BIOSYSTEMATIC NOTES ON ATRIPLEX PATULA L., A. HASTATA L., AND A. LITTORALIS L. (CHENOPODIACEAE)

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SUMMARY

In about 10—15 % of the cases a sharp distinction between *Atriplex hastata* L., *patula* L., *littoralis* L., and *glabriuscula* Edm. is not possible, both in the field and in the herbarium.

In order to establish the status of the 'intermediates' a karyological examination was undertaken of 95 samples collected in the Netherlands including both typical specimens and intermediates. It appeared that the specimens clearly representing *A. hastata, littoralis*, or *glabriuscula* are diploid (n = 9), but those representing *A. patula* tetraploid (n = 18). The 'intermediates' between *A. hastata* and *patula* are either diploid or tetraploid. Hence a sharp distinction between the latter two taxa is only possible on the chromosome number. A similar result was found for the 'intermediates' between *A. patula* and *littoralis*. It depends on the specific concept one adheres to whether these four taxa should be ranked as species; European botanists usually give them specific rank, their American colleagues infraspecific rank.

Autogamy seems to be the rule in these species. This as well as the chromosome numbers found rule out the possibility of hybridization as an explanation for the occurrence of intermediates. I have strong doubts as to the artificial hybrids reported in literature because of the technical difficulties involved and apparently not solved.

Special attention has been paid to possible characters to be derived from the leaves, the phyllotaxis, and the bracts. The variation in the leaves of the four species examined is overlapping. The same holds true for the phyllotaxis and the ripe fruits and fruiting bracteoles.

An account is given of some abnormalities which have been found during the chromosome countings.

An attempt was made to correlate morphological characters of the leaf, especially the leaf-base and leaf-index, and the chromosomes in *A. hastata* and *patula*. The results presented in the scatter diagrams show that, though on the whole there is a marked correlation between leafshape and chromosome number, no sharp distinction can be made.

Finally a provisional key is given.

INTRODUCTION

Many authors on *Atriplex* have mentioned the difficulties encountered in the delimitation of the species as well in several parts of the world as in different parts of the genus (see for Europe Turesson, 1922, 1925, Klimmek, 1960, Aellen, 1960, Aellen & Hulme, 1964; for Australia Anderson, 1930, Aellen, 1938; for North America Hall & Clements, 1923). Mention is made of polymorphism, of lack of 'constant characters', and of the occurrence of intermediates or intergrades between accepted species, leading to partly unsatisfactory taxonomies.

'The perplexing polymorphism characteristic of our *Atriplex species* is mainly due to two causes, viz. the readiness with which the different species hybridise, and the great power of modifiability on the part of the individuals' (Turesson, 1925) and Atriplex' ... is essentially a plant group in which the taxonomic worker appears to require the cooperation of the geneticist and cytologist in order to define adequately the individual species' (Anderson, 1930).

As far as I know, only two authors have tried to raise artificial hybrids (Turesson, 1922, 1925, Hulme, 1958). The results are doubtful, however, as either no mention is made how the technical difficulties which are great in this case, have been solved (Hulme), or as the method was called unsatisfactory even by the author himself (Turesson).

On the other hand Turesson (1922) stated: 'Self-fertilization seems to be the rule in most of the forms....' and 'The frequent self-fertilization, occurring also in nature, (gives) rise to the perplexing polymorphism found'.

As far as Europe is concerned three groups of species can be easily distinguished in *Atriplex sens. str.* (van der Meijden, 1968), viz. the *A. patula—hastata—littoralis* group, the *A. rosea—tatarica* group, and the *A. hortensis—heterosperma* group.

I have confined myself to the *A. patula—hastata—littoralis* group, and have tried whether the unsatisfactory delimitation based exclusively on gross morphology could be improved by using a combination of cytological and morphological data derived from living as well as from herbarium specimens.

MORPHOLOGY

Inflorescence and flower

Inflorescence mostly much-branched, branches spicoid, bearing many glomeruli each with male and female flowers. Bisalputra (1960) showed by the vascularization pattern that each cluster is a compound cymose structure.

