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The Heterodiaspory of *Capsella bursa-pastoris* (*Brassicaceae*)

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With 2 Figures

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Summary

TEPPNER H. 2003. The heterodiaspory of *Capsella bursa-pastoris* (*Brassicaceae*). – Phyton (Horn, Austria) 43 (2): 381–391, 2 figures. – English with German summary.

In *Capsella bursa-pastoris* (L.) MEDIK. two kinds of diaspores are formed: 1) the valves of the silicle containing an apical seed (i.e. the uppermost seed of each locule), which are therefore one-seeded mericarps and 2) the true (naked) seeds. Finally, of the fallen valves c. 70 % contained the apical seed; these can be easily dispersed by water and wind. Terms for heteromorphic diaspores are briefly discussed. As regards to terminology, it is proposed to restrict the term heterodiaspory, in the sense of the definition of MÜLLER-SCHNEIDER & LHOTSKÁ 1972: 408, for such cases with diaspores of different levels of morphological organisation on one individual. As an encompassing term for heterocarpy, heteromericarpy, heterospermy, heterodiaspory etc. the older term polydiaspory (MÜLLER 1955:16) can be used.

Zusammenfassung

TEPPNER H. 2003. Die Heterodiasporie von *Capsella bursa-pastoris* (*Brassicaceae*). – Phyton (Horn, Austria) 43 (2): 381–391, 2 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Capsella bursa-pastoris (L.) MEDIK. bildet zwei Typen von Diasporen: 1) die Valven, die einen apikalen Samen (das ist der oberste Same jedes Faches) enthalten und damit einsamige Merikarpien darstellen, sowie 2) die (nackten) Samen. Schließlich enthalten ca. 70 % der abgefallen Valven den apikalen Samen und kön-

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nen leicht durch Wasser und Wind ausgebreitet werden. Fachausdrücke für heteromorphe Diasporen sind kurz diskutiert. Im Hinblick auf die Terminologie wird vorgeschlagen, den Terminus Heterodiasporie, im Sinne der Definition von MÜLLER-SCHNEIDER & LHOTSKÁ 1972: 408, auf solche Fälle einzuschränken, in denen von einer Pflanze Diasporen auf verschiedenen, morphologischen Organisationsniveaus gebildet werden. Als Oberbegriff für Heterokarpie, Heteromerikarpie, Heterospermie, Heterodiasporie etc. bietet sich der ältere Ausdruck Polydiasporie (MÜLLER 1955: 16) an.

1. Introduction

1.1. Teaching and Research

The findings presented in this paper are a part of the observations gathered in course of my teaching years. During which I had the opportunity to realise the unity of teaching and research; studies for the lectures fertilized research and efforts in the field of research fruited in up to date courses and lectures. Another interesting aspect of holding practicals for first-year students was and is their great numbers (at times over 80), thus resulting in observation of more common plant material, than would have been normally possible. One such product is the detection of a female clone of *Ajuga reptans* L., now selected and grown separately (GZU 235888). In the extensive *Capsella bursa-pastoris* material collected, gynoecia with three, four and five carpels were found and forwarded to working groups concerned with the bauplan of the siliqua.

1.2. Basic Teaching and *Capsella* Fruits

Capsella bursa-pastoris is an ideal object to study the construction of the siliqua in basic practicals. The material (fully developed, though unripe fruits from plants growing naturally in the Botanic Garden) is nearly always available and the 'heart' has two 'handles'. By holding the tip of a valve, beginning from the peduncle, it is very easy to take it off; both valves detached, it leaves behind the replum with the adhering ovules (unripe seeds). In the course of discussions with the students I observed many repla with the help of a lens and it was becoming apparent to me, that the uppermost funiculi never bore ovules.

Before the discussion of *Capsella*, it is necessary to briefly check the terms in question and their proper definitions.

2. Heteromorphic Dispersal Units in Angiosperms

Within the enormous diversity of Angiosperms cases of heteromorphic dispersal units are well known since long times and the termini heterocarpy, heteromericarpy and heterospermy are of general use.

