

Compendium of Plant Genomes  
Series Editor: Chittaranjan Kole

---

Philipp Simon  
Massimo Iorizzo  
Dariusz Grzebelus  
Rafal Baranski *Editors*

# The Carrot Genome

---

# **Compendium of Plant Genomes**

## **Series Editor**

Chittaranjan Kole, ICAR-National Research Center on Plant Biotechnology,  
Pusa, Raja Ramanna Fellow, Government of India, New Delhi, India

Whole-genome sequencing is at the cutting edge of life sciences in the new millennium. Since the first genome sequencing of the model plant *Arabidopsis thaliana* in 2000, whole genomes of about 70 plant species have been sequenced and genome sequences of several other plants are in the pipeline. Research publications on these genome initiatives are scattered on dedicated web sites and in journals with all too brief descriptions. The individual volumes elucidate the background history of the national and international genome initiatives; public and private partners involved; strategies and genomic resources and tools utilized; enumeration on the sequences and their assembly; repetitive sequences; gene annotation and genome duplication. In addition, synteny with other sequences, comparison of gene families and most importantly potential of the genome sequence information for gene pool characterization and genetic improvement of crop plants are described.

**Interested in editing a volume on a crop or model plant?**

Please contact Dr. Kole, Series Editor, at [ckole2012@gmail.com](mailto:ckole2012@gmail.com)

More information about this series at <http://www.springer.com/series/11805>

---

Philipp Simon · Massimo Iorizzo ·  
Dariusz Grzebelus · Rafal Baranski  
Editors

# The Carrot Genome

 Springer

*Editors*

Philipp Simon  
Vegetable Crops Research Unit  
USDA-ARS  
Madison, WI, USA

Massimo Iorizzo  
Plants for Human Health Institute  
North Carolina State University  
Kannapolis, NC, USA

Dariusz Grzebelus  
University of Agriculture in Krakow  
Kraków, Poland

Rafal Baranski  
Faculty of Biotechnology and  
Horticulture  
University of Agriculture in Krakow  
Kraków, Poland

ISSN 2199-4781                      ISSN 2199-479X (electronic)  
Compendium of Plant Genomes  
ISBN 978-3-030-03388-0              ISBN 978-3-030-03389-7 (eBook)  
<https://doi.org/10.1007/978-3-030-03389-7>

Library of Congress Control Number: 2019934354

© Springer Nature Switzerland AG 2019

This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.

The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

The publisher, the authors and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, expressed or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Switzerland AG  
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

---

# Contents

<b>1</b>	<b>Economic and Academic Importance</b> . . . . .	<b>1</b>
	Philipp W. Simon	
<b>2</b>	<b><i>Daucus</i>: Taxonomy, Phylogeny, Distribution</b> . . . . .	<b>9</b>
	David M. Spooner	
<b>3</b>	<b>Carrot Floral Development and Reproductive Biology</b> . . . . .	<b>27</b>
	Bettina Linke, Maria Soledad Alessandro, Claudio R. Galmarini and Thomas Nothnagel	
<b>4</b>	<b>Gene Flow in Carrot</b> . . . . .	<b>59</b>
	Jennifer R. Mandel and Johanne Brunet	
<b>5</b>	<b>Carrot Domestication</b> . . . . .	<b>77</b>
	Shelby Ellison	
<b>6</b>	<b>Genetic Resources for Carrot Improvement</b> . . . . .	<b>93</b>
	Charlotte Allender	
<b>7</b>	<b>Carrot Molecular Genetics and Mapping</b> . . . . .	<b>101</b>
	Massimo Iorizzo, Shelby Ellison, Marti Pottorff and Pablo F. Cavagnaro	
<b>8</b>	<b>Carrot Molecular Cytogenetics</b> . . . . .	<b>119</b>
	Marina Iovene and Ewa Grzebelus	
<b>9</b>	<b>Classical and Molecular Carrot Breeding</b> . . . . .	<b>137</b>
	Philipp W. Simon	
<b>10</b>	<b>Genetic Engineering of Carrot</b> . . . . .	<b>149</b>
	Rafal Baranski and Aneta Lukasiewicz	
<b>11</b>	<b>The Carrot Nuclear Genome and Comparative Analysis</b> . . . . .	<b>187</b>
	Massimo Iorizzo, Alicja Macko-Podgórní, Douglas Senalik, Allen Van Deynze and Philipp W. Simon	
<b>12</b>	<b>Carrot Organelle Genomes: Organization, Diversity, and Inheritance</b> . . . . .	<b>205</b>
	David M. Spooner, Philipp W. Simon, Douglas Senalik and Massimo Iorizzo	

---

<b>13</b>	<b>Carrot Genetics, Omics and Breeding Toolboxes</b> . . . . .	225
	Hamed Bostan, Douglas Senalik, Philipp W. Simon and Massimo Iorizzo	
<b>14</b>	<b>Carrot Carotenoid Genetics and Genomics</b> . . . . .	247
	Philipp W. Simon, Emmanuel Geoffriau, Shelby Ellison and Massimo Iorizzo	
<b>15</b>	<b>Carrot Anthocyanin Diversity, Genetics, and Genomics</b> . . . . .	261
	Pablo F. Cavagnaro and Massimo Iorizzo	
<b>16</b>	<b>Carrot Volatile Terpene Metabolism: Terpene Diversity and Biosynthetic Genes</b> . . . . .	279
	Mwafaq Ibdah, Andrew Muchlinski, Mossab Yahyaa, Bhagwat Nawade and Dorothea Tholl	
<b>17</b>	<b>Genetics and Genomics of Carrot Sugars and Polyacetylenes</b> . . . . .	295
	Pablo F. Cavagnaro	
<b>18</b>	<b>Genetics and Genomics of Carrot Biotic Stress</b> . . . . .	317
	Lindsey J. du Toit, Valérie Le Clerc and Mathilde Briard	
<b>19</b>	<b>Genetics and Genomics of Carrot Abiotic Stress</b> . . . . .	363
	Dariusz Grzebelus	

---

## Contributors

**Maria Soledad Alessandro** Estación Experimental Agropecuaria La Consulta, Instituto Nacional de Tecnología Agropecuaria, Mendoza, Argentina

**Charlotte Allender** School of Life Sciences, University of Warwick, Warwick, UK

**Rafal Baranski** Faculty of Biotechnology and Horticulture, Institute of Plant Biology and Biotechnology, University of Agriculture in Krakow, Krakow, Poland

**Hamed Bostan** Plants for Human Health Institute, North Carolina State University, Kannapolis, NC, USA

**Mathilde Briard** IRHS, Agrocampus Ouest, INRA, Université d'Angers, SFR QuaSaV, Angers, France

**Johanne Brunet** USDA-Agricultural Research Service, Vegetable Crops Research Unit, Department of Entomology, University of Wisconsin, Madison, WI, USA

**Pablo F. Cavagnaro** National Scientific and Technical Research Council (CONICET), National Institute of Agricultural Technology (INTA) E.E.A. La Consulta, San Carlos, Mendoza, Argentina;  
Faculty of Agricultural Sciences, National University of Cuyo, Mendoza, Argentina;  
National Scientific and Technical Research Council (CONICET), Buenos Aires, Argentina;  
La Consulta Experimental Station, National Institute of Agricultural Technology (INTA), La Consulta, Mendoza, Argentina;  
Horticulture Institute, Faculty of Agricultural Sciences, National University of Cuyo, Lujan de Cuyo, Mendoza, Argentina

**Valérie Le Clerc** IRHS, Agrocampus Ouest, INRA, Université d'Angers, SFR QuaSaV, Angers, France

**Shelby Ellison** USDA-Agricultural Research Service, Vegetable Crops Research Unit, Department of Horticulture, University of Wisconsin-Madison, Madison, WI, USA



**Claudio R. Galmarini** Estación Experimental Agropecuaria La Consulta, Instituto Nacional de Tecnología Agropecuaria, Mendoza, Argentina; Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina;

Facultad de Ciencias Agrarias, Universidad Nacional de Cuyo, Chacras de Coria, Luján, Mendoza, Argentina

**Emmanuel Geoffriau** Agrocampus Ouest, Institut de Recherche en Horticulture et Semences – UMR 1345, Angers, France

**Dariusz Grzebelus** Faculty of Biotechnology and Horticulture, Institute of Plant Biology and Biotechnology, University of Agriculture in Krakow, Krakow, Poland

**Ewa Grzebelus** Faculty of Biotechnology and Horticulture, Institute of Plant Biology and Biotechnology, University of Agriculture in Krakow, Krakow, Poland

**Mwafaq Ibdah** Newe Ya'ar Research Center, Agriculture Research Organization, Ramat Yishay, Israel

**Massimo Iorizzo** Department of Horticultural Sciences, Plants for Human Health Institute, North Carolina State University, Kannapolis, NC, USA

**Marina Iovene** CNR, Institute of Biosciences and BioResources (CNR-IBBR), Portici, NA, Italy

**Bettina Linke** Department of Biology, Humboldt University, Berlin, Germany

**Aneta Lukaszewicz** Faculty of Biotechnology and Horticulture, Institute of Plant Biology and Biotechnology, University of Agriculture in Krakow, Krakow, Poland

**Alicja Macko-Podgórn** Faculty of Biotechnology and Horticulture, Institute of Plant Biology and Biotechnology, University of Agriculture in Krakow, Krakow, Poland

**Jennifer R. Mandel** Department of Biological Sciences, University of Memphis, Memphis, TN, USA

**Andrew Muchlinski** Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA

**Bhagwat Nawade** Newe Ya'ar Research Center, Agriculture Research Organization, Ramat Yishay, Israel

**Thomas Nothnagel** Institute for Breeding Research on Horticultural Crops, Federal Research Centre for Cultivated Plants, Quedlinburg, Germany

**Marti Pottorff** Plants for Human Health Institute, North Carolina State University, Kannapolis, NC, USA

---

**Douglas Senalik** USDA-Agricultural Research Service, Vegetable Crops Research Unit, Department of Horticulture, University of Wisconsin-Madison, Madison, WI, USA

**Philipp W. Simon** USDA-Agricultural Research Service, Vegetable Crops Research Unit, Department of Horticulture, University of Wisconsin-Madison, Madison, WI, USA

**David M. Spooner** USDA-Agricultural Research Service, Vegetable Crops Research Unit, Department of Horticulture, University of Wisconsin-Madison, Madison, WI, USA

**Dorothea Tholl** Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA

**Lindsey J. du Toit** Department of Plant Pathology, Washington State University Mount Vernon NWREC, Mount Vernon, WA, USA

**Allen Van Deynze** University of California, Davis, Seed Biotechnology Center and Plant Breeding Center, Davis, CA, USA

**Mossab Yahyaa** Neve Ya'ar Research Center, Agriculture Research Organization, Ramat Yishay, Israel



# Economic and Academic Importance

1

Philipp W. Simon

## Abstract

Carrot is a relatively recently domesticated vegetable crop that provides a significant source of dietary vitamin A to consumers. Earlier cultivar development for carrot was most extensive in temperate regions of Europe and Asia, but cultivars adapted to tropical and sub-tropical climates have contributed significantly to an increase in global carrot production in the last 50 years. Carrot germplasm includes a broad range of genotypic and phenotypic diversity that contributes to its wide adaptability. There has not been an extensive written historical record for carrot, where color and flavor were the most frequently noted attributes of the crop from its origins in Central Asia through its early development into the Middle East, North Africa, Europe, and Asia. Carotenoids and anthocyanins account for carrot colors and have been a major focus for carrot researchers, and the use of carrot in demonstrating biological totipotency and in providing the first evidence of plant transfer of mitochondrial DNA to the plastid genome has generated significant attention for carrot. The economic

importance of carrot in agriculture and academic contributions attributable to carrot that are summarized in this chapter suggest an optimistic future for improved crop production and expanded basic research opportunities that are broadened with the availability of a carrot genome sequence.

