Chapter 6
Taxonomy, Phylogeny, and the Genepool

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Abstract The presence of conspecific and interfertile wild and cultivated forms impeded the development of a stable taxonomic system of wild beet species (genus *Beta* and *Patellifolia*) in the past. Further difficulties have been caused by the proliferation of synonyms and the confusion this has caused in the nomenclature, which was only slightly reduced after Linnaeus. The frequent errors in classification solely based on plant morphology are being reduced by studying the structures of genetic diversity with molecular genetic markers. Genetic markers as well as results from interspecific crossing experiments have helped revealing the past and ongoing evolutionary processes, as well as phylogenic relationships between taxa. Despite some unresolved taxonomic questions, wild beet plants can be determined and classified with sufficient reliability today which allowed categorizing the wild taxa into the primary, secondary, and tertiary genepool of the crop.

Keywords *Beta maritima* · Taxonomy · Genus · Section · Species · Fingerprinting · Phylogenetics · Crop genepool

6.1 Pre-Linnaean Systems

The first list of types of beet is attributed to Hippocrates and Theophrastus, and it distinguished the cultivated beets (white and black) from the wild (*Limonium*, *Blitum*). The list was confirmed by Pliny (who called the wild type *Beta sylvestris*), by Dioscorides, and by other authors (see Chap. 1). This nomenclature remained almost unchanged for nearly 1500 years, as has the division, introduced by Theophrastus, of the vegetable kingdom into trees, shrubs, bushes, and herbs, within which the cultivated and wild plants are classified.

In his treatise "*De Plantis*", Cesalpino (1583) mentions the following types of beet: (i) *vulgaris* (with short and green leaves); (ii) *cum caudicantibus foliis* (with prostrate leaves); (iii) *rubra* (with red leaves and shallow roots); (iv) *radice buxea* (root resem-

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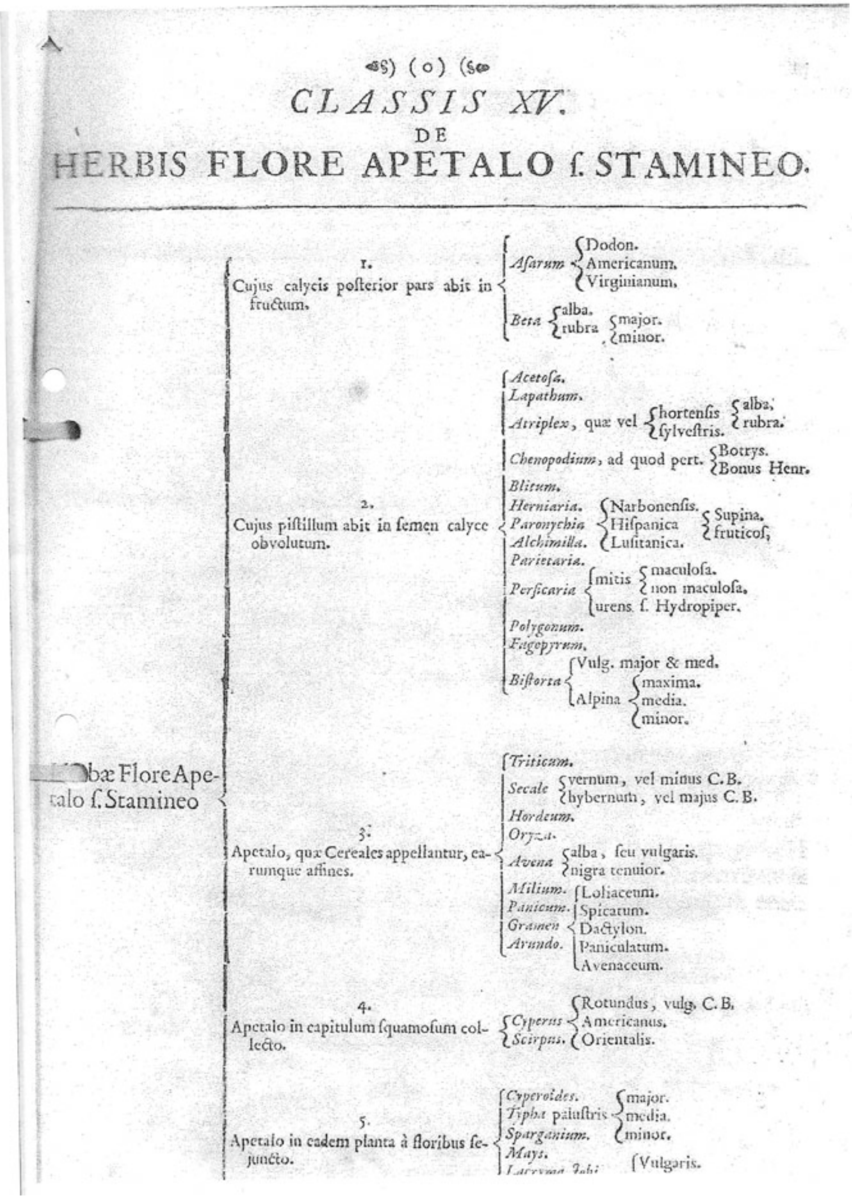
bling *Buxus sempervirens* L.). Cesalpino also cites the *Plantago* (*Plantago officinalis* L.) living in meadows and along roadsides, which is called "*Quinquinervia*" or "*Centinervia*" or "*Beta sylvestris*". The first two terms mean that the leaves bear five or more veins, respectively. The latter name is likely a mistake. In agreement with Gesner (1561), one of the first attempts of taxonomical classification was by Cordus (1551), who cited for *Beta* some unusual German names, such as Beisz-Izol, Romisch-Izol, Rograz and Mangolt. "There are two types of beets differently colored". Coles (1657) listed the following nine sorts of beets together with three sorts of "spinage" (*Spinacia oleracea*): (i) Common white; (ii) common red; (iii) common greene; (iv) Roman red; (v) Italian; (vi) prickly of Candy; (vii) sea; (viii) yellow; and (ix) flat stalked.

Cesalpino's reference to *Beta sylvestris* was corrected by de Tournefort (1700), who best described the flowering features of sea beet, considered by Cesalpino "*sine flore manifesto*" (apparently without flowers). Tournefort, in addition to *Beta sylvestris maritima* (or *Beta sylvestris spontanea marina*), lists the species of cultivated beets: (i) *Beta alba*; (ii) *Beta rubra vulgaris*; (iii) *Beta rubra radice rapae*; (iv) *Beta rubra lato caule*; (v) *Beta pallida virescens*; (vi) *Beta rubra mayor*; (vii) *Beta lutea mayor*; (viii) *Beta costa aurea*; (ix) *Beta foliis et caule flammeis*. In the Appendix of the book, other species are added: *Beta orientalis* and *Beta sylvestris* (also named *Cretica*, *maritima*, *foliis crispis*). The species are ranked under their respective "*genera*", an intermediate category between "*familiae*" and "*species*". The *genera*, including *Beta*, were chosen so well that a large proportion of them were adopted by Linnaeus (Jackson 1881). Consequently, the authority for genus *Beta* is also today the abbreviations Tourn. or Tournef. Beets were ranked in the *classis* XV: *De herbis et suffruticibus* (herbs and bushes), *sectio* I, *genus* II *Beta*. This classification was summarized by Valentini (1715) in Fig. 6.1, and was used by Tilli (1723) for the catalogue of the *Hortus Botanicus* of Pisa, Italy.

Ray (1693) divided beet into seven species: *Beta alba*, *Beta rubra*, *Beta sylvestris maritima* (*communis* or *viridis*), *Beta rubra radice rapae*, *Beta lutea mayor*, *Beta italica*, and *Beta cretica semine aculeato* (see Appendix for translation). He described the characteristics of each species, citing especially Bauhin (1623) and Parkinson. In "*Synopsis methodica stirpium Britannicarum*" (Ray 1690), the drawing of *Beta sylvestris maritima* is shown with the caption "sea-beet", which was used some years earlier by Coles. The description of *Beta cretica* is very detailed and original.

Morison (1715) classified the beets according to their uses and traits (Fig. 6.2). Note that the name of the species *Beta maritima spontanea comminis viridis* "*ad oram*" (until now) has been simplified as *Beta maritima* "*nobis*", that is, with the authority Morison himself. The proposed name "*Beta maritima*" by Morison was used by some later authors. "The Morison's copper plate engravings are very good, although small, but are cumbersome to quote because they are arranged in sections separately numbered, so that three numerals must be used to designate a particular figure" (Jackson 1881). Cupani (1696) mentioned all types of beets known at the time, including *Beta spontanea*, *Beta maritima*, *Beta communis*, *Beta viridis*, and *Beta sylvestris maritima*. The authors of the names of the species are Morison and Bauhin. Cupani also cited some Italian common names: "Gira di spiaggia", "Gira di



CLASSIS XV.

