Zeitschrift: Boissiera : mémoires de botanique systématique
Herausgeber: Conservatoire et Jardin Botaniques de la Ville de Genève
Band: 24 (1975-1976)
Heft: 1

Artikel: Specification in Mesembryanthemaceae
Autor: Hertmann, H.
DOI: https://doi.org/10.5169/seals-895514

Boissiera 24: 255-261. 1975.

Speciation in Mesembryanthemaceae

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SUMMARY

In order to exemplify evolutionary tendencies in *Mesembryanthemaceae* the author has studied the variation patterns of different morphological characters in the species complex *Argyroderma congregatum-A. crateriforme-A. delaetii.*

RÉSUMÉ

Afin d'illustrer les tendances évolutives chez les Mésembryanthemacées, l'auteur a étudié les modes de variation de divers caractères morphologiques au sein du complexe d'espèces: *Argyroderma congregatum-A. crateriforme-A. delaetii.*

Following on the previous discussion on evolution in *Mesembryanthemaceae* (Ihlenfeldt, 1975: 249-254, above), this paper shows the population variation within a species complex of the genus *Argyroderma* N. E. Br. and provides suggestions for trends in speciation on an evolutionary basis.

Description of the species complex

The three species *A. congregatum* L. Bol., *A. crateriforme* (L. Bol.) N. E. Br. and *A. delaetii* Maass possess the same type of fruit (Plate I, A) which is characterized by a ± flattened calyx tube and a short peduncle with persisting yellow bracts that enclose the capsule itself.

A. congregatum is distinguished by its branched and clump-forming habit which raises the plant above the ground (Plate I, B). The hood-shaped assimilating leaves spread when fully turgescent. They persist on whithering and turn into yellow, spreading old leaves. Yellow is the dominant flower colour. The flowering time is April and May.

A. crateriforme (Plate I, C) shares with *A. congregatum* the hood-shaped form of the assimilating leaves and the dominance of yellow flower colour, but differs markedly from the latter in its growing habit: the plants grow sunken into the ground, with age their leaves become brittle and disintegrate on whithering; also the degree of ramification is lower. Flowering occurs in April and May.

A. delaetii (Plate I, D) possesses the same growing habit as *A. crateriforme*, but differs in leaf-shape (half-egg-shaped) and ramification (mainly unbranched plants). The flowering time is April to June, the flower colour is purple or yellow. The fruits are considerably bigger than those of *A. congregatum* and of *A. crateriforme* and have more locules.

Ecology of the three species

The distribution map of the three species (Fig. 1) shows that three main areas can be recognized each of which corresponds to one species. Yet there are several

