

# Contribution to ITS phylogeny of the Brassicaceae, with special reference to some Asian taxa

Dmitry A. German · Nikolai Friesen ·  
Barbara Neuffer · Ihsan A. Al-Shehbaz ·  
Herbert Hurka

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**Abstract** Sequence data from the nuclear ribosomal internal transcribed spacer (ITS) region for 189 accessions representing 184 species in 121 genera of Brassicaceae were used to determine monophyly of tribes and genera, tribal boundaries, and component genera. Parsimony analysis and Bayesian inference suggest that the tribes Camelinae and Arabideae are polyphyletic and should be subdivided into smaller tribes. The study also supports the recent recognition of the new tribes Aphragmeae, Biscutelleae, Buniadeae, Calepineae, Conringieae, Dontostemoneae, Erysimeae, Malcolmieae, Megacarpaeae, and Turritideae. The data argue for the placement of *Borodinia* in the tribe Boechereae, *Litwinowia*

and *Pseudoclausia* in the Chorisporeae, *Atelanthera* and *Streptoloma* in the Euclidieae, and *Megacarpaea* and *Pugionium* in the Megacarpaeae, and exclusion of *Asperuginoides*, *Didymophysa*, and *Ptilotrichum* from the Alysseae, *Macropodium*, *Pseudoturritis*, and *Stevenia* from the Arabideae, and *Crucihimalaya*, *Irenepharsus*, *Pachycladon*, and *Turritis* from the Camelinae. Finally, the findings support the expansion of *Stevenia* to include both *Berteroella* and *Ptilotrichum*, *Sterigmostemum* to include *Oreoloma* and one species of *Anchonium*, *Crucihimalaya* to include *Transberingia* and several species of *Arabis*, and *Parrya* to include *Pseudoclausia*. The data also suggest that *Calymmatium* and *Olimarabidopsis* may be congeneric.

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D. A. German (✉)  
South-Siberian Botanical Garden, Altai State University,  
Lenin str. 61, 656049 Barnaul, Russia  
e-mail: oreoloma@rambler.ru

N. Friesen · H. Hurka  
Botanical Garden, University of Osnabrück, Albrechtstrasse 29,  
49076 Osnabrück, Germany

B. Neuffer  
Department of Biology, Botany, University of Osnabrück,  
Barbarastrasse 11, 49076 Osnabrück, Germany

I. A. Al-Shehbaz  
Missouri Botanical Garden, 2345 Tower Grove,  
St. Louis, MO 63110, USA

**Present Address:**  
D. A. German  
Department of Functional Genomics and Proteomics, Institute of  
Experimental Biology, Masaryk University, Kamenice 5,  
Building A2/214, 62500 Brno, Czech Republic

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## Introduction

The Brassicaceae (Cruciferae) are cosmopolitan but most abundant in temperate regions of the northern hemisphere and rather rare in the tropics except for the montane areas. The family is very attractive for evolutionary studies (Koch et al. 2003; Hurka et al. 2005; Mitchell-Olds et al. 2005) because of its:

1. remarkable ecological amplitude;
2. economic importance as a source of edible and industrial oils, condiments, vegetables, fodder, and ornamentals;
3. numerous species as colonizers or notorious weeds; and
4. most important model plant in molecular biology, *Arabidopsis thaliana* (L.) Heynh.

However, the family is still in need of comprehensive studies to resolve its major subdivisions and their relationships, to delimit its genera, and to understand its basal

members. Substantial progress has been made in the last few years, and a rather comprehensive framework of phylogenetic relationships within the Brassicaceae is emerging (Al-Shehbaz et al. 2006; Bailey et al. 2006; Beilstein et al. 2006, 2008; Al-Shehbaz and Warwick 2007; Koch et al. 2007; Warwick et al. 2007, 2008).

The most extensive molecular data set on the Brassicaceae is based on DNA sequences from the nuclear ribosomal ITS region. Although reliance on ITS as the sole source of phylogenetic evidence may have its shortcomings, because of homoplasy, orthology/paralogy, concerted evolution, and alignment problems due to indel accumulation, it remains the most commonly used marker for generating family wide, species-level phylogenetic inferences (Koch et al. 2003; Warwick and Sauder 2005; Bailey et al. 2006; Warwick et al. 2007, 2008; Khosravi et al. 2009).

Although slightly more than 50% of the 338 genera of the Brassicaceae have been surveyed for the ITS marker (Bailey et al. 2006; Warwick et al. 2007, 2008; Khosravi et al. 2009), most of the narrowly distributed or poorly known genera, especially from Asia, have not been sampled; one of the objectives of this study is to bridge that gap. The family has recently been divided into 25 tribes (Al-Shehbaz et al. 2006), and ten additional tribes have since been recognized (Al-Shehbaz and Warwick 2007; German and Al-Shehbaz 2008a; German 2009; Koch and Al-Shehbaz 2009). Obviously, the vast majority of the species and genera of the family belong to one of these tribes. However, the final number of tribes, the phylogenetic relationships among them, and the number of their component genera remain to be clarified. A step in the right direction is taken herein by the inclusion of many genera not previously studied, especially from central Asia, one of the most important centers of species diversity of the Brassicaceae (Hedge 1976; Appel and Al-Shehbaz 2003). Therefore the final choice of taxa, aimed at maximum representation of the recently recognized 28 tribes (Al-Shehbaz et al. 2006; Al-Shehbaz and Warwick 2007; Warwick et al. 2007) and the seven tribes (German and Al-Shehbaz 2008a; German 2009; Koch and Al-Shehbaz 2009) added on the basis of this study, provided the backbone for assignment of the Asian taxa sampled herein.

Tribes either absent or poorly represented in central Asia (e.g. Aethionemeae, Boechereae, Brassiceae, Halimolobeae, Heliophileae, Malcolmieae, Physarieae, and Schizopetaleae) were represented by the fewest species that ensure their accurate topology in the overall phylogeny of the family.

## Materials and methods

### Material studied, sequence accession numbers

The sample comprised 184 species in 121 genera of Brassicaceae, of which 80 species are represented by

original data, including 11 genera and 45 species studied molecularly for the first time. Taxa, collection data, vouchers, and EMBL accession numbers are listed in Table 1. Species names follow the most recent world-wide checklist of Warwick et al. (2006b) except for subsequent changes in the generic placement of a few taxa. Sequence data for other taxa were obtained from published EMBL/GenBank/DDBJ accessions.

### Sequencing, alignment

DNAs from herbarium specimens were isolated with the NucleoSpin Plant Kit (Macherey–Nagel, Düren, Germany) in accordance with the instructions of the manufacturer and were used directly in PCR amplifications. Double-stranded DNA of the complete ITS region, including the 5.8S rDNA gene, was amplified by 35 cycles of symmetric PCR using ITS primers 18F and 26R. The PCR procedure involved a hot start with 2 min at 94°C, and 35 cycles of amplification (1 min 94°C, 45 s 55°C, 45 s 72°C), final elongation step for 7 min at 72°C, and storage at 4°C. When amplification of the complete ITS region was not possible, we used the primer combination of 18F and ITS2 Primer (White et al. 1990) and 5.8F Primer (5'CTT CTG GCC GAG GGC ACG TC 3') with 26R. In some cases we applied a 5.8S primer specific for Brassicaceae newly designed by us (Brass-5.8R: 5'-TTGCGTTCAAAGACTCGATG-3'; Brass-5.8F: 5'-AGCGAAATGCGATACTTGGT-3'). The PCR products were separated on an agar gel and purified with the NucleoSpin Gel Extraction Kit (Macherey–Nagel). After checking DNA concentration on 1.8% agar gel, about 40 ng PCR products were used in a 10- $\mu$ l-cycle sequencing reaction with the ABI BigDye Terminator Kit (ABI, Foster City, CA, USA) in accordance with the instructions of the manufacturer. Products of the cycle sequencing reactions were run on an ABI 377XL automatic sequencer. Forward and reverse sequences from every individual were manually edited and combined in single consensus sequences. The sequences of all samples were aligned with CLUSTAL X (Thompson et al. 1997), and the alignment subsequently corrected manually. Many published sequences from EMBL lacked the 5.8S region, and to avoid the problems with incomplete sequences and those that may represent heterogeneous sets of polymerase chain reaction products (Bailey et al. 2006), we cut the 5.8S region from all used sequences. Alignment has been submitted to the TreeBASE database.

### Phylogenetic analyses

Phylogeny was estimated using parsimony and Bayesian methods. Parsimony analyses were performed in Paup 4.0b10 (Swofford 2002). Heuristic searches were conducted with simple and with 100 random addition sequences and

**Table 1** Taxa studied, geographical origin, source (either herbarium specimen or reference to published sequence), and GenBank accession no.

Species	Geographical origin	Collector (herbarium) or reference to published sequences	GenBank accession no.
<i>Aethionema saxatile</i> (L.) R. Br.	Germany, Osnabrück Bot. Garden	Mummenhoff et al. (2005)	AJ862697, AJ862698
<i>Alliaria petiolata</i> (Bieb.) Cavara & Grande	Germany, Osnabrück	Mummenhoff et al. (2005)	AJ862703, AJ862704
<i>Alyssum cypricum</i> Nyár.	Turkey, Burdur	Mengoni et al. (2003)	AY237948
<i>Alyssum dasycarpum</i> Steph. ex Willd.	Kyrgyzstan	Neuffer, Hurka, Friesen (OSBU 15599a)	FM164502, FM164503
<i>Alyssum klimesii</i> Al-Shehbaz	India, Ladakh	Klimeš 2070 (ALTB)	FM164504, FM164505
<i>Alyssum lenense</i> Adams	Kazakhstan, Tarbagatai mts.	Smirnov, German et al. B008 (ALTB)	FM164506, FM164507
<i>Alyssum linifolium</i> Steph. ex Willd.	Kyrgyzstan	Neuffer, Hurka, Friesen (OSBU 15599b)	FM164508, FM164509
<i>Alyssum montanum</i> L.	Italy, Tuscani	Mengoni et al. (2003)	AY237938
<i>Alyssum obovatum</i> (C.A. Mey.) Turcz.	Russia, East Siberia, Chita region	Golyakov and Mysik B033 (ALTB)	FM164510, FM164511
<i>Andrzeiowskaia cardamine</i> Reichenb.	Turkey, Vilayet	Bailey et al. (2006)	AJ628337, AJ628338
<i>Anchonium elichrysofolium</i> (DC.) Boiss.	Turkey	Warwick et al. (2007)	DQ357514
<i>Aphragmus eschscholtzianus</i> Andr. ex DC.	Canada, Yukon	Warwick et al. (2006a)	DQ165334
<i>Aphragmus involucratus</i> (Bunge) O.E. Schulz	Mongolia, Gobi Altai mts.	Neuffer and Hurka (OSBU 12042)	FM164512, FM164513
<i>Arabidopsis thaliana</i> (L.) Heynh.	Czech Republic	O'Kane et al. (1996)	U43224
<i>Arabis alaschanica</i> Maxim.	China, Inner Mongolia, Henan Shan mts.	Shurun (MO 04505376)	FM164642
<i>Arabis alpina</i> L.	Germany	Koch et al. (1999)	AJ232920
<i>Arabis axillaris</i> Kom.	Korea, Unchkhen-gan (type)	Komarov (LE)	FM164643
<i>Arabis blepharophylla</i> Hook. & Arn.	USA	Koch et al. (1999)	AJ232903
<i>Arabis kokanica</i> Regel & Schmalh.	Tajikistan, Pamir mts.	Ikonnikov 17756 (LE)	FM164644
<i>Arabis kamelinii</i> Botsch.	Tajikistan, Pamir mts.	Ikonnikov 13877 (LE)	FM164645
<i>Arabis tibetica</i> Hook. f. & Thomson	Kyrgyzstan, Alai mts.	Neuffer, Hurka, Friesen (OSBU 15740)	FM164514, FM164515
<i>Asperuginoides axillaris</i> (Boiss. & Hohen.) Rauschert	Uzbekistan	Vašák (WAG 0143231)	FM164516, FM164517
<i>Atelanthera perpusilla</i> Hook.f. & Thomson	Kyrgyzstan, Alai valley	Shmakov et al. B068a (ALTB)	FM164518, FM164519
<i>Aubrieta deltoidea</i> (L.) DC.	Germany, Bot. Garden Jena	Koch et al. (1999)	AJ232909
<i>Aurinia saxatilis</i> (L.) Desv. [as <i>Alyssum saxatile</i> L.]	–	Heenan et al. (2002)	AF401115
<i>Berteroa incana</i> (L.) DC.	Germany, Bot. Garden Osnabrück	Friesen (OSBU 16535)	FM164646
<i>Berteroella maximowiczii</i> (Palib.) O.E. Schulz	NE China	Zimmermann 424 (P)	FM164526, FM164527
<i>Biscutella laevigata</i> L.	Europa	Bailey et al. (2006)	DQ452056
<i>Boechera pinetorum</i> (Tidestrom.) Windham & Al-Shehbaz [incorrectly reported as <i>Arabis holboellii</i> Hornem.]	USA, Nevada	Roy (2001)	AF183117
<i>Boechera stricta</i> (Graham) Al-Shehbaz [as <i>Arabis drummondii</i> A. Gray]	USA, Wyoming	Koch et al. (1999)	AJ232887
<i>Boreava orientalis</i> Jaub. & Spach	Turkey, Antalya	Koch et al. (2007)	DQ249859
<i>Borodinia macrophylla</i> (Turcz.) O.E. Schulz	Russia, Far East	Kharkevich and Vyshin 79 (LE)	FM164528, FM164529