Male flower discoid, tepals 5, valvate, slightly connate at the base; stamens 5, free, epitepalous, anthers slightly versatile, latrorse; ovary reduced. The pollen is fairly large and sticky and was proven not to be transported by wind.

Female flower naked, with 2 bracteoles which are at first enveloping the thin-walled ovary with its single, erect, campylotropous ovule, later completely enclosing the young fruit which is crowned by 2 subulate stigma's.

Bisalputra (1960), working on the anatomy and morphology of Australian *Atriplex* and *Bassia*, concluded that the fruiting 'bracteoles' are similar in vascularization to leaves, and distinctly different from the one-nerved male perianth segments.

Phyllotaxis

Some authors have used the phyllotaxis to distinguish between *A. patula* and *hastata* (Aellen, 1960: *A. patula:* most leaves spirally arranged; *A. hastata:* most leaves opposite). Actually nearly all plants which I have seen, started with 4 pairs of opposite leaves. Populations of *A. hastata* growing on saline habitats often have nearly all leaves opposite; the other taxa have the higher leaves mostly spirally arranged. It may be concluded that phyllotaxis does not provide a good character to differentiate between *patula* and *hastata*.

Leaves

In the most important recent European revisions (Aellen, 1960, Aellen & Hulme, 1964) the leaf-shape is used as the main character for the distinction between *A. patula*, *hastata*, and *littoralis*. Leaf characters are given as follows:

A. patula: lower leaves mostly lanceolate, oblong, rhomboid, or rhomboid-elliptical, with cuneate or attenuate base and often with hastate teeth.

A. hastata: lower leaves mostly deltoid to triangular-hastate with truncate or ± cordate-attenuate base.

A. littoralis: all leaves linear, entire or dentate.

Are these characters good and constant? The impression one gets when looking through a herbarium collection is that there are fairly many intermediates, especially between *A. hastata* and *patula*, less so between *patula* and *littoralis*. These intermediates deserve of course the greatest interest. They may either express a general vegetative plasticity, or may be due to hybridization. The first possibility will be tested here more extensively, the latter is tested in the cytological part.

The leaf-shape is very variable in *A. patula* and *hastata*, rather constant in *littoralis*, however. Usually, in *patula* and *hastata* the lowermost 4 leaves are more or less oblong with acute or attenuate base and often with hastate teeth; the medium leaves (third to ± seventh pair) are generally the widest and those with the margin most distinctly toothed. Higher-up, the leaves are narrower, the margin is entire, but the lobing may be more distinct. The uppermost leaves are nearly always linear in *A. patula*, linear or broader in *hastata;* in *A. littoralis* nearly all leaves are linear or sometimes lanceolate-oblong.

In all 4 taxa a certain amount of variability was found between the opposite leaves of the same node. A comparison of the leaves of comparable nodes (counted from the base) of different plants of one taxon may show considerable differences in shape, base, margin, and apex. As the leaves are withering early (even before the fruits are mature, the basal and medium leaves are mostly absent) the habit of the plant is changing considerably with age. This may account for the many infraspecific taxa distinguished within *A. hastata* and *patula* (see Ascherson & Graebner, 1913, for a still incomplete survey).

Concluding, it appears that the leaf-shape is not a very valuable character for specific delimitation, because of the variability in shape 1) from below to above at the main stem, 2) between comparable parts of one specimen, 3) between comparable parts of different plants.

Fruiting bracteoles

Many authors have used shape, sculpture, innervation, consistency, and size of the bracteoles for species delimitation. For the taxa examined the results are unsatisfactory.

The characters of the bracteoles are difficult to evaluate. In the first place the bracteoles are changing considerably during the maturation of the fruit. When the ultimate form is attained, nearly all other vegetative parts of the plant are gone. For this reason a herbarium study is insufficient for detecting correlations between the form of the bracteoles and of the leaves. The total diversity in form, moreover, is great in the 4 taxa examined.

CHROMOSOMES

There is some discrepancy in literature concerning the chromosome numbers of *A. hastata* and *patula*.

