

井原正昭・井原一恵：子房の形態より見た北米産エンレイソウ属
(有花梗群)植物の分類と各分類群の地理的分布

Masaaki IHARA* & Kazue IHARA* : A Biosystematic Study on the
Pedicellate-flowered Species of the North American *Trillium*.

(1) Geographical Distribution of Major Groups and their
Gynoecium Norms**.

It is a nowadays approach to evolutionary diversification in biological science to systematize natural entities as an organic assemblage, where not a single organism but a population or its regional complex is considered to be the unit of the most conspicuous representative of the diversification. In orthodox taxonomy, the major aim is systematization of natural entities to which a taxonomic hierarchy has been adopted. It is apparent that only insufficient information would be provided as to their evolutionary processes if any natural entities have differentiated well from each other. However, such discontinuity is prerequisite to administer the hierarchical adoption to the natural entities. Where interpopulational variation in gross morphology is continuous but clinal regionally, taxonomic decision may be difficult; yet such a situation of the natural entities undoubtedly provides the most important information to the evolutionary process *per se*. This is a dilemma in orthodox taxonomy, which may require any reliable methods to inform such evolutionary status of the natural entities beyond the limit of the taxonomic hierarchy. It may be possible to document such status in nature in terms of quantitative biology; this is a fundamental idea in biosystematics.

The genus *Trillium* comprises about 20 pedicellate-flowered species and 23 sessile-flowered natural entities which inhabit as the undergrowth of the deciduous forests in eastern Asia, western and eastern North America. Despite their showy floral morphology as well as a moderate size of the group,

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**The main body of this work was accomplished at Vanderbilt University, Nashville, Tennessee, U. S. A. by the financial support of the University (1967-1969), and a part of which was read by K. IHARA, M. IHARA and R. B. CHANNELL in the 37th Annual Meeting of Japanese Society of Botany at Nagoya (1972) under the title of Analysis of Natural Populations (I).

there have been a few revisional studies covering rather limited geographical ranges (GLEASON 1906 ; BARKSDALE 1938 ; SAMEJIMA & SAMEJIMA 1962 ; FREEMAN 1975), which positively suggests that taxonomic difficulties may exist in adopting any appropriate epithets to the entities and/or in applying any orthodox species concept for recognition of the entities. Such a group of natural entities must be the best example what biosystematic study would be plausibly required.

The present study deals with the pedicellate-flowered species in which the phytogeographers have been interested as one of such species that are shared by the distantly located habitats in eastern Asia and in eastern North America since as early as the era of Asa GRAY. Even if geographically isolated natural entities may exhibit different tempo and modes of speciation, their evolutionary principle of its major factors would be equivalent. However, the species here under study provide quite contrasting information with that of the Asian species as to their breeding systems in cytogenetic studies (NARISE 1956 ; FUKUDA 1967 ; HAGA 1969) and in experiments of pollen flow and control cross pollination (IHARA 1973 ; unpublished). Further, the Asian species reveal a series of polyploidy and interspecific hybridization (HAGA 1934, 1937, 1951), whereas all of the North American relatives show diploids except for the sporadic occurrence of triploids (BALDWIN *et al* 1949 ; BAILEY 1951, 1954 ; SPARROW & POND 1950 ; RUTISHAUSER 1956 ; KURABAYASHI 1964 ; KOZUKA *et al* 1964 ; FUKUDA 1964 ; KOZUKA 1967 ; SEROTA & SMITH 1967 ; FREEMAN 1969 ; IHARA 1973).

These controversial points may relate to any diversified gross morphology in the natural entities here concerned, analysis of which is the final objective of the present investigation ; toward this end an initial concentration was made in the present study to document variation patterns and geographical distribution of some discrete assemblages in the pedicellate-flowered entities.

Materials and Methods

Of about 30,000 herbarium specimens loaned from the following 82 herbaria, more than 10,000 specimens belonged to the pedicellate-flowered entities : ALU, ASTC, AUA, BH, BKL, BM, BUF, BUT, CAS, CHARL, CINC, CM, DAV, DEN, DPU, DS, DUKE, DWC, F, FLAS, FSU, GA, GEO, GH, IA, ILL, ILLS, IND, ISC, ISM, JEPS, K, KANU, KE, KIEL, KSC, KY, LAF, LCU, LL, MIN, MISSA, MO, MSC, NA, NCU, ND, NO, NSC, NY, OC, OKL, OKLA, ORE, OS, OSC, OXF, P, PAC, PENN, PH, PUL, ROCH, SIU, SMS,

SMU, SYR, TAES, TENN, TEX, UARK, UC, UMO, US, USF, VDB, VPI, WAB, WIS, WTU, WVA and YU. The following 15 properties in gross morphology were taken from these specimens together with their localities, collectors and any ecological notes on the habitat if available : Length ratio of petal and sepal, of androecium and gynoecium, of anther and filament ; patterns in ovary, stigmatic portion, anther, petal, sepal and leaf ; colour variations in petal, sepal, anther, pollen grains and ovary. The information was recorded as classified figures, according to the range of respective classes in each property. The range of each class was chosen not by statistical sense but rather from viewpoint of its conspicuous adoption and quick operation of the materials, which essentially leads to application of a wider range of each class than than statistically recommended. However, this treatment does not change variational patterns themselves. To diminish personal bias in the classification, we calibrated our estimation by training with standardized figures of the length ratios of androecium and gynoecium as well as the other marker characters ; when either one estimated a different figure, direct measurement was employed. Properties of these marker characters were analyzed by living materials cultivated under a nursery condition at Vanderbilt University which will be independently published elsewhere as the third report of the present study. By the experiments, patterns of ovary and stigmatic shape were concluded to be the most reliable marker for representing certain assemblages of the natural entities as documented herein. Respective localities were confirmed by consulting with an old guide book to local mail stations in the United States, yet some localities remained dubious. All localities thus determined were plotted by county level for mapping. The distribution maps were also compared with patterns of physiographic provinces (FENNEMAN 1938), forest regions (BRAUN 1950), and the latest glaciation (WRIGHT & FRE

Taxonomic treatment of the pedicellate-flowered *Trillium* has been a matter of controversy. In the present study, however, the following names are adopted as the most appropriate ones in order to document the present study. Since taxonomic decision is beyond the scope of the present study, the propriety of the ranks remains to be re-examined from the viewpoint of the biological species concept, and the following enumeration should be considered as tentative. The choice of appropriate epithets was based upon the following processes together with the distribution ranges of the respective taxa herein documented : the examination of (i) the holotype, (ii) (more than)

one of the type collection or the other kinds of type specimens, (iii) photo or drawing of the type, (iv) the original description and distribution of the corresponding taxa.

Trillium pusillum MICHX. Fl. Bor.-Am. 1 : 215 (1803) - (ii).

T. pumilum PURSH, Fl. Am. Sept. 1 : 245 (1814) - (ii) ; *T. texanum* BUCKL. Proc. Acad. Sci. Philad. 443 (1860) - (iv) ; *T. ozarkanum* PALMER & STEYERM. Ann. Mo. Bot. Gard. 22 : 504 (1935) - (i) ; *T. pusillum* MICHX. var. *virginianum* FERN. Rhodora 45 : 397 (1943) - (i).

Trillium Catesbaei ELL. Sketch 1 : 429 (1817) - (iv).

T. cernuum MICHX. Fl. Bor.-Am. 216 (1803) non L. 1753. - (ii) ; *T. nervosum* ELL. l. c. 429 (1817) - (i) in CHARL ; *T. stylosum* NUTT. Gen. Am. 1 : 239 (1818) - (ii) ; *T. declinatum* RAF. Aut. Bot. 135 (1840) nec Gleason 1906. - (iv) ; *T. balduinianum* RAF. l. c. 135 (1840) - (i) in P-DU.

Trillium persistens DUNCAN, Rhodora 73 : 244 (1971) - (iv).

Trillium nivale RIDDELL, Syn. Fl. West. St. 93 (1835) - (ii & iii).

Trillium rivale S. WATS. Proc. Am. Acad. 20 : 387 (1885) - (ii).

Trillium grandiflorum (MICHX.) SALISB. Parad. Lond. t. 1 (1805).

T. rhomboideum MICHX. var. *grandiflorum* MICHX. Fl. Bor.-Am. 1 : 216 (1803) - (ii) ; *T. erythrocarpum* auct. non MICHX., Curtis, Bot. Mag. t. 855 (1805) - (iv) ; *T. amblopsis* RAF. Med. Fl. 2 : 99 (1830) - (i/i?) in P-DU.

Trillium ovatum PURSH, Fl. Am. Sept. 1 : 245 (1814) - (i & ii).

T. ovatum auct. HOOK., Fl. Bor.-Am. 2 : 180 (1838) non PURSH ; *T. californicum* KELLOGG, Proc. Calif. Acad. 2 : 50 (1863) - (iv) ; *T. crassifolium* PIPER, Erythea 7 : 104 (1899) - (i) ; *T. Scouleri* RYDB. Bull. Torr. Bot. C. 33 : 394 (1906) - A specimen of *T. ovatum* PURSH, cited as "276 *T. grandiflorum*, Columbia, (coll. by) Dr. SCOULER", of Torrey Herb. in NY, may be the type or one of the type collection of this species ; *T. venosum* GATES, Ann. Mo. Bot. Gard. 4 : 66 (1917) - (i) ; *T. ovatum* PURSH var. *stenosepalum* GATES, l. c. 61 (1917) - (i).

Trillium erectum L. var. *erectum*.

T. erectum L., Sp. Pl. 2 : 340 (1753) - (iii) ; *T. rhomboideum* MICHX. Fl. Bor.-Am. 1 : 215 (1803) - (ii) ; *T. foetidum* SALISB. Parad. Lond. t. 35 (1805) - (iii) ; *T. acuminatum* RAF. Med. Reposit. 5 : 361 (1808) - (iv) ; *T. purpureum* KIN ex ELL. Sketch 1 : 430 (1817) - (i) ; *T. nutans* RAF. Med. Fl. 2 : 99 (1830) - (iv) ; *T. flavum* RAF. l. c. 100 (1830) - (iv) ; *T. spatulatum* RAF. l. c. 101 (1830) - (iv) ; *T. divaricatum* RAF. l. c. 102 (1830) - (iv) ; *T. erectum* L. var. *viridiflorum* CURTIS, Bot. Mag. pl. 3250 (1833) - (iv) ; *T. erectum* L. Dietr. Syn. Pl. 2 : 1212 (1840), "rectum" ; *T. rhombifolium* RAF. Aut. Bot. 133 (1840) - (iv) ; *T. erectum* L. var. *flavum* TORR. Fl. N. Y. 2 : 296 (1847) - (iv) ; *T. erectum* L. forma *albiflorum* R. HOFFM. Proc. Bost. Soc. Nat. Hist. 36 : 244 (1922) - (iv) ; *T. erectum* L. var. *Chanae* FARW. Am. Midl. Nat. 9 : 266 (1925) - (i) ; *T. erectum* L. var. *horizontale* LOUIS-MARIE, La Revue d'Oka 14 : 151 (1940) - (iv) ; *T. erectum* L. var. *giganteum* LOUIS-MARIE, l. c. 151 (1940) - (iv) ; *T. erectum* L. var. *sessiloides*

BOIVIN, *Rhodora* 55 : 102 (1953) - (iv).

var. *atropurpureum* (MICHX.) PURSH, Fl. Am. Sept. 1 : 245 (1814).

