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POLLEN PHYLOGENY AND TAXONOMY EXEMPLIFIED BY AN AFRICAN ASTERACEAE GROUP

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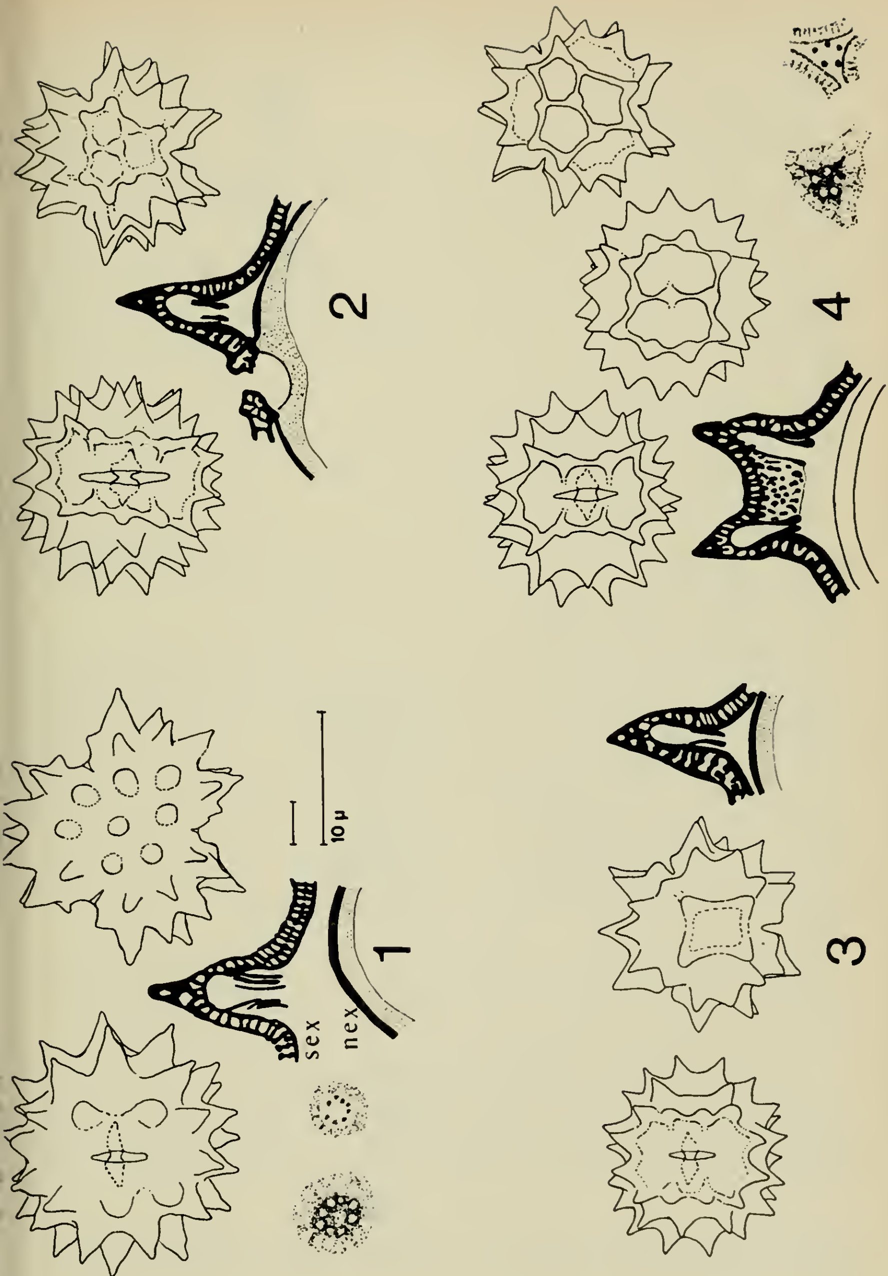
The Asteraceae group, we shall be discussing, may be outlined by the following characters: anthers sagittate; style-branches somewhat obtuse, on their whole inside with stigmatic tissue; stylar hairs reaching from the top of the style-branches to ± far beneath the point of forking of the style, where a ring of longer stylar hairs is formed; involucral bracts in several series, connate at least at the base. These are the main features of the subtribe Gorteriinae, tribe Arctotideae. The subtribe Gorteriinae, which is mainly confined to South Africa, was monographically dealt with by Roessler (1959). Roessler (l. c.) recognizes eight genera: *Berkheya* (72 species), *Cullumia* (15), *Didelta* (2), *Heterorhachis* (1), *Cuspidia* (1), *Gorteria* (3), *Hirpicium* (12) and *Gazania* (16). The relatively multiform genus *Berkheya* because of its macroscopic characters is considered to be the most primitive of the subtribe. In *Berkheya* the involucral bracts are connate only at the base, and the sterile ligulate flowers still have staminodes. The genera *Cullumia, Didelta, Heterorhachis* and *Cupsidia* are closely affiliated to *Berkheya*. The genera *Gorteria, Hirpicium* and *Gazania* are regarded as one group with most advanced macroscopic characters. Their involucral bracts are connate rather high up, and their ligulate flowers show a tendency towards disappearance of staminodes. — We shall see, what the pollen grains say to that.

