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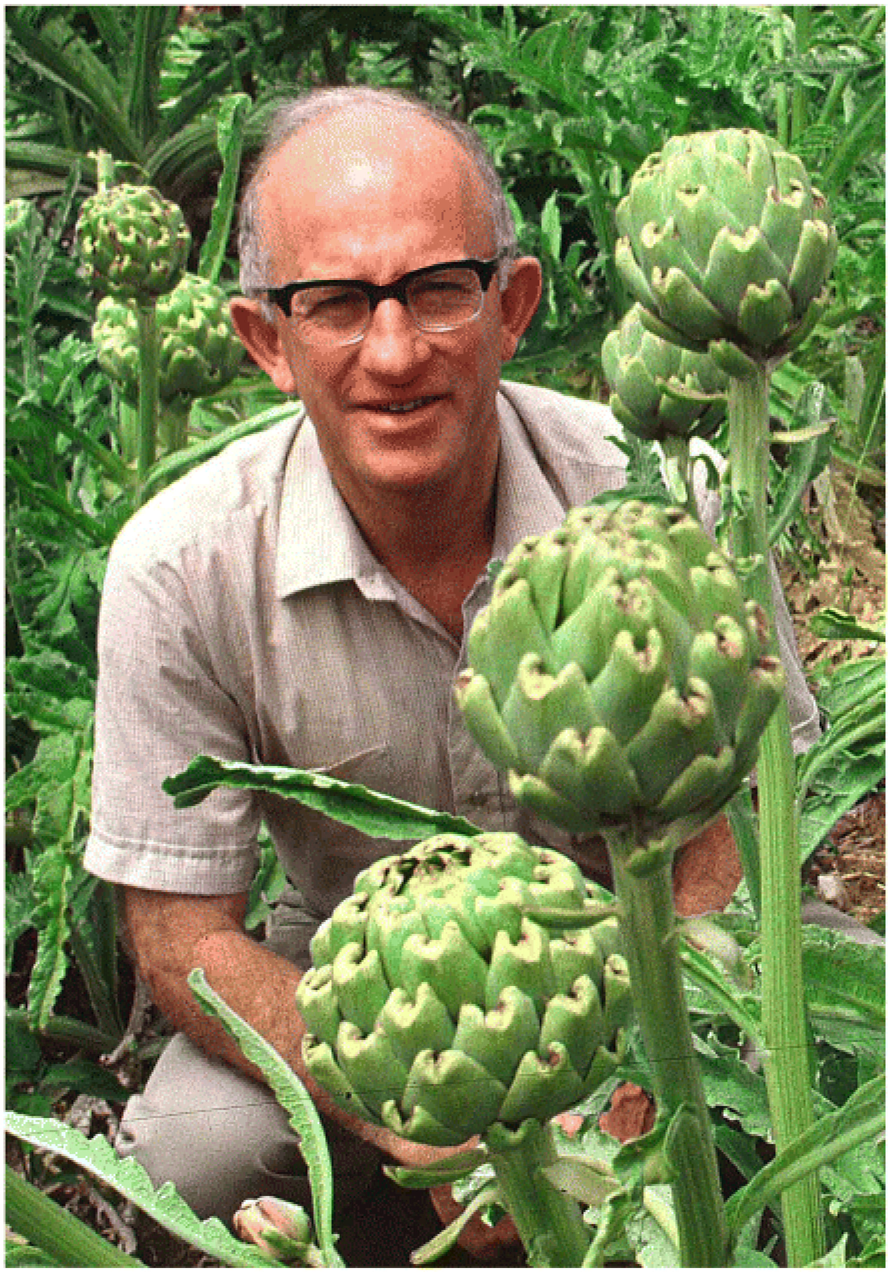

Daniel Zohary

1
Daniel Zohary: Geneticist and Explorer of Plant Domestication

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Daniel Zohary is a botanist, geneticist, and cytogeneticist. He occupies the middle link in a dynasty of three professors of biology at the Hebrew University of Jerusalem. His father, Michael Zohary, was a renowned botanist who laid the foundation to comprehensive accounts and documentation of the Flora of Israel, whereas Daniel's son, Ehud Zohary, is a neurobiologist specializing in functional magnetic resonance imaging of the brain. Professor Zohary (known to all in Israel as Danny) is mostly recognized as an explorer of plant domestication and of the rise of agriculture and Neolithic settlements in the Fertile