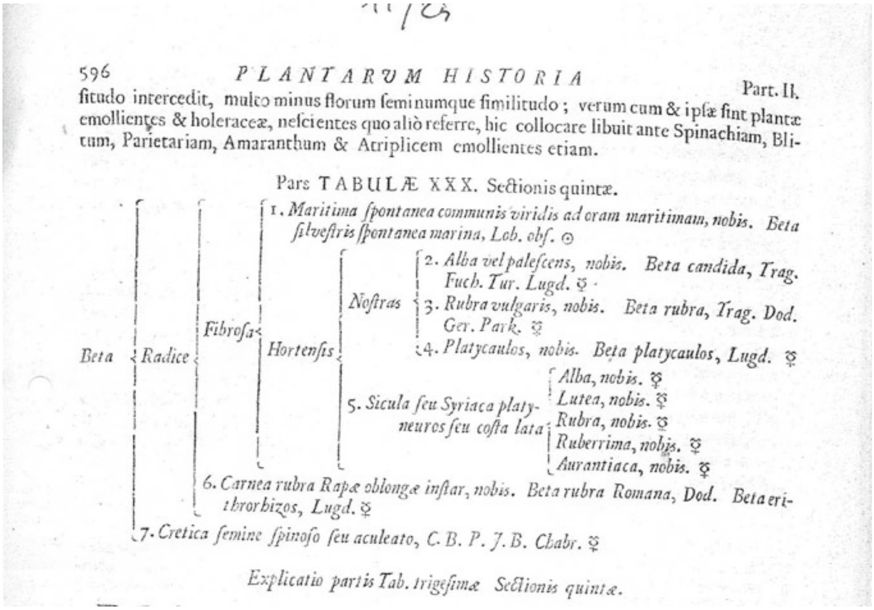
DE

HERBIS FLORE APETALO ſ. STAMINEO.

bæ Flore Apetalo ſ. Stamineo

- 1. Cujus calycis poſterior pars abit in fructum.
  - *Aſarum*
    - Dodon.
    - Americanum.
    - Virginianum.
  - *Beta*
    - alba.
    - rubra
      - major.
      - minor.
- 2. Cujus piſtillum abit in ſemen calyce obvolutum.
  - *Acetoſa.*
  - *Lapathum.*
  - *Atriplex*, quæ vel
    - hortenſis
      - alba.
      - rubra.
    - ſylveſtris.
  - *Chenopodium*, ad quod pert.
    - Botrys.
    - Bonus Henr.
  - *Blitum.*
  - *Herniaria.*
  - *Paronychia*
    - Narbonenſis.
    - Hiſpanica
      - Supina.
      - fruticoſ.
    - Luſitanica.
  - *Alchimilla.*
  - *Parietaria.*
  - *Perſicaria*
    - mitis
      - maculoſa.
      - non maculoſa.
    - urens ſ. Hydropiper.
  - *Polygonum.*
  - *Fagopyrum.*
  - *Biſtorta*
    - Vulg. major & med.
    - Alpina
      - maxima.
      - media.
      - minor.
- 3. Apetalo, quæ Cereales appellantur, earumque affines.
  - *Triticum.*
  - *Secale*
    - vernum, vel minus C. B.
    - hybernum, vel majus C. B.
  - *Hordeum.*
  - *Oryza.*
  - *Avena*
    - alba, ſeu vulgaris.
    - nigra tenuior.
  - *Milium.*
  - *Panicum.*
  - *Gramen*
    - Loliaceum.
    - Spicatum.
    - Dactylon.
    - Paniculatum.
    - Avenaceum.
  - *Arundo.*
- 4. Apetalo in capitulum ſquamoſum collecto.
  - *Cyperus*
    - Rotundus, vulg. C. B.
    - Americanus.
    - Orientalis.
  - *Scirpus.*
- 5. Apetalo in eadem planta à floribus ſejuncto.
  - *Cyperoides.*
  - *Typha* paluſtris
    - major.
    - media.
    - minor.
  - *Sparganium.*
  - *Mays.*
  - *Lacryma Jobi*
    - Vulgaris.

Fig. 6.1 Classification of species with flore "*apetalo*" i.e. without petals. *Beta* (see above) is included among the species "*cuius calycis posterior pars habit in fructus*" (the calyx takes part in the fruit) (Valentini 1715)



596 *PLANTARVM HISTORIA* Part. II.

ſitudo intercedit, multo minus florum ſeminumque ſimilitudo; verum cum & ipſæ ſint plantæ emollientes & holeraceæ, neſcientes quo aliò referre, hic collocare libuit ante Spinachiam, Blitum, Parietariam, Amaranthum & Atriplicem emollientes etiam.

Pars TABULÆ XXX. Sectionis quintæ.

- *Beta*
  - *Radice*
    - *Fibroſa*
      - 1. *Maritima ſpontanea communis viridis ad oram maritimam, nobis. Beta ſilveſtris ſpontanea marina, Lob. obſ.* ⊙
      - *Hortenſis*
        - *Noſtras*
          - 2. *Alba vel paleſcens, nobis. Beta candida, Trag. Fuch. Tur. Lugd.* ☿
          - 3. *Rubra vulgaris, nobis. Beta rubra, Trag. Dod. Ger. Park.* ☿
          - 4. *Platycaulos, nobis. Beta platycaulos, Lugd.* ☿
        - 5. *Sicula ſeu Syriaca platyneuros ſeu coſta lata*
          - *Alba, nobis.* ☿
          - *Lutea, nobis.* ☿
          - *Rubra, nobis.* ☿
          - *Ruberrima, nobis.* ☿
          - *Aurantiaca, nobis.* ☿
    - 6. *Carnea rubra Rapæ oblongæ inſtar, nobis. Beta rubra Romana, Dod. Beta erithrorbizos, Lugd.* ☿
  - 7. *Cretica ſemine ſpinoſo ſeu aculeato, C. B. P. J. B. Chabr.* ☿

Explicatio partis Tab. trigeſimæ Sectionis quintæ.

Fig. 6.2 Classification of *Beta* according to Morison (1715) see text

ripa di mari". The term "Gira" is not found in references to earlier Italian botanical authors.

In the treatise "*Prodromus theatri botanici*", Bauhin (1622) used, together with the old names "*Beta*" and "*Limonium sylvestris*", the common term "*pyrola*" mentioned by Fuchs. The words "*Beta maritima syl. spontanea*" were used on the posthumous edition of "*Stirpium illustrationes*" edited by Parkinson (1655), which detailed a second type called "*Beta maritima syl. minor*", similar to that above, but smaller in leaf and root development. In the second edition of the "*Pinax theatri botanici*", quoted by de Commerell (1778), Bauhin included "*Beta sylvestris maritima*" in the group *Minores* together with six cultivated species (*Beta alba*, *Beta communis*, *Beta rubra vulgaris*, *Beta rubra radice rapae*, and *Beta lato caule*). In the grouping *Majores*, he included *Beta pallida virens*, *Beta rubra*, and *Beta lutea* (see Appendix for translation).

Linnaeus, with a more rigorous scientific method, ordered the binomial nomenclature already widely used by botanists beginning with Mattioli, Tara, Bauhin, Pitton, de Tournefort, and so on (Greene 1909). Until the time of Linnaeus, the traditional division was into *herbae*, *suffrutices*, *arbores* (herbs, bushes, trees, etc.), or a ranking made according to their use (aromatic, medical, food, etc.). All details of the uses and properties were intentionally ignored by Linnaeus, thus simplifying the nomenclature. He also minimized the number of *genera* and *species* (Greene 1909) and simplified the names of the latter, which were becoming very long and complicated (Jackson 1881). This process of rationalization had already been adopted by Bauhin over a century earlier. Linnaeus also eliminated a large number of synonyms that confounded the precise identification of species.

In the first edition of "*Species plantarum*", Linnaeus (1753) divided the genus *Beta* into four species (*vulgaris*, *perennis*, *rubra*, and *cicla*) and eight varieties: Sea beet was named *Beta perennis* var. *sylvestris maritima*. For the remaining varieties, Linnaeus used names introduced by Bauhin (1623). The genus *Beta* was included in the *classis* V *Pentandria* and in the *ordo* II *Digyna*. The use of the term "*vulgaris*" (common) seems to go back to Cesalpino (1583). de Lobel (1576) resumed using the adjective only in the case of *Beta rubra vulgaris non turbinata*.

More complex is the origin of the term "*maritima*" (marine) used by Linnaeus, which was evidently derived from the locations preferred by the species, and partially replacing the various names and adjectives used in the past (Appendix E). The word "*maritima*" appeared in the book "*Pinax Theatri Botanici*" published by Bauhin (1623). In a list of various types of cultivated and wild beets, he used the names "*Beta syl.* (*sylvestris*) *maritima*" and "*Beta syl.* (*sylvestris*) *spontanea marina*" Lob. ob. Under the heading "*Beta*", de Lobel (1576) listed the forms known at the time, and named the wild plant "*Beta sylvestris spontanea marina*". Shortly after, he also pointed out that the plant grows in "*sabuleti maritimi*" (in sandy seashores). It is likely that Bauhin took this last adjective, which in Latin is equivalent to "*marina*" (marine), already used by Aldrovandi (1551) (cited by Baldacci et al. 1907) (Sect. 1.5). The lack of reference after the name "*Beta syl. maritima*" meant that Bauhin considered himself as the author. The name *Beta sylvestris maritima* followed by the initials of the author, abbreviation of the book, and the page (e.g., *C.B. Pin.* 118) was frequently used until Linnaeus (Dale 1730).

