03 |
| Sdh | a | | | | | | | | | 0.02 | | | 1.00 | | | 0.26 | | 0.01 | 0.07 | | |
| | b | 1.00 | 0.90 | 0.95 | 0.98 | 1.00 | 1.00 | 1.00 | 1.00 | 0.98 | 1.00 | 1.00 | | 1.00 | 1.00 | 0.74 | 1.00 | 0.89 | 0.91 | 0.96 | |
| | c | | 0.10 | 0.05 | 0.02 | | | | | | | | | | | | | 0.10 | | 0.04 | 1.00 |
| | d | | | | | | | | | | | | | | | | | | 0.01 | | |
| Mpi | a | | | | | | | 0.02 | | 0.33 | | 0.03 | 0.02 | | | | | | | | |
| | b | | 0.02 | | | 0.12 | 0.08 | | 0.02 | 0.02 | | | | 0.02 | | | | | 0.07 | | |
| | c | 0.30 | 0.30 | 0.18 | 0.20 | 0.04 | 0.13 | 0.02 | 0.18 | 0.22 | 0.30 | 0.03 | 0.48 | 0.08 | 0.31 | 0.11 | 0.34 | 0.29 | 0.29 | 0.06 | 0.02 |
| | d | 0.20 | | 0.06 | | | 0.15 | 0.03 | 0.08 | 0.10 | | | | | 0.02 | | | 0.03 | 0.26 | | 0.03 |
| | e | 0.50 | 0.66 | 0.60 | 0.68 | 0.68 | 0.60 | 0.92 | 0.65 | 0.57 | 0.63 | 0.92 | 0.37 | 0.62 | 0.67 | 0.26 | 0.61 | 0.53 | 0.31 | 0.68 | 0.86 |
| | f | | 0.02 | | | | | | | | | | | | | | | | 0.01 | | |
| | g | | | 0.16 | 0.10 | 0.16 | 0.05 | 0.02 | 0.07 | 0.05 | 0.08 | 0.02 | 0.13 | 0.02 | | 0.63 | 0.05 | 0.15 | 0.04 | 0.26 | 0.10 |
| | h | | | | 0.02 | | | | | 0.02 | | | | 0.27 | | | | | | | |
| Sod-1 | | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| Sod-2 | | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| Ak | | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |

Table 4. Gene diversity statistics for the populations examined

| Population name | P(%) | A | H |
|---|---|---|---|
| *iyoanum* | 53 | 1.41 | 0.173 |
| *maximowiczii* (1) | 53 | 1.88 | 0.165 |
| *maximowiczii* (2) | 35 | 2.18 | 0.127 |
| *serratum* (1) | 25 | 1.88 | 0.110 |
| *serratum* (2) | 59 | 2.00 | 0.137 |
| *serratum* (3) | 65 | 1.88 | 0.191 |
| *serratum* (4) | 47 | 1.76 | 0.149 |
| *serratum* (5) | 59 | 2.00 | 0.183 |
| *serratum* (6) | 53 | 2.18 | 0.130 |
| *serratum* (7) | 53 | 1.53 | 0.135 |
| *serratum* (8) | 53 | 1.53 | 0.151 |
| *serratum* (9) | 59 | 2.18 | 0.119 |
| *serratum* (10) | 41 | 2.00 | 0.120 |
| *serratum* (11) | 29 | 1.82 | 0.073 |
| *serratum* (12) | 59 | 1.70 | 0.188 |
| *serratum* (13) | 65 | 1.59 | 0.138 |
| *tosaense* | 59 | 1.94 | 0.115 |
| *yamatense* | 25 | 2.18 | 0.153 |
| *An average* of above 18 populations | 50 | 1.87 | 0.143 |
| *nikoense* | 65 | 2.06 | 0.187 |
| *undulatifolium* | 59 | 1.82 | 0.147 |

could be adaptable to the *A. serratum* group, speciation might be influenced by the drastic climatic changes in the later gracial period on the complicated topology of Japanese Islands. A hypothetical scheme for this kind of speciation in the *Saussurea nipponica* complex in Japan was given by Im (1990), although the situation in the *Arisaema serratum* group is far more complicated than in *Saussurea*. Each of the three groups of *Arisaema, Arisaema nikoense* group (Serizawa 1981, 1986), *A. undulatifolium* group (Serizawa 1980) and *A. serratum* group, appear to show examples of this kind of speciation in Japan, of which the *Arisaema serratum* group, growing most widely and abundantly, has the most complicated structure of differentiation. The results of this study support the taxonomic treatment of *A. serratum* of Ohashi and Murata (1980) where various morphologically indistinct populations were included.

