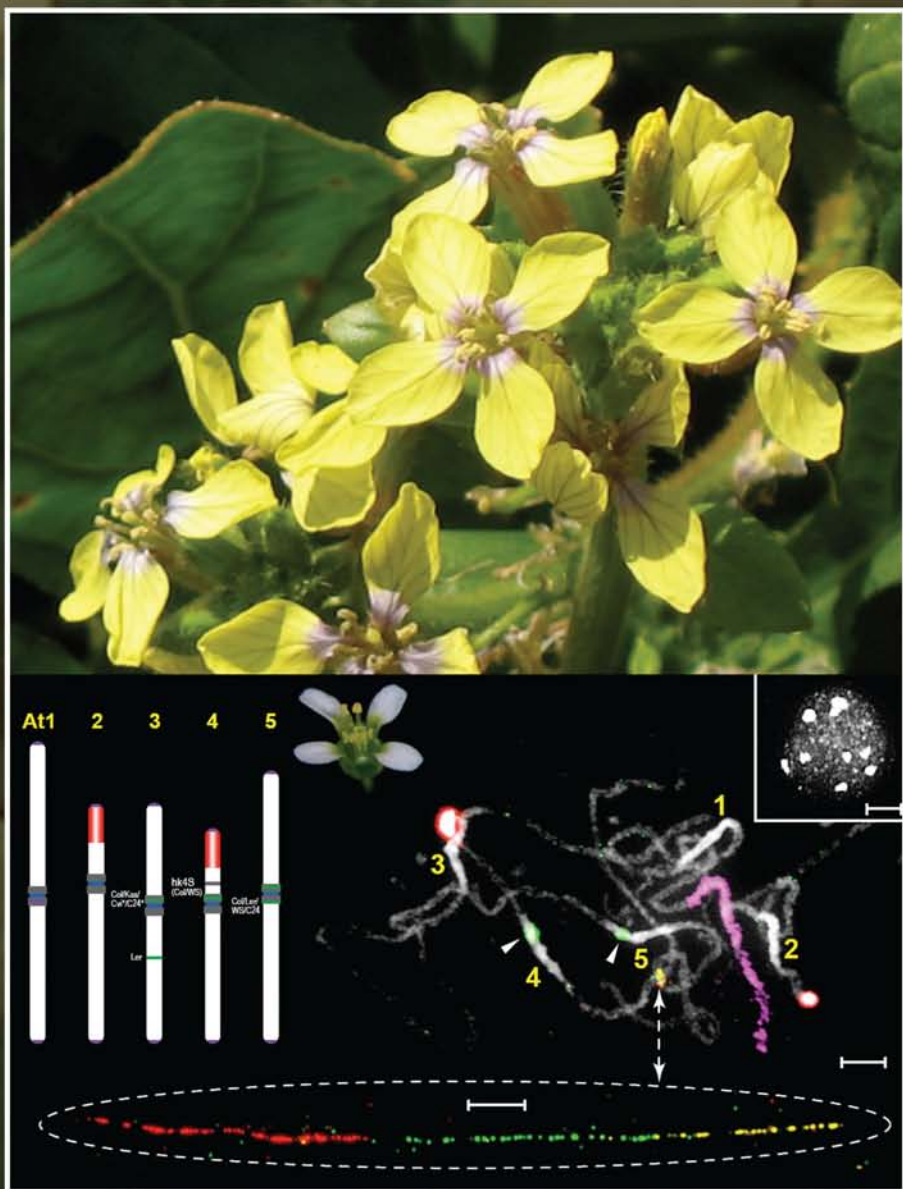


Biology and Breeding of Crucifers

Edited by **Surinder Kumar Gupta**



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Preface

Despite recent advances made in rapeseed-mustard breeding, the need and opportunities to increase its production, productivity, oil content and quality, and protein yield are as great today as they have ever been. The alien variations available in wild crucifers have been utilized enormously by the technique of chromosome and genetic engineering to develop noble varieties. Realizing the importance of crucifer crops in Europe and the rest of the countries of the world, there is an urgent need to search for new gene pools with special reference to wild species and to update the knowledge of the recent technologies developed thus far in enhancing rapeseed-mustard production at the global level. At present, no single publication available deals exclusively with crucifers, with the primary emphasis on wild species.

This book includes 18 chapters that have been well prepared by leading *Brassica* scientists around the world with extensive experience, and their contributions are well recognized worldwide. Chapters 1 and 2 deal with the systematics and phylogenies of wild crucifers, while Chapters 3 and 4 describe the major wild relatives of crucifers accompanied by beautiful photographs to assist in recognizing diagnostic characteristics and to aid in the identification of the species. This is followed by chapters on breeding methods, self-incompatibility, cytoplasmic male sterility, germination and viability, and plant-insect interactions in crucifers. Chapters 10 and 11 provide a detailed account of comparative cytogenetics and distant hybridizations involving wild crucifers. The phytoalexins and their role are discussed in Chapter 12, followed by chapters on introgression of genes from wild crucifers (Chapter 13), biotechnology (Chapter 14), and microspore culture and haploidy breeding (Chapter 15). Another chapter (Chapter 16) on genetic improvement of vegetable crucifers using wild species has been added to enhance the beauty of this book. Finally, Chapter 17 provides a brief account of industrial products from wild crucifers and Chapter 18 describes the preservation and maintenance of crucifer plant genetic resources at the global level. Although a few chapters may overlap with each other to some extent with regard to subject matter, this has been dealt with in depth by each of the contributors.

I am highly indebted to Professor Nagendra Sharma, Honorable Vice-Chancellor, Sher-e-Kashmir University of Agricultural Sciences and Technology of Jammu, India, for encouraging me to carry out research on crucifer crops with all the required modern facilities. I am also thankful to all the contributors of the various chapters for their ready response.

Help rendered by Professor Marcus Koch, Heidelberg University, Germany; Ihsan A. Al-Shehbaz, Head, Missouri Botanical Garden, Missouri, United States; Professor Suzanne I. Warwick, Eastern Cereal and Oilseeds Research Centre, Ontario, Canada; Professor Martin A. Lysak, Institute of Experimental Biology, Masaryk University, Czech Republic; Professor M. Soledade C. Pedras, University of Saskatchewan, Canada; Professor Y. Takahata, Iwate University, Japan; Professors Shyam Prakash and P.R. Kalia, Indian Agricultural Research Institute, New Delhi, India, is also gratefully acknowledged.

I am indeed grateful to Professor W.J. Zhou, Crop Science Institute, Hangzhou, China, and to Dr. César Gómez Campo, Universidad Politécnica de Madrid, Spain, for providing technical input and critically reviewing some of the chapters. Ms. Randy Brehm, assistant editor, CRC Press, deserves special thanks for bringing this book to life. Dr. Aditya Pratap, assistant professor, Division of Plant Breeding & Genetics, SKUAST-Jammu, also deserves sincere thanks for an outstanding and formidable volume of correspondence with regard to this book. Shri Madan Mohan Gupta, my father-

in-law, has been the instrumental force behind this book. Unfortunately, he has left for heavenly abode. I owe so very much to this departed soul and also to my better half, Dr. Neena Gupta, for their unstinting help and patience during the preparation of this manuscript.

S.K. Gupta
Editor

About the Editor

Dr. S.K. Gupta, born in 1959, is currently working as professor and head/chief scientist (Oilseeds) in the Division of Plant Breeding and Genetics, SK University of Agricultural Sciences and Technology, FOA, Chatha, Jammu, India, and holds a brilliant academic and service record. For almost two decades he has devoted his research interests to the area of oilseed brassicas.