Crescent. His research and long career are marked by the employment of expertise from different scientific disciplines, such as botany, cytogenetics, population genetics, ecology, and archaeology, and the synthesis of findings obtained in these fields into a coherent evolutionary description of the rise of agriculture. Danny has published more than 100 peer-reviewed papers; unlike most of his colleagues, he was also able to summarize his life work in a comprehensive book on plant domestication, which was published in four successful editions (Zohary and Hopf 1988, 1993, 2000; Zohary et al. 2012).

I. Early Days

Danny Zohary was born in Jerusalem in 1926. As a teenager with a botanist father, Danny became familiar with the rich flora of the Holy Land and the Middle East and, as a student, already started to look into relationships between plant species, at the level of plant communities and their interaction with ecological factors, and over time, as evolutionary relationships. As an undergraduate student in Botany and Geology at the Hebrew University, Zohary's studies were interrupted in 1947–1949 by his active participation in the Israeli War of Independence; eventually he graduated in 1951. In 1952 he started his Ph.D. studies at the University of California, Berkeley, where his scientific interests took him in two parallel and equally productive directions. For his thesis work with G. Ledyard Stebbins, he investigated the relationships between diploid and tetraploid forms of *Dactylis glomerata*, a common Mediterranean grass. The *Dactylis* complex provided a good example of the success of autotetraploidy, as well as of diploid–tetraploid hybrids and gene flow in natural populations, and the prevalence of supernumerary chromosomes. These studies continued upon Zohary's return to Israel in 1956, and subsequently he became one of the world's experts on polyploidy (both auto- and allopolyploidy), following his mentor Stebbins. The second line of research Zohary undertook while being a graduate student at Berkeley was that of cytogenetics of meiosis in plants, under the guidance of Spencer W. Brown. The most important outcome of these studies was the proof that cytologically observed chiasmata in lily and in maize resulted from previously occurring crossing over events (Brown and Zohary 1955; Zohary 1955), in contrast to the alternative interpretation that chiasmata resulted from overlapping chromatids, which provided opportunities for crossover events (that subsequently did or did not take place).

In the following years, Zohary's interests and academic activities continued along three main tracts of plant biology and agriculture: (i) the genetic relationships among closely related plant species and populations, (ii) the domestication of various crops and fruit trees in view of their genetic relationships with wild relatives, and (iii) the interface between crop evolution and human societies as shown by archeological findings and the impact these findings had on the origin of agriculture and on human evolution (Fig. 1.1).