**Table 1** continued

Species	Geographical origin	Collector (herbarium) or reference to published sequences	GenBank accession no.
<i>Botschantzevia karatavica</i> (Lipsch. & Pavlov) Nabiev	Kazakhstan, Karatau	Vvedensky and Kovalevskaya 73 (LE)	FM164530, FM164531
<i>Brassica juncea</i> (L.) Czern.	Cultivated	Yang et al. (1999)	AF128093
<i>Braya humilis</i> (C.A. Mey.) Robins. [as <i>Neotorularia humilis</i> (C.A. Mey.) Hedge & J. Léonard]	China	O'Kane and Al-Shehbaz (2003)	AF137566
<i>Bunias cochlearioides</i> Murr. (1)	Kazakhstan, NW	Sumnevich and Serkin (TK)	FM958513
<i>Bunias cochlearioides</i> (2)	Russia, SW Siberia	Burdakova (TK)	FM958514
<i>Bunias orientalis</i> L. (1)	Germany, Osnabrück	Neuffer (OSBU 205)	FM958515
<i>Bunias orientalis</i> (2)	Russia, Altai	Neuffer, Hurka, Friesen (OSBU 13556)	FM958516
<i>Bunias orientalis</i> (3)	Botanic Garden Dijon	Koch et al. (2007)	DQ249863
<i>Calepina irregularis</i> (Asso) Thell.	Spain	Francisco-Ortega et al. (1999)	AF039995, AF040039
<i>Calymmatium draboides</i> (Korsh.) O.E. Schulz (1)	Tajikistan, East Pamir	Kuznetsov and Varivtseva s.n. (MW)	FM958511
<i>Calymmatium draboides</i> (2)	Tajikistan, Badakhshan	Tzvelev (LE)	FM958512
<i>Camelina microcarpa</i> Andrz. ex DC.	Romania	O'Kane and Al-Shehbaz (2003)	AF137574
<i>Capsella rubella</i> Reut.	Spain, Andaluz near Cadiz	Neuffer 690 ( <i>Capsella</i> -collection Osnabrück, OSBU)	FM164647
<i>Cardamine bellidifolia</i> L.	Russia, Altai mts.	Neuffer, Hurka, Friesen (OSBU 13254)	FM164648
<i>Catolobus pendula</i> (L.) Al-Shehbaz [as <i>Arabis pendula</i> L.]	Russia, Far East	O'Kane and Al-Shehbaz (2003)	AF137572
<i>Caulanthus inflatus</i> S. Wats.	USA, California	Pepper and Norwood (2001)	AF346653
<i>Chorispora bungeana</i> Fisch. & Mey.	Kazakhstan	Warwick et al. (2007)	DQ357520
<i>Chorispora macropoda</i> Trautv.	Afghanistan	Warwick et al. (2007)	DQ357522
<i>Chrysochamela velutina</i> Boiss.	Botanic Garden, University of Copenhagen	Koch et al. (2007)	DQ249856
<i>Cithareloma lehmannii</i> Bunge	Iran	Warwick et al. (2007)	DQ357528
<i>Clausia aprica</i> (Steph.) Korn.-Tr.	Russia, East Europe	Franzke et al. (2004)	AY546110, AY546139
<i>Clausia kazachorum</i> Pavlov	Kazakhstan	Warwick et al. (2007)	DQ357530
<i>Clausia trichosepala</i> (Turcz.) Dvořák	Mongolia, Eren-Daba mts.	Kamelin, Gubanov et al. 754 (MW)	AJ628317, AJ628318
<i>Clypeola aspera</i> Turrill	Iran	Warwick et al. (2008)	EF514642
<i>Cochlearia danica</i> L.	Germany, Sylt	Mummenhoff and Mühlhausen unpublished	AJ628283, AJ628284
<i>Conringia perfoliata</i> (C.A. Mey.) N. Busch	Iran	Warwick and Sauder (2005)	AY722505
<i>Crambe arborea</i> Webb ex H. Christ	Spain, Canary Islands, Tenerife	Francisco-Ortega et al. (2002)	AF450012
<i>Crucihimalaya mollissima</i> (C.A. Mey.) Al-Shehbaz, O'Kane & R.A. Price	Afghanistan	O'Kane and Al-Shehbaz (2003)	AF137552
<i>Crucihimalaya rupicola</i> (Kryl.) A.L. Ebel & D. German	Mongolia, Altai mts.	German B056 (ALTB)	FM164538, FM164539
<i>Crucihimalaya wallichii</i> (Hook.f. & Thomson) Al-Shehbaz, O'Kane & R.A. Price	Japan, Myagi University, Sendai seed centre	Koch et al. (1999)	AJ131396
<i>Degenia velebitica</i> (Degen) Hayek	Hungary	Warwick et al. (2008)	EF514646
<i>Descurainia pinnata</i> (Walter) Britton	USA, Utah	Roy (2001)	AF183122

**Table 1** continued

Species	Geographical origin	Collector (herbarium) or reference to published sequences	GenBank accession no.
<i>Dichasianthus subtilissimus</i> (M. Pop.) Ovcz. & Junussov	Tajikistan	O'Kane and Al-Shehbaz (2003)	AF137594
<i>Didymophysa fedtschenkoana</i> Regel & Schmalh.	Kyrgyzstan, Alai mts.	Neuffer, Hurka, Friesen (OSBU 15733)	FM164544, FM164545
<i>Dilophia salsa</i> Thomson	Kyrgyzstan, Alai mts.	Neuffer, Hurka, Friesen (OSBU 16157)	FM164649
<i>Diptychocarpus strictus</i> (Fisch.) Trautv.	Afghanistan	Warwick et al. (2007)	DQ357535
<i>Dontostemon crassifolius</i> Bunge	Mongolia, Ömnögovi	Batlai Oyuntsetseg (OSBU 12356)	AY558923, AY558951
<i>Dontostemon dentatus</i> (Bunge) Ledeb.	Japan, Xoncio	Anonymous (VLA)	AY558915, AY558943
<i>Dontostemon pinnatifidus</i> (Willd.) Al-Shehbaz & H. Ohba	Mongolia, Hövsgol lake	Gubanov et al. (MW)	AY558935, AY558963
<i>Dontostemon tibeticus</i> (Maxim.) Al-Shehbaz	China, Quinghai	Ho et al. (MO)	AY558942, AY558970
<i>Draba doerfleri</i> Wettst.	Bot. Garden Osnabrück (seeds from Serbia)	Neuffer (OSBU 142)	FM164650
<i>Draba hystrix</i> Hook.f. & Thomson	Pakistan	Koch and Al-Shehbaz unpublished	AY134194
<i>Draba oreades</i> Schrenk	Mongolia, Altai	Hurka and Neuffer (OSBU 10433)	FM164651
<i>Draba sibirica</i> (Pall.) Thell.	Russia, Altai	Hurka, Neuffer, Friesen (OSBU 12973)	FM164652
<i>Draba nuda</i> (Bélang.) Al-Shehbaz & M. Koch [as <i>Drabopsis nuda</i> (Bélang.) Stapf]	Iran	O'Kane and Al-Shehbaz (2003)	AF137577
<i>Draba verna</i> L. [as <i>Erophila spathulata</i> Láng]	Austria	Koch and Al-Shehbaz (2002)	AF377952
<i>Eruca vesicaria</i> (L.) Cav. subsp. <i>sativa</i> (Mill.) Thell. [as <i>E. sativa</i> Mill.]	No locality given	Francisco-Ortega et al. (1999)	AF039996, AF040037
<i>Erysimum cheiranthoides</i> L.	USA	Kress et al. (2005)	DQ005989
<i>Erysimum mongolicum</i> D. German	Mongolia, Altai mts. (type)	German (OSBU 14802)	FM164520, FM164521
<i>Erysimum siliculosum</i> (Bieb.) DC.	Kazakhstan	Smirnov and Antonyuk (OSBU 14155)	FM164522, FM164523
<i>Euclidium syriacum</i> (L.) W.T. Aiton	Iran	Warwick et al. (2007)	DQ357544
<i>Eutrema altaicum</i> (C. A. Mey.) Al-Shehbaz & Warwick	Russia, Altai	Hurka, Neuffer, Friesen (OSBU 13363)	FM164653
<i>Eutrema botschantzevii</i> (D. German) Al-Shehbaz & Warwick	Russia, South-West Siberia (type)	Shaulo et al. (NS)	FM164654
<i>Eutrema edwardsii</i> R. Br.	Mongolia, Altai, Tavan Bogd	Hurka and Neuffer (OSBU 10405)	FM164655
<i>Eutrema parvulum</i> (Schrenk) Al-Shehbaz & Warwick [as <i>Thellungiella parvula</i> (Schrenk) Al-Shehbaz & O'Kane]	Turkey	O'Kane and Al-Shehbaz (2003)	AF137579
<i>Fibigia clypeata</i> (L.) Medik.	Botanic Garden Bordeaux	Koch et al. (2007)	DQ249852
<i>Fibigia spathulata</i> (Kar. & Kir.) B. Fedtsch.	Kazakhstan, Arkaly mts.	Botschantzev and Botschantzeva 1058 (LE)	FM164656
<i>Fibigia suffruticosa</i> (Vent.) Sweet	Turkey	Mummenhoff (OSBU 18314)	FM164657
<i>Fourraea alpina</i> (L.) Greuter & Burdet [as <i>Arabis pauciflora</i> (Grimm) Garcke]	Germany, Thüringen, Jena	Koch et al. (1999)	AJ232890
<i>Galitzkya potaninii</i> (Maxim.) V. Bocz.	Mongolia, Dzungarian Gobi	German B161 (ALTB)	FM164524, FM164525
<i>Galitzkya spathulata</i> (Steph. ex Willd.) V. Bocz.	Russia, Altai foothills	German et al. B163a (ALTB)	FM164534, FM164535

