

Pollen morphological studies in *Amaranthaceae* s.lat. (incl. *Chenopodiaceae*) and their taxonomic significance: A review

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Abstract

Amaranthaceae s.lat. is a stenopalynous family showing, in contrast, a considerable phenotypic diversity for macromorphological characters. A total of one quantitative and seven qualitative characters were reviewed in an attempt to assess their taxonomic implications. The presence of unique shape class, pore membrane sculpturing, anulopunctate tectum and pore borders clearly distinguished the subfamilies *Amaranthoideae* and *Gomphrenoideae* (*Amaranthaceae sensu stricto*) from the rest of the subfamilies of *Amaranthaceae* s.lat. Metareticulate exines are present exclusively in the subfamily *Gomphrenoideae*, in one genus of the subfamily *Corispermoideae* and encountered in one species – belonging to subfamily *Polycnemoideae*. Pore numbers although reported as a useful diagnostic feature, showed considerable intra-specific variation. The two basic pollen-types (*Amaranthus*-type and *Gomphrena*-type) within the subfamilies *Amaranthoideae* and *Gomphrenoideae* are quite distinct and gained broad acceptance, whereas the pollen types investigated for the rest of the subfamilies (belonging to *Chenopodiaceae*) are diverse and intricate. With the exception of *Anthochlamys*-type (related to *Gomphrena*-type), it was noticed that either members of one type constitute members of different subfamilies, or members of the same subfamily were scattered in different pollen-types, highlighting difficulties in recognising distinctive pollen-types in these subfamilies. The pollen-types within the subfamilies *Betoideae*, *Camphrosomoideae*, *Chenopodioideae*, *Corispermoideae*, *Salicornioideae*, *Salsoloideae*, *Suaedoideae* and *Polycnemoideae* are diverse and do not support their differentiation. Members of the subfamily *Polycnemoideae* share similarities with *Amaranthaceae* s.str. rather than members of the family *Chenopodiaceae*.

Keywords: *Chenopodiaceae*, *Amaranthaceae* s.str., *Gomphrena*-type, *Polycnemoideae*

Amaranthaceae Juss. s.lat. (incl. *Chenopodiaceae* Vent. *sensu* APG IV 2016; see also Kuhn et al. 1993; Cuenoud et al. 2002), is a cosmopolitan family including 173 genera and 2125 species (Mabberly 2017). Some authors (e.g. Hernandez-Ledesma et al. 2015) decided to maintain as separate the families *Amaranthaceae* and *Chenopodiaceae*, just accepting *Polycnemon* L. into the former (for the latter genus see e.g. Iamonico 2013; Freitag & Iamonico 2015).

According to APG-IV (Angiosperm Phylogenetic Group (APG) 2016) *Amaranthaceae* is classified into ten subfamilies: *Amaranthoideae* Burnett and *Gomphrenoideae* Schinz belong to *Amaranthaceae* s.str. (Townsend 1993), whereas *Betoideae* Ulbr., *Camphrosomoideae* Scott., *Chenopodioideae* Burnett, *Corispermoideae* Ulbr., *Salicornioideae* Ulbr., *Salsoloideae* Raf., *Suaedoideae* Ulbr. and *Polycnemoideae* Ulbr.

would belong to the family *Chenopodiaceae*. Concerning the subfamily *Polycnemoideae* it was differently treated during the time. For example, Dumortier (1827) recognised it as a tribal rank within the *Chenopodiaceae*, Moquin-Tandon (1849) regarded it as belonging to *Amaranthaceae* s.str., whereas according to Ulbrich (1934) considered it as a subfamily of the *Chenopodiaceae*. On the basis of molecular studies by Kadereit et al. (2003) and Masson and Kadereit (2013), *Polycnemoideae* was shown to be a basal lineage within the *Amaranthaceae* s.lat.

Amaranthaceae exhibits the highest pollen morphological diversity in the whole order *Caryophyllales* Juss. ex Bercht. et Presl. (see Nowicke 1994). Pollen studies were carried out at different taxonomic ranks (from family to species), and several characters (both quantitative and qualitative) were considered. Qualitative

characters include pollen and shape type, exine sculpturing, pore membrane sculpturing, pore borders, convexness of mesopori, shape of spines, etc. Quantitative characters include pollen diameter, pore number, diameter and density, exine thickness, interpore distance, punctate/spinules ratio, spinules height and density, punctae density, etc. These quantitative features show a broad range of overlap and as a consequence, they appear to be not good to distinguish taxonomic groups (see e.g. Borsch 1998; Flores-Olvera et al. 2016).

