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68

Onion and other cultivated alliums

Allium spp. (Liliaceae)

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Introduction

The genus *Allium* contains seven cultivated species of economic importance: the bulb onion (*A. cepa*), the closely related shallot (*A. cepa* var. *ascalonicum*), potato onion (*A. cepa* var. *aggregatum*), chive (*A. schoenoprasum*), Chinese chive (*A. tuberosum*), Japanese bunching onion (*A. fistulosum*), garlic (*A. sativum*), leek (*A. ampeloprasum* var. *porrum* syn. *A. porrum*), and rakkyo (*A. chinense*). In addition, Fenwick and Hanley (1985) list eighteen other *Allium* species that are consumed as a fresh vegetable, pickled or used as flavouring. The distinctive flavour or odour of the alliums occur when plant tissue is bruised, cut, or macerated and the enzyme alliinase hydrolyses *S*-alk(en)yl cysteine sulphoxide precursors to yield volatile sulphur compounds. Onion and garlic possess many traditional medicinal uses and have been used to treat many ailments, e.g. chicken-pox, the common cold, influenza, measles, rheumatism and others (Fenwick and Hanley, 1985). Antimicrobial characteristics of the alliums are probably due to the interaction of sulphur compounds in the plant with the microbes. Objective research has established that onion and garlic extracts lower sugars, lipids, and platelet aggregation and enhance fibrinolysis in the blood (Augusti, 1990). As a result, the alliums may help to prevent atherosclerosis and other diseases of the heart.

The bulb onion is the most valuable allium with a total world production in 1989 of approximately 27 Mt (FAO, 1990). The importance of the bulb onion in the diet of a wide range of cultures is reflected by the greatest overall production occurring in the most populous countries, e.g. in 1987 China (3.6 Mt), India (2.8 Mt), and the former USSR and the USA (2.0 Mt each) were the leading producers. In 1989, world-wide production of garlic was about 10 per cent that of the bulb onion (3.0 Mt). Leek and the Japanese bunching onion are the next most valuable alliums with production concentrated in Europe and the Orient respectively.

Cytotaxonomic background

The genus *Allium* is a very diverse taxon with over 600 species (Traub, 1968) and has been assigned to the Amaryllidaceae, Liliaceae and a distinct family, the Alliaceae (Hanelt, 1990). Confusion over what constitutes a distinct morphological character has resulted in classification of closely related types as separate species. Shallot was once classified as a separate species (*A. ascalonicum*) and has now been reduced to *A. cepa* var. *ascalonicum*. Likewise, leek, kurrat and great-headed garlic (originally classified as *A. porrum, A. kurrat*, and *A. giganteum* respectively) have been reclassified as *A. ampeloprasum* var. *porrum, kurrat* and *holmense* respectively.

Habitats of members of the genus are concentrated in northern temperate zones, comprising the Eurasian continent, North Africa and North America. The greatest number of *Allium* species are found in North Africa and Eurasia and over 90 per cent have a basic chromosome number of 8 (Fig. 68.1). More than 95 per cent of the North American *Allium* species have a basic chromosome number of 7 (Traub, 1968). All economically important cultivated alliums have a basic chromosome number of 8. The bulb onion, potato onion, shallot, garlic and Japanese bunching onion are diploid ($2n = 2x = 16$). Chinese chive, kurrat and leek exist primarily as tetraploids ($2n = 4x = 32$). Chive and rakkyo comprise a polyploid series with diploid, triploid and tetraploid forms; the cultivated forms of chive and rakkyo are diploid and tetraploid respectively. Great-headed garlic exists as a tetraploid and hexaploid ($2n = 6x = 48$).