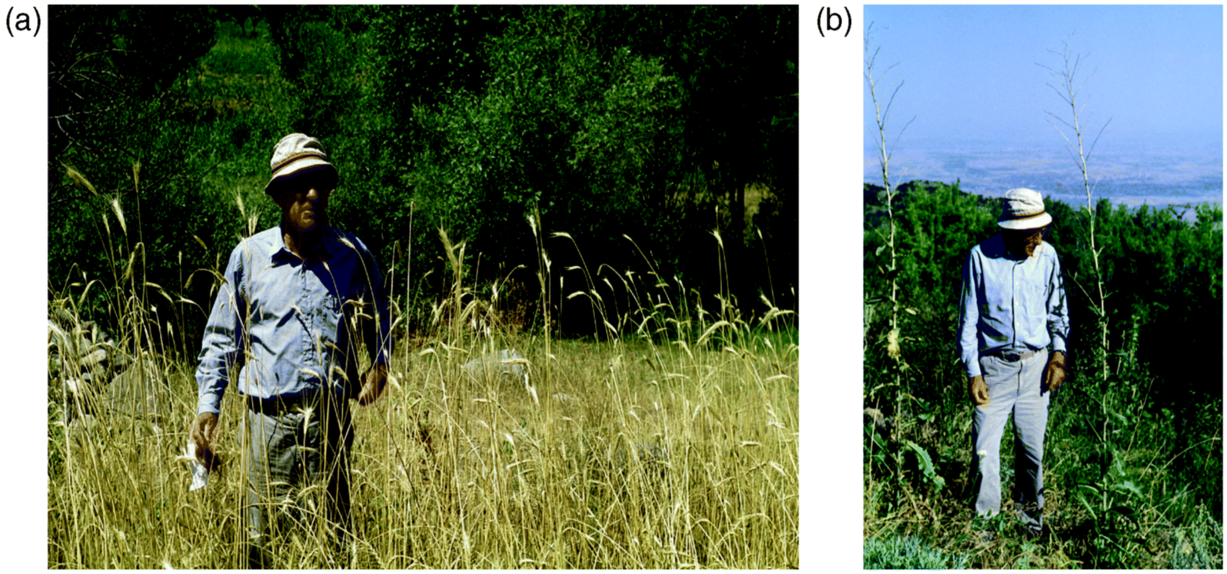

Fig. 1.1 Daniel Zohary collecting wild relatives of domesticated plants. (a) Wild rye (*Secale*) in Turkey, late 1990s. (b) Wild lettuce (*Lactuca*) in Georgia, late 1990s.

II. Genetic Relationships Among Related Plant Species

Zohary's Ph.D. thesis with Stebbins at Berkeley dealt with the *Dactylis glomerata* species complex, which consists of diploid and tetraploid populations across the Mediterranean Basin and the Near East. In locations in Israel where diploid and tetraploid plants coexisted, natural triploid hybrids were found (Zohary and Nur 1959). Plants introduced from wild populations were crossed to each other and their progeny were thoroughly examined cytologically and morphologically. Many diploid plants also contained up to three supernumerary chromosomes, and in some populations, their frequency reached 50% (Zohary and Ashkenazi 1958). Although *D. glomerata* (orchard grass) is an important forage plant, Zohary's interests soon shifted to Mediterranean genera that included the most important crops associated with the rise of agriculture, namely, wheat, barley, oats, peas, and lentils.

In the *Triticum–Aegilops* wheat group, Zohary and his students (Zohary and Feldman 1962; Feldman 1965; Pazy and Zohary 1965) investigated genetic relationships and natural hybridization among the tetraploid species ($2n$ = 28) of the Pleionathera section, which share the C^U genome; the most abundant species in this group in Israel are *Aegilops variabilis*, *Aegilops ovata*, and *Aegilops biuncialis*. The authors concluded that in addition to the common diploid genome, each of these species carries another genome that has been thoroughly modified by hybridization and introgression with neighboring species of the same group. The diploid outbreeding species *Aegilops speltoides* ($2n$ = 14, carrying the S genome) and the selfer *Aegilops longissima* (S^1 genome) were both shown to exist as mixed populations, consisting of *speltoides* and *ligustica* plants in *Ae. speltoides*, and *longissima* and *sharonensis* plants in *Ae. longissima* (Ankory and Zohary 1962; Zohary and Imber 1962); natural intercrossing within each pair was demonstrated in these studies. In other cereals, natural hybridization and evidence for genetic introgression were found between *Hordeum spontaneum* and the cultivated barley, *Hordeum vulgare* (Zohary 1959; Tovia and Zohary 1962), as well as among diploid, tetraploid, and hexaploid barley (*Avena*) species (Ladizinsky and Zohary 1968, 1971).

One significant feature common to most of these natural cases of hybridization and introgression was their occurrence in human-disturbed habitats, where new ecological niches were available to the hybrids and their descendants. In later years, Zohary collaborated with Eviatar Nevo and his colleagues and with plant pathologists, on evaluation of genetic variation in plant populations in such human-interfered habitats. Thus, for instance, allozyme variation and disease resistance genes were investigated in natural populations of wild barley and

Emmer wheat, in relation to their ecology and interaction with the corresponding cultivated crops (Nevo et al. 1979, 1982; and numerous other joint publications).