2.1. Heterocarpy

When two or more different, aerial fruit types are developed on one plant individual it is called heterocarpy. It is abundant in *Asteraceae* [e.g. *Calendula*, *Dimorphotheca* (*Calenduleae*), *Bidens* p.p. (DAKSHINI & AGGARWAL 1974, CORKIDI & al. 1991), *Synedrella* (*Heliantheae*), *Geropogon* (*Lactuceae*), many *Anthemideae*]. Furthermore *Ceratocapnos heterocarpa* DURIEU (*Fumariaceae*; RUIZ DE CLAVIJO 1994) and *Justicia heterocarpa* T. ANDERSON, *J. dinteri* S. MOORE and *J. leptocarpa* LINDAU (*Acanthaceae*; SELL 1969: 444–445, MEYER 1968: 34) may be mentioned.

The term polycarpy ('Polykarpie') used by ULBRICH 1928: 200–203 more or less in the sense of heterocarpy is a very misleading one because of its similarity with *Polycarpicae* and polycarpic.

Dimorphic fruits are also usual in amphicarpous plants [see 2.7.; e.g. *Amphicarpaea bracteata* (L.) FERNALD, *Fabaceae – Phaseoleae*] and can often be found within one dispersal unit in synaptospermous plants [e.g. *Xanthium strumarium* L. (*Asteraceae – Heliantheae*) and *Triticum baeoticum* BOISS. and *T. dicoccoides* (ASCH. & GRAEBN.) AARONS. (*Poaceae – Triticeae*)].

2.2. Heteromericarpy (incl. heteroarthrocarpy, VOYTENKO 1968)

This term is used, when the partial fruits originating from one coenocarpous (or apocarpous: only *Leguminosae*) gynoeceum are morphologically different. Under the most often discussed examples are *Torilis nodosa* (L.) GAERTNER (*Apiaceae*) and *Brassiceae*, e.g. *Cakile* and *Rapistrum*. Further examples e.g. *Cerinthe minor* L. (*Boraginaceae*, LHOTSKA 1974) and *Microparacaryum* (2 species, *Boraginaceae*, HILGER & al. 1985: 292–293). Compare e.g. HUTH 1895 and PAVOLINI 1910 (and VOYTENKO 1968 for *Brassicaceae*).

2.3. Heterocarpidy

In this case in fruits originating from a coenocarpous gynoecium the carpels are morphologically different (STOPP 1962: 69, 'Heterokarpidie') and do not separate (contrary to heteromericarpy). One of the carpels remains indehiscent, whereas the other(s) open (e. g. *Rogeria*, *Pedaliaceae*, STOPP 1962: 67–69; *Commelina* sect. *Heterocarpus* and *Heteropyxis*, *Commelinaceae*, BRÜCKNER 1930: 164, 177–179, GOEBEL 1928: 557) or in the case of opened carpels, in one carpel a part of the seeds is arrested (seed pockets; *Sesamum pedalioides* HIERN, STOPP 1962: 71).

In *Antirrhinum majus* L. (*Scrophulariaceae* or *Plantaginaceae*) the effect of heterocarpidy on dispersal is little expressed; some seeds are arrested between the placenta-margin and the septum in both locules, only seed scattering is slightly delayed in the adaxial locule because of the smaller area of the opening(s).

2.4. Heterospermy

This is the case, when only the seeds are different in an individual. A well known example is *Spergularia* [*S. salina* J. & C. PRESL and *S.media* (L.) C. PRESL] (*Caryophyllaceae*), with winged and unwinged seeds in the same capsule (e.g. SALISBURY 1958, TELENIUS 1992). Heteromorphous seeds can also often be a consequence in the other syndromes mentioned here.

