

5. Landauer, R., *Philos. Mag.*, 1970, **21**, 863.
6. Anderson, P. W., Thouless, D. J., Abrahams, E. and Fisher, D. S., *Phys. Rev.*, 1980, **B22**, 3519. Also, Anderson, P. W., *Phys. Rev.*, 1981, **B23**, 4828.
7. Abrikosov, A. A. and Ryzhkin, I. A., *Adv. Phys.*, 1978, **27**, 147.
8. For a discussion on these points see Soukoulis, C. M. and Economou, E. N., *Solid State Commun.*, 1981, **37**, 409.
9. Chandrasekhar, S., *Radiative transfer*, (Dover, New York, 1960), p 161. For a general introduction to this method, see Bellman, R. and Wing, G. M., *An introduction to invariant imbedding* (Wiley, New York) 1975.
10. van Kampen, N. G., *Phys. Rep.*, 1976, **246**, 172.
11. Jayannavar, A. M. and Kumar, N., *Phys. Rev. Lett.*, 1982, **48**, 553.
12. van Kampen, N. G., *Stochastic processes in physics and chemistry*, (North-Holland, New York) 1981.

EVOLUTION OF GARDEN NYMPHAEAS

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ABSTRACT

The genus *Nymphaea* (L.) J. E. Smith supports a wide range of ploidy levels from $2x$ (28) to $16x$ (224), both at inter- and intraspecific levels based on $x = 14$. The present study was essentially aimed to unravel the nature of cytogenetic mechanisms underlying origin and evolution of cultivated nymphaeas. The diploids, forming the core, are found in Africa and India, while the polyploid taxa occupy much larger area are adapted to diverse climates. There is no correlation between flower size and the ploidy level and the taxa are self- as well as cross-pollinated. Detailed analysis of meiotic system indicates that the polyploids are allopolyploid in character, and the present day garden nymphaeas are the result of repeated crossing involving about twelve elemental species and selection extending for 100 years which took place in Europe and North America. The main mechanisms underlying evolution are hybridization and polyploidy.

NYMPHAEA is a genus of water lilies which inhabits the tropical and temperate regions of the world and comprises of 50 species with numerous forms¹. The water lilies constitute an important element of tropical aquatic ornamental horticulture because of their strikingly beautiful flowers with wide spectrum of colours. Nymphaeas attained their widespread fame as ornamentals in Europe and North America in the early 19th century when the highly coloured hardy hybrids were gradually placed on the market. The genus has been subjected to extensive hybridization since about 1850, primarily for the development of new ornamental cultivars²⁻⁴ and the present-day garden nymphaeas are the result of repeated crossing involving about twelve elemental species and selection of approximately 100 years which took place in Europe and North America. The precise cytogenetical understanding about the origin and evolution of garden nymphaeas from their wild relatives does not

exist. The present study is aimed to bring out these events in relation to the nature of cytogenetic mechanisms underlying origin and evolution of cultivated nymphaeas.

The genus *Nymphaea* has been divided into two main sections *viz* Apocarpiae and Syncarpiae. The former has been further subdivided into two subgenera *viz* Ancephyta, Brachyceras while the latter into three—Castalia, Lotos and Hydrocallis^{4,5}. As will be clear subsequently out of 50 species, the species relevant to the origin of the present day garden water lilies are *N. odorata* Ait., *N. tuberosa* Paine., *N. alba* var. *rubra* Lonnroth, *N. tetragona* Georg., *N. pygmaea* Aiton, *N. lotus* Linn., *N. rubra* Roxburgh, *N. caerulea* Savigny, *N. capensis* Thunberg, *N. zanzibariensis* Casp., *N. flavo-virens* Lehmann, *N. mexicana* Zuccarini.

Morphological analysis of species and cultivars has shown in general considerable variation in several

morphological characters like the habit of the plant, flower size, type of flower, number of petals, number of stamens, colour of flowers, time of blooming and its duration and mode of propagation. In the elemental species the basic colours for the flowers appear to be red, white, yellow or blue. But all shades in between exist in all the garden cultivars. This has been the result of natural hybridization or due to indiscriminate hybridization carried out by nursery men.

