# A synopsis of Chenopodiaceae subfam. Betoideae and notes on the taxonomy of Beta

Authors: Kadereit, Gudrun, Hohmann, Sandra, and Kadereit, Joachim W.

Source: Willdenowia, 36(1) : 9-19

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: https://doi.org/10.3372/wi.36.36101

GUDRUN KADEREIT, SANDRA HOHMANN & JOACHIM W. KADEREIT

# A synopsis of *Chenopodiaceae* subfam. *Betoideae* and notes on the taxonomy of *Beta*


## Abstract

Kadereit, G., Hohmann, S. & Kadereit, J. W.: A synopsis of *Chenopodiaceae* subfam. *Betoideae* and notes on the taxonomy of *Beta.* – Willdenowia 36 (Special Issue): 9-19. – ISSN 0511-9618; © 2006 BGBM Berlin-Dahlem.
doi:10.3372/wi.36.36101 (available via http://dx.doi.org/)

A synopsis of the phylogeny and systematics of subfamily *Betoideae* of the *Chenopodiaceae* is provided and a modified subfamilial classification proposed. *Betoideae* contain five or six genera, i.e. *Beta, Patellifolia, Aphanisma, Oreobliton* and *Hablitzia*. The inclusion of *Acroglochin* in *Betoideae* is not clearly resolved by molecular evidence. The five genera (excl. *Acroglochin*) fall into two clades. These are *Beteae* with *Beta* only, and *Hablitzieae* with the remaining four genera. Of these four genera, *Patellifolia* formerly has been regarded as a section of *Beta (B.* sect. *Procumbentes).* The closer relationship of *Patellifolia* to *Hablitzieae* rather than to *Beta* is supported not only by molecular but also by flower morphological characters. Molecular evidence, in part newly generated, suggests that *Beta* can be divided into two well-supported groups. These are *B.* sect. *Corollinae* and *B.* sect. *Beta.* The often recognized unispecific *B.* sect. *Nanae* should be included in *B.* sect. *Corollinae*. In *B.* sect. *Beta,* probably only two species, *B. macrocarpa* and *B. vulgaris,* should be recognized.


Key words: angiosperms, beets, *Patellifolia,* phylogenetic systematics, ITS, morphology.

## Introduction

The *Betoideae* are a small subfamily of the *Amaranthaceae/Chenopodiaceae* alliance, comprising between 11 and 16 species in five genera, dependent mainly on the classification of *Beta* L. sect. *Beta.* Recent family-wide molecular studies (Kadereit & al. 2003, Pratt 2003, Müller & Borsch 2005) based on cpDNA markers produced conflicting results concerning the position of *Betoideae* within the alliance, and raised doubts about the monophyly of the subfamily. In the *rbc*L study by Kadereit & al. (2003), three betoidean clades were part of a basal polytomy that also included *Amaranthaceae* s.str., *Polycnemoideae,* and the remaining *Chenopodiaceae.* In the *ndh*F analysis by Pratt (2003) the two genera included were also part of a basal polytomy, and in the *mat*K analysis by Müller & Borsch (2005) representatives of *Betoideae* (except for *Acroglochin* Schrad.) were sister to a clade comprising *Salicornioideae, Suaedoideae* and *Salsoloideae,* and therefore were part of *Chenopodiaceae* s.str. These three studies, however, were based on a relatively small sample of *Betoideae*.

A more detailed molecular study by Hohmann & al. (2006), including all genera of the subfamily in its traditional circumscription (Ulbrich 1934, Kühn & al. 1993) and representatives of all sections of *Beta,* and using the same cpDNA markers as in the aforementioned family-wide studies plus the *trn*L intron and ITS as more variable markers, clearly showed that *Betoideae* are monophyletic and comprise *Beta, Patellifolia* A. J. Scott & al. (= *Beta* sect. *Procumbentes* Ulbr.), *Aphanisma* Nutt. ex Moq., *Hablitzia* M. Bieb. and *Oreobliton* Durieu. Only *Acroglochin,* always considered part of *Betoideae* (Volkens 1892, Ulbrich 1934, Kühn & al. 1993), belongs to the *Chenopodioideae/Corispermoideae* lineage according to the *mat*K data (Müller & Borsch 2005, Hohmann & al. 2006), or is part of a basal polytomy within the *Amaranthaceae/Chenopodiaceae* alliance according to the *rbc*L data (Kadereit & al. 2003). In the *ndh*F data, *Acroglochin* is sister to the remaining *Betoideae* without bootstrap support (Fig. 1; Hohmann & al. 2006).

The *Betoideae* share a unique fruit type, a capsule that normally opens with a circumscissile lid. The fruits of other *Amaranthaceae/Chenopodiaceae* usually are nuts or achenes, or rarely berries. The presence of a capsule with a circumscissile lid in *Acroglochin* on the one hand and the molecular data just described on the other hand do not permit a final decision on the relationships of *Acroglochin* to *Betoideae.* This should await further data. The subfamily shows high diversity in habit by comprising annual, biennial or perennial herbs, vines and subshrubs, and also in ecology (see below). This may reflect its relatively old age estimated to 48.6-35.4 million years (my) by Hohmann & al. (2006). Old age of the subfamily may also account for its disjunct geographical distribution (Fig. 2, see also below). The position of the *Betoideae* within the *Amaranthaceae/Chenopodiaceae* alliance, however, remains unclear also in the study of Hohmann & al. (2006). The aim of this paper is to summarize the phylogenetic knowledge available for *Betoideae,* to translate this into a modified classification and to characterize its constituent taxa. We also will briefly comment on the taxonomy of *Beta.* For the latter purpose, ITS1 sequences of *Beta* by Shen & al. (1998), Hohmann & al. (2006), and eleven newly generated sequences are combined and analysed.