## 1.1 Introduction

Carrot is a crop with a wide range of phenotypic variation utilized by breeders (Simon et al. 2008) and genotypic variation that is only beginning to be fully evaluated (Iorizzo et al. 2016). Carrots are among the top 10 vegetables, based on global production records of primary vegetables, after tomatoes, onions, cabbage, cucumbers, and eggplant (FAO 2017). Most of the 22 vegetables among those in that class of primary vegetables are members of the Amaryllidaceae, Brassicaceae, Compositae, Cucurbitaceae, Leguminosae, Poaceae, Solanaceae, where several major crops rank high in terms of global production for each of those families. In contrast, carrots are the only member of the Apiaceae in that class of primary vegetables, but several other vegetable crops, including celery, cilantro, fennel, and arracacha, and many spice crops are also significant Apiaceous crops grown globally (Rubatzky et al. 1999). Carrot today is grown globally with extensive adaptation to temperate production areas in Europe, Asia, and the

---

P. W. Simon (✉)  
USDA Agricultural Research Service, Vegetable  
Crops Research Unit, Department of Horticulture,  
University of Wisconsin, 1575 Linden Dr., 53706  
Madison, WI, USA  
e-mail: [philipp.simon@ars.usda.gov](mailto:philipp.simon@ars.usda.gov)

Americas, but with more recent cultivar development for sub-tropical and even tropical climate (Simon et al. 2008). Orange carrots are rich in provitamin A and carotenoids (see Chap. 9), and with the expansion of carrot production in warmer climates, they can provide a sustainable, locally produced food to contribute to reducing the incidence of vitamin A deficiency, which continues to be particularly prevalent in those warmer climates (Tanumihardjo 2012). While categorized as a cool-season crop, the adaptation of carrots to warmer climates raises a positive indication for continued expanded carrot production into the future.

---

## 1.2 Global Production and Economic Value

Global carrot production has risen steadily in the last 50 years (FAO 2017), with a threefold increase in production area (Table 1.1; Fig. 1.1) and twofold increase in yield (Table 1.2) to result in a sixfold increase in total production (Table 1.3; Fig. 1.2). With these increases, the average global increase in per capita carrot production has risen 2.7-fold in the last 50 years (Table 1.4; Fig. 1.3). All of these increases in carrot production and availability have risen slightly ahead of the averages for the 22 primary vegetables, so that carrot today accounts for 5.5% of the per capita vegetable availability globally (Table 1.4). This increase was particularly steep in Asia. A rise in the economic value of the carrot crop follows a similar trend with a sixfold increase in global production value in the last 50 years (Table 1.5) and a twofold increase in value per hectare to the grower (Table 1.6). As with production trends, economic increases in the value of the carrot crop were particularly high in Asia (Tables 1.5, 1.6).

Unfortunately, FAO statistics combine turnip production with carrot, as they do for several other primary vegetable crops, like cauliflower and broccoli. Consequently, statistics presented in Tables 1.1, 1.2, 1.3, 1.4, 1.5, 1.6 and Figs. 1.1, 1.2, 1.3 include the combined values for carrot and turnip. Carrots account for most of the production values, based on crop-specific

information available for the USA and Europe. Turnip production was less than 2% of carrot production in the USA in 1950 (USDA 1954), and publication of U.S. statistics for turnips was discontinued in 1963. Turnip production in Europe in the early 1990s was <1% that of carrot (Hinton 1991).

The portion of the carrot crop grown under organic production management practices has grown in recent decades in the more well-developed carrot markets of North America and Europe, accounting for 11% of the 2016 U.S. market (USDA 2017) and 25–30% of Danish and German markets (Willer and Lernoud 2016). Consumers place a high value on nutritional quality and flavor (Yiridoe et al. 2005), and the generally positive public impression of carrots as a nutritious food may account for increasing organically grown carrot consumption. The broad range of genetic diversity and new tools for improving carrot flavor available to breeding programs (see Chap. 16) provide promising prospects for flavor improvement, and while production of organic carrots is not without pest, disease, and weed challenges, progress has been made in managing them (Simon et al. 2017).

### 1.2.1 Historical Records

The first archeological record for carrot was seed found at Bronze Age campsites of around 4500 years ago in Switzerland and southern Germany (Neuweiler 1931), where it was speculated that seed was likely used as a spice or medicinal herb, as many other Apiaceous plants are used today (Rubatzky et al. 1999). Carrot tissue preparations were also found on a Roman shipwreck off Tuscany of around 2100 years ago where it was included in what is thought to be a medicinal preparation including several other plants (Smithsonian Insider 2010). Relatively little was written about carrot during its early history other than periodic references to its color and flavor (Banga 1957a, b, 1963). The 1963 work of Banga is the most extensive publication dedicated to carrot to date, where he reviewed and analyzed not only written historical records

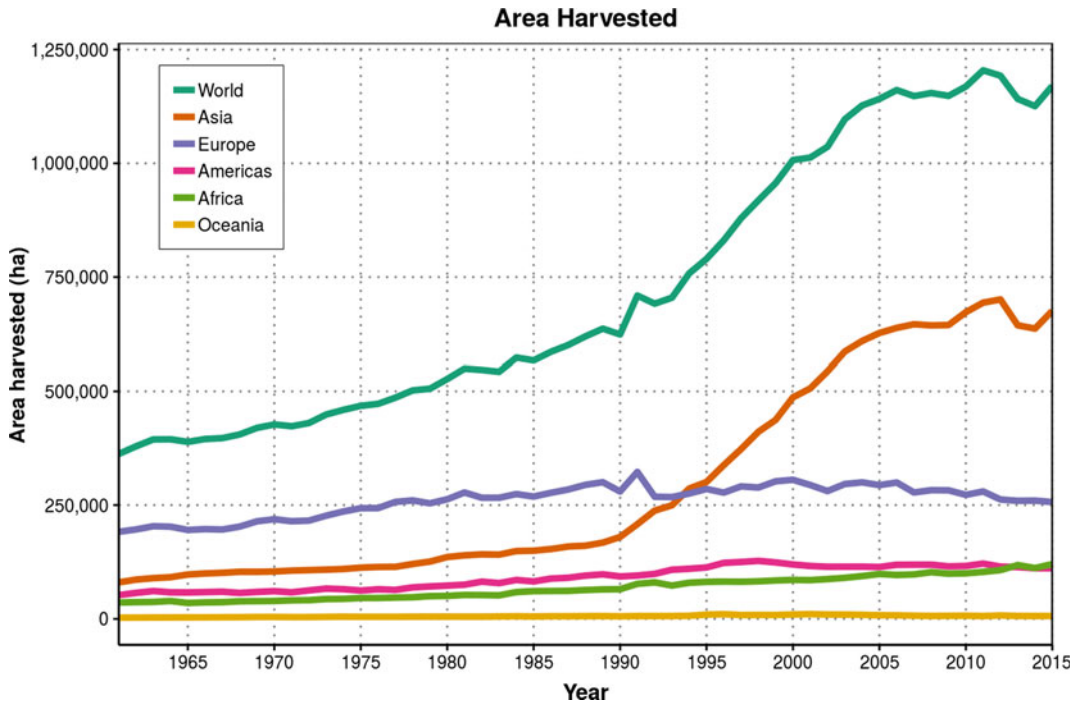
**Table 1.1** Global production area of 22 primary vegetables and of carrots + turnips comparing the average for the 1961–1965 period to the 2011–2015 period

Year	Region	Vegetables, primary (ha)	Carrots and turnips (ha)	Percent of vegetables <sup>a</sup>	Change <sup>b</sup>
1961–1965	World	13,057,559	383,965	2.9	
	Africa	1,028,571	36,782	3.6	
	Americas	1,949,102	57,351	2.9	
	Asia	5,782,030	88,985	1.5	
	Europe	4,215,052	197,915	4.7	
	Oceania	82,804	2932	3.5	
2011–2015	World	34,640,706	1,166,885	3.4	303%
	Africa	5,620,793	112,093	2.0	304%
	Americas	2,736,117	114,494	4.2	199%
	Asia	23,049,230	670,127	2.9	753%
	Europe	3,101,668	263,703	8.5	133%
	Oceania	132,899	6467	4.9	221%

Data from FAO (2017)

<sup>a</sup>Percent of vegetables is the carrot + turnip percentage of the primary vegetables

<sup>b</sup>Change is the carrot + turnip value for 2011–2015 relative to 1961–2015



**Fig. 1.1** Global and regional carrot + turnip production area 1961–2015

**Table 1.2** Global yield of 22 primary vegetables and of carrots + turnips comparing the average for the 1961–1965 period to the 2011–2015 period

Year	Region	Vegetables, primary (hg/ha)	Carrots and turnips (hg/ha)	Percent of vegetables <sup>a</sup>	Change <sup>b</sup>
1961–1965	World	95,996	166,893	174	
	Africa	66,371	93,467	141	
	Americas	106,438	213,260	200	
	Asia	89,318	127,386	143	
	Europe	114,450	183,271	160	
	Oceania	111,474	280,789	252	
2011–2015	World	184,330	329,021	178	197%
	Africa	85,937	184,041	214	197%
	Americas	220,969	303,285	137	142%
	Asia	195,966	357,687	183	281%
	Europe	246,758	324,813	132	177%
	Oceania	191,741	526,737	275	188%