**Table 1** continued

Species	Geographical origin	Collector (herbarium) or reference to published sequences	GenBank accession no.
<i>Goldbachia pendula</i> Botsch.	Mongolia, Dzungarian Gobi	Smirnov, German et al. A052 (OSBU 14762)	FM164536, FM164537
<i>Halimolobos diffusus</i> (A. Gray) O.E. Schulz	USA, Nevada	O'Kane and Al-Shehbaz (2003)	AF137567
<i>Heliophila arenaria</i> Sond.	South Africa	Mummenhoff et al. (2005)	AJ863600, AJ864811
<i>Heliophila coronopifolia</i> L.	South Africa	Mummenhoff et al. (2005)	AJ863596, AJ864814
<i>Hesperis laciniata</i> All.	Morocco	Mummenhoff et al. (2005)	AJ628315, AJ628615
<i>Hesperis sibirica</i> L.	Russia, Altai	Neuffer, Hurka, Friesen (OSBU 13609)	FM164658
<i>Hormathophylla purpurea</i> (Lag. & Rodr.) P. Küpfer	Spain, Granada	Wieringa 2730 (WAG 0061830)	FM164546, FM164547
<i>Hornungia petraea</i> (L.) Reichenb.	Morocco	Staudinger (OSBU 13661)	FM164548, FM164549
<i>Ianhedgia minutiflora</i> (Hook.f. & Thomson) Al-Shehbaz & O'Kane	Afghanistan	O'Kane and Al-Shehbaz (2003)	AF137568
<i>Iberis amara</i> L.	Botanical Garden University of Mainz, Germany	Kropf et al. (2003)	AJ440311
<i>Ionopsidium prolongoi</i> (Boiss.) Batt.	Spain, Cadiz	Bailey et al. (2006)	AJ628303, AJ628304
<i>Irenepharsus magicus</i> Hewson	Australia, NSW, South Coast	Telford 9644 (CANB, CBG 84-00-326)	FM164550, FM164551
<i>Isatis tinctoria</i> L. [as <i>I. indigotica</i> Fortune ex Lindl.]	China, Jiangsu	Bailey et al. (2006)	AF384104
<i>Iskandera alaica</i> (Korsh.) Botsch. & Vved.	Kyrgyzstan, Alai mts.	Neuffer, Hurka, Friesen (OSBU 15699)	FM164659
<i>Kerneria saxatilis</i> (L.) Sweet subsp. <i>boissieri</i> (Reut.) Nyman	Spain	Kropf et al. (2003)	AJ440313
<i>Leiospora exscapa</i> (C.A. Mey.) Dvořák	Mongolia, Mongolian Altai mts.	Hurka and Neuffer (OSBU 10410)	FM164552, FM164553
<i>Leiospora pamirica</i> (Botsch. & Vved.) Botsch. & Pachom.	Central Asia	Warwick et al. (2007)	AJ628329, AJ628330
<i>Lepidium draba</i> L.	Romania	Bot. Garden Jasi, Romania (OSBU 95-0334-10)	FM164554, FM164555
<i>Lepidium ruderales</i> L.	Germany, Oldenburg	Mummenhoff et al. (2004)	AJ582465, AJ582513
<i>Lepidium paniculatum</i> (Regel & Schmalh.) Al-Shehbaz	Kyrgyzstan, Tin Shan	Neuffer, Hurka, Friesen (OSBU 15546)	FM164556, FM164557
<i>Leptaleum filifolium</i> (Willd.) DC.	Turkmenistan	Kutafiev and Shmakov (OSBU 14773)	FM164560, FM164561
<i>Litwinowia tenuissima</i> (Pall.) Woron. ex Pavlov	Mongolia, Dzungarian Gobi	Smirnov, German et al. A064 (OSBU 14774)	FM164562, FM164563
<i>Lyrocarpa coulteri</i> Hook. & Harv.	Mexico	O'Kane and Al-Shehbaz (2003)	AF137591
<i>Macropodium nivale</i> (Pall.) W.T. Aiton	Russia, Altai mts.	Neuffer, Hurka, Friesen (OSBU 12946)	FM164660
<i>Malcolmia littorea</i> (L.) W.T. Aiton	Portugal	Warwick et al. (2007)	DQ357559
<i>Mancoa bracteata</i> (S. Wats.) Rollins	Mexico	Bailey et al. (2002)	AF307633
<i>Matthiola incana</i> (L.) W.T. Aiton	France, Bretagne	Hurka (OSBU 96-0180-10)	AJ628339, AJ628340
<i>Matthiola lunata</i> DC.	Algeria	Gómez-Campo (OSBU 91-50-0053-10)	AJ628341, AJ628342
<i>Megacarpaea megalocarpa</i> (Fisch. ex DC.) Schischk. ex B. Fedtsch.	Mongolia, Dzungarian Gobi	Smirnov, German et al. A066 (OSBU 14776)	FM164564, FM164565
<i>Megadenia pygmaea</i> Maxim.	Russia, Buryatia	Popov and Bardunov (NSK)	FM164661
<i>Microstigma brachycarpum</i> Botsch.	China	Warwick et al. (2007)	DQ357569

**Table 1** continued

Species	Geographical origin	Collector (herbarium) or reference to published sequences	GenBank accession no.
<i>Microstigma deflexum</i> (Bunge) Juz.	Mongolia, Gobi Altai	Batlai Oyuntsetseg 631 (OSBU 14828)	FM165293, FM165294
<i>Microthlaspi perfoliatum</i> (L.) F.K. Mey.	Russia, Astrakhan	Neuffer (OSBU 8811)	FM164566, FM164567
<i>Nasturtium microphyllum</i> (Boenn. ex Reichenb.) Reichenb.	Denmark, Jütland, Helgønaes	Franzke et al. (1998)	AF078029, AF078030
<i>Neotorularia torulosa</i> (Desf.) Hedge & J. Léonard	Iran	O'Kane and Al-Shehbaz (2003)	AF137571
<i>Neurotropis szowitsiana</i> (Boiss.) F.K. Mey. [as <i>Thlaspi szowitsianum</i> Boiss.]	Caucasus	Koch and Mummenhoff (2001)	AF336174, AF336175
<i>Noccaea caerulescens</i> (J. & C. Presl) F.K. Mey.	Germany, Sauerland	Koch (OSBU 95-0052-10)	FM164568, FM164569
<i>Olimarabidopsis cabulica</i> (Hook.f. & Thomson) Al-Shehbaz, O'Kane & R.A. Price	Kyrgyzstan	O'Kane and Al-Shehbaz (2003)	AF137548
<i>Olimarabidopsis pumila</i> (Steph.) Al-Shehbaz, O'Kane & R.A. Price	Arabidopsis Seed Stock Center, Sendai, Japan	Johnston et al. (2005)	AY662277
<i>Oreoloma matthiolooides</i> (Franch.) Botsch.	China	Warwick et al. (2007)	DQ357574
<i>Oreoloma sulfureum</i> Botsch.	China, Dzungaria, Argaltay mts.	Rus/Sin Altai Exped. 2004-002 (ALTB)	FM164572, FM164573
<i>Oreoloma violaceum</i> Botsch.	Mongolia, Dzungarian Gobi	Smirnov, German et al. A089 (OSBU 14799a)	FM164574, FM164575
<i>Orychophragmus violaceus</i> (L.) O.E. Schulz	E Asia	Warwick and Sauder (2005)	AY722506
<i>Pachycladon wallii</i> (Carse) Heenan & A.D. Mitchell [as <i>Cheesemanian wallii</i> (Carse) Allan]	New Zealand	Mitchell and Heenan (2000)	AF100681
<i>Pachyneurum grandiflorum</i> (C.A. Mey.) Bunge (1)	Mongolia, Mongolian Altai	German A071 (OSBU 1481)	FM164576, FM164577
<i>Pachyneurum grandiflorum</i> (2)	Russia, Altai	Neuffer, Hurka, Friesen (OSBU 13117)	FM164578, FM164579
<i>Parrya asperrima</i> (B. Fedtsch.) M. Pop.	Kyrgyzstan, Tian Shan	Neuffer, Hurka, Friesen (OSBU 16525)	FM164580, FM164581
<i>Parrya lancifolia</i> M. Pop.	Kyrgyzstan, Terskei Alatau	Lazkov (FRU)	FM164582, FM164583
<i>Parrya pulvinata</i> M. Pop.	Kazakhstan	Warwick et al. (2007)	DQ357579
<i>Parrya stenocarpa</i> Kar. & Kir.	Kyrgyzstan, Terskei Alatau	Lazkov s.n. (FRU)	FM991736
<i>Physaria didymocarpa</i> (Hook.) A. Gray	USA, Montana	O'Kane and Al-Shehbaz (2003)	AF137583
<i>Pseudoarabidopsis toxophylla</i> (Bieb.) Al-Shehbaz, O'Kane & R.A. Price	Kazakhstan	O'Kane and Al-Shehbaz (2003)	AF137558
<i>Pseudoclausia olgae</i> (Regel & Schmalh.) Botsch.	Uzbekistan, Nuratau	Pimenov et al. (MW)	FM991737
<i>Pseudoclausia turkestanica</i> (Lipsky) A. Vassil.	Kyrgyzstan, Tian Shan	Lazkov (FRU)	FM164584, FM164585
<i>Pseudoempervivum aucheri</i> (Boiss.) Pobed. [as <i>Cochlearia aucheri</i> Boiss.]	Turkey, Tossia	Koch and Mummenhoff (2001)	AF336202, AF336203
<i>Pseudoturritis turrita</i> (L.) Al-Shehbaz [as <i>Arabis turrita</i> L.]	Bot. Gard. Berlin-Dahlem	Koch et al. (1999)	AJ232905
<i>Ptilotrichum dahuricum</i> Peschkova	Mongolia, Pre-Hingan upland	Gubanov et al. 1062 (MW)	FM164588, FM164589
<i>Ptilotrichum tenuifolium</i> (Steph.) C.A. Mey.	Russia, East Siberia, Baikal lake	Bergmann (OSBU 14876)	FM164590, FM164591
<i>Pugionium pterocarpum</i> Kom.	Russia, Tuva	Lomonosova and Danilov (NS)	FM164592, FM164593

**Table 1** continued

Species	Geographical origin	Collector (herbarium) or reference to published sequences	GenBank accession no.
<i>Rhammatophyllum fruticosum</i> (C.A. Mey.) Al-Shehbaz	Kazakhstan, Tin Shan	Smirnov, German et al. B061 (ALTB)	FM164594, FM164595
<i>Rhammatophyllum kamelinii</i> (Botsch.) Al-Shehbaz & O. Appel	Mongolia, Dzungarian Gobi	Smirnov, German et al. A075 (OSBU 14785)	FM164596, FM164597
<i>Rorippa sylvestris</i> (L.) Bess.	Germany, Lower Saxony, Bad Rothenfelde	Franzke et al. (1998)	AF078023, AF078024
<i>Sandbergia perplexa</i> (L.F. Hend.) Al-Shehbaz [as <i>Halimolobos perplexus</i> (L.F. Hend.) Rollins]	USA, Idaho	Koch et al. (1999)	AJ232926
<i>Sisymbriopsis ychengica</i> (Z.X. An) Al-Shehbaz, Z.X. An & G. Yang	China	Warwick et al. (2004a)	AY353161
<i>Sisymbrium altissimum</i> L.	USA, California	Francisco-Ortega et al. (1999)	AF039997, AF040040
<i>Sisymbrium brassiciforme</i> C.A. Mey.	India, Kashmir	Koch et al. (2007)	DQ518399
<i>Sisymbrium linifolium</i> (Nutt.) Nutt. [as <i>Schoenocrambe linifolia</i> (Nutt.) Greene]	USA, Colorado	Roy (2001)	AF183088
<i>Smelowskia flavissima</i> (Kar. & Kir.) Kar. & Kir.	Kazakhstan, Tarbagatai mts.	Smirnov, German et al. A085 (OSBU 14795)	FM164598, FM164599
<i>Smelowskia jacutica</i> (Botsch. & Karav.) Al-Shehbaz & Warwick [as <i>Gorodkovia jacutica</i> Botsch. & Karav.]	Russia	Warwick et al. (2004b)	AY230646
<i>Smelowskia tibetica</i> (Thomson) Lipsky [as <i>Hedinia tibetica</i> (Thomson) Ostenf.]	China	Warwick et al. (2004b)	AY230607
<i>Solms-laubachia flabellata</i> (Regel) J.P. Yue, Al-Shehbaz & H. Sun [as <i>Desideria flabellata</i> (Regel) Al-Shehbaz]	Kyrgyzstan, Alai mts.	Neuffer, Hurka, Friesen (OSBU 15734)	FM164542, FM164543
<i>Sphaerocardamum nesliiforme</i> Shauer	Mexico	Bailey and Doyle (1999)	AF055195
<i>Spirorhynchus sabulosus</i> Kar. & Kir.	China, Dzungaria	Rus/Sin Altai Exped. 2004-159 (ALTB)	FM164600, FM164601
<i>Sterigmostemum caspicum</i> (Lam.) Rupr.	Kazakhstan, Arkaly mts.	Smirnov, German et al. A087 (OSBU 14797)	FM164610, FM164611
<i>Sterigmostemum fuhaiense</i> H.L. Yang	China, Altai mts.	Rus/Sin Altai Exped. 2004-304 (ALTB)	FM164612, FM164613
<i>Sterigmostemum ramosissimum</i> (O.E. Schulz) Rech.f.	Turkmenistan	Shmakov et al. B238 (ALTB)	FM164614, FM164615
<i>Sterigmostemum schmakovii</i> Kamelin & D. German	Kazakhstan, Zaissan depression	Smirnov, German et al. A088 (OSBU 14798)	FM164616, FM164617
<i>Stevenia alyssoides</i> Adams ex Fisch.	Mongolia, Hövsgol lake	Gubanov 5226 (MW)	FM164602, FM164603
<i>Stevenia cheiranthoides</i> DC.	Mongolia, Pre-Hingan upland	Kamelin et al. 1633 (MW)	FM164604, FM164605
<i>Stevenia incarnata</i> (Pall. ex DC.) Kamelin	Russia, East Siberia, Baikal lake	Bergmann (OSBU 14841)	FM164606, FM164607
<i>Stevenia sergievskajae</i> (Krasnob.) Kamelin & Gubanov	Mongolia, Hövsgol lake	Gubanov et al. (MW)	FM164608, FM164609
<i>Streptanthus albidus</i> Greene subsp. <i>peramoenus</i> (Greene) Kruckeb	USA, California	Pepper and Norwood (2001)	AF346651
<i>Streptoloma desertorum</i> Bunge	Turkmenistan, Ashkhabad distr., Annau	Zhilenko (MO 3149466)	FM164618, FM164619
<i>Strigosella africana</i> (L.) Botsch. [as <i>Malcolmia africana</i> (L.) W.T. Aiton]	USA, Utah	Warwick et al. (2007)	AY237307
<i>Strigosella brevipes</i> (Bunge) Botsch.	Mongolia, Dzungarian Gobi	Warwick et al. (2007)	AY558940, AY558968
<i>Stubendorffia gracilis</i> (Pavlov) Botsch. & Vved.	Kazakhstan	Bailey et al. (2006)	DQ780944, DQ780945