For *A. hastata* I found 5 records 2n = 18 (Winge, 1917; Witte, 1947, '*A. patula var. hastata*'; Tarnavschi, 1948; Gadella & Kliphuis, 1966, 1968) and one record 2n= 36 (Cooper, 1935, '*A. patula var. hastata*').

For *A. patula*, Winge (1917) and Löve & Löve (1956) recorded 2n = 36, but Kjellmark (1934) counted 2n = 18. This latter record is doubtful, however, because Kjellmark's figures only show heterochromatic particles in interphase nuclei.

For *A. littoralis*, Winge (1917) and Tarnavschi (1948) counted 2n = 18.

For *A. glabriuscula*, Wulff (1936, 1937 '*A. babingtonii*') and Löve and Löve (1956) counted 2n = 18.

TABLE 1. Account of specimens examined on chromosomes, all collected by me *) in the Netherlands.

coll. number R. v. d. Meijden	Locality	Hour grid	n	2n	Leaf Index	Leafbase class
Atriplex hastata						
651	Rotterdam	37.47	9	—	1.5	1
672	Rijsoord	37.58	9	—	1.7	4
673	id.	id.	9	—	1.4	2
678	Hellegatsplein	43.36	9	—	1.3	1.5
679	id.	id.	9	—	1.7	4.5
682	id.	id.	9	—	1.6	4.5
683	id.	id.	9	—	1.6	3
684	id.	id.	c. 9	—	1.7	2.5
686	Renesse	42.25	c. 9	—	1.7	3
690	Westenschouwen	42.35	9	—	1.7	1
691	id.	id.	9	—	1.5	1.5
692	Burghsluis	42.35	9	—	1.5	1
694	id.	id.	—	c. 18	—	—
695	id.	id.	9	—	1.5	3
697	Roompot	42.54	9	—	2.1	1.5
699	id.	id.	9	—	2.3	1
700	id.	id.	9	—	1.2	2
701	id.	id.	9	—	1.4	2.5
704	id.	id.	9	—	2.0	4
705	id.	id.	9	—	1.9	2.5
710	Scharendijke	42.27	9	—	1.6	3
711	id.	id.	9	—	2.3	2.5
717	Westenschouwen	42.34	9	—	1.6	3
720 *)	Oostvoorne	37.32	9	—	1.8	3.5
725	id.	id.	9	—	1.3	3.5
728	id.	37.31	9	—	1.4	2
731	id.	id.	9	—	1.6	1.5
742	Westervoort	40.23	—	18	1.5	4
743	id.	id.	9	—	1.6	1
745	id.	id.	—	18	1.5	3
756	Rheden	40.13	—	c. 18	1.7	2
759	id.	id.	9	—	1.7	1
761	id.	id.	—	c. 18	2.1	1.5
762	Flevopolder	26.36	—	18	1.7	2.5
763	id.	id.	9	—	1.5	1.5
765	id.	26.37	9	—	1.7	1
766	id.	id.	—	18	1.4	1
769	Nijmegen	40.42	9	—	1.8	3
771	id.	id.	—	c. 18	1.7	4
773	Oosterbeek	40.21	—	c. 18	1.5	2.5
777	Lathum	40.24	—	c. 18	—	—
778	id.	id.	—	c. 18	1.8	3
781	Doesburg	40.16	—	c. 18	1.7	1.5
786	Eysden	61.48	—	c. 18	1.8	4
787	id.	id.	9	—	—	—
788	id.	id.	—	c. 18	1.5	5
794	Roermond	58.44	—	c. 18	1.5	2
800 *)	Oostvoorne	37.32	—	18	—	—
803 *)	Boschplaat (Terschelling)	—	—	18	—	—
804 *)	id.	—	—	18	—	—
805 *)	id.	—	—	18	—	—
806 *)	Vierhuizen	—	—	18	—	—