2.5. Heteroanthocarpy

This term is used, when at least the persistent floral parts enveloping the fruit are different within one individual. E.g. *Acleisanthes obtusa* (CHOISY) STANDL. (HEIMERL 1932: 458) and *Abronia* p.p. (WILSON 1974), (*Nyctaginaceae*). Term used by KRAVTSOVA 1999 in an abstract for *Urticaceae – Boehmerieae* p.p. It refers to certain species of *Pouzolzia* (incl. *Memoralis*) in which broad-winged and only ribbed perigon occurs in the same infructescence or as polymorphism (see 2.8.) in different individuals (for details see KRAVTSOVA & al. 2003, but the term heteroanthocarpy is not used here).

2.6. Heterodiaspory

At least, by MÜLLER-SCHNEIDER & LHOTSKÁ 1972: 408, the term heterodiaspory was proposed for the cases in which a plant produces diaspores of different levels of morphological organisation: 'Wenn eine Pflanze morphologisch verschieden zusammengesetzte Diasporen ausbildet, so bezeichnen wir diese Erscheinung analog zu den Begriffen Heterokarpie und Heterospermie als Heterodiasporie. Wo es sich um echte Früchte (Samen) handelt, ist jedoch der Ausdruck Heterokarpie (Heterospermie) weiterhin am Platze.' [If a plant produces diaspores, which are morphologically different, then we denominate this phenomenon, in analogy to the terms heterocarpy and heterospermy, as heterodiaspory. But in the case of true fruits (seeds) the term heterocarpy (heterospermy) is still adequate]. E.g. *Atriplex* (*Chenopodiaceae*) with fruits plus bracteoles and nuts alone (falling out from the perigon) as dispersal units (see e.g. MANDÁK & PYŠEK 2001 for *A. sagittata* BORKH. or BECKER 1913: 122–130 for *A. hortensis* L.). Abundant in *Asteraceae*, e.g. *Sanvitalia procumbens* LAM. (*Heliantheae*; fruits from ligulate flowers with persistent corolla and three pappus-thorns), *Zinnia* (*Heliantheae*; with persistent ligules), *Filago gallica* L. (*Gnaphalieae*; outer achenes included in bracts), *Crepis foetida* L., *Crepis* sect. *Zacintha*, *Rhagadiolus stellatus* (L.) GAERTN., *Hedypnois cretica* (L.) DUM.-COURSET (*Lactuceae*; outer achenes clasped by bracts; GRIMBACH 1913) and taxa bearing achenes with and without pappus in the same head. *Aethionema* spp. (*Brassicaceae*) with dehiscent silicles and single-seeded, winged nuts (ANDERSSON & al. 1983: 4, MÜLLER-SCHNEIDER 1986: 97). In *Sinapis arvensis* L. the stylar segment usually contains one

seed and drops as one-seeded mericarp whereas the opening valvular segment sets the seeds free. *Platystemon californicus* BENTH. (*Papaveraceae*) with single seeded fragments of the carpels (mericarps) and true seeds (HANNAN 1980, BRÜCKNER 1982: 156).

But earlier, before them, VAN DER PIJL 1969: 82 (and 1982: 98–100) uses the term 'heterodiaspory' for all cases of different kinds of diaspores in a plant species, even only physiological differences included. Meanwhile, MÜLLER-SCHNEIDER 1986: 22, seems to have changed his mind and now uses the term in the same manner as VAN DER PIJL, i.e. as an encompassing term for the above and related cases. The same is true for MANDÁK 1997: 132. With this broader use of the term heterodiaspory a precise information is missing and no own special term is available for diaspores of different morphological organisation levels from one plant. Polychory is often more or less merged or synonymised with heterodiaspory; but originally it meant plants with one type of diaspores whose are dispersed in two (partly separated as diplochory) or more different ways (isokarpe Polychorie ULBRICH 1928: 200–201; BONN & POSCHLOD 1998: 25).

Thus, at least as far as I see, the only possible solution is the proposal to use the term heterodiaspory restricted to the definition of MÜLLER-SCHNEIDER & LHOTSKÁ 1972: 408, i.e., for the cases with aerial diaspores of different levels of morphological organisation [e.g. fruits or mericarps and seeds or fruits enveloped by bracts (or perigon, calyx etc.) and true fruits] in individuals of a given plant species.