This study was supported by Grant-in-Aid for Scientific Research No. 02640534 from the Ministry of Education, Science and Culture, Japan to J. M. Thanks are due to Mr. K. Fukuhara of Chiba Prefecture and Mr. J. Ohno of Shizuoka Prefecture for their help in collecting material.

Table 5. Mean genetic identities (upper triangle) and genetic distances (lower triangle) for populations of *Arisaema* examined

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *A. serratum* (9) | X | 0.98 | 0.98 | 0.99 | 0.97 | 0.98 | 0.99 | 0.98 | 0.97 | 0.91 | 0.96 | 0.95 | 0.99 | 0.95 | 0.98 | 0.92 | 0.91 | 0.98 | 0.96 | 0.88 |
| 2. *A. serratum* (2) | 0.02 | X | 0.99 | 0.99 | 1.00 | 0.99 | 0.99 | 0.99 | 0.99 | 0.92 | 0.96 | 0.94 | 0.98 | 0.97 | 1.00 | 0.90 | 0.92 | 1.00 | 0.98 | 0.88 |
| 3. *A. serratum* (7) | 0.02 | 0.01 | X | 1.00 | 0.98 | 0.99 | 0.99 | 0.99 | 0.98 | 0.90 | 0.94 | 0.94 | 0.98 | 0.94 | 0.98 | 0.89 | 0.90 | 0.99 | 0.97 | 0.90 |
| 4. *A. serratum* (8) | 0.03 | 0.02 | 0.01 | X | 0.99 | 1.00 | 1.00 | 0.99 | 0.99 | 0.92 | 0.95 | 0.94 | 0.99 | 0.96 | 0.99 | 0.91 | 0.92 | 1.00 | 0.97 | 0.90 |
| 5. *A. serratum* (1) | 0.03 | 0.00 | 0.02 | 0.02 | X | 0.99 | 0.99 | 0.98 | 0.99 | 0.91 | 0.95 | 0.93 | 0.96 | 0.97 | 1.00 | 0.89 | 0.92 | 0.99 | 0.98 | 0.86 |
| 6. *A. serratum* (3) | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 | X | 1.00 | 0.99 | 0.99 | 0.92 | 0.95 | 0.94 | 0.98 | 0.97 | 0.99 | 0.91 | 0.92 | 1.00 | 0.98 | 0.89 |
| 7. *A. serratum* (6) | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | X | 0.99 | 0.99 | 0.92 | 0.95 | 0.93 | 0.98 | 0.95 | 0.99 | 0.90 | 0.93 | 1.00 | 0.99 | 0.88 |
| 8. *A. serratum* (4) | 0.02 | 0.01 | 0.01 | 0.01 | 0.02 | 0.01 | 0.01 | X | 0.99 | 0.91 | 0.94 | 0.93 | 0.98 | 0.96 | 0.98 | 0.89 | 0.91 | 1.00 | 0.97 | 0.88 |
| 9. *A. serratum* (5) | 0.03 | 0.01 | 0.02 | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 | X | 0.90 | 0.95 | 0.94 | 0.97 | 0.97 | 0.99 | 0.91 | 0.92 | 0.99 | 0.97 | 0.86 |