## Material and methods

Herbarium specimens from M and MJG (abbreviations according to Holmgren & Holmgren 1998-) as well as material cultivated at the Botanical Garden of Mainz University (deposited at MJG) from seeds obtained from the Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK) Gatersleben were used to verify or supplement the information found in the literature and to extract DNA.

Eight ITS sequences were obtained from GenBank (species and accession number): *Aphanisma blitoides* Nutt. ex Moq.: AY858591; *Beta corolliflora* Zosimovich ex Buttler: AY858598; *B. nana* Boiss. & Heldr.: AY858596; *B. trigyna* Waldst. & Kit.: AY858595; *B. vulgaris* L.: AY858597; *Hablitzia tamnoides* M. Bieb.: AY858590; *Oreobliton thesioides* Durieu & Moq.: AY858592; *Patellifolia procumbens* (C. Sm.) A. J. Scott & al.: AY858594. Ten sequences were taken from Shen & al. (1998; species and accession number of the Beet Germplasm Collection of the University of Birmingham): *Beta lomatogona* Fisch. & C. A. Mey.: B0213; *B. macrorhiza* Steven: B0397; *B. trigyna:* B0367; *B. corolliflora:* B0537; *B. maritima* L.: B0334; *B. adanensis* Pamukç.: B0423; *B. macrocarpa* Guss.: B0588; *B. vulgaris* L. subsp. *vulgaris* var. *vulgaris* (spinach beet) B0051; *B. vulgaris* subsp. *vulgaris* var. *altissima* Döll (sugar beet): B0079; *B. nana: FD19.*

The 11 samples of the newly generated sequences were obtained from plants cultivated at the Botanical Garden of Mainz University. The seeds were kindly provided by the IPK Gaterleben. In the following, the samples are listed with the IPK Gaterleben seed collection number, voucher information and GenBank accession number: *B. macrocarpa:* BETA 331/98, Greece, DQ223061; BETA 220/97, Greece, DQ223062; *B. vulgaris* subsp. *orientalis* (Roth) Aellen: BETA 94/85, India, DQ223064; BETA 330/95, India, DQ223065; *B. vulgaris* subsp. *maritima* (L.) Thell.: BETA 308/98, Ireland, DQ223066; BETA 194/94, Libya, DQ223067; BETA 255/90, Spain, DQ223068;

*B. vulgaris* subsp. *vulgaris:* BETA 6/77, Hungary, DQ223063; BETA 245/88, Iraq, DQ223069; BETA 317/98, India, DQ223070; BETA 8109/96, Italy, DQ223071.

The new sequences were generated using the same protocols for DNA extraction, PCR amplification, primer sequences and sequencing as described in Hohmann & al. (2006). All 29 sequences were aligned using SequencherTM 4.1. Alignment was unproblematic and required only few manual corrections.

The matrix of ITS sequences was executed in PAUP* 4.0b10 (Swofford 2002) and analysed under maximum parsimony (MP) and maximum likelihood (ML) criteria. MP analysis was performed using heuristic searches with 1000 replicates of random taxon addition and tree-bisection-reconnection (TBR) branch swapping. The appropriate model of DNA substitution for the inference of phylogenetic relationships under ML was estimated using Modeltest 3.06 (Posada & Crandall 1998). The GTR+G model was chosen with gamma distribution set to 0.7105. Base frequencies were set to A = 0.25, C = 0.25, G = 0.25, and T = 0.25. The rate matrix was set to AC 1.0, AG 1.37, AT 0.25, CG 0.25, CT 2.73, and GT 1.0. The heuristic search settings were 10 random additions of taxa and TBR swapping. The settings for the ML bootstrap analysis were the same as for the ML heuristic search running 100 replicates. For the MP bootstrap analysis also 10 random additions and 100 replicates were run under the same settings as the heuristic search.

## Results and discussion

### 1. Phylogeny of *Betoideae*

The most comprehensive taxonomic treatment of *Betoideae* by Ulbrich (1934) divided the group into *Hablitzieae* with *Hablitzia, Aphanisma, Oreobliton* and *Acroglochin,* and *Beteae* with only *Beta* (including *Patellifolia* as *B.* sect. *Procumbentes*). In contrast to this, the most recent treatment of *Chenopodiaceae* by Kühn & al. (1993) abandoned the subfamily status of *Betoideae* and combined all genera in one tribe, *Beteae,* within *Chenopodioideae.*

The molecular data by Hohmann & al. (2006), which did not clarify the relationships of *Acroglochin* to *Betoideae,* show a dichotomy within *Betoideae* (excl. *Acroglochin*): *Beta* (with sect. *Beta,* sect. *Corollinae* and sect. *Nanae*) forms a clade that is sister to *Hablitzia, Aphanisma, Oreobliton* and *Patellifolia* (Fig. 1). These findings agree with the tribal classification of Ulbrich (1934) with the notable exception of *Patellifolia.* This group, described (without rank) as *Patellares* by Transhel' (1927) and renamed as *B.* sect. *Procumbentes* by Ulbrich (1934), is not part of *Beta* and the *Beteae* but rather of the *Hablitzieae. Patellifolia* had first been separated from *Beta* by Scott & al. (1977), but this treatment was never generally accepted beyond the regional Flora level (Letschert 1993). Although various molecular analyses (summarized in Shen & al. 1998) of *Beta* had identified *Patellifolia* as a very distinct cluster within the genus, the absence of other genera of *Betoideae* from all these analyses could not reveal the true relationships of this group.

