A classification system for seed (diaspore) monomorphism and heteromorphism in angiosperms

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Abstract

'Seed heteromorphism' is a broadly- and loosely-defined term used to describe differences in size/mass, morphology, position on mother plants and ecological function (e.g. dispersal, dormancy/germination) of two or more seeds or other diaspores produced by an individual plant. The primary aim of this review paper was to characterize via an in-depth classification scheme the physical structural design ('architecture') of diaspore monomorphism and diaspore heteromorphism in angiosperms. The diaspore classification schemes of Mandák and Barker were expanded/modified, and in doing so some of the terminology that Zohary, Ellner and Shmida, and van der Pijl used for describing diaspore dispersal were incorporated into our system. Based on their (relative) size, morphology and position on the mother plant, diaspores of angiosperms were divided into two divisions and each of these into several successively lower hierarchical layers. Thus, our classification scheme, an earlier version of which was published in the second edition of 'Seeds' by Baskin and Baskin, includes not only heteromorphic but also monomorphic diaspores, the *Division* to which the diaspores of the vast majority of angiosperms belong. The scheme will be useful in describing the ecology, biogeography and evolution of seed heteromorphism in flowering plants.

Introduction

'Seed (diaspore) heteromorphism' is a broadly- and loosely-defined term used to describe differences in size/mass, morphology, position on mother plant and ecological function (e.g. dispersal, dormancy/germination) of two or more seeds or other diaspores produced by an individual plant. Thus, the term is applied to a variety of situations concerning degree of distinctness of differences in size/mass, morphology and position of diaspores on a plant. For example, *Aethionema arabicum* (Brassicaceae) produces two morphologically distinct aerial diaspores with no intermediates (Arshad et al., 2019), *Heterosperma pinnatum* (Asteraceae) produces two morphologically distinct diaspores connected by a series of morphologically intermediate ones (Venable et al., 1987, 1995; Martorell and Martínez-López, 2014) and *Ceratocarpus arenarius* (Amaranthaceae) produces two morphologically distinct ground-level diaspores and a series of aerial diaspores that differ continuously in size and morphology from top to bottom of the plant canopy (Lu et al., 2013). It is no wonder, then, that in a recent paper Scholl et al. (2020) stated that defining seed heteromorphism is a challenge.

The aim of this review paper is to provide an in-depth classification scheme, an earlier version of which was published in the second edition of 'Seeds' by Baskin and Baskin (2014), based on size, morphology and position on the mother plant that will give more exactness to use of the term 'seed heteromorphism'. More generally, our aim was to characterize the diversity of structural design ('architecture') of diaspore monomorphism and heteromorphism in angiosperms.

Methods

Our classification scheme is based on information in the literature on the size/mass, morphology and position (e.g. aerial, basal and subterranean) on the mother plants of the diaspores of angiosperm taxa. Basically, we greatly expanded/modified the diaspore classification schemes of Mandák (1997) and Barker (2005), sometimes using terminology that Zohary (1937, 1962), Ellner and Shmida (1981) and van der Pijl (1982) applied to diaspore dispersal. Seeds (diaspores) were first divided into two major categories (monomorphic and heteromorphic) called divisions and each *Division* into several successively lower hierarchical layers.

Our scheme does not include the terms that Zohary (1937, 1962), Ellner and Shmida (1981), van der Pijl (1982) and/or Gutterman (1993, 1994b) used to describe agents/modes of dispersal such as anemochory (wind), hydrochory (water), ombrohydrochory (rain) and

zoochory (animals). Neither does it include genetic polymorphism, in which (1) two or more kinds of diaspores are produced by a species, (2) a population may be diaspore-monomorphic or dimorphic/polymorphic and (3) individual plants produce only one kind of diaspore, which is determined by Mendelian inheritance, i.e. a genetic segregation, not a somatic differentiation (see Appendix A).

In general, we follow Scholl et al.'s (2020) definition of 'seed heteromorphism.' According to these authors, variation in the morphology of heteromorphic diaspores can be discrete or continuous. However, if the variation is continuous the most extreme diaspores need to be widely divergent morphologically, such as occurs in *H. pinnatum* (see Introduction), for them to qualify as heteromorphic. Diaspores that do not meet one of these two criteria are, by default, considered to be monomorphic.