T. rhomboideum MICHX. var. *atropurpureum* MICHX. Fl. Bor.-Am. 1 : 215 (1803) - (ii);

T. rhomboideum MICHX. var. *album* MICHX. l. c. 215 (1803) - (ii); *T. erectum* L. var. *album* (MICHX.) PURSH, l. c. 245 (1814); *T. atropurpureum* (MICHX.) CURTIS ex BECK. Bot. N. & M. State 361 (1833); *T. Vaseyi* HARBISON forma *album* HOUSE, Muhlenbergia 6 : 73 (1910) - (i).

var. *simile* (GLEASON), comb. nov. ined.

T. simile GLEASON, Bull. Torr. Bot. Cl. 33 : 39 (1906) - (ii); *T. Vaseyi* HARBISON var. *simile* (GLEASON) BARKSDALE, Journ. E. Mitch. Sci. Soc. 54 : 285 (1938).

var. *sulcatum* BARKSDALE, valid. ined.

T. erectum L. var. *sulcatum* BARKSDALE, Journ. E. Mitch. Sci. Soc. 54 : 285 (1938) nom. nud. - (ii).

var. *vaseyi* (HARBISON) AHLES in Radford *et al*, Guide Vasc. Fl. Carol. 115 (1964).

T. Vaseyi HARBISON, Biltmore Bot. Stud. 1 : 24 (1901) - (ii).

Trillium cernuum L. Sp. Pl. 2 : 339 (1753) - (iii).

T. pendulum WILLD. Ges. Naturf. Fr. Neue Schr. 3 : 421 (1801) - (iv); *T. cernuum* BARTON, Fl. N. Am. II:13 t. 40 (1822) non L. 1753 - (iii); *T. hamosum* RAF. Med. Fl. 2 : 101 (1830) - (iv); *T. medium* RAF. l. c. 102 (1830) - (iv); *T. glaucum* RAF. l. c. 102 (1830) - (iv); *T. cernuum* L. var. *macranthum* EAMES & WIEG. *Rhodora* 25 : 191 (1923) - (i); *T. cernuum* L. var. *typicum* WHERRY forma *tangerae* WHERRY, *Bartonia* 23 : 49 (1945) - (i); *T. cernuum* L. var. *terrae-novae* BOIVIN, *Rhodora* 55 : 101 (1953) - (iv).

Trillium flexipes RAF. Aut. Bot. 133 (1840) - (iv).

T. erectum L. var. *declinatum* A. GRAY, Man. Bot. N. U. S. ed. 5, 523 (1867) - (iv); *T. declinatum* (A. GRAY) GLEASON, Bull. Torr. Bot. Cl. 33 : 389 (1906) non RAF. 1840; *T. cernuum* L. *declinatum* (A. GRAY) FARW. Rep. Mich. Acad. Sci. 21 : 363 (1920); *T. gleasoni* FERN. *Rhodora* 34 : 21 (1932); *T. erectum* L. var. *blandum* JENNISON, *Rhodora* 40 : 486 (1938) - (i).

Trillium latifolium: RAF. Med. Fl. 2 : 96 (1830), "latifolium" - (iii) & (i?) in P-DU; *T. cernuum* L. *atrorubens* WOOD ex DEAM, Fl. Indiana 324 (1940) pro syn.; *T. cernuum* L. var. *declinatum* (A. GRAY) FARW. forma *Walpolei* FARW. Rept. Mich. Acad. Sci. 21 : 363 (1920) - (iv); *T. cernuum* L. var. *declinatum* (A. GRAY) FARW. forma *Billingtonii* FARW. l. c. 364 (1920) - (iv); *T. declinatum* (A. GRAY) GLEASON forma *Walpolei* (FARW.) FRIESNER, Butler Univ. Bot. Stud. Paper 1 (3) : 34 (1929); *T. flexipes* RAF. forma *Walpolei* (FARW.) FERN. *Rhodora* 46 : 17 (1944).

Trillium affine RENDLE, Journ. Bot. 39 : 334 (1901) - (iii).

Trillium rugelii RENDLE, Journ. Bot. 39 : 331 (1901) - (iii).

When variation pattern of certain natural entity is situated at the mid-point and its proximity of discrete variations in any other entities, the natural entity

documented by a hyphenized epithets of the referred entities, e. g., "*erectum-simile*" or "*erectum-flexipes*", etc. The taxonomic rank of the entity remains uncertain until sufficient informations is accumulated.

Recent reports by Samejima (1976 a, b) deal with exactly the same entities of almost the same specimens as what we examined. However, it is almost impossible to ascertain the propriety of her results because some mis-identification of the specimens examined by her has been undoubtedly made with especially what we define as the *Erectum* major group, which in turn causes rather dubious delimitation of her respective entities. Further, any critical inferences should be retained as to some quantitative measurements like sizes of leaf length and width, of sepals, of petals and so forth for detecting any interspecific relationships until experiments demonstrate these properties to work out for the purpose. Accordingly, as far as respective independent studies are approved, the Samejima's results would not be referred in the series of the present study unless there are perfect coincidence of any results in the present study and the Samejima's.

Results

As shown in Fig. 1, patterns of ovary shape and stigmatic portion seem to be characteristic representatives of certain assemblages in the pedicellate-flowered entities, in which three major groups may be recognized according to the range and the frequency of respective patterns exhibited by them.

PUSILLUM major group. Gynoecium of every member of this group is characteristic to have a connated portion at the base of carpel prolongation, making a remarkable common style and stigmata. The following three morphs may be involved, i. e., P₁-, P₂- and P₃-type (Fig. 1). Difference between P₂-type and P₃-type is quantitative fashion at the connated part as well as due to square or round ovary. A rod-shaped ovary is allocated on P₃-type. In *Trillium pusillum* all specimens examined revealed the rod-shaped ovary of the P₁-type irrespective of their localities. The present species is sometimes split into two geographical varieties, i. e., var. *pusillum* and var. *virginianum*. The former entity is known to occupy somewhat dry rocky habitats of the Ozark Mountains and its vicinity in Missouri, Arkansas and Texas, while the latter entity occurs in bogs or boggy habitats on the Piedmont Plateau in Maryland, Virginia, North and South Carolina (Fig. 2; also SAMEJIMA 1976 a). Yet, there was no appreciable difference between these two taxa in the gynoecium morph. *Trillium Catesbaei* may be a member of this group in possessing P₁-, P₂- or P₃-type gynoecium (Fig. 1). This species grows in Virginia,

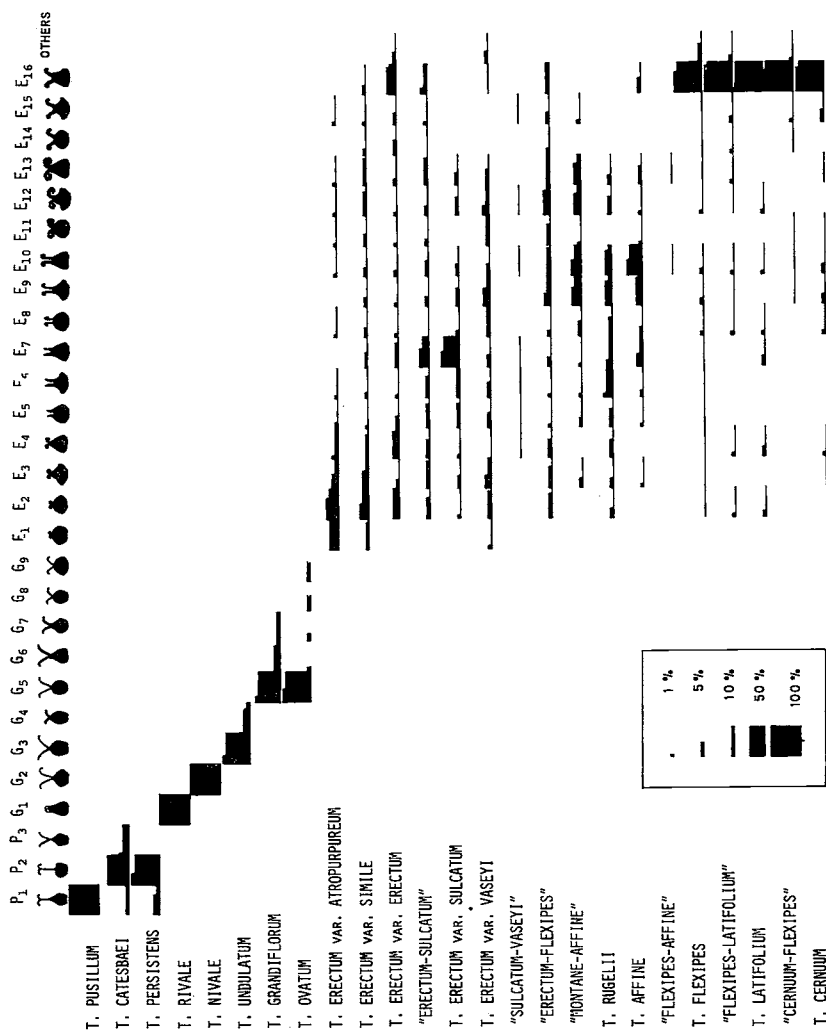


Fig. 1. Gynoecium forms and their frequency distribution in the pedicellate-flowered species of *Trillium*. Reference of the frequency in respective dendrograms is located in a corral. The number of specimens examined is as follows: all specimens in the *Pusillum* major group, including 30 specimens of *T. persistens* collected from Tallulah Falls, Ga.; all specimens in the *Grandiflorum* major group except respective 100 specimens in *T. grandiflorum* and in *T. ovatum* as covering throughout their distribution ranges; totally 5536 specimens in the *Erectum* major group. Only a bar is shown if the frequency is less than 1 per cent.

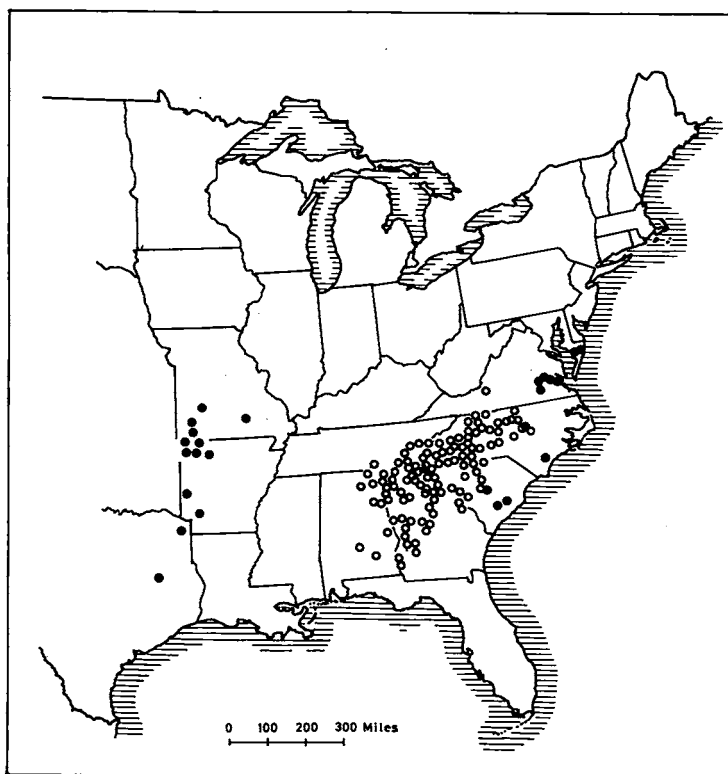


Fig. 2. Geographical distribution of the *Pusillum* major group. Respective marks denote ; (●) *T. pusillum*, (○) *T. Catesbaei*, (▲) *T. persistens*. In the figure 2 to 6, each single mark corresponds to a county from which more than one herbarium specimens were collected. Names of the counties are listed in the Appendix.