2.7. Amphicarpy

And lastly, the term amphicarpy is used, when aerial and hypogeous fruits are present on the same individual.

2.8. Fruit and seed polymorphism (diaspore polymorphism)

Different fruits or seeds on different individuals or in different lines of a species, caused by allelic differences, as in other polymorphisms. E.g. *Spergula arvensis* L., *Caryophyllaceae*, papillate and nonpapillate seeds. *Plectritis*, *Valerianaceae*, broad-winged and narrow-wingend to wingless fruits (DEMPSTER 1958, GANDERS & al. 1977), *Valerianella* p.p., *Valerianaceae*, fruits with and without wings (EGGERS WARE 1983) and also *Fedia*, *Valerianaceae* (MATHEZ & XENA DE ENRECH 1985, XENA DE ENRECH & MATHEZ 1998). *Microparacaryum*, *Boraginaceae*, nutlets with and without marginal wing (HILGER & al. 1985: 300–301). The alleged fruit polymorphism in *Macleaya cordata* (WILLD.) R.Br. (DELPINO 1894, reason for the term anisocarpy of HUTH 1895: 4) is not confirmed in the recent literature; quite possible, that DELPINO observed a mixture of *M. cordata* and *M. microcarpa* (MAXIM.) FEDDE. For fruit polymorphism PAGLIA 1910 and PAVOLINI 1910 used the term pseudo-heterocarpy ('pseudo-eterocarpia').

2.9. General Remarks

The older term polydiaspory (MÜLLER 1955: 16) can be promoted as an encompassing term for heterocarpy, heteromericarpy, heterospermy, heterodiaspory and related cases. Polydiaspory seems to have priority over heterodiaspory in the broader sense.

IMBERT 2002: 33–36 has given a very useful list (218 species from 99 genera and 18 families) with references, but he has evaded all terminological problems in classifying all cases mentioned above under 'seed heteromorphism' (as did VENABLE 1985). For a more complete list e.g. DELPINO 1894, HUTH 1895, PAGLIA 1910 and PAVOLINI 1910 are to be critically considered.

For the classification of a case of heteromorphism the highest level of organisation of a diaspore is decisive. The highest levels in *Atriplex* p.p. are nuts plus bracts and true nuts; therefore heteromorphism type is heterodiaspory, and not heterospermy, in spite of differing seeds.

3. Results and Discussion

In the fruits of *Capsella bursa-pastoris* (L.) MEDIK. [*Lepidieae* in the classic systems, probably *Arabideae* according to molecular characteristics (KOCH & al. 1999) ?] the uppermost ovule or seed (named apical seed in the following), in each valve lies immediately near and parallel to the margin at the notch of the 'heart'. A little distance away from this margin, parallel to the margin as well, an impressed groove is differentiated abaxially as well as adaxially (Fig. 1, left). In the otherwise excellent figure 34 (longitudinal section of the fruit) in Jones 1950: 91 this situation is not to be seen conclusively and the frontispiece is erroneous in this respect. The figure in STRASBURGER 2002: 841 is also wrong in these details. A good picture of a longitudinal section showing the placement of the ovules is to be seen in Anonymous 2003.

If in unripe fruits the valves are removed, as described in 1.2., the two uppermost, more or less erect funiculi lack the seeds (Fig. 1, right): these remain trapped in the valves caused by the narrowing by the grooves protruding inwards.

The same situation is true for the ripe fruits (Fig. 2). Thus one fruit produces two kinds of diaspores:

1) two valves, each containing one apical seed (i.e. functionally two one-seeded mericarps). The diaspore is much enlarged by the wing-like structure (valve) and the enclosure makes myxospermy ineffective in relation to a vector or the soil.

2) a variable number of true seeds (10–40 according to HURKA & HAASE 1982: 36; 7–39 seeds, AKSOY & al. 1998: 180; 14–30 were abundant numbers in our material).