The present study aimed to review various pollen morphological characters (with emphasis on qualitative characters) of *Amaranthaceae* s.lat. and assess their taxonomic implications.

Material and methods

A total of one quantitative (pore number) and seven qualitative characters (pollen type, shape, exine sculpturing, pore membrane sculpturing, pore borders, punctate tectum and pollen types) were examined.

Results

Pore number

The number of pores were considered as a useful diagnostic feature to characterise the pollen types in many taxa (Angelini et al. 2014; Sanchez-del Pino et al. 2016; Dehghani et al. 2020). The number of pores vary from four as in *Nothosacra brachiata* (L.) Wight (subfamily *Amaranthoideae*) to 250 as in *Froelichia floridana* (Nutt.) Moq. (subfamily *Gomphrenoideae*) (Borsch 1998).

Considerable variations were reported to exist both inter-specific between members of the same genus or intra-specific within the same species in various geographical localities. The pore number of *Chenopodium album* L. was 65–75 in America (Tsukada 1967), 118 in Korea (Chung & Lee 1996), 107 in Turkey (Pinar & Inceoglu 1999), 50–90 in Ukraine (Tsymbalyuk 2005a), 92 in Iran (Hamdi et al. 2009), 48–60 in Mongolia (Punsalpaamuu et al. 2012), 105–188 in Italy (Angelini et al. 2014), and 60–65 in Egypt (Bayoumy et al. 2020).

In addition to variations in pore number encountered in different geographical localities, an exact count of pores can never be of reliable diagnostic character and of a taxonomic significance. The lack of an accurate count and the use of a wide range of numbers in most studies may be due to uneven distribution of pores on the surface of some pollen grains (Robinson & Skvarla 2014), lack of strict isodiametry of the pollen grains (Uotila 1974), variation due to habitat moisture (Dehghani et al. 2020)

and the use of different methods for calculating the number of pores (Christensen 1986).

Various methods for calculating or estimating the pore number were encountered and in many studies the pore numbers were mentioned without giving an account of the methods used. Mc Andrews and Swanson (1967) used the *C/D* ratio (cord *versus* diameter), Toderich (2008) used spherical geometry theory, Angelini et al. (2014) used the total area of pollen grain surface divided by the area of one hexagon around each pore, Franssen et al. (2001) used the visible number of pores divided by visible surface area, whereas Monoszon (1952) and Campell (1992) multiplied the number of pores on the surface by two.

Pollen class

In spite of the fact that all the pollen grains of the family are provided with pores uniformly distributed over the surface, different terms were used to describe this phenomenon. These terms include Polyforate (Erdtman 1952), Panporate (Erdtman & Vishnu-Mittre 1956), Pantoporate (Erdtman et al. 1961), Periporate (Faegri & Iversen 1989), Peripolyporate (Moore et al. 1991), Polypantoporate (Franssen et al. 2001), and Pantopolyporate (Toderich et al. 2010). Shams and Toshiyuki (2012) and the Australian Pollen and Spore Atlas (<http://apsa.anu.edu.au>) described the pollen class of *Alternanthera sessilis* (L.) R. Br. ex DC. (subfamily *Gomphrenoideae*) and *Hemichroa diandra* R. Br. (subfamily *Polycnemoideae*) respectively as fenestrate. The latter term was not recommended to be used in description (Punt et al. 1994).

Shape class

The pollen grains may be spheroidal or subspheroidal (Flores-Olvera et al. 2006; Dehghani et al. 2020), tetrahedral, cubical or dodecahedral (Borsch 1998). Spheroidal or subspheroidal shape classes were encountered in a wide array of taxa within the family, whereas tetrahedral or cubical classes were recorded so far in at least one species in *Pseudoplantago* Suess. (subfamily *Gomphrenoideae*). Dodecahedral shape class was reported in at least 12 genera of the subfamily *Gomphrenoideae* (Borsch 1998; Chin & Lim 2011; Sanchez-del Pino et al. 2016), and in one genus (*Kyphocarpa* [Fenzl.] Schinz.) in the subfamily *Amaranthoideae* (Borsch 1998).