The pollen grains of the Gorteriinae have rather different surfaces. There are pollen grains with long spines, and others showing a lacunar surface (cf. also Stix 1960). After an extensive investigation we can distinguish seven main types:

Amongst the spiny forms one type (fig. 1) is characterized by its spines irregularly spread on the surface. We will call it the "irregular spiny" type.

Fig. 1—4. Pollen grains of Gorteriinae (equatorial and polar views, LO-analyses and sections through the exine). 1. *Berkheya armata.* 2. *Berkheya insignis.* 3. *Berkheya spekeana.* 4. *Berkheya radula.*



Its baculate sexine protrudes to form hollow spine bases. About six to eight long bacules, more or less circularly placed, project into the cavity of the spine bases. The sexine between the spines appears two-layered through thickenings on the bacules.

The following pollen type (fig. 2) is distinguished from the latter by the fact that the spines are mostly interconnected at their bases through low hollow cristae. In addition, the spines around the pole and the three colpi often form a regular pattern. Generally three spines stand on either side of a colpus. On each mesocolpium f o u r spines are found in the area of the equatorial line: this is the "four-spine" type. The sexine of the "four-spine" type is either one-layered between the spines or two-layered through thikkenings on the bacules, a difference to which we shall not attach too much importance.

The next type (fig. 3) is characterized by t h r e e spines on each mesocolpium in the outline of the polar view: this is the "three-spine" type. Again its spines are interconnected at their bases by low cristae and often arranged in a more or less regular pattern in different areas. Generally two spines are found on either side of a colpus.

Another "three-spine" type (fig. 4) has somewhat higher cristae between the spines and a more rigid pattern. On its mesocolpia there are two large fields, i. e. two shallow lacunae. On either side of a colpus and at right angles to the latter two low cristae can be observed.

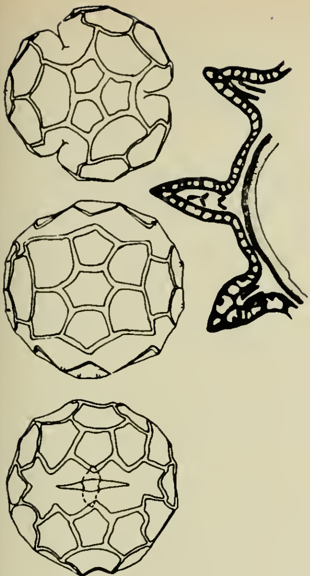
The same pattern as in that more regular "three-spine" type occurs in an entirely lacunar pollen type, which we call "lacunar *Berkheya*" type (fig. 5). The cavities at the points of intersection of the cristae, which are homologous to the cavities in the spine bases of the spiny pollen grains, have only three or four longer bacules projecting into them.

A second, entirely lacunar type (fig. 6) has a pattern on its mesocolpia which resembles somewhat the shell of a turtle; we refer to it as "turtle" type. Generally the lacunae on the margins of the mesocolpia project towards the colpi with three edges. In the hollows at the edges and the points of intersection of the cristae mostly three or four long bacules are found again.

A third lacunar pollen type which differs from all of the above types by the absence of those bacules is the "*Gazania*" type (fig. 7). It shows two lacunae on each mesocolpium and two overlapping cristae at the center of the colpi.