| 10. *A. serratum* (12) | 0.09 | 0.08 | 0.11 | 0.09 | 0.09 | 0.08 | 0.09 | 0.10 | 0.10 | X | 0.88 | 0.86 | 0.91 | 0.93 | 0.92 | 0.86 | 0.86 | 0.92 | 0.92 | 0.86 |
| 11. *A. serratum* (10) | 0.04 | 0.04 | 0.06 | 0.05 | 0.05 | 0.05 | 0.06 | 0.06 | 0.05 | 0.13 | X | 0.99 | 0.95 | 0.93 | 0.96 | 0.90 | 0.88 | 0.95 | 0.92 | 0.85 |
| 12. *A. serratum* (11) | 0.06 | 0.06 | 0.07 | 0.06 | 0.07 | 0.07 | 0.07 | 0.07 | 0.07 | 0.15 | 0.01 | X | 0.94 | 0.91 | 0.95 | 0.90 | 0.87 | 0.94 | 0.90 | 0.85 |
| 13. *A. serratum* (13) | 0.01 | 0.02 | 0.02 | 0.01 | 0.04 | 0.02 | 0.02 | 0.02 | 0.03 | 0.10 | 0.05 | 0.06 | X | 0.94 | 0.98 | 0.93 | 0.91 | 0.98 | 0.96 | 0.89 |
| 14. *A. maximowiczii* (1) | 0.06 | 0.03 | 0.06 | 0.04 | 0.03 | 0.03 | 0.05 | 0.05 | 0.03 | 0.07 | 0.07 | 0.09 | 0.06 | X | 0.98 | 0.90 | 0.90 | 0.96 | 0.94 | 0.86 |
| 15. *A. maximowiczii* (2) | 0.02 | 0.00 | 0.02 | 0.01 | 0.00 | 0.01 | 0.02 | 0.02 | 0.01 | 0.09 | 0.03 | 0.05 | 0.02 | 0.02 | X | 0.91 | 0.92 | 0.99 | 0.97 | 0.88 |
| 16. *A. undulatifolium* | 0.08 | 0.11 | 0.12 | 0.09 | 0.12 | 0.10 | 0.11 | 0.11 | 0.10 | 0.16 | 0.10 | 0.11 | 0.08 | 0.11 | 0.09 | X | 0.84 | 0.91 | 0.88 | 0.82 |
| 17. *A. iyoanum* | 0.09 | 0.09 | 0.10 | 0.08 | 0.09 | 0.08 | 0.08 | 0.10 | 0.09 | 0.15 | 0.13 | 0.14 | 0.10 | 0.11 | 0.09 | 0.17 | X | 0.92 | 0.91 | 0.80 |
| 18. *A. yamatense* | 0.02 | 0.00 | 0.01 | 0.00 | 0.01 | 0.00 | 0.01 | 0.00 | 0.01 | 0.08 | 0.05 | 0.07 | 0.02 | 0.04 | 0.01 | 0.09 | 0.08 | X | 0.99 | 0.87 |
| 19. *A. tosaense* | 0.04 | 0.03 | 0.03 | 0.03 | 0.02 | 0.02 | 0.01 | 0.03 | 0.03 | 0.08 | 0.08 | 0.11 | 0.05 | 0.06 | 0.03 | 0.13 | 0.10 | 0.02 | X | 0.86 |
| 20. *A. nikoense* | 0.13 | 0.12 | 0.10 | 0.11 | 0.15 | 0.12 | 0.13 | 0.13 | 0.15 | 0.15 | 0.17 | 0.17 | 0.13 | 0.16 | 0.13 | 0.20 | 0.22 | 0.14 | 0.15 | X |

