

EHRETIACEAE VERSUS BORAGINACEAE: EVIDENCE FROM PALYNOLOGY

Ehretiacees par rapport aux Boraginacees Arguments de la palynologie

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RESUME

Les Boraginacees s.l. sont reconnues dans les regions temperées et tropicales. La famille comprend environ 130 genres dont 26 sont présents en Afrique. Actuellement, les Boraginacees comportent cinq sous-familles dont une est consitutee par les Ehretioidees. Depuis 1809, une certaine ségrégation s'est produite au sein des Boraginacees, dont les Ehretiacees en 1827. Depuis lors, une controverse a oppose la these d'une famille unique à celle d'une subdivision en cinq familles différenciées. Par définition, les Ehretiacees comprennent des buissons et des arbres aux fruits charnus par opposition aux Boraginacees s.str. qui sont des herbes et dont les fruits se présentent sous forme de quatre petites noix. La famille des Boraginacees s.l est eurypollinée, produisant une grande diversité de types de pollens. Une comparaison des pollens des Ehretiacees et des Boraginacees s. str. ne confirme pas la reconnaissance de deux familles séparées.

ABSTRACT

Boraginaceae s.l. is represented throughout the temperate and tropical regions of the world. The family comprises about 130 genera of which 26 are represented in Africa. Currently Boraginaceae is usually classified into five subfamilies, one of which is Ehretioideae. From 1809 various "segregate families" have been separated from Boraginaceae, including Ehretiaceae proposed in 1827. Since then the question of one family versus five different families has been a matter of controversy. By definition Ehretiaceae comprises mainly shrubs and trees with fleshy fruit as opposed to Boraginaceae s. str. characterised by herbs and fruit with four nutlets. The family Boraginaceae s.l. is eurypalynous, displaying a great diversity pollen types. A comparison of pollen types in Ehretiaceae and Boraginaceae s. str. does not support the recognition of separate families.

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INTRODUCTION

Various genera and species, mainly described by Linnaeus, were classified under an order “Borragineae” by JUSSIEU (1789), who divided the genera into three different groups based on fruit type, namely (a) berry-like (*Ehretia*, *Cordia*); (b) one- or two-locular capsules (*Hydrophyllum*, *Phacelia*); and (c) four separate nutlets (*Borago*, *Heliotropium*). However, since 1809 various families have been segregated from Boraginaceae, including Ehretiaceae proposed in 1827 by Martius.

Boraginaceae *s.l.* (Forget-me-not or Alkanet family) is represented throughout the temperate and tropical regions of the world. The family comprises about 130 genera (BRUMMITT 1992), of which 26 are indigenous to the African continent (RETIEF & VAN WYK 1999). Members of a few other genera occur as naturalised weeds in Africa. Boraginaceae *s.l.*, a family of herbs, shrubs and trees, is characterised by an indumentum of setae with swollen, multicellular bases, sympetalous flowers, inflorescences with scorpioid or helicoid cymules, which uncoil and elongate as the flowers mature, a terminal or gynobasic style, and fruit consisting mostly of four nutlets. By definition Ehretiaceae comprises mainly shrubs and trees with sympetalous flowers, inflorescences with scorpioid cymules, a terminal style which is divided in the upper part, and fleshy fruit types.

The family Boraginaceae *s.l.* is eurypalynous, the pollen displaying a wide range of morphological types. Perhaps it is unexpected that a family so morphologically uniform, at least in northern Europe and North America, should exhibit such palynological diversity (NILSSON & PRAGLOWSKI 1992). It does so nevertheless, both with respect to pollen size, which ranges from the tiny pollen grains of some *Myosotis* species, 3–4 µm, to grains measuring more than 20 µm in diameter. The aperture and tectum also display a great diversity of form and structure.

