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***Molecular Systematics and Evolution of "wild" crucifers (Brassicaceae or Cruciferae)***

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**Abstract.** This chapter summarizes and introduces the current knowledge on the systematics and evolution of the Cruciferae or Brassicaceae (mustard family), with a special emphasis on the tribal classification and relationships. Within the past two decades, the utilization of molecular markers has dramatically changed our perspectives on almost every biological aspect of this fascinating and economically important family. These findings are discussed herein together with the newest classification of the family and the ongoing projects to introduce the family as a model for evolutionary biology of plants, along with its well-known model organisms such as *Arabidopsis thaliana* and some *Brassica* species. Genome-wide studies, combined with findings from other fields (e.g., cytogenetics, cell biology, development, phylogeography, molecular phylogeny), enable us to use also the whole genome for comparative studies. These studies enriched our knowledge about the evolution of characters, evolutionary history, past migrations, and the infrastructure and circumscription of the major lineages within the family.

The past two decades are characterized by the tremendously increasing number of studies focusing on systematics, development, phylogenetics, and phylogeography of cruciferous plants (mustards). The Brassicaceae (Cruciferae) is a large plant family (338 genera and 3709 species; see Warwick et al., 2006b) of major scientific and economic importance. Almost a century after Hayek's (1911) major taxonomic account, which was followed by the more thorough monograph of Schulz (1936), we are now closer to the first comprehensive phylogenetic system of the mustard family. The increasing importance of *Arabidopsis* and *Brassica* species as model organisms in the plant sciences has greatly advanced the research in systematics, taxonomy, evolution, and development on the entire family, including the cultivated taxa and their wild relatives.

The first attempt to summarize knowledge of the family was provided over 30 years ago (Vaughan et al., 1976). It was followed by Tsunoda et al. (1980) that dealt with the biology and breeding of *Brassica* crops and their wild allies. During the last 20 years, molecular biology and DNA techniques revolutionized plant systematics and evolution, and because of the selection of *Arabidopsis thaliana* as the model flowering plant, the Brassicaceae have been at the forefront of scientific research. Except for the highly specific monograph on *Brassica* (Gómez-Campo, 1999), no family-wide symposium or textbook was devoted to its systematics and evolution. That gap was abridged in a special symposium organized by Koch and Mummenhoff (2006) during the XVII International Botanical Congress in Vienna. The symposium, entitled "Evolution and Phylogeny of the Brassicaceae" and dedicated to Herbert Hurka's 65<sup>th</sup> birthday and his contributions to evolutionary studies in the family, addressed diversified fields such as phylogeny, systematics, phylogeography, polyploidy, hybridization, comparative genomics, and developmental genetics, and the contributed papers appeared in a special issue of *Plant Systematics and Evolution* (Volume 259(2-4), 2006) that included a comprehensive checklist of all species of the family (Warwick et al., 2006b) and a compilation of chromosome numbers to that date (Warwick and Al-Shehbaz, 2006).

Many recent contributions (e.g., Koch et al., 2000, 2001, 2003a; Koch, 2003; Appel and Al-Shehbaz, 2003; Beilstein et al., 2006; Al-Shehbaz et al., 2006; Bailey et al., 2006; Koch and Mummenhoff, 2006; Warwick and Al-Shehbaz, 2006; Warwick et al., 2006; Koch et al., 2007; Warwick et al., 2007) have paved the way to a better understanding of the phylogenetic relationships within the Brassicaceae and to the delimitations of the major lineages based on comprehensive morphological and taxonomical treatments in light of molecular data. As a result, a phylogenetically based tribal classification of the family emerged and being refined (e.g., Al-Shehbaz et al., 2006; Al-Shehbaz and Warwick, 2007; German and Al-Shehbaz, 2008).

What are the most important milestone accomplishments during the past two decades? In principle, and aside from the wealth of knowledge on the model organisms in *Arabidopsis*, *Brassica*, and *Capsella*, they are four: I) achieving a new infrafamiliar classification based on phylogenetically circumscribed new tribes, II) recognition and assignment of monophyletic genera, III) unravelling the principles in crucifer evolution and exploring detailed examples for species or genus-specific evolutionary histories, and IV) phylogenetic circumscription of the order Capparales and the determination of Cleomaceae as the closest and sister family to the Brassicaceae. In this introductory chapter we will deal mainly with the first issue. Few of these issues are discussed in more detail in subsequent chapters. Others are outlined in various contributions presented in this book.

### **Recognition of infrafamiliar taxa: the tribal system**

The history of tribal classification systems is long and is well-summarized in various reviews (e.g., Appel and Al-Shehbaz, 2003; Koch, 2003; Koch et al., 2003a; Mitchell-Olds et al., 2005; Al-Shehbaz et al., 2006) and need not be repeated here. Prior to 2005, the most important conclusion reached in phylogenetic studies was that except for the Brassicaceae, the other tribes are artificially delimited and do not reflect the phylogenetic relationships of their component genera.



