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Cytotaxonomy of *Cerastium holosteoides*

By

Áskell Löve & M. S. Chennaveeraiah

Institut Botanique de l'Université de Montréal, Montréal, Canada

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Among the genera of complex species which have defied the efforts of many taxonomists and remained critical and confused, the genus *Cerastium* seems to have a position of its own. Few other genera include as many species or complexes with disordered nomenclature, and better examples of taxonomical perplexity are hard to find. More or less stray cytological studies of some of the species, but especially the thorough investigations by Favarger 1950, Favarger & Söllner 1949, and Söllner 1950, 1952, 1953a, b, 1954, have shown that much of the confusion may be caused by different degrees of auto- and alloploidy accompanied by minor morphological differentiation in characteristics often dismissed as being of no taxonomical importance, and then followed by some hybridization between the species of each complex, or even between some of the complexes, to complicate the separation of the units in the field. In most of the groups the apparent mixing of characters, however, is not caused by hybridization in the exact meaning of the word, but rather by the complex kind of alloploidy at the higher levels of polyploidy. The complicated alloploidy has, doubtlessly, resulted in the belief that here we have a case of "world-wide introgression" (Hultén 1956) since it often seems to indicate the occurrence of hybridization between different species of the same alloploid complex. It is evident that even a very careful analysis of such groups is difficult or perhaps impossible if the diploid species are either unknown or neglected. Even modifications of essential characters are of interest in the species with northern distribution, and only by aid of carefully planned genecological experiments can these non-heritable variations be separated from the characteristics of evolutionary significance.

Although it is evident from the investigations already performed that the application of cytological and taxonomical methods combined will likely solve many of the most difficult problems of this genus, cytological information from some of its complexes seem rather to blur and complicate the picture. Reports of chromosome numbers from some of the most critical species, based on only a preliminary taxonomical analysis, have resulted in a long list of numbers even for some small units so that careful taxonomists may have felt more confused by trying to incorporate these data into their classification.

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Although not the most confused complex of the genus *Cerastium*, the species *C. holosteoides* and its subspecies seems to be a typical example in which several cytological reports are distressing at the same time as the nomenclature problems are of a considerable magnitude.

The nomenclatural confusion in the *C. holosteoides* group started with LINNAEUS 1753, who referred in part to the species we now know as *C. holosteoides* under the name *C. viscosum*, at least regarding the material from Lappland; this he repeated in 1755, but in 1762 he seems to have included the same taxon in *C. vulgatum*, which is supposed to have originally referred only to what is at present known as *C. glomeratum* THUILL. Both these Linnaean names are now rejected as being ambiguous, on very good grounds (HYLANDER 1945).

Until HYLANDER 1945 and MÖSCHL 1948 solved the confusion by rejecting all but the name *C. holosteoides* FR. as restricted by HYLANDER 1945, authors of manuals have listed the species in question as *C. vulgatum* L., *C. triviale* LINK, *C. caespitosum* GILIB., *C. vulgare* HARTM., or *C. viscosum* L., but rarely in a restricted sense; therefore other related taxa have been included under the same broad descriptions. The plant is indigenous in Europe, although its area is greatly affected by human activities, and some races are roadside weeds. In North America, however, two of the European subspecies are met with as introductions, and although the nomenclatural confusion had been solved in Europe years before the publication of the most recent American manuals, FERNALD 1950 still uses the name *C. vulgatum* for the plant, while GLEASON 1952 apparently confuses it in both *C. vulgatum* and *C. viscosum*. As mentioned above, HYLANDER 1945 clearly showed that both these latter names are to be rejected as nomina ambigua. The name *C. triviale* is illegitimate, and so is also *C. caespitosum* since it was a renaming without redefinition of *C. viscosum* L.

HYLANDER 1945, 1955 included three varieties in the species *C. holosteoides*, namely, var. *vulgare* (HARTM.) HYL., var. *glabrescens* (G. F. W. MEYER) HYL., and var. *glaberrimum* (K. JOH.) HYL. The eminent Austrian *Cerastium* specialist MÖSCHL 1948 replaced the var. *vulgare* with the name subsp. *triviale* (LINK) MÖSCHL, united the varieties *glabrescens* and *glaberrimum* in the subsp. *glabrescens* (G. F. W. MEYER) MÖSCHL, and described as new the subsp. *pseudoholosteoides* MÖSCHL from southern Scandinavia and the Baltic Sea region. According to the present International Code, the subsp. *triviale* is to be renamed subsp. *holosteoides*, whereas the two latter names are legitimate.