What are the relationships between these pollen types? — It would not be reasonable to place all the spiny types in one group and all the lacunar types in a second. It can be supposed that the three lacunar types with their fairly rigid patterns form the terminal points of three phylogenetic lines

Fig. 5—7. Pollen grains of Gorteriinae. 5. *Berkheya heterophylla* (section through the exine from *Cullumia aculeata).* 6. *Cullumia setosa.* 7. *Gazania othonnites.*



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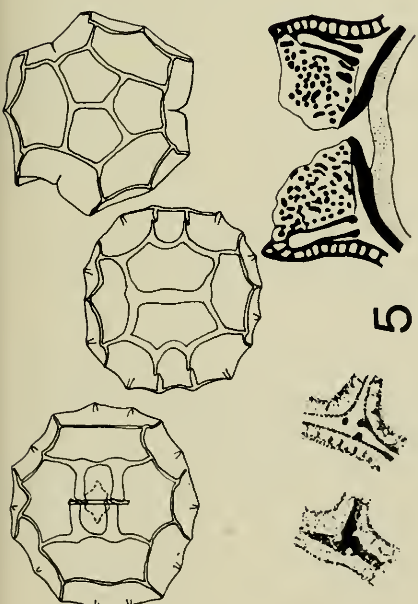

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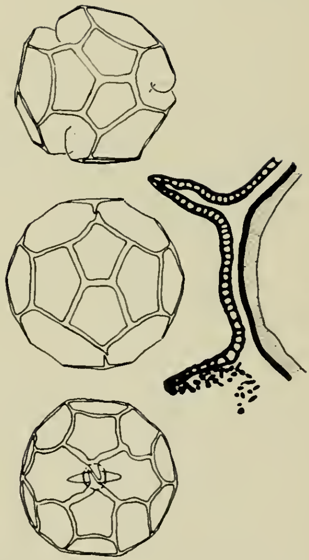

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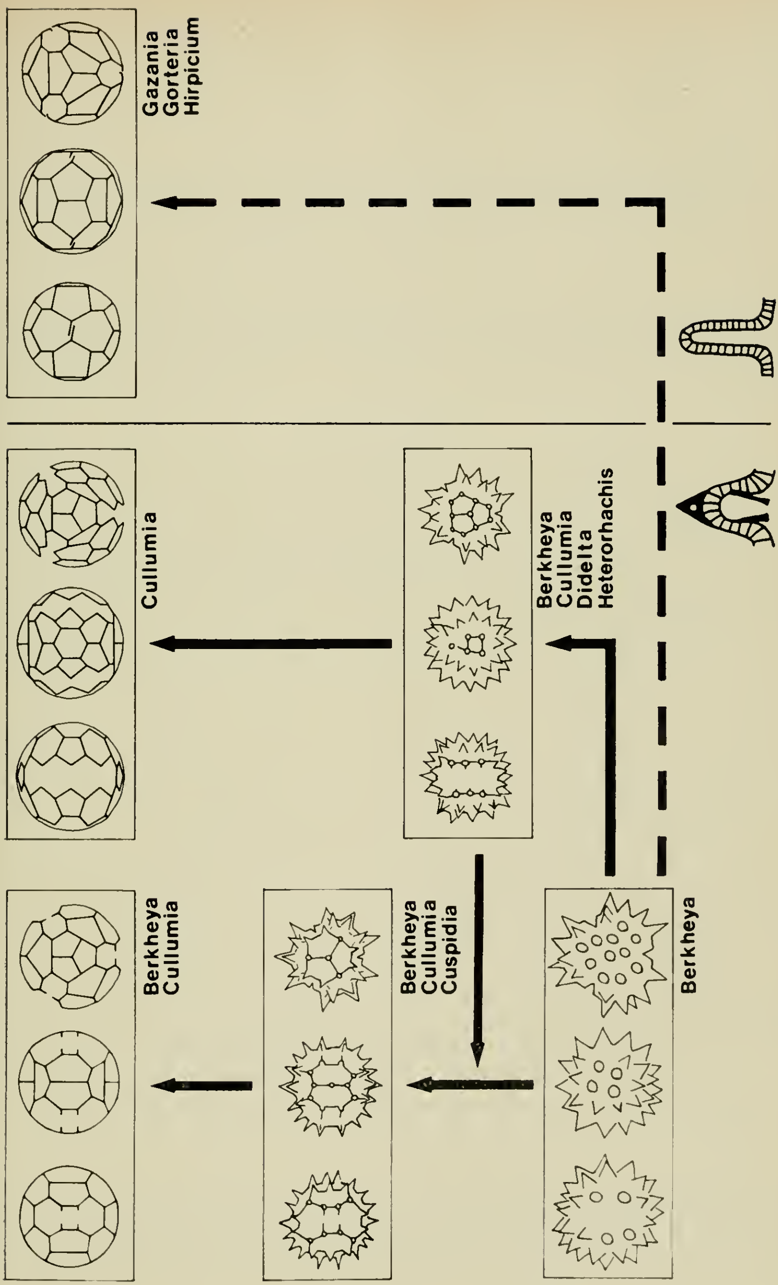
(fig. 8). The "irregular spiny" type, with its free spines, would form the starting-point. From this starting-point we can trace a nearly continuous progression via the "three-spine" types to the "lacunar *Berkheya*" type: The pattern of the pollen surface gradually becomes more rigid; the cristae between the spines become higher and higher; the number of bacules in the cavity of the spine bases decreases. The lacunar "turtle" type, being the terminal point of a parallel phylogenetic line, may be connected with the "four-spine" type. The absence of spiny forms with a more rigid pattern causes a break in the continuity of that line. The "four-spine" type is closely connected with the "irregular spiny" type. It is also possible, that the "four-spine" type with its still variable pattern leads over to the less regular "three-spine" type. Finally, the "*Gazania*" type occupies a rather isolated position and consequently must be regarded as the end of an independent phylogenetic line of which no intermediate stages are known.