Data from FAO (2017)

<sup>a</sup>Percent of vegetables is the carrot + turnip percentage of the primary vegetables

<sup>b</sup>Change is the carrot + turnip value for 2011–2015 relative to 1961–2015

**Table 1.3** Global crop production of 22 primary vegetables and of carrots + turnips comparing the average for the 1961–1965 period to the 2011–2015 period

Year	Region	Vegetables, primary (ton)	Carrots and turnips (ton)	Percent of vegetables <sup>a</sup>	Change <sup>b</sup>
1961–1965	World	133,903,539	6,413,270	4.8	
	Africa	7,705,073	343,979	4.5	
	Americas	22,366,990	1,222,371	5.5	
	Asia	55,344,331	1,134,616	2.1	
	Europe	47,578,050	3,629,651	7.6	
	Oceania	909,095	82,654	9.1	
2011–2015	World	724,328,890	38,352,663	5.3	598%
	Africa	51,501,312	2,061,469	4.0	599%
	Americas	67,561,800	3,469,613	5.1	284%
	Asia	520,393,097	23,919,717	4.6	2108%
	Europe	82,140,041	8,560,515	10.4	236%
	Oceania	2,732,641	341,350	12.5	413%

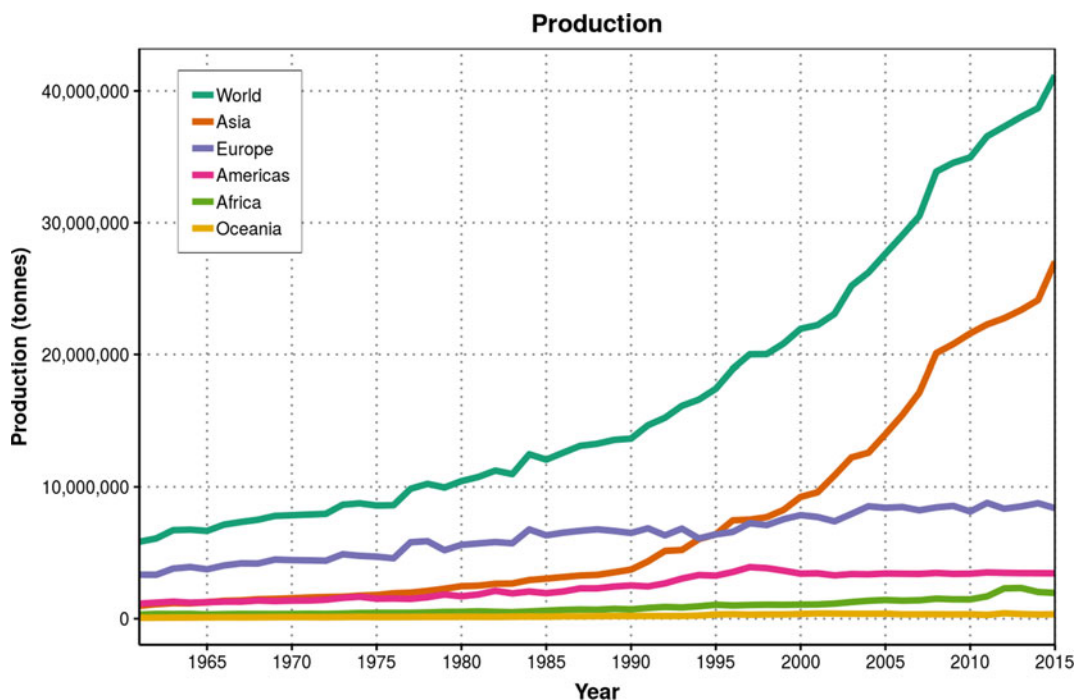
Data from FAO (2017)

<sup>a</sup>Percent of vegetables is the carrot + turnip percentage of the primary vegetables

<sup>b</sup>Change is the carrot + turnip value for 2011–2015 relative to 1961–2015

thought to refer to carrot, but also artwork thought to depict carrot, and early seed catalog illustrations and descriptions of carrots. The early written and illustrative evidence attributed to

carrots as a root crop two millennia ago was disputed by Banga who was not convinced that carrot was the root crop described. He concluded that carrot was not developed as a root crop



**Fig. 1.2** Global and regional carrot + turnip total crop production 1961–2015

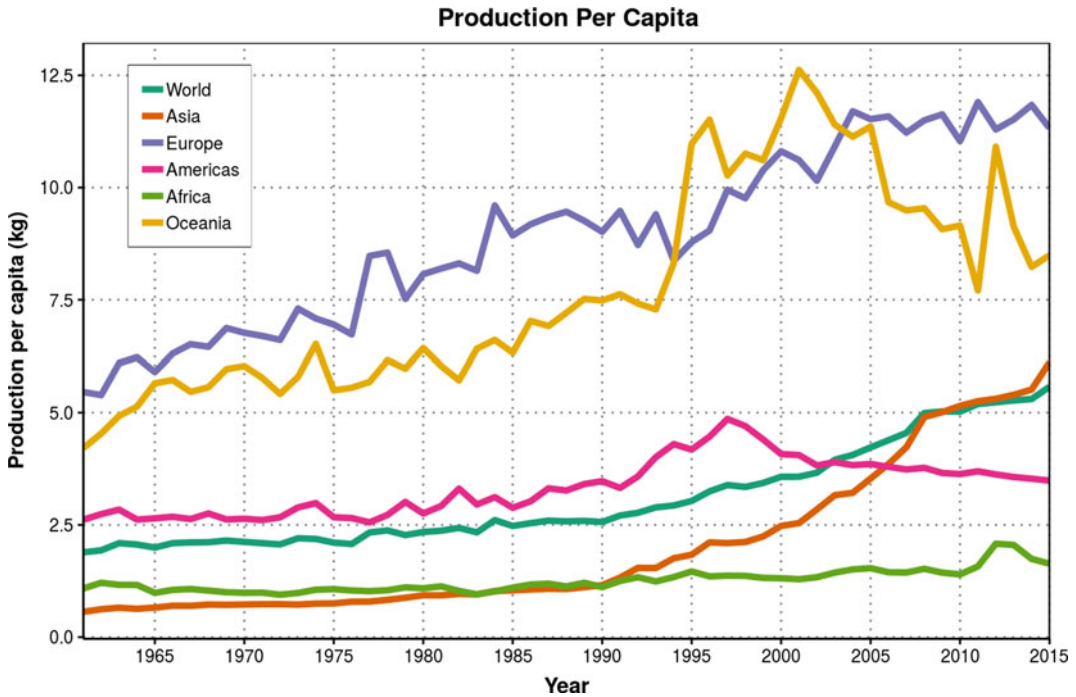
**Table 1.4** Global production per capita of 22 primary vegetables and of carrots + turnips comparing the average for the 1961–1965 period to the 2011–2015 period

Year	Region	Vegetables, primary (kg)	Carrots and turnips (kg)	Percent of vegetables <sup>a</sup>	Change <sup>b</sup>
1961–1965	World	41.70	1.99	4.8	
	Africa	25.07	1.12	4.5	
	Americas	49.27	2.69	5.5	
	Asia	30.62	0.63	2.0	
	Europe	76.25	5.81	7.6	
	Oceania	53.91	4.89	9.1	
2011–2015	World	100.39	5.32	5.3	266%
	Africa	45.35	1.82	4.0	162%
	Americas	69.68	3.58	5.1	133%
	Asia	120.12	5.52	4.6	882%
	Europe	111.06	11.58	10.4	199%
	Oceania	71.19	8.89	12.5	182%

Data from FAO (2017)

<sup>a</sup>Percent of vegetables is the carrot + turnip percentage of the primary vegetables

<sup>b</sup>Change is the carrot + turnip value for 2011–2015 relative to 1961–2015



**Fig. 1.3** Global and regional carrot + turnip production per capita 1961–2015

**Table 1.5** Global gross production value of 22 primary vegetables and of carrots + turnips comparing the average for the 1961–1965 period to the 2011–2015 period

Year	Region	Vegetables, fresh (1000 Int. \$)	Carrots and turnips (1000 Int. \$)	Percent of vegetables <sup>a</sup>	Change <sup>b</sup>
1961–1965	World	12,120,283	1,600,105	13.2	
	Africa	991,392	85,822	8.7	
	Americas	826,997	304,980	36.9	
	Asia	7,449,353	283,086	3.8	
	Europe	2,809,668	905,594	32.2	
	Oceania	42,873	20,622	48.1	
2011–2015	World	52,135,962	9,568,951	18.4	598%
	Africa	3,527,670	514,334	14.6	599%
	Americas	1,413,772	865,665	61.2	284%
	Asia	44,987,006	5,967,945	13.3	2108%
	Europe	2,095,569	2,135,840	101.9	236%
	Oceania	111,945	85,166	76.1	413%

Data from FAO (2017)

<sup>a</sup>Percent of vegetables is the carrot + turnip percentage of the primary vegetables

<sup>b</sup>Change is the carrot + turnip value for 2011–2015 relative to 1961–2015



**Table 1.6** Global value per hectare of production of 22 primary vegetables and of carrots + turnips comparing the average for the 1961–1965 period to the 2011–2015 period

Year	Region	Vegetables, fresh (1000 Int. \$/ha)	Carrots and turnips (1000 Int. \$/ha)	Percent of vegetables <sup>a</sup>	Change <sup>b</sup>
1961–1965	World	0.9282	4.1673	449	
	Africa	0.9639	2.3333	242	
	Americas	0.4243	5.3178	1253	
	Asia	1.2884	3.1813	247	
	Europe	0.6666	4.5757	686	
	Oceania	0.5178	7.0339	1359	
2011–2015	World	1.5050	8.2004	545	197%
	Africa	0.6276	4.5885	731	197%
	Americas	0.5167	7.5608	1463	142%
	Asia	1.9518	8.9057	456	280%
	Europe	0.6756	8.0994	1199	177%
	Oceania	0.8423	13.1690	1563	187%

Data from FAO (2017)

<sup>a</sup>Percent of vegetables is the carrot + turnip percentage of the primary vegetables

<sup>b</sup>Change is the carrot + turnip value for 2011–2015 relative to 1961–2015

during the Roman Empire, but rather about 1100 years ago, and was Central Asian in origin, as Vavilov suggested and molecular evidence supports (Iorizzo et al. 2013). More recently, Stolarczyk and Janick (2011) evaluated evidence for an earlier origin of carrots as a root crop in Turkey, Greece, and Italy, including support for orange storage and carrot color. As new archeological and artistic evidence for carrot arises, the early history of carrot will hopefully become clearer.