Representatives of the subfamily *Polycnemoideae* were described by Tsymbalyuk (2005b, 2008) as possessing characteristic polyhedral shapes, rounded-angular or angular shapes.

Exine sculpturing

Various exine sculpturing were encountered. These sculpturings were described as micro-echinate or micro-echinate scabrate by Nazish et al. (2019), scabrate or granulate by Bayoumy et al. (2020), psilate by Mudie et al. (2005), psilate-scabrate (El Ghazali 1993), verrucate by Malih (2017) and metareticulate by Borsch and Barthlott (1998). These features with the exception of metareticulate sculpturing have no taxonomic significance, since they are diverse even within the same genus. The exine sculptures are micro-echinate in *Chenopodium album* L., micro-echinate scabrate in *C. ficifolium* Sm. and scabrate in *C. botrys* L. (= *Dysphania botrys* [L.] Mosyakin et Clemants) (Nazish et al. 2019).

The term 'metareticulate sculpture' was proposed by Borsch and Barthlott (1998) to describe pantoporate pollen with a reticulum-like structure of vaulted mesopori and sunken pores with width to the height ratio of mesopori less than one. Previously, various authors, e.g. Rioulet and Bonnefile (1976), Praglowski (1971), regarded these pollen grains as reticulate, Erdtman (1966) described them as reticulate or undulati-tegillate infra reticulate, whereas Robertson (1981) considered them as reticulate with deeply recessed pores. Metareticulate sculpture as defined by Borsch and Barthlott (1998), was encountered in several genera (at least 12) of the subfamily Gomphrenoideae, and at least in one genus (*Psilotrichopsis* C.C. Towns) of the subfamily Amaranthoideae (Borsch 1998). These two subfamilies (Gomphrenoideae and Amaranthoideae) belong to the former *Amaranthaceae* s.str.

In spite of the fact that the term metareticulate gained acceptance by many authors and widely adopted, it is still not followed throughout, and descriptive phrases were used instead. Nowicke and Skvarla (1979) and Nowicke (1975) described the pollen grains of *Anabasis* L., *Aellenia* Ulbr. (syn. *Halothamus* Jaub. et Spach.), *Halocharis* Moq. and *Traganum* Del. (subfamily Salsoloideae), *Aerva* Forssk. and *Marcellipsis* Schinz. (subfamily Amaranthoideae), and *Nitrophila* S. Watson (subfamily Polycnemoideae), as with sunken pores and convex mesoporial exines.

Pore membrane sculpturing

The pollen grains of the *Amaranthaceae* may be operculate (with ectexinous elements on the pore membrane) or nonoperculate. The presence/absence of opercula, may occur even within the same genus. The pollen grains of *Arthrocnemum macrostachyum* (Moric.) K. Koch. are operculate, whereas, those of *Arthrocnemum indicum* (Willd.) Moq. (= *Halosar-*

cia indica [Willd.] P.G. Wison) are nonoperculate (Perveen & Qaiser 2012).

The absence of ectexinous elements on the pores (nonoperculate) were encountered in at least one species of a diverse number of genera, e.g. *Anabasis* L., *Bassia* All., *Chenopodium* L., *Spinacia* L. (Bayoumy et al. 2020).

In operculate pollen grains, the sculpture of their pore membranes were described as having hook-shaped stellately arranged ectexinous bodies (Muller & Borsch 2005), with ectexinous bodies arranged in a mosaic-like pattern (Borsch 1998), micro-echinate (isolated or fused) (Lu et al. 2019), conical tuberculate (Hamdi et al. 2009), with conical spinules (Pinar & Inceoglu 1999) and scabrate (Perveen & Qaiser 2012).

The hook-shaped stellate pore sculpture is unique within the Angiosperms (Borsch 1998). This phenomenon which was also described as star-like structures (Nowicke 1975) and angular flecks of sexine (Shinwari et al. 2004) is known in only ten genera (Muller & Borsch 2005); nine genera of these belong to the subfamily Amaranthoideae and one genus (*Pseudoplantago* Suess.) belongs to the subfamily Gomphrenoideae.