Following Ulbrich (1934), *Hablitzieae* are characterized by an epigynous ovary, a membranous fruiting perianth and stamens that are basally united into a membranous ring. In contrast, *Beteae* have a partly hypogynous ovary, a fruiting perianth that becomes woody at the base, and stamens that are basally united into a fleshy bulge. According to our own observations, *Patellifolia* like *Beta* has perigynous ovaries, but shares a membranous fruiting perianth and a membranous ring at the base of the stamens with the other genera of *Hablitzieae*. Accordingly, the latter two characters support the molecular finding of a closer relationship of *Patellifolia* to *Hablitzieae* than to *Beta* (Fig. 1). *Patellifolia* further differs from *Beta* in having short tepals that do not overtop the fruit (Ulbrich 1934, Letschert 1993).

Within *Hablitzieae, Aphanisma* and *Oreobliton* always are sister to each other in the molecular analyses. The relationships of the *Aphanisma/Oreobliton* clade to *Patellifolia* and *Hablitzia,* however, are not unambiguously resolved. In the *trn*L intron and *mat*K analyses *Hablitzia/Patellifolia* are sister to *Aphanisma/Oreobliton,* and in the ITS and *ndh*F analyses *Hablitzia* is sister to the remaining *Hablitzieae* (Fig. 1 and 3, Hohmann & al. 2006). These conflicting topologies result from the fact that *Hablitzia* shares a number of mutations with both *Patellifolia* and *Apha-*

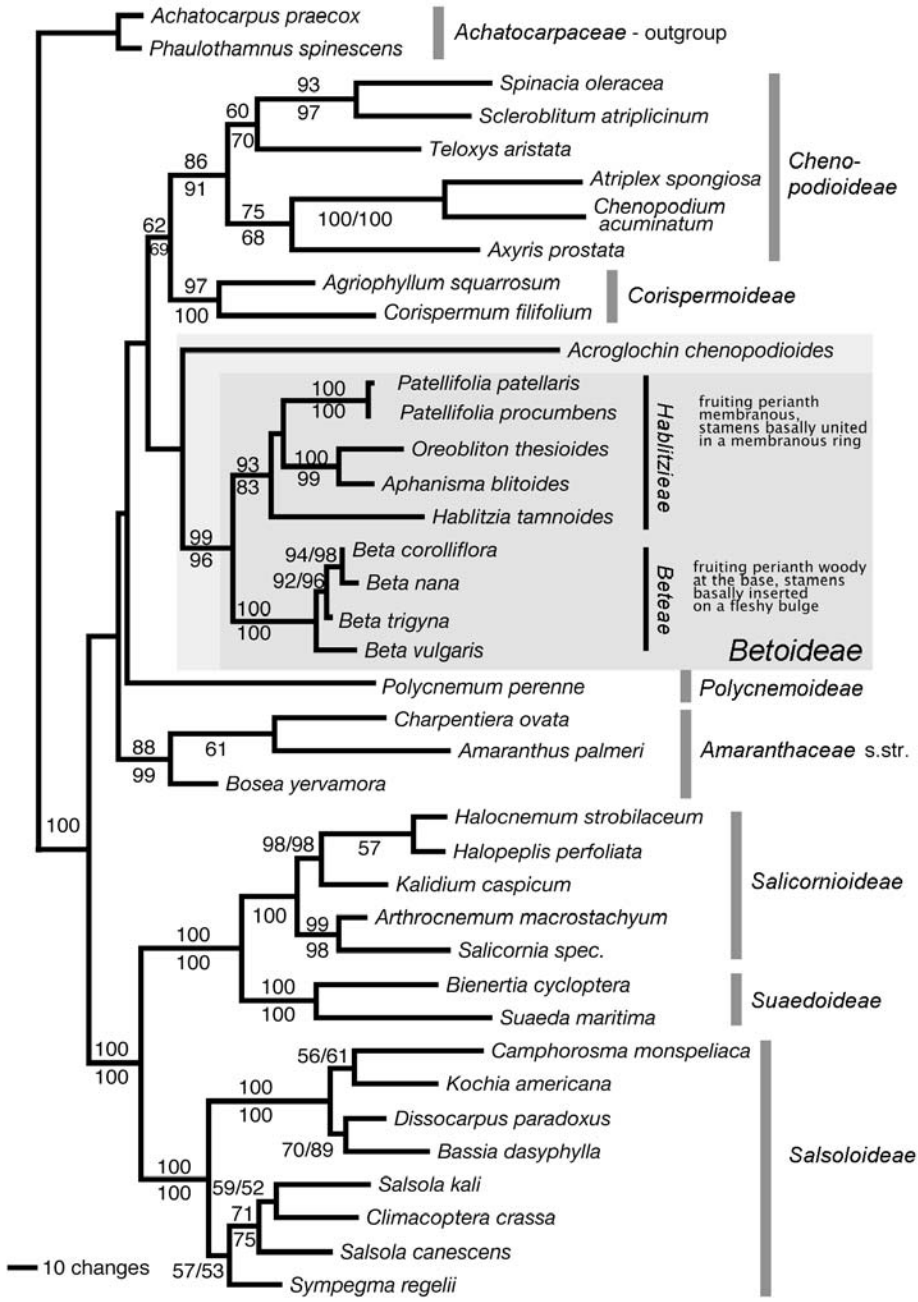


Fig. 1. Maximum Likelihood tree based on 37 *ndh*F sequences of the *Amaranthaceae/Chenopodiaceae* alliance including ten representatives of *Betoideae* taken from Hohmann & al. (2006). The tree was rooted with two representatives of *Archatocarpaceae,* values above and below branches are bootstrap values of the ML and MP analyses, respectively.