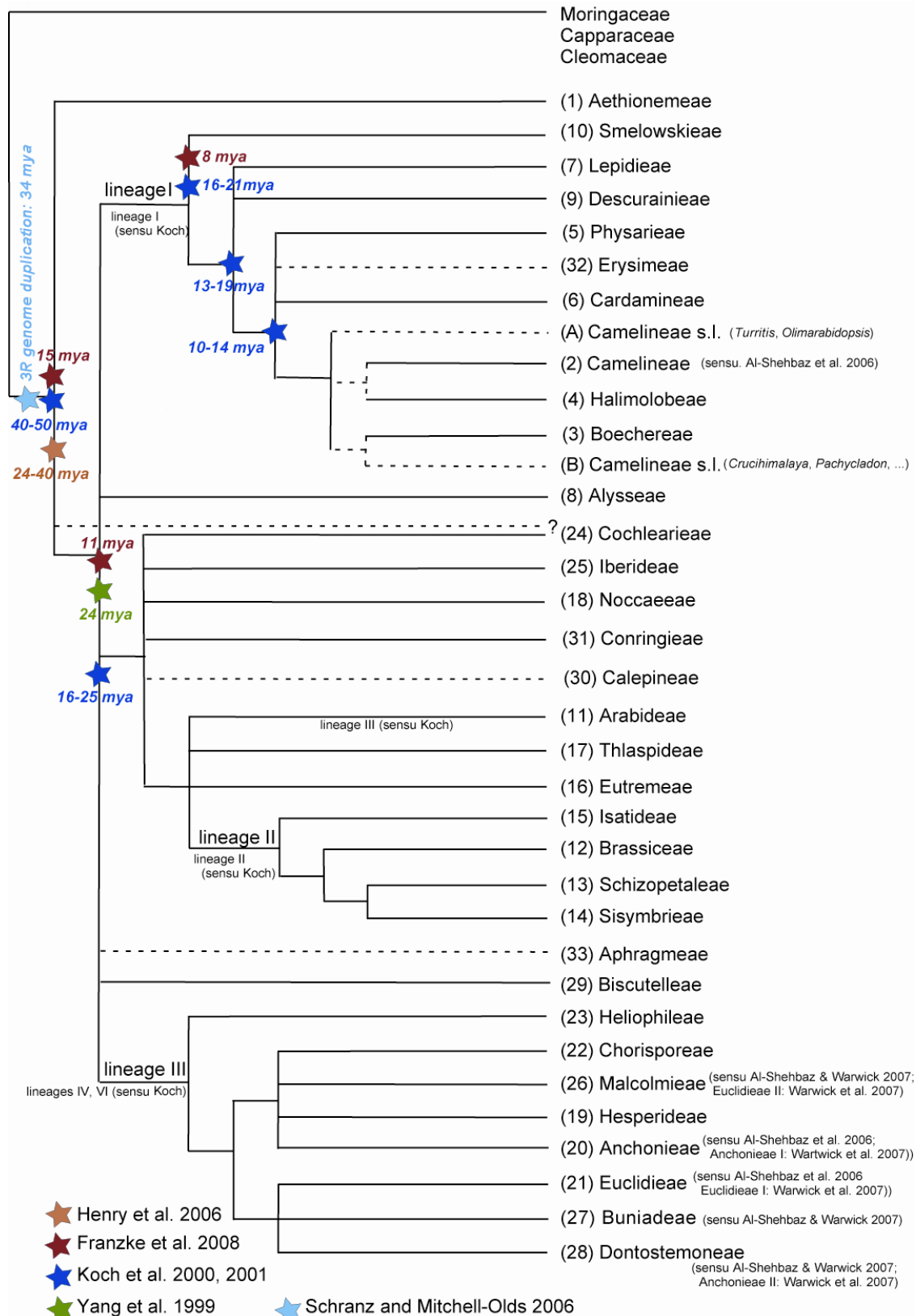
The other exception was thought to be the tribe Lepidieae (e.g., Zunk et al., 1999), but that too was shown to be artificially circumscribed (Al-Shehbaz et al., 2006). Of the 49 infrafamilial taxa (19 tribes and 30 subtribes) recognized by Schulz (1936), nine tribes (Alysseae, Arabideae, Brassiceae, Euclidieae, Heliophileae, Hesperideae, Lepidieae, Schizopetaleae, and Sisymbrieae) were maintained by Al-Shehbaz et al. (2006), though the limits of all except the Brassiceae and Heliophileae were substantially altered. These authors also recognized 16 additional tribes that were either described as new or re-established. The first comprehensive phylogeny of the Brassicaceae, in which 101 genera were sampled, was based on the plastidic gene *ndhF* (Beilstein et al. 2006). It identified three, significantly supported major clades (Fig. 1). The study provided the main foundation on which a new tribal classification was introduced (Al-Shehbaz et al., 2006). A subsequent, ITS-based study (Bailey et al., 2006) provided substantial support to the new system. In a more recent analysis focusing primarily on the evolution of plastid *trnF* pseudogene in the mustard family, a supernetwork was reconstructed based on nuclear alcohol dehydrogenase (*adh*), chalcone synthase (*chs*), and internal transcribed spacer of nuclear ribosomal DNA (ITS) and plastidic maturase (*matK*) sequence data (Koch et al., 2007). In this paper the corresponding *trnL-F* derived phylogeny was largely in congruence with this supertree, and all three major lineages identified by Beilstein et al. (2006) were confirmed. The supertree approach clearly demonstrated that there is a substantial conflicting “phylogenetic signal” at the deeper nodes of the family tree resulting in virtually unresolved phylogenetic trees at the genus level. However, other similarities are in congruence when comparing the supertree with the *ndhF* phylogeny of Beilstein et al. (2006). For example, the tribes Arabideae, Thlaspidaeae, Eutremeae, and Isatideae are closely related to lineage II comprising the tribes Schizopetaleae, Sisymbrieae, and Brassiceae. Furthermore, the tribe Alysseae is more closely related to lineage I (all have the *trnF* pseudogenes) (Fig. 1). On the other hand, some results are contradictory, such as the ancestral position of Cochlearieae (Koch et al., 2007), which is not confirmed by the results from *ndhF* (Beilstein et al., 2006) or ITS data (Bailey et al., 2006). Remarkably, a phylogenetic study focusing on the mitochondrial *nad4* (Franzke et al., 2008) is highly congruent with the ITS and *ndhF* studies. In a recent Bayesian analysis (Franzke et al., 2008), the Heliophileae fell in lineage III, which disagrees with the *ndhF* data. In an ongoing research on genome-size evolution in the family (Lysak and Koch, unpublished), the Heliophileae was also placed in lineage III, using a supertree approach (*adh*, *chs*, ITS, *matK*, *trnL-F*). In summary, most of the tribes recognized by Al-Shehbaz et al. (2006) are clearly delimited, but strong support for the intertribal relationships is still lacking.

Despite the use of multigene phylogenies, the lack of resolution in the skeletal backbone of the family is not yet understood, and two hypotheses explain that. First, early radiation events were quite rapid and were characterized by low levels of genetic variation separating the different lineages. Second, reticulate evolution (e.g., as found in the tribe Brassiceae) resulted in conflicting gene trees that did not reflect species phylogenies. The mitochondrial *nad4* intron data presented by Franzke et al. (2008) perhaps favour the first hypothesis. This scenario was also favoured by Koch et al. (2007), who found that the micro-structural evolutionary changes may be useful for inferring early events of divergence. In fact, the two structural rearrangements described by Koch et al. (2007) for the *trnL-F* region identify ancient patterns of divergence supported by phylogenetic analysis of that region excluding the micro-structural mutations. Further support is also found from analyses of the nuclear ITS sequence data (Bailey et al., 2006) and is discussed below.

The recently proposed tribal classification of Al-Shehbaz et al. (2006) recognized 25 tribes (1-25, see below). More recently, Franzke et al. (2008) presented a family phylogeny based on the mitochondrial *nad4* intron. Although the sampling in the latter study was smaller, both cpDNA (Beilstein et al., 2006) and mtDNA (Franzke et al., 2008) phylogenies were totally congruent with each other. However, it is still unclear why there are major inconsistencies between these two phylogenies and those generated from the nuclear genome, such as the ITS by Bailey et al. (2006) or the *adh* and *chs* by Koch et al. (2000, 2001).