Dr. Gupta obtained his post-graduate degrees (M.Sc., Ph.D.) from Punjab Agricultural University, Ludhiana, India, in 1984 and 1987, respectively. He is the recipient of a post-doctoral fellowship in plant biotechnology, and has published more than 100 research papers in esteemed national and international journals, mostly on brassicas. He has already developed five varieties of rapeseed-mustard. In addition, he has written two books on plant breeding and edited two volumes: one on *Recent Advances in Oilseed Brassicas*, Kalyani Publishers, New Delhi, India, and the second on *Rapeseed Breeding-Advances in Botanical Research*, Vol. 45, Academic Press, Elsevier Publishers. For his excellent scientific endeavors, he has been conferred with the Young Scientist Award: 1993–1994 by the State Department of Science and Technology.

Contributors

D.P. Abrol

Division of Entomology
Sher-e-Kashmir University of Agricultural
Sciences and Technology
Chatha, Jammu, India

Ihsan A. Al-Shehbaz

Head, Department of Asian Botany
Missouri Botanical Garden
St. Louis, Missouri, USA

San Woo Bang

Laboratory of Plant Breeding
Faculty of Agriculture
Utsunomiya University
Utsunomiya, Japan

S.R. Bhat

National Research Centre on Plant
Biotechnology
Indian Agricultural Research Institute
New Delhi, India

Vinitha Cardoza

BASF Corporation
26 Davis Drive
Durham, North Carolina, USA

Mei Desheng

Institute of Oil Crops Research
Chinese Academy of Agricultural Science
Wuhan, P.R. China

Ting-Dong Fu

The National Key Laboratory of Crop Genetic
Improvement
Huazhong Agricultural University
Wuhan, P.R. China

César Gómez-Campo

Universidad Politécnica de Madrid
Departamento de Biología Vegetal
E.T.S. Ingenieros Agrónomos
Ciudad Universitaria
Madrid, Spain

S.K. Gupta

Division of Plant Breeding and Genetics
Sher-e-Kashmir University of Agricultural
Sciences and Technology
Chatha, Jammu, India

Jocelyn C. Hall

Department of Biological Sciences
University of Alberta
Edmonton, Alberta, Canada

Pritam Kalia

Division of Vegetable Science
Indian Agricultural Research Institute (IARI)
New Delhi, India

H. Kitashiba

Graduate School of Agricultural Science
Tohoku University
Sendai, Japan

Marcus Koch

Heidelberg Institute of Plant Sciences
Heidelberg University
Heidelberg, Germany

D. Liu

Institute of Crop Science
Zhejiang University
Hangzhou, P.R. China

Martin A. Lysak

Department of Functional Genomics and
Proteomics
Masaryk University
Brno, Czech Republic

Yasuo Matsuzawa

Laboratory of Plant Breeding
Faculty of Agriculture
Utsunomiya University
Utsunomiya, Japan

Peter McVetty

Department of Plant Science
University of Manitoba
Winnipeg, Manitoba, Canada

M.S. Naeem

Institute of Crop Science
Zhejiang University
Hangzhou, P.R. China

Takeshi Nishio

Graduate School of Agricultural Science
Tohoku University
Sendai, Japan

M. Soledade C. Pedras

Department of Chemistry
University of Saskatchewan
Saskatoon, Saskatchewan, Canada

Shyam Prakash

National Research Centre on Plant
Biotechnology
Indian Agricultural Research Institute
New Delhi, India

Aditya Pratap

Division of Crop Improvement
Indian Institute of Pulses Research (ICAR)
Kanpur, India

Hu Qiong

Institute of Oil Crops Research
Chinese Academy of Agricultural Science
Wuhan, P.R. China

R. Raziuddin

Institute of Crop Science
Zhejiang University
Hangzhou, P.R. China

C. Neal Stewart, Jr.

Department of Plant Sciences
University of Tennessee
Knoxville, Tennessee, USA

Y. Takahata

Faculty of Agriculture
Iwate University
Morioka, Japan

G.X. Tang

Institute of Crop Science
Zhejiang University
Hangzhou, P.R. China

G.L. Wan

Institute of Crop Science
Zhejiang University
Hangzhou, P.R. China

Suzanne I. Warwick

Eastern Cereal and Oilseeds Research Centre
Agriculture and Agri-Food Canada
Ottawa, Ontario, Canada

Kaneko Yukio

Laboratory of Plant Breeding
Faculty of Agriculture
Utsunomiya University
Utsunomiya, Japan

Li Yunchang

Institute of Oil Crops Research
Chinese Academy of Agricultural Science
Wuhan, P.R. China

Carla Zelmer

Department of Plant Science
University of Manitoba
Winnipeg, Manitoba, Canada

Qingan Zheng

Department of Chemistry
University of Saskatchewan
Saskatoon, Saskatchewan, Canada

W.J. Zhou

Institute of Crop Science
Zhejiang University
Hangzhou, P.R. China

1 Molecular Systematics and Evolution

Marcus A. Koch and Ihsan A. Al-Shehbaz

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INTRODUCTION

The past two decades can be characterized by the tremendously increasing number of studies focusing on the systematics, development, phylogenetics, and phylogeography of cruciferous plants (mustards). *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 research into the systematics, taxonomy, evolution, and development of the entire family, including the cultivated taxa and their wild relatives.

The first attempt to summarize knowledge of the family was provided more than 30 years ago (Vaughan et al., 1976). It was followed by Tsunoda et al. (1980), who dealt with the biology and breeding of *Brassica* crops and their wild allies. During the past 20 years, molecular biology and DNA techniques have 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 bridged 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 65th 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. 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; Al-Shehbaz et al., 2006; Bailey et al., 2006; Beilstein 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 toward 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 has been refined (e.g., Al-Shehbaz et al., 2006; Al-Shehbaz and Warwick, 2007; German and Al-Shehbaz, 2008).

What were 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*, there are four: (1) achieving a new infrafamilial classification based on phylogenetically circumscribed new tribes; (2) recognition and assignment of monophyletic genera; (3) unraveling the principles in crucifer evolution and exploring detailed examples for species- or genus-specific evolutionary histories; and (4) phylogenetic circumscription of the order Capparales and the determination of Cleomaceae as the closest and sister family to the *Brassicaceae*. This introductory chapter deals mainly with the first issue. Some 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 Brassiceae, 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), 9 tribes (Alysseae, Arabideae, Brassiceae, Euclidieae, Heliophileae, Hesperideae, Lepidieae, Schizopetaleae, and Sisymbrieae) were maintained by Al-Shehbaz et al. (2006), although 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 reestablished. 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 (Figure 1.1). The study provided the main foundation on which a new tribal classification was introduced (Al-Shehbaz et al., 2006). A subsequent internal transcribed spacer (ITS)-based study (Bailey et al., 2006) provided substantial support for 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 an ITS of nuclear ribosomal DNA and plastidic maturase (*matK*) sequence data (Koch et al., 2007). In that article, 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, Thlaspidiae, 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) (Figure 1.1). 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 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 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 favor the first hypothesis. This scenario was also favored by Koch et al. (2007), who found that the microstructural 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 microstructural mutations. Further support is also found from analyses of the nuclear ITS sequence data (Bailey et al., 2006) and is discussed below.