III. Domestication of Crops and Fruit Trees

The major contributions of Daniel Zohary, for which he is most widely known, relate to the domestication of plants in the Old World and the role of plant domestication in the origin and rise of agriculture and of organized human society. There were numerous studies by Zohary and his associates on these issues that were later summarized in *Domestication of Plants in the Old World*, published by Oxford University Press in four editions. This book will be discussed in a later section of this chapter. Here we shall only highlight major findings by Zohary and colleagues in this area, and the interested reader may refer to the recent edition of the book for further details.

The seminal publication in this area was that of Harlan and Zohary (1966), which analyzed the distribution of wild barley (*H. spontaneum*, $2n = 14$), diploid Einkorn wheat (*Triticum boeticum*, $2n = 14$), and tetraploid Emmer wheat (*Triticum dicoccoides*, $2n = 28$) in the Near East. The authors showed that the geographical distribution of these plant populations overlaps the earliest known sites of Neolithic farming in the area known as the Fertile Crescent, and may well have been the sites where agricultural practices were first employed. These cereals were probably first harvested in dense stands of the wild plants and subsequently, ~10,000 years ago, used for seed stocks; thus started the development of agricultural practices and the establishment of Neolithic communities. Agricultural domestication, however, was also associated with genetic changes in the plants that facilitated the collection of seed (harvesting). Thus, domestication of barley and wheat involved selection for nonbrittleness of the spikes, a characteristic of clear disadvantage to the ancestral wild plants because it compromises seed dispersal. Moreover, a significant insight into the occurrence of present-day dense stands of these wild cereals is that they are found in relatively undisturbed ecological habitats, at the centers of distribution of the species, and their robust morphology (along with large grain) suggests that they could indeed be profitably harvested by man before they were fully domesticated. At the perimeter of distribution of these wild cereals, more weedy races occupy largely disturbed habitats; these do not form continuous stands, and therefore Harlan and Zohary (1966) suggest that they were less likely to have attracted the attention of ancient humans at the onset of agriculture.

Zohary collaborated with the German botanist/archaeologist Maria Hopf on the study of the origin of cultivated legumes (pulses). Their conclusions about domestication of pulses (Zohary and Hopf 1973) were based largely on carbonized seed remains at the sites of early Neolithic farming villages in the Near East, as well as on cytogenetics and on crosses in the laboratory between the cultivated and wild relatives, and on the occasional finding of wild populations containing plants of intermediate morphologies. Thus, it was determined that cultivated pea, *Pisum sativum*, probably originated from *Pisum humile* or *Pisum elatius* (Ben-Zeev and Zohary 1973), and lentil (*Lens culinaris*) may have originated from *Lens orientalis* (Zohary 1972; Garfinkel et al. 1988). The conclusions regarding the origins of broad bean and chickpea were however more tentative (Zohary and Hopf 1973).

The artichoke (*Cynara scolymus*) is another crop that was thoroughly investigated by Zohary and colleagues regarding its origin and domestication (Zohary and Basnizky 1975; Rottenberg and Zohary 1996). These studies led to the transformation of artichoke from a perennial, vegetatively propagated crop into an annual, seed-planted vegetable, adjusted to modern, mechanized cultivation and new successful cultivars (Basnizky and Zohary 1987, 1994) as shown in the frontpiece photograph taken in the 1990s.

Several important fruit trees originated from wild species still found in the Near East, and thus Zohary's attention naturally focused on the olive, grape, date, and fig (Zohary and Spiegel-Roy 1975). Domestication of all four fruit trees was associated with changes in their breeding behavior, especially the adoption of vegetative propagation. Numerous archaeological remains suggest that domestication of these fruit trees took place several thousands of years after the establishment of Neolithic agriculture in the Near East, which was originally based on cereals (wheat and barley) and pulses (pea and lentil). Zohary also published numerous articles on the wild relatives and domestication of other fruit trees, including plum (Zohary 1992), almond (Browicz and Zohary 1996; Zohary 1998), pistachio (Zohary 1996), wild apple and pear (Zohary 1997), and carob (Zohary 2002).