Results and discussion

The classification scheme we assembled for diaspore monomorphism and heteromorphism is shown in Table 1. However, as pointed out by Imbert (2002) and Scholl et al. (2020) seed heteromorphism (and thus monomorphism) is not easy to define. According to Harper et al. (1970), most individual plants and populations have a normal or skewed (continuous) distribution for seed size or shape, but that 'It is, however, characteristic of some species to produce two or more sharply defined types of seed.' Thus, the word 'monomorphic' does not mean that all seeds on an individual plant have a single size/mass or morphology (or that they have the same degree of dormancy). In fact, there is considerable variation in these traits (especially mass) among monomorphic seeds on an individual plant and even among those on the same infructescence or within a fruit as various authors have reported (e.g. Janzen, 1977a, b; Ernst, 1981; Thompson, 1981; Pitelka et al., 1983; Stanton, 1984; Thompson, 1984; Wolf et al., 1986; Wulff, 1986; Michaels et al., 1988; McGinley, 1989; Winn, 1991; Fenner, 1992; Susko and Lovett-Doust, 2000). Monomorphic simply means that seeds cannot easily be sorted into two or more clearly-defined (distinct) groups based on traits such as size/mass and/or morphology. Monomorphic seeds may show differences in dormancy/germination: cryptic polymorphism (i.e. ecological differentiation in the absence of obvious morphological differences) of Venable (1985). Heteromorphic seeds, on the other hand, means that seeds on an individual plant readily can be sorted into two or more distinct groups that differ in size/mass and/or morphology.

An excellent example of cryptic seed heteromorphism has been reported by Liyanage et al. (2016) for two species of Fabaceae (*Bossiaea heterophylla* and *Viminaria juncea*) whose seeds have physical dormancy. They found that individual plants of the two species, which occur in fire-prone ecosystems in southeastern Australia, produce seeds with a high threshold temperature and a low threshold temperature for physical dormancy break. There were no significant differences in mass or visible differences in shape or color of high- and low threshold temperature seeds from individual plants of either species. Seeds with a low threshold temperature for dormancy break could germinate after exposure to temperatures of a low-intensity fire (40–60°C), whereas those with a high threshold temperature for dormancy break could germinate only after exposure to temperatures of a high-intensity fire (≥80°C). Further, under competition with seedlings of *Acacia linifolia* (Fabaceae), a co-occurring species, seedlings of *B. heterophylla*

emerging after low-intensity fire temperature grew better than those emerging after high-intensity fire temperature. Competition would be more intense following low- than high-intensity fire due to the survival of more plants in the low- than high-intensity-burned community. Thus, although low and high threshold temperature seeds did not exhibit differences in mass or morphology they differed in their dormancy-breaking response to fire intensity and in seedling growth response to competition resulting from different fire intensities.

Overall, we show that there is considerable structural diversity in design ('architecture') of diaspore-heteromorphic angiosperm species based on diaspore size, morphology and position on the mother plant and of diaspore-monomorphic angiosperms based on diaspore position (e.g. aerial, basal and subterranean) on the mother plant. To date, only a few hundred of the >250,000 extant angiosperm species have been reported to produce heteromorphic diaspores (Imbert, 2002; Wang et al., 2010; Baskin et al., 2014; Scholl et al., 2020; Zhang et al., 2020), apparently meaning that the vast majority of flowering plants produce monomorphic diaspores.

In a recent survey for homomorphic (=our monomorphic) and heteromorphic species in the North American deserts, using information in various floras for the area, Scholl et al. (2020) identified 458 monomorphic species and 101 heteromorphic taxa, of which 75 of the latter were annuals. They also reported that their study brought the total number of known seed heteromorphic species to 378. The flora of this area contains many annuals, the climate is arid/semiarid and amount and timing of rainfall is unpredictable, which are conditions that favor bet-hedging via diaspore heteromorphism as a life history strategy (Scholl et al., 2020; Gianella et al., (2021). Thus, the North American deserts undoubtedly are highly over-represented in proportion of heteromorphic species compared to other bioclimatic regions. In which case, we should expect that the proportion of diaspore-heteromorphic species in the world's flora is much lower than that in the North American deserts.