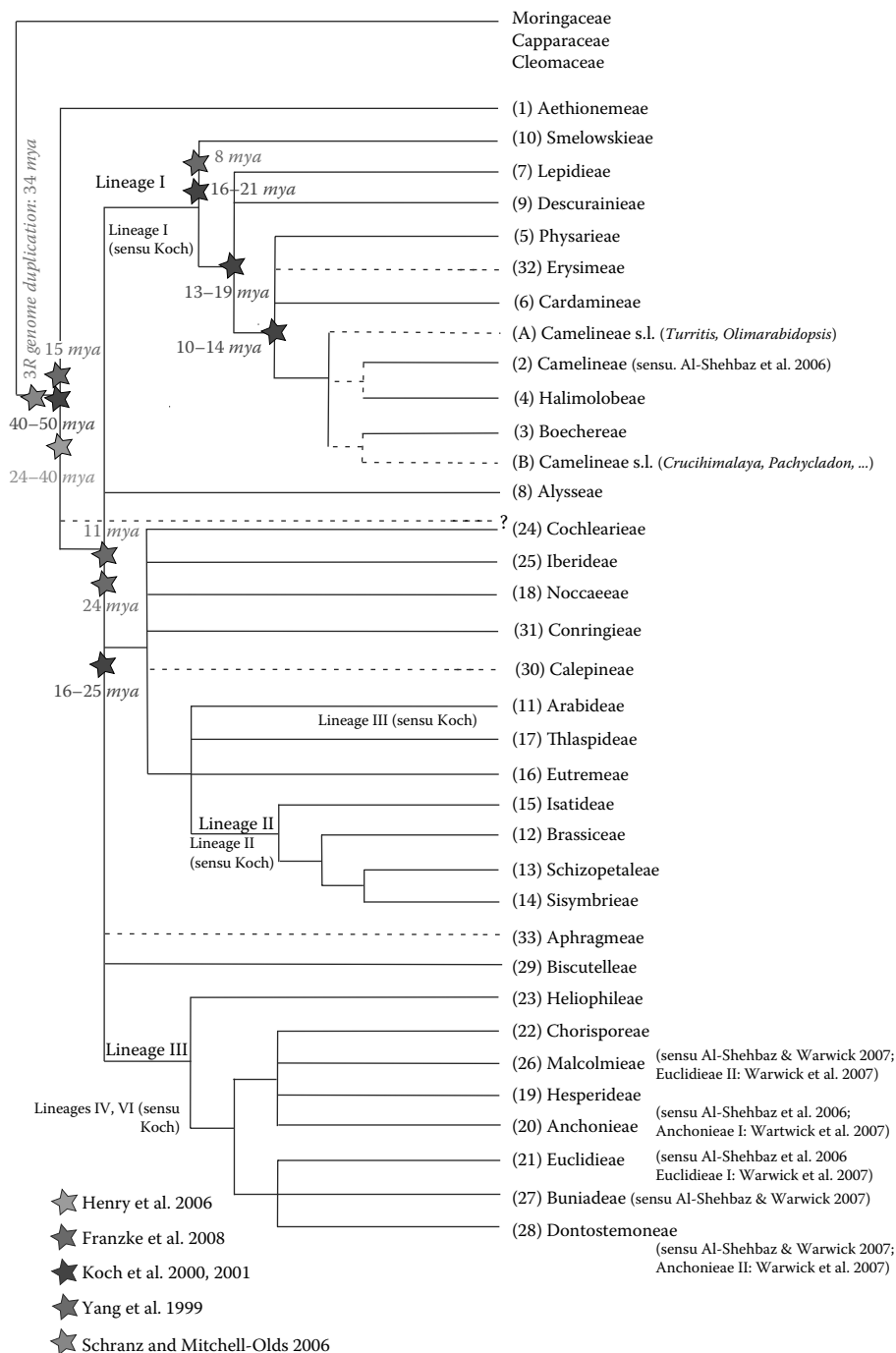


FIGURE 1.1 (See color insert following page 128.) Synopsis of phylogenetic hypothesis from various sources of tribal relationships in the *Brassicaceae* family (for details, refer to the text). Lineages I–III are described in Beilstein et al. (2006). Koch et al. (2007) used different numbers given also as “sensu Koch,” and we suggest the use of Beilstein’s version only 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.

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).

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 reestablished the tribe Buniadeae (tribes 26–28). The studies 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 reestablishment 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 1.1). An overview of these various tribes and a synopsis of the relationships among them are presented in Figure 1.1. 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 limited value (Koch et al., 2001; Koch et al., 2007). To have a comprehensive phylogeny of the entire family, several problematical genera must 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 the 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 the *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 of genome size and duplication, base chromosome number, evolutionary trends, most basal taxa, and monophyly of *Aethionema* is undoubtedly valuable in understanding the evolution and early radiation of the entire family.

2. TRIBE CAMELINEAE

As delimited by Al-Shehbaz et al. (2006), the Camelinae have recently been shown to be paraphyletic and consist of a heterogeneous assemblage of genera (Bailey et al., 2006; Warwick et al., 2007; Koch et al., 2007; German and Al-Shehbaz 2008; Koch, unpublished). 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 be about 35 species. The tribe includes the genera *Arabidopsis* (10 spp.),

TABLE 1.1
Overview on the Tribes and the Number of Genera and Species of the
***Brassicaceae* as Scored Herein**

Tribe	Genera	Species	Ref.
1. Aethionemeae	1	45	This chapter
2. Camelineae	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. Descurainieae	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 and Warwick (2006)
17. Thlaspidiae	7	27	Al-Shehbaz et al. (2006)
18. Noccaeeae	3	90	This chapter
19. Hesperideae	1	45	Al-Shehbaz et al. (2006)
20. Anchonieae	8	68	Al-Shehbaz and Warwick (2007)
21. Euclidieae	13	115	Al-Shehbaz and Warwick (2007)
22. Chorisporaeae	3	47	Al-Shehbaz and Warwick (2007)
23. Heliophileae	1	80	Al-Shehbaz et al. (2006)
24. Cochleariaeae	1	21	Al-Shehbaz et al. (2006)
25. Iberideae	1	27	Al-Shehbaz et al. (2006)
26. Malcolmieae	8	37	Al-Shehbaz and Warwick (2007)
27. Buniadeae	1	3	Al-Shehbaz and Warwick (2007)
28. Dontostemoneae	3	28	Al-Shehbaz and Warwick (2007)
29. Biscutelleae	1	53	German and Al-Shehbaz (2008)
30. Calepineae	3	8	German and Al-Shehbaz (2008)
31. Conringieae	2	9	German and Al-Shehbaz (2008)
32. Erysimeae	1	180	German and Al-Shehbaz (2008)
33. Aphragmeae	1	11	German and Al-Shehbaz (2008)
34. Unnamed-I (A)	2	5	This chapter
35. Unnamed-II (B)	3	20	This chapter
Total	212	3249	

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.

Due to the extensive use of *Arabidopsis thaliana* in basically every field of experimental biology, the genus and its relatives above received considerable study (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, unpublished; Mitchell and Heenan, 2000; Al-Shehbaz and O’Kane, 2002a; Heenan and Mitchell, 2003; Heenan et al., 2002).

3. TRIBE BOECHEREAEE

This tribe of 7 genera and 118 species is almost exclusively North American, and only *Boechera furcata* grows in the Russian Far East (Al-Shehbaz, 2005). Except for *Boechera* (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 *Boechera* and simple in *Nevada*). The majority are perennials with well-defined basal rosette.

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

4. TRIBE HALIMOLOBEAEE

The Halimolobeae is a New World tribe of 5 genera and 39 species mostly distributed in northern and central Mexico (Bailey et al., 2007), although 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 7 genera and 133 species distributed primarily in North America. *Physaria* (105 spp.) is disjunct into South America (5 spp., northern Argentina and southern 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 is nested the previously 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, northern Europe, and northern Russia), which occupies such habitats, should 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) consist of *Lepidium*, a genus recently 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 also belong here.