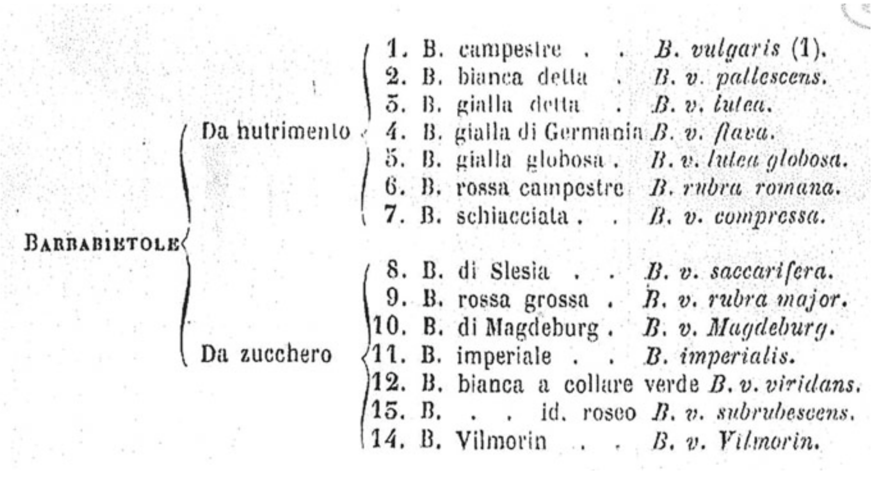
Beta maritima was considered as a separate species in the second edition of "*Species plantarum*" dated 1762. The *genus* was split into two species: the main distinction between *Beta vulgaris* (cultivated beets) and *Beta maritima* (wild or sea beets) was based on the behavior of the seed stalk: erect in *vulgaris* and "*decumbens*" (prostrate) in *maritima* (Fig. 3.18); however, in reality, the stalk is often erect even in *Beta maritima* (Fig. 3.17). The flowers described by Linnaeus "*solitariis aut binis*" (single or double) are actually composed of two or more flowers; only quite rarely they are single. *Beta vulgaris* differs from *maritima* through its biennial cycle "at least in Mediterranean areas" (Greene 1909).

In "*Systema naturae*" on page 276, Linnaeus (1735) split the cultivated species, *Beta vulgaris*, into the sub-species *vulgaris* and *cicla*: the first was grown for the root and the second for the leaves. "*Cicla*" was the ancient Latin name given to the leaf beets. According to Linnaeus, *Beta maritima* differed from *Beta vulgaris* due to the double flowers not being "*congestis*" (numerous) as they were in *vulgaris*, and because it flowered in the first year (annual) rather than in the second (biennial). Between the last two editions, Linnaeus proposed some different classifications for the genus *Beta* (Letschert 1993). Because "*Systema vegetabilium*" was the last book he edited, the latter classification (in which *Beta maritima* is a species and not subspecies) can be considered as definitive. Several authors disagree with this as the final classification. Letschert (1993) gives a detailed review of the taxonomic pre- and post-Linnaean treatment of the genus *Beta*.

6.2 Post-Linnaean and Current Classification

Willdenow (1707) was unwilling to follow the Linnaean system, and divided the genus *Beta* into four species: *Beta vulgaris*, *Beta patula*, *Beta cicla*, and *Beta maritima*, each having several sub-species. Stokes (1812) subdivided the genus *Beta* into *Beta esculenta*, *Beta alba*, *Greenleaved beet*, *Reddishleaved beet*, *Beta rubra*, *Root of scarcity*, *Beta rubra radice rapae*, and *Beta lutea mayor*, including about 50 sub-species, but *Beta maritima* was not mentioned. "Root of scarcity" was the initial English name given to the "Mangel Würzel" (fodder beet) based on the literal translation of the first German word (Fig. 6.3) (de Commerell 1778).

After Linnaeus, several modifications of the taxonomy were proposed, among others, by Desfontaines (1789), Kitaibl and Waldstein (1813) (cited by von Lippmann 1925), Hornemann (1813) (cited by von Proskowetz 1896), Marschall (1819), Roxburgh (1832), Mutel (1836), Boissier (1879), and Hohenacker (1838). Desfontaines listed three types of cultivated beets (*Beta vulgaris*, *Beta rubra vulgaris*, and *Beta rubra*) and two wild types (*Beta maritima* and *Beta sylvestris maritima*). Hornemann reported six species of wild and cultivated beets, and described *Beta maritima*, as having the following characteristics "*floribus geminis*, *foliis cordatis triangularibus attenuatis*" (double flowers, triangular or heart-shaped leaves). Marschall attributed to genus *Beta* the species *maritima*, *trigyna*, and *macrorhyza*, and explained that the first species flowered in November, developing inflorescences with 1–4 flowers, bearing *folia subcarnosa* (almost fleshy leaves), and favoring salty water. Mutel (1836) recognized only two species, commune (*Beta vulgaris*) and marine (*Beta maritima*). Lenz (1869) cited Bieberst, who had been referenced by Linnaeus for other sub-species, as author of the name *Beta maritima*.



BARBABIETOLE	Da nutrimento	1.	B. campestre	*B. vulgaris* (1).
		2.	B. bianca detta	*B. v. pallescens.*
		3.	B. gialla detta	*B. v. lutea.*
		4.	B. gialla di Germania	*B. v. flava.*
		5.	B. gialla globosa	*B. v. lutea globosa.*
		6.	B. rossa campestre	*B. rubra romana.*
		7.	B. schiacciata	*B. v. compressa.*
	Da zucchero	8.	B. di Slesia	*B. v. saccarifera.*
		9.	B. rossa grossa	*B. v. rubra major.*
		10.	B. di Magdeburg	*B. v. Magdeburg.*
		11.	B. imperiale	*B. imperialis.*
		12.	B. bianca a collare verde	*B. v. viridans.*
		13.	B. . . . id. roseo	*B. v. subrubescens.*
		14.	B. Vilmorin	*B. v. Vilmorin.*

Fig. 6.3 Classification of beets according to their use "da nutrimento" (as food) and "da zucchero" (for sugar extracion") (Berti-Pichat 1866)

Moquin-Tandon (1840) completely changed the classification of Linnaeus in "*Chenopodearum monographia enumeratio*" in which he brought together the family *Chenopodiaceae*, and split genus *Beta* into eight species (*trigyna*, *longispicata*, *macrorhiza*, *vulgaris*, *orientalis*, *procumbens*, *webbiana*, and *patula*). The species *vulgaris* comprised nine sub-species (*pilosa*, *maritima*, *macrocarpa*, *cicla*, *flavescens*, *purpurescens*, *alba*, *lutea*, and *rubra*), that is, all the cultivated beets and some of the wild beets. *Beta maritima* was described as a plant "*gracilis et glabra. In littoralibus Ocean et Medit.*" (delicate and smooth leaved. It lives on Atlantic and Mediterranean shores.)

In "*Prodromus systematis naturalis regni vegetalibus*" published by de Candolle (1849), Moquin-Tandon proposed a new classification, in which the genus *Beta* was divided into ten species. The species *Beta vulgaris* was split into three groups: (i) Bette; (ii) Poirées; and (iii) Bette-raves. The first included the wild species, (α) *pilosa*; (β) *maritima*; (γ) *orientalis*; and (δ) *macrocarpa*. *Beta villosa* (with hairy or velvet leaves) probably corresponded to the above-mentioned *Beta cretica*. It should be noted that the species *Beta villosa* (*cretica*, *pilosa*, etc.), placed by various authors in the Greek islands, Egypt, Corsica, Sicily, and so on disappeared entirely in subsequent classifications. The genus *Beta*, in the Linnaean taxonomy, belonged to the family "*Salsolaceae*" authored Moq. or Moquin.

Another classification was developed by Bertoloni (1837). Although he maintained the Linnaean membership to class *Pentandria*—order *Digyna*, he split the genus *Beta* into three species: *cicla*, *macrocarpa*, and *maritima*. After he listed *maritima* as being found in Italy, he gave a very particular botanical characterization of the species; the flowers were described as "double, rarely triple, and seldom single at the apex of the branches". Berti-Pichat (1866) gave a unique classification of beets based on their two major uses (Fig. 6.4). Gandoger (1910) divided the species *maritima* into two sub-species, *agrigentina* and *atriplicifolia* (leaf similar to *Atriplex* species). The first, given the authority Gdgr. (Gandoger), was declared to be widespread near Agrigento (Sicily), and the second in Spain. The author did not provide any details on other distinctive traits. A somewhat confused classification of genus *Beta* partially taken from Linnaeus was given by Steudel (1871), in which he named *Beta maritima*, *Beta decumbens*, with the authority attributed to Moench without mentioning the written reference.

Some minor changes to classifications within genus *Beta* were made by Joseph Koch (1858), Karl Koch (1839), Ledebour (1846), Heldreich (1877), Boissier (1879), and Radde (1866). Bunge (cited by von Proskowetz 1896) listed under genus *Beta* (Tournef.) 14 species and their respective ranges. Kuntze (1891) divided *Beta maritima* into the following "forms": *macrocarpa*, *orientalis*, *brevibracteolata*, *trigynoides*. The last two were named by Kuntze himself, and were found at Funchal (Madeira) and Garachico (Tenerife), respectively. Gürke (1897) proposed another classification, in which genus *Beta* was divided into seven species; *Beta maritima* was included in the species *vulgaris* together with the sub-species *foliosa*, *pilosa*, *cicla*, and *esculenta.* Some synonyms of *Beta vulgaris maritima* were given, which included *marina*, *deccumbens*, *triflora*, *carnulosa*, *erecta*, and *noëana*. As was proposed by de Wildeman and Durand (1899), *Beta maritima* became the only species of

Fig. 6.4 Painting of *Beta perennis* (Reichenbach and Reichenbach 1909)

the sub-family *Betoideae* (family *Chenopodiaceae*) whereas *Beta vulgaris* contained all the cultivated beets.

As we discussed, in the taxonomic evolution of genus *Beta* post 1900, the abbreviations of authorities for genera, species, sub-species, varieties, and so on will be cited only if necessary. As example, the denominations (basionyms) of *Beta maritima* and the respective authors are given (www.tropicos.org).