coll. number R. v. d. Meijden	Locality	Hour grid	n	2n	Leaf Index	Leafbase class
Atriplex patula						
650	Rotterdam	37.47	—	c. 36	2.5	6
653	id.	id.	—	c. 36	2.6	7
654	id.	id.	—	c. 36	3.3	7.5
670	Rijsoord	37.58	18	—	—	—
671	id.	id.	—	c. 36	3.0	8
693	Burghsluis	42.35	18	—	2.4	7
722	Oostvoorne	37.32	c. 18	—	—	—
758	Rheden	40.13	18	—	2.3	6
770	Nijmegen	40.42	18	—	5.9	8
775	Oosterbeek	40.21	18	—	2.8	7
776	Lathum	40.24	—	c. 36	4.5	7.5
779	Doesburg	40.16	—	36	2.8	6
780	id.	id.	—	c. 36	—	—
791	Maastricht	61.28	—	c. 36	6.3	8
792	id.	id.	—	c. 36	4.6	8
793	Roermond	58.44	—	c. 36	7.5	8
795	id.	id.	—	c. 36	4.4	6.5
798	Lattrop	29.21	—	c. 36	4.3	7
799	id.	id.	18	—	3.2	7
Atriplex littoralis						
659	Rotterdam	37.46	9	—	9	8
660	id.	id.	9	—	11	8
661	id.	id.	—	c. 18	21	8
662	id.	id.	9	—	9.5	8
675	Hellegatsplein	43.36	9	—	17	8
688	Westenschouwen	42.35	9	—	15	8
696	Roompot	42.54	9	—	12	8
721	Oostvoorne	37.32	9	18	14	8
Atriplex glabriuscula						
727	Oostvoorne	37.31	9	—	—	—
730 *)	id.	id.	9	—	2.3	4
801 *)	id.	id.	—	18	—	—
Intermediates of A. hastata and A. patula						
685	Renesse	42.25	9	—	2.4	3
687	id.	id.	9	—	2.1	6
689	Westenschouwen	42.35	c. 9	—	1.9	4.5
702	Roompot	42.54	c. 18	—	2.0	6.5
703	id.	id.	c. 9	—	2.5	3.5
712	Scharendijke	42.27	9	—	2.6	4
716	Westenschouwen	42.34	9	—	2.0	5
723	Oostvoorne	37.32	c. 18	—	2.1	5
757	Rheden	40.13	18	—	2.0	5
760	id.	id.	—	c. 36	2.1	3
772	Nijmegen	40.42	—	c. 18	2.1	3
774	Oosterbeek	40.21	—	c. 18	2.3	4.5

*) Of some fruiting collections countings were made of the offspring of these grown in the greenhouse; the countings were performed on the vegetative apex.

Collection numbers 803—805 were collected by P. Ketner (I.B.P., Terschelling). Collection number 806 was collected by W. Joenje (Haren, Groningen).

Collection number 800 belongs to the same population as 720; number 801 to the same as 730.

Material and method

In July and August 1968 95 samples of the four *Atriplex* taxa mentioned above were collected at 24 localities in the Netherlands (see table 1). The samples consisted of young inflorescences and occasionally of root-tips or young fruits. In 57 samples the meiosis could be examined. In the remaining 38 samples, mitotic configurations were studied from young flowers or from the meristematic zone of the radicula.

The material was fixed according to Östergren & Heneen (1962). After 4 months storage at — 20 °C the quality of the fixed material was still excellent. The chromosomes were stained with aceto-carmine.

From all samples examined voucher specimens are deposited in the Laboratorium voor Experimentele Plantensystematiek, Leiden.

Results (see table 1)

The haploid number n = 9 was counted in 47 samples (43 counted exactly), (38 *A. hastata*, 7 *littoralis*, and 2 *glabriuscula*).

The diploid number 2n = 18 was counted in 25 samples (only 5 counted exactly), (22 *hastata*, 2 *littoralis*, and 1 *glabriuscula*).

The haploid number n = 18 was found in 10 samples (5 counted exactly), all belonging to *A. patula*. In 13 samples the tetraploid number 2n = 36 (one counted exactly) was found, all belonging to *A. patula*.

Winge (1917, p. 199) suggested an allopolyploid origin of *A. patula* with *hastata* and *littoralis* as parent species.

