THE CHROMOSOME NUMBERS OF THE BRITISH *MENTHAE*

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The mints provide an excellent basis for cytological study. The taxonomic position of many is uncertain, minor variation is abundant, putative hybrids frequently occur, and many polyploids exist. An investigation into the chromosome numbers of this group was undertaken in the hope that they would help to clarify the taxonomic position, the main objects of the work being, (*a*) to ascertain the extent of polyploidy, (*b*) to determine whether the chromosome numbers support the suggested hybrid origin and parentage of many mints, (*c*) to provide the basis for an investigation into the association between polyploidy, hybridity and speciation.

The material for this work was collected from many parts of Great Britain and cultivated in the Botanic Gardens of King's College in the University of Durham. Also continental material of several British mints was obtained for purposes of comparison. Chromosome counts were made from root-tip preparations using a section technique. The roots were prefixed in a saturated aqueous solution of paradichlorobenzene for a period of one and a half hours. The chromosomes of most mints are short, but their large number, small size, and close proximity in the metaphase plate make counting difficult. Prefixation in paradichlorobenzene solution reduces them to a length little greater than their breadth and thus facilitates counting. Fixation was in Langlet's Modification of Navaschin's Fluid; sections were cut at 8 to 10 μ and staining was by Newton's Gentian Violet Method. The illustrations are camera-lucida drawings from such preparations.

Herbarium material of all the plants which have been used in this work is, for the time being, housed in the writer's own collections. Additional specimens of many of these plants are also in the herbarium of Mr. R. A. Graham.

Chromosome counts for several of the British species of *Mentha* have been published (see Darlington & Janaki, 1945 ; A. & D. Löve, 1948 ; Maude, 1939 ; Tischler, 1938). These counts were, however, based on non-British material. The diploid numbers are summarised below :

Species	*2n*	*Authority*
M. aquatica	96	Ruttle
	36	Schürhoff
	c. 96	Junell
M. arvensis	72	Ruttle, Schürhoff, Lietz
	12, 60-62, 72	Junell
	64, c. 90, 92	Nagao
M. longifolia	18	Heimans, Schürhoff
	24	Ruttle
	48	Nagao
M. × *niliaca*	24, 56	Ruttle
M. × *piperita*	36	Schürhoff, Wolf
	66, 68, 70	Ruttle
	36, 64 (128*)	Glotov

* Experimentally produced.

Species	$2n$	*Authority*
var. *officinalis*	72, 84	Nagao
var. *vulgaris*	68, 72	Nagao
M. rotundifolia	18	Heimans
	24	Ruttle, Nagao
	c. 54	Schürhoff
M. × *verticillata*	54	Schürhoff
	96, c. 120	Junell
M. spicata	36	Junell, Schürhoff
	48	Junell, Ruttle
	36, 48, 84	Nagao
(*M. canadensis*)	54	Schürhoff, Wolf
M. pulegium	20, 40	Ruttle

The variation of chromosome number within the species as shown by this list is probably exaggerated. The genus shows greater morphological variation on the Continent, but the affinities of some of these variants are imperfectly known, hence unrelated plants may have been grouped together. It is difficult to draw any conclusions from this list without material of the actual plants from which these chromosome numbers were obtained. My own results suggest a greater uniformity in the chromosome numbers of each species, and material from Continental sources has rarely differed in this respect.

The Chromosome Numbers of Plants from British Sources

(a) *The Species and their Varieties*

M. aquatica L. A wide range of this very variable mint, collected in the following vice-counties, has been examined : v.cs. 13, 17 (4), 20, 21 (3), 65 (2), 66 (15), 67 (2), 70, 80, 102 and 104 (4). All thirty-five plants had a diploid number of 96. They included plants referable to vars. *major* Sole, *lobeliana* Becker (in the sense of Briquet and Fraser), and *hirsuta* (Huds.) besides other variations in leaf shape and dentation, pubescence, pigmentation, number of inflorescences, position of the stamens (whether included or exserted), habit, etc. Hence it is clear that the considerable variation of this species cannot be attributed to numerical chromosomal differences. The behaviour under cultivation, of the above and many other plants, showed that the trend of variation originally noted in the field was usually still recognisable, but much less pronounced. Far more noticeable was the " levelling out " effect produced by the cultivation of transplanted material under relatively uniform conditions. Hence I am of the opinion that the commonly occurring varieties of *M. aquatica* are the result of the complementary inter-reaction of minor genetical variation and the environment.