There is a great variation in flower size within a single species or cultivar according to the food supply and other conditions. But there is no correlation between the size of the flower and the ploidy level since the pygmy of the genus (*N. tetragona*) and one of the largest flowered (*N. gigantea*) both are high polyploids with $2n = 112$ and $2n = 224$ respectively⁵. In the present investigation also it was observed that the hexaploid ($2n = 84$) cultivars possess small flowers of size ranging from 4 to 10 cm. and the diploids ($2n = 28$), triploids ($2n = 42$), tetraploids ($2n = 56$) and higher poly-aneuploids ($2n = 154$, $2n = 206$) possess comparatively larger flowers of size ranging from 12 to 24 cm. The genus *Nymphaea* reproduces asexually through rhizomes, leaves and even by flowers.

With regard to the breeding system, the floral morphology would suggest that the taxa are self- and cross-pollinated.

The present cytological analysis of 6 species and about 30 cultivars have revealed the existence of a polyploid series of $2x$, $3x$, $4x$, $6x$, $8x$, $11x$ based⁶ on $x = 14$. Besides one of the cultivars was found to be aneuploid with $2n = 15 \times - 4 = 206$ and another cultivar 'Director G. T. Moore' was found⁷ to be trisomic with $2n = 28 + 1$. The negligible number of multivalents and predominant bivalent formation in all the polyploid species studied presently indicate an allopolyploid nature of taxa either genomically or functionally.

The meiosis in different polyploids of garden cultivars was characterised by the occurrence of bivalents, univalents with a negligible number of multivalents, reduced chiasma frequency, unequal segregation of chromosomes, lagging and precocious division of univalents⁶. The fairly large number of univalents in triploids, tetraploids, hexaploids and higher poly-aneuploids may be attributed due to the absence of exact homologues. This is because garden cultivars have evolved after tremendous reshuffling of parental genomes as a result of repeated and indiscriminate hybridization between elemental species at different ploidy levels as in gladioli⁸. This is further

substantiated by the predominant bivalent formation in the induced hexaploid of triploid *Nymphaea* hybrid, *N. daubeniana*⁹. Almost all the cultivars are sterile. However, sterility has no consequence on the survival of the cultivars as they are propagated vegetatively.

The correlation of level of polyploidy with general geographical distribution of *Nymphaea* has shown that the diploids which form the core are found in Africa and India, while the polyploid taxa occupy much larger area than the diploids and hence are adopted to more diverse climates. The occurrence of intra-specific polyploidy in species of *N. stellata*, *N. rubra* and *N. lotus* in India, shows that this sub-continent has been an active centre for the evolution of these species.

Like most ornamental plants¹⁰ garden nymphaeas also have a short history of domestication. The direction of evolution of garden nymphaeas was provided by the shift of emphasis from nymphaeas as starch yielding plants in the earliest times to nymphaeas for colourful and large flowers and greater adaptability to cold climate. The water lilies culture began in the large estates and botanic gardens of England with the introduction of *N. odorata* from America in 1786. From that time until 1812, several species were brought to English gardens. From England the interest spread to many parts of Europe and back to America. Since their first introduction into cultivation as ornamentals, an immense range of variation has appeared resulting in a variety of new colours and shape and size of blooms.

A perusal of the relevant literature^{2,4,11-15} shows that broadly speaking water lilies can be divided horticulturally into three distinct groups namely Hardy water Lilies, Night-blooming Tropical water Lilies and Day-blooming Tropical water Lilies. These correspond to hybrids within three distinct subgenera namely Castalia, Lotos and Brachyceras respectively with no hybrids in between (figure 1). A number of interspecific hybrids involving a number of species have been produced ever since 1851 when the first hybrid between *N. lotus* and *N. rubra* was raised⁴. The major developments took place during the first 50 years (1850-1900 A.D.) when the elemental species from Africa and America were introduced into Europe and hybridized with the species native of Europe to produce various hybrid groups^{4,13}. The selection from these hybrid segregates resulted in the modern water lilies.

The real breakthrough in *Nymphaea* culture was achieved after the introduction of tropical and temperate species into European gardens which have a