**Figure 1.** Synopsis of phylogenetic hypothesis from various sources of tribal relationships in the Brassicaceae family (for details refer to the text). Lineage I-III are described in Beilstein et al. (2006). Koch et al. (2007) used different numbers given also as „sensu Koch“, and we suggest to use Beilstein’s version only in order to avoid future confusion. Dashed lines indicate uncertain phylogenetic position. However, it should be kept in mind, that this synopsis is not derived from one single phylogenetic analysis.



Additional studies have shown that some the tribes proposed by Al-Shehbaz et al. (2006) were broadly delimited or paraphyletic and needed further splitting. For example, the tribes Euclidieae and Anchonieae were shown by Warwick et al. (2007) and Al-Shehbaz and Warwick (2007) to consist of more than one lineage, and they recognized the new tribes Malcolmieae and Dontostemoneae and re-established the tribe Buniadeae (tribes 26-28). The study by German et al. (2008) of primarily Asian taxa have also resulted in the description of the new tribes Aphragmeae and Conringieae, as well as the re-establishment of the tribes Calepineae, Biscutelleae, and Erysimeae (tribes 29-33). The ITS studies of Bailey et al. (2006) and Koch (unpublished) justify the recognition of the last tribe. They also demonstrated that the tribe Camelinae sensu Al-Shehbaz et al. (2006) is paraphyletic and requires further division, herein recognized as tribes 34 (A) and 35 (B) (Table 1). An overview of these various tribes and a synopsis of their relationships among are presented in Fig. 1. However, this figure does not represent the outcome of an overall analysis, and a family-wide phylogenetic study is needed to achieve that. Furthermore, it is important to emphasize that phylogenetic hypotheses based individually on one marker (e.g., plastid, mitochondrial, or nuclear) would be of a limited value (Koch et al., 2001; Koch et al., 2007). In order to have a comprehensive phylogeny of the entire family, several problematical genera need to be sampled and adequately assigned to tribes (Al-Shehbaz et al., 2006).

The present study does not deal with generic level delimitations, and the interested reader should consult Appel and Al-Shehbaz (2003) and database of Warwick et al. (2006b). As for the prior tribal assignments of various genera and tribal limits, the reader is advised to consult Al-Shehbaz et al. (2006).

**1. Tribe Aethionemeae.** This unigeneric tribe of about 45 spp. consists of *Aethionema* including *Moriera*. The vast majority of species are endemic to Turkey, and only a few grow as far east as Turkmenistan and west into Spain and Morocco.

*Aethionema* was previously placed in the tribe Lepidieae (e.g., Hayek 1911, Schulz 1936). However, Al-Shehbaz et al. (2006) placed it in its own tribe because molecular data consistently show its sister position to the rest of Brassicaceae. The genus is highly variable in habit, fruit and floral morphology, and chromosome number (Appel and Al-Shehbaz, 2003; Al-Shehbaz et al., 2006). Knowledge on genome size and duplication, base chromosome number, evolutionary trends, most basal taxa, and monophyly of *Aethionema* are undoubtedly valuable to understand the evolution and early radiation of the entire family.

**2. Tribe Camelinae.** As delimited by Al-Shehbaz et al. (2006), the Camelinae has recently been shown to be paraphyletic and consists of a heterogeneous assemblage of genera (Bailey et al., 2006; Warwick et al., 2007; Koch et al., 2007; German and Al-Shehbaz 2008; Koch unpubl.). Indeed, the tribe should be subdivided into at least four monophyletic tribes, of which the unigeneric Erysimeae (ca. 180 spp.) is now recognized (German and Al-Shehbaz, 2008). Therefore, the species total in the Camelinae s.str. (following the removal of *Erysimum*, *Turritis*, *Olimarabidopsis*, *Crucihimalaya*, *Transberingia*, and *Pachycladon*) would about 35 species. The tribe includes the genera *Arabidopsis* (10 spp.), *Capsella* (3 spp.), *Catolobus* (1 sp.), *Camelina* (8 spp.), *Neslia* (2 spp.), *Pseudoarabidopsis* (1 sp.), and perhaps the Australian-endemic *Stenopetalum* (10 spp.). The tribe is primarily Eurasian, and only two species of *Arabidopsis* are native to North America.

Because of extensive use of *Arabidopsis thaliana* in basically every field of experimental biology, the genus and its relatives above received considerable studies (e.g., Mummenhoff and Hurka, 1994, 1995; Price et al., 1994, 2001; O’Kane and Al-Shehbaz, 1997, 2003; O’Kane et al., 1997; Al-Shehbaz et al., 1999; Koch et al., 1999a, 2000, 2001, 2007, unpubl.; Mitchell and Heenan, 2000; Al-Shehbaz and O’Kane, 2002a; Heenan and Mitchell, 2003; Heenan et al., 2002).





Table 1. Overview on the number of tribes, genera and species of the Brassicaceae as scored herein.

	genera	species	Reference
1. Aethionemeae	1	45	This chapter
2. Camelinaeae	7	35	This chapter
3. Boechereae	7	118	Al-Shehbaz et al. (2006)
4. Halimolobeae	5	39	Bailey et al. (2007)
5. Physarieae	7	133	This chapter
6. Cardamineae	9	333	This chapter
7. Lepidieae	4	235	This chapter
8. Alysseae	15	283	This chapter, Warwick et al. (2008)
9. Desurainieae	6	57	Al-Shehbaz et al. (2006)
10. Smelowskieae	1	25	Al-Shehbaz et al. (2006)
11. Arabideae	8	470	This chapter
12. Brassiceae	46	230	Al-Shehbaz et al. (2006)
13. Schizopetaleae s.l.	28	230	Al-Shehbaz et al. (2006)
14. Sisymbrieae	1	40	Al-Shehbaz et al. (2006)
15. Isatideae	2	65	This chapter
16. Eutremeae	1	26	Al-Shehbaz & Warwick (2006)
17. Thlaspidiae	7	27	Al-Shehbaz et al. (2006)
18. Noccaeae	3	90	This chapter
19. Hesperideae	1	45	Al-Shehbaz et al. (2006)
20. Anchonieae	8	68	Al-Shehbaz & Warwick (2007)
21. Euclidieae	13	115	Al-Shehbaz & Warwick (2007)
22. Chorisporeae	3	47	Al-Shehbaz & Warwick (2007)
23. Heliophileae	1	80	Al-Shehbaz et al. (2006)
24. Cochlearieae	1	21	Al-Shehbaz et al. (2006)
25. Iberideae	1	27	Al-Shehbaz et al. (2006)
26. Malcolmieae	8	37	Al-Shehbaz & Warwick (2007)
27. Buniadeae	1	3	Al-Shehbaz & Warwick (2007)
28. Dontostemoneae	3	28	Al-Shehbaz & Warwick (2007)
29. Biscutelleae	1	53	German & Al-Shehbaz (2008)
30. Calepineae	3	8	German & Al-Shehbaz (2008)
31. Conringieae	2	9	German & Al-Shehbaz (2008)
32. Erysimeae	1	180	German & Al-Shehbaz (2008)
33. Aphragmeae	1	11	German & Al-Shehbaz (2008)
34. Unnamed-I (A)	2	5	This chapter
35. Unnamed-II (B)	3	20	This chapter
<b>Total</b>	<b>212</b>	<b>3,249</b>	