M. crispa L. This mint has been considered both as a variety of *M. aquatica* and as a hybrid between this species and *M. spicata* or between *M. spicata* and *M. rotundifolia*. Material from the Gardens of the Royal Horticultural Society at Wisley had a diploid number of 96, hence the suggestion that this plant is a variety of *M. aquatica* appears to be the most probable.

M. arvensis L. All seven plants examined from the following vice-counties had a diploid number of 72 : v.cs. 13, 17 (2), 21 (2), 66, 102. This included both annual and perennial forms. Continental material from Essen Botanic Gardens also had the same chromosome number.

M. longifolia (L.) Huds. There is some difficulty in separating this species from its hybrid *M.* × *nemorosa*. However, it appears certain that at least two cytotypes exist in Britain with diploid numbers of 36 and 48. No morphological differences between these two cytotypes have been noted. In addition, a plant from Amsterdam Botanic Gardens had a diploid number of 24, but was not identical with British material.

M. rotundifolia (L.) Huds. Material of this species from nine sources all had a diploid number of 24. Three of these sources were British (v.cs. 17 and 66 (2)), and the remainder Continental (Paris, Nantes, Lund, Brussels, Sacarvem and Liége Botanic Gardens).

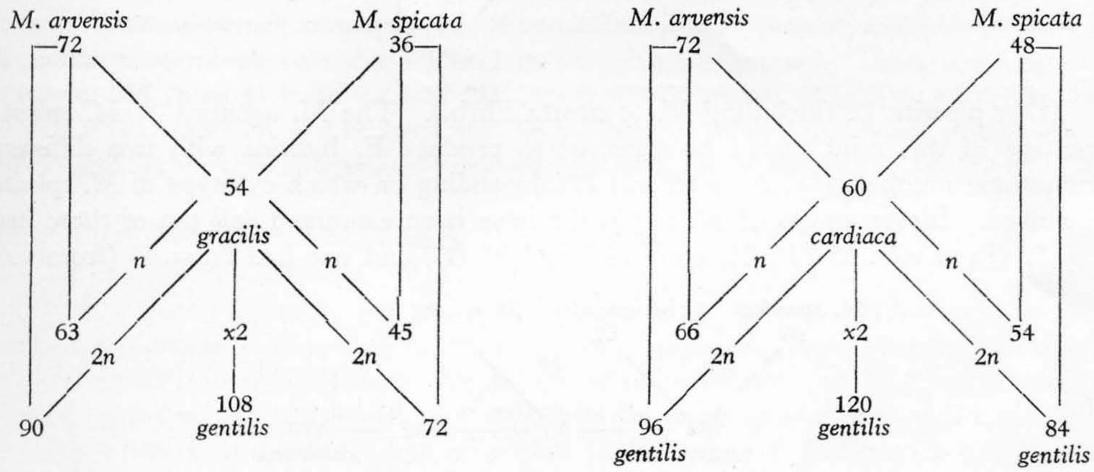
M. spicata L. Two different chromosome numbers occur in this species, 2n = 36 and 48. Plants with 36 chromosomes were obtained from v.cs. 21 (2), 66 (6) and 70. Also a plant referable to var. *ciliata* Druce from v.c. 66 and another referable to var. "*lacerata*" from the Gardens of the Royal Horticultural Society at Wisley had this chromosome number. Plants with 48 chromosomes were obtained from v.cs. 21 (3) and 66 and from the Gardens of the Royal Horticultural Society at Wisley (a very hairy plant). In addition Continental material with 2n = 36 was supplied by Liége, Geneva (2) and Warsaw (2) Botanic Gardens, and with 2n = 48 by Paris, Lund, Copenhagen, Warsaw, Amsterdam (2) and Geneva Botanic Gardens. This material was received under a variety of names – *i.e. M. sativa, M. piperita, M. gentilis, M. longifolia, M. arvensis, M. canadensis, M. lacerata* and *M. crispata*, but it all grew into plants identical with, or very closely related to, British forms of *M. spicata*.