Abnormalities

The proportion of individuals with meiotic abnormalities seems to be rather high.

In 2 out of 7 samples (*v. d. Meijden 675* and *696*) of *A. littoralis*, some anthers contained pollen mother-cells with apparently 8 instead of 9 chromosomes. In *v. d. Meijden 675* not one of the *c.* 40 first metaphase plates counted had 9 chromosomes. In this case all chromosomes were of approximately the same size. In *v. d. Meijden 696*, each of the *c.* 40 first metaphase plates counted had 8 chromosomes, one of wihch was strikingly larger than the other chromosomes and apparently tripartite. Another case of tripartite chromosomes in *Atriplex* is reported by Billings (1934). In both specimens the great majority of the anthers proved to have pollen mother-cells with the normal haploid number n = 9. In this connection it may be interesting to note that Gadella & Kliphuis (1968) found in one plant of *A. hastata* in root tips the numbers 2n = 18, 36, *16*, and *32*.

In one tetraploid sample *(v. d. Meijden 670)* all PMC's had, judged from the appearance of their 'callose special wall' (Waterkeyn, 1964) just passed telophase II. Instead of the normal heterochromatic particles they showed *c.* 15—20 contracted chromosomes appearing like those of metaphase I. Here again, the meiose in the other anthers was normal. Winge (1917, p. 179—180, fig. 16b) seems to have found a comparable abnormality in *A. littoralis*.

COMPARISON OF CYTOLOGICAL AND MORPHOLOGICAL DATA

From each voucher specimen the leaf-index (the proportion of length and width of the leaf including the petiole) and the leaf-base class (defined as in fig. 1) has been established of 2 medium leaves from the main axis. The term 'medium' must be understood as being the third to sixth or seventh leaf pair (counted from below) in which the leaves are either opposite or no more than 4 cm shifted.

In diagram 1, the leaf-index and the leaf-base class of the 95 specimens investigated are combined.

As could be expected there is a general agreement between leaf-base class and leaf-index. It appears also clearly that the higher leaf-indices, above *c.* 2.2, nearly all belong to tetraploids. Unfortunately there are exceptions. The majority of the diploids, on the other hand, has a low leaf-index and a low leaf-base class, but again there is no sharp distinction.

The same procedure, but based upon 100 sufficiently complete herbarium specimens in the Rijksherbarium, is represented in diagram 2. This provides essentially the same picture.

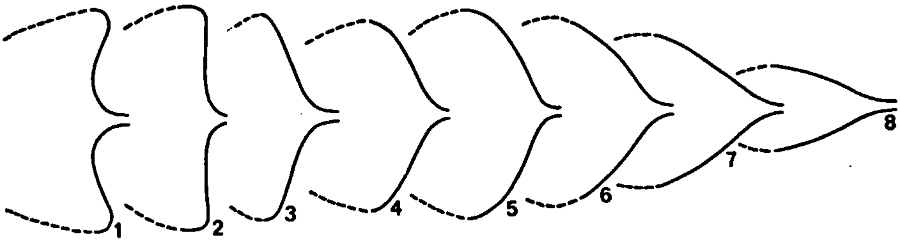

Fig.1

Explanation of the leaf base classes referred to in diagrams 1 and 2.

DISCUSSION

The taxonomic difficulties in the *patula* — *hastata* — *littoralis* group may have their cause in two factors: polyploidy and autogamy. The influence of polyploidy has been investigated, especially between tetraploid *A. patula* and diploid *A. hastata*. As is shown these taxa seem to be separated genetically in nature, as triploids have not been found, but are partly overlapping in morphological characters; they must be treated as different taxa. The diploid taxon with the low leaf-index (diagram 1) corresponds with *hastata*, the tetraploid with high leaf-index with *patula*. In my opinion, polyploidy is not the factor which causes the greatest difficulties in this case.

As mentioned before, it must be re-examined whether hybridization is possible, the records of Turesson (1925) and Hulme (1958) being unsatisfactory. In fact, the role of the pollen in the reproduction should be studied, that being possibly the key to the problem in this genus. It must be examined, for instance, whether autogamy, as suggested by Turesson (1922), or apogamy does occur.