According to de Vries (1905), "Some authors have distinguished specific types among the wild forms. While the cultivated beets are collected under the heading of *Beta vulgaris*, separate types with more or less woody roots have been described as *Beta maritima* or *Beta patula*". Reichenbach and Reichenbach (1909) classified *Beta maritima* as a "*perennis*" (perennial) variant of *Beta vulgaris* (Fig. 6.5). In this case, genus *Beta* was included in the sub-tribe *Betae*, in the tribe *Chenopodieae*, and in the family *Chenopodiaceae*. Ascherson and Graebner (1919) were quite confused when they subdivided genus (Gesamtart) *Beta* into two species, *Beta trigyna* and *Beta vulgaris*. The wild plants were named *Beta vulgaris perennis*, and under this heading different sub-species and variety synonyms of *Beta maritima* were listed: *perennis*, *marina*, *decimbens*, *triflora*, *noëana*, *annua*, *glabra*, *pilosa*, and so on, with the respective authorities.

Transchel (1927) divided the genus *Beta* into three undefined "groups": *Vulgares*, *Corollinae*, and *Patellares* (Coons 1954; de Bock 1986). Ulbrich (1934) called Transchel's groups "sections" and added a fourth section, *Nanae*. He changed the name *Patellares* to *Procumbentes*, a decision supported by Buttler (1977) later. This left genus *Beta* divided into four sections: I *Vulgares*, II *Corollinae*, III *Nanae*, and IV *Procumbentes*. The section *Vulgares* had the widest distribution and was believed to be the primordial species group of the genus *Beta* (Campbell 1984). Ulbrich (1934) divided section *Beta* into two species: *vulgaris* and *macrocarpa*. A cluster analysis based on RFLP DNA fingerprinting showed a higher similarity of *Beta macrocarpa* accession to section *Corollinae* than to section *Beta* accessions (Jung et al. 1993) which supports the proposal of Ulbrich (1934). He considered *Beta maritima* a variety of the species *vulgaris*, which belonged to the sub-species *perennis* along with six other varieties. The division into four sections remained essentially unchanged until recently (Table 6.1).

Coons (1954) adapted Ulbrich's classification, changing the name of section IV back to *Patellares*, and ordering the taxa into sections, species, sub-species, and varieties. As a result, the Latin name of sea beet became "*Beta vulgaris* subsp. *perennis* var. *maritima*". Many other minor changes have been made or proposed by, among others, Komarow (1936) (see Ford-Lloyd 2005), Zossimovitch (1934), Aellen (1938), Ernauld (1945), Helm (1957), Krassochkin (1959) (see de Bock 1986), Mansfeld (1959), Tutin et al. (1964), Davis (1937), Aellen (1967), Buttler (1977) (reviewed in Letschert 1993). We will briefly review the taxonomies developed by Zossimovitch (1934), Burenin and Garvrilynk (1982), and Ford-Lloyd et al. (1975). Zossimovitch subdivided the genus *Beta* into three groups according to their "ecogeographic isolation and the area": (i) eastern (*Beta lomatogona* including *Beta nana*, *Beta trigyna* (Fig. 6.5), and *Beta macrorhiza*); (ii) central (*Beta vulgaris* with the variety *annua*,

Fig. 6.5 Painting of *Beta trigyna*

Table 6.1 Taxonomy of the genus *Beta* according to Ulbrich (1934)

Genus	Section	Species
Beta	I *Vulgares*	*vulgaris*
		maritima
		macrocarpa
		patula
		atriplicfolia
	II *Corollinae*	*macrorhiza*
		trigyna
		foliosa
		lomatogona
	III *Nanae*	*nana*
	IV *Procumbentes*	*patellaris*
		procumbentes
		webbiana

patula, *macrocarpa*, and *maritima*); (iii) western (*Beta patellaris*, *Beta procumbens*, and *Beta webbiana*).

According to Ford-Lloyd et al. (1975), section *Vulgares*, which subsequently would become section *Beta* (Buttler 1977; Barocka 1985), included only the species *vulgaris*, which was divided into seven sub-species (Table 6.2). The species *maritima* was split into six varieties with the same names as used by Coons (1954). The classification within sections *Nanae* and *Procumbentes* remained the same. In section *Corollinae*, the species named *foliosa* was changed to "*corolliflora*", and was brought into the species *intermedia*. Krasochkin (1959) returned to the classification of *Beta maritima* as species, split into two subspecies: *mediterranea* and *danica*. The former was further subdivided into four varieties: (i) *prostrata*; (ii) *erecta*; (iii) *macrocarpa*; and (iv) *atriplicifolia*.

Another significant revision proposed by Ford-Lloyd and Hawkes (1986) was to divide *Beta* section *Beta* into four sub-species (i) *vulgaris* (including the cultivated beets except leaf beets); (ii) *cicla* (leaf beets); (iii) *maritima* (northern sea beet); (iv) *macrocarpa* (southern sea beets). The International Plant Genetic Resources Institute (IPGRI) in 1993 supported the taxonomy proposed by Ford-Lloyd and Hawkes (1986) with minor changes. *Beta vulgaris* subsp. *maritima*, *Beta prostrata* and *Beta erecta* were no longer considered as separate species. The species *Beta vulgaris* subsp. *vulgaris* was divided into three varieties: *conditiva*, *crassa*, and *altissima* (IPGRI, 1993). The cultivated species were included in *Beta vulgaris* subsp. *cicla* (Swiss chard or leaf beet) and in subsp. *vulgaris* (red beet, fodder beet, and sugar beet).

For the genus *Beta*, including the genus *Patellifolia*, 142 taxon names have been listed of which Hanelt and the Institute of Plant Genetics and Crop Plant Research (2001) only listed 25 names as the accepted taxa (http://mansfeld.ipk-gatersleben.de/apex/f?p=185:145:::NO::P3_BOTNAME:Beta). For *Beta maritima* the USDA-

Table 6.2 Taxonomy of the genus *Beta* according to Ford-Lloyd et al. (1975)

Genus	Section	Species	Sub-species	Variety
Beta	I *Vulgares*	*vulgaris*	*maritima*	*maritima*
				trojana
				macrocarpa
				atriplicifolia
				prostrata
				erecta
			orientalis	
			adanensis	
			cicla	*cicla*
				flavescens
			vulgaris	
			lomatogonoides	
			Patula	
	II *Corollinae*	*macrorhiza*		
		Trigyna		
		Foliosa		
		lomatogona		
	III *Nanae*	*Nana*		
	IV *Procumbentes*	*patellaris*		
		procumbens		
		webbiana		

ARS GRIN taxonomy site (www.usda-grin.gov) and Letschert (1993) listed 25 and 21 synonyms, respectively. Thus, the multiplication of the names of taxa included in the species *Beta vulgaris* continued. This process also involves *Beta maritima*, considered alternatively as species, sub-species, or variety as reviewed by Letschert (1993). According to Letschert et al. (1994), the difficulties of obtaining a satisfactory taxonomic treatment of the genus *Beta* were due, not only to the coexistence of wild and cultivated species, and the difficulties of getting representative samples of all taxa for research, but also to the different professional and cultural background of plant breeders and taxonomists trying to resolve the taxonomic problems.

Today, taxonomists can also rely on molecular marker technologies such as isoenzyme analysis (e.g., van Geyt et al. 1990), various kinds of DNA markers (e.g., Jung et al. 1993; Shen et al. 1996, 1998; Andrello et al. 2017), and comparative genomics (Dohm et al. 2013). The use of genetic markers allows the analysis of the heritable diversity underlying the morphological differentiation of the wild beet taxa. Information on the genetic relatedness has been used to improve the taxonomy of the genus *Beta* (Letschert 1993). However, the variability present within the species still creates problems, and every method applied on a limited number of samples or without a full understanding of the geographic distribution of the species may give varying results.

Based on the literature studies and the analysis of morphological, ecological, and molecular traits, Letschert proposed a revision of the section *Beta* (Letschert 1993; Letschert et al. 1994). According to this revision, the section *Beta* consisted of three species, *vulgaris* (with the sub-species *vulgaris*, *adanensis*, and *maritima*), *macrocarpa*, and *patula*. The Italian scientist Giovanni Arcangeli had also divided the species *vulgaris* into the subsp. *vulgaris* and subsp. *maritima*, as published in the "*Compendium florae italicae*" (Arcangeli 1882). In addition to the usual Linnaean authority for the species (L.), the authority of Arcangeli (Arcang.) was added, resulting in the officially accepted taxon name *Beta vulgaris* (L.) subsp. *maritima* (Arcang.).

The taxonomy proposed by Letschert (1993) for the section *Beta* (syn. *Vulgares*) and for section *Procumbentes* (syn. *Patellares*) (Buttler 1977) seems to have been confirmed by RFLP analysis (Mita et al. 1991). Jung et al. (1993) found a low degree of homology (34%) between the sugar beet and *Patellifolia procumbens* (syn. *Beta procumbens*) after cross-hybridization of sugar beet RFLP probes with *Patellifolia procumbens* probes. In addition, a spinach (*Spinacia olearcea*) sample clustered together with *Patellifolia procumbens* and *Patellifolia webbiana* accession. Scott et al. (1977) suggested ranking section *Procumbentes* as a genus named *Patellifolia*. The cross-hybridization experiment and the high genetic similarity between *Spinacia* and *Patellifolia* accessions further substantiated the proposal.

From Ulbrich (1934) until just a few decades ago, the genus *Beta* was included in the family Chenopodiaceae (Cronquist 1988). Most recently, Kadereit et al. (2006) have suggested the re-introduction of the sub-family Betoideae (excluding Acroglochin), proposed first by Ulbrich (1934), because it resolved as a monophyletic group in molecular analysis (Hohmann et al. 2006) and is morphologically distinct from other sub-families of the Chenopodiaceae/Amaranthaceae alliance. Kadereit et al. (2006) corroborated that the section *Procumbentes* (Ulbrich 1934) should be given the rank of a genus and to keep section *Beta* and *Corollinae* within the genus *Beta* (Table 4.3). This classification also has been supported by the analysis of nuclear ribosomal DNA (Santoni and Bervillè 1992) (Table 6.3).