Stearn (1944) described the history of *Allium* taxonomy. Detailed scientific descriptions of *Allium* began in 1601 with Clusius's *Rariorum Plantarum Historis*. Clusius travelled about central and southern Europe and wrote accurate accounts of more *Allium* species than any of his predecessors. However, he

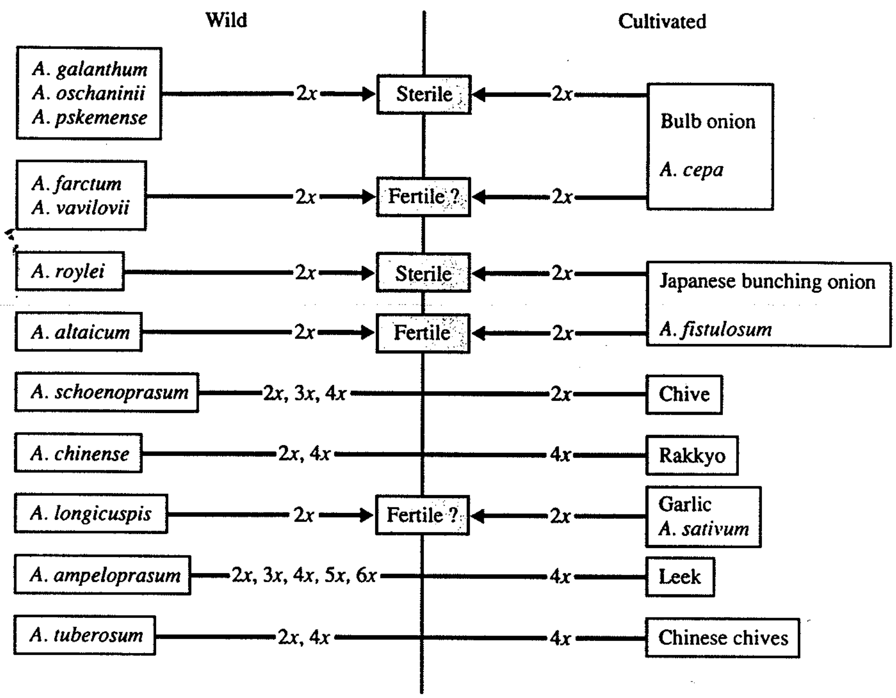

Fig. 68.1 Germplasm introgression from wild to cultivated alliums. Basic chromosome number (x) = 8.

considered the cultivated alliums (bulb onion, chive, garlic, and leek) to be too common and excluded them from his treatise. Early taxonomists working after Clusius placed the onion, leek, and garlic into different genera. Haller was responsible for collecting all alliaceous plants into one group. In 1745, Haller published a monograph on *Allium*, recognizing the synonymy of some species and combining them under a single name. Linnaeus built upon the work of Clusius and Haller and described 31 *Allium* species in detail. The next major taxonomic description of *Allium* was in 1832 by Don, who described 129 species in considerable detail; however, many species have since been combined. In 1875, Regel described 262 species of *Allium* including many new species from collections in Turkestan, a region rich in diversity for *Allium* and thought to be the centre of origin for the bulb onion. *Allium* species from the eastern Mediterranean region to India were described in 1882 by Boissier, who described 141 species and added new ones to the growing genus.

A detailed description of *Allium* in the former Soviet Union was published by Vvedensky (1944), a botanist who worked in Tashkent near the mountains where *Allium* reaches its greatest diversity in the Old World. Vvedensky presented accurate descriptions of 228 species, including 40 new *Allium* species, and fitted them into a logical framework. However, the policy of Russian taxonomists of the Komarov school was to designate a separate species for all populations possessing consistent inherent features, no matter how closely related (Stearn, 1944; Hanelt, 1990). Therefore, many of Vvedensky's species may correspond to subspecies or varieties. The bulb onion exists only in cultivation and may have originated in the area now comprising Afghanistan, Iran and the southern former Soviet Union (Jones and Mann 1963). Vvedensky's classification is important because onion has no clear progenitor and he identifies closely related wild species. The bulb onion was placed in section *Cepa* with *A. galanthum, A. oschaninii, A. pskemense* and *A. vavilovii*. The grouping of the bulb onion with these wild species has been supported by geography, serology of seed proteins, numerical taxonomy, karyotypes and the banding patterns of esterases (Hanelt, 1990). Another species *A. farctum*, from Afghanistan and west Pakistan (Wendelbo, 1969), was not included in Vvedensky's classification and may be an additional wild species closely related to the bulb onion. Although *A. cepa* and these wild *Allium* species may have arisen from a common progenitor, the high sterility/low fertility exhibited by interspecific hybrids indicates that their use in the genetic improvement of the bulb onion will be difficult (Fig. 68.1). Embryo rescue has successfully increased the numbers of progeny from interspecific hybridizations, but the hybrids show a high degree of sterility (Novak *et al.*, 1986).