Hybridization can hardly play a role of any importance, because of the density of the ± simultaneously flowering male and female flowers and of other facts of the flower-biology (sticky pollen, no pollinating animals).

The technical difficulties to examine the reproduction-mechanism are great, as castration is particularly difficult to perform. In my opinion the only way seems to be a rather involved one, removing young female flowers, pollinating these, and raising them in vitro under sterile conditions.

The evaluation of the 4 taxa examined remains a question of appreciation. In my opinion they form one complex species in which at least three infraspecific taxa must be distinguished, namely diploid *hastata* [and its allied taxa, e.g. *A. glabriuscula* Edm., *A. calotheca* (Rafn) Rafn & Fries, *A. longipes* Drej., *A. prostrata* Boucher, *A. triangularis*

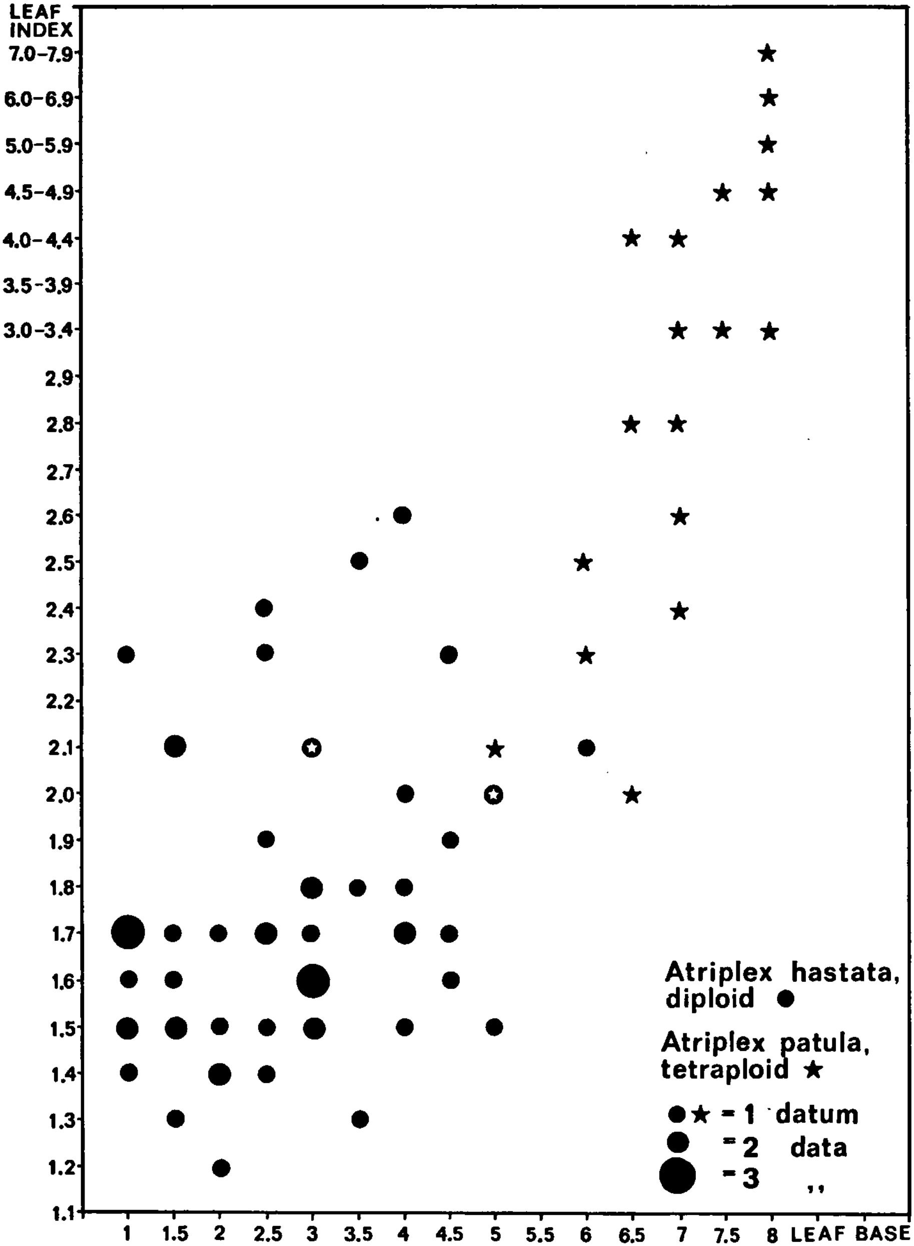
LEAF INDEX
7.0-7.9
6.0-6.9
5.0-5.9
4.5-4.9
4.0-4.4
3.5-3.9
3.0-3.4
2.9
2.8
2.7
2.6
2.5
2.4
2.3
2.2
2.1
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
6.5
7
7.5
8
LEAF BASE CLASS
Atriplex hastata, diploid ●
Atriplex patula, tetraploid ★
●★ = 1 datum
● = 2 data
● = 3 ,,