Pore borders

The borders circumscribing the pores exhibit a wide range of variations. The borders may be indistinct or with differentiated areas around them. The latter may be described as with annuli as in *Amaranthus hybridus* L. (subfamily Amaranthoideae) (Azzazy 2011), flat-ringing as in *Alternanthera albida* (Moq.) Griseb. (subfamily Gomphrenoideae), irregular border lines as in *Nototrichium humile* Hillebr. (subfamily Amaranthoideae), ring-shaped structure as in *Kyphocarpa angustifolia* (Moq.) Lopr. (subfamily Amaranthoideae) (Borsch 1998), and torus as in *Tidestromia* Standl. (subfamily Gomphrenoideae) (Sanchez-del Pino 2001).

Pores with indistinct borders were encountered to exist in *Polycnemonum arvensis* L., *Polycnemonum majus* A. Braun ex Bogenh., *Nitrophila occidentalis* (Moq.) S. Watson (subfamily Polycnemoideae), *Horaninowia anomala* Moq., *Noea spinosissima* L., *Girgensohnia oppositiflora* (Pall.) Fenzl., *Nanophyton erinaceum* (Pall.) Bunge (subfamily Salsoloideae) (Tsymbalyuk 2005a, 2005b).

Punctate tectum

High resolution scanning electron microscopy (SEM) revealed punctuate tectum in all members of the family (Nowicke & Skvarla 1979). These punctae (perforations) are sometimes annulate, i.e. anulopunctate. Anulopunctate tectum was encountered within the subfamily Amaranthoideae in: *Deeringia* R. Br., *Henonia*

Moq., *Celosia* L., *Hemmbstaedia* Rchb., *Chamissoa* Kunth., *Indobanalia* A.N. Henry et B. Roy., *Lagrezia* Moq., *Digera* Forssk., *Pleuropterantha* Franch. (Borsch 1998), *Mechowia* Schinz., *Psilotrichum* Blume (Muller & Borsch 2005). Elsewhere within the family, it occurs only in one species (*Iresine borschii* Zumaya et Flores Olv.) belonging to subfamily Gomphrenoideae (Flores-Olvera et al. 2016).

Pollen types

Previous studies on pollen types were restricted to Amaranthaceae s.str. and Chenopodiaceae, and no study was encountered to investigate the pollen types within the family Amaranthaceae s.lat. at the family level. The family Amaranthaceae s.str. was recognised by Erdtman (1952) and accepted by Nowicke (1975) to possess two basic pollen types: *Amaranthus*-type (subfamily Amaranthoideae) and *Gomphrena*-type (subfamily Gomphrenoideae). Additional pollen types were described within these two basic pollen types by subsequent authors (Vishnu-Mittre 1963; Borsch 1998). These newly described pollen types were regarded informative for intrafamilial taxonomy (Borsch 1998).

However, within the family Chenopodiaceae, Bayoumy et al. (2020) recognised four pollen types, Lu et al. (2019) reported six pollen types and Perveen and Kaiser (2012) outlined four types. With the discovery of *Anthochlamys*-type, as a new pollen type in the family by Mosyakin and Tsybalyuk (2002), Tsybalyuk (2005a) proposed two basic pollen types for the family Chenopodiaceae: *Anthochlamys*-type and *Chenopodium*-type. *Anthochlamys*-type consists of members of the genus *Anthochlamys* Fenzl. (subfamily Corispermoidae), and considered by Mosyakin and Tsybalyuk (2002) as similar to the *Gomphrena*-type (subfamily Gomphrenoideae) due to the presence of metareticulate surface pattern. *Chenopodium*-type was divided into 28 types and 50 subtypes, and constitute members of the rest of the subfamilies including the genus *Corispermum* L. (subfamily Corispermoidae). All previous studies on the pollen types in the family Chenopodiaceae showed that these pollen types are diverse and intricate. According to Perveen and Kaiser (2012), Lu et al. (2019) and Bayoumy et al. (2020), *Haloxylon*-type encompasses exclusively members of the subfamily Salsoideae, *Atriplex stocksii*-type (Bayoumy et al. 2020) constitutes members of the subfamilies Chenopodioideae, Camphrosomoideae, Betoideae, Salicornioideae and Salsoloideae, whereas members of the same subfamily (e.g. Salsoloideae) were scattered in different types (*Kalidum*-type, *Haloxylon*-type, *Iljinia*-type) (Lu et al. 2019). Moreover, Tsybalyuk (2005a) recognised seven types and 32 subtypes in Chenopodioideae, seven types and eight subtypes in Salsoloideae, five

types and two subtypes in Betoideae, three types and two subtypes in Camphrosomoideae, two types in Polycnemoideae, two types in Suaedaoideae, one type and three subtypes in Salicornioideae and one type and three subtypes in Corispermoidae.