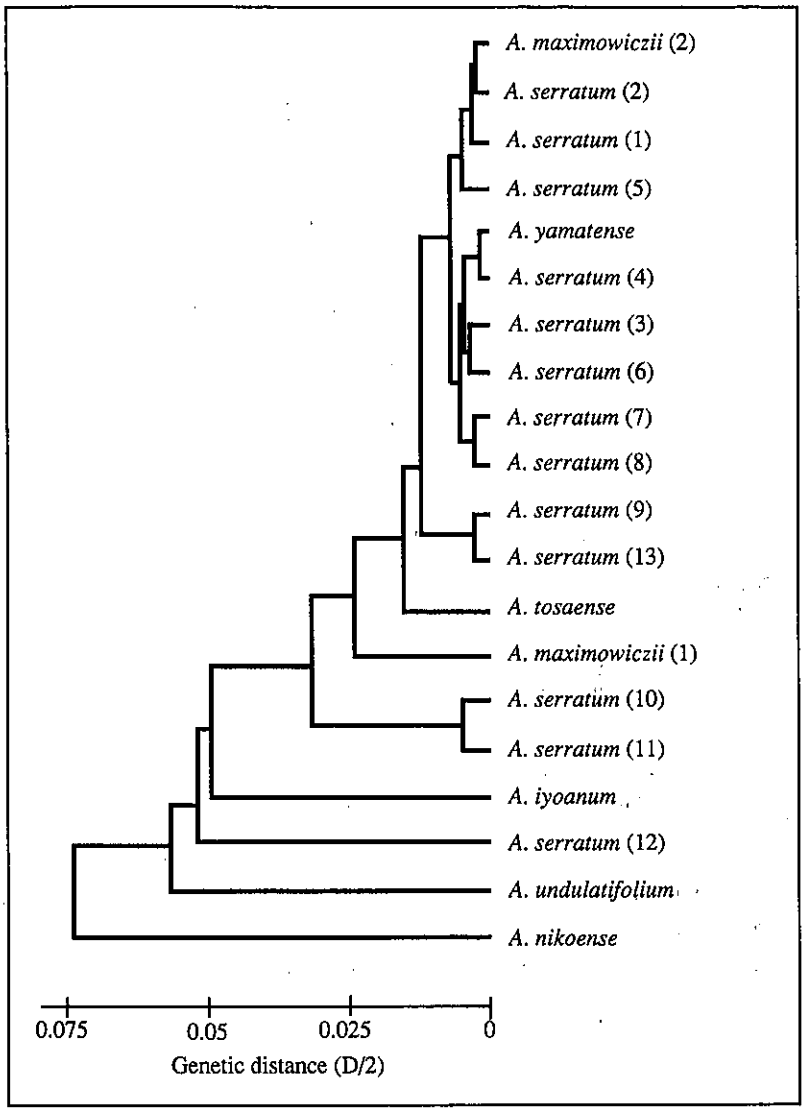


Fig. 5. A genetic distance phenogram of populations examined by UPGMA method.

## References

Cardy, B.J., Stuber, C.W. and Goodman, M.M. 1981. Technics for starch gel electrophoresis of enzyme from maize (*Zea mays*), revised. Instl. Stat. Mimeogr. Ser. 1317. North Carolina State University.

Crawford, D.J. 1983. Phylogenetic and systematic inferences from electrophoreticstudies. *In*: Tanksley, S.O. and Orton, T.J. (eds.), Isozyme in plant genetics and breeding, Part A, pp. 257-287. Elsvier, Amsterdam.

Crawford, D.J. 1989. Enzyme Electrophorasis and Plant systematics. *In*: Soltis, D.E. and Soltis, P.S. (eds.), Isozymes in plant biology. pp. 146-164. Dioscorides Press, Portland.

Crawford, D.J., Ornduff, R. and Vasey, M.C. 1985. Allozyme variation within and between *Lasthenia minor* and its derivative species, *L. maritima* (Asteraceae). Am. J. Bot. 72: 1177-1184.

Crawford, D.J., Whitkus, R. and Stussey, T.F. 1987. Plant evolution and speciation on oceanic islands. *In*: Urbanska, K. (ed.), Differentiation patterns in higher plants. pp. 183-199. Academic Press, London.

Hamrick, J.L. and Godt, J.W. 1990. Allozyme diversity in plant species. *In*: Brown, H.D., Clegg, M.C., Kahler, A.L. and Weir, B.S. (eds.), Plant population genetics, breeding, and genetic