MATERIALS AND METHODS

Herbarium specimens housed in the National Herbarium (PRE), National Botanical Institute, Pretoria, were used in gathering pollen data on various species. These were supplemented by an extensive literature review. A list of specimens examined is supplied in RETIEF & VAN WYK (1999). Untreated and acetolysed pollen grains were studied. Pollen was acetolysed by the standard method of ERDTMAN (1960). For scanning electron microscopy, prepared samples were transferred to aluminium stubs, coated with gold and studied with an ISI-SX-25 SEM. Although acetolysis is the basic technique used by virtually all pollen morphologists, untreated pollen grains were also studied because certain characters are destroyed by the treatment.

FAMILY DELIMITATION

Boraginaceae *s.l.* comprises about 2500 species (MABBERLEY 1997), traditionally divided into five subfamilies: Wellstedioideae, Ehretioideae, Cordioideae, Heliotropioideae and Boraginoideae. Currently most workers accept the family in a broad, more or less conservative sense. In his concept of the family, JUSSIEU (1789) even included genera such as *Hydrophyllum* and *Phacelia*, both closely related to Boraginaceae in pollen and fruit characters, but currently classified under Hydrophyllaceae. The following authors are among those who have accepted Boraginaceae in an inclusive sense: CANDOLLE (1845), GÜRKE (1897), JOHNSTON (1951), KAZMI (1970), CHANDA & MUKHERJEE (1978), EDMONDSON (1978), SAHAY (1978), CRONQUIST (1981), MILLER (1989), MARTINS (1990), VERDCOURT (1991), BRUMMIT (1992), THORNE (1992), RIEDL (1997), TAKHTAJAN (1997) and THE ANGIOSPERM PHYLOGENY GROUP (1998).

In 1809 Brown segregated a group of genera from Boraginaceae subsequently classified under Cordiaceae. MARTIUS (1827) placed *Ehretia*, *Tournefortia*, *Rhabdia* and *Bourreria* in the family Ehretiaceae. Martius also proposed a family Heliotropiaceae with *Heliotropium* and *Preslea* as members. Presently Ehretiaceae is regarded as consisting of subfamilies Ehretioideae and Cordioideae, with the following genera (MILLER 1989, NOWICKE & MILLER 1990): *Ehretia*, *Bourreria*, *Carmona*, *Coldenia*, *Cortesia*, *Halgania*, *Lepidocordia*, *Pteleocarpa*, *Rocheportia*, *Rotula* and *Tiquilia* in Ehretioideae; *Cordia*, *Auxemma*, *Patagonula* and *Sacculium* in Cordioideae. Authors in favour of segregate families include: MARTIUS (1827), NOVÁK (1943), MERXMÜLLER (1960), FRIEDRICH-HOLZHAMMER (1967), HUTCHINSON (1969), AIRY SHAW (1973), DAHLGREN (1989), HEYWOOD (1997) and LE BRUN & STORK (1997).

DIAGNOSTIC PALYNOLOGICAL AND MACROMORPHOLOGICAL CHARACTERS IN EHRETIACEAE

Palynological and macromorphological characters of Ehretiaceae and Boraginaceae *s. str.* are compared below to establish whether to accept various segregate families or to regard Boraginaceae as an unquestionably natural unit' as VERDCOURT (1991) thought.

PALYNOLOGICAL CHARACTERS

Ehretiaceae as such is palynologically diverse. According to SAHAY (1978), HEUBL *et al.* (1990), NOWICKE & MILLER (1990) and our own observations, the pollen of this segregate family can be described as follows: Pollen grains isopolar; tricolporate, tricolporoidate, tricolpate, heterocolpate or triporate; spheroidal, oblate spheroidal, prolate spheroidal, subprolate. Shape in polar view triangular to circular, shape in equatorial view hexagonal, rectangular, elliptic to spheroidal. Apertures very long, broad or rather narrow in diameter, mesocolpium centres present. Tectum reticulate, spinulose, microperforate, verrucose, striate or rugulose.