Although the taxonomical treatment by HYLANDER 1945, 1955 and MÖSCHL 1948 of this critical complex was based on morphological and geographical characters of the most reliable kind, its clarity seemed to be somewhat diminished by the fact that various chromosome numbers had apparently been reported from the complex by several authors. Many of

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these numbers were mentioned by MÖSCHL 1948 who, however, did not try to identify them with any of his subspecies. The first chromosome number to be reported from this group was n = c. 55 counted on material named *C. vulgatum* from Germany by HEITZ 1926. ROHWEDER 1939, also studying German populations, found the number to be 2n = 144, whereas HAGERUP 1944 counted n = 63 in Danish plants of *C. triviale*. BRETT 1952 reported the number 2n = 72 from British material. The number 2n = 144 has later been confirmed from different regions by MATTICK (in TISCHLER 1950), SÖLLNER 1952, 1954, BRETT 1953, and LÖVE & LÖVE 1956. It is worth mentioning that SÖLLNER 1954 found the gametic number to vary somewhat between n = 67 and 72, BRETT 1955 reported variation between n = 68 and 76, whereas BLACKBURN & MORTON 1957 listed 2n = 72, 126, 144, and 180. Most of the numbers were reported without closer references to race, except in the cases studied by SÖLLNER who used plants belonging to the subsp. *holosteoides* and *glabrescens*.

The present writers have studied several collections of *C. holosteoides* from northern Europe and Iceland and also from eastern North America. The three distinct subspecies were easily recognized, but although hybrids between them could be studied, these do not seem to be frequent in the field and only occasionally did they occur in the experiments. It seems likely that this is caused by the preponderance of autogamy, since the hybrids are always as fertile as pure populations and their meiotic divisions are equally regular. Therefore, it seems safe to conclude that the subspecies are true intraspecific races produced by gradual morphological differentiation in ecologically or geographically somewhat distinct parts of the natural area of the species and later brought together by human agencies.

The mitotic chromosome number was studied on material of all the subspecies from northwestern Europe. In addition, the typical subspecies and subsp. *glabrescens* were studied from Iceland and eastern North America. Since it was possible that the present writers might have misidentified some of the material, seeds of the two subspecies *glabrescens* and *pseudoholosteoides* (collected from cultures in Austria in 1956) were sent to us by Dr. Wilhelm MÖSCHL, and the plants were cultivated in a greenhouse in Montreal. The seeds of subsp. *glabrescens* (MÖSCHL No. 7532) originated from a collection made in July 1955 by Mr. PEDERSEN at Lakolk on Romö in Denmark, whereas those of subsp. *pseudoholosteoides* (MÖSCHL No. 7538) had been collected in May 1955 by Mr. PEDERSEN at Eskebjerg, Vesterling, in Denmark. On the basis of these cultures it was possible to identify other collections and also to study suspected natural hybrids as compared to artificial hybrids between these Danish populations.

The mitotic chromosome number of all the collections studied by the present writers, of the pure subspecies and their hybrids, was always found to be 2n = 144, or at least very close to this number. Not even in suspected natural hybrids were other numbers observed. This is the number pre-

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viously reported from Schleswig-Holstein by ROHWEDER 1939, from Britain by BRETT 1953, 1955, from the Austrian Alps by MATTICK (in TISCHLER 1950), from Switzerland, Italy, Portugal, Denmark, and Newfoundland by SÖLLNER 1954, from Iceland by LÖVE & LÖVE 1956, and from Britain and Portugal by BLACKBURN & MORTON 1957.

We are inclined to believe that the 16-ploid chromosome number $2n = 144$ is the only correct number for the species *Cerastium holosteoides* and its subspecies. The four numbers $2n = 72$, c. 110, 126, and 180, reported from this species by different authors, may have been counted on related but distinct taxa or on rare hybrids, or they may be too low estimates resulting from the great difficulties in counting so many chromosomes in meiotic divisions in which multivalents occur rather frequently. Although we did not observe any natural hybrids between this and related species, such hybrids may be more frequent than indicated by available material, and some of the previously reported chromosome numbers seem to support such a suggestion. Further experiments may reveal the correctness of such an assumption.

The above results fully confirm the classification of the species *Cerastium holosteoides* and its subspecies as proposed by HYLANDER 1945 and MÖSCHL 1948, despite conflicting cytological reports. They are additional evidence of the fact that careful morphological observations of considerable herbarium material usually result in a fully satisfactory solution even in critical groups, particularly if the observer has gained an adequate knowledge of the taxa in question and does not base his judgment on preconceived ideas. They also show that conflicting cytological reports by different authors cannot always be accepted as an indication of heterogeneity within a taxonomical unit. It must be remembered, however, that if certain cytological phenomena connected with morphological and geographical differences are ignored, this may tend to even more misleading taxonomical conclusions. The genus *Cerastium* includes groups in which cytologists and taxonomists alike have been misled by uncritical acceptance or ignorance of data of both kinds.

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Summary

The species *Cerastium holosteoides*, including the three subspecies *holosteoides*, *glabrescens*, and *pseudoholosteoides*, was a very confused taxon until HYLANDER and MÖSCHL, respectively, clarified its synonymy and divided it into proper subspecies. Since cytological reports seemed to indicate

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that this classification might be insufficient from biosystematical points of view, cytological studies were performed on correctly determined material of all the races and their hybrids. All the populations studied were found to have $2n = 144$ chromosomes. It is, therefore, concluded that only this number is typical of the species and that other numbers reported must be regarded either as mistakes or as inexact estimations. The classification proposed by HYLANDER and MÖSCHL fully agrees with the biosystematical observations made in this paper.

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