**3. Tribe Boechereae.** This tribe of seven genera and 118 species is almost exclusively North American, and only *Boechea furcata* grows in the Russian Far East (Al-Shehbaz, 2005). Except for *Boechea* (110 species), the remaining genera are either monospecific (*Anelsonia*, *Nevada*, *Phoenicaulis*, *Polycytenium*) or bispecific (*Cusickiella*, *Sandbergia*).

All members of the tribe typically have a base chromosome number of  $x=7$ , mostly entire leaves (except *Polycytenium* and one *Sandbergia*), and branched trichomes (absent or in few *Boechea* and simple in *Nevada*). The majority are perennials with well-defined basal rosette.

Rollins (1993) treated all species of *Boechea* as members of *Arabis*, but extensive molecular studies (summarized in Al-Shehbaz 2003 and Al-Shehbaz et al. 2006), the two genera belong to different tribes.

**4. Tribe Halimolobeae.** The Halimolobeae is a New World tribe of five genera and 39 species mostly distributed in northern and central Mexico (Bailey et al., 2007), though genera such as *Exhalimolobos* (9 spp.), *Mancoa* (8 spp.), and *Pennellia* (10 spp.) are also disjunctly distributed in northern Argentina, Bolivia, and Peru (Bailey et al., 2002; Fuentes-Soriano, 2004). Three species of *Halimolobos* (8 spp.) grow in the southern United States, whereas *Sphaerocardamum* (4 spp.) is endemic to Mexico.

Members of the Halimolobeae have branched trichomes, white (rarely purplish flowers), seeds mucilaginous when wetted, ebracteate racemes (except two *Mancoa*), often spreading sepals, and a base number of  $x=8$ .

**5. Tribe Physarieae.** The tribe consists of seven genera and 133 species distributed primarily in North America. *Physaria* (105 spp.) is disjunct into South America (5 spp., N Argentina and S Bolivia) and has one species, *P. arctica*, distributed from northern Canada and Alaska into arctic Russia. The tribe also includes *Dimorphocarpa* (4 spp.), *Dithyrea* (2 spp.), *Lyrocarpa* (3 spp.), *Nerisyrenia* (9 spp.), *Paysonia* (8 spp.), and *Synthlipsis* (2 spp.). *Lesquerella* is paraphyletic and within which nested is the earlier-published *Physaria*, which necessitated their union into one genus (Al-Shehbaz and O'Kane, 2002b).

The Physarieae are readily separated from the rest of the Brassicaceae by having pollen with four or more colpi (the rest of Brassicaceae are tricolpate). The only exception is *Lyrocarpa coulteri*, in which a reversal to the tricolpate state apparently occurred. Other features of the tribe, none unique, are discussed by Al-Shehbaz et al. (2006).

**6. Tribe Cardamineae.** The tribe includes 333 species most of which belong to the genera *Cardamine* including *Dentaria* (ca. 200 spp.), *Rorippa* (86 spp.), and *Barbarea* (25 spp.). Except for *Barbarea*, which does not occur in South America, the genera are represented by native species on all other continents. The other genera are *Nasturtium* (5 spp.; 2 native to Mexico and the United States), and the North American *Iodanthus* (1 sp.), *Leavenworthia* (8 spp.), *Ornithocarpa* (2 spp.), *Planodes* (1 sp.), and *Selenia* (5 spp.).

Species of the Cardamineae grow predominantly in mesic or aquatic habitats, and *Subularia* (2 spp., one in Africa and the other in North America, N Europe, and N Russia), which occupies such habitats, need to be checked molecularly to determine whether or not it belongs here. The majority of species are glabrous or with simple trichomes only and have divided leaves, accumbent cotyledons, and a base chromosome number of  $x = 8$ .

**7. Tribe Lepidieae.** The Lepidieae (235 species) consists of *Lepidium*, a genus recently been expanded by Al-Shehbaz et al. (2002) to include *Cardaria*, *Coronopus*, and *Stroganowia*. It is represented by native species on all continents except Antarctica. The monospecific *Acanthocardamum* (Afghanistan) and the Middle Eastern and Central Asian *Winklera* (3 spp.) and *Stubendorffia* (8 spp.) most likely belong here too.



The tribe is distinguished by the angustiseptate fruits (secondarily inflated in two species formerly assigned to *Cardaria*), one ovule per locule, often mucilaginous seeds, and simple or no trichomes.

Schulz (1936) artificially delimited the Lepidieae solely on the presence of angustiseptate fruits and included genera assigned by Al-Shehbaz et al. (2006) to some 12 tribes. Evidently, the independent evolution of angustiseptate fruits in the Brassicaceae took place in the majority of tribes.

**8. Tribe Alysseae.** Dudley and Cullen (1965) expanded the limits of Alysseae to include genera now assigned to different tribes. For example, *Ptilotrichum* is removed to the Arabideae (Al-Shehbaz et al., 2006; Warwick et al., 2008; Koch, unpubl.). The Alysseae is distributed in Eurasia and N Africa, and only one species (*Alyssum obovatum*) extends its distribution to Canada and Alaska. The tribe includes some 253 species in the genera *Alyssum* (ca. 180 spp.), *Alyssoides* (6 spp.), *Aurinia* (13 spp.), *Berteroa* (5 spp.), *Bornmuellera* (7 spp.), *Clastopus* (2 spp.), *Clypeola* (10 spp.), *Degenia* (1 sp.), *Fibigia* (16 spp.), *Galitzkya* (3 spp.), *Hormathophylla* (7 spp.), *Physoptychis* (2 spp.), and *Strausiella* (1 sp.).