Carrot root color was a primary focus of early descriptions of the crop as noted above, and Vilmorin (1859) also wrote quite extensively about the origins of orange color in carrots where he evaluated intercrosses of wild and cultivated carrots. The genetics of carrot color due to carotenoids continues to be a major focus for carrot research today (also see Chap. 14), but it was the development of in vitro methods for plant propagation that brought carrot most widely into the basic scientific literature.

### 1.3 Totipotency and Future Directions

On the occasion of the 125th anniversary of Science magazine, the editors generated 125 questions that point to critical knowledge gaps addressing the question: What don't we know? In this broad-ranging sweep of questions characterized as "opportunities to be exploited" (Siegfried 2009), compelling scientific questions that could not be answered were raised, and most of those questions dealt with physics, mathematics, and human health. Only six dealt specifically with plant sciences, and the only one of those six to be included among the 25 top questions that were included as separate articles in that 125th anniversary issue of Science was "How does a single somatic cell become a whole plant" (Miller 2009). This article noted that nearly 50 years earlier "scientists learned they could coax carrot cells to undergo... embryogenesis in

the lab”, referring to the seminal work of Steward et al. (1958, 1964) that provided the foundation for the concept that became known as totipotency in plants and the inspiration for pluripotent stem cell research in humans. Totipotency has, in fact, been a focus of numerous research efforts, yet the biology of totipotency, having been observed in not only carrot but also in many other plants, remains a largely unanswered question.

Significant efforts have been made in carrot, advancing the basic scientific knowledge of totipotency, carotenoid accumulation, and a wide range of other research topics, and applied research has increased the productivity and improved the quality of the crop significantly in the last 50 years. Carrot genomic information has already contributed to our understanding of organelle evolution with first evidence of plant transfer of mitochondrial DNA to the plastid genome discovered in carrot, as highlighted in Chap. 12. The availability of the carrot genome sequence will provide future research efforts with an additional valuable tool to better understand and improve this important vegetable crop.

## References

- Banga O (1957a) Origin of the European cultivated carrot. *Euphytica* 6:54–63
- Banga O (1957b) The development of the original European carrot material. *Euphytica* 6:64–76
- Banga O (1963) Main types of the western carotene carrot and their origin. W.E.J. Tjeenk Willink, Zwolle, The Netherlands
- FAO (2017). [www.fao.org/statistics](http://www.fao.org/statistics)
- Hinton L (1991) The European market for fruit and vegetables. Elsevier, London
- Iorizzo M, Senalik DA, Ellison SL et al (2013) Genetic structure and domestication of carrot (*Daucus carota* L. subsp. *sativus* L.) (Apiaceae). *Am J Bot* 100:930–938
- Iorizzo M, Ellison S, Senalik D, Zeng P et al (2016) A high-quality carrot genome assembly provides new insights into carotenoid accumulation and asterid genome evolution. *Nat Genet* 48:657–666
- Miller G (2009) How does a single somatic cell become a whole plant? *Science* 209:86
- Neuweiler E (1931) Die Pflanzenreste aus dem spätbronzezeitlichen Pfahlbau “sumpf” bei Zug. *Vierteljahrsschr Naturf Ges Zurich* 76:776–732
- Rubatzky VE, Quiros CF, Simon PW (1999) Carrots and related vegetable Umbelliferae. CABI, New York
- Siegfried T (2009) Praise of hard questions. *Science* 309:75
- Simon PW, Freeman RE, Vieira JV et al (2008) Carrot. In: Prohens J, Carena MJ, Nuez F (eds) *Handbook of crop breeding, vol 1. Vegetable breeding*. Springer, Heidelberg, pp 327–357
- Simon PW, Zystro J, Roberts PA et al (2017) The CIOA (Carrot Improvement for Organic Agriculture) project: location, cropping system, and genetic background influence carrot performance including top height and flavor. *Acta Hort* 1153:1–8
- Smithsonian Insider (2010) DNA sequencing reveals simple vegetables in ancient Roman medicines. <https://insider.si.edu/2010/10/dna-sequencing-reveals-simple-vegetables-in-ancient-roman-medicines/>
- Steward FC, Mapes MO, Smith JO (1958) Growth and organized development of cultured cells. I. Growth and division of freely suspended cells. *Am J Bot* 45:693–703
- Steward FC, Mapes MO, Kent AE, Holsten RD (1964) Growth and development of cultured plant cells. *Science* 743:20–27
- Stolarczyk J, Janick J (2011) Carrot: history and iconography. *Chron Hortic* 51:13–18
- Tanumihardjo S (ed) (2012) Carotenoids and human health. Springer, New York
- Vilmorin M (1859) Notice sur l’amelioration de la carotte sauvage. In: Vilmorin L (ed) Notice sur l’amelioration des plantes par le semis. Librairie Agricole, Paris, pp 5–29
- USDA (2017). [www.nass.usda.gov/Publications/Todays\\_Reports/reports/census17.pdf](http://www.nass.usda.gov/Publications/Todays_Reports/reports/census17.pdf)
- USDA (1954). [www.nass.usda.gov](http://www.nass.usda.gov)
- Willer H, Lernoud J (2016) The world of organic agriculture—statistics and emerging trends. Research Institute of Organic Agriculture (FiBL) and IFOAM, Berlin
- Yiridoe EK, Bonti-Ankomah S, Martin RC (2005) Comparison of consumer perceptions and preference toward organic versus conventionally produced foods: a review and update of the literature. *Renew Agric Food Syst* 20:193–205

# *Daucus*: Taxonomy, Phylogeny, Distribution

# 2

David M. Spooner

## Abstract

Cultivated carrot (*Daucus carota* subsp. *sativus*) is the most important member in the Apiaceae family in terms of economy and nutrition and is considered the second most popular vegetable in the world after potato. Despite its global importance, the systematics of *Daucus* remains under active revision at the species, genus, and subtribal levels. The phylogenetic relationships among the species of *Daucus* and close relatives in the Apioideae have been clarified recently by a series of molecular studies using DNA sequences of the plastid genes *rbcL* and *matK*; plastid introns *rpl16*, *rps16*, *rpoC1*; nuclear ribosomal DNA internal transcribed spacer (ITS) sequences; and plastid DNA restriction sites. Of these DNA markers, the ITS region consisting of ITS1, the intervening spacer, and ITS2 has served as the main marker used. Recently, next-generation DNA sequencing methodologies have been used. We review these techniques and how they are impacting the taxonomy of the genus *Daucus*.

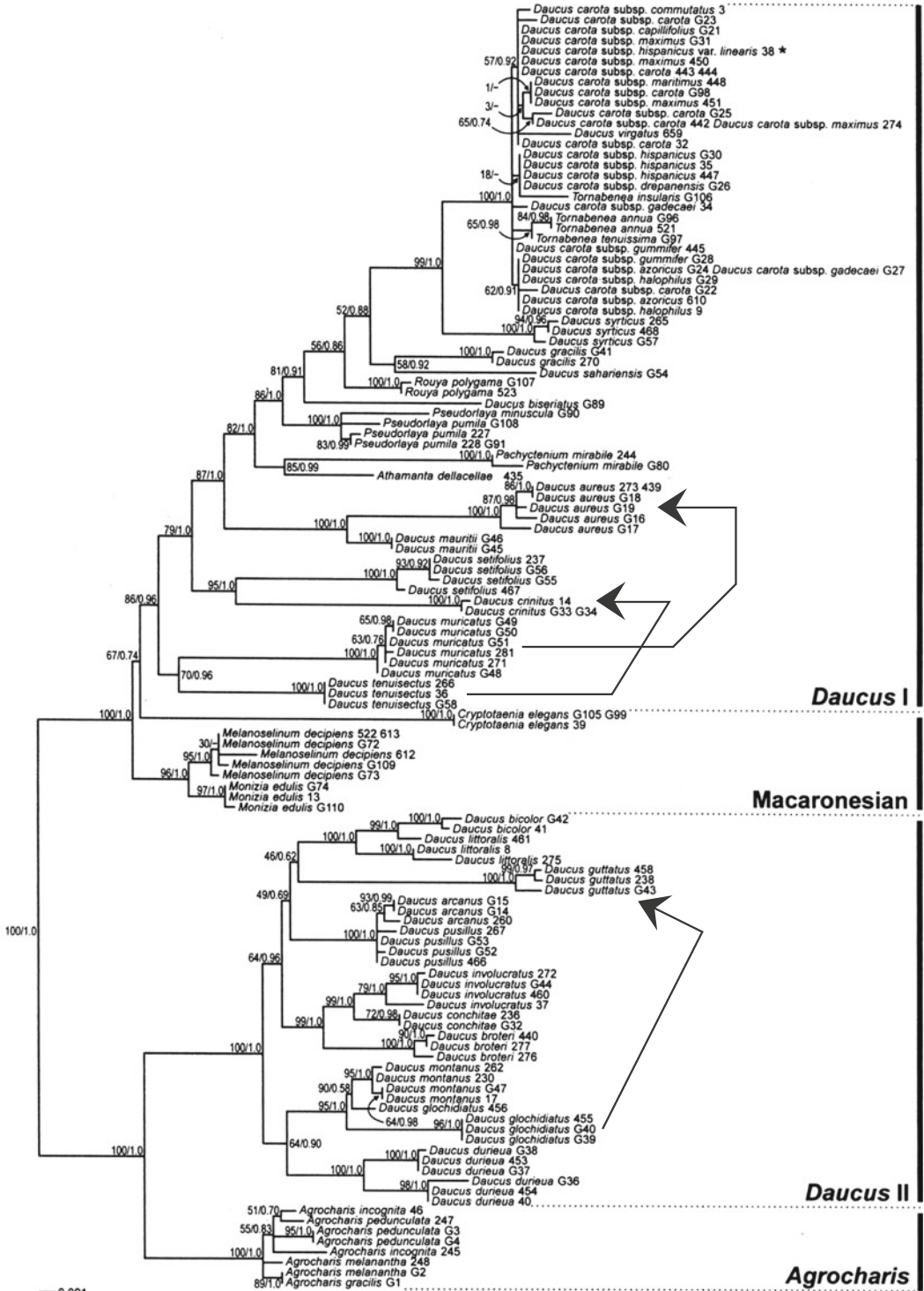
## 2.1 Taxonomy of the Apiaceae (Umbelliferae)

The Apiaceae (Umbelliferae) family contains 466 genera and 3820 species (Plunkett et al. [in press](#)) and is one of the largest families of seed plants. It is nearly cosmopolitan in distribution, but most diverse in temperate regions of the northern hemisphere (Downie et al. [2000a, b, c](#); Heywood [1983](#)). It is well supported as a monophyletic family, closely related to the families Araliaceae, Pittosporaceae, and Myodocarpaceae, and these, along with three smaller families, constitute the order Apiales, containing about 5400 species (Judd et al. [2016](#); Plunkett et al. [1996b](#)).