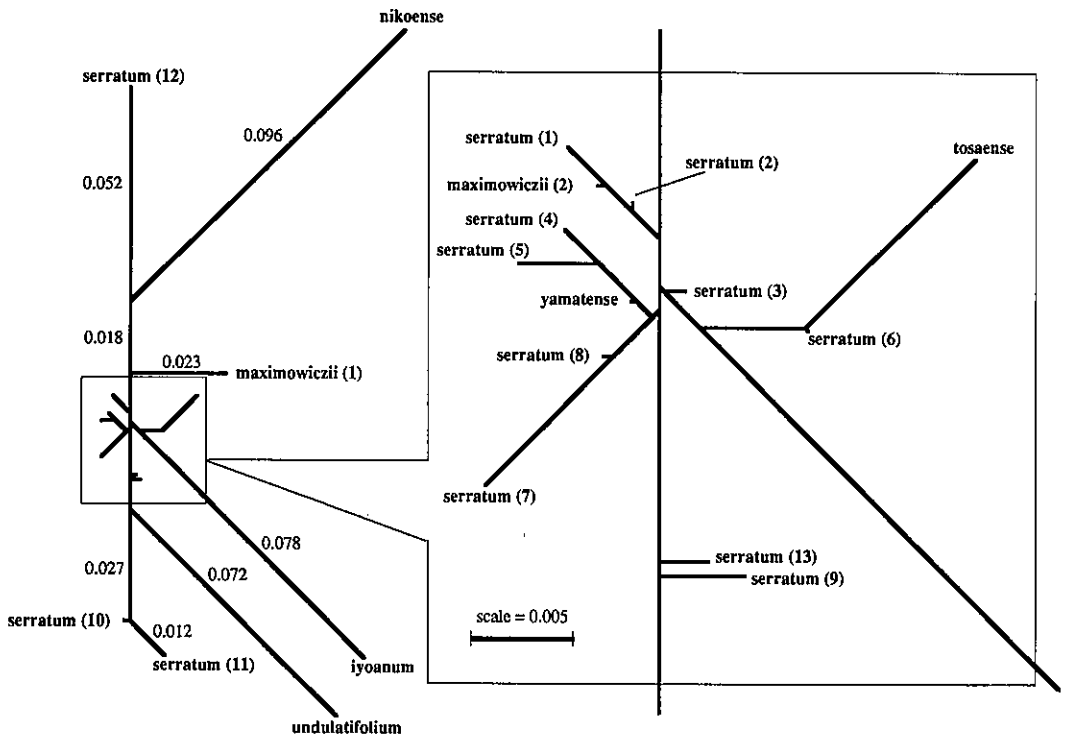


Fig. 6. A genetic distance phenogram of populations examined by neighbour-joining method. Values are standard genetic distance.

resources, pp. 43-63. Sinauer, Sunderland.

Hamrick, J.L., Linhart, Y.B. and Mitton, J.B. 1979. Relationships between life history characteristics and electrophoretically-detectable genetic variation in plants. Annu. Rev. Ecol. Syst. **10**: 173-200.

Im, H-T. 1991. Electrophoretic study of Taxonomic relationships in the *Saussurea nipponica* complex (Compositae). Pl. Spec. Biol. **6**: 11-18.

Loveless, M.D. and Hamrick, J.L. 1984. Ecologocal determinants of genetic structure in plant populations. Annu. Rev. Ecol. Syst. **15**: 65-95.

Lowrey, T.K. and Crawford, D.J. 1985. Allozyme divergence and evolution in *Tetramolopium* (Compositae: Asteraceae) on the Hawaiian Islands. Syst. Bot. **10**: 64-72.

Murata, J. 1986. Comments on the taxonomic characters and taxonomy of Japnese *Arisaema* (Araceae). (2) Length of the peduncle and the number of ovules per ovary, with special reference to *A. kishidae* Makino and *A. undulatifolium* Nakai. Acta Phtotax. Geobot. **37**: 27-41 (in Japanese with English summary).

Murata, J. 1991.The systematic position of *Arisaema nepenthoides* and *A. wattii* (Araceae). Kew Bull. **46**: 119-128.

Murata, J. and Kawahara, T. 1994. Allozyme differentiation in *Arisaema* (Araceae) (1). Sections *Clavata* and *Tortuosa*, with special reference to the systematic position of *A. negishii*. J. Phytogeogr. Taxon. **42**: 11-16.

Murata, J., Kawahara, T. and Darnaedi, D. 1994. Allozyme differentiation in *Arisaema* (Araceae) (2). Section *Fimbriata*. J. Phytogeogr. Taxon. **42**: 17-20.

Nei, M. 1972. Genetic distance between populations. Am. J. Bot. **63**: 2448-1453.

Ohashi, H. and Murata, J. 1980. Taxonomy of the Japanese *Arisaema* (Araceae). J. Fac. Sci. Univ. Tokyo. III, **12**: 281-336.

Odrzycoski, I.J. and Gottlieb, L.D. 1984. Duplications of genes coding 6-phosphogluconate dehydrogenase in *Clarkia* (Onagraceae) and their phylogenetic implications. Syst. Bot. **9**: 479-489.

Serizawa, S. 1980. Studies on the Genus *Arisaema* in Japan (2) Group of *Arisaema yamatense*. J.