North and South Carolina, Georgia, Alabama and Tennessee (Fig. 2 ; also SAMEJIMA 1976 a). It is southernmost distribution in the pedicellate-flowered entities, occurring near the boundary of the Oak-Chestnut forest region at the foot hills of the Southern Appalachian and extending to the southeastern ever-green region where it sometimes grows with *T. erectum* var. *simile* in the former region and with either *T. underwoodii* or *T. decipiens* of the sessile-flowered entities in the latter region. Its northwestern boundary seems to be concord with the location of Ridge and Valley Section in the Oak-Chestnut forest region except for some locations in Tennessee and Alabama on Lookout

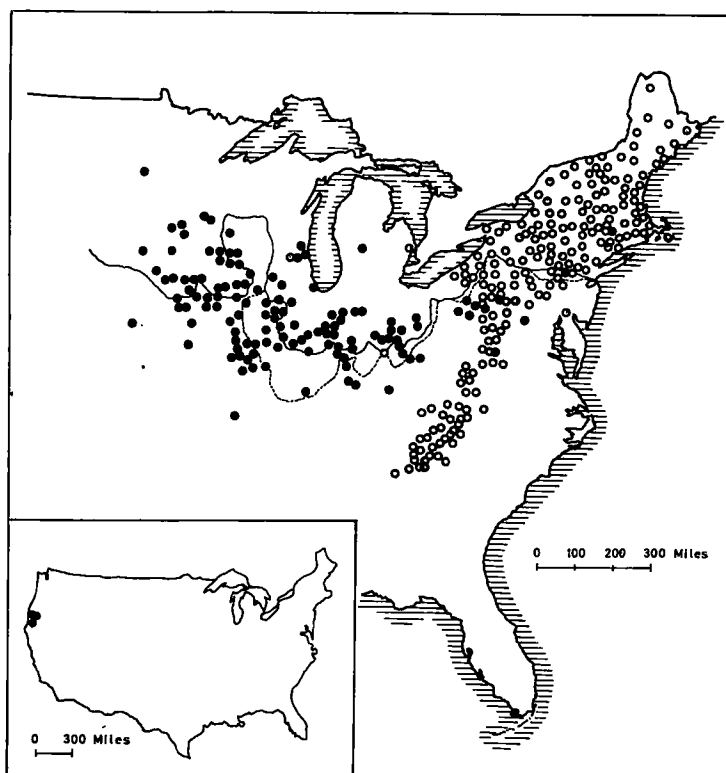


Fig. 3. Geographical distribution of *T. rivale* (●), bottom left.

Fig. 4. Geographical distribution of *T. nivale* (●) and *T. undulatum* (○).

The solid line in the map shows the Wisconsin border, and the broken line represents the extent of the Illinoian glaciation.

Mountain belonging to the Cumberland Plateau of the Mixed Mesophytic forest regions (see Appendix and compare BRAUN 1950). The distribution range of *T. Catesbaei* is superimposed by that of *T. grandiflorum* and *T. undulatum* at the Southern Appalachian and the Cumberland Plateau as well as that of the *erectum* complex and the *flexipes* complex at the Oak-Pine forest region in Alabama, Georgia, South and North Carolina and Virginia. However, cohabitation is only seen with *T. erectum* var. *simile* in the member of the pedicellate-flowered entities at the Southern Appalachian. Therefore, the above-mentioned association of remarkably discrete natural entities may reflect some evolutionary significance, and so we designated such association as an ecological species

compound which may follow the same sociological and/or evolutionary fate. A natural entity which has either P_1 - or P_2 -type gynoeceium occurs at the centre of the geographical distribution range of *T. Catesbaei* in Georgia. Recently, this entity was described as a new species, *T. persistens*, as we had expected (cf. DUNCAN *et al.* 1971). From its gynoeceium form, this entity may relate to *T. Catesbaei* and *T. pusillum*, which is also supported by their close similarity in chromosomal morphology, all possessing 2 pairs of large sub-median chromosomes instead of one pair of large median chromosome customarily denoted as chromosome A in the member of the *Grandiflorum* major group, the *Erectum* major group and in all members of the sessile-flowered entities (IHARA & IHARA ms. in preparation; also cf. BALDWIN *et al.* 1949). We have carefully examined the Georgian dried as well as living specimens in the natural population and under a nursery condition at Vanderbilt University, yet the Duncan's description of "*Peduncul arcuati ad erectiusculi*" sounds to be misleading of the entity because of arched peduncles occurring in *T. Catesbaei*. In this connection we are not sure whether the specimens from Oconee Co., South Carolina should belong to the present entity; all specimens we examined from this county were identified as *T. Catesbaei*.

All the entities thus involved in this group are pale-green in ovary colour; futher, a slender rhizome is characteristic to *T. pusillum*. It may be noteworthy that these morphological characteristics together with the occurrence of the conspicuous common style are common to those in certain members of the genus *Paris*. Judging from gross and chromosomal morphology, the west coast region lacks any counterparts of this group; but it does not imply there are any direct relationships whatsoever between the *Pusillum* major group and the *Erectum* major group. However, it may be suspected that the *Pusillum* major group would be a kind of spinning-out as if they have still retained some morphological remnants.

GRANDIFLORUM major group. This group comprises somewhat heterogeneous components in gross morphology as well as in geographical distribution, so that the assemblage may be artificial rather than natural. All the member of this group expressed inconspicuous or no common style, revealing slender or tentacle-like stigmata except that *T. rivale* shows extremely short or no carpel prolongation. All specimens examined in *T. rivale* were rod-shaped in the gynoeceium form (G_1 -type) like that of *T. pusillum*. However, there seems to be no close similarity in their chromosome morphology as mentioned in the previous section. This west coast species occurs at a very restricted area in California

and Oregon (Fig. 3; also cf. SAMEJIMA 1976 a) and reveals a characteristic chromosome C, short arm of which used to result in a thread-like elongation in the metaphase to anaphase figures of the usual 3 : 1 fixed specimens (cf. WARMKE 1937; IHARA & IHARA ms. in preparation). Because of the above-mentioned discontinuity, there are difficulties to confirm relationships between the present natural entity and any other known entities. Geographical distribution of *T. nivale* ranges from Massachusetts westwards to Pennsylvania, Ohio, Michigan, Indiana, Illinois, Wisconsin, Minnesota, Iowa and Missouri (Fig. 4; also cf. SAMEJIMA 1976 a), most of which are glaciated in the Wisconsinan; the southernmost extension of the lobe is shown by a solid line in the Fig. 4. Contrasting with abundant occurrence in the glaciated region, several specimens came from the unglaciated region, viz., Maryland, West Virginia, Kentucky and Nebraska. That the most concentrated distribution ranges fall into some glaciated areas not only in the Illinoian but also in the Wisconsinan suggests that the distribution ranges of *T. nivale* may have established before the Wisconsin Ice Age and that a post-glacial recovery has taken place at the area of the Wisconsinan glaciation. Some unglaciated localities may imply remnants of its southerly expansion. However, the extent of the historical expansion is obscure because two of such unglaciated locations are situated at the Ridge and Valley Section of the Oak-Chestnut forest region and others are in the Western Mesophytic forest region and in the Oak-Hickory forest region extending to the Prairie.

Gross morphology of *T. undulatum* is distinguished from those of any natural entities, viz., undulated petals of showy painted base with reddish purple colour, definitely petiolated leaves, slender ellipsoid ovary (G_3 - and G_4 -type in Fig. 1) and pink or red coloured berry. Difference between these two morphs in the gynoeceium form is based upon quantitative one as to the carpel prolongation. However, these characteristics in gross morphology lead to an indistinctive relation to any known natural entities; yet the karyotype indicates that the present entity belongs to the *Grandiflorum* major group. The range of geographical distribution goes northwards along the Appalachian Mountains from Georgia, South and North Carolina, Tennessee, West Virginia, Kentucky, Virginia, Maryland, Delaware, Pennsylvania, New Jersey, New York, Connecticut, Rhode Island, Massachusetts, Vermont, New Hampshire and Maine; Ashtabula Co. and Hamilton Co., Ohio, St. Clair Co., Michigan and Jefferson Co., Wisconsin seem to be not very isolated locations of the species, but some localities are dubious for naturality (Fig. 4). These localities mostly locate

on the Oak-Chestnut forest region and its adjacent region, i. e., the eastern part of the Hemlock-White Pine-Northern Hardwood region, which must associate with its more wet habitat condition than that of *T. grandiflorum* (cf. Figs. 4 & 5). This may also be suspected by the following points: The range of geographical distribution in *T. undulatum* is almost exactly superimposed by that of *T. grandiflorum*; yet the realm of the present species is restricted at the eastern part of the geographical distribution of *T. grandiflorum* (Figs. 4 & 5). Further, northern part of respective distribution ranges of both species is situated at the glaciated area, to which they would have expanded since the onset of the post-glacial age; on the other hand, the size of the contemporary realm may have correlated to their maximum expansion in the southern part of their distribution. In the above-mentioned three comparisons, *T. grandiflorum* occupies wider range than *T. undulatum*. In the Southern Appalachian, an ecological species compound was consisted of *T. undulatum*, *T. erectum* var. *Vaseyi* and *T. luteum*; another compound was formed by *T. undulatum* and *T. erectum* var. *simile*. Thus, that no sympatry was seen between *T. undulatum* and *T. grandiflorum* may be another supporting evidence of their different habitat preference. However, from viewpoints of chromosomal morphology and of similarity in the components of the ecological species compound of *T. grandiflorum* or *T. luteum*, it may be reasonable that *T. undulatum* is included in the *Grandiflorum* major group.