Diagram 1

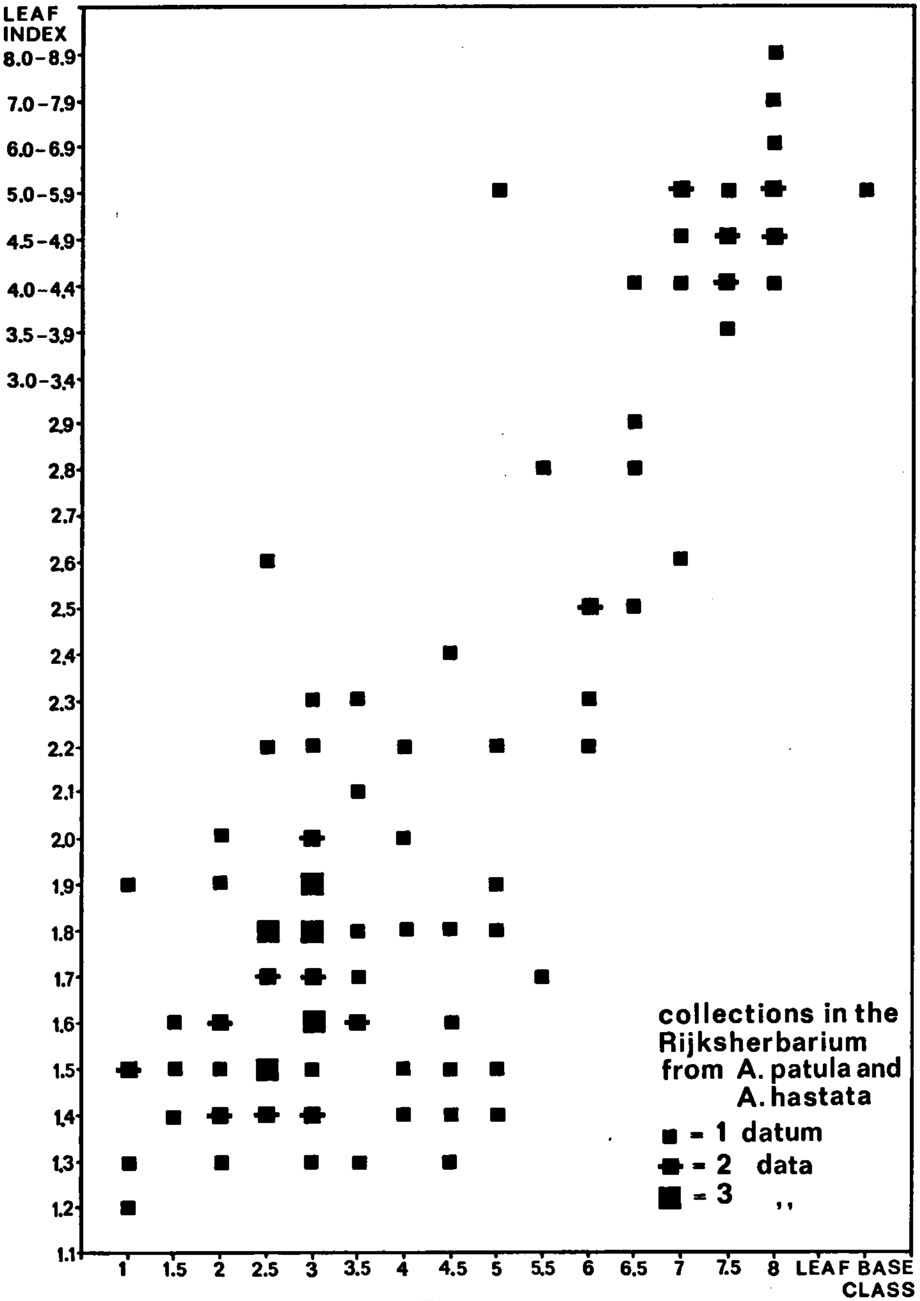
LEAF INDEX
8.0-8.9
7.0-7.9
6.0-6.9
5.0-5.9
4.5-4.9
4.0-4.4
3.5-3.9
3.0-3.4
2.9
2.8
2.7
2.6
2.5
2.4
2.3
2.2
2.1
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
6.5
7
7.5
8
LEAF BASE CLASS
collections in the Rijksherbarium from A. patula and A. hastata
■ = 1 datum
■ = 2 data
■ = 3 ,,