Discussion and conclusions

The pollen of all studied members of the family Amaranthaceae s.lat. are characterised by the presence of uniformly distributed pores. Different terms were used for this pollen class by various authors (e.g. Erdtman 1952; Erdtman & Vishnu-Mittre 1956; Erdtman et al. 1961; Faegri & Iversen 1989). With respect to this pollen class, it was regarded by Erdtman (1966) as belonging to a stenopalynological group. The latter group includes a total number of 54 angiosperm families and only seven of them possess exclusively the same pollen class (Prieu et al. 2017). The family Amaranthaceae in spite of being stenopalynous with respect to pollen class and in some genera, the pollen grains are stenopalynous with respect to all characters (e.g. *Kyphocarpa* [Fenzl.] Schinz. et *Tidestromia* Standl.) (Borsch 1998), considerable diversity exists in different other characters.

Within the characters here investigated, the subfamilies Amaranthoideae and Gomphrenoideae were noticed to share dodecahedral shape class (Borsch 1998; Chin & Lim 2011; Sanchez-del Pino et al. 2016), metareticulate exine (Borsch 1998; Borsch & Barthlott 1998), hook-shaped stellate pore sculpture (Muller & Borsch 2005), anulopunctate tectum (Borsch 1998; Muller & Borsch 2005; Flores-Olvera et al. 2016) and distinct pore borders (Borsch 1998; Sanchez-del Pino 2001; Azzazy 2011). These five palynological characters support the unique position of the two subfamilies; Amaranthoideae and Gomphrenoideae and the basic pollen-types (*Gomphrena*-type and *Amaranthus*-type) investigated in the family Amaranthaceae s.str. (Erdtman 1952; Nowicke 1975), gained wide acceptance and all subsequent pollen types that were added by Vishnu-Mittre (1963) and Borsch (1998) are in fact within these two basic pollen types.

However, with the exception of the *Anthochlamys*-type which was reported in only one genus (*Anthochlamys* Fenzl.) of the subfamily Corispermoidae, the pollen types within the Chenopodiaceae are quite diverse and difficult to interpret from the taxonomic point of view. It was noted that either several pollen types constitute members of the same subfamily (Tsybalyuk 2005a), or members of one type are scattered in several subfamilies (Bayoumy et al. 2020).

Members of the subfamily Polycnemoideae possess peculiar palynological characters that distinguished them from those of the Chenopodiaceae (Tsybalyuk 2005a, 2005b). Moreover, *Nitrophila occidentalis* (Moq.) S. Watson (subfamily Polycnemoideae) produces a polyhedral-like shape similar to *Aerva* Forssk. and *Marcellipsis* Schinz. (subfamily Amaranthoideae) (Nowicke & Skvarla 1979), whereas *Hemichroa diandra* R.Br. (subfamily Polycnemoideae) was described in Australian Pollen and Spore Atlas (<http://apsa.anu.edu.au>) as with reticulate (metareticulate) surface pattern similar to members of the subfamily Gomphrenoideae. Both these subfamilies (Amaranthoideae and Gomphrenoideae) constitute members of the family Amaranthaceae s.str. These palynological characters indicated that the subfamily Polycnemoideae share similarities with family Amaranthaceae s.str., endorsing previous treatments by Moquin-Tandon (1849), Kadereit et al. (2003) and Hernandez-Ledesma et al. (2015).

Acknowledgements

The author would like to thank Dr Zoya M. Tsybalyuk, National Academy of Science of Ukraine for valuable comments on earlier version of the manuscript.

Funding

This work was supported by the National Centre for Research, Sudan [NCR-12].

Disclosure statement

No potential conflict of interest was reported by the author.

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