M. pulegium L. Efforts to obtain living material of this now rare mint from British sources were unsuccessful. However, material was obtained from several Continental sources and this proved to have a euploid series with a base number of 5. The diploid numbers obtained were, 10 (Liége Botanical Gardens), 20 (Geneva and Nantes Botanical Gardens), 30 (Liége Botanical Gardens), 40 (Sacarvem Botanical Gardens). In addition material belonging to the related *M. gattefossii* Maire was received from Mainz Botanic Gardens and had 2n = 40. Both taxonomic and cytological characters indicate that *M. pulegium* belongs to a different section of the genus from all the other British species.

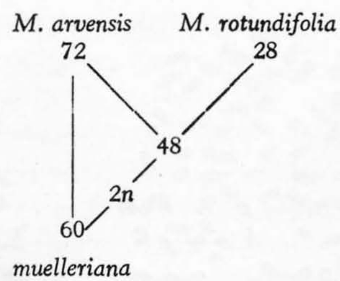
(b) *The Hybrids*

M. × *alopecuroides* Hull is usually considered as a hybrid involving *M. rotundifolia* and *M. longifolia*. If this is the case the diploid chromosome number of 36, in the three plants examined from v.cs. 17 (2) and 31, indicates that this mint is probably the F_1 hybrid between these two species. The marked stability of this mint suggests that it may be a completely sterile hybrid. The suggested parentage is difficult to reconcile with the existence of another, and different looking, hybrid (*M.* × *nemorosa*) of the same parentage and chromosome number, and showing the greater range of variation so frequently associated with hybridity. Further evidence on seed production and fertility etc. is required before any conclusions can be reached on the status or origin of *M.* × *alopecuroides*.

M. × *gentilis* L. (including *M.* × *cardiaca* (Gray) Baker and *M.* × *gracilis* Sole). This range of hybrids forms one of the most interesting and complex in the genus. A consideration of their chromosome numbers provides an explanation of their origin and parentage. The two species involved are *M. arvensis* and *M. spicata*. Diploid numbers of 54, 60, 84, 96, 108 and 120 were found in the eighteen plants which were examined. The vice-county distribution of these plants was : 2n = 54 from v.c. 21; 2n = 60 from v.c. 17; 2n = 84 from v.cs. 17, 65, 66 (4) and 67; 2n = 96 from v.cs. 66 and 67 (2); 2n = 108 from v.cs. 67 and 104; 2n = 120 from v.cs. 40, 67, 70, and 77. The plant with a diploid number of 54 was referable to *M.* × *gracilis* and the one with a diploid number of 60 was referable to *M.* × *cardiaca.* Further material of both these is required in order to determine whether these numbers are constant. The diagram below indicates the main hybrid combinations and recombinations which are theoretically possible between *M. arvensis* and both cytotypes of *M. spicata.* It is noteworthy that both forms of *M. spicata* can take part in the formation of the *M.* × *gentilis* complex, though it appears that the one with 2n = 48 is most frequently involved. *M.* × *gentilis* with 2n = 84 is known to set fertile seed on occasions, and young plants have been raised from such seed, but these had not flowered up to the time of writing. Hybrid swarms are frequently encountered and the ones examined have been combinations of *M.* × *gentilis* (2n = 84) and *M. arvensis.* The plants in such swarms show every intermediate between *M.* × *gentilis* and *M. arvensis* and frequently set well-formed seed.

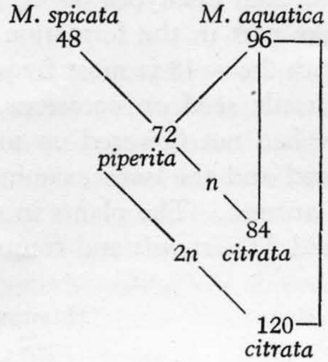


M. × *muelleriana* F. W. Schultz. Material of this very rare mint, from its original Devon locality, was found to have a diploid chromosome number of 60. *M. arvensis* and *M. rotundifolia* are obviously the parents involved in this hybrid, and the above chromosome number indicates a back-cross of the F_1 hybrid with the *M. arvensis* parent.