IV. The Scientific Approach and Methodology of Daniel Zohary

Danny Zohary's successful scientific career was largely based on his unusual combination of interests and expertise, which originated in his family background as well as in his early academic training. As a boy he became a competent field botanist, learning plant systematics from his father Michael Zohary, who was an expert on the rich flora of Israel and the Near East. At an early age he could identify most plants in their natural habitats and acquired a profound understanding of the roles different species had in the so-called plant community, consisting of various species that commonly associate with each other and are usually found together in a defined habitat, of a unique ecology. As a student at the Hebrew University of Jerusalem in the late 1940s and early 1950s, Danny majored in Botany and Geology, wrote his MSc thesis on plant communities in the Negev Desert, and published the first vegetation map of the Negev. When he went to Berkeley in the 1950s, Zohary became a real geneticist. He learned cytogenetics from Spencer Brown and plant evolution (especially polyploidy) from G. Ledyard Stebbins, his Ph.D. adviser. This unique combination of skills was the foundation for his prolific scientific work in the subsequent 50–60 years.

Later in his career, Zohary added to his arsenal other scientific tools and approaches that he acquired through collaboration with prominent archaeologists, notably the late Maria Hopf. He thus arrived at a novel understanding of plant domestication by ancient humans, which was primarily based on the unconscious selection of genetic characteristics in crops and trees, which enabled the latter to economically sustain settled human communities. This thesis explained the transformation of nomad groups of food gatherers (and hunters) into people primarily engaged in agriculture. Zohary and colleagues later extended this principle of unconscious selection to the domestication of animals (sheep and goats) (Zohary et al. 1998).

Zohary also collaborated extensively with plant breeders, especially on artichoke breeding (Basnizky and Zohary 1987, 1994) and on cultivation of anemones (*Anemone* *coronaria*), which became one of the most common ornamental flowers grown in Israel (Horovitz et al. 1975).

V. The Book

The magnus opus *Domestication of Plants in the Old World* may be regarded as the culmination of Danny Zohary's scientific work, as it summarizes his most important papers, as well as those of his colleagues in this field. His collaboration with Maria Hopf started as a joint paper in *Science* on the domestication of pulses (Zohary and Hopf 1973), but soon the additional insight into issues of plant domestication that came from archaeological findings won Zohary's attention and keen interest. He felt that plant domestication and the rise of agriculture involved several steps of unconscious manipulation by humans. In this way desirable traits were selected, and the plants that were chosen and propagated were also modified in important aspects of their genetics, especially regarding the breeding systems and dispersal mechanisms. Subsequently, the chosen plants underwent improvement of their nutritional characteristics and adaptation to the cultivation routines used by the settled human communities, and thus started agriculture. In the four editions of the book, Zohary and his coauthors Maria Hopf and Ehud Weiss tried to understand and follow domestication of each agricultural plant in the Old World, based on the genetic and ecological evidence on the one hand and on a huge amount of archaeological findings on the other. Each edition is a major revision of the previous one and reflects the rapid progress in the field during the period between 1988 and 2012, and the accumulation of new findings in the fields pertinent to the book. The full name of the book (4th edition) is *Domestication of Plants in the Old World: The Origin and Spread of Domesticated Plants in South-West Asia, Europe,* *and the Mediterranean Basin*. The syntheses arrived at by the authors for so many domesticated species are most enlightening and make the reader comprehend that domestication and the rise of agriculture were not merely chance events, but rather the products of predictable interactions between ancient humans and the plant species around them.

The seven major chapters of the book (4th edition) are entitled “Cereals,” “Pulses,” “Oil- and Fibre-Producing Crops,” “Fruit Trees and Nuts,” “Vegetables and Tubers,” “Condiments,” and “Dry Crops” (dye plants). A detailed section is presented on each domesticated species. Thus, in the chapter dealing with pulses, there are separate sections on lentil, pea, chickpea, faba bean, bitter vetch, common vetch, grass pea, Spanish vetchling, fenugreek, and lupins. Preceding the major chapters of the book, there are two important introductory chapters. The first is entitled “Current State of the Art” and consists of a summary of the findings and of the authors' views on plant domestication. The second chapter presents the methodologies used to study plant domestication.

