SCIENCE CHINA
Life Sciences

A comparative study of distant hybridization in plants and animals

Chen Jie, Luo Mi, Li Shengnan, Tao Min, Ye Xiaolan, Duan Wei, Zhang Chun, QIN Qinbo, Xiao Jun and Liu Shaojun

Citation: SCIENCE CHINA Life Sciences ; doi: 10.1007/s11427-017-9094-2

View online: http://engine.scichina.com/doi/10.1007/s11427-017-9094-2

Published by the Science China Press

SCIENCE CHINA
Life Sciences

• REVIEW •

doi: 10.1007/s11427-017-9094-2

A comparative study of distant hybridization in plants and animals

Jie Chen[1,2†], Mi Luo[1,2†], Shengnan Li[1,2†], Min Tao[1,2], Xiaolan Ye[1,2], Wei Duan[1,2], Chun Zhang[1,2], Qinbo QIN[1,2], Jun Xiao[1,2] & Shaojun Liu[1,2*]

[1]*State Key Laboratory of Developmental Biology of Freshwater Fish, Hunan Normal University, Changsha 410081, China;*
[2]*College of Life Sciences, Hunan Normal University, Changsha 410081, China*

Received February 27, 2017; accepted March 29, 2017; published online August 28, 2017

Distant hybridization refers to crosses between two different species, genera, or higher-ranking taxa, which can break species limits, increase genetic variation, and combine the biological characteristics of existing species. It is an important way of creating genetic variation, fertile strains, and excellent characteristics in new strains and populations. Combining analyses and summaries from many inter-related documents in plants and animals, both domestic and international, including examples and long-standing research on distant hybridization in fish from our laboratory, we summarize and compare the similarities and differences in plant and animal distant hybridization. In addition, we analyze and review the biological characteristics of their different ploidy progenies and the possible causes of disparity in survival rates. Mechanisms of sterility in animal and plant distant hybrids are also discussed, and research methods for the study of biological characteristics of hybrids, including morphology, cytology, and molecular cytogenetics are presented. This paper aims to provide comprehensive research materials and to systematically compare the general and specific characteristics of plant and animal hybrids with regards to reproduction, genetics, growth traits, and other biological characteristics. It is hoped that this paper will have great theoretical and practical significance for the study of genetic breeding and biological evolution of plant and animal distant hybridization.

animals and plants, distant hybridization, reproductive isolation, different ploidy, lineage

Citation: Chen, J., Luo, M., Li, S., Tao, M., Ye, X., Duan, W., Zhang, C., Qin, Q., Xiao, J., and Liu, S. (2017). A comparative study of distant hybridization in plants and animals. Sci China Life Sci 60. doi: 10.1007/s11427-017-9094-2

INTRODUCTION

Distant hybridization refers to crosses between distant species, in contrast to close hybridization, which occurs between varieties of the same species or subspecies. Distant hybridization can combine the biological characteristics of distant species, which breaks species limits and amplifies genetic variations, resulting in genotypic and phenotypic changes and the creation of new variations or species (Liu, 2014). The concept of distant hybridization has also been expanded to geographically distant hybridization, which refers to hybridization between biotypes with different geographical distributions.

Close hybridization, or intraspecific hybridization, can also lead to gene mutation in the hybrid offspring; however, the resulting ranges of variation and genetic breeding are limited. Distant hybrids may contain the genomes of different species, laying the foundation for recombination and communication between the genes of different species. The formation of fertile distant hybrid strains can create new types of

---

†Contributed equally to this work
*Corresponding author (email: lsj@hunnu.edu.cn)

variation, and even new species. In terms of phenotype, distant hybridization integrates the strengths of both parents to confer hybrid advantages in relation to appearance, growth, survival rates, disease resistance, and other traits. In terms of genotype, distant hybridization causes genome-level changes to produce diploids, triploids, and tetraploids. At the DNA scale, distant hybridization also leads to the emergence of recombinant DNA variation in offspring. Moreover, the micro-chromosome of natural gynogenetic diploid fish, which result from distant hybridization, can lead to sub-chromosomal changes (Liu, 2010; Liu, 2014; Zhang et al., 2014).