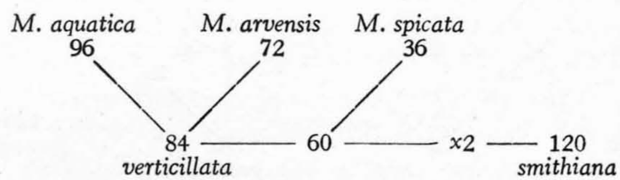


M. × *nemorosa* Willd. Morphological characters suggest a *M. longifolia* × *M. rotundifolia* parentage for this mint. Plants belonging to this hybrid frequently so closely resemble the former parent that so far I have been unable to separate them. A diploid number of 36 was obtained in material from v.c. 91 which is definitely referable to this hybrid. The presence of at least two cytotypes (2n = 36 and 48) in *M. longifolia,* one of which (2n = 36) is the same as would be expected to occur in *M.* × *nemorosa,* prevents the separation of the species from its hybrids on a cytological basis. As already mentioned

M. × *alopecuroides* is generally believed to have the same parents as *M.* × *nemorosa* but is a very different plant in its appearance. A possible explanation may lie in the way in which these hybrids have arisen, *M.* × *alopecuroides* being produced when *M. rotundifolia* is the female parent and *M.* × *nemorosa* when *M. longifolia* is the female parent. Additional material of both *M.* × *nemorosa* and *M. longifolia* is required from as many sources as possible for further study.



M. × *piperita* L. (including *M.* × *citrata* Ehrh.). The *M. aquatica* × *M. spicata* parentage of this mint would be expected to produce F_1 hybrids with two different chromosome numbers (*i.e.* 2n = 66 and 72) depending on which cytotype of *M. spicata* is involved. Eleven plants of *M.* × *piperita* have been examined and ten of these had 2n = 72 (from v.cs. 17 (2), 21, 66 (4), 90 and 91 (2)) and one had 2n = 66 (from v.c.



81). Those with 2n = 72 were referable to var. *vulgaris* Sole, var. *officinalis* Sole, and f. *hirsuta* (J. Fraser) R. A. Graham. Two plants of *M.* × *citrata* were examined and these had 2n = 84 (v.c. 21) and 2n = 120 (v.c. 62). These two numbers indicate back-crosses of *M.* × *piperita* with the *M. aquatica* parent, in the first case a normal gamete of *M.* × *piperita* being involved, and in the latter an unreduced gamete.

Fig. 1

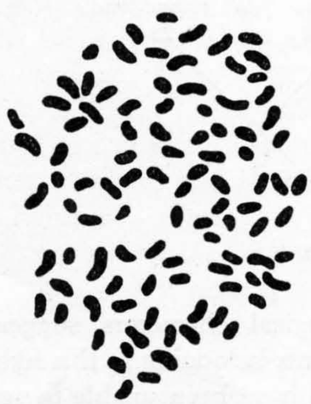


Fig. 2

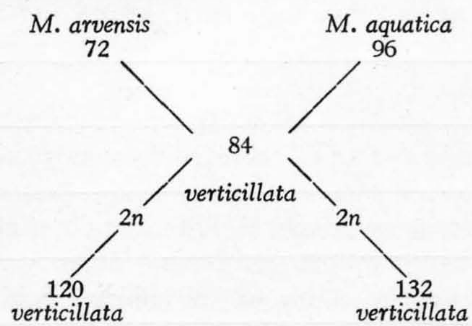
Fig. 3

Fig. 1. Root-tip metaphase plate in *Mentha rotundifolia* (L.) Huds. × 3750. (2n = 24).
Fig. 2. Root-tip metaphase plate in *Mentha aquatica* L. × 3750. (2n = 96).
Fig. 3. Root-tip metaphase plate in amphidiploid *Mentha* × *gentilis* L. × 3750 (as in Fig. 1). (2n = 120).

M. × *smithiana* R. A. Graham. The triple parentage of this mint is supported by its chromosome number. Two plants (from v.cs. 17 and 21) were examined and both had 2n = 120. This number can only be satisfactorily accounted for on the basis of an amphidiploid hybrid involving *M.* × *verticillata* and *M. spicata.*

The gametes of *M.* × *verticillata* are shown to be fertile from the occurrence of both back-crosses and fertile seed in this hybrid. Amphidiploidy is of frequent occurrence in hybrid plants and is a common means by which stability and fertility are attained. Whether *M.* × *smithiana* produces fertile seed is not known, and field and experimental observations on this point are needed. The plant is, however, very stable and shows little variation when considered in the strict sense. It is probable that some plants referable to *M.* × *gentilis* with 2n = 120 have been included under *M.* × *smithiana* in the past. They show a similar long tubular calyx but this is smaller than that of *M.* × *smithiana* and the plants have not the distinct habit associated with this latter mint.