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 based 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 Alyseae 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). The Alyseae are distributed in Eurasia and North 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 northwestern Africa and Macaronesia (Appel and Al-Shehbaz, 2003). All members of *Farsetia* and *Lobularia* are pubescent with exclusively malpighiaceae trichomes. However, this type of trichome occurs sporadically in species of other tribes, although 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 6 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 *Ianhedkea* (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, one- to three-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 7 species in North America and 18 species 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 8 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 neighboring central Asia, but it is absent in Australia and all except northwestern Africa. *Arabis* (70 spp.) is primarily Eurasian, with 15 spp. in North America, and only a few in northwestern 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, latiseptate 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 (latiseptate 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., unpublished).

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), 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 southwestern 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 component “genera” of both clades exhibit tremendous fruit diversity, which are the main characters used in their delimitation. 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 should be maintained. As a result, the Schizopetaleae will have many fewer species and genera all restricted to South America, whereas the Thelypodieae include genera in both North and South America. Therefore, the Thelypodieae sensu Al-Shehbaz (1973), minus *Macropodium*, should be expanded to include all 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), this 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 tribe species 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, two-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 2 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, unpublished). Further studies are needed to determine if *Chartoloma*, *Tauscheria*, *Glastaria*, and *Schimpera* belong to this tribe. Members of the Isatideae have indehiscent, often pendulous, one- or two-seeded fruits; yellow or rarely white flowers; auriculate stem leaves; and simple or no trichomes.

16. TRIBE EUTREMEAE

This unigeneric tribe comprises *Eutrema* (26 spp.), a genus distributed primarily in Asia, especially the Himalayas and neighboring central Asia, with two species extending their ranges into North America (Al-Shehbaz and Warwick, 2005). 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 Eutremeae are glabrous or with simple trichomes and have white flowers, incumbent cotyledons, and often palmately veined basal leaves.

17. TRIBE THLASPIDAEAE

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, 2001; Beilstein et al., 2006) have shown 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 4 species in the New World (Koch and Al-Shehbaz, 2004), 5 species in the Himalayas (Al-Shehbaz, 2002), and others to be transferred from *Aethionema* and other genera, including all of the other segregates (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 HESPERIDAE

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 northwestern Africa. The Hesperideae are unique in the *Brassicaceae* for their unicellular glands on uniseriate, few-celled stalks.

20. TRIBE ANCHONIEAE

As delimited by Al-Shehbaz et al. (2006), the Anchonieae included 12 genera and approximately 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 8 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* are in need of thorough study 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, two-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 more than 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 redefined.

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

22. TRIBE CHORISPOREAE

This tribe of 3 genera and 47 species is primarily Asian and only 4 of the 35 species of *Parrya* are North American. The other genera are *Chorisporea* (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 and 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 extending into northern North America and Asia and one into Northwest 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 this tribe.

Members of the Cochlearieae have rosulate, undivided basal leaves; white petals; often sessile cauline leaves; terete or angustiseptate siliques; 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 Northwest Africa, and Southwest and Central Asia.

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

26. TRIBE 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 8 primarily Mediterranean genera, although some are distributed into Southwest Asia, the 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. TRIBE BUNIADAE

This unigeneric tribe includes only *Bunias* (3 spp.), a genus distributed exclusively in Eurasia, although two species are weeds naturalized in North America. Molecular studies (Beilstein et al., 2006; Koch, unpublished) 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 sili-
cles, and spiral cotyledons.

28. TRIBE 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 other tribes with multicellular glands on multiseriate-multicel-
lular stalks by the lack of branched trichomes and the presence of often united or winged filaments,
entire stigmas, and rounded repla.

29. TRIBE 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 years ago, the Biscutelleae was not recognized by subsequent authors and
has only recently been reinstated by German and Al-Shehbaz (2008). It is distinguished from the
other tribes by its didymous, angustiseptate, two-seeded fruits; long styles; entire stigmas; simple
trichomes; and auriculate cauline leaves.

30. TRIBE CALEPINEAE

The tribe was first established by Horaninow some 160 years ago and was not recognized since
then. 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 previ-
ously 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., unpublished) clearly support its exclusion from this tribe.

The tribe includes annuals with indehiscent, woody, one- to three-seeded fruits; entire stigmas;
simple or no trichomes; and undivided, often auriculate cauline leaves.

31. TRIBE CONRINGIEAE

Based on molecular studies (German et al., unpublished), German and Al-Shehbaz (2008) estab-
lished this new tribe. It consists of nine, primarily Southwest Asian species in the genera *Conringia*
(6 spp.) and *Zuvanda* (3 spp.), although 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. TRIBE ERYSIMAEAE

This unigeneric tribe consists of *Erysimum* (ca. 180 spp.), a genus centered primarily in Eurasia, with
8 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., unpublished) clearly support its placement in a distinct tribe. Another genus,
Chrysocamela (3 spp.) should perhaps be added to the Erysimeae (Koch et al., unpublished).

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

33. TRIBE APHRAGMEAE

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

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., unpublished; German et al., unpublished). We suggest that the genera *Turritis* (2 spp.) and *Olimarabidopsis* (3 spp.) be placed in one tribe, and that *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, unpublished) led to the tribal adjustments recently proposed by Al-Shehbaz and Warwick (2007) and German and Al-Shehbaz (2008). Table 1.1 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, and Koch) aims to cover more than 95% of all accepted genera. The major difficulty lies in obtaining adequate material for molecular studies on species of numerous monospecific or oligospecific genera (see Figure 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* are 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 (Figure 1.1) are still controversial. The usage of Ks values, as presented by Schranz and Mitchell-Olds (2006) and Maere et al. (2005), are more reliable because they do not 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 (Ks = 0.67) reflecting the last and third major genome duplication event (3R or α 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 value is 0.82, which refers to 41 mya as the divergence time estimate between these two families, provided that the same evolutionary mutational rate is applied.

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2 Phylogeny of *Brassica* and Wild Relatives

Suzanne I. Warwick and Jocelyn C. Hall

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INTRODUCTION

The genus *Brassica* and its wild relatives are included in the tribe Brassiceae, one of approximately 25 to 30 tribes in the *Brassicaceae* or *Cruciferae* family (Al-Shehbaz et al., 2006; Al-Shehbaz and Warwick, 2007). The tribe Brassiceae has long been considered a monophyletic group (Hedge, 1976; Al-Shehbaz, 1985; Koch et al., 2001, 2003; Appel and Al-Shehbaz, 2003). The Brassiceae comprise 48 genera and approximately 240 species (Table 2.1, revised from Warwick and Sauder, 2005; Warwick et al., 2006). Except for the four species of *Cakile* that are native to North America, the tribe is primarily distributed in the Mediterranean and southwestern Asia, with a range extension southward into South Africa. It is geographically centered in the southwestern Mediterranean region (Algeria, Morocco, and Spain), where approximately 40 genera are either endemic or exhibit maximum diversity (Hedge, 1976; Gómez-Campo, 1980, 1999; Al-Shehbaz, 1985; Al-Shehbaz et al., 2006).