Allium fistulosum also exists only in cultivation and may have originated in central China. Vvedensky placed the Japanese bunching onion in section *Phyllodolon* with *A. altaicum* and *A. microbulbum* Hanelt (1990) described *A. microbulbum* as an obscure species that may be extinct. *Allium altaicum* is a wild species indigenous to Mongolia and Siberia and may be a wild form of *A. fistulosum* (McCollum, 1976). Hybrids have been successfully generated between *A. fistulosum* and *A. roylei*, but the progeny were sterile. *Allium fistulosum* possesses characteristics potentially useful in the genetic improvement of the bulb onion, including resistance to pink root, thrips and smut (Jones and Mann, 1963). Interspecific hybrids between *A. cepa* and *A. fistulosum* have been generated by direct crossing and embryo rescue. The consistently low fertility of the hybrids is probably due to poor chromosomal pairing. Progeny from backcrosses of hybrids to *A. cepa* and *A. fistulosum* often resemble recurrent parent species and show near-normal meiosis, suggesting that functional gametes are close to parental species types. Amphidiploids from natural or induced doubling of the chromosomes of *A. cepa* by *A. fistulosum* hybrids generally show low fertility. The cultivar Beltsville Bunching is a seed-propagated allotetraploid derived from a hybrid between *A. cepa* and *A. fistulosum* and grown in the USA as a green bunching onion. Another interspecific *Allium* hybrid commercially grown in the USA is Delta Giant shallot, generated from the backcross to *A. cepa* of an amphidiploid from a shallot by *A. fistulosum* hybrid.

Garlic and leek were assigned by Vvedensky to section *Porrum* G. Don with possible progenitors *A. longicuspis* (possibly wild garlic) and wild forms of *A. ampeloprasum* (Fig. 68.1). *Allium longicuspis* exists in the former Soviet Central Asian Republics and is vegetatively propagated. Wild tetraploid *A. ampeloprasum* is widespread and may show cross-fertility with leek and kurrat (McCollum, 1976). Chive and Chinese chive were assigned to section *Rhizirideum*. Vvedensky omitted rakkyo, an oriental cultivated species, from his classification scheme. Chive is a widespread, highly polymorphic species found in the Old and New Worlds. Both Chinese chive and rakkyo are primarily grown in the Orient. Cultivated Chinese chive closely resembles wild *A. tuberosum*.

More recent classification schemes have been proposed for the cultivated Alliums. Traub (1968) assigned the bulb onion, chive, Japanese bunching onion, and rakkyo to section *Cepa*; garlic and leek to section *Allium*; and Chinese chive to section *Rhizirideum*. Wendelbo (1969) stated that the division of *Allium* into relatively few sections was outdated and described four subgenera and new sections to accommodate newly described species indigenous to Iran and Afghanistan.

Early history

Stearn (1944), Jones and Mann (1963), and Fenwick and Hanley (1985) have reviewed the historical use of alliums as food crops. The following description was adapted from McCollum (1976). References to onion, garlic and leek as food, medicines, or religious objects can be traced back to the 1st Egyptian dynasty (3200 BC) and to the biblical account of the exodus of the Israelites from Egypt (1500 BC). The use of onion and garlic in medicine in India in the sixth century BC can be inferred from later Indian writings. Greek and Roman authors, e.g. Hippocrates (430 BC), Theophrastus (322 BC), and Pliny (AD 79), described several onion cultivars as long or round; white, yellow or red; and mild or pungent. As onion cultivation spread to new climates and environments, selection occurred for diverse types of shape, colour, flavour, response to daylength and storage ability.

Allium fistulosum has long been the main garden onion of China and Japan. Domestication of *A. fistu-*

losum may have occurred in north-west China and written accounts appear in Chinese writings as early as 100 BC (McCollum, 1976). It appears in Japanese literature at about AD 720 after introduction from China (Inden and Asahira, 1990). *Allium fistulosum* does not bulb and is grown for its edible tops and leaf bases. Specific cultivars have been selected for tender leaves, thicker sheaths and various degrees of tillering (Jones and Mann, 1963).