Diagram 2

Willd.], diploid *littoralis*, and tetraploid *patula* (and allied taxa); as no chromosome number is known to me from the closely allied Central European *A. oblongifolia* W. & K., its relation is uncertain.

Although this concept may be new for Europe, it is used by many American authors (Britton & Brown, 1913; Hall & Clements, 1923; Gleason, 1952; Gleason & Cronquist, 1963), following A. Gray (1867) who combined them under *A. patula*, subordinating *hastata* and *littoralis*.

The American authors cited above have neglected nomenclature, but merely used the specific epithetets on a lower rank. In this case, it seems to me to be an example to be followed. Strict application of the Rules of Nomenclature will be difficult and time-consuming.

Merely for the sake of clearity, I have used binomia in this paper; certainly this does not mean that I regard the taxa as 'good' species.

In order to facilitate identification it appeared useful to frame a key to the taxa discussed. I must emphasize that it seems impossible to me to identify each specimen. Moreover, it is impossible to distinguish *A. littoralis* by leaf characters alone from narrow-leaved forms of *A. patula*. As the two are not or only very rarely found together I have added their ecology.

KEY TO THE TAXA

1. All leaves linear or linear-lanceolate.
    2. Bracteoles embracing the fruit, mostly triangular- to rhomboid-ovate, the free margins with 3 or more pairs of ± equal teeth, shiny white inside, densely farinaceous above and often around the fruit; appendages (0—)2(—4) on one or both bracteoles, basally thickened, tooth-like, rarely ± leaf-like or laciniate. Pericarp basally longitudinally wrinkled. Seed black. On saline habitats, occasionally introduced elsewhere with sand . . . . **A. littoralis** L.
    2. Not all these characters combined: at least part of the female flowers with bracteoles only partly or just fully embracing the fruit. Fully developed bracteoles ± rhomboidal, the free margins often with only one pair of hastate teeth, inside glabrous or slightly farinaceous, never shiny white; appendages never strongly thickened at base, leaf-like, simple, laciniate, or absent. Pericarp not wrinkled. Seed black, reddish, or yellowish, often mixed in one inflorescence. A typical weed of disturbed places, exceptionally saline . . . . narrow-leaved forms of **A. patula** L.
1. At least the basal leaves wider, mostly triangular to oblong-hastate.
    3. Third to seventh leaf-pair at the main stem (counted from the base) oblong to linear (leaf-index 2.0 to more than 5), with an obtuse to narrowly cuneate base . . . . **A. patula** L.
    3. Third to seventh leaf-pair deltoid to triangular (leaf-index 1.2 to 2.6) with an ± cordate-attenuate to widely obtuse base . . . . **A. hastata** L.

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