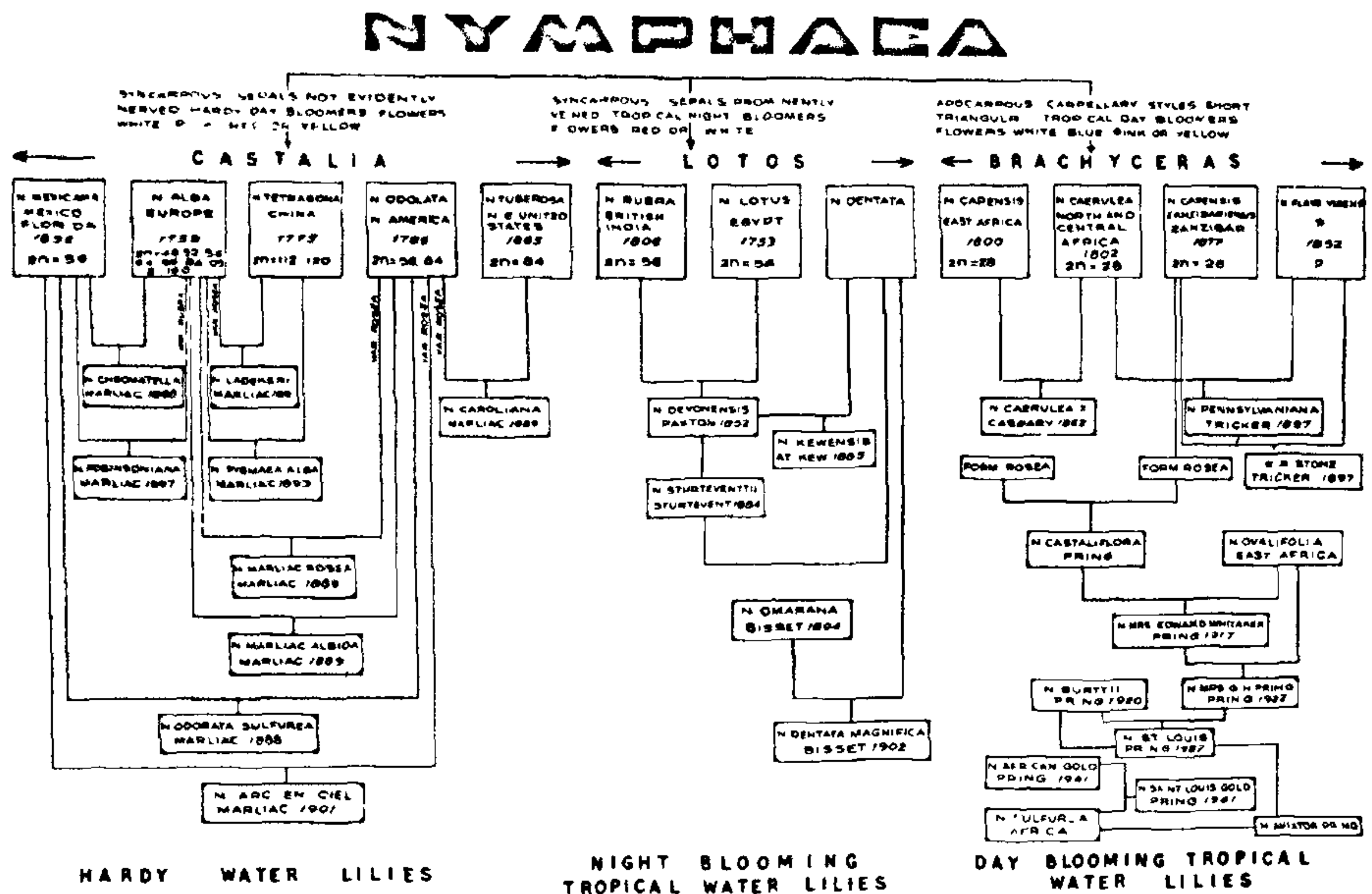


Figure 1. Origin of cultivated water lilies.

range of ploidy from $2x$ to $16x$. The different tropical and temperate species belong to the three different subgenera such as *Castalia*, *Lotos* and *Brachyceros*. The species of *Castalia* group have a range of ploidy from $4x$ to $8x$, while in the *Lotos* and *Brachyceros* groups the range is from $2x$ to $4x$ and $2x$ to $16x$ respectively. In *Castalia* group the crosses between octoploid and tetraploid levels merged the genepool of the species at hexaploid level. In *Lotos* group the crosses between tetraploid species combined the gene pool of the species at the same level, while in *Brachyceros* group the crosses between diploid and diploid and tetraploid species merged the genepool of the species at diploid and triploid levels respectively. This was followed by repeated cycles of hybridization involving other diploid and polyploid species over a period of about 50 years followed by further selection (figure 1). These processes have resulted in the release of tremendous genetic variability due to recombination between multiple sets of genomes. But soon the individuals with better texture and thicker flower parts, imparting greater durability and flower size