Following Scott et al. (1977), the genus *Patellifolia* consists of three species, namely *Patellifolia patellaris* (Moq.) A. J. Scott, Ford-Lloyd, and J. T. Williams (syn. *Beta patellaris* Moq.), *Patellifolia procumbens* (C. Sm.) A. J. Scott, Ford-Lloyd, and J. T. Williams (syn. *Beta procumbens* C. Sm.), and *Patellifolia webbiana* (Moq.) A. J. Scott, Ford-Lloyd, and J. T. Williams (syn. *Beta webbiana* Moq.). However, the difficulties in distinguishing the species led some authors to refer an uncertain number of species—two or three (e.g., Wagner et al. 1989; Hohmann et al. 2006; Kadereit et al. 2006) or even only one (Santoni and Bervillè 1992; Thulin et al. 2010). The proposal of Thulin et al. (2010) is based on the analysis of ITS regions of five specimens, namely *Patellifolia procumbens* and *Patellifolia patellaris* from Gran Canaria, *Patellifolia webbiana* and *Patellifolia patellaris* from Tenerife as well as one specimen from *Tetragonia pentrandra* from Socotra (Yemen). While the taxonomic debate continues, the taxonomic system of Scott et al. (1977), which is commonly

Table 6.3 Comparison between the taxonomies of the genus *Beta* proposed by Ford-Lloyd (2005) left; and Kadereit et al. (2006) right

Ford-Lloyd (2005)	Kadereit et al. (2006)
Beta Section *Beta*	*Beta* Section *Beta*
Beta vulgaris L.	*Beta vulgaris* L.
Beta. vulgaris L. subsp. *vulgaris* cultivated form	
Beta vulgaris L. subsp. *maritima* (L.) Arcang.	*Beta vulgaris* L. subsp. *maritima* (L.) Arcang.
Beta vulgaris L. subsp. *adanensis*	*Beta vulgaris* L. subsp. *adanensis*
Beta macrocarpa	*Beta macrocarpa*
Beta patula	
Beta Section *Corollinae*	*Beta* Section *Corollinae*
Beta corolliflora	*Beta corolliflora*
Beta lomatogona	*Beta lomatogona*
Beta intermedia	*Beta trigyna*
Beta trigyna	*Beta nana*
Beta Section *Nanae*	
Beta nana	
Beta Section *Procumbentes*	
Beta procumbens	
Beta patellaris	
Beta webbiana	

used in plant breeding and also applied in threat assessment studies (Bilz et al. 2011), should be used for pragmatic reasons (Frese et al. 2018).

The sections *Beta*, *Corollinae*, and *Nanae* have been differentiated by restriction analyses of the chloroplast DNA (Komarnitsky et al. 1990). Nevertheless, Kadereit et al. (2006) also suggested the elimination of the section *Nanae*, and incorporated *Beta nana* (the lone species in that section) into section *Corollinae*.

Section *Beta* consists of wild and cultivated taxa. The cultivated taxa share a common ancestor with *Beta maritima* as indicated by the RFLP DNA fingerprinting results presented by Jung et al. (1993). Accessions belonging to the genus *Beta* were analyzed using DNA fingerprinting. The results confirmed the taxonomy accepted at this time with the exception that there was too narrow differentiation of *Beta atriplicifolia* and *Beta orientalis* to consider them as distinct species. A high level of similarity was found between Atlantic sea beet populations and cultivated varieties, whereas sugar and leaf beets were widely diverged. Jung et al. (1993) concluded that the hypothesis (Fischer 1989) that sugar beet was derived from an unintentional cross between fodder and leaf beet is unlikely. It also seems probable that there has been more recent gene flow between sugar beet and *Beta maritima* than earlier suspected. Recent research with sequence variations in the ITS1 region of nuclear ribosomal DNA and the molecular structure of the *matK* chloroplast gene has proven useful for phylogenetic discrimination among species within *Beta* (Mglinets 2008; Shen et al. 1998). Ford-Lloyd (2005) revised and updated the current taxonomy taking into account the new research findings. The section *Beta* was modified, as suggested by Lange et al. (1999) and has been accepted for use by the International Database of *Beta* (Germeier and Frese 2004). Compared to the past two centuries of systematic taxonomic investigations, today researchers have access to the full range of genotypes (populations) of the various wild beet taxa and can apply highly sophisticated molecular genetic methods to study the past and ongoing speciation processes generating the interspecific and intraspecific diversity we are trying to classify today. The taxonomy of wild beets will likely be revised again in future when outstanding issues will be resolved. Should *Beta vulgaris* subsp. *adanensis* be treated as species or sub-species? Is the tetraploid form of *Beta macrocarpa* a separate species or a sub-species o*f Beta macrocarpa*. Does it make sense to keep *Beta intermedia* and *Beta trigyna* as separate species despite these forms belonging to a highly variable polyploid hybrid complex? Is the genus *Patellifolia* a single, but highly variable species? These are some of the questions still pending (Buttler 1977; Villain 2007; Thulin et al. 2010).

There is often disagreement among taxonomists especially with regard to the classification of the cultivated types (Letschert et al. 1994). Two different approaches have been applied to create a taxonomic system for cultivated beets. In Eastern Europe the cultivated types were given varietas and forma names. Experts familiar with this system immediately know what the material looks like as the name circumscribes specific colors, root, or petiole shapes and further traits of interest to breeders, growers, and consumers. The disadvantage of this so-called "splitter system" is that it does not always allow a clear classification of all types since the trait variation of an outbreeding crop is complex and hampers the unambiguous delineation of forms based on classical taxonomic traits. For this reason Lange et al. (1999) proposed to classify cultivated material according to the use. The resulting "lumper system" is composed of four cultivar groups only and does not require intimate knowledge of the meaning of varietas and forma names, compared to the splitter system names that only provide information on the use type. Therefore, a lumper system should be integrated into an information system that is able to document and provide trait data, that is, trait scores or trait measurements.

Cultivated beets are classified into four cultivar groups or "*culta*" based on their use. The Leaf Beet Group is composed of two types: (i) spinach beet which produces leaves similar to spinach and is used in the same way, and (ii) Swiss chard with developed, white (or colored), and tender petioles and midribs. The unselected root shape has remained similar to that of sea beet.

The Garden Beet Group has a round root more or less flattened, and the skin and flesh often show a deep red color. The beet may also be white or of varying shades and intensities of yellow to orange. The beet (crown, hypocotyl, and taproot) is primarily an enlarged hypocotyl, making up about 85% of the weight. The leaves can be dark-green or red-purple as well. The root contains little fiber and, if harvested at the appropriate time lends itself to be eaten raw or cooked.

The Fodder Beet Group is of any color, shape, and proportion of hypocotyl: taproot. It was developed for easy manual removal from the soil and winter storage. Its high total digestible nutrients make it suitable for feeding all classes of livestock. Beets are very large and can protrude almost completely from the ground.

The Sugar Beet Group has been selected for sucrose production. The roots are ivory white, and cone-shaped, more or less elongated (Fig. 4.1). Root and leaves have uniform characteristics, so that they are not used to distinguish among commercial varieties. The crown protruding from the soil of the taproot is limited. More information regarding cultivated beets is given in Chap. 9.

In 1995, after the publication of the "International Code of Nomenclature for Cultivated Plants" (Trehane et al. 1995), the taxonomy of the section *Beta* was slightly revised (Lange et al. 1999). The changes concerned the species *Beta vulgaris*, which was divided into subsp. *maritima*, subsp. *adanensis*, and subsp. *vulgaris*. *Beta vulgaris* subsp. *vulgaris* was changed to incorporate all beets, including the weedy and wild (feral) beets, which were derived in any way from the cultivated beet crops (Ford-Lloyd 2005). The names indicating the four cultivated groups (*culta*) were slightly modified (Lange et al. 1999). This new approach was endorsed by the World *Beta* Network (WBN), which recommended its use (Frese 2003).

6.3 Phylogeny

Today's distribution area of wild beet species (genus *Patellifolia* and *Beta*) can be divided into two regions of differing phylogenetic significance: the Macaronesian archipelago and the east Mediterranean region. Burenin and Garvrilynk (1982) and Zosimovich (1968, cit. in Burenin and Garvrilynk (1982)) assumed that the genus *Beta* as well as the genus *Patellifolia* (syn. *Beta* section *Procumbentes*) evolved from a hypothetical ancestral form called "Protobeta". Protobeta occurred in the region of the Tethys, an ancient ocean extending from the Caribbean, and the Mediterranean basin to the western shore of Indonesia during the tertiary period 25 million years ago. During the Miocene epoch (late tertiary period), the homogeneity of the Tethys faunas was abruptly disturbed (Hallam 1972). The causes of this phenomenon must have also affected the flora of the Tethys region. It can be assumed that the change from the tropical–subtropical climate of the Miocene and Pliocene epoch to the cool climate of the Pleistocene had a strong impact on the fauna and flora. Along with geological changes induced by the continental plate drift, climate change was also likely to have been an important driver of evolution taking place in the Mediterranean region which is known today as the center of genetic diversity of the genus *Beta* and *Patellifolia*. The climate change was accompanied by the southwards expansion of glaciers in the northern hemisphere. The northwards progression of the deserts in the current Sahara region and the decreasing temperature in the northern hemisphere caused the extinction of many species from the Tethys. Geological and oceanological studies suggest that the continental drift split off the islands Lanzarote and Fuerteventura from North Africa. Thereby parts of the Tethys flora, including prototypes of the genus *Patellifolia*, were on the one hand saved from extinction and, on the other hand, evolved toward geographically isolated relict species (Bramwell and Bramwell 1974) which colonized later sites in South Spain and West Portugal.