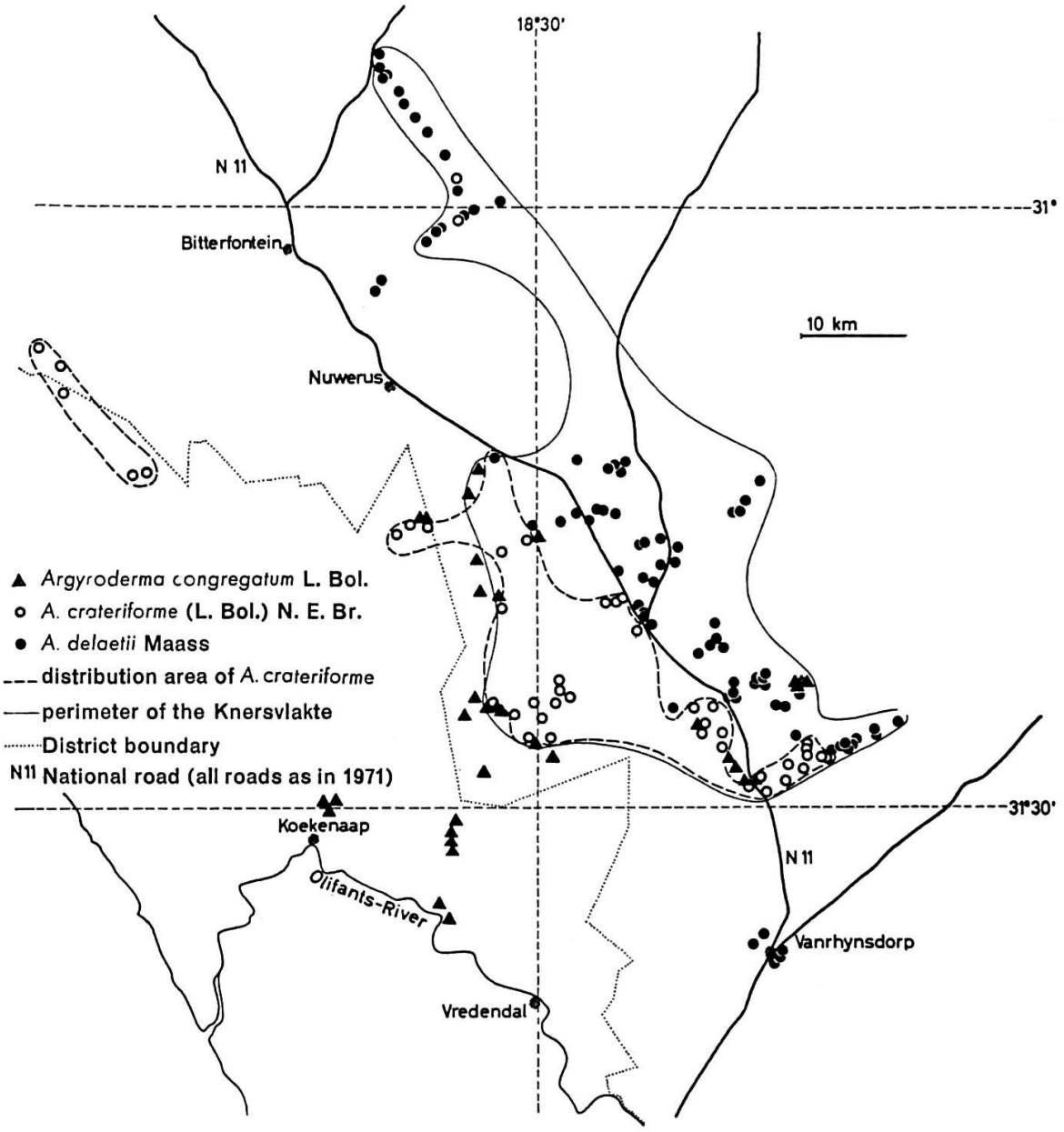


Fig. 1. — Distribution of the species complex *A. congregatum* L. Bol.-*A. crateriforme* (L. Bol.) N. E. Br.-*A. delaetii* Maass.

localities where two species grow very close together, and others where one species is occasionally found within the main distribution area of another. This peculiar pattern is due to the particular ecology of each species, and in reality there is not one sympatric locality.

A. congregatum at the western border of the Knersvlakte grows on rather rough hard soil covered loosely with quartz pebbles or stones up to head-size . It is mostly found underneath bushes on slopes or koppies. Since, west of the Knersvlakte, the quartz outcrops occur mainly in places exposed by the incisions of the rivers, it is not surprising to find *A. congregatum* here. As such favourable areas are often of considerable size, populations can be large and wide-spread.

A. delaetii, on the contrary, occupies the eastern flat parts of the Knersvlakte where small or large patches of rather soft soil are densely covered with small white quartz pebbles. These patches are formed from decomposed outcorps of quartz bands and differ greatly in size and distance from each other. On these patches *A. delaetii* often forms pure colonies: there seem to exist no competing species on this well-drained shallow type of soil.

A. crateriforme takes an intermediate position between the two species described above: the sunken habit indicates that it grows in soft soil, but the quartz cover found in these localities is rather loose as in those frequented by *A. congregatum*, and the size of the pebbles varies more than in the *A. delaetii*-localities. The association is mostly dominated by shrubs, as in *A. congregatum* stations.

Thus it is obvious that the east-western differentiation between the three species is closely related to ecological and to edaphic conditions in particular. In order to discuss the evolutionary trends and to interprete the mechanisms of speciation, the variation of different characters within the three species will be considered.