Mesocolpium centres, as in Ehretiaceae, are known in species of *Wellstedtia* and members of Hydrophyllaceae, but occur also in Boraginaceae *s.str.* Polyaperturate pollen grains are found in, for example, *Lithospermum*, *Anchusa* and *Borago*, genera of Boraginoideae *s. str.*, but are absent in Ehretiaceae. Members of the tribe Boragineae are also characterised by an equatorial girdle around the pollen grain where endoapertures fuse (an endocingulum), not present in Ehretiaceae.

MACROMORPHOLOGICAL CHARACTERS

Habit

Ehretiaceae comprises mainly shrubs or trees, but also includes also the monotypic genus *Coldenia*, which is herbaceous. Boraginaceae *s. str.* is a family dominated by herbaceous taxa. However, in *Lobostemon* (Boraginaceae *s.l.*: Boraginoideae), for example, a number of species are small shrubs up to about 1.5 m high.

Style

Ehretiaceae is characterised by an ovary with a terminal style. This state is also found in *Wellstedtia* (Boraginaceae *s.l.*: Wellstedioideae) and *Heliotropium* (Boraginaceae *s.l.*: Heliotropioideae). It is well-known that the majority of Boraginaceae *s. str.* possesses a gynobasic style, a state also found in the Lamiaceae.

Fruit

Fruit characters are often used in support of the recognition of Ehretiaceae, known for its bright red or orange drupaceous fruit with a thin leathery exocarp, fleshy to mucilaginous mesocarp and bony endocarp with one to four stones which vary in surface sculpturing. These colourful fruit attract birds which are responsible for seed dispersal. In most Boraginaceae *s. str.* the fruit consists of four nutlets varying in surface sculpturing, often with glochidia (barbed hairs) which facilitate attachment for dispersal.

Fig. 1 & 2 illustrate some pollen grains and characteristics of the tectum in Boraginaceae *s.l.*

CONCLUSION

Palynologically some members of Ehretiaceae show strong similarity to certain members of the Hydrophyllaceae and *Wellstedtia* (Boraginaceae *s.l.*: Wellstedioideae or sometimes placed in a family of its own, Wellstediaceae) in reticulate or rugulose tectum morphology. Pollen grains with similar broad mesocolpium centres (pseudocolpi) and relatively broad apertures are known in members of Ehretiaceae, Hydrophyllaceae and *Wellstedtia*. BAILLON (1890) classified Hydrophyllaceae under Boraginaceae, but BRAND (1913) restored Hydrophyllaceae to family status and this has been followed by subsequent workers. Morphological and palynological similarities between members of the Hydrophyllaceae, *Wellstedtia* and Ehretiaceae may point to the

sharing of a common ancestor or even to their placement in an entity of their own. However, those species of Ehretiaceae characterised by narrow mesocolpium centres (pseudocolpi) and rectangular to elliptic equatorial outlines in their pollen do not support this view. Narrow mesocolpium centres and long, narrow apertures are also found in *Heliotropium* (Boraginaceae *s. str.*). In *Cordia* (Boraginaceae *s.l.*: Cordioideae) of the Ehretiaceae the tectum ornamentation of some species is reticulate, bearing resemblance to pollen grains of *Ehretia* and supporting the possible recognition of Ehretiaceae. On the contrary, similarity in suboblate pollen grains between other species of *Cordia* and *Trichodesma* (Boraginaceae *s. str.*: Trichodesmeae) does not support the recognition of a segregate family. In comparing the tectum ornamentation of Ehretiaceae with Boraginaceae *s. str.* it is also observed that the reticulate tectum of *Lobostemon*, for example, a genus closely related to *Echium* (Boraginaceae *s.l.*: Boraginoideae), shows similarity to Ehretiaceae. The tectum ornamentation of pollen grains in Boraginaceae *s. str.* is mostly psilate.