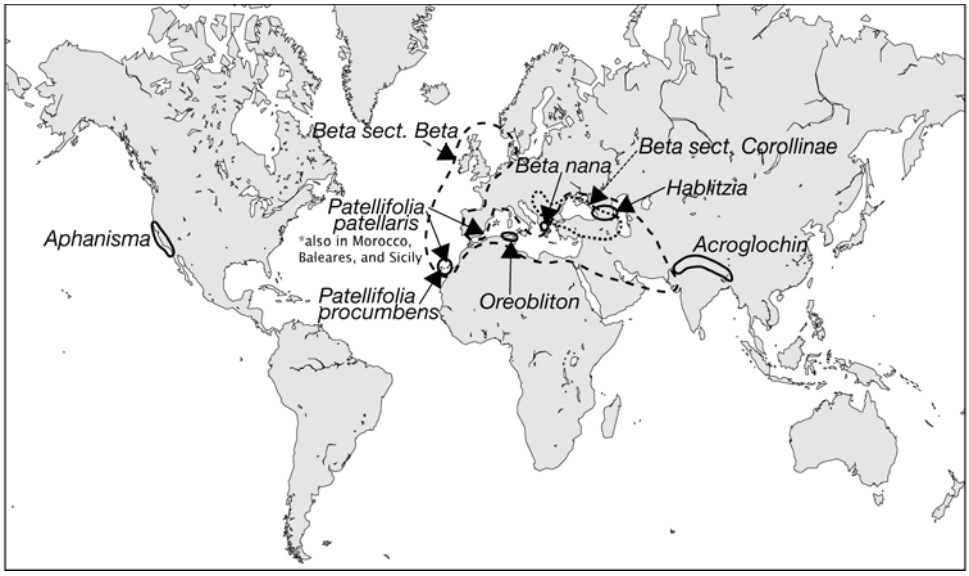


Fig. 2. Geographical distribution of *Betoideae*.

*nisma/Oreobliton.* All three clades are old (32.7-18.6 my according to Hohmann & al. 2006), morphologically and genetically heterogeneous and species-poor. Therefore, they are best interpreted as relict taxa as suggested by Kadereit & al. (2003). The *Hablitzieae* probably experienced dramatic extinction, which might obscure the true interrelationships of the three clades found.

### 1.1. *Hablitzieae*

*Aphanisma and Oreobliton.* – The unispecific *Aphanisma* (*A. blitoides* Nutt. ex Moq.) occurs in coastal habitats in California (Munz 1974, Shultz 2003). *Aphanisma* is an annual plant with prostrate and erect branches. The inflorescences consist of three to five (or fewer) flowers tightly aggregated in the axils of foliose bracts. The flowers have only three tepals and one stamen. This is unique in *Betoideae,* which normally have five tepals and five stamens. In fruit the tepals are not spreading as in *Oreobliton* and *Hablitzia* but tightly enclose the lower half of the fruit. The unispecific N African *Oreobliton* (*O. thesioides* Durieu & Moq.) is sister to *Aphanisma. Oreobliton* is found in the Algerian and Tunesian Atlas (Maire 1961), where it grows in calcareous rock fissures at 400-1000 m altitude. It is a subshrub, and the pentamerous flowers are arranged in few-flowered thyrses in the axils of foliose bracts. It shares some morphological characters with *Aphanisma,* including tepals with only one nerve, a globose, longitudinally compressed capsule opening above the lower third with a smooth-rimmed lid, and seeds with a crustaceous testa.

The peculiar North American/N African disjunction of the *Aphanisma/Oreobliton* clade was estimated to be 15.4-9.2 my old by Hohmann & al. (2006). These authors, also considering the possibility of long distance dispersal, interpret this disjunction as a remnant of a Beringian ancestral range. Such interpretation implies that the evolution of the two genera into dry habitats took place in parallel in western Eurasia and western North America.

*Hablitzia.* – The perennial *Hablitzia* is unispecific (*H. tamnoides* M. Bieb.) and one of the very few vines in *Chenopodiaceae.* The genus is restricted to the Caucasian floristic region (Meusel & al. 1965), where it grows in mesic deciduous forests (Grossgeim 1945). Apart from its climbing habit, *Hablitzia* is characterized by a persistent fleshy root whereas the above-ground stems die off in autumn. The pentamerous flowers are arranged in often many-flowered thyrses in the axils

of foliose bracts. In each terminal cyme, the lateral flowers are present only as vestigial buds below the terminal flower. *Oreobliton* and *Hablitzia* are similar in flower morphology and share the star-like arrangement of the persistent tepals in fruit.

*Patellifolia.* – *Patellifolia* comprises two or three species, *P. patellaris, P. procumbens* and *P. webbiana* (Moq.) A. J. Scott & al. Whereas the latter two species are restricted to the Canary Islands, *P. patellaris* is also found in southern Spain, the Balearic Islands, Sicily, Algeria and Morocco (Fig. 2). *Patellifolia* comprises perennial procumbent plants with glomerules of 1-3 flowers in the axils of foliose bracts. *P. procumbens* and *P. patellaris* form a strongly supported monophyletic group (Fig. 1). A 600 bp fragment of *ndh*F of the third species *(P. webbiana)* sequenced from the more variable 3' end of the gene is identical with that of *P. procumbens,* and therefore was not included in further analyses (S. Hohmann, unpubl. data). Curtis (1968) doubted whether *P. procumbens* and *P. webbiana* are separate species. His experiments showed that the tetraploid (2n = 36) *P. patellaris* is self-compatible and that the other two species are diploid and self-incompatible. Whereas attempts of hybridisation between *P. patellaris* and the other two species failed, *P. procumbens* and *P. webbiana* could be hybridized easily. The three species also differ in their resistance to eelworms (*Heterodera schachtii* Schm.). Whereas the resistance of *P. patellaris* is not complete, eelworms never develop to maturity in the other two species (Curtis 1968). An isozyme analysis by Wagner & al. (1989) revealed no differences between *P. procumbens* and *P. webbiana,* and very little difference was found in an RFLP analysis of total RNA by Mita & al. (1991). These and similar results from other molecular studies (summarized in Shen & al. 1998) can be regarded as support of Curtis' (1968) observations.