Considerable variability was exhibited by the gynoeceum morph of *T. grandiflorum* and *T. ovatum*, which may be classified into five kinds (Fig. 1), i. e., roundish or depressed ovoid (G_9 -type), ellipsoid (G_5 - and G_8 -type) and ovoid (G_6 - and G_7 -type). The most frequent form is the G_5 -type, being common to both species; the other morphs occur infrequently. It is very remarkable that the carpel prolongation of *T. grandiflorum* is long, irrespective of ovary shape. These morphologically resembled entities are separated by the intermountain region. This disjunction may correspond to the extent of the Prairie (cf. BRAUN 1950). Since we have not examined the natural populations of *T. ovatum*, we can not provide enough information as to the sociological sketches of its habitat except for some available information recorded on the herbarium sheets. Of 336 herbarium sheets with any sociological records, 207 sheets informed that the entity lives in woods or deciduous forests; the number of sheets informing coniferous woods, mixed deciduous and coniferous woods, and boggy woods were 120, 6, and 3, respectively. The coniferous woods thus informed in the herbarium records may be comprised of

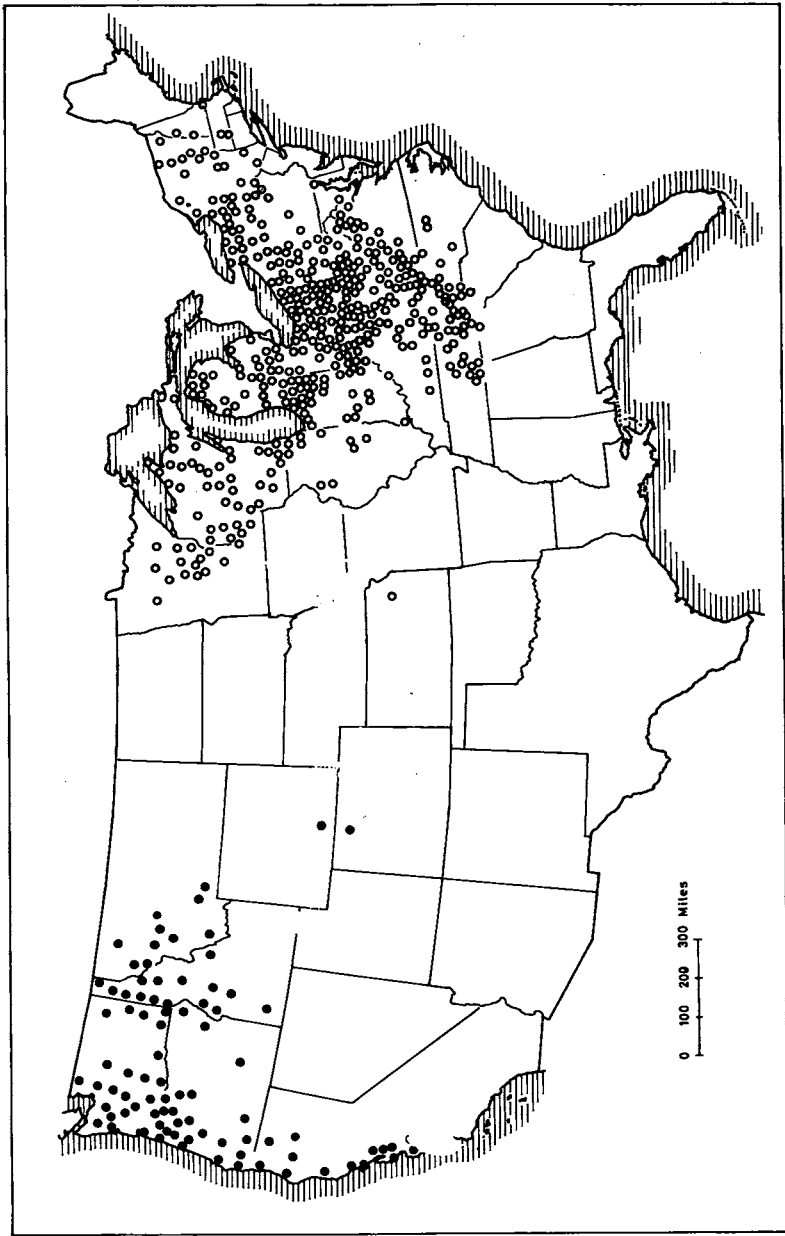


Fig. 5. Geographical distribuion of *T. grandiflorum* (○) and *T. ovatum* (●).

Sequoia sempervirens, *Pseudotsuga Menziesii* and other coniferous woods (cf. MUNZ 1968), which is quite contrasting with the habitat of *T. grandiflorum*. The geographical distribution range of *T. grandiflorum* spreads over mainly in eastern deciduous forests (Fig. 5), viz., the Mixed Mesophytic forest region, the Oak-Chestnut forest region, northeastern part of the Western Mesophytic forest region, the Beech-Maple forest region, northern division of the Oak-Hickory forest region, the Maple-Basswood forest region, and the Hemlock-White Pine-Northern Hardwoods region (cf. BRAUN 1950). This implies that the natural entity may have expanded to somewhat moist habitat as far as its continuity is provided. Therefore, their naturality may be guaranteed as to the following two localities in the Forest-Prairie Transition Area of the Oak-Hickory forest region, i.e., Harrison Co., Iowa and Shawnee Co., Kansas. This is so indicative that the distribution range of both *T. grandiflorum* and *T. ovatum* would have separated by a successive development of the Prairie, suggesting their recent isolation from sole natural entity if not homogeneous at all. The assumption may be supported by the occurrence of the common variation pattern in the gynoeceum form as well as chromosomal morphology which expresses a close similarity to the karyotype of the *Erectum* major group. *ERECTUM* major group. We have discerned 17 natural entities which may belong to an assemblage designated as the *Erectum* major group, in which the most conspicuous common characteristics are their karyotype and their physiological or pre-adapted nature of microsporogenesis responding to the environmental conditions, especially to temperature (IHARA, M. ms. in preparation). Their gynoeceum forms are variable in the ovary shape as well as in the stigmatic portion, though the variability *per se* characterizes the present assemblage. The gynoeceum morph may be categorized into 17 kinds according to the combination between 4 ovary shapes (i.e., globose, depressed or roundish ovoid, intermediate forms between ovoid and conical, and conical or flask-shaped ovary) and 5 kinds of the carpel prolongation (i.e., teat-like, antelope-horned, proboscidean, truncated and goat-horned). Since intra- and interpopulational analyses as to the intra- and interspecific variation in gross morphology will be reported in the third paper of the series of the present study, only a summarized representation is made in the present paper.

As shown in the Fig. 1, there may be no discrete discontinuity of the frequency distribution of the gynoeceum morphs among these 17 entities, indicating their similarity in the property. However, the following two points are remarkable: The most frequent morph of respective entities gradually changes

from *T. erectum* var. *atropurpureum* (the top-situated dendrogram) to *T. cernuum* (the bottom one); the peak of the frequency distribution in the lower 5 entities is definitely deviated from the main body of the variation. Although it should be reminded that each dendrogramized information is arranged subjectively, the above-mentioned properties of the variation must implicate any evolutionary significance. The followings are the reasons: Locations of respective entities thus categorized quite correspond to certain geographical area if not exactly; namely seven entities (the first 7 counted from the top to the bottom in Fig. 1) are almost exactly situated at the Mesophytic forest region, the Oak-Chestnut forest region and the eastern part of the Hemlock-White Pine-Northern Hardwoods; the remainders mainly occur out of the above-mentioned forest regions (Fig. 6). At the northern part of the superimposed geographical area, we could easily discern any counterparts belonging to the bottom five entities because of their characteristic gynoeceum form. Therefore, the first seven entities may be a discernible biological assemblage from the remaining natural entities. We define the first seven entities as the *Trillium erectum* complex and the remainders as the *T. flexipes* complex for convenience (cf. Fig. 1).

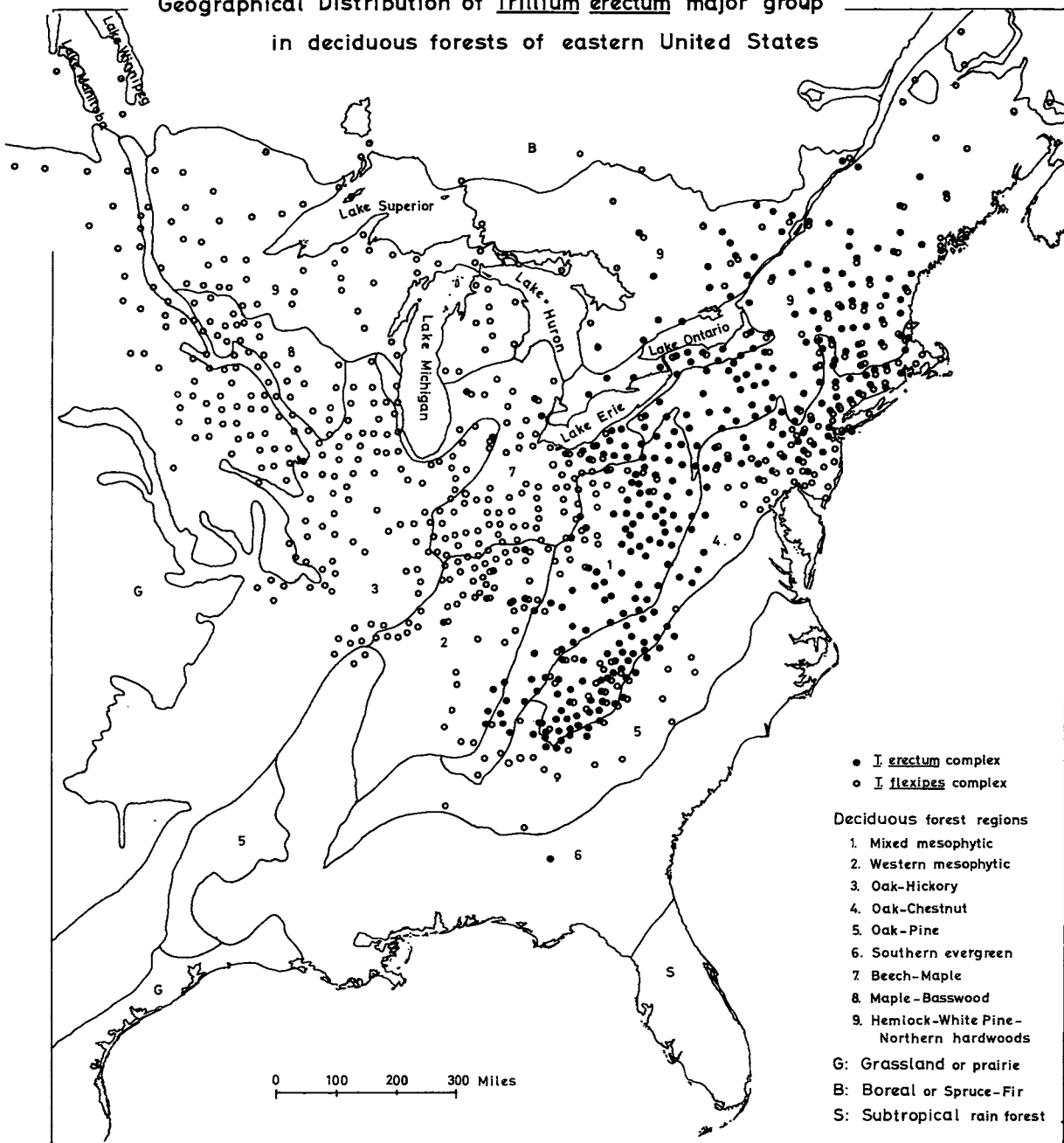
Here it should be emphasized that the variability of these complexes is not correlated to their absolute range of geographical distribution at all, which in turn reinforces that their variation patterns are specific to respective complexes. Thus those natural entities which inhabit the central part of the whole distribution range exhibit more variability in the gynoeceum morph than the peripheral entities. This is one of the remarkable characteristics in the *Erectum* major group whatever the origin of such pattern may be. Accordingly, it may be a natural conclusion that these five entities of the *flexipes* complex, which are circumjacent to the distribution range of the *erectum* complex, express wider variation ranges than those of the peripheral natural entities of the *flexipes* complex; we are assuming here that any sorting-out of the member of the *Erectum* major group would have accompanied with the loss of the variability in gross morphology. This may be principally the same idea as exemplified for the foundation of the deciduous forest regions in the eastern United States by Braun (1950). Alternatively, the variability of such circumjacent entities may be illustrated as it might have been retained by recurrent and/or extensive gene-exchanges among the member of the *erectum* complex and that of the *flexipes* complex. In fact, an intermediate variation pattern between the *erectum* complex and the peripheral entities of the *flexipes* com-

plex is revealed by the circumjacent entities; which is very familiar pattern to any interspecific hybridization proposed by Anderson and Hurbicht (1938), yet the carriers of the intermediate variation patterns occur neither at the disturbed habitats (cf. ANDERSON & STEBBINS 1954) nor at the sympatric populations of the putative parental entities but at somewhat climatically specific area like a transitional zone from a certain forest regions to another one or at the vicinity of the Ohio River and the Sasquehanna River.