The "irregular spiny" pollen type is confined to three species of the genus *Berkheya*. Pollen grains of the "three-spine" types are found in several species of *Berkheya*, in three species of *Cullumia* and in the genus *Cuspidia*. Apart from *Berkheya*, the "lacunar *Berkheya*" type also appears in a few *Cullumia* species. The "four-spine" type is represented in the genera *Didelta* and *Heterorhachis* and also in certain species of *Berkheya* and *Cullumia*. The "turtle" type is found in some *Cullumia* species only. The lacunar "*Gazania*" type is confined to *Gazania*, *Gorteria* and *Hirpicium*.

Our palynological results agree with the clear seperation of the three undoubtedly related genera *Gazania*, *Gorteria* and *Hirpicium* from all the other Gorteriinae as mentioned by Roessler. Furthermore, our pollen morphological investigations confirm that *Berkheya* is the most primitive genus within the subtribe. Only in this eurypalynous genus we still find pollen grains distinguished by free and irregularly spaced spines. It is interesting to note that the genus *Cullumia* shows nearly the same stages in pollen phylogeny as *Berkheya* (*Cullumia* only lacks the most primitive "irregular spiny" type and shows a further step in the phylogenetic line of the "four-spine" type forming a second lacunar type, the "turtle" type). This supports the assumption that *Cullumia* evolved from different *Berkheyas*. However, the vegetative uniformity of the *Cullumia* species may not be in favour of a heterogeneous origin.

How are the Gorteriinae related to other groups? — The neighbouring subtribe Arctotidinae, which is closely related to Gorteriinae as far as the morphology of the anthers and styles is concerned, may be differentiated by its free involucral bracts. The pollen grains of Arctotidinae as far as investigated have in principle the same interior spine structure as those in the Gorteriinae. But the cavity in the spine base is typically cylindrical and longer bacules, if present, are closely adjacent to the wall of the cavity (cf. also

Fig. 8. The phylogenetic lines of the pollen grains of the Gorteriinae.



Stix 1960). In this respect the pollen grains of Arctotidinae seem to form a definite group. According to our present knowledge they have not reached the lacunar level. In this connection it might further be mentioned, that the genus *Heterolepis*, which until now was placed in the Inuleae-Arthrixiinae, probably also belongs to the Arctotidinae (Besold, thesis).

The same interior spine structure as in many Gorteriinae is observed in the monotypic genus *Eremothamnus* of SW Africa. The genus first was included in the Senecioneae-Liabinae, but later was related to the Inuleae. The recent palynological and morphological investigation (Leins 1970) shows that it is very closely related to the Gorteriinae. In some respects *Eremothamnus* is still more primitive than *Berkheya*. Its pollen grains possess very numerous spines and its involucral bracts are still free. It is therefore proposed to place *Eremothamnus* just before the Gorteriinae in a separate subtribe.

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