Leek and kurrat were known to ancient civilizations of the Near East and closely resemble wild *A. ampeloprasum*. Leek was grown in Europe in the Middle Ages and many varieties have been selected for long, white, edible leaf bases with green tops, winter hardiness and resistance to bolting (i.e. early flowering). Kurrat is primarily grown in Egypt and other Near Eastern countries for the green leaves and as a seasoning (Jones and Mann, 1963). Great-headed garlic is vegetatively propagated by large cloves or smaller ground bulblets. It is less pungent than garlic and has been marketed in the USA as a mild 'garlic'. It flowers profusely but sets few or no seeds.

Garlic is an ancient crop of central Asian origin and mentioned in ancient Chinese, Egyptian and Greek writings. It is vegetatively propagated by cloves and, in those cultivars that still bolt, by inflorescence bulbils. Some modern cultivars may produce flowers mixed with the bulbils, but flowers rarely set seed. Garlic presents an interesting problem as to the origin of strains differing in maturity, bulb size, clove size and number, scale colour, bolting, scape height, number and size of inflorescence bulbils and presence or absence of flowers. It is not clear how much variation was selected while *A. sativum* or its ancestors were still sexual and how much has arisen after garlic became vegetatively propagated.

Cultivated chive may have originated in the Mediterranean area and is not recorded earlier than in sixteenth-century Europe. Chive crosses readily with the polymorphic, wide-ranging ecotypes of *A. schoenoprasum* and may have been brought into cultivation many times from wild populations. Chinese chive and rakkyo have been domesticated since ancient times in the Orient. Chinese chive is a seed-propagated perennial that spreads by rhizomes. It is cultivated for the leaves and inflorescences which have been used as a herbal medicine and to relieve fatigue. Cultivated forms of rakkyo are propagated vegetatively by bulb multiplication. It is fried or the small bulbs are pickled in brine or vinegar.

Recent history

The bulb onion, chive, Chinese chive, Japanese bunching onion and leek are seed propagated and have been historically maintained as open pollinated populations. They are outcrossers and show inbreeding depression. The genetic improvement of the commercially important alliums is slow because 2 years are generally required to complete one generation (seed-to-bulb and bulb-to-seed). Because the primary economic product is the bulb or pseudostem, a breeder must select for the desirable type and against bolting. At present, high-quality open pollinated populations of these alliums with excellent seeding ability represent a significant component of commercial production.

Onion populations show severe inbreeding depression and vigour is restored by crossing between inbred lines. The hybrids are higher yielding than the parental populations and more uniform for maturity and bulb size, shape, and colour. At present, a significant proportion of onions produced in North America, Europe and Japan are hybrids. Production of hybrid onion seed became economically feasible with the discovery of cytoplasmic male sterility (CMS). In 1962, Jones and colleagues were inbreeding plants of the cultivar Italian Red to develop a hybrid red onion for storage (Jones and Mann, 1963). One plant did not set seed after self-pollination and was saved by virtue of bulbils in the inflorescence. Sterility in Italian Red was cytoplasmically inherited (CMS-S) with fertility restored by a dominant allele (*Ms*) at a single nuclear restorer locus. Male-sterile plants possess the sterile cytoplasm and are homozygous recessive at the restorer locus (*S* msms). Male-sterile lines can be maintained by crossing the sterile line with a maintainer line with normal cytoplasm and homozygous recessive at the restorer locus (*N* msms). When planted together in isolation, the sterile and maintainer are propagated by harvesting seed separately from each line. Significant progress in the development of onion hybrids has been realized. Due to low seed yield, many hybrid onions in the USA are generated by three-way crosses, i.e. the commercial hybrid of sale results from crossing a male sterile F_1 seed parent with a third inbred line. Extraction of maintainer lines from some onion populations, e.g. the American short-day cultivar Grano or the Japanese cultivar Sapporo-Ki, has been difficult due to the high frequency of the restorer allele.

Although hybrid onion cultivars are available, open-pollinated populations still represent most of the production in subtropical and tropical areas. Unknown numbers of cultivars are maintained by individual farmers throughout the world. Shallots are also maintained in the subtropics and tropics and prized for their strong pungent taste. Recently, the genetic improvement and eradication of viruses from tropical shallots has been discussed (van der Meer and Permadi 1990).