Tribal members are morphologically characterized by having conduplicate cotyledons (i.e., the cotyledons longitudinally folded around the radicle in the seed), and/or transversely segmented

TABLE 2.1
List of 48 Genera in the Tribe Brassiceae (*Calepina*
Adanson and *Conringia* Heist. ex Fabr. excluded)

Genus	No. of Species	Base Chromosome No. (n)
<i>Ammosperma</i> Hook. f.	2	—
<i>Brassica</i> L.*	39	7, 8, 9, 10, 11
<i>Cakile</i> Mill.*	6	9
<i>Carrichtera</i> DC.	1	8
<i>Ceratocnemum</i> Coss. & Balansa*	1	8
<i>Chalcanthus</i> Boiss.	1	7
<i>Coincya</i> Porta & Rigo ex Rouy*	6	12
<i>Cordylocarpus</i> Desf.*	1	8
<i>Crambe</i> L.*	34	15
<i>Crambella</i> Maire*	1	11
<i>Didesmus</i> Desv.*	2	8
<i>Diplotaxis</i> DC.*	32	7, 8, 9, 10, 11, 13
<i>Douepia</i> Cambess. ex Jacquem.	2	8
<i>Enarthrocarpus</i> Labill.*	5	10
<i>Eremophyton</i> Bég.*	1	-
<i>Eruca</i> Mill.	4	11
<i>Erucaria</i> Gaertn.*	10	6, 7, 8
<i>Erucastrum</i> C. Presl*	25	7, 8, 9
<i>Fezia</i> Pit. ex Batt.*	1	11
<i>Foleyola</i> Maire	1	16
<i>Fortuynia</i> Shuttlw. ex Boiss.*	2	16
<i>Guiraoa</i> Coss.*	1	9
<i>Hemicrambe</i> Webb*	3	9
<i>Henophyton</i> Coss. & Durieu	2	42
<i>Hirschfeldia</i> Moench*	1	7
<i>Kremeriella</i> Maire*	1	12
<i>Moricandia</i> DC.	8	11, 14
<i>Morisia</i> J. Gay*	1	7
<i>Muricaria</i> Desv.*	1	12
<i>Orychophragmus</i> Bunge	2	12
<i>Otocarpus</i> Durieu*	1	8
<i>Physorhynchus</i> Hook.*	2	14, 16
<i>Pseuderucaria</i> (Boiss.) O.E. Schulz	2	14
<i>Pseudofortuynia</i> Hedge	1	7
<i>Psychine</i> Desf.	1	15
<i>Quezeliantha</i> H. Scholz ex Rauschert	1	-
<i>Raffenaldia</i> Godr.*	2	7
<i>Raphanus</i> L.*	3	9

—continued

TABLE 2.1 (continued)
List of 48 Genera in the Tribe Brassiceae (*Calepina*
Adanson and *Conringia* Heist. ex Fabr. excluded)

Genus	No. of Species	Base Chromosome No. (n)
<i>Rapistrum</i> Crantz*	2	8
<i>Rytidocarpus</i> Coss.	1	14
<i>Savignya</i> DC.	1	15
<i>Schouwia</i> DC.	1	18
<i>Sinapidendron</i> Lowe	4	9, 10
<i>Sinapis</i> L.*	4	7, 8, 9, 12
<i>Succowia</i> Medik.	1	18
<i>Trachystoma</i> O.E. Schulz*	3	7, 8
<i>Vella</i> L.	7	17
<i>Zilla</i> Forssk.	2	16

Note: Recent generic changes include placement of *Boleum* Desv. and *Euzomodendron* Coss. in *Vella* (Warwick and Al-Shehbaz, 1998); *Dolichorhynchus* Hedge & Kit Tan in *Douepea* (Appel and Al-Shehbaz, 2001); *Quidproquo* Greuter & Burdet in *Raphanus* (Al-Shehbaz and Warwick, 1997); *Nesocrambe* A.G. Mill. (Miller et al., 2002) in *Hemicrambe* (Al-Shehbaz, 2004); *Brassica* includes subgenus *Brassicaria* Gómez-Campo [= *Guenthera* Andr. (Gómez-Campo, 2003)].

* Indicates the presence of heteroarthrocarpic fruit.

Source: Adapted from Warwick and Sauder, 2005, taxonomic literature included therein; and Warwick et al., 2006, with base chromosome numbers from Warwick and Al-Shehbaz, 2006.

fruits that have seeds or rudimentary ovules in both segments (heteroarthrocarpic; Appel, 1999) and, if present, only simple trichomes or hairs (Gómez-Campo 1980, 1999; Al-Shehbaz, 1985). The first two features are unknown elsewhere in the family. The few exceptions to this character combination are the genera *Ammosperma* and *Pseuderucaria*, neither of which has the conduplicate cotyledons or the segmented fruits. Classical taxonomic delimitation in the tribe Brassiceae has depended mainly upon fruit characters, with considerable debate centered on the circumscription and relationships among subtribes and genera. In the most comprehensive taxonomic treatment of the tribe, Schulz (1919, 1923, 1936) recognized seven subtribes: Brassicinae, Cakilinae, Moricandiinae, Raphaninae, Savignyinae, Vellinae, and Zillinae. Gómez-Campo (1980) proposed a reduction to six subtribes, by including the Savignyinae in the Vellinae. The Brassicinae and Moricandiinae are characterized by elongated, siliquose fruit, whereas the other subtribes generally have reduced, shortened fruit; the morphological distinctness of subtribes Brassicinae, Moricandiinae, and Raphaninae is not well substantiated (Al-Shehbaz, 1985; Warwick and Black, 1994). The Moricandiinae, for example, were separated from the Brassicinae on the basis of two characters: (1) beak (a sterile upper segment, distinct from the upper segment of heteroarthrocarpic fruits), and (2) absence of median nectaries; the latter are present in the Brassicinae and the seeds are usually present in the distal segment. As we see below, recent molecular-based phylogenetic data have provided support for alternative tribal, subtribal, and generic circumscriptions.

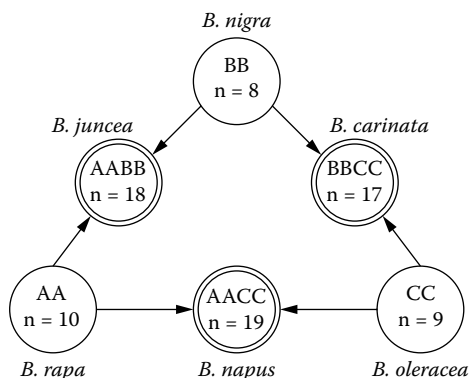


FIGURE 2.1 Relationships among the six *Brassica* crop species; Triangle of U. (Source: From U, 1935)

HISTORICAL REVIEW OF MOLECULAR PHYLOGENETIC STUDIES IN THE TRIBE

Because of its economic importance, extensive molecular-based phylogenetic studies have been conducted on members of the tribe. Earlier studies focused on *Brassica* crops and relatives. Relationships between the three diploid *Brassica* crop species [*B. nigra* ($n = 8$, BB), *B. rapa* ($n = 10$, AA), and *B. oleracea* ($n = 9$, CC)] and related amphidiploid species [*B. napus* ($n = 19$, AACC), *B. carinata* ($n = 17$, BBCC), and *B. juncea* ($n = 18$, AABB)] were first proposed by U in 1935 (Figure 2.1). Palmer et al. (1983) and Erickson et al. (1983) were the first to use restriction site data from the chloroplast DNA (cpDNA) to document the origins of the amphidiploid taxa, the results of which were later confirmed by Song et al. (1988)

using nuclear RFLP markers. Yanagino et al. (1987) compared the cpDNA of 11 species in the tribe and found that the genus *Brassica* was not monophyletic, as *Brassica* taxa were intermixed with five allied genera rather than with each other. Song et al. (1990) studied the nuclear RFLPs of some 15 *Brassica* species and three additional genera, and found similar incongruities with traditional taxonomy.