The majority of species in the tribe have stellate trichomes, latiseptate or terete (rarely angustiseptate), mostly few-seeded silicles, often winged seeds, and usually winged, toothed, or appendaged filaments. *Farsetia* (26 spp.) and *Lobularia* (4 spp.) are somehow distinct, but were retained in this tribe (Warwick et al. 2008). *Farsetia* is distributed from northern and eastern Africa through Southwest Asia into Pakistan and western India, whereas *Lobularia* is restricted to NW Africa and Macaronesia (Appel & Al-Shehbaz, 2003). All members of *Farsetia* and *Lobularia* are pubescent with exclusively malpighiaceae trichomes. However, this type of trichomes occurs sporadically in species of other tribes, though often in combination with other trichome types. From these, they are distinguished by have latiseptate silicles or sometimes siliques, often winged seeds, petiolate, often entire cauline leaves, and accumbent cotyledons.

**9. Tribe Descurainieae.** The tribe consists of six genera and some 57 species. *Descurainia* (47 spp.), including *Hugueninia*, is distributed in three centers: North American (17 spp.), South American (ca. 20 spp.), and Canarian (7 spp.), plus three species in Eurasia. The tribe also includes the European *Hornungia* (3 spp.), central Asian *Ianhedgia* (1 sp.), North-South American *Tropidocarpum* (4 spp.), and (if distinct from *Descurainia*) the monospecific Middle Eastern *Robeschia* and Patagonian *Trichotolinum*.

The tribe is characterized by the petiolate, 1–3-pinnatisect stem leaves, dendritic or rarely only forked trichomes, incumbent cotyledons, and mostly yellow flowers. *Descurainia* is unique in the Brassicaceae for the presence in some species of unicellular, glandular papillae.

**10. Tribe Smelowskieae.** This unigeneric tribe consists of *Smelowskia* (25 spp.), a genus with seven species in North America and 18 in central and eastern Asia. Based on molecular studies by Warwick et al. (2004b), the genus was expanded by Al-Shehbaz and Warwick (2006) to include *Gordokovia*, *Hedinia*, *Redowskia*, *Sinosophiopsis*, and *Sophiopsis*.

Members of the Smelowskieae have branched trichomes, petiolate, pinnatisect cauline leaves, white to purple (rarely cream) flowers, nonmucilaginous seeds, and incumbent cotyledons.

**11. Tribe Arabideae.** The tribe consists of at least eight genera and some 470 species. *Draba* (370 spp.), which includes *Drabopsis*, *Erophila*, and *Schivereckia*, is the largest genus in the family. It is represented by 119 spp. in North America, 70 in South America, and over 100 in the Himalayas and neighbouring central Asia, but it is absent in Australia and all except NW Africa. *Arabis* (70 spp.) is primarily Eurasian, with 15 spp. in North America, and only a few in NW and alpine tropical Africa. Other genera of the tribe are the Eurasian *Aubrieta* (15 spp.), Eurasian *Ptilotrichum* (ca. 10





spp.), Chinese *Baimashania* (2 spp.), western North American *Athysanus* (2 spp.), European *Pseudoturritis* (1 sp.), and central Asian *Berteroella* (1 sp.).

Species of the Arabideae primarily have branched trichomes, accumbent cotyledons, latisepate or terete fruits nonmucilaginous seeds, and mostly a base number of  $x = 8$ .

Prior to the molecular studies of Koch et al. (1999, 2000) and O’Kane and Al-Shehbaz (2003), *Arabis* was so broadly delimited that it was estimated to include about 180 species (Al-Shehbaz, 1988). Subsequent studies (e.g., Al-Shehbaz, 2003; 2005) led to the removal of many of its species to the genera *Arabidopsis*, *Boechera*, *Catolobus*, *Fourraea*, *Pennellia*, *Pseudoturritis*, *Rhammatophyllum*, *Streptanthus*, and *Turritis*, which are presently assigned to at least five tribes. Obviously, the characters on which *Arabis* was delimited (latisepate fruits, accumbent cotyledons, branched trichomes) evolved independently numerous times in the Brassicaceae. *Arabis* is much in need of comprehensive molecular studies, and despite the removal of nearly 65% of its species to other genera, it remains paraphyletic because its type species (*A. alpina*) is sister to *Draba* and *Aubrieta* rather than to most species still assigned to it (Koch et al., 2003a; Koch et al., unpubl.).

**12. Tribe Brassiceae.** This tribe of 46 poorly defined “genera” and some 230 species includes the most economically important plants in the family (e.g., species of *Brassica*, *Eruca*, *Raphanus*, *Sinapis*). It has been subjected to extensive molecular (Warwick and Black, 1997a, 1997b; Warwick and Sauder, 2005, and references therein) and taxonomic and other studies (Tsunoda et al. 1980, Gómez-Campo 1999).

The vast majority of species in the Brassiceae have conduplicate cotyledons and/or segmented (heteroarthrocarpic) fruits. The tribe is distributed primarily in the Mediterranean region, adjacent SW Asia, and South Africa, and only four species of *Cakile* are native to North America.

Molecular studies (see the review chapter by Warwick and Hall) on the tribe amply show that the traditional generic boundaries recognized by Schulz (1936) and Gómez-Campo (1999) do not hold. Only a few genera (e.g., *Cakile*, *Vella*, *Crambe*) are monophyletic (Warwick and Black, 1994, 1997b; Francisco-Ortega, 1999, 2002), but the majority of them form two groups (the rapa and nigra clades) that are well supported by chloroplast but not nuclear data and are basically indistinguishable morphologically. The components “genera” of both clades exhibit tremendous fruit diversity, which are the main characters used in their delimitation. In order to have a taxonomy that reflects phylogenetic relationships, the generic boundaries in the Brassiceae need radical revision. As a result, some genera (e.g., *Diplotaxis*, *Eruca*, *Erucastrum*, *Hemicrambe*, *Hirschfeldia*, *Raphanus*, *Rapistrum*, *Sinapidendron*) may have to be abandoned.

**13. Tribe Schizopetaleae.** The tribe was broadly delimited by Al-Shehbaz et al. (2006) to consist of some 230 species in over 28 genera, including those previously assigned to the tribe Thelypodieae. However, molecular studies in progress (Warwick et al.) show that both tribes ought to be maintained. As a result, the Schizopetaleae will have much fewer species and genera all restricted to South America, whereas the Thelypodieae includes genera on both North and South America. Therefore, the Thelypodieae sensu Al-Shehbaz (1973), minus *Macropodium*, should be expanded to include all of the North American genera placed in the Schizopetaleae by Al-Shehbaz et al. (2006). The South American genera to be restored in the Thelypodieae will be added following the completion of research by Warwick and colleagues. Little else can be gained herein by speculating any further about the limits of both tribes.

The combined Schizopetaleae and Thelypodieae exhibit enormous floral diversity not observed elsewhere in the Brassicaceae. This aspect is further discussed by Al-Shehbaz et al. (2006), and in these tribes, the floral features are far more useful than fruit characters in the delimitation of genera.