We are in agreement with SAHAY (1978) and CHANDA & MUKHERJEE (1978) who stated that the segregation of Ehretiaceae from Boraginaceae is not supported by palynological evidence and that the taxa concerned should be retained in Boraginaceae as primitive members. Fossil evidence suggests that *Ehretia* already existed in the Tertiary. *Davisella ehretioides*, a fruit described from the Lower Eocene, is now included in modern *Ehretia* (CHANDLER 1964). We therefore follow workers such as TAKHTAJAN (1997) and the ANGIOSPERM PHYLOGENY GROUP (1998) in recognising an inclusive Boraginaceae with five subfamilies.

Furthermore, certain macromorphological characters also show similarities supporting the recognition of Boraginaceae *s.l.* *Coldenia procumbens* (Ehretiaceae) is herbaceous and has a dry fruit of four nutlets, linking Ehretiaceae with Boraginaceae *s. str.* Terminal styles occur in *Heliotropium* (Boraginaceae *s.l.*: Heliotropioideae), whereas species of *Echium* (Boraginaceae *s. str.*: Boraginoideae) with a gynobasic style, has the style bilobed in the upper part, thus showing similarity to members of Ehretiaceae.

Resemblances between different pollen types, the presence of similar growth forms, styles, trichome and fruit types within the genera thus support that the view that the family Boraginaceae is a natural unit. A classical evolutionary taxonomical approach presents evolutionary relationships in phylogenetic trees, considering both evolutionary branching and the extent of divergence that has occurred in a lineage since it branched from a stem group. In accepting Boraginaceae as a family consisting of five subfamilies, these subfamilies can be regarded as branches of a tree with Wellstedioideae and Ehretioideae, the oldest with Boraginoideae the youngest.

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Fig. 1. SEM micrographs of pollen types in various subfamilies of Boraginaceae s.l. and in Hydrophyllaceae. A. Hydrophyllaceae: *Codon royenii* (LEACH & CANNELL 13810) – triaperturate. B. Wellstedioideae: *Wellstedia dinteri* (OLIVER & MÜLLER 6397) – tricolporoidate. C. Ehretiodeae: *Ehretia* sp.nov. (HANEKOM 1859) – heterocolpate. D. Cordioideae: *Cordia caffra* (WARD 3554) – triaperturate. E. Heliotropioideae: *Heliotropium steudneri* (RETIEF 1516) – heterocolpate. F. Boraginoideae: *Cynoglossum spelaeum* (HILLIARD & BURTT 18242) – heterocolpate. G. Boraginoideae: *Lobostemon paniculatus* (THOMPSON 3372) – triaperturate. H. Boraginoideae: *Lithospermum cinereum* (VAN DER BERG 3914) – polyaperturate. I. Boraginoideae: *Myosotis afropalustris* (ZIETSMAN 491) – heterocolpate. Scale bars: A = 2.7 μm ; B = 2.6 μm ; C = 2.5 μm ; D = 5.7 μm ; E = 3.3 μm ; F = 0.9 μm ; G = 1.4 μm , I = 1.3