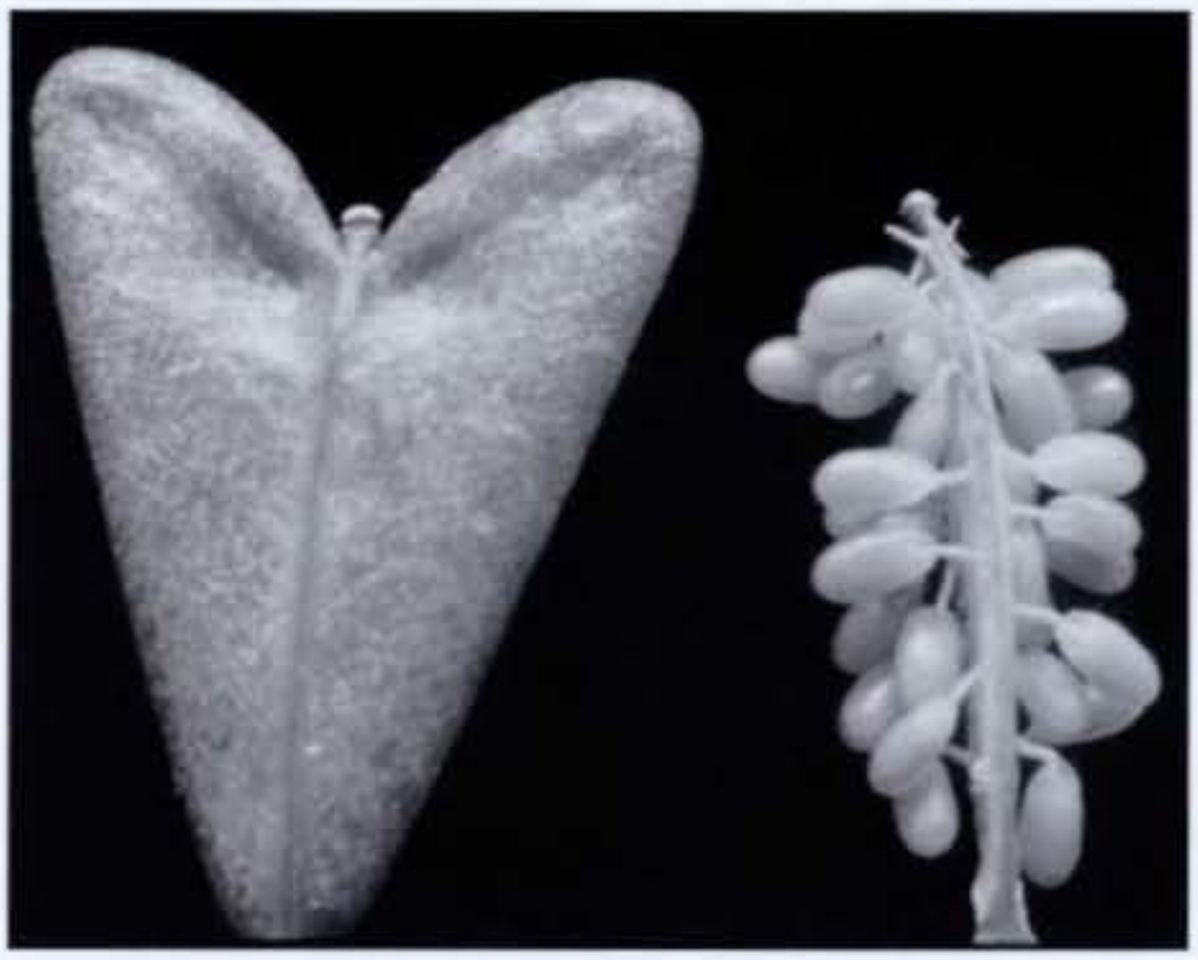

Fig. 1. *Capsella bursa-pastoris*. Fully developed though unripe fruits. – Left: whole fruit with the grooves parallel to the apical notch. – Right: valves detached, the two uppermost, erect funiculi without their seeds. – Length of the seeds 1.1–1.2 mm. – Bot. Garden Inst. Bot. Univ. Graz, May 31, 1990.