**14. Tribe Sisymbrieae.** Based on extensive molecular data (Warwick et al. 2002, 2005), the tribe was delimited by Al-Shehbaz et al. (2006) to consist of about 40 species of *Sisymbrium* (including



*Lycocarpus* and *Schoenocrambe*). Except for the North American *S. linifolium*, the remaining species of the tribe are distributed in Eurasia and Africa. This is in contrast to Schulz's (1924, 1936) delimitation of the Sisymbrieae which included 70 genera and about 400 species.

Species of the Sisymbrieae have yellow flowers, pinnately divided basal and lowermost stem leaves, 2-lobed stigmas, terete siliques, a base chromosome number of  $x = 7$ , and simple or no trichomes (only the South African *Sisymbrium bruchellii* has branched trichomes).

**15. Tribe Isatideae.** This tribe of about 65 species and two genera consists of the monospecific *Myagraum* and *Isatis* (ca. 64 spp.), including *Boreava*, *Pachypterygium*, *Sameraria*, and *Tauscheria*. The union of the last four genera with *Isatis* is based on extensive morphological and molecular studies (Moazzeni et al., 2007; unpubl.). Further studies are needed to determine if *Chartoloma*, *Tauscheria*, *Glastaria*, and *Schimperea* belong to this tribe. Members of the Isatideae have indehiscent, often pendulous, 1- or 2-seeded fruits, yellow or rarely white flowers, auriculate stem leaves, and simple or no trichomes.

**16. Tribe Eutremae.** This unigeneric tribe comprises *Eutrema* (26 spp.), a genus distributed primarily in Asia, especially the Himalayas and neighbouring central Asia, with two species extending their ranges into North America (Al-Shehbaz and Warwick, 2006). Molecular studies by Warwick et al. (2004a, 2006a) strongly suggested that the limits of *Eutrema* be expanded to include the genera *Neomartinella*, *Platycraspedum*, *Taphrospermum*, and *Thellungiella*. Members of the Eutremae are glabrous or with simple trichomes and have white flowers, incumbent cotyledons, and often palmately veined basal leaves.

**17. Tribe Thlaspideae.** This European and Southwest Asian tribe includes 27 species in the genera *Alliaria* (2 spp.), *Graellsia* (8 spp.), *Pachyphragma* (1 sp.), *Parlatoria* (2 spp.), *Peltaria* (4 spp.), *Pseudocamelina* (4 spp.), and *Thlaspi* (6 spp.). Further studies are needed to establish if the Southwest Asian *Sobolewsia* (4 spp.) belongs here. Species of the tribe have striate or coarsely reticulate seeds, undivided cauline leaves, often palmately veined basal leaves, and simple or no trichomes.

*Thlaspi* used to include about 90 species, but seed anatomy (Meyer, 1973, 1979, 2001a) and extensive molecular studies (Koch and Mummenhoff, 2001; Mummenhoff et al., 1997a, 1997b, 2001b; Beilstein et al., 2006) showed that it consists of only six species, and the bulk of its previous members should be assigned to *Noccaea* (see below).

**18. Tribe Noccaeeae.** The tribe includes some 90 species, of which four belong to *Microthlaspi* (Meyer, 2003), three to *Neurotropis* (Meyer, 2001b), the rest to *Noccaea*. The last genus includes 67 species in Europe, Africa, and Southwest Asia (Meyer, 2006), but it also includes four species in the New World (Koch and Al-Shehbaz, 2004), five in the Himalayas (Al-Shehbaz, 2002), and others to be transferred from *Aethionema* and other genera, including all of the other segregates by (Meyer, 1973).

Members of the Noccaeeae were subjected (as *Thlaspi* or *Microthlaspi*) to extensive molecular studies (see Koch, 2003; Koch et al., 1998; Koch and Hurka, 1999; Koch and Bernhardt, 2004). They are glabrous plants with angustiseptate fruits, smooth seeds, and often auriculate cauline leaves.

**19. Tribe Hesperideae.** This unigeneric tribe includes about 45 spp. in *Hesperis*, a genus much in need of systematic and molecular studies. It is distributed primarily in the Middle East and Europe, with fewer species in central Asia and NW Africa. The Hesperideae is unique in the Brassicaceae for its unicellular glands on uniseriate, few-celled stalks.



**20. Tribe Anchonieae.** As delimited by Al-Shehbaz et al. (2006), the Anchonieae included 12 genera and ca. 130 species. However, Warwick et al. (2007) have shown the tribe to be polyphyletic, and Al-Shehbaz and Warwick (2007) redefined its limits to include eight genera and 68 species. The genera are *Anchonium* (2 spp.), *Iskandera* (2 spp.), *Matthiola* (48 spp.), *Microstigma* (3 spp.), *Oreoloma* (3 spp.), *Sterigmostemum* (7 spp.), *Synstemon* (2 spp.), and *Zerdana* (1 sp.). *Matthiola* and *Sterigmostemum* need of thorough studies because Warwick et al. (2007) demonstrated that they are polyphyletic.

The Anchonieae is distributed primarily in Eurasia and eastern and northern Africa. It is distinguished by the presence of multicellular glands on multicellular-multiseriate stalks, 2-lobed stigmas, erect sepals, and often branched trichomes.

**21. Tribe Euclidieae.** This tribe was also broadly delimited by Al-Shehbaz et al. (2006) to include some 25 genera and over 150 species. It was also found to be polyphyletic (Warwick et al., 2007). As a result, Al-Shehbaz and Warwick (2007) and Yue et al. (2008) adjusted its boundaries to include only 13 genera and 115 species distributed primarily in Eurasia and northern and eastern Africa. The tribe includes *Braya* (17 spp., 7 in North America), *Cryptospora* (3 spp.), *Leiospora* (6 spp.), *Neotorularia* (11 spp.), *Rhammatophyllum* (10 spp.), *Sisymbriopsis* (5 spp.), *Solms-laubachia* (26 spp.), *Strigosella* (23 spp.), *Tetracme* Bunge (10 spp.), and the monospecific *Dichasianthus*, *Euclidium*, *Leptaleum*, and *Shangrilaia*. *Desideria* is nested within *Solms-laubachia* and is united herein with the latter (Yue et al., 2006, 2008). Both *Neotorularia* and *Sisymbriopsis* are polyphyletic (Warwick et al., 2004a), and their boundaries need to be re-defined.

With the removal of several genera from the Euclidieae to the Malcolmieae (see below), the former becomes monophyletic and can easily be distinguished from the latter by the presence of simple and 2- to several-rayed (vs. sessile stellate) trichomes.