The northern movement of the African plate closed not only the northern flank of the Tethys Ocean but also compressed the Eurasian plate leading to the rise of the Alpine orogenetic belt. The orogenetic activities reached a maximum 20 mya, gradually reducing for the past 5 million years and ending with the extinction of volcanic activities during the past million years. During the Alpine orogeny, mountains in Greece, Turkey, and the Caucasus region were formed. The alternating cold and warm periods during the Pleistocene shaped the mountainous areas as we know them today. The last cold period ended only 10,000 years ago.

The progenitors of the section *Corollinae* and section *Beta* presumably shared a number of similar plant traits and formed the evolutionary basis of two phylogenetic lines within the genus *Beta* (Buttler 1977). During the alpidic orogenesis, species of section *Corollinae* may have evolved through adaptation to the harsh environmental conditions of mountains in Greece as well as in the Taurus and Caucasus region. Buttler (1977) realized that the ancestral form of the section *Corollinae* should have had a similar ecological potential comparable to the current species. If only the strong difference in frost tolerance between section *Beta* and *Corollinae* species are taken into account, the existence of two progenitors with very different adaptive potential within the genus *Beta* seems likely. Buttler (1977) regarded *Beta macrorhiza* and *Beta corolliflora* as the primordial taxa with distribution areas in the oriental-turanian region and the east Mediterranean region as well. Both species represent the first phylogenetic line within the section *Corollinae*. *Beta lomatogona* is completely restricted to the oriental-turanian region, specifically adapted to arid habitats, morphologically clearly distinct from *Beta macrorhiza* and *Beta corolliflora* and could be considered the second phylogenetic line. The phylogenetic position of *Beta nana*, a highly specialized species of snow patch vegetation of alpine regions in Greece, has only recently been investigated due to the lack of material.

The progenitor of the section *Beta* occurred in coastal areas of the east Mediterranean basin, spread westwards and finally northwards along the Atlantic coasts when the glaciers withdrew at the end of the last cold period. Populations from the Atlantic part of the distribution area most likely constitute evolutionarily the youngest component of *Beta maritima* (Boughey 1981; Villain 2007).

The hypotheses of Buttler (1977), Burenin and Garvrilynk (1982), Boughey (1981), and Bramwell and Bramwell (1974) based on geology, paleobotany, and geobotany agree with the results of studies using molecular markers. Santoni and Bervillè (1992) constructed rDNA physical maps of *Beta* section *Beta* and section *Corollinae* as well as *Patellifolia* species. The diversity of restriction sites was higher in sections *Beta* and *Corollinae* when compared to *Patellifolia*. The simple intergenic spacer of *Patellifolia* is likely to be evolutionarily older than the sequences of the *Beta* species. Romeiras et al. (2016) analyzed ITS, matK, trnH-psbA, trnL intron, and rbcL gene sequences to reveal the relationships within the Betoidae sub-family and constructed a molecular clock-dated phylogenetic tree. The genera *Patellifolia* and *Beta* diverged around 25.3 mya (range: 35.9–16.1 mya) which agrees well with the conclusions of Burenin and Garvrilynk (1982) and Bramwell and Bramwell (1974) reached from geological and paleological knowledge. Sections *Corollinae* and *Beta* started to diverge around 7.2 mya (range: 11.5–3.5) which falls into the period of the alpinic orogeny. An Atlantic group (*Beta maritima*, *Beta macrocarpa*) arose 1.4 mya (range: 2.1–0.7) and separated into distinct *Beta maritima* and *Beta macrocarpa* around 0.9 mya (range: 1.9–0.2 mya). The latter taxon is the youngest among the investigated material with an average divergence time of 0.3 mya (range: 0.7–0.1 mya).

The genetic diversity of *Beta maritima* is high compared to *Beta vulgaris* subsp. adanensis, *Beta macrocarpa* (2x and 4x) and *Beta patula* (Letschert 1993; Villain 2007). Letschert (1993) found significantly higher levels of genetic diversity in south eastern and middle Mediterranean populations compared to the Atlantic material. Leys et al. (2014) investigated the spatial distribution of genetic diversity of *Beta maritima* distributed from the Bay of Biscay to the south of Morocco and found a much higher genetic diversity in Morocco as compared to the material sampled north of the Straits of Gibraltar. *Beta maritima* from the Gibraltar region exhibited a particularly high number of private alleles. The results corroborate with Villain (2007), who explained the current spatial distribution patterns of genetic diversity by the existence of three glacial refugia where the species survived cold periods during the Pleistocene. Refugium 1 was located in the northwestern part of the Iberian Peninsula from where sites north of Portugal were recolonized at the end of the Würm glaciations. Refugium 2 existed in Morocco and refugium 3 in the middle to eastern Mediterranean region. Leys et al. (2014) supported this hypothesis and described the Gibraltar region as a refugium and historical buffer zone maintaining genetic diversity of *Beta maritima* without which range expansion after cold periods would not have been possible. The present-day geographic pattern of genetic diversity is the result of a complex microevolutionary process that is not yet fully understood (Villain 2007; Leys et al. 2014; Touzet et al. 2018).

Villain (2007) used polymorphic chloroplastic and nuclear genetic markers to analyze the genetic relationship between *Beta maritima* and *Beta macrocarpa* as well as *Beta maritima* and *Beta vulgaris* subsp. *adanensis*. Within the haplotype network constructed from chloroplastic genetic marker data, *Beta macrocarpa* samples formed a clearly distinct group. Interestingly, a mutation named HK 550 located on the fragment of trnH-psbA distinguishes *Beta vulgaris* from diploid *Beta macrocarpa* and can be used as diagnostic feature. A major haplotype of *Beta macrocarpa* is distributed from the eastern Mediterranean distribution area to the Canary Islands. Villain (2007) concluded from the results that the diploid *Beta macrocarpa* evolved from *Beta maritima* and, in terms of the microevolutionary timescale, spread rapidly. The phylogenic trees constructed from nuclear genetic markers also showed a clear phylogenetic separation between *Beta maritima* and *Beta macrocarpa*. The tetraploid form of *Beta macrocarpa* first detected by Buttler (1977) on the Canary Islands evidently is an allotetraploid species. Lange and de Bock (1989) investigated tetraploid *Beta macrocarpa* and observed a regular diploidized meiosis which is typical for alloploid species. Villain (2007) found in *Beta maritima* and tetraploid *Beta macrocarpa* the same chloroplastic haplotype and concluded that the tetraploid form developed from crosses between *Beta maritima* x *Beta macrocarpa*. All of the diploid *Beta macrocarpa* samples from the Canary Islands proved to be invariable at nine SSR loci while all tetraploid forms, with very few exceptions, showed variation at all of the nine loci. It seems therefore that the time span from the first colonization of the Canary Islands by the diploid *Beta macrocarpa* till today was too short for mutations to have accumulated. The diploid *Beta macrocarpa* on the Canary Islands likely forms the youngest phylogenetic branch of the species and the allotetraploid *Beta macrocarpa* the preliminary end point of speciation within section *Beta*. Self-fertilization is the main mode of reproduction of the diploid and tetraploid *Beta macrocarpa*. Although diploid *Beta macrocarpa* can occur at the same locations, the chance for crosses between *Beta maritima* and *Beta macrocarpa* is low due to the large difference in flowering time. Temporal isolation is a strong reproductive barrier between both taxa and maintains the differences between both species.

The phylogenetic position of *Beta patula* is not yet fully understood. The species is morphologically clearly distinct from all other taxa of the section *Beta*. The substantial morphological divergence and the extremely low allozyme variation was proposed by Letschert (1993) as the signature of an isolated *Beta maritima* population located at the edge of the species' distribution range which adapted rapidly to the environmental conditions of the archipelago of Madeira. As with the diploid *Beta macrocarpa* from the Canary Islands (Villain 2007), the time between the colonization and the present time was probably too short to allow for allozyme polymorphisms to occur (Letschert 1993). This is not the case for the 25 SSR markers applied to study the genetic diversity of *Beta patula*. On average 4.5 alleles per marker locus were observed and only three out of the 25 markers were monomorphic. Compared to the mutation rate for protein coding loci such as allozymes, the mutation rate at SSR loci is higher (Allendorf and Luikart 2007) which may explain the seemingly contradictory results. The principal component analysis grouped *Beta maritima* individuals with those of *Beta patula* from Ilheu Chaos (Madeira) indicating a close genetic relationship between both species (Frese et al. 2012). The results agree with those of Letschert (1993) who calculated the genetic distance between all taxa of the section *Beta* from allozyme data. *Beta patula* was included in the cluster of *Beta vulgaris* sensu lato while diploid *Beta macrocarpa* accessions formed a clearly distinct cluster (Letschert 1993). Andrello et al. (2017) applied 9724 SNP markers to analyze the genetic diversity within a collection of 1512 individuals taken from 1080 Genebank accessions of section *Beta* (cultivated and wild taxa), that is, one to few individuals per accession. The discriminant analysis of principal components (Jombart et al. 2010) was used to identify genetically similar individuals by the k-means algorithm of the ex nihilo cluster method. The single individual of *Beta patula* was assigned to a cluster consisting almost exclusively of *Beta macrocarpa* individuals. In view of the high number of SNP markers used, this finding cannot be interpreted as a random effect caused by the small sample size. It rather shows that the different marker systems detect different kinds of diversity.