Mandák's (1997) classification scheme for seed (diaspore) heteromorphism divides heteromorphic diaspores into Amphicarpy and Heterodiaspory and distinguishes three subgroups for the latter category: heterocarpy (Heteromericarpy of van der Pijl, 1982), heteroarthrocarpy and heterospermy. (See Table 1 for definition of each of these three terms and of those mentioned in the following.) Barker's (2005) diaspore classification scheme deals only with basicarpy, geocarpy and amphicarpy. His scheme includes full geocarpy, with three subtypes, i.e. active geocarpy, geophytic geocarpy and passive geocarpy; and basicarpy, also with three subtypes, i.e. aerial amphicarpy, amphi-geocarpy and amphi-basicarpy. Note that all of the categories in Mandák's (1997) scheme fit under our Division II (Heteromorphic), whereas the scheme of Barker (2005) includes terms under both our Division I (e.g. Full geocarpy) and Division II (e.g. Amphi-basicarpy). Imbert (2002) recognized two categories of diaspore heteromorphism: heterocarpy and heterospermy.

Many species of grasses (Poaceae) produce cleistogamous (CL) axillary spikelets within leaf sheaths at nodes on flowering culms (Connor, 1979, 1981; Campbell et al., 1983). Some grasses, e.g. the well-studied species *Triplaris purpurea* (e.g. Chase, 1908, 1918; Cheplick, 1996; Cheplick and Sung, 1998), produce these clandestine spikelets at all nodes on the flowering culm, which is terminated by an inflorescence of chasmogamous (CH) spikelets. Caryopsis mass decreases continuously [in a log-linear (or nearly so) fashion] from the lowermost to one of the upper leaf sheaths,

Table 1. A classification system for monomorphic and heteromorphic diaspores in angiosperms based on size/mass, morphology and position on mother plant.