Although *Patellifolia* appears to be a rather old genus (30.9-15.3 my) based on different markers), its diversification took place only in the late Pliocene or early Quarternary (*ndh*F: c. 1 mya, *trn*L-intron: c. 3.5 mya; Hohmann & al. 2006). The geographical distribution of the three (or two) species, with *P. procumbens* and *P. webbiana* growing only in the Canary Islands, and *P. patellaris* in the Canary Islands and the W Mediterranean area, in combination with ploidy level, raises the interesting and unusual possibility that the Mediterranean area was colonized from the Canary Islands by the tetraploid selfer *P. patellaris.*

### 1.2. *Beteae*

*Beta.* – *Beta* comprises annual, biennial and perennial herbs. Similar to *Patellifolia,* 1-3 flowers are arranged in tight axillary glomerules, but bracts can be either bracteose or foliose. Transhel" (1927) divided *Beta* into three informal groups, i.e. *Vulgares, Corollinae* and *Patellares.* Ulbrich (1934) treated these three groups at sectional rank and introduced *B.* sect. *Nanae* with only *B. nana* from Greece as a fourth section. He also renamed Transhel"'s (1927) *Patellares* as *B.* sect. *Procumbentes.* His naming of *B.* sect. *Vulgares,* containing the type of the genus, was corrected to *B.* sect. *Beta* by Coons (1954). As discussed above, *B.* sect. *Patellares* needs to be excluded from the genus and classified as a separate genus, *Patellifolia.* Different problems are related to the remaining sections.

*Beta* sect. *Corollinae* is the least problematic, and most authors have considered this group to contain four species, *B. lomatogona, B. macrorhiza, B. corolliflora* and *B. trigyna,* growing at inland localities mostly above 300 m (Ford-Lloyd & Williams 1975) in the E Mediterranean area and SW Asia. Tepals are corolla-like and whitish, yellowish or reddish in *B. trigyna* and *B. corolliflora,* but greenish in *B. lomatogona* and *B. macrorhiza.* The inclusion of *B. trigyna* in *B. corolliflora* by Buttler (1977a) is not supported by several molecular analyses (summarized in Shen & al. 1998) including our own. The species appears to be more closely related to *B. macrorhiza* than to *B. corolliflora* (Fig. 3).

Although the specific status of the Greek mountain endemic *Beta nana,* a perennial plant with small rosettes and procumbent inflorescences with 1-flowered partial inflorescences (Tan 1997), has never been doubted, its classification in a section of its own *(B.* sect. *Nanae)* is questionable. Thus, the studies by, e.g., Shen & al. (1998) and Jung & al. (1993) resolve *B. nana* in a position within *B.* sect. *Corollinae.* Our sequence data are not conclusive at this point. Here, *B. nana* is part