Jpn. Bot. **55**: 353-357 (in Japanese with Latin description).
Serizawa, S. 1981. Studies on the Genus *Arisaema* in Japan (3) Group of *Arisaema nikoense*. J. Jpn. Bot. **56**: 90-96 (in Japanese with Latin description).
Serizawa, S. 1982. Studies on the Genus *Arisaema* in Japan (6) Group of *Arisaema maximowiczii*. J. Jpn. Bot. **57**: 85-90.
Serizawa, S. 1986. Supplementary notes on the classification of *Arisaema nikoense* s. lat. J. Jap. Bot. **61**: 22-29.
Saitou, N. and Nei, M. 1987. The neighbour-joining method; A new method for reconstructing phylogenetic trees. Mem. Biol. Evol. **24**: 189-204.
Sneath, P.H. and Sokal, R.R. 1973. Numerical Taxonomy. W.H. Freeman and Company, San Fransisco.
Soltis, D.E. 1985. Allozymic differentiation among *Heuchera americana, H. parviflora, H. pubescens* and *H. villosa* (Saxifragaceae). Syst. Bot. **10**: 193-198.
Soltis, D.E., Hauer, C.H., Darrow D.C. and Gastony G.J. 1983. Starch gel electrophoresis of ferns: a complication of grinding buffers, gel and electrode buffers, and staining schedules. Am. Fern J. **73**: 9-27.
Stutz, H.C. 1978. Explosive evolution of perrenial *Atriplex* in Western North America. *In*: Harper, K.T. and Reveal, J.L. (eds.), Intermountain Biogeography: a symposium. Great Basin Naturalist memories No. 2., pp. 161-168.
Thorpe, J.P. 1982. The molecular clock hypothesis: biochemical evolution, genetic differentiation, and systematics. Annu. Rev. Ecol. Syst. **13**: 136-168.

## 摘　要

日本産テンナンショウ属植物は大部分マムシグサ節に含められる。マムシグサ節では栄養器官の形質に関連が見られ，小葉の数が多いものほど小葉間の葉軸がより発達し，また偽茎が長い傾向がある（図1, 2)。このうち一方の極端は，葉が三小葉に分裂し葉軸が発達しないミツバテンナンショウ，ムサシアブミである。本論文で扱うマムシグサ群はもう一方の極端にあるもので，葉が7小葉以上に細かく分裂し，小葉間に葉軸が発達し，一般に長い偽茎を持つという特徴でまとめられる。Ohashi & Murata (1980)はマムシグサに近縁な種の分類学的問題について議論し，これらは形態的に識別が困難であるとして24種を *Arisaema serratum* ただ1種にまとめている。本論文で扱うマムシグサ群はこの *Arisaema serratum* のほかに，ツクシテンナンショウ群 (Serizawa 1980)，ムロウテンナンショウ群 (Serizawa 1982)，およびヒトツバテンナンショウとオモゴテンナンショウからなるヒトツバテンナンショウ群，アオテンナンショウとムロウマムシグサからなるアオテンナンショウ群を含む（表1)。

本研究では広義のマムシグサ群合計16集団と，形態的分化の大きな例としてマムシグサ群からはっきり識別できるユモトマムシグサ1集団および外部形態的にはマムシグサ群とユモトマムシグサ群の中間的であるが胚種数が多いことが特徴であるヒガンマムシグサを加え，計20集団（表2）を対象とし，電気泳動法により集団間のアロザイム分化を解析した。この結果，UPGMA法による他集団との平均距離は，最も離れているユモトマムシグサの集団で D=0.15であった。この値はすでに報告されたマイヅルテンナンショウ節やアマミテンナンショウ節の異種の集団間 (Murata & Kawahara 1994)，あるいはフデボテンナンショウ節の異種の集団間 (Murata et al. 1994) の値 (D=0.29—1.51) に比べて著しく小さかった。マムシグサ節では種間の遺伝的分化が一般に小さいのではないかと推定される。マムシグサ群内の集団間ではさらに分化の程度が小さかったが，オモゴテンナンショウ (*iyoanum* 集団)，ホソバテンナンショウ (*serratum*(12)集団)，ヒガンマムシグサ (*undulatifolium* 集団) とアオテンナンショウ (*tosaense* 集団)，染色体数が異数化しているハチジョウテンナンショウ (*serratum*(10)および *serratum*(11)集団)，花序が葉に先だって開く性質によりヒガンマムシグサ群に似ているマムシグサ (*serratum*(9)) とヒトヨシテンナンショウ (*serratum*(13)) などは少し離れていた。狭義のマムシグサ内の大部分の集団はさらに近縁なクラスターを形成した。。

マムシグサ群では集団間の遺伝的距離 (D) が特に小さいことから，種分化の初期の段階を示していると推定した。マムシグサ群は，氷河時代の末期に日本列島の複雑な地形の上で集団が一時的に様々に分断されることによって形態的分化を生じた小集団の集まりであるかも知れない。このような状況のもとでは，マムシグサ群のうち識別が困難な小集団をまとめて1種とするOhashi & Murata (1980)の分類学的処置は妥当なものだと考えられる。

(received November 24, 1993; accepted September 27, 1994)