In China, extensive research has investigated the distant hybridization of rice, corn, soybean, rapeseed, wheat, cotton, and other crops. Many excellent crop varieties have been obtained and popularized in large areas. For instance, the distant hybridization of couch grass (*Elytrigia repens*), common wheat (*Triticum aestivum*), and rye (*Secale cereale*) resulted in the creation of new crop species that do not exist naturally, including new trititrigia and octoploid triticale. The introduction of exogenous genes through distant hybridization has become an important means of expanding genetic variation between plants (Sharma and Gill, 1983). With respect to distant hybridization in animals, agricultural records indicate that distant hybridization was first used in China in 202 BC to improve livestock features. Among vertebrates, Genner created the world's first recorded hybrid, via hybridization between carp (*Cyprinus carpio*) and goldfish (*Carassius auratus*) in the 1450s. From 1558 to 1980, 56 families and 1,080 species of fish were used for experimental research on crossbreeding, with approximately 3,759 studies performed (Schwartz, 1972; Schwartz, 1981). In nature, approximately 10% of animals and 25% of plants have undergone hybridization with at least one other species, and more than 40% of hybrid introgression has involved angiosperms. Distant hybridization facilitates the formation of species and evolutionary radiation. As allopolyploidization resulting from hybridization may underlie the dynamics of new species forming, distant hybridization constitutes the main facilitator of genome evolution and the formation of new species (Mallet, 2005; Grant et al., 2005; Mallet, 2007). In addition, those authors stated that distant hybridization may form new fertile polyploid strains and species as well as new fertile diploid strains and species. With breeding development, genetic resources have been gradually exhausted. Expanding the scope of genetic resources through distant hybridization is of great importance. Based on an analysis of the large body of domestic and foreign literature on distant animal and plant hybridization, and on results from the author's laboratory on the distant hybridization of fish over long periods, this paper presents a relatively systematic and comprehensive comparison and analysis of research and related problems concerning distant hybridization in plants and animals.

GENERAL OVERVIEW OF DISTANT HYBRIDIZATION IN ANIMALS AND PLANTS

General overview of distant hybridization in plants

In traditional plant taxonomy, plants are divided into lower plants (e.g., fern and algae) and higher plants (e.g., mosses, ferns, and seed plants) (Li et al., 2015). Distant hybridization occurs widely in plants and mostly refers to the interspecific hybridization of plants of the same genus or the intergeneric hybridization of plants of different genera. The use of dynamic methods to import plant exogenous genetic material can have effects similar to those of distant hybridization. For instance, by importing garlic (*Allium sativum*), shallot bulb (*Allium fistulosum*), and maize (*Zea mays*) genes into somatic cells of *Brassica chinensis*, it is possible to obtain completely hybridized garlic-greens, shallot bulb-greens, and maize-greens, respectively, between different classes (Zhu, 1986). In the same manner, it is possible to obtain super-phylum hybrid plants, such as mushroom-cabbage (Zhu, 1988).

Distant hybridization of lower plants

Sexual distant hybridization between xianggu mushroom (*Lentinus edodes*, ♂), which belongs to Agaricales, Tricholomataceae, *Lentinus*, and cap fungus (*Pleurotus ostreatus*, ♀), which belongs to Agaricales, Pleurotaceae, *Pleurotus*, can generate delicious new sweet mushroom varieties with hard and crisp qualities with high biological efficiency (Liu et al., 1991; Chen, 1996; Hua, 2004). Hybridization between *Pleurotus ferulae* and fragrant mushrooms can generate new types of Xiangwei mushrooms with a sweet flavor of ferulae and the strong resistance of fragrant mushrooms (Chen and Lin, 1998). In 2007, A mushroom farmer in Gutian mixed sowing seeds of Shiitake mushrooms and *Pleurotus eryngii* Quei and cultivated a sweet apricot mushroom similar to Shiitake mushrooms and *P. eryngii* Quei, which was confirmed to be a hybrid (Fu et al., 2008; Ruan et al., 2012).

The distant hybridization of different genera of algae using whole floating leaf algae (*Pelagophycus porra*, ♀) and giant kelp (*Macrocystis angustifolia*, ♂) resulted in a small increase in the number of generated sporophytes. The sporophytes had a normal form but exhibited unique morphological characteristics of the two genera (Mitsumoto et al., 1983). The hybridization of a female kelp gametophyte (*Laminaria japonica*) and a male sugar kelp gametophyte (*Laminaria saccharina*) resulted in high yields of a distant hybrid, which exhibited early maturity after five consecutive years of breeding, and was denoted as yuanza No. 10 (Jin et al., 2009).

Distant hybridization of higher plants

Examples of distant hybridization in Bryophytes include moss ball (*Phascum cuspidatum*) and short tooth moss (Pottia truncate), which are hermaphrodites, which resulted in 50%

malformation and 50% normal hybridization; 2% of the offspring survived and exhibited a morphology intermediate to that of the parents (Ulychna, 1977). Hybridization between the hermaphrodite *Bruchia microspora* (♀) and *Trematodon longicollis* (♂) generated 7% normal sporophytes, and the morphology of the offspring was most similar to that of the female parent (Rushing and Snider, 1985). Hybrids of *Orthotrichum diaphanum* (♀) and *Orthotrichum sprucei* (♂) vary in size, and are most similar to the male parent (Philibert, 1883). However, the morphologies of gametophytes between *O. gymnostomum* (♀) and *O. obtusifolium* (♂) are between those of the parents (Hedderson, 1986).