**Table 1** continued

Species	Geographical origin	Collector (herbarium) or reference to published sequences	GenBank accession no.
<i>Synthlipsis greggii</i> A. Gray	Mexico, Nuevo Leon	O'Kane and Al-Shehbaz (2003)	AF137590
<i>Tauscheria lasiocarpa</i> Fisch. ex DC.	Kazakhstan, Altai mts.	Smirnov, German et al. B258 (ALTB)	FM164620, FM164621
<i>Teesdalia nudicaulis</i> (L.) R. Br.	Germany, Bramsche	Koch and Mummenhoff (2001)	AF336214, AF336215
<i>Thlaspi alliaceum</i> L.	Bot. Garden Düsseldorf, Germany	Koch and Mummenhoff (2001)	AF336156, AF336157
<i>Transberingia bursifolia</i> (DC.) Al-Shehbaz & O'Kane [as <i>Beringia bursifolia</i> (DC.) O'Kane, Al-Shehbaz & R.A. Price]	Russia	O'Kane and Al-Shehbaz (2003)	AF137557
<i>Turritis glabra</i> L. [as <i>Arabis glabra</i> (L.) Bernh.]	Germany	Koch et al. (1999)	AJ232925
<i>Yinshania henryi</i> (Oliv.) Y.H. Zhang	China, Hubei, Shenlngjia	Koch et al. (1999)	AJ232930
<i>Werdermannia anethifolia</i> (Phil.) I.M. Johnst.	Chile	Warwick et al. (2002)	AF531645
<i>Zilla spinosa</i> (L.) Prantl subsp. <i>macroptera</i> (Coss.) Maire & Weiller	No locality given	Crespo et al. (2000)	AF263397
<i>Zuvanda crenulata</i> (DC.) Askerova	Israel	Warwick et al. (2007)	DQ357606
<i>Cleome lutea</i> Hook.	USA, Utah	O'Kane and Al-Shehbaz (2003)	AF137588

Herbaria acronyms according to Index Herbariorum

TBR branch swapping. Maximum tree limit was set at 50,000 most parsimonious trees. Statistical support of the branches of the 50% majority-rule consensus tree was tested by Bootstrap (1,000 replicates) and Jackknife (100 replicates) analyses. Bayesian inference used the program MrBayes 3.1 (Ronquist and Huelsenbeck 2003). Sequence evolution models were evaluated using the Akaike information criterion with the aid of Modeltest 3.7 (Posada and Crandall 1998). The GTR+I+G model was chosen as the best fit. There were two independent runs each of eight chains, 10 million generations, sampling every 100 trees, and 25% of initial trees were discarded as burn-in. The remaining 28,000 trees were combined into a single data set, and a majority-rule consensus tree was obtained. Bayesian posterior probabilities were calculated for that tree in MrBayes 3.1.

*Cleome lutea* Hook. was used as outgroup, because Cleomaceae was shown to be the sister family to the Brassicaceae (Hall et al. 2002, 2004).

## Results

### Sequence data

The aligned ITS data matrix consisted of 473 characters across 184 Brassicaceae taxa and *Cleome lutea* (outgroup)

(GenBank numbers are given in Table 1). Sixty-two characters were constant, and of the 412 variable characters, 370 were potentially parsimony informative. Problems were caused by *Bunias orientalis* L. (but not by *B. cochlearioides* Murr.): in the two samples studied by us, PCR amplification resulted in three fragments instead of one, as for all other accessions studied, two weak bands of ca. 500 and 700 bp, respectively, and one stronger band of ca. 1,250 bp. Direct sequencing of the 700-bp fragment failed except for ITS 2 when using the primer 26R (as for the 500-bp fragment, see below.) Sequencing the 1,250 bp fragment revealed a sequence of 1,162 bp. The first 111 bp were homologous with the beginning of the Brassicacean ITS1 region, whereas the last 337 bp of the *Bunias orientalis* 1,162 bp sequence were homologous with the 5.8S region and with the complete ITS2 region. The segment from position 112 to position 825 (length 714 bp) is of unknown homology. BLAST search gave no results. For the alignment of the *Bunias orientalis* sequences, this 714 bp segment was discarded, and only the first 111 bp of the ITS1 region and the ITS2 region were taken into account. The *Bunias orientalis* sequence accession no. DQ249863 taken from GenBank (Table 1) was submitted by Koch et al. (2007). In their analysis, PCR amplification resulted in a ca. 500-bp fragment, which corresponded to our 500-bp fragment. The first 111 bp were homologous with the beginning of ITS1, and the last 337 bp

homologous with the 5.8S region and ITS2, comparable with our results with the 1,250 bp fragment, although with a much shorter insertion which was also of unknown homology.

Apart from the problems with *Bunias orientalis*, we had difficulties with the alignment of species of the tribe Chorisporaee, except for species of *Chorispora* R.Br. ex DC. An insertion of about 48 bp at the beginning of the ITS2 region (position no. 322–369) prevented unequivocal alignment. This region was cut off, and the alignment we were working with is based on 473 bp. The alignment is given in Supplement 2.

### Phylogenetic analyses

The 50,000 most parsimonious trees had a length of 4,482 steps and a consistency index  $CI = 0.2048$  ( $CI = 0.1951$  excluding uninformative characters) and retention index  $RI = 0.6319$ . These values are in the range of previously studied family or “lineage” wide ITS phylogenies (e.g. Bailey et al. 2006; Warwick et al. 2007). The strict consensus tree is available in Supplement 1 along with results of Bootstrap and Jackknife analyses. Figure 1 presents the Bayesian majority-rule consensus tree of the 28,000 post-burn-in trees from that analysis. Bayesian posterior probabilities and bootstrap supports from the parsimony analyses are shown on the branches of the tree (see numbers and asterisks above branches in Fig. 1; for Jackknife support values, see Supplement 1).

### Tree topology

Both Bayesian and parsimony analyses supported largely congruent topologies (Fig. 1). In general, the tree topology (Fig. 1) agrees fairly well with the molecular phylogenies published to date (Koch 2003; Koch et al. 2003; Bailey et al. 2006; Beilstein et al. 2006; Warwick et al. 2008; Khosravi et al. 2009). *Aethionema* W.T. Aiton is sister to an unresolved basal polytomy including the rest of the family. Most of the tribes can be assigned to the three *ndhF* “lineages” of Beilstein et al. (2006, 2008) which are also supported by data from other markers (Koch et al. 2007; Franzke et al. 2009; Lysak et al. 2009). The “core group” of lineage I includes Camelinae sensu Al-Shehbaz et al. (2006), Physarieae, Halimolobeae, and Boechereae, and is mirrored in Fig. 1. The assignment of other tribes of this lineage (Cardamineae, Lepidieae, Descurainieae, Smeulowskieae) was well supported by Bayesian values only (Fig. 1). Lineage II comprises the tribes Brassiceae, Isatideae, Schizopetaleae, and Sisymbrieae, and this grouping is fully supported by our analysis as is lineage III (Chorisporaee, Hesperideae, Euclidieae, Anchonieae; the last two tribes sensu Al-Shehbaz et al. 2006) (Fig. 1).

The tree topology clearly support the view that the Camelinae sensu Al-Shehbaz et al. (2006) is polyphyletic, which agrees with Bailey et al. (2006), Clauss and Koch (2006), Koch et al. (2007), Lysak et al. (2009), and some earlier works (Heenan et al. 2002). The ITS data also show that the Arabideae sensu Al-Shehbaz et al. (2006) is split into two strongly supported monophyletic subclades (Fig. 1) revealed in earlier studies (Heenan et al. 2002; Koch et al. 1999, 2000, 2001; Koch 2003). The study also supports the recent recognition of the new tribes Aphragmeae, Biscutelleae, Buniadeae, Calepineae, Conringieae, Dontostemoneae, Erysimeae, Malcolmieae, Megacarpaceae, and Turritideae (Al-Shehbaz and Warwick 2007; German and Al-Shehbaz 2008a; German 2009). Our data also argue for tribal replacement of different genera and for the expansion of some genera to include additional species or hitherto independent genera. Monophyly of tribes and genera, tribal boundaries, and component genera are discussed below, especially when contradicting earlier work (Al-Shehbaz et al. 2006; Bailey et al. 2006; Warwick et al. 2007, 2008; Al-Shehbaz and Warwick 2007).

### Discussion

It is well known that ITS-based phylogenies might be biased because of homoplasy, orthology/paralogy, concerted evolution, and alignment problems due to indel accumulation. We also realize possible incongruencies between phylogenies derived from different genomes (i.e., organelle versus nuclear genomes), which, however, currently appear as only minor in the Brassicaceae (Koch et al. 2007; Franzke et al. 2009). We are fully aware of all these possible shortcomings, which, in general and often forgotten, more or less apply to any molecular marker. Family-wide molecular phylogenies in the Brassicaceae show major similarities in the analyses of multiple molecular markers, and the overall tree topology of our ITS data (Fig. 1) agrees fairly well with the molecular phylogenies published to date: basal split between Aethionemeae and the rest of the family; lack of significant resolution of deeper nodes; assignment of the majority of tribes to the three lineages of Beilstein et al. (2006) and Al-Shehbaz et al. (2006) (section “Tree topology”). Some minor discrepancies compared with the phylogenies published to date are predominantly caused, as tested by us at the preliminary stages of tree construction, by differences in the taxon sampling, and, to much lesser degree, by differences between alignments. This led us to assume that our data, our alignments, and our phylogenetic analyses are accurate and meaningful. The following discussion is not only based on molecular data but includes evaluation of morphology and biogeography as important and independent data sets.