**22. Tribe Chorisporeae.** This tribe of three genera and 47 species is primarily Asian and only four of the 35 species of *Parrya* are North American. The other genera are *Chorispora* (11 spp.) and *Diptychocarpus* (1 sp.). Molecular data (Warwick et al., 2007) strongly support the assignment of *Parrya* to this tribe.

The Chorisporeae are distinguished by the presence of multicellular glands on multicellular-multiseriate stalks, connivent stigmas, and erect sepals, and by the lack of branched trichomes.

**23. Tribe Heliophileae.** The tribe was defined by Appel & Al-Shehbaz (1997) to include six genera, but based on molecular studies (Mummenhoff et al., 2005), Al-Shehbaz and Mummenhoff (2005) united all genera into *Heliophila* (80 spp.). The Heliophileae are exclusively South African and are easily distinguished by the dipicolobal cotyledons, often appendaged petals and/or staminal filaments, and simple or no trichomes.

**24. Tribe Cochlearieae.** This unigeneric tribe consists of *Cochlearia* (21 spp., including five of *Ionopsidium*). *Cochlearia* is distributed primarily in Europe, with the ranges of three species extended into northern North America and Asia and one into NW Africa. The genus received detailed molecular studies (Koch, 2002; Koch et al., 1996, 1999b, 2003b), and further work is needed on *Bivonaea* and *C. aragonensis* to determine if they belong in the tribe.

Members of the Cochlearieae have rosulate, undivided basal leaves, white petals, often sessile cauline leaves, terete or angustiseptate silicles, entire stigmas, biseriate seeds, ebracteate racemes, and no trichomes.

**25. Tribe Iberideae.** This tribe consists only of *Iberis* (27 spp.), a genus centered mainly in Europe, with a few species in NW Africa, and SW and central Asia.

Species of the Iberideae are glabrous or with simple trichomes and have angustiseptate, 2-seeded fruits, zygomorphic flowers, and corymbose infructescences.



**26. Malcolmieae.** This newly established tribe (Al-Shehbaz and Warwick, 2007) was segregated from the Euclidieae sensu Al-Shehbaz et al. (2006). It includes 37 species in eight primarily Mediterranean genera, though some are distributed into SW Asia, Canary Islands, and Africa. The genera are *Cithareloma* (3 spp.), *Diceratella* (11 spp.), *Eremobium* (1 sp.), *Malcolmia* (10 spp.), *Maresia* (3 spp.), *Morettia* (3 spp.), *Notoceras* (1 sp.), and *Parolinia* (5 spp.).

The Malcolmieae are characterized by having often sessile stellate trichomes, decurrent stigmas, and mostly accumbent cotyledons.

**27. Buniadeae.** This unigeneric tribe includes only *Bunias*. (3 spp.), a genus distributed exclusively in Eurasia, though two species are weeds naturalized in North America. Molecular studies (Beilstein et al., 2006; Koch, unpubl.) show that *Bunias* groups close to the tribes Euclidieae and Anchonieae, but should be excluded from the latter, as was done by Al-Shehbaz and Warwick (2007).

The Buniadeae have multicellular glands on multicellular-multiseriate stalks, indehiscent silicles, and spiral cotyledons.

**28. Dontostemoneae.** Members of the tribe are distributed exclusively in central and eastern Asia. It comprises 28 species in the genera *Clausia* (6 spp.), *Dontostemon* (12 spp.), and *Pseudoclausia* (10 spp.).

The Dontostemoneae differ from the other tribes with multicellular glands on multiseriate-multicellular stalks by the lack of branched trichomes and the presence of often united or winged filaments, entire stigmas, and rounded repla.

**29. Biscutelleae.** This unigeneric tribe comprises the genus *Biscutella* L. (53 spp.), a primarily North African-European genus but with only a few species reaching the Middle East. Although established by Dumortier more than 180 ago, the Biscutelleae was not recognized by subsequent authors and has only recently been re-instated by German and Al-Shehbaz (2008). It is distinguished from the other tribes by its didymous, angustiseptate, 2-seeded fruits, long styles, entire stigmas, simple trichomes, and auriculate cauline leaves.

**30. Calepineae.** The tribe was first established by Horaninow some 160 years ago and was not recognized since. As delimited by German and Al-Shehbaz (2008), the tribe includes eight Asian species in *Goldbachia* (6 spp.) and the monospecific *Spirorrhynchus* and *Calepina*. The last genus was previously assigned to the Brassiceae (Schulz, 1936; Gomez-Campo, 1999), but recent molecular studies (Anderson and Warwick, 1999; Francisco-Ortega, 1999; Lysak et al., 2005; Beilstein et al., 2006, German et al., unpubl.) clearly support its exclusion from this tribe.

The tribe includes annuals with indehiscent, woody, 1–3-seeded fruits, entire stigmas, simple or no trichomes, and undivided, often auriculate cauline leaves.

**31. Conringieae.** Based on molecular studies (German et al., unpubl.), German and Al-Shehbaz (2008) established this new tribe. It consists of nine primarily Southwest Asian species in the genera *Conringia* (6 spp.) and *Zuvanda* (3 spp.), though the range of *C. planisiliqua* extends into the Himalayas and *C. orientalis* is a naturalized Eurasian weed.

As in *Calepina*, *Conringia* was previously included in the Brassiceae (Schulz, 1936; Gomez-Campo, 1999), but molecular data (see references under *Calepina*) clearly support its removal from that tribe. Species of the Conringieae are glabrous or with simple trichomes and have sessile auriculate cauline leaves, linear fruits, capitate or conical and decurrent stigmas, and often incumbent cotyledons.





**32. Erysimeae.** This unigeneric tribe consists of *Erysimum* (ca. 180 spp.), a genus centered primarily in Eurasia, with eight species in northern Africa and Macaronesia and 15 in North America. The genus was placed in the broadly circumscribed Camelinae sensu Al-Shehbaz et al. (2006), but molecular studies (Bailey et al., 2006; German et al., unpubl.) clearly support its placement in a distinct tribe. Another genus, *Chrysocamela* (3 spp.) should perhaps be added to the Erysimeae (Koch et al., unpubl.).

The tribe is distinguished by the exclusively sessile, stellate and/or malpighiaceae trichomes, often yellow or orange flowers, and many-seeded siliques.

**33. Aphragmeae.** This tribe includes only *Aphragmus* (11 spp.), a genus distributed mainly in the Himalayas and central Asia, with only *A. eschscholtzianus* growing in the Russian Far East and arctic Alaska and adjacent Canada. The Aphragmeae has recently been described as new by German and Al-Shehbaz (2008) based on molecular studies by German et al. (unpubl.).