DIVISION I. Monomorphic. One type of fruit and one type of seed produced by an individual plant (see Discussion for further explanation).
Supergroup 1. Monomorphic aerial. Fruits/seeds produced on aerial stems (not including basal part of aerial stem at ground-level).
Group A. All fruits/seeds produced by chasmogamous (CH) flowers; includes most angiosperm species.
Group B. Fruits/seeds produced by both CH and cleistogamous (CL) flowers; includes a few hundred angiosperm species, e.g. many, but not all, *Viola* species (Violaceae) (Uphof, 1938; Lord, 1981; Culley and Klooster 2007).
Group C. All fruits/seeds produced by CL flowers (complete cleistogamy) (Uphof, 1938; Lord, 1981; Culley and Klooster, 2007), e,g, species in the mycoheterotropic genus *Gastrodia* (Orchidaceae) (Suetsuga, 2013, 2014, 2016).
Supergroup 2. Monomorphic basal or subterranean. One type of fruit and one type of seed produced at or near ground-level or underground.
Group A. Basicarpy. Flowers and fruits at or near ground-level but not subterranean, e.g. *Asteriscus pygmaeus (*Asteraceae) (Zohary, 1962; Ellner and Shmida, 1981), *Oenothera triloba* (Onagraceae) (Walck and Hidayati, 2007), *Trigonella stellata* (Fabaceae) (Zohary, 1962; Ellner and Shmida, 1981), holoparasitic plants [with 'dust seeds' and undifferentiated embryo (Baskin and Baskin 2022)] in Balanophoraceae and Cytinaceae (Barker, 2005).
Group B. Geocarpy. Subterranean fruits from subterranean or aboveground flowers.
Subgroup a. Full geocarpy (**protogeocarpy** *sensu* Zohary, 1962). Flowers and fruits subterranean, e.g. *Rhizanthella gardneri* (Orchidaceae) (Warcup, 1985).
Subgroup b. Active geocarpy (**hysterogeocarpy** *sensu* Zohary, 1962). Flowers aboveground. After fertilization, ovary is pushed or pulled underground, where the fruit develops, e.g. *Arachis hypogaea* (Fabaceae) (Smith, 1950), *Holocarpha* spp. (Asteraceae) (Barker, 2005) and *Trifolium subterraneum* (Fabaceae) (Darwin, 1888; Katznelson and Morley, 1965).
Subgroup c. Geophytic geocarpy. Stigma aboveground but ovary remains belowground at all times, e.g. the holoparasitic genera [with 'dust seeds' and undifferentiated embryo (Baskin and Baskin 2022)] *Hydnora* (Hydnoraceae) (Bolin et al., 2009) and *Lophophytum* (Balanophoraceae) (Borchsenius and Olesen, 1990) and Iridaceae species (Barker, 2005). In some geophytic species in the monocot families Amaryllidaceae, Colchicaceae and Iridaceae with bulbs or corms, the flower is raised into the air by elongation of the perianth tube, which acts as a pedicle, and the ovary remains belowground. The peduncle elongates after flowering and raises the fruit above the level of the soil surface. In *Syringodea leipoldtii* (Iridaceae), the upper part of the ovary is raised aboveground, and the lower part remains belowground. In *Crinum acaule* (Amaryllidaceae), the short peduncle may, or may not, lift the ovary above ground (Burtt, 1970, 1977).
Subgroup d. Dioecious geocarpy. Male flowers produced on aerial stems of male plants and single-flowered female inflorescences produced belowground (or below ocean-sediment surface in seagrasses) on horizontal rhizomes of female plants. The ephemeral stigma protrudes aboveground (or above ocean-sediment surface in seagrasses), where it is pollinated by wind, e.g. *Alexgeorgea* (Restionaceae) (Carlquist, 1976; Meney et al., 1990), or water, e.g. geocarpic species in the seagrass genera *Cymodocea* and *Halodule* (Cymodoceaceae) and *Halophila* (Hydrocharitaceae) (Kuo and Kirkman, 1992; Ackerman, 2006; Orth et al., 2006).
Subgroup e. Passive geocarpy. Flowers and fruits at ground-level, but fruits become covered via natural soil (sand) disturbance, e.g. the sea strand plant *Arctotheca populifolia* (Asteraceae) (Barker, 2005)
DIVISION II. Heteromorphic [**somatic polymorphism** *sensu* Harper et al. (1970) and Harper (1977), which Harper (1977, p. 69) defines as ' … the production of seeds of different morphologies or behavior on different parts of the same plant – not a genetic segregation but a somatic differentiation.']. Two or more distinct kinds of fruits and/or seeds (produced by an individual plant) that differ in size/mass and/or morphology; fruits sometimes with accessory parts such as phyllary, bracteoles or perianth; different morphs usually show definite differences in dispersal and/or dormancy. The proportion of diaspore morphs produced can vary between years, habitats, populations and individuals within a population, and the variation may have a genetic, progeny- environmental and/or a maternal (and even a great grandmother or grandmother) environmental component (transgenerational plasticity) (Baker and O'Dowd, 1982; Cheplick and Quinn, 1983; Venable et al., 1987; Venable and Búrquez. 1989; 1995; Mandák and Pyšek, 1999; Imbert and Ronce, 2001; Wang and Wei, 2007; Lu et al., 2012, 2021; Talavera et al., 2012; Baskin and Baskin, 2014; Martorell and Martínez-López, 2014; Yang et al., 2015a,b; Zhang et al., 2017; Gan et al., 2020; Wang et al., 2021). For *Heterotheca subaxillaris*, an invasive species (from the USA) on the eastern shore of the Mediterranean Sea in Israel, Robinson et al. (2023) found that not only was the proportion of dispersing (disc) cypselae greater in the leading-edge populations than in the core populations but the investment in pappus of the dispersing cypselae was greater in the leading-edge populations. Some genetic aspects of diaspore heteromorphism are discussed by Baskin and Baskin (2014, see Table 8.14 and text page 351).
Group A. Heterodiaspory. Two or more types of diaspores (or of fruits within diaspores) produced aboveground (in some species including a few at or near ground-level, i.e. basal).
Subgroup a. Heterocarpy. Two, three or more kinds of fruits/seeds.
Type 1. Between-diaspore (inter-diaspore) variation. e.g. *Atriplex* spp. (Amaranthaceae) (Flores-Olvera et al., 2011), *Garhadiolus papposus* (Asteraceae) (Sun et al., 2009) and other Asteraceae species (Imbert, 2002), some of which have morphologically distinct diaspores connected by a series of morphologically intermediate ones [e.g. *Heterosperma pinnatum* (Asteraceae) (Venable et al., 1987)] and the *Rumex bucephalophorus* species complex (five subspecies) (Polygonaceae) [for plants of this species complex that produce aerial diaspores only(Talavera et al., 2010, 2011, 2012)]. See additional information about the *R. bucephalophorus* species complex under Amphicarpy *sensu lato.* Note that in addition to within-diaspore variation (see below), at least some species of *Aegilops* (Poaceae) exhibit between diaspore (inter-diaspore) variation within a spike, e.g. *A. cylindrica* (Donald and Ogg, 1991; Fandrich and Mallory-Smith, 2006) and *A. tauschii* (Wang et al., 2023). Thus, some *Aegilops* species fit into both between-diaspore and within-diaspore heteromorphism.
Type 2. Within-diaspore (intra-diaspore) variation (**synaptospermy**, i.e. two or more seeds or fruits joined together forming a compound diaspore, *sensu* Ellner and Shmida, 1981), e.g. *Aegilops* spp. (diaspore is spikelet or whole spike, depending on the species) (Waisel and Adler, 1959; Wurzburger and Leshem, 1967; Datta et al., 1970; Wurzburger et al., 1974; Wurzburger and Koller, 1976; Marañon, 1989; Donald and Ogg, 1991; Dyer 2004; Fandrich and Mallory-Smith, 2006; Guzzon et al., 2018; Gianella et al., 2020, 2022; Wang et al., 2022, 2023); *Eremopyrum distans* (Poaceae, diaspore is a spikelet) (Wang et al., 2010); wild emmer wheat (*Triticum dicoccoides*) (Poaceae, diaspore is a spikelet) (Horovitz et al., 2013; Nave et al., 2016; Volis, 2016); and *Xanthium* spp. (Asteraceae, diaspore is an indehiscent bur with hooked prickles that develops from the involucre and contains two cypselae) (Arthur, 1895, 1906; Crocker, 1906; Wareing and Foda, 1957; Esashi and Leopold, 1968; Martin and Carnahan, 1983; Hockling and Liddle, 1986). If the seeds in the compound diaspore differ in dormancy-breaking/germination requirements, it is referred to as **heteroblasty** (Zohary and Imber, 1963). Thus, all the species mentioned in this section are heteroblastic.