The Apiaceae is well defined morphologically by a suite of characters, typically including herbs with compound leaves, stems usually hollow in the internodes and with secretory canals containing ethereal oils, resins, and other compounds; alternate compound leaves or simple and deeply divided or lobed leaves with sheathing petioles; determinate inflorescences containing simple to compound umbels often subtended by involucre bracts; small flowers with 5 sepals, 5 petals, 5 stamens, and 2 connate carpels with an inferior ovary; 2 small stigmas; with the fruit a schizocarp (dry fruits breaking into one-seeded segments) with each of the two mericarps attached to an entire and deeply divided forked central stalk (carpophore) (Judd et al. [2016](#)).

---

D. M. Spooner (✉)  
 USDA-Agricultural Research Service, Vegetable  
 Crops Research Unit, Department of Horticulture,  
 University of Wisconsin–Madison, 1575 Linden Dr,  
 53706-1590 Madison, WI, USA  
 e-mail: [David.Spooner@ars.usda.gov](mailto:David.Spooner@ars.usda.gov)



◀ **Fig. 2.1** Reproduction of the upper part of the *Daucus* maximum likelihood phylogeny of Banasiak et al. (2016), using combined nuclear internal transcribed spacer region of ribosomal DNA (ITS) and plastid (*rps16* intron, *rpoC1* intron, and *rpoB-trnC* intergenic spacer) data, with

This large suite of distinctive characters makes the Apiaceae and its constituent species easily recognized to family, but divisions within the family have been the subject of long dispute including circumscription and relationships of the genus *Daucus* (Constance 1971; Plunkett and Downie 1999). Traditionally, the Apiaceae has been divided into three subfamilies, the Saniculoideae, Hydrocotyloideae, and Apioideae, with the Apioideae, containing the genus *Daucus*, by far the largest of these three traditional subfamilies. Drude (1898) recognized 8 tribes and 10 subtribes within the Apioideae. Molecular phylogenetic studies have confirmed the monophyly of the subfamily Apioideae but not many of its tribes and subtribes (Downie et al. 2001). Downie et al. (2001) recognized nine tribes in the Apiaceae subfamily Apioideae, and placed *Daucus*, and 12 other genera, in tribe *Scandiceae* Spreng., subtribe *Daucinae* Dumort. (the other 12 genera being *Agrocharis* Hochst., *Ammodaucus* Coss. and Durieu, *Cuminum* L., *Laser* Borkh. ex P. Gaertn., B. Mey. and Schreb., *Laserpitium* L., *Melanoselinum* Hoffm., *Monizia* Lowe, *Orlaya* Hoffm., *Pachyctenium* Maire and Maire and *Polemannia* Eckl. and Zeyh., *Polylophium* Boiss., *Pseudorlaya* (Murb.) Murb., and *Thapsia* L.).

A genus-level treatment of *Daucus* by Sáenz Laín (1981) used morphological and anatomical data and recognized 20 species. Rubatzky et al. (1999) later estimated 25 species of *Daucus*. The phylogenetic relationships among the species of genus *Daucus* and close relatives in the Apioideae have been clarified by a series of molecular studies using DNA sequences of the plastid genes *rbcL* and *matK*; plastid introns *rpl16*, *rps16*, *rpoC1*; nuclear ribosomal DNA internal transcribed spacer (ITS) sequences; and plastid DNA restriction sites (e.g., Arbizu et al. 2014b, 2016a, b; Banasiak et al. 2016; Downie and Katz-Downie 1996; Downie et al. 1996, 1998,

numbers above the branches representing bootstrap support and posterior probability values. The arrows show hard incongruence between Banasiak et al. (2016) and the nuclear ortholog phylogenies of Arbizu et al. (2014b, 2016b)

2000a, b, c, 2001, 2010; Katz-Downie et al. 1999; Lee 2002; Lee and Downie 1999, 2000, 2006; Plunkett et al. 1996a; Spalik and Downie 2007; Spalik et al. 2001a, b; Weitzel et al. 2014). Of these DNA markers, the ITS region consisting of ITS1, the intervening spacer, and ITS2 has served as the main marker. A recent study of ITS, and other DNA regions proposed as standard barcodes (*psbA-trnH*, *matK*, and *rbcL*) in 1957 species in 385 diverse genera in the Apiaceae have shown ITS to serve to identify species 73.3% of the time, higher than any of the other individual markers tested (Liu et al. 2014).

A study by Banasiak et al. (2016) using DNA sequences from nuclear ribosomal ITS and three plastid markers (*rps16* intron, *rpoC1* intron, and *rpoB-trnC* intergenic spacer) is the latest of a series of studies to investigate ingroup and outgroup relationships of *Daucus* (Fig. 2.1). This study redefined and expanded the genus *Daucus* to include the following genera and species into its synonymy: *Agrocharis* Hochst. (4 species), *Melanoselinum* Hoffm. (1 species), *Monizia* Lowe (1 species), *Pachyctenium* Maire and Pamp. (1 species), *Pseudorlaya* (Murb.) Murb. (2 species), *Rouya* Coincy (1 species), *Tornabenea* Parl. (6 species), *Athamanta dellacellae* E. A. Durand and Barratte, and *Cryptotaenia elegans* Webb ex Bolle (these latter two genera with only some of its members transferred to *Daucus*).

Banasiak et al. (2016) made the relevant nomenclatural transfers into *Daucus* (Table 2.1) and following this classification, the genus *Daucus* contains ca. 40 species and now includes winged and completely unadorned (“obsolete”) fruits in addition to its traditionally recognized spiny fruits. As summarized in Banasiak et al. (2016) and presented in graphic form in Fig. 5 of this paper, winged versus spiny versus obsolete fruits presented major traditional taxonomic characters at higher levels in the Apiaceae (e.g.,

**Table 2.1** Taxonomic circumscription of *Daucus* following Arbizu et al. (2014b, 2016b) and Banasiak et al. (2016), their cladistic relationships, and diploid chromosome numbers

Taxon	$2n$	Heywood (1978)— sections within <i>Daucus</i>	Siéenz Lain (1981)— sections within <i>Daucus</i>	Clade (Arbizu et al. 2014b, 2016b; Banasiak et al. 2016)	Banasiak et al. (2016)— sections within <i>Daucus</i>	Fruit type— secondary ribs (Banasiak et al. 2016)	Countries of occurrence
<i>Daucus arcanus</i> García-Martín and Silvestre	22			Daucus II	<i>Anisactis</i>	Spiny	Spain
<i>Daucus aureus</i> Desf.	22	<i>Chrysodaucus</i> Thell.	<i>Chrysodaucus</i>	Daucus I	<i>Daucus</i>	Spiny	Spain (Canary Islands), Algeria, Egypt, Libya, Morocco, Tunisia, Cyprus, Israel, Lebanon, Syria, Italy
<i>Daucus bicolor</i> Sm.	–	<i>Pseudoplatyspermum</i> (Thell.)	<i>Platyspermum</i>	Daucus II	<i>Anisactis</i>	Spiny	Greece, Turkey
<i>Daucus biseriatus</i> Muurb.	–			Daucus I	<i>Daucus</i>	Spiny	Algeria
<i>Daucus carota</i> subsp. <i>capillifolius</i> (Gilli) C. Arbizu	18	<i>Daucus</i>	<i>Daucus</i>	Daucus I	<i>Daucus</i>	Spiny	Libya, Tunisia
<i>Daucus carota</i> subsp. <i>carota</i> L.	18	<i>Daucus</i>	<i>Daucus</i>	Daucus I	<i>Daucus</i>	Spiny	Widely naturalized worldwide
<i>Daucus carota</i> subsp. <i>gummifer</i> (Syme) Hook. f.	18	<i>Daucus</i>	<i>Daucus</i>	Daucus I	<i>Daucus</i>	Spiny	Coastal Mediterranean, coastal Atlantic in UK, France, Tunisia, Italy
<i>Daucus carota</i> subsp. <i>maximus</i> (Desf.) Ball	18	<i>Daucus</i>	<i>Daucus</i>	Daucus I	<i>Daucus</i>	Spiny	Spain, Algeria, Morocco, Tunisia, Afghanistan, Cyprus, Iran, Israel, Jordan, Lebanon, Syria, Turkey, Pakistan, Greece, Italy (former) Yugoslavia, France, Portugal, Spain
<i>Daucus carota</i> subsp. <i>sativus</i> (Hoffm.) Arcang.	18	<i>Daucus</i>	<i>Daucus</i>	Daucus I	<i>Daucus</i>	Spiny	Cultivated worldwide
<i>Daucus conchitae</i> Greuter	–		Incertae sedis	Daucus II	<i>Anisactis</i>	Spiny	Greece
<i>Daucus crinitus</i> Desf.	22 (18 possibly an error)	<i>Meoides</i> Lange	<i>Daucus</i>	Daucus I	<i>Daucus</i>	Spiny	Algeria, Morocco, Tunisia, Portugal, Spain
<i>Daucus durieua</i> Lange	22	<i>Anisactis</i> DC.	<i>Anisactis</i>	Daucus II	<i>Anisactis</i>	Spiny	Spain, Algeria, Libya, Morocco, Tunisia, Cyprus, Israel, Lebanon, Syria, Portugal, Spain
<i>Daucus glochidiatus</i> (Labil.) Fisch. and C. A. Mey.	44	<i>Anisactis</i>	<i>Anisactis</i>	Daucus II	<i>Anisactis</i>	Spiny	Australia, New Zealand
<i>Daucus gracilis</i> Steinh.	–	<i>Daucus</i>	<i>Daucus</i>	Daucus I	<i>Daucus</i>	Spiny	Algeria, Tunisia
<i>Daucus guttatus</i> Sm.	20, 22	<i>Daucus</i>	<i>Daucus</i>	Daucus II	<i>Anisactis</i>	Spiny	Egypt, Libya, Cyprus, Iran, Iraq, Israel, Lebanon, Syria, Turkey, Albania, Bulgaria, Greece, Italy, Romania (former), Yugoslavia
<i>Daucus hochstetteri</i> A. Braun ex Drude	–	<i>Anisactis</i>		Daucus II		Spiny	Eritrea, Ethiopia
<i>Daucus involucratus</i> Sm.	20, 22	<i>Daucus</i>	<i>Daucus</i>	Daucus II	<i>Anisactis</i>	Spiny	Cyprus, Turkey, Greece