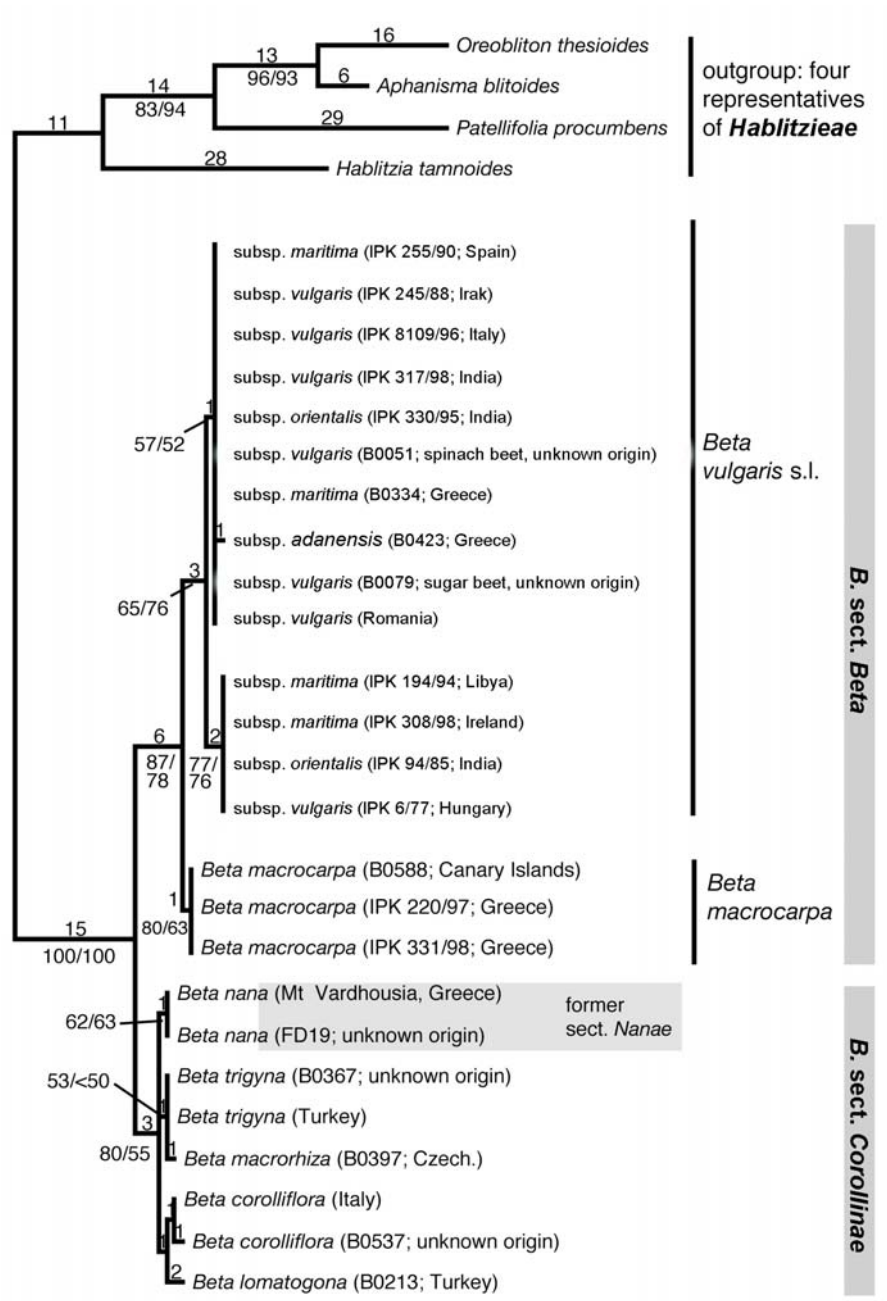


Fig. 3. ML tree of *Beteae* based on 29 ITS1 sequences including four members of *Hablitzieae* which served as outgroup (best score 1040.4.5; bootstrap values (MP value/ML value) below branches, number of character changes above branches). The data matrix comprised 251 characters of which 147 were invariable, 47 variable but uninformative, and 57 parsimony informative. The MP analysis (not shown because of nearly identical topology) found four shortest trees of 157 steps length with CI = 0.841 and RI = 0.885. The data matrix contained eight informative indels. If these were coded in a 0/1 matrix and included in the MP analysis, again four shortest trees with the same topology but of 167 steps length were found.

of an unresolved trichotomy with *B. trigyna/B. macrorhiza* and *B. corolliflora/B. lomatogona* (Fig. 3). Considering these results and the distribution of *B. nana* well within the range of *B.* sect. *Corollinae,* we here suggest to merge the two sections as earlier suggested by Zosimovic (1940). In all molecular analyses (summarized by Shen & al. 1998), *B.* sect. *Corollinae* plus sect. *Nanae* are clearly distinct from *B.* sect. *Beta.* This is supported by our results, where the basal dichotomy in the genus separates *B.* sect. *Beta* from *B.* sect. *Corollinae* and sect. *Nanae.* These two clades are in fact the only supraspecific clades with acceptable bootstrap support (Fig. 3).

The subdivision of *Beta* sect. *Beta,* characterized by greenish tepals that are dorsally ridged, have hooded tips and are partly appressed to the fruit, with their free upper parts being mostly longer than the fruit, is most problematic. As summarized by Buttler (1977b), between one and seven wild and cultivated species and between five and 35 wild and cultivated infraspecific taxa have been recognized by different authors. It seems very likely that all wild plants of *B.* sect. *Beta* either grow in coastal or in saline habitats (Ford-Lloyd & Williams 1975, Jalas & Suominen 1980, Greuter & al. 1984, Lange & al. 1999) and that inland plants from other than saline habitats are either cultivated or feral. Although we realize that our sampling of *B.* sect. *Beta* is far from ideal, the major taxa recognized by most modern authors are contained in our ITS1 analysis (e.g., Letschert 1994). The results of this analysis suggest that at least *B. macrocarpa* is different from the *B. vulgaris* group and should be treated at specific rank (Fig. 3). *B. adanensis* Pamukç., recognized by Ball & Akeroyd (1993), groups among the *B. vulgaris* accessions. The status of *B. patula* Aiton, recognized by Letschert (1993, 1994), remains unclear in the absence of material of this taxon. Although we most certainly do not want to suggest a re-classification of *B.* sect. *Beta* based on a limited sample and very few molecular characters, and without critical examination of phenotypic variation of a large sample of plants, we note that the recognition in sect. *Beta* of only *B. macrocarpa* and *B. vulgaris* would be fully congruent with the approach taken by Ball (1964) in the first edition of Flora Europaea. *Beta macrocarpa* is a coastal taxon from the southern Iberian Peninsula and NW Africa, Sicily and Italy, and Greece, Crete and the Aegean as well as Israel (Jalas & Suominen 1980, Greuter & al. 1984). Different authors use partly different characters to distinguish this species (at whatever rank) from *B. vulgaris.* Thus, Aellen (1960) mainly relies on tepal shape and texture, Ball (1964) on the presence and distribution of bracts in the inflorescence, Gutiérrez Bustillo (1990) on the relative length of bracts and partial inflorescences, and Tan (1997) on habit, inflorescence bracts and tepal texture.

A phylogenetic study with the aim to fully resolve relationships within *Beta* should be able to cope with hybridisation, polyploidisation as well as apomixis (Jassem 1976, 1980, Boudry & al. 1993).