Subgroup b. Heteroarthrocarpy (**heteromericarpy** *sensu* van der Pijl, 1982). One type of fruit with distinct proximal and distal segments, each typically bearing a single seed that is a distinct morph, e.g. *Cakile* spp. (Barbour, 1970; Rodman, 1974; Keddy, 1980; Payne and Maun, 1981; 1982; Hocking, 1982; Maun and Payne, 1989; Maun et al., 1990; Zhang, 1994; Donohue, 1997) and other species of Brassicaceae, tribe Brassiceae (Hall et al., 2011).

Subgroup c. Heterospermy. One or more types of fruits (F), without proximal/distal segments, containing seeds (S) that differ within and/or between fruits. Examples include (1) two types of fruits, each with a different type of seed (2S : 2F), e.g. annual species of *Aethionema* (Brassicaceae) (Zohary and Fahn, 1950; Arshad et al., 2019), *Diptychocarpus strictus* (Brassicaceae) (Lu et al., 2010) and *Suaeda aralocaspica* (Amaranthaceae) (Wang et al., 2008); (2) two types of fruits with three types of seeds (3S : 2F), e.g. *Ceratocapnos heterocarpa* (Fumariaceae) (Ruiz de Clavijo, 1994); and (3) one type of fruit with two types of seeds in same fruit (2S : 1F), e.g., *Capsella bursa-pastoris* (Brassicaceae) (Toorop et al., 2012; Gomez-Cabellos et al., 2022) and *Plantago coronopus* (Plantaginaceae) (Dowling, 1933; Schat, 1981).

Group B. Amphi-basicarpy. Flowers and fruits produced at or near ground-level and on aerial parts of stem. Aerial and ground-level diaspores may differ in morphology and/or size.

Subgroup a. *sensu stricto*. Diaspores on aerial part of stem do not exhibit a continuous change in morphology or size, e.g. *Trionptiles solitaria* and some other Cyperaceae (Haines, 1971; Haines & Lye, 1977; Browning, 1992; Bruhl, 1994; Smith et al., 2006); and *Nassella clarazii* (Poaceae) (Lerner et al., 2008).

Subgroup b. *sensu lato*. Diaspores on aerial part of stem (canopy) exhibit a continuous change in morphology and size, e.g. *Ceratocarpus arenarius* (Amaranthaceae) (Lu et al., 2013). Cleistogamous grasses such as *Triplasis purpurea* (see Discussion), *Amphibromus scabrivalvis* (Cheplick and Clay, 1989) and *Achnatherum brachychaetum* (Lerner et al., 2008) might fit here.

Group C. Amphicarpy. One type of fruit or more than one type of fruit produced both above- and belowground (Note exception in the *Rumex bucephalophorus* species complex, Amphicarpy Subgroup b. *senso lato*.) that differ in ecological function, e.g., dispersal and dormancy (Baskin and Baskin, 2014; Zhang et al., 2020).