The Japanese bunching onion is primarily maintained in the Orient by individual farmers as open-pollinated populations. However, commercial production of seed is becoming more common. Cultivars are selected for uniformity, quality, heat tolerance and resistance to bolting. Superior gene combinations through recombination and selection may occur rarely because *A. fistulosum* shows a peculiar localization of chiasmata which may result in large chromosome regions being inherited *en bloc*. Economic production of hybrids of the Japanese bunching onion has become a possibility with the discovery of a source of CMS. Fertility is restored by a dominant allele at either of two loci Ms_1 and Ms_2 (Inden and Asahira, 1990).

The genetic improvement of leek has primarily relied on mass or family selection for yield, uniformity, and resistance to yellow stripe virus and bolting (Currah, 1986). The development of hybrid leeks is complicated by tetraploidy; severe inbreeding depression occurs due to the persistence of deleterious recessive alleles in the population. Strict bivalent pairing in leek in ensured by localization of chiasmata as in *A. fistulosum*. Hybrids between selected cultivars or slightly inbred lines have demonstrated heterosis for economically important traits (Currah, 1986). The commercial production of hybrid leek seed is dependent on a source of male sterility. Although male-sterile plants often occur in open-pollinated leek cultivars, the genetics of this sterility has not been described. A CMS system like that of onion would be difficult to develop because a maintainer line must possess four recessive alleles at each restorer locus. An alternative approach would be the multiplication of individual male-sterile plants by tissue culture.

Cultivars of chive are maintained as open-pollinated populations and can be quite variable. Hybrids yield better than conventional open-pollinated cultivars and sources of CMS have been identified. Little information exists on the genetic improvement of Chinese chive and rakkyo. The flower structure of both alliums indicates that they are or were outcrossers (McCollum, 1976).

Prospects

The economic importance, widespread use and potential health benefits of the alliums are an impetus to continued research on the phylogeny, breeding and genetics of this important genus. Recurrent selection will continue to improve open-pollinated *Allium* populations for quality, uniformity and resistance to diseases and bolting. High-quality open-pollinated cultivars represent and will continue to represent a significant proportion of world production. However, the greater uniformity and significant heterosis expressed by hybrids will remain as a stimulus to their continued development. Exploitation of male sterility will be a primary factor in the economic production of hybrid seed.

The onion would benefit from increased resistance to diseases and pests. Inbreds or cultivars highly resistant to pink root (*Pyrenochaeta terrestris*) and basal rot (*Fusarium oxysporum* f.sp. *cepae*) have been selected. Additional sources of disease or pest resistance are known, e.g. resistance to thrips (*Thrips tabaci*) conditioned by glossy foliage, but have not been incorporated into commercially acceptable cultivars. Identification of germplasm resistant to leaf blight (*Botrytis squamosa*), neck rot (*B. allii*), white rot (*Sclerotium cepivorum*), maggot (*Delia antiqua*), smut (*Urocystis magica*), downy mildew (*Peronospora destructor*), purple blotch (*Alternaria porri*), bacterial rots (*Erwinia carotovora* and *Pseudomonas alliicola*), nematodes (*Ditylenchus dipsaci* and *Meloidogyne hapla*), or yellow dwarf virus and incorporation into élite cultivars could result in greater yield stability and significant reductions in pesticide use. In addition, market trends will require onion breeders to develop new cultivars with specific characteristics to meet processing requirements (uniform ring size for breaded onion rings or high dry matter for dehydration) or changes in consumer preferences (lower pungency in the USA). In subtropical and tropical production areas, highly pungent onions with long dormancy are demanded.

In the future, tissue culture may play a more significant role in the development of superior cultivars and hybrids. Successful micropropagation, callus and protoplast culture, and embryo rescue of alliums have been reported (Novak *et al.*, 1986). Meristem tip culture is widely used to free garlic plants from virus. *In vitro* evaluations for resistance to pink root or *Fusarium* based rot by treating cultured onion cells with toxins produced by these fungi are being developed. Culture of the inflorescence or basal plate can be used to propagate male-sterile plants without a maintainer line. Vegetatively propagated female parents of the hybrid would be transplanted directly in the field for pollination. The use of this technology will depend directly on the cost of propagating the female versus the increased revenue generated by hybrid seed. Another potentially useful application of tissue culture is the extraction of haploid plants by ovule culture (Muren, 1989). The chromosome number of haploid plants can be doubled to generate completely homozygous plants. If these doubled haploid plants can be maintained by seed, the process will yield numerous inbred lines avoiding the 2 year-per-generation cycle. Assuming that this technology will be generally applicable to diverse populations, inbred lines could be quickly extracted and tested in hybrid combinations.