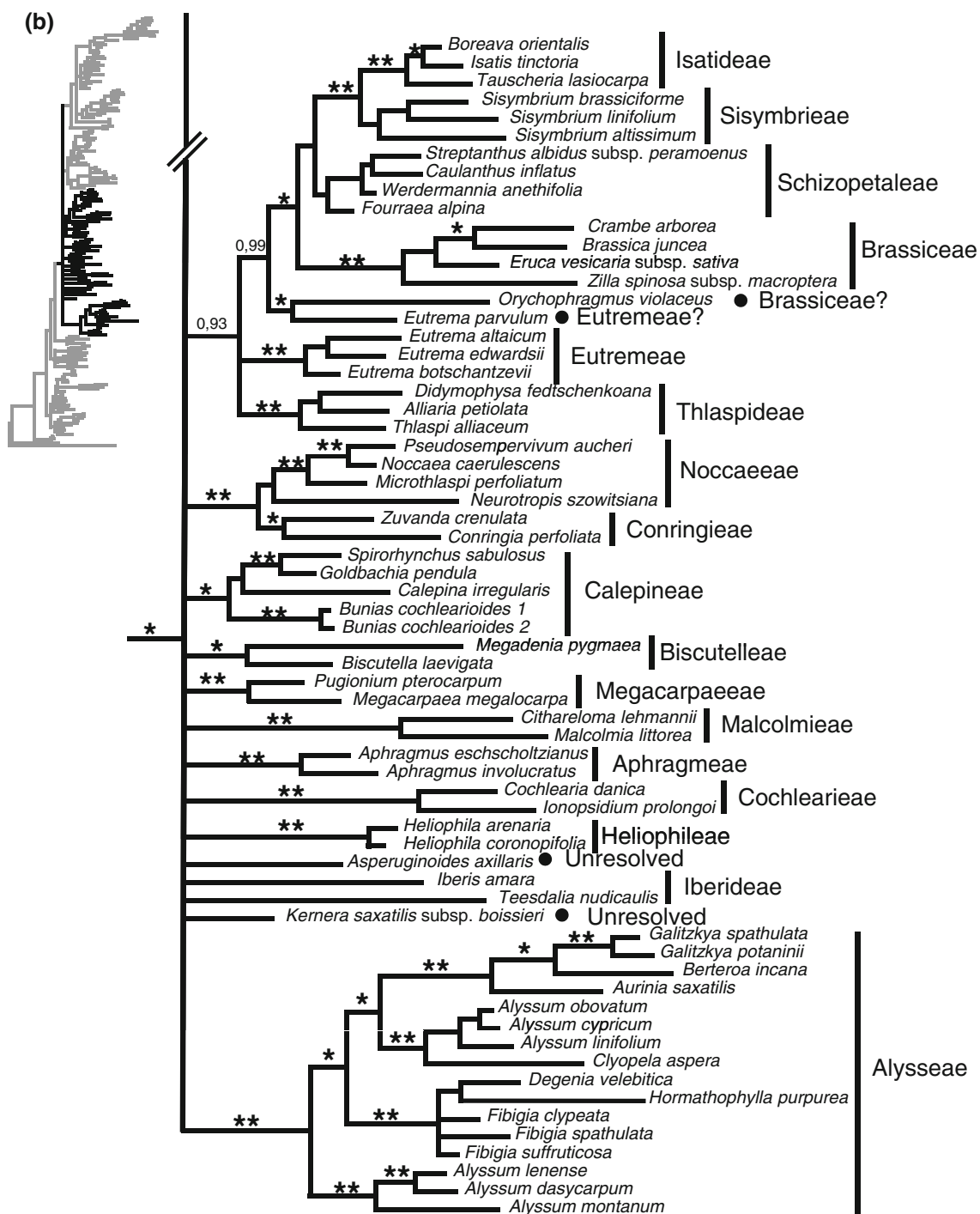


Fig. 1 continued

## Tribe Camelineae DC.

The Camelineae s.l. were split into five clades intermixed with the tribes Boechereae, Halimolobeae, and Physarieae (Fig. 1) to form a well-resolved major clade corresponding in part to lineage I of Beilstein et al. (2006, 2008). *Erysimum* L., which was also assigned to the Camelineae by Al-

Shehbaz et al. (2006), formed an independent, well-resolved clade within the family polytomy (Fig. 1); our preliminary analyses were consistent with results summarized by Koch and Al-Shehbaz (2009) regarding its closer relationship to the tribes Descurainieae, Smelowskieae, Lepidieae, and Cardamineae. The molecular and morphological data (German and Al-Shehbaz 2008a) clearly

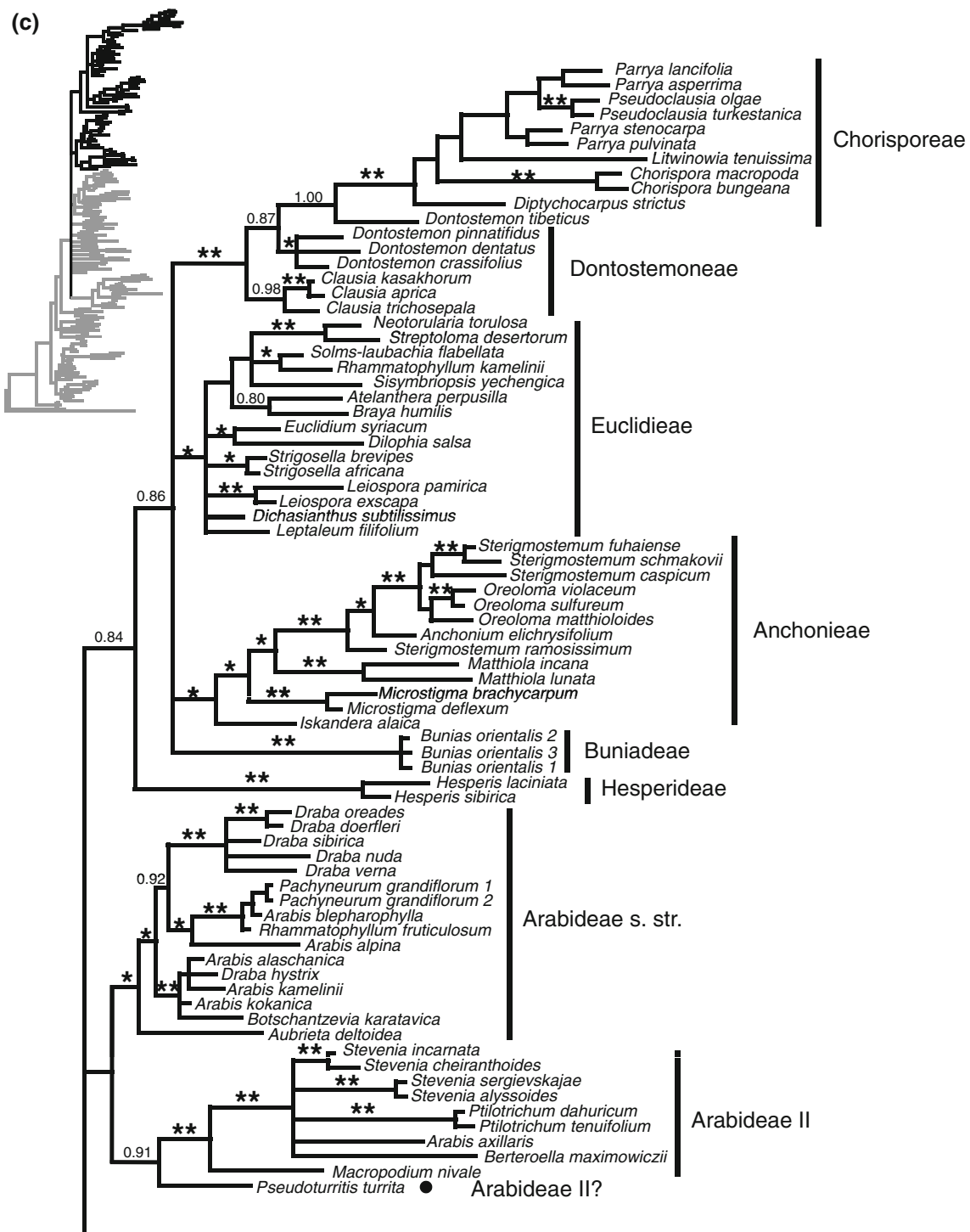


Fig. 1 continued

support the recognition of the large genus *Erysimum* (223 spp. sensu Warwick et al. (2006b), but certainly smaller) into the unigeneric Erysimeae Dumort.

*Erysimum siliculosum* (Bieb.) DC. and *E. mongolicum* D. German formed with *E. cheiranthoides* L., the generic type, a monophyletic clade with 100% BS support (Fig. 1).

The first species is a type of a previously accepted genus, *Syrenia* Andr. ex Bess., but our data clearly support its union with *Erysimum*, a position taken earlier by Appel and Al-Shehbaz (2003).

*Crucihimalaya* Al-Shehbaz, O’Kane & R. A. Price & *Transberingia* Al-Shehbaz & O’Kane were placed by

Al-Shehbaz et al. (2006) in the tribe Camelinae, but our data do not support that assignment. Instead, these two genera plus *Arabis tibetica* Hook.f. & Thomson, *A. rupicola* Kryl., and *Alyssum klimesii* Al-Shehbaz formed a well-defined clade (100% support in all analyses; Fig. 1; Supplement 1) that merits recognition as an independent tribe. *Arabis rupicola* and *Transberingia bursifolia* (DC.) Al-Shehbaz & O’Kane have already been transferred to *Crucihimalaya* (German 2005; German and Ebel 2005), but *A. tibetica* has not. The position of *Alyssum klimesii* was quite perplexing, although it has recently been established with *Crucihimalaya* by Koch et al. (2007). *Alyssum klimesii* differs from the rest of this clade by being a dwarf (1–3 cm high) pulvinate plant with entire fleshy leaves, few-flowered racemes, and few-seeded silicles (Al-Shehbaz 2002). By contrast, *Crucihimalaya* consists of taller (up to 1 m), annuals or non-pulvinate perennials with non-fleshy, dentate to pinnately divided leaves, many-flowered racemes, and many-seeded linear siliques (Al-Shehbaz et al. 1999; Appel and Al-Shehbaz 2003). Our data suggest that either all taxa above be united into one highly heterogeneous genus, or at least two or three genera be recognized. The systematic position of *A. klimesii* will be dealt with in a forthcoming paper.

Finally, the position of *Turritis* L. within lineage I was established earlier (Koch et al. 1999, 2000), and is closely related to the other tribal-rank clades within this lineage. Therefore, we suggest its placement in the monogeneric tribe Turritidae (German 2009).

Another clade of the Camelinae sensu Al-Shehbaz et al. (2006) is formed by *Irenepharsus* Hewson and *Pachycladon* Hook.f. Although the phylogeny of Australian taxa is beyond the scope of this study, the position of both genera emphasizes the need for further phylogenetic studies of the tribe.

Eight genera (*Calymmatium* O.E. Schulz, *Olimarabidopsis* Al-Shehbaz, O’Kane & R. A. Price, *Chrysochamela* Boiss., *Arabidopsis* (DC.) Heynh., *Catolobus* (C.A. Mey.) Al-Shehbaz, *Camelina* Crantz, *Pseudoarabidopsis* Al-Shehbaz, O’Kane & R. A. Price, and *Capsella* Medik.) formed a monophyletic clade recognized herein as Camelinae s.str. Although previous ITS (Bailey et al. 2006) and combined (Koch et al. 2007) studies fully agree with ours on the polyphyly of Camelinae s.l., further studies are needed to properly assign additional genera and establish the monophyly of Camelinae s.str.

The closer phylogenetic relationship of *Calymmatium* to *Olimarabidopsis* and their morphological similarities (e.g. both annuals with short-stalked to sessile 2–5-rayed trichomes, usually auriculate-sagittate stem leaves, usually yellow flowers, and incumbent cotyledons) suggest they may be congeneric. As recently revealed by Khosravi et al. (2009), morphologically similar SW Asian *Alyssopsis*

Boiss. also belongs to this group of affinity. However, further studies are needed to finally clarify relationships among these genera.

#### Tribe Boechereae Al-Shehbaz, Beilstein & E. A. Kellogg

On the basis of morphological and cytological ( $2n = 14$ ) data, German (2004) suggested close affinity of the monospecific *Borodinia* N. Busch (E Siberia, Russian Far East) and the primarily North American *Boechera* Á. Löve & D. Löve. This relationship was also suspected by Bailey et al. (2006) and recently demonstrated in a significant way by Kiefer et al. (2009). Our ITS data support the placement of *Borodinia* in the tribe Boechereae. *Borodinia macrophylla* (Turcz.) O.E. Schulz and *Boechera falcata* (Turcz.) Al-Shehbaz (E Siberia, Russian Far East) are the only representatives of the tribe Boechereae in the Old World.