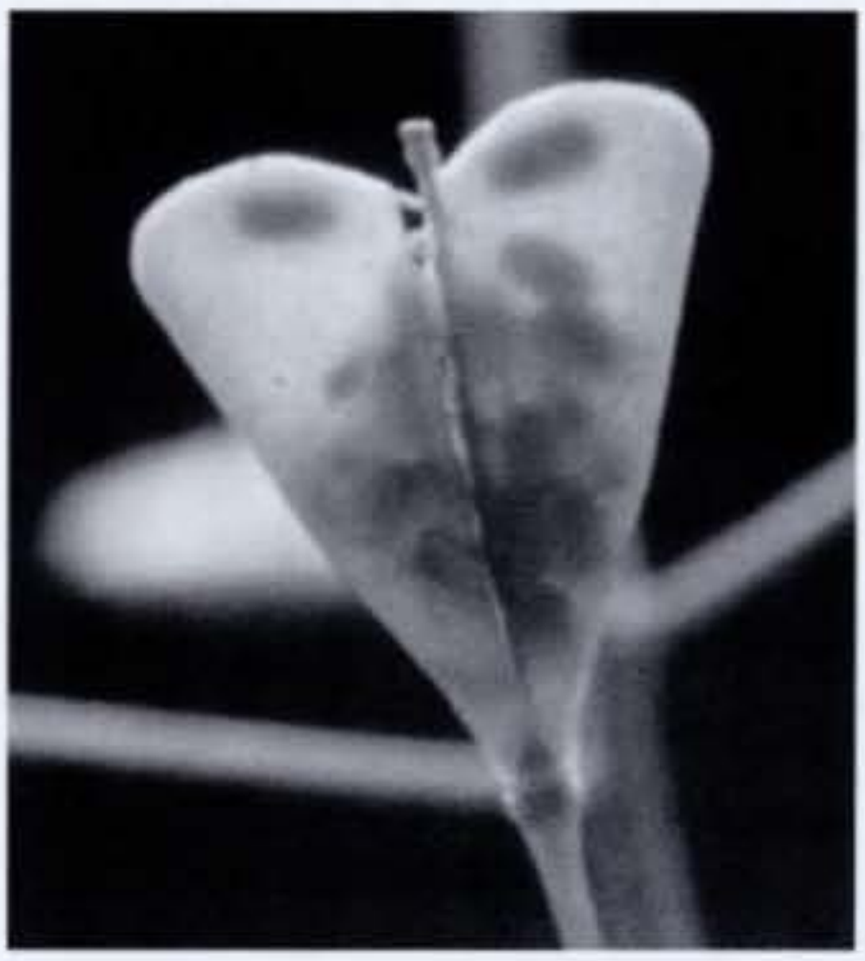

Fig. 2. *Capsella bursa-pastoris*. Full ripe fruit in transmission light, one valve a little loosened. The apical seed in the tip of each valve, the left one already broken away from its funiculus. – Length of the valves 5.6 mm. – Bot. Garden Inst. Bot. Univ. Graz, July 7, 1990.

Thus, *C. bursa-pastoris* is heterodiasporous in the sense of the restricted definition proposed above (2.6.), because it produces mericarps as well as seeds as dispersal units on the same individual. A check of our herbarium material (GZU) has shown, that *C. bursa-pastoris* possesses this character all around the world.

C. bursa-pastoris is often described as ombrohydrochorous, but feeding the seeds by birds, brushing against and trampling must also be effective for removing the valves and seeds. According to HURKA & HAASE 1982:

36 'Under natural conditions, vibration and contact caused by men, animals, wind, rain drops etc. on the one hand, and fluctuating humidity on the other hand apparently favour fruit opening and seed scattering.' See also AKSOY & al. 1998: 180.