## 2. Taxonomy

*Betoideae* Ulbr., Nat. Pflanzenfam., ed. 2, 16c: 455. 1934
- *Beteae* Moq. in Candolle, Prodr. 13(2): 43, 49. 1849
  - *Beta* L., Sp. Pl.: 222. 1753
    - *Beta* sect. *Beta*
    - *Beta* sect. *Corollinae* Ulbr., Nat. Pflanzenfam., ed. 2, 16c: 462. 1934 (incl. *B.* sect. *Nanae* Ulbr., l.c.)
- *Hablitzieae* Ulbr., l.c.
  - *Aphanisma* Nutt. ex Moq. in Candolle, Prodr. 13(2): 43, 54. 1849
  - *Hablitzia* M. Bieb. in Mém. Soc. Imp. Naturalistes Moscou 5: 24. 1817
  - *Oreobliton* Durieu in Rev. Bot. Recueil Mens. 2: 428. 1847
  - *Patellifolia* A. J. Scott & al. in Taxon 26: 284. 1977
- position uncertain: *Acroglochin* Schrad. in Schultes, Mant. 1: 69: 227. 1822

Key to tribes, genera and sections of *Betoideae* (incl. *Acroglochin*)

1. Terminal branches of inflorescence needle-like and without flowers, tepals sparsely covered with hairs . . . . . *Acroglochin*

– Terminal branches of inflorescence not needle-like, tepals glabrous . . . . . 2
2. Stamens basally inserted on a thickened bulge surrounding the visible part of the ovary; tepals conspicuously modified in fruit; flowers fused at their indurated bases . . . . . 3 *(Beteae, Beta)*
– Stamens basally united in a membranous ring; tepals not conspicuously modified in fruit; flowers free . . . . . 4 *(Hablitzieae)*
3. Tepals not hooded at apex, often petaloid, white, yellowish, reddish or greenish . . . . . *Beta* sect. *Corollinae*
– Tepals hooded at apex, not petaloid, green . . . . . *Beta* sect. *Beta*
4. Vine; one or two vestigial buds present beneath each terminal flower (Caucasia and Transcaucasia) . . . . . *Hablitzia*
– Subshrubs or perennial or annual herbs; no vestigial buds present beneath terminal flowers . . . . . 5
5. Tepals 3; stamen 1 (California) . . . . . *Aphanisma*
– Tepals 5, stamens 5 (Old World) . . . . . 6
6. Free part of tepals spreading in fruit (mountains of Tunesia and Algeria) . . . *Oreobliton*
– Free part of tepals appressed to fruit (coasts of Canary Islands, southern Spain, Morocco, Algeria, Baleares, Sicily) . . . . . *Patellifolia*

**Acknowledgements**

We acknowledge the IPK Gatersleben (Germany) for providing seed material, H. Freitag (Kassel) and B. V. Ford-Lloyd (Birmingham) for helpful reviews of the manuscript, D. Franke and L. Klöckner for help with the figures, and the Deutsche Forschungsgemeinschaft (DFG) for financial support to G. Kadereit (Cl188/1-1 and KA1816/1-3).

**References**

Aellen, P. 1960: *Beta* L. – Pp. 550-569 in: Rechinger, K. H. (ed.), Hegi, Illustrierte Flora von Mitteleuropa, ed. 2, **3(2).** – München.

Ball, P. W. 1964: *Beta* L. – Pp. 91-92 in: Tutin, T. G., Heywood, V. H., Burges, N. A., Valentine, D. H., Walters, S. M. & Webb, D. A. (ed.), Flora europaea, ed. 1, **1.** – Cambridge, etc.

— & Akeroyd, J. R. 1993: *Beta* L. – Pp. 110-111 in: Tutin, T. G., Burges, N. A., Chater, A. O., Edmondson, J. R., Heywood V. H., Moore, D. M., Valentine, D. H., Walters, S. M. & Webb, D. A. (ed.), Flora europaea, ed. 2, **1.** – Cambridge, etc.

Boudry, P., Mörchen, M., Saumitou-Laparade, P., Vernet, P. & Van Dijk, H. 1993: The origin and evolution of weed beet: consequences for the breeding and release of herbicide resistent transgenic sugar beets. – Theor. Appl. Genet. **87:** 471-478. [CrossRef]

Buttler, K. P. 1977a: Revision von *Beta* section *Corollinae (Chenopodiaceae)* I. Selbststerile Basisarten. – Mitt. Bot. Staatssamml. München **13:** 255-336.

— 1977b: Variation in wild populations of annual beet *(Beta, Chenopodiaceae).* – Pl. Syst. Evol. **128:** 123-136. [CrossRef]

Coons, G. H. 1954: The wild species of *Beta.* – Proc. Amer. Soc. Sugar Beet Technol. **8:** 142-147.

Curtis, G. J. 1968: Observations on fruit shape and other characters in the species of the section *Patellares,* genus *Beta.* – Euphytica **17:** 485-491.[CrossRef]

Ford-Lloyd, B. V. & Williams, J. T. 1975: A revision of *Beta* section *Vulgares (Chenopodiaceae),* with new light on the origin of cultivated beets. – Bot. J. Linn. Soc. **71:** 89-102.

Greuter, W., Burdet, H. M. & Long, G. 1984: Med-Checklist **1.** – Genève & Berlin.

Grossgeim, A. A. 1945: Flora kavkaza **3.** – Baku.

Gutiérrez Bustillo, A. M. 1990: *Beta* L. – Pp. 478-484 in: Castroviejo, S., Lainz, M., López González, G., Montserrat, P., Muñoz Garmendia, F., Paiva, J. & Villar, L. (ed.), Flora iberica **2.** – Madrid.

Hohmann, S., Kadereit, J. W. & Kadereit, G. (in press): Understanding Mediterranean-Californian disjunctions: evidence from *Chenopodiaceae-Betoideae.* – Taxon.