Since these initial studies, sampling of the tribe has been extensive; all but seven genera (Table 2.2) have now been included in phylogenetic studies. In a series of studies based on the presence/absence of cpDNA restriction sites (Warwick and Black, 1991, 1993, 1994, 1997a; Warwick et al., 1992), analyses of relationships were extended to the whole tribe. Pradhan et al. (1992) also evaluated relationships in more than 60 species from ten genera of the tribe using cpDNA and mitochondrial DNA (mtDNA) RFLP data. The remaining studies analyzed DNA sequence variation, although they vary with regard to taxa and region sampled. ITS (internal transcribed spacers ITS-1 and ITS-2 of nuclear DNA, and the 5.8 rRNA gene) sequence-based phylogenetic studies were conducted on subtribe Vellinae (Crespo et al., 2000) and the genus *Crambe* (Francisco-Ortega et al., 1999, 2002). Focusing on 21 species, Lysak et al. (2005) analyzed sequences from the *trnL* (UAA)-*trnF* (GAA) region. Recent phylogenetic studies include sequences from the chloroplast gene maturaseK (*matK*) and nuclear gene phytochrome A (*phyA*; Hall et al., unpublished) with a particular focus on subtribe Cakilinae. The study by Warwick and Sauder (2005) represents the most extensive taxonomic sampling of the tribe to date. These analyses were based on the ITS region and *trnL* sequence data. ITS sequences were obtained from 86 species of the tribe Brassiceae, representing subtribes Brassicinae (includes Moricandiinae and Raphaninae), Cakilinae, Vellinae, and Zillinae, and controversial tribe members *Calepina*, *Conringia*, and *Orychophragmus*. *trnL* sequences were obtained for 95 tribal species.

PHYLOGENETIC RELATIONSHIPS

TRIBAL LIMITS

In general, molecular studies support a monophyletic origin for the tribe (e.g., Anderson and Warwick, 1999; Francisco-Ortega, 1999; Lysak et al., 2005; Warwick and Sauder, 2005; Bailey et al., 2006; Beilstein et al., 2006). In fact, the delimitation of the tribe has not changed drastically since the detailed work of Schulz (1919, 1923; Al-Shehbaz et al., 2006). The Chinese genus *Spryginia* was excluded early from the tribe (Gómez-Campo, 1980). However, the placement

TABLE 2.2
Assignment of Genera to Phylogenetic Lineages

Rapa/Oleracea					
Lineage	Nigra Lineage	Cakile Lineage	Vella Lineage	Zilla Lineage	Savignya Lineage
<i>Brassica</i>	<i>Brassica</i>	<i>Cakile</i>	<i>Carrichtera</i>	<i>Foleyola</i>	<i>Psychine</i>
<i>Diplotaxis</i>	<i>Ceratocnemum</i>	<i>Crambella</i>	<i>Vella</i>	<i>Fortuynia</i>	<i>Savignya</i>
<i>Enarthrocarpus</i>	<i>Coincya</i>	<i>Didymus</i>		<i>Physorhynchus</i>	NEW
<i>Eruca</i>	<i>Cordylocarpus</i>	<i>Erucaria</i>		<i>Schouwia</i>	<i>Henophyton</i>
<i>Erucastrum</i>	<i>Diplotaxis</i>			<i>Zilla</i>	<i>Pseuderucaria</i>
<i>Moricandia</i>	<i>Erucastrum</i>				
<i>Morisia</i>	<i>Guiraoa</i>				NEW
<i>Raphanus</i>	<i>Hemicrambe</i>				<i>Orychophragmus</i>
<i>Rapistrum</i>	<i>Hirschfeldia</i>				
<i>Rytidocarpus</i>	<i>Kremeriella</i>		Not Studied:	<i>Annosperma</i>	
	<i>Muricaria</i>			<i>Chalcanthus</i>	
	<i>Otocarpus</i>			<i>Douepia</i>	
	<i>Raffanaldia</i>			<i>Eremophyton</i>	
	<i>Sinapidendron</i>			<i>Fezia</i>	
	<i>Sinapis</i>			<i>Pseudofortuynia</i>	
	<i>Trachystoma</i>			<i>Quezeliantha</i>	

of *Calepina* (1 sp.), *Conringia* (6 spp.), and *Orychophragmus* (2 spp.) (Gómez-Campo, 1980; Al-Shehbaz, 1985) within the tribe remains controversial and, as a result, has been the subject of several recent studies. *Calepina* and *Conringia* were once included in the Brassiceae (Schulz, 1936; Al-Shehbaz, 1985; Gómez-Campo, 1999). Gómez-Campo (1980) excluded these two genera from the tribe, but then tentatively re-included *Calepina* and *Orychophragmus* (Gómez-Campo, 1999). Parsimony analyses of the cpDNA, ITS, and combined ITS/*trnL* sequence data support a monophyletic origin for the tribe, including the controversial members *Calepina*, *Conringia*, and *Orychophragmus* (Warwick and Sauder, 2005). In all four data sets (cpDNA, ITS, *trnL*, and ITS/*trnL*), *Calepina* and *Conringia* formed a separate and well-supported clade (with bootstrap values of 91%, 88%, 73%, and 95%, respectively) that was sister to the rest of the tribe. Based on bootstrap support for the broader tribal clade (85% in combined ITS/*trnL*) and low (<50%) bootstrap support for the remaining Brassiceae (Figure 2.4), Warwick and Sauder (2005) retained *Calepina* and *Conringia* in the tribe. In contrast, other recent molecular studies (Anderson and Warwick, 1999; Francisco-Ortega, 1999; Lysak et al., 2005; Beilstein et al., 2006) clearly support their exclusion from the Brassiceae. For example, *Calepina* formed a clade with the four outgroup taxa rather than with the rest of the tribe in the ITS-based phylogenetic analysis of Francisco-Ortega et al. (1999). Phylogenetic relationships based on the chloroplast *trnL-trnF* region and estimated divergence times based on sequence data of the chalcone synthase gene are congruent with comparative chromosome painting data in placing *Calepina* and *Conringia* outside the clade of Brassiceae species with triplicated genomes (Lysak et al., 2005; see Chapter 10 in this book). Earlier evidence of isozyme duplication for *Pgm-2* and *Tpi-1* (Anderson and Warwick, 1999) in all tribal members, except *Calepina* and *Conringia*, also supported their exclusion from the tribe. Al-Shehbaz et al. (2006) suggested that both genera should be removed from the Brassiceae, and further that the alleged conduplicate cotyledons present in *Calepina* and one of the six species of *Conringia* are likely not homologous to those of typical members of the tribe.

The last problematic genus, *Orychophragmus* (2 spp., China), has been retained in the tribe (Warwick and Sauder, 2005; Lysak et al., 2005). Earlier isozyme duplication studies (Anderson and Warwick, 1999) supported its inclusion in the tribe as it had both *Pgm-2* and *Tpi-1* duplications, like all other genera in the tribe. Hybridization data (reviewed in Warwick et al., 2000; Warwick and Sauder, 2005) between *Orychophragmus violaceus* and the six cultivated *Brassica* species also support its inclusion in the tribe. The position of *Orychophragmus* within the tribe, however, has not been resolved; it was sister to the *Calepina/Conringia* clade in one of two most parsimonious cpDNA trees, but most closely associated with the Vellinae clade in the ITS/*trnL* analyses (Warwick and Sauder, 2005).