were preferred. Such individuals happened to be triploids particularly in Day-blooming Tropical *Nymphaeas*. Incidentally triploidy also turned out to be the optimum level of ploidy, with the result a large majority of the garden *nymphaeas* are triploids. Furthermore, in vegetatively propagated ornamentals, more often than not, triploids give excellent performance, because this level of ploidy combines in itself the gigantism of polyploidy and heterotic effect associated with hybridity¹⁶. The sterility associated with triploids is a definite bottleneck to future possibilities in *Nymphaea* breeding. In the present study fertility was restored in a sterile triploid *N. daubeniana* by inducing hexaploidy and thus opened up a new avenue for further breeding in *Nymphaea*⁹.

It is now evident from the foregoing account that repeated cycles of interspecific hybridization followed by selection and polyploidy have played a major role in the origin and evolution of garden *Nymphaeas* as in several vegetatively reproduced ornamentals such as roses, cannas, irises, gladioli, bougainvilleas etc.^{8,10,17}. However, the resultant sterility due to

hybridity has been of little significance as nymphaeas are maintained and propagated by effective vegetative means which has made fixing of useful genotypes easy.

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1. Cook, C. D. K., *Water Plants of the world*, Pitman Press, Bath, Avon, England, 1974.
2. Marliac Latour R. Mons, *J. Hort. Soc.*, 1898, **22**, 287.
3. Paxton, Jos, *Gard. Chron.*, 1852.
4. Conard, H. S., *The water Lilies. A monograph of the genus Nymphaea*, Rubls Carnegie Inst. Washington, 1905.
5. Sculthorpe, C. D., *The Biology of aquatic plants*, Edward Arnold, London, 1967.
6. Subrahmanyam, G. V. and Khoshoo, T. N., *Caryologia* (Communicated).
7. Subrahmanyam, G. V., *Curr. Sci.*, 1979, **48**, 34.
8. Ohri, D., *Cytogenetics of garden gladiolus and bougainvilleas*, Ph. D. thesis, Panjab Univ., Chandigarh, 1979.
9. Subrahmanyam, G. V. and Khoshoo, T. N., *The Nucleus*, 1981, **24**, 56.
10. Khoshoo, T. N., In *Progress in Plant Research*, (eds) T. N. Khoshoo and P. K. K. Nair, Today and Tomorrow Printers, New Delhi, 1979, **2**, 1.
11. Innes, W. T., *Gold Fish varieties and water gardens*, Inner Publishing Co., Philadelphia, USA.
12. Niklitschek, A., *Water lilies and water plants*, Great Britain, 1932.
13. Perry, F., *Water Gardening*, Robert Maclehose and Co. Ltd., London, 1938.
14. Pring, G. H., *Missourie Bot. Gard. Bull.*, 1958, **46**, 57.
15. Richard Gorer, *The Development of Garden Flowers*, Eyre and Spottiswoode Ltd., 1970.
16. Khoshoo, T. N., *Indian J. Genet.*, 1968, **28**, 187.
17. Stebbins, G. L., *Variation and Evolution in Plants*, Columbia University Press, N.Y., 1950.

ANNOUNCEMENT

BETTER PROTEIN SEPARATION

After a year of intensive research, a group of LKB in Bromma, Sweden, led by Dr Bengt Bjellqvist, has succeeded in developing a new method for isoelectric focusing. The research project has now resulted in a new product, the Immobiline system, which provides its users with precise results in the separation of biochemical samples. It is now possible to separate proteins which were previously thought to be homogeneous. In addition, the new method is said to ensure high reproducibility. The Immobiline system gives a 10-fold higher resolution, and allows a 5-fold increase in the amount of sample which can be analysed.

In the past, electrofocusing has mostly been confined to research work. The new development, however, opens up possibilities for routine applications in

several interesting areas: the food industry, which will probably be the greatest user, employs the method for continual quality control of various foodstuffs; in plant breeding, the method can be used to analyse the proteins present in the seeds of interest; clinical chemistry laboratories may use Immobiline to examine how well a diabetic has managed his diet over the previous two or three weeks; and, using a combination of electrofocusing and electrophoresis, one can produce a chart of the several thousand proteins present in a cell type; changes in position of a certain protein can be used in diagnosis of disease.

Further details can be had from: John Morrison, Search, Lloyd Media, PO Box 340, Mona Vale, NSW 2103.