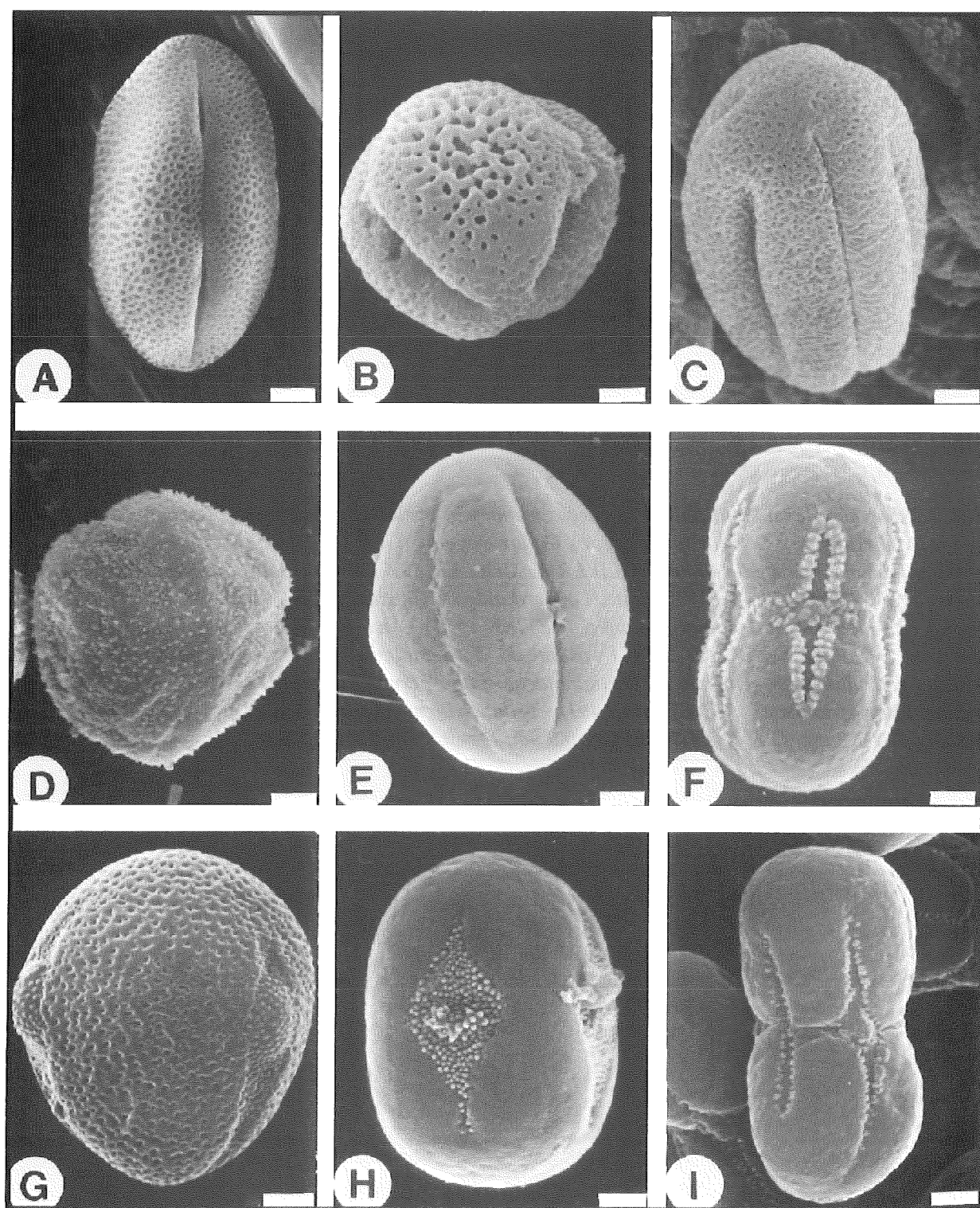


Fig. 2. SEM micrographs of pollen surfaces (tectum) in various subfamilies of Boraginaceae s.l. and in Hydrophyllaceae. A. Hydrophyllaceae: *Codon royenii* (GERMISHUIZEN 5510) – reticulate. B. Wellstedioideae: *Wellstedia dinteri* (OLIVER & MÜLLER 6397) – reticulate. C. Ehretioideae: *Ehretia obtusifolia* (FOURIE 2848) – reticulate. D. Cordioideae: *Cordia caffra* (WARD 3554) – spinulose. E. Heliotropioideae: *Heliotropium steudneri* (RETIEF 1516) – psilate. F. Boraginoideae: *Cynoglossum spelaum* (HILLIARD & BURTT 18242) – psilate. G. Boraginoideae: *Echium plantagineum* (BALSINHAS 3546) – reticulate with gemmae. H. Boraginoideae: *Lithospermum cinereum* (VAN DER BERG 3914) – psilate. I. Boraginoideae: (ZIETSMAN 491) – psilate with micropores. Scale bars: A & F = 0.6 μm ; B = 0.5 μm ; C = 1.2 μm ; D & E = 1.7 μm ; G = 0.9 μm ; H = 0.8 μm , I = 0.7 μm .