Holmgren, P. K. & Holmgren, N. H. 1998- (continuously updated): Index herbariorum. – http://sciweb.nybg.org/science2/IndexHerbariorum.asp

Jalas, J. & Suominen, J. 1980: Atlas Florae Europaeae **5.** – Helsinki.

Jassem, B. 1976: Embryology and genetics of apomixis in the section *Corollinae* of the genus *Beta.* – Acta Biol. Cracov., Bot. **19:** 149-172.

— 1980: Origin and reproduction of higher polyploids within the *Corollinae* section of the genus *Beta.* – Genet. Polon. **21:** 18-27.

Jung, C., Pillen, K., Frese, L., Fähr, S. & Melchinger, A. E. 1993: Phylogenetic relationships between cultivated and wild species of the genus *Beta* revealed by DNA "fingerprinting". – Theor. Appl. Genet. **86:** 449-457.[CrossRef]

Kadereit, G., Borsch, T., Weising, K. & Freitag, H. 2003: Phylogeny of *Amaranthaceae* and *Chenopodiaceae* and the evolution of C4 photosynthesis. – Int. J. Pl. Sci. **164:** 959-986.[CrossRef]

Kühn, U., Bittrich, V., Carolin, R., Freitag, H., Hedge, I. C., Uotila, P. & Wilson, P. G. 1993: *Chenopodiaceae.* – Pp. 253-281 in: Kubitzki, K., Rohwer, J. G. & Bittrich, V. (ed.), The families and genera of vascular plants **2.** – Berlin, etc.

Lange, W., Brandenburg, W. A. & de Bock, T. S. M. 1999: Taxonomy and cultonomy of beet (*Beta vulgaris* L.). – Bot. J. Linn. Soc. **130:** 81-96.[CrossRef]

Letschert, J. P. W. 1993: *Beta* section *Beta:* biogeographical patterns of variation, and taxonomy. – Wageningen.

— , Lange, W., Frese, L. & Berg, R. G. van den 1994: Taxonomy of *Beta* Section *Beta.* – J. Sugar Beet Res. **31:** 69-85.

Maire, D. R. 1961: Flore de l'Afrique du Nord **8.** – Paris.

Meusel, H., Jäger, E. & Weinert, E. 1965: Vergleichende Chorologie der zentraleuropäischen Flora **2.** – Jena.

Mita, G., Dani, M., Casciari, P., Pasquali, A., Selva, E., Minganti, C. & Piccardi, P. 1991: Assessment of the degree of genetic variation in beet based on RFLP analysis and the taxonomy of *Beta.* – Euphytica **55:** 1-6.[CrossRef]

Müller, K. & Borsch, T. 2005: Phylogenetics of *Amaranthaceae* based on *mat*K/*trn*K sequence data – evidence from parsimony, likelihood, and Bayesian analyses. – Ann. Missouri Bot. Gard. **92:** 66-102.

Munz, P. A. 1974: A Flora of southern California. – Berkeley, etc.

Posada, D. & Crandall, K. A. 1998: Modeltest: testing the model of DNA substitution. – Bioinformatics **14:** 817-818.

Pratt, D. 2003: Phylogeny and morphological evolution of *Chenopodiaceae-Amaranthaceae* alliance. – Ph. D. Thesis, Iowa State University, Ames.

Scott, A. J., Ford-Lloyd, B. V. & Williams, J. T. 1977: *Patellifolia,* nomen novum *(Chenopodiaceae).* – Taxon **26:** 284.[CrossRef]

Shultz, L. M. 2004: *Chenopodiaceae* Ventenat: 3. *Aphanisma.* – P. 264 in: Flora of North America Editorial Committee (ed.), The flora of North America **4.** – New York & Oxford.

Shen, Y., Ford-Lloyd, B. V. & Newbury, H. J. 1998: Genetic relationships within the genus *Beta* determined using both PCR-based marker and DNA sequencing techniques. – Heredity **80:** 624-632.[CrossRef]

Swofford, D. L. 2002: PAUP*: Phylogenetic analysis using parsimony (*and other methods), Version 4.0.beta10. – Sunderland, MA.

Tan, K. 1997: *Beta* L. – Pp. 110-112 in: Strid, A. & Tan, K. (ed.), Flora hellenica **1.** – Königstein.

Transhel", V. A. 1927: Obzor vida roda *Beta*. – Trudy Prikl. Bot. Genet. Selek. **17:** 203-223.

Ulbrich, E. 1934: *Chenopodiaceae.* – Pp. 379-584 in: Engler, A. & Prantl, K. (ed.), Die natürlichen Pflanzenfamilien, ed. 2, **16c.** – Leipzig.

Volkens, G. 1892: *Chenopodiaceae.* – Pp. 36-91 in: Engler, A. & Prantl, K. (ed.), Die natürlichen Pflanzenfamilien, ed. 1, **1a.** – Leipzig.

Wagner, H., Gimbel, E. M. & Wricke, G. 1989: Are *Beta procumbens* Chr. Sm. and *Beta webbiana* Moq. different species? – Pl. Breed. (New York) **102:** 17-21.

Zosimovich, V. P. 1940: Dikie vidy i proishozhdenie kul'turnoj svekly. – Sveklovodstvo **1:** 17-85.

Address of the authors:
Gudrun Kadereit, Sandra Hohmann, Joachim W. Kadereit, Institut für Spezielle Botanik und Botanischer Garten, Johannes Gutenberg-Universität Mainz, D-55099 Mainz; e-mail: Kadereit@uni-mainz.de