In comparison with *Beta macrocarpa*, *Beta vulgaris* subsp. *adanensis* is more difficult to distinguish from *Beta maritima* based on morphological traits. The results of allozyme, nuclear and chloroplastic genetic markers indicate a weak differentiation between *Beta maritima* and *Beta vulgaris* subsp. *adanensis*. The main distribution area of *Beta vulgaris* subsp. *adanensis* encompasses the Aegean Islands, Cyprus and adjacent Turkish coastlines where the two taxa can be found in close proximity. Villain (2007) suggested two hypotheses to explain the lower level of genetic diversity of *Beta vulgaris* subsp. *adanensis* compared to *Beta maritima* and the low level of genetic differentiation between the taxa. The current structure of the *Beta maritima*/*Beta vulgaris* subsp. *adanensis* complex could be explained as a recent and ongoing speciation process with *Beta maritima* as the progenitor of *Beta vulgaris* subsp. *adanensis*. According to the second hypothesis, the speciation process started from *Beta maritima* populations which survived in isolated East Mediterranean refugia during the past glacial period. However, the microevolutionary time span was not long enough to generate strong reproductive barriers between the autogamous *Beta vulgaris* subsp. *adanensis* and its allogamous ancestor *Beta maritima*. Today, gene flow between the taxa prevents the completion of the speciation process and emergence of a reproductively isolated new species "adanensis".

The ancestor of all cultivated beets, *Beta maritima*, is known to be a diploid species with $2n = 18$ chromosomes. Within the section *Beta*, section *Corollinae* and the genus *Patellifolia* ploidy complexes exist. Interspecific hybridization generates novel genetic diversity and can increase the adaptive potential (Castro et al. 2017). The existence of mixed ploidy populations at sites where species grow sympatrically indicates ongoing speciation processes (Castro et al. 2018). Such sites and populations are evolutionary hot spots and should be given high priority by plant genetic resources conservation programs (Frese et al. 2018).

6.4 The Genepool

Crop wild relatives are those genetically related species that can be used to broaden the genetic base of the crop. The phylogenetic distance between the potential donor and the crop species determines the amount of investment into breeding research required to introgress a target trait into the crop's breeding pool and to develop improved varieties. To indicate the degree of relatedness Harlan and de Wet (1971) suggested categorizing species into primary, secondary and tertiary genepools. The primary genepool is composed of all forms of the cultivated species (GP-1A) and closely related wild species (GP-1B). Among the species of GP-1 crossing is easy, the hybrids are fertile and gene segregation is approximately normal. Species of the secondary genepool (GP-2) can be crossed but introgression of a trait into the crop is more difficult due to limited seed set, only partially fertile hybrids, insufficient chromosome pairing or other phenomena. Seed set after crosses between the crop and species of the tertiary genepool (GP-3) is more or less possible but seedlings may show a range of abnormalities for instance lack of root formation.

Researchers have been interested in utilizing the genetic resources of wild species since the emergence of sugar beet breeding programs at the end of the nineteenth century and the beginning of the twentieth century (see Chap. 1). As compared to other wild species of the genus *Beta* and *Patellifolia*, an impressive number of *Beta maritima* population has been sampled in the wild and preserved in Genebanks (Frese 2010). From the plant breeder's perspective, *Beta maritima* is the most valuable species as it not only contains several important resistance genes but can be easily crossed with the sugar beet.

Experimental crosses between species within the genus *Beta* (including *Patellifolia* species) have been conducted for two reasons: (i) to enlarge or replenish the sugar beet breeding pool and (ii) to investigate the genetic and evolutionary relationships between species. Interspecific hybrids have played a key role for enhancing the yield and yield stability of the sugar beet crop. Indeed, wild germplasm has been (and is) used in breeding programs to improve the genetic resistance to sugar beet diseases and pests important for economically and ecologically sound sugar beet production worldwide (see Chap. 8).

Crossing experiments along with cytological studies have been the only way to study the phylogeny of wild beet species until the development of molecular marker technologies. Today, the results of cytological studies can be combined with the results from genetic marker-based phylogenetic studies to describe the position of wild beet species in the crop genepool with greater precision. An enormous amount of detailed information on crossing experiments has been published since then and can be applied to categorize wild beet species according to the genepool concept. A division of wild beet species into the primary, secondary, and tertiary genepool has been suggested by Frese (2010).

Abe and Shimamoto (1989) found no consistent reproductive barriers between *Beta vulgaris* subsp. *vulgaris* and *Beta maritima*. A high percentage of male sterile plants in the backcross generation of *Beta macrocarpa* (A1171) crossed with sugar beet observed by Oldemeyer (1957) is likely the first documented evidence of reproductive barriers between *Beta vulgaris* subsp. *vulgaris* and *Beta macrocarpa*. Abe and Shimamoto (1989) observed pollen and seed abortion in F1 hybrids between *Beta macrocarpa* and *Beta patula*, respectively, with *Beta maritima* and *Beta vulgaris* subsp. *vulgaris* and noted chlorotic plants, dwarf plants, complete male sterile plants and semi-fertile plants in the F2. In addition, significant deviation from the expected F2 segregation ratios of three isozyme loci was observed in the F2 of *Beta macrocarpa* x *Beta vulgaris* subsp. *vulgaris* (Abe et al. 1984) and the reciprocal cross (Abe and Tsuda 1986). By backcrossing the material, Abe and Tsuda (1987) even produced B2F1-plants. Weak reproductive barriers clearly exist but species crosses and backcrosses within section *Beta* are straightforward. Placing *Beta macrocarpa* and *Beta patula* into the GP1 B is therefore justified.

Section *Corollinae* includes *Beta corolliflora*, *Beta macrorhiza*, and *Beta lomatogona*, which Buttler (1977) considers as the base species of derived kinship groups. *Beta nana* and the three base species are sexually isolated and morphologically clearly distinct, populate differing habitats and distribution areas, and therefore match the main criteria for true species (Buttler 1977; Phitos et al. 1995). Filutowicz and Dalke (1976) and Cleij et al. (1976) first introduced genome formulae to designate the genome components in kinship groups and progenies derived from interspecific crosses (see Table 6.4).

Table 6.4 Genome formula of wild beet species according to Cleij et al. (1976), Filutowicz and Dalke (1976), and Dechyeva and Schmidt (2009). *Beta* section *Beta* and section *Corollinae* as well as the genus *Patellifolia* form polyploidy complexes. Not all possible combinations are presented here

Species	Genome formula
Beta vulgaris subsp. *vulgaris* (varieties)	VV, VVV, VVVV
Beta vulgaris subsp. *maritima*, *Beta vulgaris* subsp. *adanensis, Beta patula*	VV
Beta macrocarpa	VV, VVVV
Beta corolliflora	CCCC
Beta macrorhiza	MM
Beta lomatogona	LL
Beta trigyna	LLCCCC
Beta intermedia	?
Beta nana	NN[a]
Patellifolia procumbens	PP[a]
Patellifolia webbiana	PP[a]
Patellifolia patellaris	PP??

[a] Suggested by the authors of this book chapter

Very comprehensive cytological studies were conducted mainly in Poland and in The Netherlands to investigate the phylogeny of *Corollinae* species and to find ways to tap the secondary genepool for sugar beet breeding. These studies have greatly contributed to our understanding of the relationships between *Corollinae* species and the ploidy complex existing within section *Corollinae*. Dalke (1977) crossed sugar beet ($2 = 36$) with *Beta corolliflora* and backcrossed the F1 with sugar beet to introgress mosaic virus resistance from the wild species. Of 1570 B2 to B4 plants, 517 virus-resistant plants were selected with chromosome numbers ranging between 18 and 40. Three diploid-resistant B3 plants probably contained only a small wild species chromosome fragment as indicated by the regular course of the meiosis. Vasilchenko and Zhuzhzhalova (2011) paired *Beta vulgaris x Beta corolliflora* and produced triploid hybrid plants. Selection in the progenies gave plants with conical roots, cytoplasmic male sterility, and a high percentage of monogerm plants. The introgression of *Beta corolliflora* genes into the sugar beet breeding lines was evidenced with a *Beta corolliflora*-specific genetic marker. The chromosomes of *Beta corolliflora* can be distinguished clearly from *Beta vulgaris* chromosomes with the genomic in situ hybridization technique (Desel et al. 2002). The authors noticed a weak hybridization of *Beta vulgaris* chromosomes with *Beta corolliflora* DNA and interpreted this observation as hybridization between repetitive sequences that are conserved in both species.