MAJOR MOLECULAR LINEAGES IN THE TRIBE

As indicated above, six or seven lineages are currently recognized in the tribe, some of which are consistent with traditional subtribal delimitations. Recent morphological, hybridization, and molecular data sets have provided support for alternative subtribal and generic circumscriptions. Restriction site analyses of cpDNA (Figures 2.2 and 2.3; Warwick and Black, 1993, 1994, 1997a) and *matK* sequence data (Hall et al., unpublished) provided support for the recognition of subtribes Cakilinae, Vellinae, and Zillinae, but little support for the Brassicinae, Moricandiinae, and Raphaninae. Results from the cpDNA analyses divided the latter three subtribes into two clades, designated the Rapa/Oleracea and Nigra lineages (Warwick and Black, 1991, 1993, 1994, 1997a; Warwick et al., 1992), also referred to as the *Brassica* and *Sinapis* lineages, respectively, by other authors. Lysak et al. (2005) observed the two lineages in a *trnL-trnF*-based phylogeny and dated the split of the two lineages at 7.9 mya. Results from the ITS- and ITS/*trnL*-based clades (Figure 2.4; Warwick and Sauder, 2005) are similar to those obtained with cpDNA restriction site data (Figure 2.2; Warwick and Black, 1994, 1997a), which provided support for the recognition of

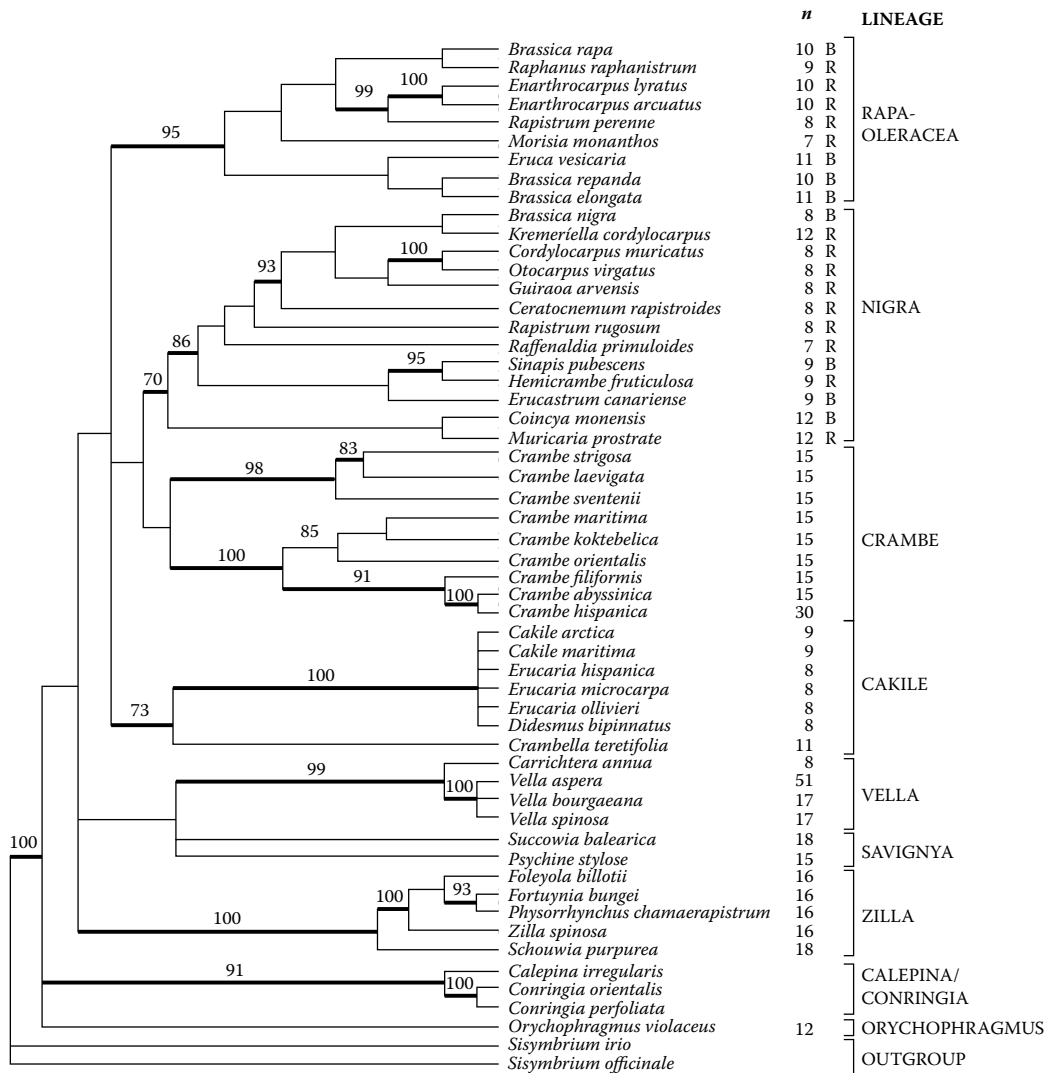


FIGURE 2.2 Strict consensus tree of the tribe Brassiceae based on maximum parsimony analysis of chloroplast DNA restriction site polymorphisms. Bolded branches have bootstrap support 70% or higher. Major lineages indicated to the right include *Rapa-Oleracea* lineage, *Nigra* lineage, *Crambe* lineage, *Cakile* lineage, *Vella* lineage, *Savignya* lineage, *Zilla* lineage, *Calepina/Conringia*, *Orychophragmus*, and the outgroup. Assignment to subtribes: Brassicinae (B) and Raphaninae (R). Chromosome numbers (*n*) are indicated at right. (Source: Adapted from Warwick and Black, 1997a, and Warwick and Sauder, 2005.)

taxonomic subtribes Cakilinae, Vellinae, and Zillinae; but as with previous cpDNA studies, there was little support for subtribes Brassicinae, Moricandiinae, and Raphaninae. The close genetic relatedness of the latter three subtribes is consistent with hybridization data where genetic exchange is possible among members of these subtribes (reviewed in Warwick et al., 2000).

Despite significant progress in identifying lineages within Brassiceae, our knowledge of how these lineages are related to one another is limited. Phylogenetic analyses of the Brassiceae based on nucleotide sequences of the S-locus related gene *SLR1* showed a close relationship between members of the Brassiceae and Raphaninae (Inaba and Nishio, 2002). Analyses of *matK* sequence