In the *erectum* complex in which the most plausible representation is provided by anther-filament length ratio, the following seven natural entities may be distinguished: *Trillium erectum* var. *atropurpureum* seems to be a highland form of the complex, exhibiting a globose or slightly depressed ovoid ovary with teat-like stigmata (E_1 - and E_2 -type) as a typical norm but varying its petal colour and size considerably. The most typical populations may be seen near the Indian Gap of the Great Smoky Mountain and near Forkridge Overlook of the Blue Ridge. The former population is variable in the petal colour and the latter shows rather uniform petal colour and size, but specimens from these populations are quite compatible with the Michaux's type collection except for colour variation. *Trillium erectum* var. *simile* reveals the same variation range as the previous entity does, except that the present entity expresses slightly higher frequency than that of var. *atropurpureum* in the conical or flask-shaped ovary with various stigmatic forms. This must positively correspond to the present entity's occurring at lower elevation of the Southern Appalachian, where sometimes it forms an ecological compound with *T. grandiflorum* and/or *T. luteum* as *T. erectum* var. *sulcatum* does. However, var. *simile* seems to show extremely variable patterns of the H-segments in the chilled chromosomal sets while var. *sulcatum* does not (cf. KOZUKA 1967; IHARA & IHARA ms. in preparation). In this consequence, we may define var. *simile* as a heterogeneous representative at the Southern Appalachian, although the type population is situated at Mt. Tryon, South Carolina. *Trillium erectum* var. *erectum* may be delimited as a northern form of the *erectum* complex, consisting of several characteristic norms of the gynoeceum form as well as of the typical globose ovary but larger than that of the highland entity, namely, flask-shaped ovary either with teat-like stigmata (E_4 -type) or with truncated (E_7 -type) or goat-horned stigmata (E_{16} -type). These forms with the stout

Fig. 6. Geographical distribution of the *erectum* complex (●) and the flexipes complex (○) in the various forest regions of eastern United States.

Geographical Distribution of *Trillium erectum* major group
in deciduous forests of eastern United States



stigmata are usually seen in the specimen come from New England, the vicinity of the Alleghany Mountains and of the Finger Lakes, in which the Northern Appalachian highland protrudes into the Hemlock-White Pine-Northern Hardwoods region. The main body of an intermediate form designated as *erectum-sulcatum* frequently occurs in Kentucky, West Virginia and southern Pennsylvania corresponding to the northern part of the Mixed Mesophytic region, but it does not conform a pure stand by itself. The gynoeceium form varies almost as the same range as that of var. *erectum*, yet the most frequent norm in these localities may be indiscernible with that of var. *sulcatum*, viz., the flask-shaped ovary with truncated stigmata (E₇-type). A distributional transition from the realm of the *erectum-sulcatum* to that of var. *sulcatum* seems to correspond to any climatic conditions, which is more plausibly shown by a discontinuous distribution of the member of the *flexipes* complex at the eastern part of the Appalachian Mountain ranges. We define it as the Virginian Disjunction; this problem will be discussed later. *Trillium erectum* var. *sulcatum* may be a conspicuous southern representative of the *erectum* complex, occurring at the Cumberland Plateau and the northern part of the Blue Ridge. It reveals the conical ovary with truncated stigmata (E₇-type), petals with sulcated tip and maroon colour in carpel, anther, petal and pollen grains except that some colour variants occur in extremely low frequency. As mentioned before, this entity conforms an ecological species compound with *T. grandiflorum* and/or *T. luteum*. Another discrete southern form of the *erectum* complex may be represented by *Trillium erectum* var. *Vaseyi*. This entity is usually treated as a species probably because of its large conspicuous maroon flower with a long stalk nodding beneath the leaves. On the contrary with the constancy in the flower size, the gynoeceium morphs cover with almost whole variation range, indicating considerable variability. Some natural populations consist of the typical form of the present entity and of var. *sulcatum* together with their intermediate forms, designated as *sulcatum-Vaseyi*, which suggests that these natural entities may interconnect somehow. In consequence, a varietus rank may be a better treatment to the present entity until more critical information will be available. Extremely isolated two localities, i. e., Randolph Co., Georgia and Hartford Co., Connecticut(!), may be a supporting evidence to the above-mentioned assumption as well as to a possible southern expansion of the *erectum* complex historically.

Summing up the variation norm of the gynoeceium form in the *erectum* complex, these morphs are quantitatively different from each other, mak-

ing a series of the variation norm from north to south or low-to highland. Therefore it is probable that these clinal variations may depend upon any pre-adapted nature of environmental response because a mere transplantation to a nursery condition would not change the original norm appreciably, otherwise the entities are killed (IHARA & IHARA ms. in preparation).

There may be two sub-groups in the *flexipes* complex as exemplified in the Fig. 1, i. e., those taxa with a discrete gynoeceium form of the flask-shaped ovary with truncated (E₇-type) or goat-horned stigmata (E₁₆-type), and those entities exhibiting various combination forms of the ovary shape and the stigmatic norm. Every member of the former sub-group occupies the peripheral range while that of the latter sub-group grows at the so-defined circumjacent range of the whole distribution of the *flexipes* complex. We discerned the following five entities in the former sub-group: *Trillium flexipes*, *flexipes-latifolium*, *T. latifolium*, *cernuum-flexipes* and *T. cernuum*.

The first entity occurs at Tennessee northwards to Kentucky, Missouri, Iowa, Illinois and Wisconsin. In Kentucky, Illinois, Indiana and Ohio, the second and the third entities grow, sometimes altogether conforming a mixed stand; they may be discernible from the first entity by anther-filament length ratio and both larger ovary and smaller petals with sometimes pale pink colour than those of *T. flexipes*, the most typical populations of which stand in Missouri to Illinois. However, what would be a pure stand of *T. latifolium* is not homogeneous as to the above-documented properties and other gross morphology, exhibiting certain common norms to *T. flexipes*. An intermediate form between *T. flexipes* and *T. cernuum*, typically these two are distinguished by their difference in the anther-filament length ratio as well as in the norm of pedicel declination, lives in several natural populations locating in Wisconsin, Minnesota, and North Dakota; their variation norms reveal as if they are descendants in hybrid swarms (IHARA & IHARA ms. in preparation). The last entity, *T. cernuum*, is a discrete northern form of the *flexipes* complex, exhibiting a hooked pedicel, greyish purple anther and the anther-filament length ratio being unity. It grows in North and South Dakota, Minnesota, Wisconsin eastwards to Michigan, Ontario, Quebec, New York, Vermont, New Hampshire, Maine southwards to Massachusetts, Rhode Island, Pennsylvania, Maryland, Delaware and Virginia. A geographical disjunction of about 200 miles distance lays down between the southern limit of *T. cernuum* and the northern limit of *T. affine*, belonging to the other sub-group of the complex. We defined this distributional gap as the Virginian Disjunction. As eastern inhabitant of *T.*

cernuum is sometimes treated as var. *macranthum* for separating the western counterpart because of its more stout norm in the floral parts than that of the western relative. The typical form may be seen at the lowland populations in New England; yet its anther-filament length ratio is unity, which suggests that there is no necessity to split the species into two geographical varieties.

Another sub-group of the *flexipes* complex may comprise the following five entities; *erectum-flexipes*, *montane affine*, *T. rugelii*, *flexipes-affine* and *T. affine*. These entities look like members of the *erectum* complex in their gynoeceum norm. However, the most frequent morph is remarkably deviated from that of the *erectum* complex. *Trillium affine* predominantly grows in the Oak-Pine forest region or in the Piedmont Province, northern part of which is occupied by dry habitats, being transition into the Virginian Disjunction. An intermediate form, designated as the *flexipes-affine*, between *T. flexipes* and *T. affine* sometimes conforms a pure stand in Alabama, the region of which may be a narrow transitional zone from the Oak-Pine forest to the Western Mesophytic forest where *T. decumbens* of the sessile-flowered species predominates (cf. FREEMAN 1975), so conforming an ecological compound with the entity here under consideration. *Trillium rugelii*, a discrete entity possessing recurved petals with the conspicuous purple veined base, inhabits in Buncombe Co. and Henderson Co., North Carolina, where a transitional cove type forest between the Mixed Mesophytic and the rich chestnut slope forest grow in Black Mountain (cf. BRAUN 1950). The Ashville Basin locates in the vicinity of the above-mentioned transitional zone and inside the Oak-Chestnut forest region, where what we inform as a natural entity of the *montane affine* inhabits. This nodding trillium possesses a flask-shaped to depressed ovoid ovary with proboscidean stigmata (E_8 -, E_9 - and E_{10} -type) or with truncated stigmata (E_5 -, E_6 - and E_7 -type), so that it looks like *T. affine* to some extent. However, respective natural populations of this entity are composed of various forms in gross morphology; some individuals in a population may fall into the same variation range of either one of *T. affine*, *T. flexipes* and another heterogeneous entity, the *erectum-flexipes*. Accordingly, we define the *montane affine* as a representative of the heterogeneous *affine*-like trilliums. It may be noteworthy that this entity conform an ecological compound with *T. grandiflorum* and/or *T. luteum* as some members of the *erectum* complex do in the Appalachian Mountains, suggesting that the entity may have still preserved any relic morphs in connection with those of the *erectum* complex. The last

entity of the sub-group is an intermediate form between *T. flexipes* and *T. erectum*; some mass collections reveal a considerable variation in the gynoeceium form as well as in other gross morphology except for the pedicel's declining, resembling almost exactly to *T. flexipes* or to a white form of *T. erectum*. Their localities are situated somewhat disorderly, viz., in the vicinity of the Finger Lakes, of the Sasquehanna River at eastern part of Pennsylvania, of the Ohio River at the southwestern corner of Pennsylvania, and of the Tennessee River at Knoxville. It is still uncertain whether the present entity would be reduced into either *T. flexipes* or *T. erectum* var. *erectum*.

Discussion

It is now evident that the morphological diversities which have brought on many debates in taxonomy as well as in evolutionary biology should have been exclusively encountered in the *Erectum* major group. Comparing with the variational patterns of gynoeceium morph in the *Pusillum* major group and the *Grandiflorum* major group, it is noteworthy that the same property reveals such a wide range of variability in the members of the *Erectum* major group, extending through most of the natural entities there involved. Yet, there are remarkable clinal variations of frequency distributions successively changing from the *erectum* complex to the *flexipes* complex. Thus E_1 -type and E_2 -type occur most frequently in the former complex while E_{16} -type may be conspicuous representative of the latter complex. This tendency is quite compatible with their geographical distribution. Namely the *erectum* complex predominantly inhabits the central part of the geographical distribution range of the *Erectum* major group, where the Mixed Mesophytic forests and the Oak-Chestnut forests occupy the Appalachian Mountains (cf. BRAUN 1950). On the contrary, the realm of the *flexipes* complex surrounds the region of the *erectum* complex by *T. latifolium* at the western part and the *montane affine* at the eastern part of the foot hills of the Mountains, respectively and *T. cernuum* cohabits mainly with *T. erectum* var. *erectum* at the northern part of the distribution range; furthermore, *T. flexipes*, *T. affine* and *T. rugelii* are circumjacent to the above-mentioned surroundings, altogether making not only an equicircular pattern, if not exactly, of respective geographical distributions but also that of the frequency distributions in their gynoeceium morphs. This concordance in the variation patterns of the gynoeceium morph and the geographical distribution patterns is exhibited by the *Erectum* major group while such concordance to the contemporary events is not expressed by the other major groups, which implicates

that different tempo and modes may have operated in the evolutionary processes of these three major groups.