Berkutenko (2003, 2005) reduced *Borodinia* to synonymy with *Arabis* L. on the basis of having branched trichomes, white petals, latiseptate siliques, and accumbent cotyledons. As shown by Al-Shehbaz (2003, 2005), Koch et al. (2003), and Al-Shehbaz et al. (2006), that combination of characteristics is highly homoplasious and evolved many times across the whole family. Berkutenko (2003, 2005) placed *A. alaschanica* Maxim. (N China) in synonymy with *B. macrophylla*, but the molecular data (Fig. 1) and morphological differences (fruit type and width, seed shape, indumentum) strongly support their placement in the remotely related tribes Arabideae and Boechereae. Further studies are needed to clarify the phylogenetic position of *Borodinia* within the Boechereae, especially with regard to the larger (110 spp.) and taxonomically difficult *Boechera* (Windham and Al-Shehbaz 2006, 2007a, b).

#### Tribe Arabideae DC.

The core Arabideae (Arabideae s.str.) consisted of *Arabis*, *Draba* L., *Aubrieta* Adans., monospecific *Pachyneurum* Bunge, *Botschantzevia* Nabiev, and *Dendroarabis* (C.A. Mey.) D. German & Al-Shehbaz. The core of the second subclade, hereafter Arabideae-II, is a strongly supported group of predominantly E/C Asian-Siberian taxa which consists of *Stevenia* Fisch., *Ptilotrichum* C.A. Mey., monospecific *Berteroella* O.E. Schulz, and bispecific *Macropodium* W.T. Aiton. Monospecific and predominantly Mediterranean *Pseudoturritis* Al-Shehbaz had weak but constant affinity to this subclade.

#### *Arabideae* s.str

*Aubrieta* was invariably sister to the rest of this core group. *Draba* (including *Drabopsis* C. Koch, *Erophila*

DC., and *Schivereckia* Andr. ex DC. and excluding *D. hystrix* Hook.f. & Thomson) showed 100% BS support (Fig. 1), and these findings agree with earlier studies (e.g. Al-Shehbaz et al. 2006; Bailey et al. 2006; Koch 2003; Koch and Al-Shehbaz 2002; Koch et al. 2003, 2007). *Draba hystrix* is anomalous in the genus, because of its needle-like leaves, large fruits and seeds, and long-setose trichomes (Jafri 1973), and we suggest its exclusion from *Draba*.

Despite extensive morphological (Al-Shehbaz 2003, 2005) and molecular (Koch et al. 1999, 2000, 2001; O'Kane and Al-Shehbaz 2003) studies, the limits of *Arabis* remain problematic (Al-Shehbaz et al. 2006; Koch et al. 2003; Zhou et al. 2001). The addition herein of taxa not previously studied molecularly associate the generic type, *A. alpina* L., with *Pachyneurum* and *Botschantzevia*, although their positions relative to each other varied according to the algorithm used.

The monospecific *Pachyneurum*, together with the central Asian *Dendroarabis* and western North American *Arabis blepharophylla* Hook. & Arn., formed a well-defined subclade with 100% BS support (Fig. 1). The subclade included *A. hirsuta* (L.) Scop. (not shown here) and other species of *Arabis* (Clauss and Koch 2006; Koch 2003; Koch et al. 1999, 2000).

The position and status of *Pachyneurum* have been treated in different ways by various authors (Table 2) but our ITS (Fig. 1) and cpDNA *trnL* intron data (not shown) strongly support the recognition of *Pachyneurum* as a distinct genus in the Arabideae, as suggested by Vassilyeva (1969) and Botschantzev (1972) and later accepted by Al-Shehbaz et al. (2006). A closer relationship between *Pachyneurum* and *Noccaea* Moench (tribe Noccaeeae) revealed by Koch et al. (2007) is a consequence of misidentification of the cited voucher specimen (M. Staudinger 5493, deposited in W with duplicates in WU and HEID) which, in fact, belongs to *Noccaea cochleariformis* (DC.) Á. Löve & D. Löve (see GenBank annotation by M. Koch). Overall morphology (e.g. the presence in *Pachyneurum* of latiseptate siliques vs. angustiseptate silicles and malpighiaceus trichomes vs. simple ones or none, etc.) support the placement of *Pachyneurum* in the Arabideae and not in *Noccaeeae*.

Species of the Central Asian *Rhammatophyllum* O.E. Schulz were assigned to various genera in the tribes Anthonieae, Arabideae, Alysseae, and Hesperideae (Al-Shehbaz and Appel 2002). The placement herein of *R. kamelinii* (Botsch.) Al-Shehbaz & O. Appel, a very close relative of the generic type *R. pachyrrhizum* (Kar. & Kir.) O.E. Schulz, into the Euclidieae agrees with Al-Shehbaz et al. (2006). However, the placement herein of *R. fruticosum* in the Arabideae demonstrates that the genus sensu Al-Shehbaz (2005) is polyphyletic. Our molecular

data prompted German and Al-Shehbaz (2008b) to place the species in the monospecific *Dendroarabis*.

Three species of *Arabis* (*A. alaschanica*, *A. kamelinii* Botsch., and *A. kokanica* Regel & Schmalh.), *Draba hystrix*, and *Botschantzevia karatavica* (Lipsch.) Nabiev form a well supported (Fig. 1), predominantly central Asian subclade. These woody perennials (*B. karatavica* is a subshrub) grow in rock crevices and have well-developed rosettes and few, non-auriculate cauline leaves. Although the generic placement of the last species fluctuated between *Arabis*, *Erysimum*, and *Parrya*, the molecular data (Fig. 1) and trichome morphology (Dvořák 1968; Nabiev 1972) strongly support its recognition in a monospecific *Botschantzevia* assigned to the Arabideae, rather than to the Erysimeae or Chorisoporeae. These three species of *Arabis* strongly resemble *A. karategina* Lipsky, *A. popovii* Botsch. & Vved., *A. saxicola* Edgew., *A. setosifolia* Al-Shehbaz, especially in their morphology, ecology, and distribution, and it is likely that these seven species form an independent genus.

As delimited herein, the Arabideae s.str. remain in need of further phylogenetic studies and considerable taxonomic adjustments. Depending on the algorithm used, the sister position of *Arabis alpina* L. was unstable in relation to the subclades including *Pachyneurum*, *Botschantzevia*, or even the rest of Arabideae s.str. minus *Aubrieta* (Clauss and Koch 2006; Heenan et al. 2002; Koch et al. 1999, 2000). We believe that a monophyletic *Arabis* would be a rather small genus consisting of its type, *A. alpina*, and its nearest relatives (e.g. *A. caucasica* Willd., *A. tianschanica* Pavlov). The vast majority of *Arabis* species must be placed in other genera, and systematics can be only solved by including the genus *Draba* and its various segregates (Koch et al., work in progress), and several taxa will have to be circumscribed in a different generic context, as was partially done by Al-Shehbaz (2003, 2005).

#### Arabideae-II

This clade is strongly supported (Fig. 1), and its component genera are also highly resolved. The southern Siberian *Macropodium nivale* (Pall.) W.T. Aiton is sister to a polytomy including four species of *Stevenia*, two of *Ptilotrichum*, *Arabis axillaris* Kom., and monospecific *Berteroella* (hereafter the *Stevenia* alliance). *Macropodium pterospermum* F. Schmidt (eastern Asia) has not yet been studied molecularly.

*Macropodium* was assigned to the Thelypodieae, a tribe considered by many to include most extant primitive Brassicaceae (Hayek 1911; Busch 1939; Takhtajan 1986; Dvořák 1972; Al-Shehbaz 1973; Hedge 1976; Avetisyan 1990) because of the superficial floral similarities of its genera and *Cleome*. However, others (Prantl 1891; Busch

**Table 2** Revised tribal assignment of the studied Brassicaceae genera and their previous taxonomic treatments

Genus	De Candolle (1821)	Bentham and Hooker (1862)	Prantl (1891)	Hayek (1911)	Schulz (1936)	Janchen (1942)	Dvořák (1972)	Kamelin (2002)	Al-Shehbaz et al. (2006)	Subsequent treatments <sup>a</sup>	This study
<i>Aphragmus</i> Andr. ex DC.	–	Camelineae (Braya p. p.)	Sinapeae/ Alliariinae	Arabideae/ Arabidinae	Sisymbriaceae/ Pachycladinae	–	–	Sisymbriaceae/ Brayinae	–	–	Aphragmeae
<i>Asperuginoides</i> Rauschert (Buchingera Boiss. et Hohen.)	–	Alyseae	Hesperideae/ Alyssinae	Alyseae/ Alyssinae	Alyseae	Alyseae/ Alyssinae	–	Clypeoleae	? Alyseae	Unresolved	Unresolved
<i>Atlanthera</i> Hook. f. et Thomson	–	Arabideae	Hesperideae/ Malcolmiinae	Alyseae/ Hesperidinae	Hesperideae	–	Sisymbriaceae/ Brayinae	Sisymbriaceae/ Brayinae	? Euclidieae	–	Euclidieae
<i>Berteroella</i> O. E. Schulz	–	–	–	–	Sisymbriaceae/ Brayinae	–	–	Sisymbriaceae/ Brayinae	? Arabideae	? Arabideae	Arabideae II
<i>Biscutella</i> L.	Thlaspidaceae	Thlaspidaceae	Sinapeae/ Lepidinae	Lepidideae/ Lepidinae	Lepidideae/ Iberidinae	Lepidideae/ Iberidinae	–	Megacarpaeae	Unresolved	Unresolved	Biscutelleae
<i>Boreava</i> Jaub. et Spach	–	Isatideae	Sinapeae/ Sisybriinae	Arabideae/ Buniadinae	Euclidieae	Sisymbriaceae/ Buniadinae	–	Parabraceae/ Buniadinae	Isatideae	Isatideae	Isatideae
<i>Borodinia</i> N. Busch	–	–	–	–	Arabideae	–	–	Arabideae/ Drabinae	? Boechereae	–	Boechereae
<i>Botschantzevia</i> Nabiev	–	–	–	–	–	–	–	Arabideae/ Arabidinae	–	Arabideae	Arabideae
<i>Bunias</i> L.	Buniadaceae	Isatideae	Hesperideae/ Hesperidinae	Arabideae/ Buniadinae	Euclidieae	Sisymbriaceae/ Buniadinae	–	Parabraceae/ Buniadinae	? Anchemieae	Buniadaceae	Buniadaceae
<i>Calepina</i> Adans.	Zillaceae	Isatideae	Sinapeae/ Sisybriinae	Brassicaceae/ Raphaninae	Brassicaceae/ Raphaninae	Brassicaceae/ Raphaninae	–	Parabraceae/ Buniadinae	Unresolved	Unresolved	Calepineae
<i>Calymmatium</i> O. E. Schulz	–	–	–	–	Sisymbriaceae/ Brayinae	–	–	Lepidideae/ Cochlearinae	–	–	Camelineae
<i>Chorisporea</i> R. Br. ex DC.	Raphaneae	Raphaneae	Hesperideae/ Hesperidinae	Alyseae/ Brayinae	Matthioleae	Hesperideae/ Matthiolinae	Hesperideae/ Anchemiinae	Parabraceae/ Chorisporeinae	Chorisporeae	Chorisporeae	Chorisporeae
<i>Clausia</i> Korn.-Tr.	–	Sisymbriaceae (Hesperis p. p.)	Hesperideae/ Hesperidinae	Alyseae/ Hesperidinae	Hesperideae (Hesperis p. p.)	Hesperideae/ Matthiolinae	Hesperideae/ Matthiolinae	Arabideae/ Hesperidinae	Anchemiinae	Dontostemoneae	Dontostemoneae
<i>Conringia</i> Heist. ex Fabr.	–	Sisymbriaceae	Hesperideae/ Moricandiinae	Brassicaceae/ Moricandiinae	Brassicaceae/ Moricandiinae	Brassicaceae/ Moricandiinae	–	Brassicaceae/ Moricandiinae	Unresolved	Unresolved	Conringieae
<i>Cryptospora</i> Kar. et Kir.	–	Raphaneae	Hesperideae/ Malcolmiinae	Alyseae/ Hesperidinae	Hesperideae	–	Sisymbriaceae/ Brayinae	Arabideae/ Hesperidinae	Euclidieae	Euclidieae	Euclidieae
<i>Dichasanthus</i> Ovez. et Junussov	–	–	–	–	–	–	–	Sisymbriaceae/ Brayinae	Euclidieae	Euclidieae	Euclidieae
<i>Didymophya</i> Boiss.	–	Thlaspidaceae	Sinapeae/ Cochlearinae	Lepidideae/ Thlaspidinae	Lepidideae/ Physarinae	Lepidideae/ Physarinae	–	Lepidideae/ Lepidinae	? Alyseae	Unresolved	Thlaspidaceae
<i>Dilophia</i> Thomson	–	Lepidideae	Sinapeae/ Cochlearinae	Lepidideae/ Thlaspidinae	Lepidideae/ Cochlearinae	–	–	Lepidideae/ Lepidinae	Euclidieae	Euclidieae	Euclidieae
<i>Dontostemon</i> Andr. ex C. A. Mey.	–	Sisymbriaceae	Hesperideae/ Hesperidinae	Alyseae/ Brayinae	Arabideae	–	Hesperideae/ Anchemiinae	Arabideae/ Hesperidinae	Anchemiinae	Dontostemoneae	Dontostemoneae