Szota (1995) crossed sugar beet with *Beta macrorhiza*, *Beta lomatogona*, and *Beta corolliflora* and noticed strong disturbance in meiosis likely caused by a lack of chromosome homology between *Beta vulgaris* subsp. *vulgaris* (sugar beet group) and

Corollinae species. Interspecific hybrids with *Beta corolliflora* or *Beta lomatogona* as male parent were generally partial to fully sterile. Cleij et al. (1976) produced backcross progenies ((sugar beet 2x x *Beta lomatogna* 4x) x sugar beet 2x) and identified plants with amphidiploid genome composition (VVLL). Furthermore, amphihaploid, male sterile offspring of VVLL plants showed some bivalent pairing in meiosis, indicating partial homology between *Beta vulgaris* and *Beta lomatogona* chromosomes. Fertile hybrids were obtained from sugar beet x *Beta macrorhiza* crosses. These hybrids showed regular meiosis and their chromosomes paired in bivalents. Szota (1995) concluded from the experimental results that *Beta macrorhiza* may be phylogenetically closer to *Beta vulgaris* than *Beta corolliflora* and *Beta lomatogona*. The experimental results evidence that introgression of a trait from the base species of section *Corollinae* into the crop species is difficult due to limited seed set, only partially fertile hybrids, insufficient chromosome pairing or other disorders, but it is not impossible. *Beta corolliflora*, *Beta macrorhiza*, and *Beta lomatogona* thus clearly match the criteria of species belonging to the secondary genepool. *Beta nana*, however, has never been used in crossing experiment. Barocka (1985) suggested a close relationship between *Corollinae* species and *Beta nana*. Phylogenetic studies using plastid DNA substantiated this assumption (Fritzsche et al. 1987). Gao et al. (2000) found high homology between the *Beta corolliflora*-specific satellite sequences pBC1279 and pBC1944 with *Beta nana*-specific repeat sequence pRN1 (Kubis et al. 1997). They assumed that the three sequences originated from a common ancestor. Kadereit et al. (2006) finally decided to place *Beta nana* into section *Corollinae* as mentioned earlier in this chapter. Since the criteria of Harlan and de Wet (1971) cannot be applied to the close phylogenetic relationship between *Corollinae* species and *Beta nana* justifies placing this species in the secondary genepool, too.

Two additional accepted taxa of *Corollinae* exist: *Beta trigyna* and *Beta* x *intermedia* (see the USDA-ARS GRIN taxonomy site, www.usda-grin.gov) which Buttler (1977) considers the hybrid species within section *Corollinae*. *Beta trigyna* includes the autotetraploid parental species *Beta corolliflora* and the diploid *Beta lomatogona*. The first indications on the autotetraploid nature of *Beta corolliflora* were given by Ramos-Büttner and Wricke (1993) and this assumption was further substantiated by Gao et al. (2000). Paesold et al. (2012) found two pairs of chromosome 1 in a sample of *Beta corolliflora*, which is further evidence of the autotetraploid nature of the species. Filutowicz and Dalke (1976) concluded from their crossing experiments that *Beta trigyna* ($2n = 54$, genome formula LLCCCC) stems from crosses between *Beta lomatogona* ($2n = 18$; genome formula LL) x *Beta corolliflora* ($2n = 36$, genome formula CCCC). Arapova (1987) crossed diploid *Beta vulgaris* with hexaploid *Beta trigyna*. After pollination of *Beta vulgaris* with *Beta trigyna* only a single hybrid plant was obtained (0.7% of all harvested seeds) while no hybrid plant was found in the reciprocal crosses. Cleij et al. (1968) succeeded to produce F1-hybrid plants and backcross progenies with a tetraploid plant named *Beta intermedia* as pollinator and tetraploid *Beta vulgaris* as seed parent. The hybrid species can be crossed with crop species and backcross progenies can be produced without need for the application of special techniques. The categorization of *Beta trigyna* and *Beta intermedia* as members of the secondary genepool is therefore justified.

Polish researchers paired the base species of section *Corollinae* in different combinations to unravel the phylogeny of the section *Corollinae* species (all possible combinations except for *Beta corolliflora* x *Beta macrorhiza* and *Beta lomatogona* x *Beta corolliflora*). Jassem and Jazdzewska (1980) crossed *Beta macrorhiza* x *Beta lomatogona* (2n = 18) and obtained fertile progeny. Some spontaneous polyploid and fertile apomicts were found in the progeny of *Beta macrorhiza* x *Beta lomatogona* (2n = 18) showing that apomicts can be created by crossing normally sexually reproducing *Corollinae* species. Jassem et al. (1985) said that *Beta macrorhiza* (2n = 18) and *Beta lomatogona* (2n = 18) could be crossed rather easily and gave fertile progeny. Both tended to develop unreduced male gametes, which leads to the development of polyploids. The meiosis of *Beta macrorhiza* (2n = 18) x *Beta lomatogona* (2n = 18) proved to be regular and bivalents were formed (Szota 1995), which indicates a close relationship between both amphimictic species.

Apomixis is strongly expressed in *Beta lomatogona* (2n = 36) and *Beta trigyna* (2n = 54). Chromosome pairing in bivalents and quadrivalents was often observed in offspring of *Beta macrorhiza* (2n = 18) x *Beta trigyna* (2n = 54), whereas chromosome pairing occurred only sporadically in offspring of *Beta lomatogona* (2n = 18) x *Beta trigyna* (2n = 54). The chromosome homology between *Beta macrorhiza* x *Beta trigyna* seems to be stronger as compared to *Beta lomatogona* x *Beta trigyna* indicating that *Beta macrorhiza* is phylogenetically closer to *Beta trigyna* (Szota and Kuzdowicz 1978). Sufficient potential for species crosses within the section *Corollinae*, the tendency to polyploidy combined with facultative apomixis results in the development and fixation of different hybrid forms within the natural habitat and creates a hybrid swarm and a common agamic complex. Jassem (1992) reviewed the extensive crossing experiments and cytological studies of the Polish researchers and concluded from the experimental results that *Beta macrorhiza* is phylogenetically closer to section *Beta* species, *Beta lomatogona* more distant and *Beta corolliflora* maintains an intermediate position. Conclusions with respect to the phylogenetic position of the agamic ploidy complex (*Beta trigyna*, *Beta* x *intermedia*) were not drawn indicating the need for further research.

Patellifolia species have been considered a genetic resource for sugar beet breeding since the beginning of systematic sugar beet breeding (for instance, de Vilmorin 1923). Interestingly, the great potential of *Beta maritima* as gene donor has been overlooked or underestimated and breeding researchers focused efforts on *Beta* section *Corollinae*. Useful pre-breeding material developed from interspecific crosses did not result from the extensive research work (Barocka 1959; Szota 1995; Cleij et al. 1968, 1976). Instead, *Patellifolia* species that proved to be most difficult to handle were the first of the distantly related wild beet species contributing an economically highly valuable trait, the resistance to the beet cyst nematode (*Heterodera schachtii*), to the sugar beet breeding pool.

Szota (1995) conducted crosses among *Patellifolia* species. The F1-generation of *Patellifolia procumbens* 2x x *Patellifolia webbiana* 2x and reciprocal crosses showed a high percentage (>77.9%) of pollen mother cells without any disturbances at anaphase I, II and tetrad stages and a high percentage of viable pollen (87.2–91.1%). When using the self-compatible tetraploid species *Patellifolia patellaris* as pollinator, the percentage of undisturbed PMC at all stages ranged between 14.8 and 42.1% and the pollen viability dropped to between 13.9 and 34.1%. The lack of crossing barriers between *Patellifolia procumbens* and *Patellifolia webbiana* indicates that both outbreeding species are closely related or may even be genetically strongly differentiated forms of the same species. Indeed, there is increasing evidence from diversity studies using isozyme markers (Wagner et al. 1989), RFLP markers (Mita et al. 1991), DNA fingerprinting (Jung et al. 1993), and SSR markers (Frese et al. 2018) that *Patellifolia webbiana* constitutes a spatially isolated population of *Patellifolia procumbens* adapted to a specific habitat. These pieces of evidence have relevance with respect to assumptions on the evolution of *Patellifolia patellaris* which Walia (1971) supposed to be an allotetraploid species. Dechyeva and Schmidt (2009) labeled *Patellifolia procumbens* as well as *Patellifolia patellaris* chromosomes with *Patellifolia procumbens* satellite DNA (clone pTS5) and found in the tetraploid *Patellifolia patellaris* probe the same number of signals as observed in *Patellifolia procumbens*. This genomic in situ hybridization pattern suggests that *Patellifolia procumbens* could be one of the parent species of the likely allopolyploid *Patellifolia patellaris*. Mesbah et al. (1997a, b) characterized monosomic addition lines of sugar beet carrying different chromosomes from *Patellifolia patellaris*. The presence or absence of the *Heterodera schachtii* resistance gene in specific families could best be explained by the existence of two homologous chromosomes 1 in an allotetraploid *Patellifolia patellaris* carrying the resistance gene and two homeologous chromosomes without that gene. Mesbah et al. (1997a, b) found chromosome addition families derived from *Patellifolia patellaris* to be completely resistant to *Polymyxa betae*. However, the introgression of traits suited to enhance the resistance of sugar beet to pests and diseases is very difficult. Desel et al. (2002) used genomic DNA of *Patellifolia procumbens* to detect chromatin of *Patellifolia procumbens* in nematode resistant *Beta vulgaris* introgression lines. They observed, unlike the weak labeling of *vulgaris* chromosomes with *Beta corolliflora* DNA, no labeling of the *Beta vulgaris* chromosomes with *Patellifolia procumbens* DNA. Their observation further underpins that the phylogenetic difference between *Patellifolia* species and *Beta vulgaris* is greater than the difference between section *Corollinae* species and *Beta vulgaris*.

In hybrids between sugar beet and *Patellifolia* species almost no chromosome pairing occurs in meiosis causing development and fertility distortions. Speckmann and de Bock (1982) and Löptien (1984) reported the main problems impeding the introgression of traits from the *Patellifolia* species into the sugar beet. *Beta vulgaris* x *Beta procumbens* F1 and BC1 plants lacked functioning roots and seedlings need to be grafted to *Beta vulgaris* hypocotyls to produce flowering plants. F1-plants show high degrees of sterility and even plants of backcross generations do not thrive well. Only after extensive crossing and screening work Savitsky (1978) succeeded to select introgression lines carrying the resistance to *Heterodera schachtii* from *Patellifolia procumbens*. There is therefore sufficient experimental evidence that

Patellifolia species match the criteria of Harlan and de Wet (1971) for species of the third genepool.

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