In fact, it is evident that the geographical distribution pattern of the *Pusillum* major group may be directly concord with neither one of physiographic provinces, the forest regions and other climatic changes in Pleistocene era and that no direct influence of the glaciation would work out there because of its occurring more northerly. However, there is no plausible hypothesis to explain the distribution pattern. On the other hand the distribution pattern of the *Grandiflorum* major group may provide rather probable information as to its modifying events: Habitats of *T. nivale* are mainly seen from the area of the glaciated front northward, which suggests that the contemporary distribution pattern must positively correspond to the Illinoian as well as the Wisconsinan retardation of the ice lobes. The post-glacial recovery is also probable in their northern habitats of *T. grandiflorum* and *T. undulatum*. Despite its extreme similarity to *T. grandiflorum* in the gynoeceum morph as well as other gross morphology, *T. ovatum* has been ranked as a discrete natural entity, probably because the intermountain disjunction lays down between their geographical distribution ranges. Since the disjunction seems to agree with the range of the Prairie, the isolation may have been due to a post-glacial or the contemporary development of the range rather than any events in the glacial era. Certain missing links exist among discontinuous variation patterns of gross and chromosomal morphology in *T. rivale*, *T. nivale* and *T. undulatum*, although they were assembled under the *Grandiflorum* major group because of their contemporary association with either *T. grandiflorum* or *T. ovatum* as the ecological compound as well as of their karyotypic similarity.

Evidently from the theoretical point of view, isolation itself by no means provides any genetic differentiation among the isolated populations. Here the followings may be reminded as the example: *Trillium pusillum* is sometimes split into two geographical taxa, i.e., var. *pusillum* and var. *virginianum*. However, there is no discreteness among these two except for their geographical disjunction and habitat preferences. Likewise, *T. grandiflorum* and *T. ovatum* may be referable to the case because of their common variation in gross morphology as well as in chromosomal morphology (IHARA & IHARA ms. in preparation). It may be therefore accepted that the pedicellate-flowered species reveal two facets of the tempo and modes of evolutionary diversification, namely isolation or sorting-out of populations with less variations in gross morphology, and that with diversification irrespective of the

range of the geographical distribution as well as the contemporary association or dissociation in the form of the species compound. This reinforces such an evolutionary principle that goes on not only in the member of the *Pusillum* major group but also in the *Grandiflorum* major group is a stochastic process, resulting in different degrees of genetic differentiation in respective populations even if they have been isolated for the same chronological time.

For the diversified gross morphology in the *Erectum* major group, the following two explanations may be reliable as previously suggested; namely, operation of natural selection would have separated the *flexipes* complex from the *erectum* complex as worked out for sorting-out the deciduous forest types on one hand, and extensive gene-exchanges would have retained any intermediates or heterogeneous members between the above-mentioned complexes as illustrated by many examples for the interspecific deviants on the other. However, it seems to be unlikely that these two evolutionary forces would operate simultaneously to have brought out two complexes. The first factor operates effectively, turning out ineffective operation of the second factor, and *vice versa*. Further, it is also unlikely that re-association would occur between different species of the different complexes beyond their ecological interlocking with certain major communities. In consequence, it would be only a possibility of such a local differentiation to have attained through the following process meanwhile respective entities here concerned will have been engaged as the undergrowth of certain forest communities: Changes in ravines of the forest, which may have run steadily but abruptly form new branches or different runnings due to a heavy rain-fall, followed by a forced isolation or a local migration of the populations of the natural entities, would altogether bring about a random change of genetic component of the new populations owing to a random choice of the inhabitants. This implies that a stochastic process operates as an effective evolutionary force to follow any local foundations of the populations which may be composed of genetically different components from those of the mother populations. Ample examples which are assumed to be resultants of the above-mentioned process have been provided by the natural populations of the following entities inhabiting the Southern Appalachian where the most heterogeneous components of the deciduous forests have been preserved as the members of the so-called cove type forest; namely, those heterogeneous constituents of the populations in the *montane affine* and *Trillium erectum* var. *simile*, and rather homogeneous constituents of the populations in *T. rugelii*. Populations of the *erectum-flexipes*, occurring in

the vicinity of the Tennessee River at Knoxville, of the Ohio River and Sasquehanna River in Pennsylvania and of the Finger Lakes, may be added to these examples.

However, it may be asked whether or not differences in the fitness of respective entities would have any role on the above-mentioned process, corresponding to various environmental conditions of their habitats. The following facts may be indicative : Geographical distribution ranges of *Trillium erectum* var. *erectum* and *T. cernuum* are superimposed in New England in which they may have invaded after the latest Ice Age ; yet there seems to be little synpatry as well as no intermediate between these two, suggesting a remarkable difference in their habitat preferences and no gene-exchange at all. On the southern realm of the *Erectum* major group, there is a discrete disintegration of their distribution ranges in the *erectum* and the *flexipes* complex ; yet some populations which consist certain morphological recombinants between these complexes *occupy their own habitats inside the distribution range* of the *erectum* complex. It may be concluded therefore that a rapid migration might occur irrespective of minor difference in the fitness of respective entities when a certain favourite habitat condition is given, and that the difference in the fitness may effectively work out only when the invaders successively descend their offspring to supply any loss of the inhabitants.

Since recent advances in molecular evolution, which is acknowledged as the stochastic process, have positively asked whether any parallelism exists in the different types of evolution between molecular and morphological levels, these discrete natural entities here studied are good examples to examine degree of genetic differentiation in relation to their diversification in gross morphology in this concern.

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APPENDIX

List of counties in each State in which more than one herbarium specimen were ex-

amined in the present study.*

- T. pusillum** **TEXAS**—Cass, Houston ; **ARKANSAS**—Benton, Carroll, Hempstead, Madison, Newton, Polk, Washington ; **MISSOURI**—Barry, Lawrence, Polk, Shannon ; **SOUTH CAROLINA**—Berkeley, Calhoun, Dorchester ; **NORTH CAROLINA**—Pender, Wake ; **VIRGINIA**—Charles City, Chesterfield, Dinwiddie, Henrico, James City ; **WEST VIRGINIA**—Somerset, Worchester :
- T. Catesbaei** **ALABAMA**—Calhoun, Cleburne, DeKalb, Jackson, Lee, Lowndes, Marshall, Pike ; **GEORGIA**—Baldwin, Bartow, Bibb, Burke, Chattooga, Clarke, Clay, Cobb, Dawson, Early, Elbert, DeKalb, Floyd, Fulton, Gordon, Greene, Franklin, Habersham, Hall, Haralson, Hart, Houston, Jackson, Lee, Lumpkin, Marion, Merriwether, Murray, Oconee, Oglethorpe, Polk, Putnam, Rabun, Richmond, Sumter, Talbot, Towns, Troup, Twiggs, Union, Upson, Walker, Webster, Wilkes ; **SOUTH CAROLINA**—Aiken, Calhoun, Cherokee, Chester, Edgefield, Fairfield, Greenville, Lancaster, McCormick, Newberry, Oconee, Pickens, Richland, Spartanburg, Union, York ; **TENNESSEE**—Blount, Marion, Monroe, Polk, Sevier ; **NORTH CAROLINA**—Alamance, Alexander, Buncombe, Burke, Cherokee, Cleveland, Davidson, Davie, Durham, Gaston, Guilford, Haywood, Henderson, Iredell, Jackson, Johnston, Lee, Lincoln, Macon, McDowell, Mecklenburg, Montgomery, Orange, Person, Polk, Randolph, Rutherford, Stanly, Stokes, Surry, Transylvania, Wake, Watauga, Wilkes, Yadkin ; **VIRGINIA**—Roanoke :
- T. persistens** **GEORGIA**—Rabun :
- T. rivale** **CALIFORNIA**—Del Monte ; **OREGON**—Curry, Josephine :
- T. nivale** **MISSOURI**—Clark, Daviess, Lewis, Lincoln, Marion, Monroe, Montgomery, Pike, Ralls, Texas ; **KENTUCKY**—Jessamine ; **WEST VIRGINIA**—Pendleton ; **MARYLAND**—Washington ; **NEBRASKA**—Lancaster ; **IOWA**—Adair, Allamakee, Benton, Boon, Calhoun, Cherokee, Chikasaw, Clayton, Clinton, Decatur, Dubuque, Emmet, Fayett, Gathrie, Hamilton, Hardin, Henry, Howard, Jasper, Johnson, Jones, Linn, Lyon, Madison, Mahaska, Marion, Mitchell, Muscatine, Polk, Poweshiek, Sac, Tama, Van Buren, Webster, Winneshiek ; **ILLINOIS**—Adams, Brown, Bureau, Cass, Champaign, Coles, Cook, Fulton, Hamilton, Henry, Jersey, Knox, La Salle, Logan, Macon, Marshall, McLean, Ogle, Peoria, Piatt, Pike, Sangamon, Starke, Stephenson, Tazewell, Vermilion ; **INDIANA**—Carroll, Cass, Cawford, Fountain, Harrison, Huntington, Johnson, Lawrence, Marion, Monroe, Montgomery, Owen, Parke, Putnam, Tippecanoe, Wabash, Warren, Wayne, White ;

* More precise informations of each locality may be available from Dr. R. B. Channell at Vanderbilt University, Nashville, Tennessee 37204 U. S. A. Informations as to the *Erectum* major group (names of entities, their localities, sources of the specimens etc.,) may be provided by Mrs. Kazue Ihara for personal request before the third paper of this series will be published.