Subgroup a. *sensu stricto* (**amphi-geocarpy** *sensu* Barker, 2005). Flowers aerial (CH or CH/CL) and subterranean (CL only); fruits aerial and subterranean. Examples include *Amphicarpaea bracteata* (Fabaceae), *Amphicarpum amphicarpon* (Poaceae), *Cardamine chenopodifolia* (Brassicaceae), *Commelina benghalensis* (Commelinaceae) and *Vigna minima* (Fabaceae) (Zhang et al., 2020). In *Amphicarpum* and three other genera of grasses, the subterranean spikelets with large caryopses are produced on specialized rhizomes called rhizanthogenes (Dobrenz and Beetle, 1966; Campbell et al., 1983).

Subgroup b. *sensu lato*. Flowers aerial (CH) and at or near ground-level (CH); fruits aerial and subterranean [or aerial and (basal → subterranean) in the *Rumex bucephalophorus* species complex (see below)], e.g., *Catananche lutea* (Asteraceae) (Ruiz de Clavijo, 1995; Ruiz de Clavijo and Jiménez, 1998), *Emex spinosa* (Polygonaceae) (Ortiz et al., 2009, *Gymnarrhena micrantha* (Asteraceae) (Koller and Roth, 1964) [Various authors have reported erroneously that subterranean fruits of *C. lutea*, *E. spinosa* and *G. micrantha* are produced by CL flowers, when, in fact, they are produced by CH flowers that are insect pollinated (see Baskin and Baskin, 2017).] and plants of the *R. bucephalophorus* species complex that produce both buried and aerial types of diaspores. Plants in some populations of the *R. bucephalophorus* species complex that form a basal rosette may produce female flowers and mature diaspores in the leaf axils that are buried by the action of contractile roots (buried diaspores) as well as aerial hermaphrodite flowers and diaspores. Plants that do not form a rosette produce only aerial flowers and diaspores. Altogether, one buried and three aerial diaspore types are produced by this species complex (Talavera et al., 2010, 2011, 2012). *C. lutea* and *G. micrantha* are examples of Asteraceae species with two types of capitula, i.e. aerial and basal (partly underground) (Burtt, 1977).

above which there is little or no change in mass of caryopses, including those in the terminal CH spikelets. Chase (1908, 1918) used the term 'cleistogene' to describe the solitary sessile single floret with palea and lemma but without glumes in the lower leaf sheaths of *T. purpurea*. Chase (1918) applied the term 'chasmogene' to the terminal ('ordinary') spikelet. Her illustrations clearly show that the caryopsis from the cleistogene is much larger than that from the chasmogene. We have (cautiously) suggested that *T. pupurea* might fit subgroup B of amphi-basicarpy (Table 1).

Monomorphic aerial CH/CL plants/populations may produce only CH or only CL flowers (Wilken, 1982; Sun, 1999; Hayamizu et al., 2014). *Corallorhiza bentleyi* (Orchidaceae), is an example of a species in which some populations produce only CL and others both CH and CL (see Freudenstein, 1999; Culley and Klooster, 2007). Small or young individuals of some CL species or individuals growing under unfavorable conditions produce only CL (Coker, 1962; Minter and Lord, 1983; Oakley et al., 2007; Hayamizu et al., 2014). *Epifagus virginiana* (Orobanchaceae) is an annual CL holoparasite with 'dust seeds' and an undifferentiated embryo that is host-specific on the roots of American beech (*Fagus grandifolia*). However, most, and sometimes all, of the flowers are CL, and the CH flowers usually are sterile. Thus, most seeds are produced by CL flowers (Schrenk, 1894; Cooke and Schively, 1904; Thieret, 1969, 1971; Musselman, 1982).

Lloyd and Schoen (1992) state that CH and CL seeds in most CL species differ in size, dispersal and germination. However, seeds from CH and CL flowers of our Group B of Supergroup 1 (monomorphic aerial) may or may not differ in these respects

(Baskin and Baskin, 2014, 2017). When there is a difference in mass of CH and CL seeds, the mass of CH seeds usually is greater than that of CL seeds (e.g. Cope, 1966; Hiratsuka and Inoue, 1988; Cheplick, 2005; Eckstein et al., 2006; Albert et al., 2011; Huebner, 2011; Munguía-Rosas et al., 2012). Differences in germination of CH and CL diaspores are more likely to occur in amphicarpic *sensu stricto* species than in aerial CL species. In 58 of 65 case studies (89.2%) for amphicarpic *sensu stricto* species, seeds from CH and Cl flowers differed in germination percentage, whereas in aerial CL species 83 of 132 case studies (62.9%) of seeds from CH and Cl flowers differed in germination percentage (Baskin and Baskin, 2017). Further study may show that a new category needs to be split out of Group B (Supergroup I, Division I) and incorporated into Division II. The new category would include species in which fruits/seeds produced by CH and CL flowers are morphologically distinct and (presumably) differ in ecology.