M. × *verticillata* L. The hybrids included under this name all have a *M. aquatica* × *M. arvensis* parentage. *M.* × *verticillata* is very variable and several different chromosome numbers have been found in the plants examined. These are: 2n = 42 from v.c. 66; 2n = 84 from v.cs. 17 (5), 21 (3), 65 (2) and 66 (4); 2n = 120 from v.cs. 65 and 66 (3); and 2n = 132 from v.c. 66. These numbers are derived from the F_1 hybrid and its unreduced gametes back-crossed with either parent.



The plant with a diploid number of 42 is of interest because it contains only half the normal chromosome complement and presumably must have developed from an unfertilized gamete.

The various hybrids appear to be correlated with several named varieties. The normal plant, and also var. *paludosa* (Sole) Druce (which rarely retains its characters under cultivation) have 2n = 84. The back-cross with *M. arvensis* very closely resembles this parent and is referable to *M. arvensis* var. *densifoliata* Briq. The back-cross with *M. aquatica* has the verticils concentrated in the upper nodes and the bracts much smaller. It is subglabrous and has the narrower leaves associated with var. *acutifolia* (Sm.) Fraser. *M.* × *verticillata* with 2n = 84 is frequently sterile but on occasions it has been observed to produce a varying amount of seed. Whether this is fertile is not known. The plants with 2n = 120 have produced a full crop of seed, some at least of which was fertile.

M. × *villosonervata* Opiz. A plant which appears to belong to this hybrid between *M. longifolia* and *M. spicata* was found to have a diploid number of 48. It was discovered growing with the parents on waste land at Sherburn Hill (v.c. 66). The inflorescence is very poorly developed and few flowered. The flowers have included stamens and open several weeks later than those of either parent. All those examined died without setting seed.

British Mints – Their chromosome numbers, polyploidy and status or parentage

Name	2n	2×	4×	6×	7×	8×	9×	10×	11×	12×	14×	16×	18×	20×	22×	*Status or Parentage*
M. aquatica	96											×				Species
var. *crispa*	96											×				
M. arvensis	72									×						Species
M. longifolia	36			×												Species
	48					×										
M. rotundifolia	24		×													Species
M. spicata	36			×												Species
	48					×										
var. *ciliata*	36			×												
var. *lacerata*	36			×												
M. pulegium	10	×														Species
(from non-British material)	20		×													
	30			×												
	40					×										
M. × *alopecuroides*	36			×												Probably ♀ *rotundifolia* × ♂ *longifolia*
M. × *gentilis*	120													×		Amphidiploid *arvensis* × *spicata* (48)
	108												×			Amphidiploid *arvensis* × *spicata* (36)
	96											×				(*arvensis* × *spicata* 48) unreduced × *arvensis*
	84										×					(*arvensis* × *spicata* 48) unreduced × *spicata* (48)
var. *cardiaca*	60							×								*arvensis* × *spicata* (48)
var. *gracilis*	54						×									*arvensis* × *spicata* (36)
M. × *muelleriana*	60							×								(*arvensis* × *rotundifolia*) unreduced × *arvensis*
M. × *nemorosa*	36			×												Probably ♀ *longifolia* × ♂ *rotundifolia*
M. × *piperita*	66								×							*aquatica* × *spicata* (36)
	72									×						*aquatica* × *spicata* (48)
var. *citrata*	84										×					*piperita* (reduced) × *aquatica*
	120													×		*piperita* (unreduced) × *aquatica*
M. × *smithiana*	120													×		Amphidiploid, *verticillata* × *spicata* (36)
M. × *verticillata*	84										×					*aquatica* × *arvensis*
	42				×											Haploid *verticillata*
(*M. arvensis* var. *densifoliata*)	120													×		*verticillata* (unreduced) × *arvensis*
var. *acutifolia*	132														×	*verticillata* (unreduced) × *aquatica*
M. × *villoso-nervata*	48					×										*longifolia* × *spicata*

Discussion

The above account of the chromosome numbers of the various species and hybrids clearly indicates the importance of polyploidy in the genus *Mentha*. There are two distinct polyploid series : the section *Pulegium* with a base number of 5, and the section *Mentha*. with a base number of 6. The former provides a complete euploid series from 10 to 40, and the latter from 24 to 132. These chromosome numbers are apparently the result of both autopolyploid and allopolyploid changes in the genus.