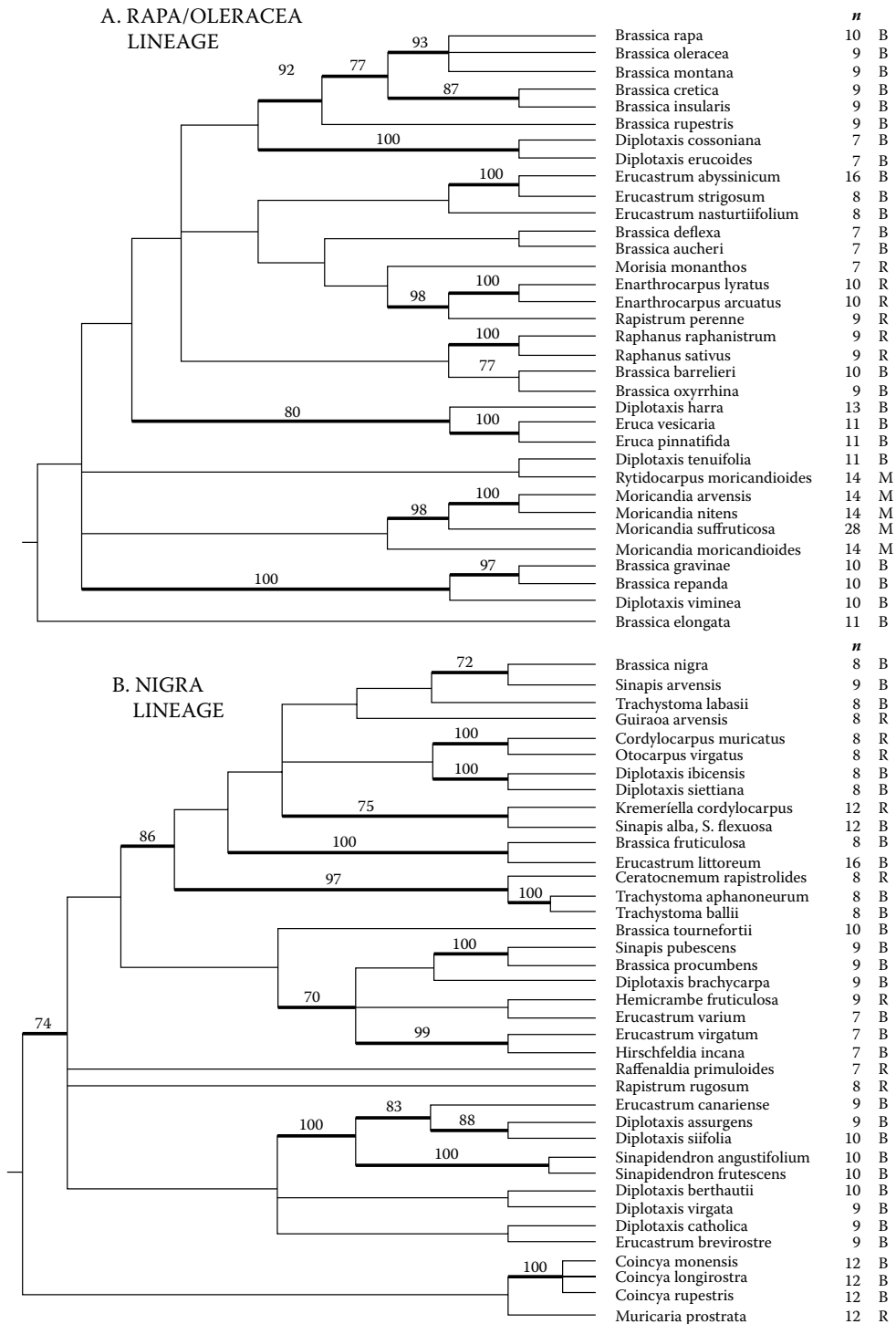
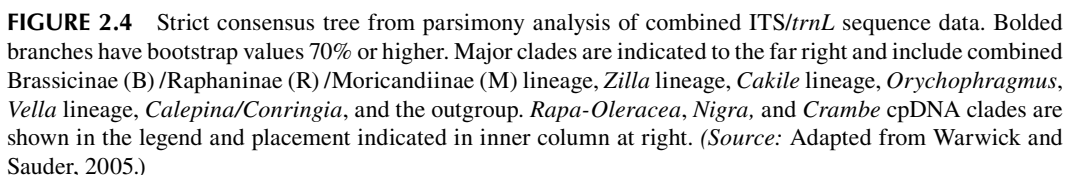


FIGURE 2.3 Strict consensus tree from parsimony analysis of chloroplast DNA restriction site polymorphisms for (A) *Rapa-Oleracea* lineage and (B) *Nigra* lineage in the tribe Brassiceae. Bolded branches have bootstrap values 70% or higher. Assignment to subtribes: Brassicinae (B), Raphaninae (R), and Moricandiinae (M). Chromosome numbers (*n*) are listed to the right. (Source: Adapted from Warwick and Black, 1997a.)



data (Hall et al., unpublished) support the *Zilla* lineage (*Schouwia* and *Zilla*) as sister to all other Brassiceae. There is little or no support for other relationships among lineages, which is surprising given the number of taxa sampled and the range of molecular markers utilized to examine relationships in the tribe. The unresolved backbone may be due to a lack of appropriate variation in molecular markers studied, or due to a lack of variation as the result of rapid radiation of the tribe. Although more molecular and morphological data are required, there is some evidence that this striking pattern may be the result of rapid radiation near the base of the tribe. The lineage is young, based on molecular dating information (ca. 7.9–14.6 mya; Lysak et al., 2005; Koch et al., 2001). An intriguing hypothesis is that the proposed radiation is perhaps due to either the evolution of the heteroarthrocarpic fruit and/or to the genome duplication that occurred at the base of the Brassiceae.

Each lineage shown in Table 2.2 is discussed in turn.

CAKILE LINEAGE

Phylogenetic analyses (Figure 2.2; Warwick and Black, 1997a) based on cpDNA provided evidence for the inclusion of the Cakilinae genera *Cakile* ($n = 9$), *Erucaria* (includes *Reboudia*; $n = 6,7,8$), and former Raphaninae genera *Crambella* ($n = 11$) and *Didesmus* ($n = 8$), in a *Cakile* lineage. ITS *trnL* sequence data for *Cakile* and *Erucaria* (Figure 2.4; Warwick and Sauder, 2005), and more recently *matK*- and *phyA*-based phylogenies based on extensive sampling for all four genera (Hall et al., unpublished), confirmed support for the lineage. Interestingly, the former study indicated that *Crambella* is sister to all other genera, whereas the latter study indicated that the monotypic genus is more derived in the clade. *Cakile*, *Didesmus*, and *Erucaria* were very closely related and, indeed, formed a single intermixed clade rather than three distinct generic clades.

The *Cakile* lineage uniformly has heteroarthrocarpic fruits with one to a few seeds in the upper segment, but the cotyledonary position is variable. *Crambella*, *Didesmus*, and some *Erucaria* (species formerly in *Reboudia*) have conduplicate cotyledons, a defining trait for the tribe, but *Cakile* has incumbent or accumbent cotyledons and the remaining *Erucaria* have incumbent or spiral cotyledons (Schulz, 1919, 1923, 1936).

ZILLA LINEAGE

Phylogenetic analyses (Warwick and Black, 1994) based on cpDNA provided evidence for the inclusion of the $n = 16$ Zillinae genera *Foleyola*, *Fortuynia*, *Physorhynchus*, and *Zilla*, and the former Vellinae genus *Schouwia* ($n = 18$) in the *Zilla* lineage. The latter genus was the sister group to other Zillinae genera in these analyses. A number of studies support the *Zilla* lineage: ITS sequences for *Fortuynia*, *Schouwia*, and *Zilla* (Crespo et al., 2000); ITS and *trnL* sequences for *Fortuynia* and *Zilla* (Warwick and Sauder, 2005); combined ITS/*trnL* sequences for *Zilla* plus *Schouwia* (Figure 2.4; Warwick and Sauder, 2005); and more recently *matK* and *phyA* sequences (Hall et al., unpublished data) for *Zilla* plus *Schouwia*.

Morphologically, members of the *Zilla* lineage are all adapted to xeromorphic conditions; share a similar cotyledon shape, which is large with a shallow obtuse notch; and have heteroarthrocarpic fruit, the upper segment of which is always fertile. Chromosome numbers are high — $n = 16, 18$.

VELLA AND SAVIGNYA LINEAGES

Phylogenetic analyses (Warwick and Black, 1994) based on cpDNA provided evidence for the inclusion of the Vellinae genera *Boleum* ($n = 51$), *Carrichtera* ($n = 8$), *Euzomodendron* ($n = 17$), and *Vella* ($n = 17$) in the *Vella* lineage. This result led to the transfer of monotypic genera *Boleum* and *Euzomodendron* to the genus *Vella* (Warwick and Al-Shehbaz, 1998). The ITS-sequence-based phylogeny of subtribe Vellinae (Crespo et al., 2000) generally confirmed the cpDNA-based Vellinae lineage, as did the ITS and ITS/*trnL* sequences for *Carrichtera* and *Vella* in studies by Warwick and