Table 2 continued

Genus	De Candolle (1821)	Bentham and Hooker (1862)	Prantl (1891)	Hayek (1911)	Schulz (1936)	Janchen (1942)	Dvořák (1972)	Kamelin (2002)	Al-Shehbaz et al. (2006)	Subsequent treatments <sup>a</sup>	This study
<i>Erysimum</i> L.	Sisymbriaceae	Sisymbriaceae	Hesperideae/Erysimumae	Arabideae/Erysimumae	Hesperideae	Hesperideae/Hesperidinae	Erysimeae	Arabideae/Erysimumae	Camelineae	Camelineae	Erysimeae
<i>Euclidium</i> W. T. Aiton	Euclidieae	Isatideae	Hesperideae/Malcolmiinae	Alyseae/Euclidinae	Euclidieae	Hesperideae/Euclidinae	–	Parabrassicaceae/Buniadinae	Euclidieae	Euclidieae	Euclidieae
<i>Goldbachia</i> DC.	Anchonieae	Raphaneae	Sinapeae/Sisymbriinae	Arabideae/Buniadinae	Hesperideae	Sisymbriaceae/Buniadinae	–	Parabrassicaceae/Chorisporinae	? Isatideae	Unresolved	Calepineae
<i>Iskandera</i> N. Busch	–	–	–	–	–	–	Hesperideae/Matthiolinae	Arabideae/Hesperidinae	Anchonieae	Anchonieae	Anchonieae
<i>Leiospora</i> (C. A. Mey.) Dvořák	–	–	–	–	–	–	Hesperideae/Matthiolinae	Arabideae/Hesperidinae	Euclidieae	Euclidieae	Euclidieae
<i>Leptaleum</i> DC.	Sisymbriaceae	Camelineae	Hesperideae/Malcolmiinae	Alyseae/Brayinae	Hesperideae	Hesperideae/Hesperidinae	Sisymbriaceae/Brayinae	Arabideae/Hesperidinae	Euclidieae	Euclidieae	Euclidieae
<i>Litwinovia</i> Woron.	–	–	–	–	Euclidieae (Euclidium p. p.)	Hesperideae/Euclidinae	–	Parabrassicaceae/Buniadinae	–	–	Chorisporaeae
<i>Macropodium</i> W. T. Aiton	Arabideae	Arabideae	Hesperideae/Turritinae	Thelypodieae	Stanleyeae	–	–	Macropodieae	Arabideae	Arabideae	Arabideae-II
<i>Megacarpaea</i> DC.	Thlaspidaceae	Thlaspidaceae	Sinapeae/Lepidinae	Lepidieae/Lepidinae	Lepidieae/Iberidinae	Lepidieae/Iberidinae	–	Megacarpaeaceae	Unresolved	–	Megacarpaeaceae
<i>Megadenia</i> Maxim.	–	–	Sinapeae/Cochleariinae	Lepidieae/Thlaspidinae	Lepidieae/Iberidinae	–	–	Megacarpaeaceae	–	–	Biscutelleae
<i>Microstigma</i> Trautv.	–	–	–	–	Matthioleae (Matthiola p. p.)	–	–	Matthioleae	Anchonieae	Anchonieae	Anchonieae
<i>Oreoloma</i> Botsch.	–	–	–	–	–	–	–	Arabideae/Hesperidinae	Anchonieae	Anchonieae	Anchonieae
<i>Orychophragmus</i> Bunge	–	Brassicaceae	Hesperideae/Moricandinae	Brassicaceae/Moricandinae	Brassicaceae/Moricandinae	–	–	Brassicaceae/Moricandinae	–	Brassicaceae/Vellinae	Unresolved
<i>Pachyneurum</i> Bunge	–	Arabideae (Parrya p. p.)	Hesperideae (Parrya p. p.)	Alyseae/Hesperidinae (Parrya p. p.)	Arabideae	–	–	Arabideae/Arabidinae	? Arabideae	? Noccaeae	Arabideae
<i>Parrya</i> R. Br. (Neuroloma Andr., Achoriphragma Soják)	–	Arabideae	Hesperideae/Hesperidinae	Alyseae/Hesperidinae	Matthioleae	Hesperideae/Matthiolinae	Hesperideae/Matthiolinae	Arabideae/Hesperidinae	Chorisporaeae	Chorisporaeae	Chorisporaeae
<i>Pseudoclausia</i> M. Pop.	–	–	–	–	–	–	–	Arabideae/Hesperidinae	Anchonieae	–	Chorisporaeae
<i>Ptilotrichum</i> C. A. Mey.	–	Alyseae (Alyssum p. p.)	Hesperideae/Alyssinae	Alyseae/Alyssinae	Alyseae	Alyseae/Alyssinae	–	Arabideae/Alyssinae	? Arabideae	Arabideae	Arabideae-II
<i>Pugionium</i> Gaertn.	Euclidieae	Isatideae	Hesperideae/Malcolmiinae	Lepidieae/Thlaspidinae	Lepidieae/Isatidinae	Lepidieae/Pugioninae	–	Parabrassicaceae/Chorisporinae	–	–	Megacarpaeaceae
<i>Rhammatophyllum</i> O. E. Schulz	–	–	–	–	Hesperideae	–	Sisymbriaceae/Brayinae	Arabideae/Arabidinae	Euclidieae	Euclidieae	Euclidieae

Table 2 continued

Genus	De Candolle (1821)	Bentham and Hooker (1862)	Prantl (1891)	Hayek (1911)	Schulz (1936)	Janchen (1942)	Dvořák (1972)	Kamelin (2002)	Al-Shehbaz et al. (2006)	Subsequent treatments <sup>a</sup>	This study
<i>Sisymbriopsis</i> Botsch. et Tzvel.	–	–	–	–	–	–	–	Sisymbrieae/Brayinae	Euclidieae	Euclidieae	Euclidieae
<i>Solms-laubachia</i> Muschl.	–	–	–	–	Matthioleae	–	–	Arabideae/Hesperidinae	Euclidieae	Euclidieae	Euclidieae
<i>Spirorhynchus</i> Kar. et Kir.	–	Isatideae	Sinapeae/Sisymbriinae	Arabideae/Buniadinae	Euclidieae	Sisymbrieae/Buniadinae	–	Parabrassicaceae/Chorisporinae	? Isatideae	–	Calepineae
<i>Sterigmostemum</i> Bieb. (Sterigma DC.)	–	Anchonieae Raphaneae	Hesperideae/Hesperidinae	Alyseae/Brayinae	Hesperideae	Hesperideae/Hesperidinae	Hesperideae/Anchominae	Arabideae/Hesperidinae	Anchonieae	Anchonieae	Anchonieae
<i>Stevenia</i> Fisch.	–	Arabideae (Arabis p. p.)	Hesperideae/Turritinae (Arabis p. p.)	Arabideae/Arabidinae (Arabis p. p.)	Arabideae	–	–	Arabideae/Arabidinae	? Arabideae	–	Arabideae-II
<i>Streptoloma</i> Bunge	–	Sisymbrieae	Hesperideae/Malcolmiinae	Alyseae/Brayinae	Sisymbrieae/Brayinae	–	Sisymbrieae/Brayinae	Sisymbrieae/Brayinae	–	–	Euclidieae
<i>Strigosella</i> Boiss. (Fedtschenkoa Regel et Schmalh.)	–	Sisymbrieae (Malcolmia p. p.)	Hesperideae/Malcolmiinae	Alyseae/Brayinae	Hesperideae (Malcolmia p. p.)	Hesperideae/Hesperidinae (Malcolmia p. p.)	Sisymbrieae/Brayinae	Arabideae/Hesperidinae	Euclidieae	Euclidieae	Euclidieae
<i>Tauscheria</i> DC.	–	Isatideae	Sinapeae/Sisymbriinae	Arabideae/Isatidinae	Euclidieae	Sisymbrieae/Isatidinae	–	Parabrassicaceae/Isatidinae	? Isatideae	Isatideae	Isatideae
<i>Zavanda</i> (Dvořák) Askerova	–	–	–	–	–	–	–	–	–	Unresolved	Conringieae

<sup>a</sup> Al-Shehbaz and Warwick (2007), Koch et al. (2007), Warwick et al. (2007, 2008)

1926; Al-Shehbaz et al. 2006) placed it in the Arabideae s.l., a position supported by our molecular data.

The *Stevenia* alliance is characterized by a uniform indumentum (sessile or subsessile 2–4-branched with pinnate rays), absence of simple hairs, entire and sessile or subsessile cauline leaves, dilated filaments, lack of median nectaries, often latiseptate fruits, usually long and slender styles, minute stigmas, and non-mucilaginous, usually flattened seeds. This characteristic combination, with the molecular data herein, support the treatment of this alliance as one genus, the oldest generic name in which is *Stevenia*.

The Mediterranean *Pseudoturritis turrita* (L.) Al-Shehbaz showed a weak relationship to *Berteroella* (Koch 2003), which is somewhat confirmed by our analysis (Fig. 1). Despite the support only in Bayesian analysis (0.91; Fig. 1), the association of *Pseudoturritis* with Arabideae is stable, and we believe that its morphological similarity to the tribe was the product of parallel evolution.

If the Arabideae s.l. is maintained, *Pseudoturritis* would most likely be one of its members. However, our data support the division of this tribe into at least two, of which the Arabideae-II needs a new tribal name.

#### Tribe Alysseae DC.

As delimited by Dudley and Cullen (1965) and Al-Shehbaz et al. (2006), the Alysseae are polyphyletic. The tribe has recently been studied phylogenetically by Warwick et al. (2008), and our data (Fig. 1) fully agree with their findings in excluding *Didymophysa* Boiss., *Asperuginoides*, *Ptilotrichum*, and *Alyssum klimesii* from the tribe. With the exclusion of these four taxa and placement of *Lobularia* Desv. and *Farsetia* Turra in the Malcolmieae (Warwick et al. 2008), the tribe becomes monophyletic.

The position of Alysseae relative to the other tribes varied substantially depending on the marker used. For example, in the *ndhF* phylogeny (Beilstein et al. 2006), the tribe was related to the Brassiceae in lineage II, whereas in the ITS phylogeny (Bailey et al. 2006) it appeared either related to *Erysimum* (their Camelinae; our Erysimeae) or unrelated to any tribe, and in the *trnL* intron–*trnL*-F intergenic spacer analysis (Koch et al. 2007) it was related to the Noccaeeae, and in ITS-based tree of Khosravi et al. (2009) it grouped together with the tribes Chorisporeae, Hesperideae, and Malcolmieae. Our ITS data did not shed additional light.