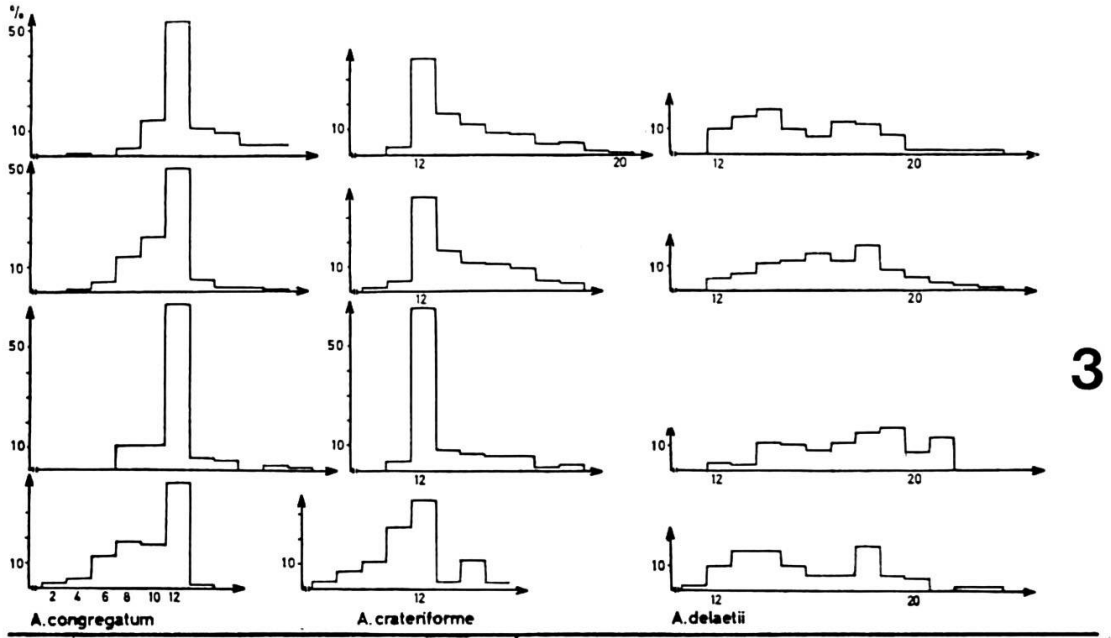
Variation within populations

Flower colour

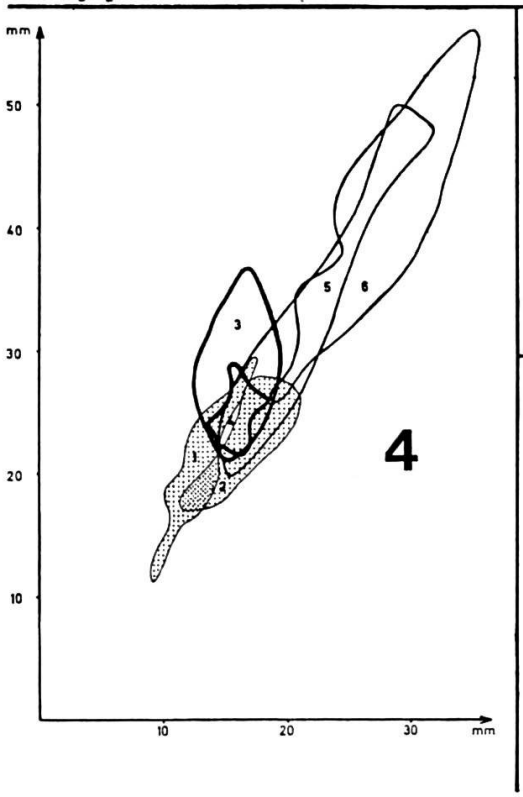
In *Argyroderma*, 9 different floral colours have been distinguished. These can occur in 19 different combinations each of which is defined as a colour-type (Hartmann, 1974). The number of colour-types per population indicates significant differences between these three species (Fig. 2): From *A. congregatum* through *A. crateriforme* to *A. delaetii*, a decrease in the percentage of homogeneous species populations is demonstrated. Consequently, in the same sequence an increase of heterogeneous populations of each species is observed. In accordance with the fact that yellow flowering populations in *Argyroderma* possess high homogeneity in colour type, it is to be noted that most populations of *A. congregatum* and *A. crateriforme* have yellow flowers. The higher variation of floral colour in *A. delaetii* corresponds to a predominance of purple flower colour.