These chapters give a detailed analysis of archaeological findings and of studies of present-day domesticated plants and their wild progenitors; the studies employ methods of genetics and cytogenetics, DNA marker variation, and geographical distribution of the supposed progenitors in relation to the archaeological sites in which domesticated plant remains were found. The last chapter of the book summarizes the information on domesticated plant remains retrieved from individual Neolithic and Bronze Age sites in the Mediterranean and European areas. All in all, it is a very important book in the field of plant domestication, which will be used by researchers in the field for a long time to come.

VI. Awards, Honors, and Recognition

Danny has always been fully devoted to his research and scientific work. He was appointed Lecturer at the Hebrew University of Jerusalem in 1956, rose through the ranks and became Professor of Genetics in 1969, and retired in 1997. He was elected Chairman of the Institute of Life Sciences at the Hebrew University and served for a brief period (1979–1983), but did not really enjoy this largely administrative role. Zohary was not after prizes and awards, although he received the J. Belling Award in Genetics from the University of California, Berkeley (1959), and was elected Distinguished Economic Botanist by the Society for Economic Botany (2003). He has been a member of several learned societies, including being a Fellow of the Linnean Society, London.

Daniel Zohary is recognized as a world leader in the field of plant domestication, largely due to the visibility and impact of his comprehensive book mentioned above (Zohary et al. 2012). Zohary's work served as the basis for descriptions of the rise of agriculture in Jared Diamond's (1997) Pulitzer Prize-winning book *Guns, Germs, and Steel* and it strongly influences the accounts therein of plant domestication by humans in the Fertile Crescent (p. 134–146 and 180–183) and of individual crops (development of nonbitter almonds, p. 118–119, of edible peas, p.120, and of nonshattering wheat and barley, p. 120–121). Indeed, in the *Further Readings* section recommended by Diamond (1997, p. 435), one finds the following statement: “Among references specifically about plant domestication, Daniel Zohary and Maria Hopf, *Domestication of Plants in the Old World*, 2nd ed. (Oxford: Oxford University Press, 1993), stands out. It provides the most detailed account of plant domestication available for any part of the world.”

VII. Personality

Danny's boyish appearance and enthusiasm remained part of his personality until advanced age. Even as an established field botanist, his Jeep-mounted expeditions were legendary. He would identify interesting specimens in the field while driving the vehicle, and on a couple of occasions almost caused road accidents by abruptly stopping and running out of the Jeep to look at suspected plants. Some of these field trips were very extensive and took several weeks, during which vast territories were covered, in Turkey, Iran, Armenia, and Georgia (Fig. 1.1). As an MSc student, this writer participated in one of Danny's earliest expeditions to Greece and Turkey in 1962, which lasted 45 days and extended to the eastern borders of Turkey. Other participants were Professor Michael Zohary and Moshe Feldman, a Ph.D. student in Danny's laboratory. This was a most rewarding experience, from which all four of us gained insight into the biology of populations of wild relatives of major crops, and initial understanding of the processes of plant domestication, which Daniel Zohary later elaborated on and developed further.

Among Zohary's numerous ex-students, several have developed successful careers in plant breeding and genetics in Israel: Moshe Feldman, Gideon Ladizinsky, Aliza Vardi, Eli Putievski, Jossi Hillel, and Giora Simchen.

Danny married in 1949 to Devora and they had three children. Their eldest child Tamar Zohary is an aquatic microbial ecologist with the Israel Oceanographic and Limnological Research Institute, Ruth (Zohary) Shouval is an artist in Texas, and Ehud Zohary is a neurophysiologist at the Hebrew University of Jerusalem, specializing in vision. Danny has six grandchildren and two great-grandchildren. Devora died of cancer in 1976, and a few years later, Danny married Lilly, with whom he has been living happily in Jerusalem for the past 35 years (Fig. 1.2).

Fig. 1.2 Daniel Zohary with his wife Lilly, 2007.

Unfortunately, Daniel Zohary is no longer active in research and in academic affairs. The heritage he has left us is evident, however, in his scientific publications, his book, and the impact he has had on the field of plant domestication and evolution.

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