Although *Alyssum* has been estimated to include ca. 195 species (Warwick et al. 2006b), the genus sensu Appel and Al-Shehbaz (2003) is polyphyletic (Bailey et al. 2006; Koch et al. 2007; Warwick et al. 2008; Khosravi et al. 2009), and our tiny sample of six species supports that. Our preliminary data agree with Warwick et al. (2008) that species of sect. *Alyssum* (*A. montanum* L., the generic type, and *A. lenense* Adams) grouped together with a member of

sect. *Psilonema* (C.A. Mey.) Hook.f. (*A. dasycarpum* Steph. ex Willd.) in a well-resolved clade (Fig. 1), whereas those of sect. *Odontarrhena* (C.A. Mey.) Hook.f. (*A. cypricum* Nyár., *A. obovatum* (C.A. Mey.) Turcz.) grouped with *A. linifolium* Steph. ex Willd. (sect. *Meniocus* (DC.) Hook.f.) in a similarly strongly supported clade (Fig. 1). Extensive sampling, however, is needed before any meaningful generic adjustments are made.

Both *Fibigia suffruticosa* (Vent.) Sweet and *F. clypeata* (L.) Medik. fell in a polytomy (Warwick et al. 2008; herein in Fig. 1) confirming the polyphyly of this genus of 13 species. Better sampling is needed to resolve its polyphyly and the position of *F. spathulata* (Kar. & Kir.) B. Fedtsch. (Kazakhstan), which was transferred by Boczantzeva (1976, 1977) to the independent genus *Pterygostemon* V. Bocz.

#### Tribe Chorisporeae C.A. Mey.

The Chorisporeae sensu Al-Shehbaz et al. (2006) included *Chorisporea* and *Diptychocarpus* Trautv. Warwick et al. (2007) added *Parrya* R.Br., and herein we add *Pseudoclausia* M. Pop. (10 spp.), monospecific *Litwinowia* Woron., and *Dontostemon tibeticus* (Maxim.) Al-Shehbaz.

*Dontostemon* Andr. ex C.A. Mey. becomes polyphyletic (Fig. 1) if *D. tibeticus* (Al-Shehbaz 2000) is maintained in it. On the basis of recent molecular studies (Warwick et al. 2007), the genus is now recognized in the tribe Dontostemoneae (Al-Shehbaz and Warwick 2007). Our molecular data and morphology (strongly two-lobed stigmas with subdecurrent lobes and deeply pinnatifid leaves with numerous decurrent lobes) support the placement of the species into a new genus in the Chorisporeae.

*Parrya* was reduced to a monospecific genus (Botschantzev 1972), and its remaining species were recognized in *Achoriphragma* Soják (*Neuroloma* Andr., nom. illeg.). *Parrya* is heterogeneous and much in need of thorough phylogenetic and systematic studies to test its monophyly, to determine its component species, and to check the merit of the genera segregated from it. Our preliminary cpDNA data (not shown here) indicate that *P. arctica* R.Br., the generic type, and some *Parrya* species belong to the Chorisporeae, but more species should be examined to address these concerns. The current data indicate parphyly of *Parrya* with *Pseudoclausia* nested within it. The latter genus was considered to be related to *Clausia* (e.g. Warwick et al. 2007), but our data do not support that. Further studies should help in testing the relationships between *Parrya* and *Pseudoclausia*.

#### Tribe Euclidieae DC.

The Euclidieae sensu Al-Shehbaz et al. (2006) was shown by Warwick et al. (2007) to be polyphyletic and split into

two clades recognized by Al-Shehbaz and Warwick (2007) as the tribes Euclidieae s.str. and Malcolmieae. Both tribes were identified in our studies, and the Euclidieae s.str. was monophyletic with moderate support (Fig. 1) The monospecific *Atelanthera* Hook.f. & Thomson is studied herein for the first time, and it belong to the Euclidieae. A similar position is revealed for *Streptoloma* Bunge (two spp.) first studied independently by Khosravi et al. (2009). Both genera have features typical of the tribe as redefined by Al-Shehbaz and Warwick (2007).

As for the tribe Malcolmieae, represented in our analysis by *Cithareloma lehmannii* Bunge and *Malcolmia littorea* (L.) W.T. Aiton, its position within a polytomy of other tribes was unstable depending on the sampled taxa and the algorithm used.

#### Tribe Anchonieae DC.

The current data agree well with earlier studies (Warwick et al. 2007; Al-Shehbaz and Warwick 2007) in recognizing two tribes, Anchonieae and Dontostemoneae, instead of one (sensu Al-Shehbaz et al. 2006). However, the circumscription of *Oreoloma* Botsch. and its relationship to *Sterigmostemum* Bieb. varied in the two studies. *Oreoloma* was monophyletic in Warwick et al. (2007), but in our analysis (Fig. 1) it formed a monophyletic lineage and together with *Anchonium elichrysofolium* (DC.) Boiss. was nested in *Sterigmostemum*. Botschantzev (1980) separated *Oreoloma* from *Sterigmostemum* by having long-clawed (vs. short-clawed) petals abruptly (vs. gradually) expanded to limb and basally saccate (vs. non-saccate) lateral sepals. As indicated by Kamelin and German (2001), these differences are trivial because some species of *Sterigmostemum* (e.g. *S. schmakovii* Kamelin & D. German) have petals well differentiated into a claw and limb and have non-saccate sepals. Based on morphology and our molecular data and those of Warwick et al. (2007), we recommend the expansion of *Sterigmostemum* to include both *A. elichrysofolium*, as initially placed in *Sterigmostemum* (de Candolle 1821), and *Oreoloma*. As a result, *Anchonium* becomes monospecific, with its type *A. billardieri* DC. sister to the expanded *Sterigmostemum* (Warwick et al. 2007).

#### Tribe Buniadeae DC.

Our data show that the recently recognized monogeneric tribe Buniadeae (Al-Shehbaz and Warwick 2007) is monophyletic if *Bunias cochlearioides* Murr. is excluded from it. The latter species differs from the other two congeners, *B. erucago* L. (generic type) and *B. orientalis* L., in the lack of multicellular glands and branched trichomes. With members of the recently restored

tribe Calepineae Horan. (German and Al-Shehbaz 2008a) *Bunias cochlearioides* formed a highly resolved clade (Fig. 1).

It is interesting to mention that the diploid ( $2n = 14$ ) *B. orientalis* and *B. erucago* share the biggest genome sizes (GS) among all Brassicaceae species studied to date (Lysak et al. 2009).

#### Tribe Brassiceae DC.

This tribe was subjected to extensive molecular studies summarized by Warwick and Sauder (2005) who retained within it the genera *Calepina* Adans., *Conringia* Heist. ex Fabr., and *Orychophragmus* Bunge. Subsequent studies (Bailey et al. 2006; Beilstein et al. 2006, 2008; Koch et al. 2007; Lysak et al. 2005, 2009; Mandáková and Lysak 2008) strongly supported the exclusion of *Calepina* and *Conringia* from the tribe.

*Calepina* and *Conringia* formed a well-supported monophyletic group in Warwick and Sauder (2005) but not in Lysak et al. (2005), who suggested that this discrepancy in the ITS phylogeny probably resulted from concerted evolution. Our ITS-based phylogeny (Fig. 1) agrees with that of Bailey et al. (2006), and with the *ndhF* phylogeny of Beilstein et al. (2006), the *trnL-F* phylogeny of Koch et al. (2007), and chromosome painting of Lysak et al. (2005) in the placement of *Calepina* (together with *Goldbachia* DC., *Spirorhynchus* Kar. & Kir., and *Bunias cochlearioides*) and *Conringia* (with *Zuvanda* (Dvořák) Askerova) in unrelated clades recognized by German and Al-Shehbaz (2008a) as the tribes Calepineae and Conringieae, respectively.

Warwick and Sauder (2005) found *Orychophragmus* nested within the Brassiceae, but our data show *O. violaceus* (L.) O.E. Schulz to be outside the tribe, though its position remains unresolved. Other lines of evidence regarding its phylogenetic position are controversial. For example, successful experimental hybridization between the species and different members of *Brassica* (Warwick and Sauder 2005) support its retention in the tribe, whereas its East Asian distribution (vs. predominantly Mediterranean/Saharo-Sindian distribution for the Brassicaceae) agree with our molecular data. Further studies are needed to unravel the phylogenetic position of this genus. Its grouping with *Conringia planisiliqua* Fisch et Mey., recently found by Khosravi et al. (2009) and recognized as “*Orychophragmus* clade”, seems to be a good step in this direction.

#### Tribe Eutremeae Al-Shehbaz, Beilstein & E.A. Kellogg

This tribe includes the monospecific *Chalcanthus* Boiss. and recently expanded *Eutrema* R.Br. (Al-Shehbaz and Warwick 2005; Al-Shehbaz et al. 2006; Warwick et al.

2006a). Our study suggests the tribe is polyphyletic if *E. parvulum* (Schrenk) Al-Shehbaz & Warwick is maintained within the genus. In O’Kane and Al-Shehbaz (2003) and Koch (2003) the species (as *Thellungiella parvula* (Schrenk) Al-Shehbaz & O’Kane) formed a well-supported clade with species later assigned to *Eutrema*. Discrepancies among these data and ours may represent a case of gene-tree/species-tree incongruence similar to that proposed for *Draba funiculosa* Hook.f. by Bailey et al. (2006). Alternatively, *E. parvulum* may represent a new monospecific genus, and some morphological data (e.g. mucilaginous seeds, reduced petals) and geographical distribution (Irano-Turanian region) support that.

#### Other clades

Our current data (Fig. 1) on the genera *Biscutella* with *Megadenia*; *Goldbachia* together with *Spirorhynchus*, *Calepina*, and *Bunias cochlearioides*; *Aphragmus* Andr. ex DC.; and *Conringia* with *Zuvanda* have resulted in the recognition (respectively) of the tribes Biscutelleae, Calpeinae, Aphragmeae, and Conringiae (German and Al-Shehbaz 2008a). These genera and tribes were discussed at some length in that publication, and the interested reader should consult it for prior tribal assignments, generic and tribal boundaries, number of species, distinguishing characteristics, and distribution.

The remaining discussion focuses on *Pugionium* Gaertn. and *Megacarpaea* DC., both of which were not subjected to prior molecular studies. They were assigned to different tribes or subtribes (Table 2), and in a few accounts only (Grubov 1982; Kuan 1987; Zhou et al. 2001) were placed next to each other. Because of its angustiseptate silicles, *Megacarpaea* was traditionally placed in the Thlaspidiae or Lepididae (Table 2), but Kamelin (2002) suggested that it, with genera having didymous silicles (e.g. *Biscutella*, *Megadenia*), should be assigned to the new tribe Megacarpaeae (nom. nud.). Our molecular data do not support the association of the last two genera with *Megacarpaea*, and didymous fruits evolved independently several times in the Brassicaceae (Al-Shehbaz et al. 2006).

The systematic position of *Pugionium* varied substantially in prior classification systems, and the genus was not mentioned by Al-Shehbaz et al. (2006). Its winged and/or spiny fruits are bizarre in the Brassicaceae, which led Hedge (1976, p 22) to consider it “a genus without any obvious allies.” By contrast, Janchen (1942) placed *Pugionium* in a monogeneric subtribe Pugioniinae (nom. nud.). Molecular data (Fig. 1) place *Pugionium* and *Megacarpaea* in a well-resolved clade recognized as the tribe Megacarpaeae Kamelin ex D. German (German 2009). However, further studies on the remaining two species of *Pugionium* and eight of *Megacarpaea* are

needed to firmly establish their monophyly and position in relation to other tribes.

#### Supratribal classification

Although 35 tribes are currently recognized (Al-Shehbaz et al. 2006; Al-Shehbaz and Warwick 2007; German and Al-Shehbaz 2008a; German 2009; Koch and Al-Shehbaz 2009; Warwick et al. 2008), it is obvious that several additional ones will be established upon completion of a molecular generic survey of the entire family. Supertribes were proposed by Avetisyan (1990) mostly on the basis of morphological characteristics, and a similar approach was taken by Dorofeyev (2004) who ignored the wealth of molecular data available. These systems are equally artificial to all prior ones. A few major groups above the tribal rank are gradually emerging, especially with regard to the sister relationship of the Aethionemeae to the rest of the family and the three major lineages recognized by Beilstein et al. (2006, 2008) and Koch and Al-Shehbaz (2009). However, it is premature to go beyond the tribal rank because of the need for a complete molecular phylogeny based on a combination of several nuclear, plastidic, and mitochondrial markers for most if not all genera.

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