(continued)



**Table 2.1** (continued)

Taxon	2n	Heywood (1978)— sections within <i>Daucus</i>	Saenz Lain (1981)— sections within <i>Daucus</i>	Clade (Arbizu et al. 2014b, 2016b; Banasiak et al. 2016)	Banasiak et al. (2016)— sections within <i>Daucus</i>	Fruit type— morphology secondary ribs (Banasiak et al. 2016)	Countries of occurrence
<i>Daucus jordanicus</i> Post	–	<i>Daucus</i>	<i>Daucus</i>	–	Incertae sedis	Spiny	Libya, Israel, Jordan
<i>Daucus tinoralis</i> Sm.	–	<i>Daucus</i>	<i>Platyspermum</i>	Daucus II	<i>Anisactis</i>	Spiny	Egypt, Libya, Cyprus, Iran, Israel, Jordan, Lebanon, Syria, Turkey
<i>Daucus mauritii</i> Semmen	–	–	–	–	–	Spiny	Morocco
<i>Daucus montanus</i> Humb. and Bonpl. ex Schult.	66	<i>Anisactis</i>	<i>Anisactis</i>	Daucus II	<i>Anisactis</i>	Spiny	Mexico, Costa Rica, El Salvador, Guatemala, Honduras, Venezuela, Bolivia, Colombia, Ecuador, Peru, Argentina, Chile
<i>Daucus muricatus</i> (L.) L.	22	<i>Platyspermum</i> (Hofm.) DC.	<i>Platyspermum</i>	Daucus I	<i>Daucus</i>	Spiny	Portugal, Algeria, Libya, Morocco, Tunisia, Italy, France, Portugal, Spain
<i>Daucus pusillus</i> Michx. (= <i>D. montevidensis</i> Link ex Spreng.)	22	<i>Leptodaucus</i> Thell.	<i>Daucus</i>	Daucus II	<i>Anisactis</i>	Spiny	Canada, United States, Mexico, Brazil, Argentina, Chile, Uruguay
<i>Daucus sahariensis</i> Murb.	18	<i>Daucus</i>	<i>Daucus</i>	Daucus I	<i>Daucus</i>	Spiny	Algeria
<i>Daucus setifolius</i> Desf.	22	<i>Meoides</i>	<i>Daucus</i>	Daucus I	<i>Daucus</i>	Spiny	Algeria, Morocco, Tunisia, Portugal, Spain
<i>Daucus setulosus</i> Guss. ex DC.	–	<i>Meoides</i>	<i>Meoides</i>	Daucus I	<i>Daucus</i>	Spiny	Greece, Turkey
<i>Daucus syriacus</i> Murb.	–	<i>Daucus</i>	<i>Daucus</i>	Daucus I	<i>Daucus</i>	Spiny	Egypt, Libya, Tunisia
<i>Daucus tenuisectus</i> Coss. ex Batt.	–	<i>Daucus</i>	<i>Daucus</i>	Daucus I	<i>Daucus</i>	Spiny	Morocco
<i>Daucus virgatus</i> (Poir.) Maire	–	–	–	Daucus I	<i>Daucus</i>	Winged	Algeria, Tunisia
<b>New <i>Daucus</i> species following the taxonomic expansion of Banasiak et al. (2016)</b>							
<i>Daucus annuus</i> (Bég.) Wojew. et al. (= <i>Tornabenea annua</i> Bég.)	–	–	–	Daucus I	<i>Daucus</i>	Winged	Cape Verde
<i>Daucus dellacellae</i> (Asch. and Barbey ex E. A. Durand and Baratte) Spalik, Banasiak and Reduron = <i>Athamanta dellacellae</i> Asch. and Barbey ex E. A. Durand and Baratte	–	–	–	Daucus I	<i>Daucus</i>	Obsolete	Libya
<i>Daucus insularis</i> (Pari. ex Webb) Spalik et al. (= <i>Tornabenea insularis</i> (Pari. ex Webb) Pari.)	–	–	–	Daucus I	<i>Daucus</i>	Winged	Cape Verde
<i>Daucus tenuissimus</i> (A. Chev.) Spalik et al. (= <i>Melanoselinum tenuissimum</i> A. Chev. (= <i>Tornabenea tenuissima</i> (A. Chev.) A. Hansen and Stueding)	–	–	–	Daucus I	<i>Daucus</i>	Winged	Madeira
<i>Daucus royi</i> Spalik and Reduron (= <i>Roiza</i> <i>polygama</i> (Desf.) Coincey)	20	–	–	Daucus I	<i>Daucus</i>	Winged	Algeria, Tunisia, Italy (Corsica, Sardinia)

(continued)

Table 2.1 (continued)

Taxon	2n	Heywood (1978)— sections within <i>Daucus</i>	Sáenz Lain (1981)— sections within <i>Daucus</i>	Clade (Arbizu et al. 2014b, 2016b; Banasiak et al. 2016)	Banasiak et al. (2016)— sections within <i>Daucus</i>	Fruit type— morphology secondary ribs (Banasiak et al. 2016)	Countries of occurrence
<i>Daucus pumilus</i> (L.) Hoffmanns. and Link (≡ <i>Pseudorhiza pumila</i> (L.) Grande)	26			Daucus I	<i>Daucus</i>	Spiny	Portugal, Spain, Morocco, France, Italy, Greece, Israel
<i>Daucus minusculus</i> Pau ex Font Quer (≡ <i>Pseudorhiza minuscula</i> (Pau ex Font Quer) Lainz)	16			Daucus I	<i>Daucus</i>	Spiny	Portugal, Spain, Morocco
<i>Daucus mirabilis</i> (Maire and Pamp.) Reduron et al. (≡ <i>Pachytenium mirabile</i> Maire and Pamp.)	–			Daucus I	<i>Daucus</i>	Spiny winged proximally, naked dorsally	Libya
<i>Daucus dellacellae</i> (E. A. Durand and Barratte) Spalik et al. (≡ <i>Athamanta dellacellae</i> E. A. Durand and Barratte)	–			Daucus I	<i>Daucus</i>	Obsolete	Libya
<i>Daucus elegans</i> (Webb ex Bolle) Spalik et al. (≡ <i>Cryptotaenia elegans</i> Webb ex Bolle)	16			Macronesian	<i>Daucus</i>	Obsolete	Canary Islands
<i>Daucus decipiens</i> (Schrad. and J. C. Wendl.) Spalik et al. (≡ <i>Melanoselinum decipiens</i> Schrad. and J. C. Wendl. (≡ <i>Melanoselinum decipiens</i> (Schrad. and J. C. Wendl.) Hoffm.)	–			Macronesian	<i>Melanoselinum</i>	Winged	Madeira
<i>Daucus edulis</i> (Lowe) Wojew. et al. (≡ <i>Monizia edulis</i> Lowe)	22			Macronesian	<i>Melanoselinum</i>	Winged	Madeira
<i>Daucus incognitus</i> (C. Norman) Spalik, Reduron and Banasiak, comb. nov. ≡ <i>Caucalis incognita</i> C. Norman ≡ <i>Agrocharis incognita</i> (C. Norman) Heywood and Jury	44			Agrocharis	<i>Agrocharis</i>	Spiny	Tropical Africa
<i>Daucus melananthos</i> (Hochst.) Reduron, Spalik and Banasiak, comb. nov. ≡ <i>Agrocharis melanantha</i> Hochst.	–			Agrocharis	<i>Agrocharis</i>	Winged	Tropical Africa
<i>Daucus pedunculatus</i> (Baker f.) Banasiak, Spalik and Reduron, comb. nov. ≡ <i>Caucalis pedunculata</i> Baker f. ≡ <i>Agrocharis pedunculata</i> (Baker f.) Heywood and Jury in Lautert	–			Agrocharis	<i>Agrocharis</i>	Winged	Tropical Africa
<b>Possibly <i>Daucus</i> but not yet examined with molecular data</b>							
<i>Agrocharis gracilis</i> Hook. f.	–			Unknown	Unknown	Spiny	Tropical Africa
<i>Daucus dellacellae</i> (Asch. and Barbey ex E. A. Durand and Barratte) Spalik, Banasiak and	22			Unknown	Unknown		Libya

(continued)



**Table 2.1** (continued)

Taxon	2n	Heywood (1978)— sections within <i>Daucus</i>	Sáenz Lain (1981)— sections within <i>Daucus</i>	Clade (Arbizu et al. 2014b, 2016b; Banasiak et al. 2016)	Banasiak et al. (2016)— sections within <i>Daucus</i>	Fruit type— morphology secondary ribs (Banasiak et al. 2016)	Countries of occurrence
<i>Reduron</i> , comb. nov. ≡ <i>Athamanta dellacellae</i> Asch. and Barbey ex E. A. Durand and Barratte	—						
<i>Daucus jordanicus</i> Post	—	<i>Daucus</i>	<i>Daucus</i>	Unknown	Unknown	Spiny	Libya, Israel, Jordan
<i>Daucus microscius</i> Borrm. and Gauba	—			Unknown	Unknown	Spiny	Iran, Iraq
<i>Daucus reboudii</i> Coss.	—			Unknown	Unknown	Spiny	Algeria, Tunisia
<i>Tornabenea bischoffii</i> J. A. Schmidt	—			Unknown	Unknown	Winged	Cape Verde
<i>Tornabenea humilis</i> Lobin and K. H. Schmidt	—			Unknown	Unknown	Winged	Cape Verde
<i>Tornabenea ribeirensis</i> K. H. Schmidt and Lobin	—			Unknown	Unknown	Winged	Cape Verde

Drude 1897–1898). Winged fruits are considered to be adapted to wind dispersal (Jongejans and Telenius 2001; Theobald 1971), and spiny fruits to animal dispersal (Jury 1982; Spalik et al. 2001a; Williams 1994) and likely under strong selective pressure. The above phylogenetic analyses, however, show these fruit characters to be highly homoplastic and of limited value in delimiting monophyletic groups.