Although at present vegetatively propagated, strains of seed-propagated garlic may be developed; Etoh (1986) collected seed-propagated garlic plants from the former Soviet Central Asia. Successive generations of sexual reproduction may produce garlic populations that can be subjected to recurrent selection for such traits as high solids, uniformity and virus resistance. Selection of seed-propagated strains of garlic would be a highly significant and economically important development in the cultivation of *Allium*.

A better understanding of the phylogenetic relationships between the cultivated alliums and their wild relatives is a necessary research goal. The wealth of genetic variability in wild and cultivated alliums has not been extensively exploited for the improvement of the bulb onion, e.g. resistance to white rot in *Allium ampeloprasum*, downy mildew in *A. roylei* or pink root in *A. fistulosum*. Although successful hybridizations between the bulb onion and other *Allium* species have been reported, little information is available on successful introgression of desired traits. Identification and characterization of the progenitor(s) of the cultivated alliums especially the bulb onion and Japanese bunching onion, are important because the habitat of some wild alliums is threatened (Hanelt, 1990). Once identified, wild *Allium* species closely related to the cultivated forms must be collected and maintained in germplasm collections. Research must evaluate the crossability of the cultivated alliums with each other and their wild relatives. The low degree of fertility exhibited by the hybrids between *A. cepa* and the *Allium* species of section *Cepa* indicate that introgression of genes will be difficult. Embryo rescue offers the possibility of increasing the number of hybrids, but introgression of beneficial genes by conventional crossing may be restricted by low fertility.

The long generation time for exclusively vegetative propagation makes the application of biotechnology to the genetic improvement of the alliums very attractive. Few genetic markers have been described in the cultivated alliums. Our understanding of the genetic diversity and phylogeny of the alliums would benefit from identification and mapping of biochemical markers, e.g. isozymes and RFLPs. Marker-facilitated selection would allow for identification of desired chromosome regions early and reduce the numbers of bulbs or pseudostems harvested and stored through the dormancy period prior to flowering. Introduction of specific traits, e.g. disease resistances, into the asexually propagated types such as garlic, great-headed garlic, and rakkyo would have great economic potential. Transformation of *Allium* by *Agrobacterium* has been reported (Dommisse *et al.*, 1990). However, the application of transformation to *Allium* will depend on the availability of cloned genes.

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69

Okra

Abelmoschus esculentus, A. caillei, A. manihot, A. moschatus (Malvaceae)

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Introduction

Okra is a very popular, tasty, gelatinous vegetable. Tender green pods 3–5 days old are used as a vegetable, generally marketed in the fresh state but sometimes in canned form (USA, Turkey). In dry areas, fruits are cut into slices, dried in the sun and stored for long periods (Sahel in Africa, India). They are relished because of their high mucilage content.

Four species are cultivated. The main crop (*Abelmoschus esculentus*) is an annual vegetable, grown from seed, in tropical, subtropical and mediterranean climatic zones. In West and Central Africa it is cultivated, in association with *A. caillei* where the former, which flowers earlier, is known as 'the rainy season okra', and the latter, which has a longer cycle (up to 1 year), is known as the 'dry season okra'. Plants of *A. manihot*, whose pods are too prickly to be consumed and have sometimes lost their flowering ability, are only cultivated in Papua New Guinea for their leaves. *Abelmoschus moschatus* has seeds which are used as musk mallow (ambrette). This species is sometimes used in several animism practices in West Africa (south Togo and Benin).

Okra has a relatively good nutritional value and is a good complement in developing countries where there is often a great alimentary imbalance. Moisture (89.6 per cent), K (103 mg), Ca (90 mg), Mg (43 mg), P (56 mg), vitamin C (18 mg) are found in 100 g of fresh fruit. Metals such as iron and aluminium

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