(a) *Autopolyploidy*

Only three British species were found to have more than one chromosome number, namely *M. pulegium*, *M. longifolia* and *M. spicata*. *M. pulegium* has four different numbers, but no correlation between these and any morphological characters, or annual and perennial habit, could be found in the available material. In *M. spicata* the two cytotypes are probably separable by distinct though minor taxonomic characters. Further attention is being devoted to them in order to determine the reliability of these characters. The two cytotypes appear to be genetically isolated for no plants with an intermediate number of chromosomes have been encountered even though both forms frequently grow in close proximity. The occurrence of cytotypes with 36 and 48 chromosomes in both *M. spicata* and *M. longifolia* suggests that ancestral types with a diploid number of 24 may occur in both species. Ruttle (in Darlington & Janaki, 1945) has reported the existence of such a plant in *M. longifolia*. As far as is known no similar plant has been encountered in *M. spicata* but further work may well lead to its discovery.

(b) *Allopolyploidy*

In the type section, *Mentha*, of this genus the main cause of variation in chromosome number is the frequent occurrence of hybrids. The position is further complicated by amphidiploidy, the production of diploid gametes, and the occurrence, in one case, of a haploid plant. The existence of amphidiploid plants has already been noted in the *M.* × *gentilis* complex and in *M.* × *smithiana*. These amphidiploid mints are noticeably more stable than most of the other hybrids in the genus. However stability in this case is probably due to sexual sterility and reproduction by vegetative means rather than to the attainment of a normal fertility and seed production. Neither of the two amphidiploid forms of *M.* × *gentilis* has set seed in the plants under observation but further observations are required to confirm this point. *M.* × *smithiana* has been observed in the wild state to produce a varying amount of seed, but this is not always well formed and no information on its fertility is available.

The production of functional diploid gametes has clearly been of importance in the formation of several hybrid mints. In *M.* × *muelleriana* and the *M.* × *gentilis* and *M.* × *verticillata* complexes only back-crosses produced from the unreduced hybrid gametes are known. In *M.* × *piperita* both types of gamete must, on occasions, be fertile because *M.* × *citrata* can arise from either type. The three remaining hybrid mints which have been investigated are apparently F_1 hybrids. *M.* × *alopecuroides* and *M.* × *villosonervata* are probably highly sterile. Little is known about the third hybrid, *M.* × *nemorosa*, but its greater variability suggests that it may be partially fertile and back-cross with the parents.

An important feature in this genus is the part played by vegetative reproduction in the propagation of the species and their hybrids. By this means the effects of disorders in sexual reproduction, which may cause varying degrees of sterility, have been overcome. Thus hybrids, even when formed very infrequently, are maintained and dispersed, and somatic variation in the sexually reproducing species is perpetuated.

ACKNOWLEDGMENTS

I would like to express my appreciation of the advice and assistance afforded to me by Mr. R. A. Graham. In particular his assistance in obtaining many rare and interesting mints has greatly facilitated this work. Also my thanks are due to Professor M. Thomas, F.R.S. and Dr. K. B. Blackburn of the Department of Botany, King's College, University of Durham, for their interest during the course of this work and for affording the facilities under which most of it was carried out.

SUMMARY

The chromosome numbers of British species and hybrids of the genus *Mentha* have been determined from root-tip preparations and are summarised in the accompanying table. In addition material from several Continental sources has been examined. The status of these mints and the parentage of the hybrids are discussed.

The mints contain two euploid series, the section *Pulegium* having diploid numbers of from 10 to 40 and a base number of 5, and the section *Mentha* with diploid numbers of from 24 to 132 and a base number of 6. Many of these numbers have arisen by allopolyploidy, but autopolyploid races occur in several of the species. The production of functional diploid gametes and the occurrence of amphidiploidy in several of the hybrids are noted. Vegetative reproduction plays an important part in the propagation both of the species and of the hybrids in this genus.

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