In *Ceratocarpus arenarius*, the basicarps differ in morphology and mass (and in embryo mass) from the aerial dispersal/germination units, which show continuous variation (increase or decrease) in morphology (see Supplementary Table S1 in Lu et al., 2013). Thus, there is discontinuous variation in this species between the basicarps (a) and aerial dispersal units (b)–(f) (Lu et al., 2013). Gao and Wei (2007) and Gao et al., (2008) recognized only two morphological types of fruits on plants of this species, namely subterranean (the two basicarps, which are, in fact, basal and not subterranean) and aerial.

In *Pisum fulvum* (Fabaceae), there is a gradient from amphicarpic plants (*sensu stricto*) with both aerial and subterranean

flowers and fruits to plants that produce only aerial flowers and fruits (Mattatia, 1977). One of the stages in the gradient is a basicarpic form that produces CH flowers near the soil surface, which Mattatia (1977) called 'subamphicarpic.' Thus, this species consists of both monomorphic (e.g. basicarpic form) and heteromorphic (e.g. amphicarpic form) plants.

Some species may exhibit plasticity as to the diaspore classification category to which they belong. For example, species that are amphicarpic and produce both aerial and subterranean diaspores under favorable environmental conditions may produce only underground fruits under stressful conditions and thus be 'facultatively geocarpic', e.g. *Amphicarpaea edgeworthii* (Fabaceae) (Zhang et al., 2017), *Amphicarpum amphicarpon* (Poaceae) Cheplick and Quinn, 1983) and *Gymnarrhena micrantha* (Asteraceae) (Koller and Roth, 1964; Zeide, 1978; Loria and Noy-Meir, 1979/80). In which cases, individuals of these two annual species have the capacity to be either diaspore-heteromorphic (amphicarpic) or monomorphic (geocarpic).

Unlike these amphicarpic species, the cold desert annual diaspore-polymorphic amphi-basicarpic species *Ceratocarpus arenarius* produces both basal (typically two) and aerial diaspores in the most stressful conditions in which it grows in its cold desert habitat. In the cold deserts of northwest China, we have observed that the smallest (5 cm tall, no branches) and largest (35 cm tall, bushy) plants of this species produce both basal and aerial diaspores, albeit in different basal morph:aerial morph and within-aerial morph ratios. Detailed experimental garden studies on the effect of abiotic (e.g. soil physicochemistry) and biotic (i.e. inter- and intraspecific competition) stress on phenotypic plasticity of the growth and reproduction of *C. arenarius*, including variation in diaspore morph ratios, have been published by Gan et al. (2020) and Lu et al. (2021).

Concluding remarks

We have documented via a hierarchical-based classification system the considerable diversity in structural design ('architecture') of diaspore monomorphism and heteromorphism in angiosperms. The scheme will enable investigators working on the broad topic of 'seed heteromorphism' to more precisely communicate their research to others, in part at least by giving more exactness to the term. It also will aid plant biologists in the preparation of a profile (spectrum) of the kinds (hierarchical categories) of diaspore monomorphism and heteromorphism for the various ecological and biogeographical units on earth. Finally, a detailed classification scheme that includes both diaspore monomorphism and hetermorphism is required for addressing the phylogenetic/evolutionary aspects of 'seed heteromorphism' in angiosperms (e.g. see Fernández et al., 2001; Cruz-Mazo et al., 2009, 2010). All that being said, however, it is likely that more hierarchical categories will need to be added to our system and/or existing ones revised/refined as literature and field research continues on diaspore monomorphism and heteromorphism in angiosperms.

Conflict of interest. The authors declare that they have no competing interests.