The two diaspore types clearly behave in different manners. Under dry conditions the one-seeded mericarps (valves) may be affected by wind, whereas in water they float. Thus the mericarps with the apical seeds are very well adapted for long-distance dispersal. There are many references concerning dispersal of the seeds, e.g. HURKA & HAASE 1982, who also consider myxospermy: The mucilage on the one hand attaches the majority of seeds fallen to the ground near the mother plants on the soil and on the other hand it sticks seeds on a vector for long-distance dispersal.

A simple experiment was carried out to check the effect of moisture on these two different diaspores. Twenty seeds and twenty valves containing the apical seed were placed on the water surface in Petri dishes. After ten minutes the first seed sank, after c. 40 minutes all seeds had sunk, whereas all valves still floated; c. two days after wetting the (stored) naked seeds contained seedlings with ca. 0,5–1,5 mm long roots (c. 26 °C). From the valves after five days only one had sunk, the others still floated and most of the seeds inside were relatively dry (no slime, no germination). If the apical seeds were taken from the valves, the behaviour in imbibition, adherence on a slide by dried mucilage and germination was the same as in the other seeds.

Early total abortion of an ovule as well as degeneration of ovules and seeds at all stages of development is possible. Small predators may feed on some seeds within a silicle. It was also observed that after desiccation of the valves of ripe fruits bendings and shrivelings of the wall sometimes can cause the apical seed to fall out. Thus, it was of interest to know the real percentage of valves with or without apical seeds. For this purpose during a dry weather period in a rich stock of full ripe plants with dry infructescences in the Botanic Garden the valves of the silicles were striped off with caution. Then, valves with and without apical seed were separated. In both the cases it was seen that one or few of the other seeds accidentally remained captured in the valve. Because of foregoing wetting, sometimes one to many seeds may adhere within, or, more rarely, outside on the valves; all these latter cases were not counted separately. From 2 030 valves counted, 70.54 % contained the apical seed. In an earlier counted small sample (221 valves) from another locality in Graz c. 82 % of the valves contained the apical seed.

Thus in all reflections on long-distance dispersal and population structure of *C. bursa-pastoris* the dispersal of mericarps (valves with the apical seed) has to be taken into consideration.

The case of *Capsella* mericarps seems to be unique within the family. As far as other *Brassicaceae* are concerned, the following remarks may be

added. Heterodiaspory in *Aethionema* and *Sinapis* is mentioned under 2.6. In *Biscutella*, *Dithyrea* and *Megacarpaea* all seeds are obligately enclosed in the valves and each gynoecium forms two single-seeded, winged mericarps; *Coronopus didymus* (L.) SM. shows subglobose mericarps. In *Lunaria* the seeds adhere to the loosing valves (detached by storms, brushing against etc.), but can secondarily detach.

During the check of literature for terms and examples for heteromorphisms, it has been very surprising to see, how often botanists have confused fruits and seeds (or even flowers and heads in composites). The interpretation of the literature is thus very difficult if one has no own experience in each entity. More discipline and precision in this respect is highly desirable.

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Addenda

Chapter 2.3. Heterocarpidy, p. 383

In *Cymbalaria* (*Plantaginaceae*, former *Scrophulariaceae*) the adaxial capel is smaller than the abaxial one (SPETA 1986: 28-30, 34). Each carpel contains at least one large and some small seeds (p. 36-43).

Chapter 2.6. Heterodiaspory, p. 384

In *Cymbalaria muralis* (SPETA 1986: 36-38) one seed (rarely two seeds) is affixed to the base of each carpel. The same is true for *Veronica agrestis* and *V. persica* (SPETA 1986: 38-39). In *C. longipes* the large seeds remain included in the capsule (SPETA 1986: 34). Thus capsules with affixed seeds, remaining on the mother plant, and freely dispersed seeds are produced (SPETA 1986: 43) as different dispersal units.

SPETA F. 1986. Heterokarpidie, Dehiszenz, Heterospermie und basifixe Samen bei *Cymbarlaria* HILL (*Scrophulariaceae*) und systematische Schlußfolgerungen. – Phyton (Horn, Austria) 26(1): 23-57.