The above classification philosophy followed by Banasiak et al. (2016) in placing all members of a monophyletic clade into a single genus (here *Daucus*) is not universally accepted, and others may revise the circumscription of these genera. For example, a dissenting classification philosophy of relying solely on molecular data for classification is presented by Stuessy and Hörandl (2014), who recognize a “holophyletic” group as one that includes the immediate ancestor and all its descendants, independent of whatever divergence occurs within each of the derivative lineages (Ashlock 1971). A paraphyletic group, in contrast, is one that derives from a common ancestor but that does not contain all its descendants (Hennig 1966) and is an unacceptable taxon following cladistic conventions. Stuessy and Hörandl (2014) point out that adaptive radiation, common in oceanic islands, produces patterns where new populations continue to accrue reproductive isolation and speciation such that they produce quite distinctive new forms, often recognized as new genera, leaving parental populations intact. As examples in the Daucinae, Stuessy et al. (2014) cite the genus *Monizia* in the Madeira Islands, but other possibilities could be the genus *Tornabenea* or the species *Cryptotaenia elegans* on the Cape Verde Islands or the genus *Melanoselinum* on the Madeira Islands. Critical data bearing on this classification question rest in the distinctiveness and divergence of these new island forms. Because we have not studied these subsumed genera in detail, we currently take no position on these differences in classification, awaiting additional data and perspectives from others, such as Martínez-Flores (2016) and Plunkett et al. (in press) who maintain more traditional classifications of *Daucus*.

## 2.2 Distribution of *Daucus*

Phylogenetic analysis of ITS sequences supports southern Africa as the ancestral origin of the Apiaceae subfamily Apioideae (Banasiak et al. 2013). Phylogenetic analysis of ITS sequences supports an Old World Northern Hemisphere origin for *Daucus*, with one or two dispersals to the Southern Hemisphere (Spalik et al. 2010). The center of diversity of *Daucus* in its traditional sense is in the Mediterranean region (Sáenz Lain 1981). *Daucus* species also occur elsewhere, with one species (*D. glochidiatus*) in Australia, four species in the American continent (*D. carota*, *D. montanus*, *D. montevidensis*, *D. pusillus* Michx.). Following the expanded classification of *Daucus* by Banasiak et al. (2016), the now included genus *Agrocharis* extends the range of *Daucus* into tropical Africa (Townsend 1989).

## 2.3 New Taxonomic Approaches: Next-Generation Sequencing (NGS)

A major innovation in plant systematics is the development of high-throughput, “next-generation” DNA sequencing (NGS) to infer phylogenetic relationships (Egan et al. 2012; E. M. Lemmon and A. R. Lemmon 2013). NGS typically first involves large-scale sequencing of all components of the genome, with the Illumina platform currently the most commonly used. Some genomes, such as plastid and mitochondria, have much higher coverage than single- to low-copy nuclear DNA and can be factored out of the nuclear genome in NGS data by coverage statistics. The utility of NGS sequencing is markedly improved when a high-quality whole-genome “reference” sequence is available that serves as a heterologous template to guide mapping of sequences of related germplasm. Such whole-genome reference sequences are available in carrot for the plastid genome (Ruhlman et al. 2006) and for the plastid and nuclear genome (Iorizzo et al. 2016). As summarized below, recent phylogenetic studies in *Daucus* have used high-throughput DNA sequencing to infer phylogenetic relationships at the

genus level using orthologous nuclear DNA sequences, also at the genus level using whole plastid DNA sequences, and at the species level using genotyping-by-sequencing (GBS).

### 2.3.1 Next-Generation DNA Phylogenetic Studies at the Genus Level Using Orthologous Nuclear DNA Sequences

In the past, there has been a paucity of validated nuclear orthologs for phylogenetic studies, and hence, most molecular taxonomic studies have relied heavily on a few plastid and/or ribosomal genes (Small et al. 2004). Phylogenies reconstructed with only one or a few independently inherited loci may result in unresolved or incongruent phylogenies due to data sampling (Graybeal 1998), horizontal gene transfer, or differential selection and lineage sorting at individual loci (Maddison 1995). Following a phylogenetic study by Spooner et al. (2013) where eight nuclear orthologs were used in *Daucus* but designed without NGS techniques, Arbizu et al. (2014b) identified 94 nuclear orthologs in *Daucus*, constructed a phylogeny with these, and determined 10 of them to provide essentially the same phylogeny as all 94, paving the way for additional and most cost-effective nuclear ortholog phylogenetic studies in carrot. The 94 (and 10) nuclear ortholog phylogeny was highly resolved, with 100% bootstrap support for most of the external and many of the internal clades. They resolved multiple accessions of many different species as monophyletic with strong support, but failed to support other species. This phylogeny had many points of agreement with Banasiak et al. (2016), including resolving two major clades (*Daucus* I and II in their study, labeled clade A and B in Arbizu et al. 2014b), with a clade A' containing all examined  $2n = 18$  chromosome species (*D. carota* all subspecies, *D. capillifolius*, *D. syrticus*), with the other clade A species being *D. aureus* and *D. muricatus* (as sister taxa), and *D. tenuisectus*. Two non-*Daucus* species (*Rouya polygama* and

*Pseudorlaya pumila*) resolved sister to *Daucus* clade A'. Clade B (*Daucus* II in Banasiak et al. 2016) contained six wild *Daucus* species *D. glochidiatus*, *D. guttatus*, *D. involucratu*s, *D. littoralis*, and *D. pusillus*, but *D. guttatus* was not monophyletic within this clade.

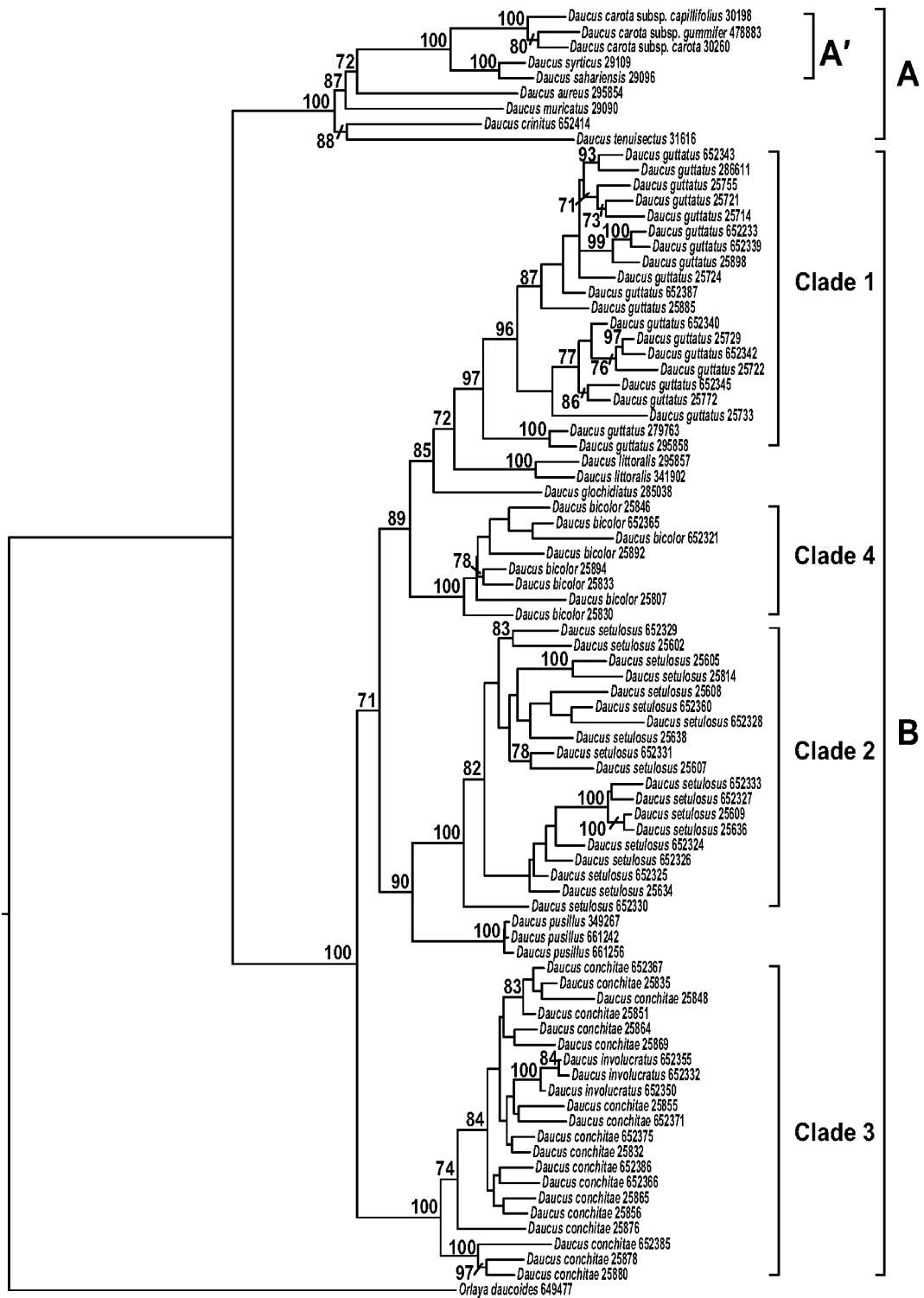
### 2.3.2 An Expansion of the Above Study—The *Daucus Guttatus* Complex

As mentioned above, the nuclear ortholog study of Arbizu et al. (2014b) resolved a monophyletic group (clade B) of six wild *Daucus* species *D. glochidiatus*, *D. guttatus*, *D. involucratu*s, *D. littoralis*, and *D. pusillus*. Some of these species are morphologically similar and difficult to distinguish, causing frequent misidentifications. Arbizu et al. (2016b) used the group of ten nuclear orthologs mentioned above in the study of Arbizu et al. (2014b), and morphological data (Arbizu et al. 2014a), and a greatly expanded subset of accessions of these species, to refine phylogenetic structure of the group. The nuclear ortholog data resolved four well-supported clades (Fig. 2.2), that in concert with morphological data, and nomenclatural data from a study of type specimens (Martínez-Flores et al. 2016) served to identify four phenetically most similar species *D. bicolor*, *D. conchitae*, *D. guttatus*, and *D. setulosus*. Internested among these four similar species were phenetically more distinctive species *D. glochidiatus*, *D. involucratu*s, *D. littoralis*, and *D. pusillus*. They presented a key to better distinguish all of these eight species. In summary, their research clarified species variation in the *D. guttatus* complex, resolved interspecific relationships, provided the proper names for the species, and discovered morphological characters allowing proper identification and key construction of members of the *D. guttatus* complex and related species.