OHIO—Adams, Clark, Clinton, Delaware, Franklin, Greene, Highland, Jefferson, Miami, Montgomery, Preble, Scioto, Shelby ; **PENNSYLVANIA** — Allegheny, Beaver, Cambria, Monroe, Washington, Westmoreland ; **MINNESOTA** — Blue Earth, Brown, Dakota, Goodhue, Nicollet, Winona ; **WISCONSIN** — Milwaukee, Washington, Waukesha ; **MICHIGAN** — Ionia ; **MASSACHUSETTS** — Hampden :

T. undulatum **GEORGIA** — Murray, Rabun, Towns, Union ; **SOUTH CAROLINA** — Greenville ; **TENNESSEE** — Blount, Cocke, Greene, Johnson, Sevier, Unicoi ; **NORTH CAROLINA** — Alleghany, Ashe, Buncombe, Caldwell, Clay, Graham, Haywood, Jackson, Macon, McDowell, Mitchell, Swain, Transylvania, Watauga Yancey ; **KENTUCKY** — Letcher ; **VIRGINIA** — Augusta, Giles, Grayson, Highland, Patrick, Russell, Smyth, Washington, Wise ; **WEST VIRGINIA** — Fayette, Grant, Greenbrier, Mercer, Mineral, Nicholas, Pendleton, Pocahontas, Preston, Raleigh, Randolph, Summers, Tucker ; **MARYLAND** — Alleghany, Garrett ; **DELAWARE** — New Castle ; **WISCONSIN** — Jefferson ; **MICHIGAN** — St. Clair ; **OHIO** — Ashtabula, Hamilton ; **PENNSYLVANIA** — Armstrong, Bedford, Blair, Bradford, Cambria, Carbon, Centre, Clarion, Clearfield, Clinton, Crawford, Cumberland, Dauphin, Elk, Erie, Fayette, Forest, Huntingdon, Indiana, Jefferson, Lackawana, Lebanon, Lehigh, Luzerne, Lycoming, McKean, Mercer, Monroe, Pike, Potter, Schuylkill, Snyder, Somerset, Susquehanna, Tioga, Union, Venango, Warren, Wayne, Westmoreland, Wyoming ; **NEW JERSEY** — Passaic, Sussex ; **NEW YORK** — Albany, Alleghany, Broome, Cattaraugus, Cayuga, Chautauqua, Chemung, Chenango, Clinton, Columbia, Cortland, Delaware, Erie, Essex, Franklin, Genessee, Greene, Hamilton, Herkimer, Jefferson, Lewis, Madison, Monroe, Niagara, Oneida, Onondaga, Ontario, Orange, Oswego, Otsego, Rensselaer, Saratoga, Schoharie, Seneca, St. Lawrence, Sullivan, Tioga, Tompkins, Ulster, Warren, Washington, Wayne, Westchester, Yates ; **CONNECTICUT** — Hartford, Litchfield, Middlesex, Tolland, Windham ; **ROHDE ISLAND** — Providence ; **MASSACHUSETTS** — Berkshire, Bristol, Essex, Franklin, Hampden, Hampshire, Middlesex, Nantucket, Norfolk, Plymouth, Suffolk, Worcester ; **VERMONT** — Addison, Bennington, Caledonia, Chittenden, Franklin, Lamoille, Orange, Orleans, Rutland, Washington, Windham, Windsor ; **NEW HAMPSHIRE** — Belknap, Carroll, Chesire, Coos, Grafton, Hillsboro, Merrimack, Rockingham, Strafford ; **MAINE** — Aroostook, Cumberland, Franklin, Hancock, Knox, Lincoln, Oxford, Penobscot, Piscataquis, Somerset, Waldo, Washington, York :

T. grandiflorum **GEORGIA** — Union ; **SOUTH CAROLINA** — Greenville ; **TENNESSEE** — Bledsoe, Blount, Campbell, Claiborne, Coffee, DeKalb, Franklin, Grundy, Hawkins, Knox, Marion, Monroe, Moore, Morgan, Putnam, Roane, Sevier, Van Buren ; **NORTH CAROLINA** — Ashe, Avery, Buncombe, Caldwell, Clay, Durham, Graham, Haywood, Henderson, Iredell, Jackson, Macon, Madison, McDowell, Mitchell, Orange, Polk, Stanly, Stokes, Swain, Watauga, Yancey ; **KENTUCKY** — Bell, Carter, Elliot, Harlan, Knox, Letcher, Lewis, Madison, Metcalfe, Oldham, Perry, Powell, Rockcastle, Russell, Warren, Wolfe ; **VIRGINIA** — Augusta, Bath, Bedford,

Bland, Botetourt, Clarke, Craig, Dickinson, Frederick, Giles, Grayson, Greene, Highland, Loudoun, Madison, Montgomery, Nelson, Page, Patrick, Prince William, Pulaski, Rappahannock, Roanoke, Rockbridge, Rockingham, Russell, Smyth, Tazewell, Warren, Washington, Wythe; **WEST VIRGINIA**—Barbour, Braxton, Brooke, Cabell, Calhoun, Doodridge, Fayette, Gilmer, Greenbrier, Hancock, Harrison, Kanawha, Lewis, Lincoln, Logan, Marion, Marshall, McDowell, Mercer, Mineral, Mingo, Monongalia, Ohio, Pendleton, Pleasants, Pocahontas, Preston, Raleigh, Randolph, Ritchie, Summers, Taylor, Tucker, Tyler, Upshure, Wayne, Webster, Wirt, Wyoming; **MARYLAND**—Allegany, Cecile, Dist. Columbia; **KANSAS**—Shawnee; **IOWA**—Harrison; **ILLINOIS**—Champaign, Coles, Cook, Du Page, Henry, Kankakee, Knox, Lake, McHenry, Piatt; **INDIANA**—Allen, Brown, DeKalb, Elkhart, Fountain, Franklin, Huntington, Kosciusko, Lagrange, Lake, La Porte, Marion, Marshall, Monroe, Noble, Parke, Porter, Posey, Putnam, Randolph, St. Joseph, Steuben, Union, Wabash, Wayne, Wells, Whitley; **OHIO**—Adams, Allen, Ashland, Ashtabula, Athens, Belmont, Brown, Butler, Carroll, Champaign, Clark, Clinton, Columbiana, Coshocton, Crawford, Cuyahoga, Darke, Delaware, Erie, Fairfield, Franklin, Gallia, Geauga, Green, Guernsey, Hamilton, Hardin, Harrison, Highland, Hocking, Holmes, Huron, Jackson, Jefferson, Knox, Lake, Lawrence, Licking, Logan, Lorain, Lucas, Madison, Mahoning, Marion, Medina, Meigs, Miami, Monroe, Montgomery, Morgan, Morrow, Muskingum, Ottawa, Perry, Pickaway, Pike, Portage, Preble, Richland, Ross, Sandusky, Scioto, Seneca, Stark, Summit, Trumbull, Tuscarawas, Union, Vinton, Warren, Washington, Wayne, Williams, Wood, Wyandot; **PENNSYLVANIA**—Allegheny, Armstrong, Beaver, Bedford, Butler, Cambria, Clarion, Clearfield, Crawford, Elk, Erie, Fayette, Forest, Huntingdon, Indiana, Jefferson, Lackawana, McKean, Mercer, Potter, Somerset, Snyder, Susquehanna, Tioga, Venango, Warren, Wayne, Westmoreland, Wyoming; **MINNESOTA**—Aitkin, Benton, Carlton, Cass, Chisago, Clearwater, Crow Wing, Goodhue, Hennepin, Itaska, Kanabec, Mille Lacs, Morrison, Pine, St. Louis, Wabasha, Winona; **WISCONSIN**—Barron, Brown, Buffalo, Clark, Dane, Door, Dunn, Florence, Fond du Lac, Forest, Iowa, Jackson, La Crosse, Langdale, Lincoln, Marathon, Milwaukee, Outagamie, Pierce, Polk, Portage, Racine, Rock, Sauk, Sawyer, Shawano, Vernon, Walworth, Washington, Waukesha, Wood; **MICHIGAN**—Alger, Baraga, Bay, Branch, Berrien, Calhoun, Carkland, Cass, Charlevoix, Cheboygan, Clinton, Eaton, Emmet, Genessee, Gladwin, Gogebic, Gratiot, Hillsdale, Houghton, Huron, Ingham, Ionia, Iron, Jackson, Kalamazoo, Kent, Lake, Leelanau, Livingston, Mackinac, Manistee, Marquette, Mecosta, Menominee, Midland, Montmorency, Neweenaw, Ontonagon, Oscoda, Otsego, Ottawa, Presque Isle, St. Clair, St. Joseph, Shiawassee, Van Buren, Washtenaw, Wayne, Wexford; **NEW YORK**—Albany, Allegany, Broome, Cattaraugus, Cayuga, Chemung, Chenango, Cortland, Delaware, Dutchess, Erie, Essex, Genessee, Jefferson, Livingston, Madison, Monroe, Niagara, Oneida, Onondaga, Ontario, Orange, Oswego, Rensselaer, St. Lawrence, Schenectady, Seneca,

Tioga, Tompkins, Washington, Wayne, Wyoming, Yates ; **CONNECTICUT**—Hartford ; **MASSACHUSETTS**—Essex, Hampden, Hampshire ; **VERMONT**—Addison, Bennington, Caledonia, Chittenden, Franklin, Rutland ; **NEW HAMPSHIRE**—Grafton, Sullivan :

T. ovatum **CALIFORNIA**—Alameda, Contra Costa, Del Monte, Humbolt, Marin, Mendocino, Monterey, San Benito, Santa Clara, Santa Cruz, Sonoma, Shasta, Siskiyou, Trinity ; **OREGON**—Baker, Benton, Clackamas, Clatsop, Coos, Curry, Douglas, Harney, Hood River, Jackson, Josephine, Klamath, Lane, Lincoln, Linn, Marion, Multnomah, Polk, Tillamook, Willamette, Wasco, Washington, Yamhill ; **WASHINGTON**—Asotin, Benton, Chelan, Clark, Columbia, Grays Harbor, Jefferson, King, Kitsap, Kittitas, Klickitat, Lewis, Mason, Pierce, Skamania, Snohomish, Spokane, Stevens, Thurston, Whatcom, Whitman, Yakima ; **IDAHO**—Adams, Benewah, Boise, Bonner, Boundary, Clearwater, Idaho, Kootenai, Latah, Lemhi, Nez Perce, Owyhee, Shoshone, Valley, Washington ; **MONTANA**—Beaverhead, Flathead, Gallatin, Granite, Lewis and Clark, Mineral, Missoula, Park, Powell, Sanders ; **WYOMING**—Carbon ; **COLORADO**—Routt :

Erectum complex **GEORGIA**—Dade, Dawson, Fannin, Gilmer, Lumpkin, Murray, Pickens, Rabun, Randolph, Stephen, Towns, Union, White ; **SOUTH CAROLINA**—Oconee, Pickens ; **TENNESSEE**—Anderson, Blount, Campbell, Carter, Claiborne, Cocke, Coffee, DeKalb, Grundy, Franklin, Hamilton, Hancock, Hawkins, Johnson, Knox, Marion, Monroe, Morgan, Polk, Putnam, Rhea, Roane, Scott, Sevier, Sullivan, Unicoi, Van Buren ; **NORTH CAROLINA**—Allegany, Ashe, Avery, Buncombe, Burke, Caldwell, Cherokee, Clay, Graham, Haywood, Henderson, Jackson, Macon, Madison, Mitchell, Polk, Rutherford, Surry, Swain, Watauga, Wilkes, Yancey ; **KENTUCKY**—Bell, Daviess, Elliott, Fayette, Jefferson, Harlan, Letcher, Lewis, Madison, McReary, Perry, Powell, Wolfe ; **VIRGINIA**—Augusta, Bath, Bland, Buchanan, Carroll, Dickenson, Floyd, Giles, Grayson, Patrick, Roanoke, Rockingham, Smyth, Tazewell, Washington ; **WEST VIRGINIA**—Barbour, Braxton, Brooke, Cabell, Calhoun, Clay, Fayette, Gilmer, Grant, Greenbrier, Hampshire, Hancock, Kanawha, Lewis, Lincoln, Logan, Marion, McDowell, Mercer, Mineral, Mingo, Monongalia, Nicholas, Ohio, Pleasants, Preston, Raleigh, Randolph, Ritchie, Summers, Taylor, Tucker, Tyler, Upshure, Wayne, Wetzel, Wirt ; **MARYLAND**—Garrett, Harford ; **ILLINOIS**—Kane ; **INDIANA**—Jefferson, Steuben ; **OHIO**—Ashtabula, Belmont, Cuyahoga, Geauga, Hamilton, Hocking, Jefferson, Lake, Lawrence, Lorain, Mahoning, Medina, Miami, Monroe, Noble, Portage, Ross, Stark, Summit, Trumbull ; **PENNSYLVANIA**—Allegheny, Armstrong, Beaver, Bedford, Berks, Blair, Bradford, Bucks, Butler, Cambria, Carbon, Centre, Clarion, Clearfield, Clinton, Crawford, Dauphin, Elk, Erie, Fayette, Forest, Greene, Huntingdon, Indiana, Jefferson, Lackawana, Lancaster, Lawrence, Luzerne, Lycoming, McKean, Mercer, Mifflin, Monroe, Montgomery, Montour, Northampton, Perry, Pike, Philadelphia, Potter, Schuylkill, Snyder, Somerset, Sullivan, Susquehanna,