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Appendix A Genetic diaspore polymorphism in angiosperms

Genetic diaspore polymorphism is best known in the family Valerianaceae, including *Plectritis* (Ganders et al., 1977a,b; Carey and Ganders, 1980) and *Valerianella* (Eggers Ware, 1983). In *Plectritis congesta*, experimental crosses showed that the kind of fruit morph is monogenically inherited with the allele for winged fruits dominant over wingless fruits (Ganders et al., 1977a). In *Plectritis brachystemon*, homozygous winged plants (i.e. selfed plants produced only winged fruits) x homozygous wingless fruits (i.e. selfed plants produced only wingless fruits) → F$_1$ hybrids, all of which produced winged fruits. The F$_2$ (F$_1$ selfed) consisted of 27 plants that produced winged fruits and nine that

produced wingless fruits (a 3:1 ratio). Thus, fruit dimorphism in *P. brachystemon* is controlled by a single locus with the allele for winged fruit dominant (Ganders et al., 1977b). In *Valerianella ozarkana*, crosses between forma *ozarkana* (winged) and forma *bushii* (fusiform) indicated that there was a simple monogenic relationship in which the *ozarkana* (winged) allele is dominant over the *bushii* (fusiform) allele (Eggers-Ware, 1983). It should be pointed out that not all species that produce two or more kinds of diaspores fit either somatic polymorphism or genetic polymorphism, i.e. they neither fit one nor the other. *Fedia cornucopiae* and *F. grandflora* (Valerianaceae) have been shown to exhibit both somatic and genetic polymorphism (Mathez and Xena de Enrich, 1985a, 1985b).,

Genetic diaspore heteromorphism (only one morph per plant) has been reported in the two grass species *Aegilops speltoides* (e.g. Zohary and Imber, 1963; Belyayev and Raskina, 2013; Ruban and Badaeva, 2018) and *Achnatherum hymenoides* (Jones and Nielson, 1999; Jones et al., 2007). In one of the two morphotypes of *A. speltoides* (i.e. form *aucheri*), the spike is the dispersal unit, and in the other morphotype (form *ligustica*) the spikelet is the dispersal unit. In *A. hymenoides*, seed size, i.e. jumbo > globose > elongate) is under genetic control, and degree of seed dormancy decreases from jumbo to globose to elongate.

A kind of genetic polymorphism for capitulum type occurs in British populations of *Senecio vulgaris* (Asteraceae). Plants of this species have radiate and non-radiate capitulum morphs, which are under genetic control. The radiate morph originated via introgressive hybridization between the native non-radiate allotetraploid *S. vulgaris* and the introduced diploid radiate *S. squalidus*. Two tightly-linked genes of *S. squalidus* were introgressed into *S. vulgaris*. A short-rayed form (a heterozygote) is produced from crosses between radiate and non-radiate forms of *S. vulgaris*. Fresh cypselae from radiate and non-radiate morphs differ in germination phenology. There also were differences in germination percentages after cypselae from radiate and non-radiate morphs were stored in the laboratory from October to June, during which time after-ripening may have occurred (e.g. Trow, 1912; Richards, 1975; Ingram et al., 1980; Abbott, 1986, 1992; Abbott et al., 1988, 1992, 1998; Abbott and Horrill, 1991; Chapman and Abbott, 2010).

Spergula and *Spergularia* are two genera in the Caryophyllaceae containing species that produce heteromorphic seeds with a genetic component. *Spergula arvensis* produces papilate (P) and smooth, i.e. non-papilate (NP), seeds and a hybrid (P × NP) intermediate between the two morphs; the hybrid is produced in a low frequency. Inheritance of seed coat character is controlled by one gene, one locus and two alleles. The intermediate morph is heterozygous with incomplete dominance (New, 1958, 1959, 1961, 1978; New and Herriott, 1981; Wagner, 1986, 1988; Kucewicz and Gojło, 2013).

Several species of *Spergularia* (e.g. *S. marina* and *S. media*) produce winged and non-winged seeds and a heterzygous intermediate with a narrow wing produced in a low frequency (Salisbury, 1958; Sterk, 1969a,b,c,d; Sterk and Dijkhuizen, 1972; Telenius and Torstensson, 1989, 1991; Telenius, 1992; Ceynowa-Giełdon, 1993; Redbo-Torstensson, 1994; Redbo-Torstensso and Telenius, 1995; 1999; Mazer and Lowrey, 2003; Memon et al., 2010). Seeds of *Spergularia diandra* collected near Sede Boker in the Negev Desert of Israel consisted of three genotypes (hairy, partly-hairy and smooth). Each genotype had three seed-color phenotypes (black, brown and yellow), and there were differences in germination of the phenotypes. Thus, there were nine seed morphs, i.e. 3 phenotypes × 3 genotypes = 9 types of seed morphs (Gutterman, 1994a, 1996, 1997a, b, 1998, 2000).