Number of locules per fruit

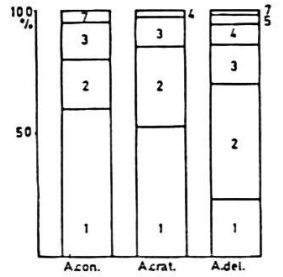
Since the fruits of the three species discussed above belong to the same type (Plate I, A) they therefore cannot be distinguished morphologically. Yet the number of locules per fruit and the diameter of the latter allow the distinction between *A.*


%
A.congregatum
A. crateriforme
A.delaetii

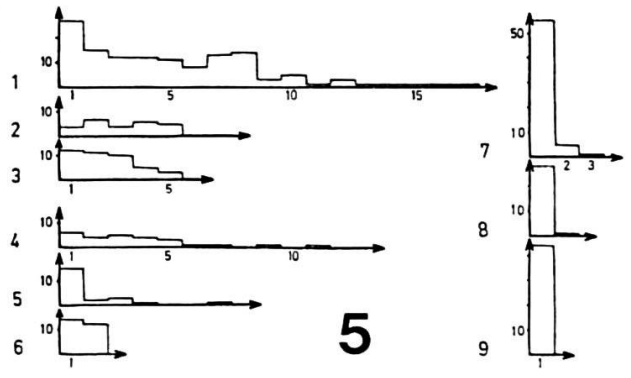
3


mm

4


100 %
A.con.
A.crat.
A.del.

2



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delaetii (with bigger fruits of 14-20 locules) and *A. congregatum/A. crateriforme* (with smaller fruits of ± 12 locules). In addition to these characters, the variation pattern of locule-numbers per fruit within populations is a specific character; *A. congregatum* and *A. crateriforme* fruits can only be separated in this way.

Figure 3 shows four populations of each species with typical distribution curves. Two features become obvious: the variation within populations increases from *A. congregatum* (left) through *A. crateriforme* (centre) to *A. delaetii* (right) as can be seen from the total amount of locule-numbers within a population.

Secondly it can be observed that there is a reduction of the maximum value from above 50% to below 20% and a shifting from a nearly normal distribution *(A. congregatum)* over a skewed one (mainly to the right, *A. crateriforme*) to a ± bimodal distribution *(A. delaetii)*.

Leaf size

The distribution pattern for leaf size in this species complex shows no discontinuation (Fig. 4). Yet *A. delaetii* has bigger leaves, whereas *A. congregatum/A. crateriforme* have smaller leaves and can not be separated by means of their leaf measurements. An analysis of variation in leaf size underlines the fact that *A. congregatum* and *A. crateriforme* cannot be distinguished on this basis. The variation within populations of these two species is similar and comparatively restricted. In contrast, *A. delaetii* not only exhibits larger leaves but also a much wider variation within populations.

Fig. 2. — Variation in flower colour.

Each species is represented by one column. These columns are divided into blocks, each of which shows the percentage of populations that share the same number of colour-types (1-7: number of colour-types per population); only those populations were taken into account where 3 or more flowers were seen. The totals of the populations studied are: *A. congregatum* (A. con.): 20, *A. crateriforme* (A.crat.): 33, *A. delaetii* (A. del.): 51.

Fig. 3. — Variation of the number of locules per fruit.

Ordinate of each graph: amount of fruits (in %); abscissa of each graph: number of locules per fruit. The graphs are arranged in such a way that the numbers of locules for each species lie in identical columns. Populations from top to bottom (the total number of measured capsules is given within brackets): *A. congregatum* L. Bol.: Hartmann 1374 (74), 1756 (127), 1859 (81), and 1391 (102); all HBG ! — *A. crateriforme* (L. Bol.) N. E. Br.: Ihlenfeldt & Hartmann 5182 (326), 4349 (361), 4458 (87), and Hartmann 1818 (28); all HBG ! — *A. delaetii* Maass: Hartmann 1666 (60), 1538 (242), 1871 (62), and 1870 (71); all HBG !

Fig. 4. — Variation in leaf size.

Ordinate: maximum length of leaf-pair as seen from above (for technical reasons, the length of the leaf-pair and not the length of one leaf was measured); abscissa: maximum width of leaf (= maximum width of leaf-pair). Each conture represents the range of measurements of one population. Two typical populations of each species are shown. — 1-6: Populations; behind the collecting number (all Hartmann, HBG !), the number of measured plants is given within brackets, Dotted: *A. congregatum* L. Bol. 1: 1693 (23), 2: 1768 (16); Fat conture: *A. crateriforme* (L. Bol.) N. E. Br. 3: 1466 (10), 4: 1690 (10); Thin conture: *A. delaetii* Maass 5: 1408 (15), 6: 1433 (13).

Fig. 5. — Variation in ramification.