The tribe includes herbaceous annuals or perennials with minute, forked or simple trichomes, bracteate racemes, non-auriculate cauline leaves, entire stigmas, incumbent cotyledons, and white to deep purple petals.

**Other tribes.** As discussed above, the tribe Camelinae sensu Al-Shehbaz et al. (2006) is polyphyletic. After the removal of *Erysimum* into the Erysimeae, the Camelinae remains polyphyletic (Koch et al., unpubl.; German et al., unpubl.). We suggest that the genera *Turritis* (2 spp.) and *Olimarabidopsis* (3 spp.) be placed in one tribe and *Crucihimalaya* (9 spp.), *Pachycladon* (10 spp.), and *Transberingia* (1 sp.) be placed in another. Studies by the present authors are underway to recognize these two tribes.

### Recognition and assignment of genera.

Although a complete tribal classification system of the Brassicaceae is not yet available, we are gradually approaching that goal. Following the first phylogenetic tribal classification of the family (Al-Shehbaz et al., 2006), subsequent molecular studies (e.g., Bailey et al., 2006; Warwick et al., 2006a, 2007, 2008; Koch et al., 2007, unpubl.) lead to the tribal adjustments recently proposed by Al-Shehbaz and Warwick (2007) and German and Al-Shehbaz (2008). Table 1 summarizes and updates our present knowledge of the tribal placement of nearly two-thirds (62.7%) of the 338 genera and 87.6% of the 3709 species compiled by Warwick et al. (2006b).

An ongoing comprehensive phylogenetic study of the family (involving Warwick, Al-Shehbaz, Mummenhoff, Koch) aims to cover more than 95% of all accepted genera. The major difficulty is obtaining adequate material for molecular studies on species of numerous monospecific or oligospecific genera (see Fig. 2 in Koch and Kiefer 2006 and the estimates by Al-Shehbaz et al. 2006). Many of these are known only from the type collections of their species. Although most of the larger genera of the family (e.g., *Draba*, *Lepidium*, *Cardamine*, *Erysimum*, *Heliophila*, *Rorippa*) are reasonably well-surveyed molecularly and are shown to be monophyletic, it is the smaller and medium-sized genera (especially of the tribes Brassiceae and Schizopetaleae s.l.) that need further studies. We suspect that many of these genera will be merged with others, and the total number of genera in the family will be substantially reduced.

### Family limits and age estimates

Based on strictly morphological studies, Judd et al. (1994) indicated that the Brassicaceae is nested within the paraphyletic Capparaceae (including Cleomaceae) and suggested their union as one family, Brassicaceae s.l. However, molecular studies (Hall et al., 2002, 2004; Schranz and Mitchell-Olds, 2006) clearly demonstrated that the Brassicaceae are sister to Cleomaceae and both are sister to Capparaceae. As a result, three families are currently recognized.

Divergence time estimates (Fig. 1) are still controversial. The usage of Ks values, as presented by Schranz and Mitchell-Olds (2006) and Maere et al. (2005), are more reliable since





they don't make any assumptions about molecular clocks. Schranz and Mitchell-Olds (2006) estimated a divergence time and very early radiation of the Brassicaceae at 34 mya (million years ago). This was based on a genome-wide estimated Ks average ( $K_s=0.67$ ) reflecting the last and third major genome duplication event (3R or  $\alpha$  duplication) and using *Arabidopsis thaliana* as a reference (Bowers et al., 2003; Simillion et al., 2002; De Bodt et al., 2005). Genome-wide comparison of Ks values from Cleomaceae and Brassicaceae suggest that the corresponding mean Ks-values is 0.82, which refer to 41 mya as divergence time estimate between these two families, provided that the same evolutionary mutational rate is applied.

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Table 1. Overview on the number of tribes, genera and species of the Brassicaceae as scored herein.

	genera	species	Reference
1. Aethionemeae	1	45	This chapter
2. Camelinaeae	7	35	This chapter
3. Boechereae	7	118	Al-Shehbaz et al. (2006)
4. Halimolobeae	5	39	Bailey et al. (2007)
5. Physarieae	7	133	This chapter
6. Cardamineae	9	333	This chapter
7. Lepidieae	4	235	This chapter
8. Alysseae	15	283	This chapter, Warwick et al. (2008)
9. Desurainieae	6	57	Al-Shehbaz et al. (2006)
10. Smelowskieae	1	25	Al-Shehbaz et al. (2006)
11. Arabideae	8	470	This chapter
12. Brassiceae	46	230	Al-Shehbaz et al. (2006)
13. Schizopetaleae s.l.	28	230	Al-Shehbaz et al. (2006)
14. Sisymbrieae	1	40	Al-Shehbaz et al. (2006)
15. Isatideae	2	65	This chapter
16. Eutremeae	1	26	Al-Shehbaz & Warwick (2006)
17. Thlaspidiae	7	27	Al-Shehbaz et al. (2006)
18. Noccaeae	3	90	This chapter
19. Hesperideae	1	45	Al-Shehbaz et al. (2006)
20. Anchonieae	8	68	Al-Shehbaz & Warwick (2007)
21. Euclidieae	13	115	Al-Shehbaz & Warwick (2007)
22. Chorisporeae	3	47	Al-Shehbaz & Warwick (2007)
23. Heliophileae	1	80	Al-Shehbaz et al. (2006)
24. Cochlearieae	1	21	Al-Shehbaz et al. (2006)
25. Iberideae	1	27	Al-Shehbaz et al. (2006)
26. Malcolmieae	8	37	Al-Shehbaz & Warwick (2007)
27. Buniadeae	1	3	Al-Shehbaz & Warwick (2007)
28. Dontostemoneae	3	28	Al-Shehbaz & Warwick (2007)
29. Biscutelleae	1	53	German & Al-Shehbaz (2008)
30. Calepineae	3	8	German & Al-Shehbaz (2008)
31. Conringieae	2	9	German & Al-Shehbaz (2008)
32. Erysimeae	1	180	German & Al-Shehbaz (2008)
33. Aphragmeae	1	11	German & Al-Shehbaz (2008)
34. Unnamed-I (A)	2	5	This chapter
35. Unnamed-II (B)	3	20	This chapter
<b>Total</b>	<b>212</b>	<b>3,249</b>	



Figure 1. Synopsis of phylogenetic hypothesis from various sources of tribal relationships in the Brassicaceae family (for details refer to the text). Lineage I-III are described in Beilstein et al. (2006). Koch et al. (2007) used different numbers given also as „sensu Koch“, and we suggest to use Beilstein’s version only in order to avoid future confusion. Dashed lines indicate uncertain phylogenetic position. However, it should be kept in mind, that this synopsis is not derived from one single phylogenetic analysis.