Tioga, Union, Venango, Warren, Washington, Westmoreland, Wyoming, York ; **NEW JERSEY**—Essex, Hunterdon, Mercer, Sussex, Union, Warren ; **MICHIGAN**—Kent, Oakland, St. Clair, Wayne ; **NEW YORK**—Albany, Allegany, Broome, Cayuga, Chautauqua, Chemung, Chenango, Clinton, Columbia, Cortland, Delaware, Dutchess, Erie, Essex, Franklin, Genessee, Greene, Hamilton, Jefferson, Livingston, Madison, Monroe, Montgomery, Nassau, New York, Niagara, Oneida, Onondaga, Ontario, Orange, Orleans, Oswego, Putnam, Rensselaer, Rockland, Saratoga, Schenectady, Schuyler, Seneca, St. Lawrence, Sullivan, Tioga, Tompkins, Ulster, Warren, Washington, Wayne, Westchester, Yates ; **CONNECTICUT**—Fairfield, Hartford, Litchfield, Middlesex, New Haven, New London, Tolland, Windham ; **RHODE ISLAND**—Kent ; **MASSACHUSETTS**—Berkshire, Franklin, Hampden, Hampshire, Middlesex, Suffolk, Worcester ; **VERMONT**—Addison, Bennington, Caledonia, Chittenden, Lamoille, Orange, Orleans, Rutland, Washington, Windham, Windsor ; **NEW HAMPSHIRE**—Belknap, Carroll, Chesire, Coos, Grafton, Hillsboro, Rockingham, Strafford, Sullivan ; **MAINE**—Aroostook, Cumberland, Franklin, Hancock, Kennebeck, Knox, Oxford, Penobscot, Piscataquis, Somerset, York ;

Flexipes complex **ALABAMA**—Blount, Cherokee, DeKalb, Lee, Limestone, Madison, Marshall, St. Clair, Tuscaloosa ; **GEORGIA**—Bartow, Cobb, DeKalb, Fannin, Floyd, Hall, Oglethorpe ; **SOUTH CAROLINA**—Lancaster, McCormick, Pickens ; **TENNESSEE**—Carter, Claiborne, Davidson, Hickman, Robertson, Unicoi, Washington, Wayne ; **NORTH CAROLINA**—Avery, Buncombe, Davie, Guilford, Haywood, Henderson, Jackson, Madison, McDowell, Mecklenburg, Mitchell, Polk, Randolph, Rutherford, Swain, Yancey ; **KENTUCKY**—Adair, Anderson, Bullitt, Campbell, Casey, Clark, Daviess, Edmonson, Estill, Fayette, Harrison, Jefferson, Jessamine, Kenton, Lyon, Meade, Mercer, Nelson, Oldham, Union, Woodford ; **VIRGINIA**—Fauquier, Rockbridge ; **MARYLAND**—Baltimore, Carroll, Frederick, Howard ; **DELAWARE**—New Castle ; **MISSOURI**—Bollinger, Boone, Callaway, Cape Girardeau, Cole, Cooper, Madison, Marion, Perry, Pike, Ralls, Scot, St. Charles, St. Louis, Stoddard, Warren, Wayne ; **IOWA**—Allamakee, Benton, Black Hawk, Buena Vista, Calhoun, Cedar, Cerro Gordo, Chickasaw, Clay, Clayton, Clinton, Delaware, Dickinson, Dubuque, Emmet, Fayette, Floyd, Franklin, Grundy, Hancock, Hardin, Howard, Humbolt, Iowa, Jackson, Johnson, Jones, Kossuth, Linn, Mahaska, Mitchell, Muscatine, Poweshiek, Shelby, Story, Tama, Washington, Webster, Winnebago, Winneshiek, Wright ; **ILLINOIS**—Adams, Alexander, Boone, Bureau, Calhoun, Carroll, Cass, Champaign, Christian, Cook, Crawford, DeKalb, Du Page, Edger, Fulton, Gallatin, Green, Hancock, Hardin, Henderson, Henry, Jackson, Jasper, Jersey, Jo Daviess, Johnson, Kane, Kankakee, Knox, Lake, La Salle, Lawrence, Lee, McHenry, McLean, Ogle, Peoria, Piatt, Pope, Rock Island, Sangamon, Schuyler, Stark, Stephenson, Union, Vermilion, Wabash, Whiteside, Will, Williamson, Winnebago ; **INDIANA**—Adams, Bartholomew, Blackford, Brown, Carroll, Cass, Clark, Clay, Clinton, Crawford, Daviess, Decature, Dearborn, Dela-

ware, Fayette, Floyd, Fountain, Franklin, Fulton, Grant, Greene, Hancock, Harrison, Hendricks, Henry, Howard, Jackson, Jefferson, Jennings, Kosciusko, Laporte, Lawrence, Marion, Martin, Marshall, Miami, Monroe, Montgomery, Morgan, Newton, Ohio, Owen, Parke, Perry, Porter, Posey, Putnam, Randolph, Ripley, St. Joseph, Scot, Shelby, Spencer, Steuben, Tippecanoe, Vigo, Warren, Washington, Wayne, Wells ; **OHIO**—Adams, Allen, Anglaize, Ashland, Athens, Butler, Champaign, Clark, Clermont, Clinton, Columbiana, Coshocton, Crawford, Cuyahoga, Darke, Delaware, Erie, Fairfield, Franklin, Fulton, Green, Guernsey, Hamilton, Hardin, Harrison, Highland, Hocking, Holmes, Huron, Knox, Lawrence, Licking, Logan, Lorain, Lucas, Marion, Medina, Meigs, Mercer, Montgomery, Monroe, Muskingum, Ottawa, Pike, Preble, Richland, Ross, Scioto, Seneca, Stark, Summit, Tuscarawas, Vinton, Warren, Wayne, Williams ; **PENNSYLVANIA**—Adams, Beaver, Berks, Bucks, Chester, Dauphin, Delaware, Erie, Franklin, Huntingdon, Lancaster, Lebanon, Lehigh, Luzerne, Mifflin, Monroe, Montgomery, Northampton, Pike, Philadelphia, Washington, York ; **NEW JERSEY**—Atlantic, Bergen, Burlington, Camden, Cape May, Gloucester, Hunterdon, Mercer, Monmouth, Morris, Ocean, Salem, Sussex, Union, Warren ; **SOUTH DAKOTA**—Brookings, Roberts ; **NORTH DAKOTA**—Cass, Cavalier, Bottineau, Grand Forks, Griggs, Richland, Rollete ; **MINNESOTA**—Aitkin, Anoka, Beltrami, Benton, Big Stone, Blue Earth, Brown, Carlton, Carver, Cass, Chippewa, Chisago, Clay, Clearwater, Cook, Crow Wing, Dakota, Douglas, Fillmore, Freeborn, Goodhue, Grant, Hennepin, Houston, Hubbard, Itasca, Kanabec, Kandiyohi, Kittsou, Koochiching, Lake, Lake of the Woods, Lincoln, Martin, McLeod, Meeker, Mille Lacs, Morrison, Murray, Nicollet, Norman, Olmstead, Otter Tail, Pine, Polk, Pope, Ramsey, Red Lake, Rice, Roseau, St. Louis, Scott, Stearns, Steel, Swift, Todd, Wabasha, Waseca, Washington, Winona, Wright ; **WISCONSIN**—Adams, Ashland, Brown, Columbia, Dane, Dodge, Florence, Grant, Green, Iowa, Jefferson, La Crosse, Lafayette, Langlade, Manitowac, Milwaukee, Oneida, Ozaukee, Pierce, Polk, Racine, Rusk, St. Croix, Sauk, Sawyer, Shawano, Vernon, Vilas, Walworth, Waukesha, Winnebago ; **MICHIGAN**—Alger, Alpena, Arenac, Baraga, Bay, Branch, Cass, Cheboygan, Chippewa, Crawford, Delta, Emmet, Gogebic, Gratiot, Houghton, Ingham, Ionia, Jackson, Kalkaska, Karamazoo, Kent, Keweenaw, Lenawee, Mackinac, Marquette, Midland, Monroe, Newaygo, Oakland, Oceana, Ontonagon, Otsego, Roscommon, Schoolcraft, Shiawassee, Van Buren, Washtenaw, Wayne ; **NEW YORK**—Albany, Columbia, Dutchess, Fulton, Greene, Monroe, Nassau, New York, Oswego, Queens, Rensselaer, Rockland, St. Lawrence, Suffolk, Tompkins, Washington, Westchester ; **CONNECTICUT**—Fairfield, Hartford, Middlesex, New Haven, New London, Tolland, Windham ; **RHODE ISLAND**—Providence ; **MASSACHUSETTS**—Berkshire, Barnstable, Bristol, Essex, Franklin, Hampden, Hampshire, Middlesex, Norfolk, Plymouth, Suffolk, Worcester ; **VERMONT**—Addison, Caledonia, Rutland, Windsor ; **NEW HAMPSHIRE**—Grafton, Hillsboro, Merrimack,

Rockingham, Sullivan ; MAINE—Aroostook, Hancock, Oxford, Penobscot, Somerset, Waldo, York :

この研究は北アメリカに産する有花梗群エンレイソウ属植物の自然分類群を明らかにする目的で行った。1万点以上のさく葉標本から得られた15の形態特性のうち、特に今回は、子房と花柱のパターンに依るふり分けを行い、その結果得られた分類群をそれぞれの核型(シリーズ第二編で発表予定)に依るふり分けと良い一致を見る三群に大別した。これら三群(*Pusillum* 群, *Grandiflorum* 群, *Erectum* 群)に属する各分類群のうち、前二群に属するものは、それぞれの分布圏や生態的種共同体(Ecological Species Compound)を作る様子から自然群と見做して差しつかえなからう。又、この二群に属する分類群に見られる不連続性のために、古典分類学的問題点は無い。最後の *Erectum* 群に属する植物では基本核型の共通性を除くと子房と花柱のパターン及び他の形態特性でも様々な変異があり(シリーズ第三編で発表予定)、分類群に対する古典的概念と通常の処理方法では、さく葉標本や自然集団から得られる情報の整理はほとんど不可能である。第三編で明らかにする様にこの群の変異を統一的に把握する上で、葯長/花糸長の比が最も有効であり、本論文ではその結果をふまえて2つの種複合体(Species Complex)を見出し、その中に17の分類群を人為的に設定して子房と花柱に於ける変異パターンを比較し、同時に特定の変異パターンを示す人為分類群がどのような地理的及び群落的背景を荷っているかを考察した。更に、その様な変異パターンがどのようにして生ずる可能性があるか、進化機構論的見地から論じた。尚、この17の人為分類群は最終的には幾つかの自然群に統合縮小されるであろう。その根拠となる実験及び自然集団の形態特性解析結果は、このシリーズの第二編以降に報告される。