Ordinate of each graph: number of plants; abscissa of each graph: number of leaf-pairs per plant. Three populations of each species have been chosen to demonstrate typical variation patterns. (All collections: Hartmann, HBG !). — 1-3: *A. congregatum* L. Bol. 1: 1369 (129 plants); 2: 1756 (28); 3: 1859 (41). 4-6 *A. crateriforme* (L. Bol.) N. E. Br. 4: 1899 (26 plants); 5: 1690 (22); 6: 1754 (26). 7-9: *A. delaetii* Maass: 7: 1433 (61 plants); 8: 1541 (29); 9: 1442 (44).

Ramification

In *Argyroderma*, as a rule, one leaf-pair is produced per season which whithers at the beginning of the following season. Branching is not rare and can result in compact plants of up to 50 leaf-pairs. The three species discussed here show considerable differences in ramification, as can be seen from Figure 5 where the number of branched plants per population and thus the degree of ramification is demonstrated.

In *A. congregatum*, the number of branched plants exceeds the amount of unbranched ones. Exceptions are rare, 4 out of 26 populations. The degree of branching can attain 17 leaf-pairs per plant. In *A. crateriforme*, the number of branched plants often exceeds the unbranched ones and the distribution pattern is similar to that of *A. congregatum*, yet the degree of branching hardly exceeds 5 and reaches 11 leaf-pairs at the most. In fact, several populations (11 out of 32) show a marked tendency towards an unbranched habit.

Plants with one leaf-pair are dominant in all populations of *A. delaetii*. In only 4 populations out of 44, plants were seen with 5 or more leaf-pairs; 10 populations consisted of entirely unbranched plants.

An obvious increase in ramification can be seen from *A. delaetii* through *A. crateriforme* to *A. congregatum*, where the ramification patterns are most variable.

Conclusions

The analyses of variation within populations show that in floral colour and in locule-number an increase in variation from *A. congregatum* through *A. crateriforme* to *A. delaetii* occurs. In the same sequence, a decrease in ramification can be seen, and in the number of pattern types *A. crateriforme* exceeds both the other species. In leaf size, the high variation of *A. delaetii* differs markedly from the more limited variation in the two other species.

In connection with the ecological data, the following suggestions for evolutionary trends of speciation are put forward. *A. congregatum* is considered to be the most primitive of the three species: in its yellow persistant, old leaves and its high degree of ramification it resembles the primitive subgenus *Roodia;* the species is ecologically least specialized and shows great homogeneity in all characters in spite of the fact that the distances between the populations are great. The latter indicates that, today, *A. congregatum* represents the relicts of an old stabilized form. Only one isolated population group in the eastern Knersvlakte (Hartmann 1767, 1768, 1773 and 1774 in Herb. HBG, see Fig. 1) having slightly different characteristics (ramification less than normal, flower colour mainly purple although homogeneous) is suggestive of a further step in evolution.

Evolution from *A. congregatum* to *A. delaetii* via *A. crateriforme* is understood as a neotenic process during which the adaptation to shallow quartz fields was obtained by ontogenetic abbreviation, i.e. by the determination of the seedling-shape (Hartmann, 1974) and -habit as a fertile adult. This explains the very limited variation in ramification and growth type. At the same time, an increased variability in the ecologically not adapted characters, such as flower colour, locule number and leaf size, could take place. It seems as if neotenic processes set free potentials of variation that have

been so far bound up in other genetic connections. In contrast to variability in primitive groups, this feature should be called secondary variability. Thus the position of *A. delaetii* can be seen from two angles: on the one hand *A. delaetii* is the ecologically and morphologically stabilized final stage of a neotenic process which includes a strict adaptation to a special habitat; on the other hand it forms a swarm of highly variable and therefore adaptive populations. Since these populations grow semi-isolated (because the favourable soil conditions, viz. quartz fields, allow development in restricted but not too distant areas) the possibilities of building up isolating mechanisms exist. Thus it is possible that *A. delaetii* represents a source of new species.

In the evolutionary sequence *A. congregatum-A. crateriforme-A. delaetii*, *A. crateriforme* represents an early stabilized form where certain steps of adaptation (growing habit, ramification) and a considerable range of variability (flower colour, ramification) have been reached, but the existence of *A. delaetii* demonstrates that *A. crateriforme* represents only a first step in the evolution of the discussed species complex.