### 2.3.3 Next-Generation DNA Phylogenetic Studies at the Genus Level Using Whole Plastid DNA Sequences

The plastid genome has many features that make it useful for plant phylogenetic studies, including its small size (generally 120–160 kbp), high copy number (as many as 1000 per cell), generally conservative nature (Wolfe et al. 1987), and varying rates of change in different regions of the genome, allowing studies at different phylogenetic levels (Raubeson and Jansen 2005). Hence, earlier sequence-based plant phylogenetic studies used genes or gene regions from the plastid. Relative to the Apiaceae, the subfamily of the Apiaceae including *Daucus*, systematic studies have used plastid restriction site data; DNA sequence data from plastid genes; from plastid introns; from plastid intergenic spacer regions. Using NGS sequencing approaches, Downie and Jansen (2015) sequenced five complete plastid genomes in the Apiales (Apiaceae + Araliaceae): *Anthriscus cerefolium* (L.) Hoffm., *Crithmum maritimum* L., *Hydrocotyle verticillata* Thunb., *Petroselinum crispum* (Mill.) Fuss, and *Tiedemannia filiformis* (Walter) Feist and S. R. Downie subsp. *greenmanii* (Mathias and Constance) Feist and S. R. Downie, and compared the results obtained to previously published plastomes of *Daucus carota* subsp. *sativus* and *Panax schin-seng* T. Nees. They discovered the *rpl32-trnL*, *trnE-trnT*, *ndhF-rpl32*, *5'rps16-trnQ*, and *trnT-psbD* intergenic spacers to be among the most fast-evolving loci, with the *trnD-trnY-trnE-trnT* combined region presenting the greatest number of potentially informative characters overall that may possess ideal phylogenetic markers in these families.

Spooner et al. (2017) explored the phylogenetic utility of entire plastid DNA sequences in *Daucus*, using Illumina sequencing, and

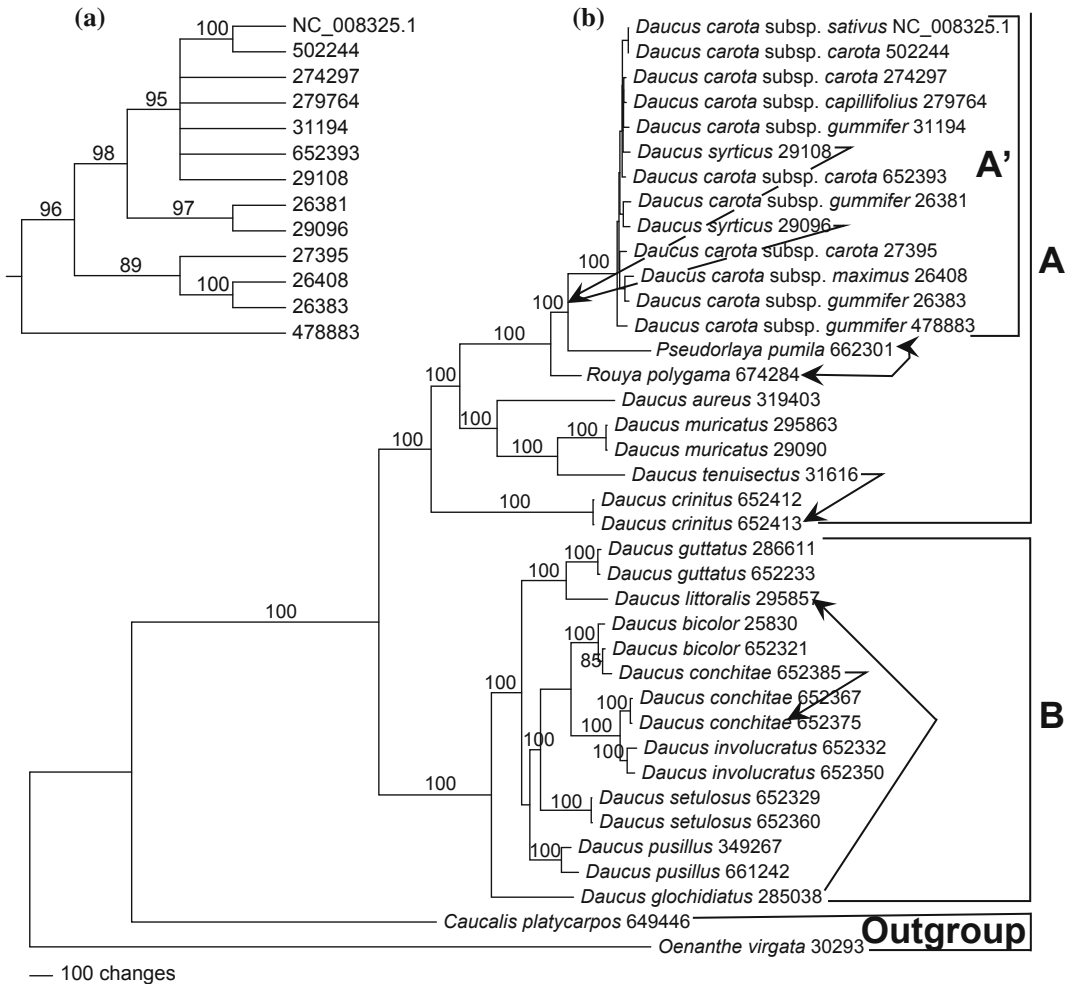


◀ **Fig. 2.2** Maximum parsimony phylogenetic reconstruction of the *Daucus guttatus* complex using 10 nuclear orthologs showing resolution of the species in the *Daucus*

*guttatus* complex. Numbers above branches represent bootstrap values. Clades 1, 2, and 3 were identified in Arbizu et al. (2014b)

compared the results with prior phylogenetic results using plastid and nuclear DNA sequences. The phylogenetic tree of the entire data set (Fig. 2.3) was highly resolved, with 100% bootstrap support for most of the external and many of the internal clades. Subsets of the plastid data, such as *matK*, *ndhF*, or the putative maximally informative regions of the plastid genome

outlined by Downie and Jansen (2015) are only partly successful in *Daucus*, resulting in polytomies and reduced levels of bootstrap support. Additionally, there are areas of hard incongruence (strongly supported character conflict because of differences in underlying evolutionary histories) with phylogenies using nuclear data (Fig. 2.1).



**Fig. 2.3** Maximum likelihood cladogram of the entire plastid DNA sequences of Spooner et al. (2017), with the three main clades indicated, with arrows highlighting hard topological incongruence with the nuclear ortholog phylogenies of Arbizu et al. (2014b, 2016b); the two

accessions of *Daucus syrticus* resolve as a sister group to all accessions of *D. carota*. **a** Represents expanded topological detail of the upper portion of the entire tree shown on **b**. The values above the branches are bootstrap support values

Incongruence between plastid and nuclear genes are not uncommon in phylogenetic studies in the Apiaceae (e.g., Lee and Downie 2006; Yi et al. 2015; Zhou et al. 2009), indeed throughout many angiosperms (Wendel and Doyle 1998). These incongruent results showed the value of resequencing data to produce a well-resolved plastid phylogeny of *Daucus*, and highlighted caution to combine plastid and nuclear data, if at all. The value of generating phylogenies from both nuclear and plastid sequences is that hard incongruence can be quite informative, suggesting such evolutionary processes as “plastid capture” where incongruence can be caused by a history of hybridization between plants with differing plastid and nuclear genomes (Rieseberg and Soltis 1991), and backcrossing to the paternal parent but retaining the plastid genome that is (typically) maternally inherited. Other possible processes that can lead to such incongruence, however, are gene duplication (Page and Charleston 1997), horizontal gene transfer (Doolittle 1999), and incomplete lineage sorting (Pamilo and Nei 1988).

### 2.3.4 Next-Generation DNA Phylogenetic Studies at the Species Level—Genotyping-by-Sequencing (GBS) for the *Daucus Carota* Complex

The genus *Daucus* contains cultivated carrot (*Daucus carota* L. subsp. *sativus* Hoffm.), the most important member of Apiaceae in terms of economic importance and nutrition (Rubatzky et al. 1999; Simon 2000), and is considered the second most popular vegetable worldwide after potato (Heywood 2014). *Daucus carota* has many formally named subspecies and varieties, and the species is widely naturalized in many countries worldwide. The great morphological variation in *D. carota* has resulted in more than 60 infraspecific taxa, making *D. carota* the most problematic species group in the Apiaceae (Heywood 1968a, b; Small 1978; Thellung 1926). Cultivated carrots and closely related wild

carrots (other subspecies and varieties of *D. carota* sensu lato) belong to the *Daucus carota* complex. Its constituent taxa all possess  $2n = 18$  chromosomes and have weak biological barriers to interbreeding. *D. carota* undergoes widespread hybridization experimentally and spontaneously with commercial varieties of carrot and the wild subspecies of *D. carota* (e.g., Ellis et al. 1993; Hauser 2002; Hauser and Bjørn 2001; Krickl 1961; McCollum 1975, 1977; Nothnagel et al. 2000; Rong et al. 2010; Sáenz de Rivas and Heywood 1974; Steinborn et al. 1995; St. Pierre and Bayer 1991; St. Pierre et al. 1990; Umiel et al. 1975; Vivek and Simon 1999; Wijnheijmer et al. 1989). In addition, there are other closely related wild species with  $2n = 18$  chromosomes (*D. sahariensis*, *D. syrticus*) based on shared karyotypes (Iovene et al. 2008), the genus-level phylogenetic studies summarized above, and they represent gene pool 1 species to cultivated carrot. The haploid chromosome number for the genus *Daucus* (sensu stricto) ranges from  $n = 8$  to  $n = 11$ . In addition to the  $n = 8$  diploid species, diploid chromosome numbers in *Daucus* range from  $2n = 16$  to  $22$ , and a tetraploid (*D. glochidiatus*) and a hexaploid (*D. montanus*) species have been reported (Table 2.1).

To put the taxonomic problem of the *Daucus carota* complex into historical context, several molecular approaches have examined its diversity and genetic relationships. St. Pierre et al. (1990) used isozymes to study 168 accessions of the *D. carota* complex from 32 countries and could not separate named subspecies into distinct groups. Nakajima et al. (1998) used random amplified polymorphic DNA (RAPD) and amplified fragment length polymorphism (AFLP) data and showed all accessions of *D. carota* group into a major clade. Vivek and Simon (1998, 1999) used restriction fragment length polymorphisms (RFLPs) of nuclear, plastid, and mitochondrial DNA and interpreted their results to be generally concordant with the classification proposed by Sáenz Laín (1981), but studied just one additional subspecies (subsp. *drepanensis*). Using AFLPs, Shim and Jørgensen (2000) showed wild and cultivated carrot clustered separately. Bradeen et al. (2002) used AFLPs and