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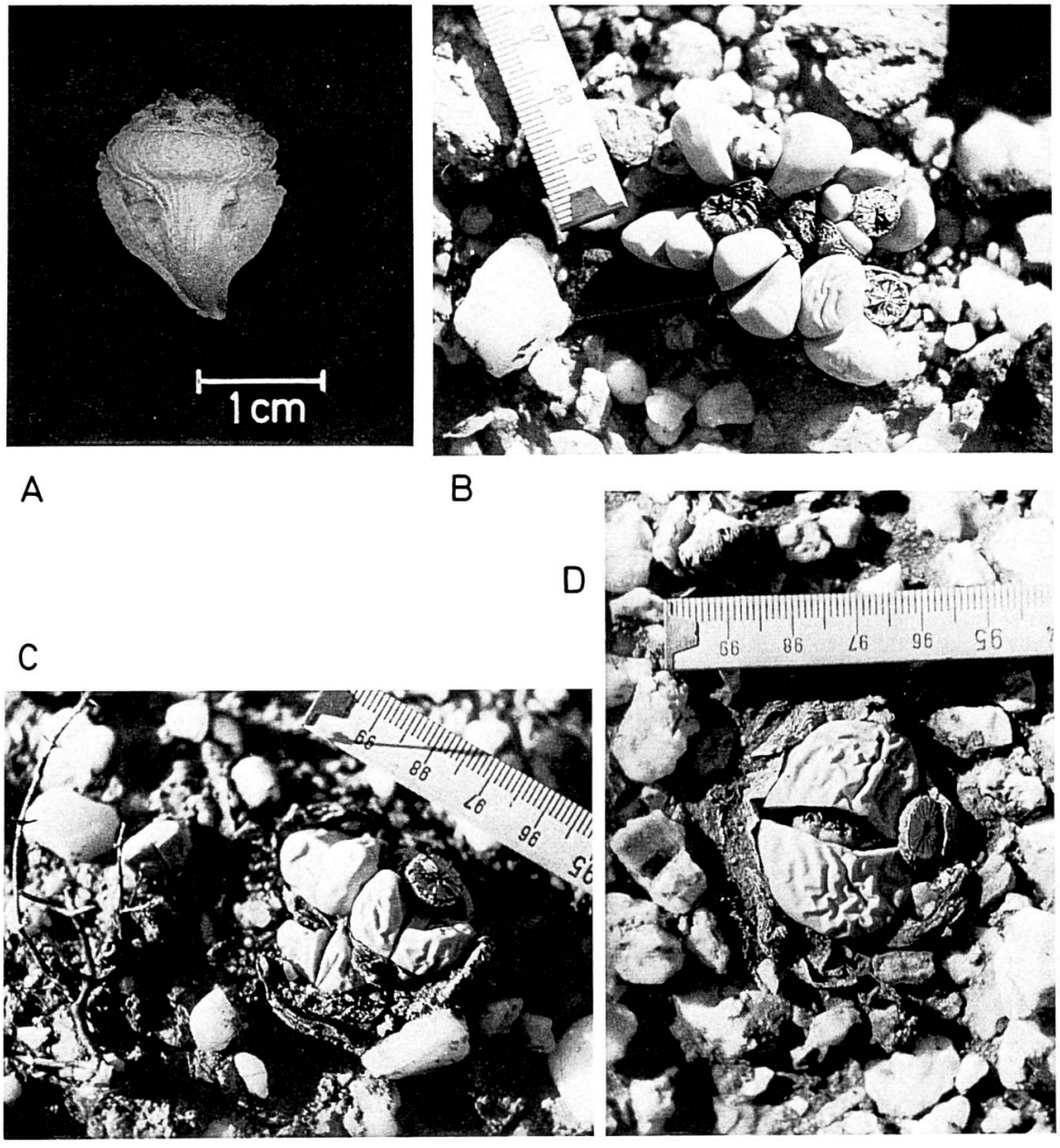

A, fruit type. Side-view of fruit of *A. delaetii* Maass (Ihlenfeldt & Hartmann 5127 HGB!).
B, *A. congregatum* L. Bol. in its natural habitat (Hartmann 1762 HGB!).
C, *A. crateriforme* (L. Bol.) N. E. Br. in its natural habitat (Hartmann 1722 HBG!).
D, *A. delaetii* Maass in its natural habitat (Hartmann 1536 HBG!).