Examples of distant hybridizations in ferns include those between *Asplenium antiquum* (♀) and *A. prolongatum* (♂), which yielded the hybrid *A. kenzoi* (Murakami and Iwatsuki, 1999). *Woodsia abbeae* is believed to be a hybrid of *Woodsia oregana* (♀) and *Woodsia ilvensis* (♂) (Wagner, 1987). Spleenwort (*A. trichomanes*) is a species widely distributed throughout the world, particularly in the temperate zone of countries in the northern hemisphere with sporadic distribution in the southern hemisphere (Lovis, 1955). Spleenwort includes a large number of taxonomic groups, which have similar morphologically but different ecology and microscopic structures (Bennert and Fischer, 1993; Lovis, 1964). Spleenworts include three cellular types: diploid, tetraploid, hexaploid, and hybridization between diploid×tetraploid or each tetraploid subspecies, can produce filial generations. Furthermore, hybridization with *A. tripteropus*, *A. viride*, *A. azoricum*, *A. petrarchae*, or other species, can also produce offspring (Reichstein, 1981; Bennert et al., 1989; Bennert et al., 1988; Mokry et al., 1986; Manton, 1950; Lovis and Reichstein, 1977; Lovis et al., 1965; Hou and Wang, 2000). For example, an interspecies cross between the tetraploid *A. azoricum* (♀) and *A. scolopendrium* (♂) can form triploid *Asplenium santamariae* (Rumsey et al., 2004). Additionally, hybridization between *A. azoricum* (♂) and *A. onopteris* (♀) can produce triploid *A. diasii*, also found that one of the genome from *Asplenium onopteris*, and two other genomes from *Asplenium azoricum* (Rumsey et al., 2004)

Examples of distant hybridization in gymnosperms include: pond cypress (*Taxodium ascendens* (Taxodiaceae *Taxodium*), ♀)×China fir (*Cunninghamia lanceolata* (Taxodiaceae *Cunninghamia*, ♂)) (Jiangsu Institute of Botany, 1975), *T. ascendens* (♀)×Japan cedar (*Cryptomeria fortunei* (Taxodiaceae *Cryptomeria*), ♂) (Jiangsu Institute of Botany, 1975), *T. ascendens* (♀)×cedar (*Cedrus deodara* (Cedrus Pinaceae), ♂) (Jiangsu Institute of Botany, 1975), sabino (*T. distichum* (Taxodiaceae *Taxodium*), ♀)×*T. ascendens* (♂) (Jiangsu Institute of Botany, 1975), *T. distichum* (♀)×*C. lanceolata* (♂) (Jiangsu Institute of Botany, 1975), *T. distichum* (♀)×*C. deodara* (♂) (Jiangsu Institute of Botany, 1975); all of these combinations gained fruits. The shape of F_1, whose female parent is *T. distichum*, tends to follow that of the female parent, only with a somewhat different size. The F_1 having *T. ascendens* as the female parent exhibits intermediate characteristics regardless of the size or size of fruit. Examples of interspecific hybridization in gymnosperms includes *Pinus thunbergii* (♀)×Chinese red pine (*Pinus massoniana*, ♂) (Tree breeding group et al., 1973), *P. thunbergii* (♀)×*Pinus yunnanensis* (♂) (Tree breeding group et al., 1973), *P. thunbergii* (♀)×slash pine (*Pinus elliottii*, ♂) (Tree breeding group et al., 1973), *P. thunbergii* (♀)×*Pinus taeda* (♂) (Tree breeding group et al., 1973), *P. thunbergii* (♀)×*Pinus palustris* (♂) (Tree breeding group et al., 1973), *P. massoniana* (♀)×*P. thunbergii* (♂) (Tree breeding group et al., 1973), *P. taeda* (♀)×*P. yunnanensis* (♂) (Tree breeding group et al., 1973), *P. tabuliformis* (♀)×*P. latteri* (♂) (Tree breeding group et al., 1973), *P. taeda* (♀)×*P. elliottii* (♂) (Tree breeding group et al., 1973), *P. taeda* (♀)×*P. rigida* (♂) (Tree breeding group et al., 1973), *P. rigida* (♀)×*P. taeda* (♂) (Tree breeding group et al., 1973), and *P. pinaster* (♀)×*P. elliottii* (♂) (Tree breeding group et al., 1973); the characteristics of the F_1 generation were mostly intermediate between those of the parents (Tree breeding group et al., 1973).

Orchid, the main species of monocotyledons, has a long history of hybridization. *Paphiopedilum* has been subjected to distant hybridization for more than 160 years. The first distant hybrid *P. harrisianum* is a cross between *P. barbatum* (♀)×*P. villosum* (♂) (Zeng et al., 2010). There are 20,262 hybrids on record at the Royal Horticultural Society (RHS), with 48 generic cross hybrids in *Paphiopedilum* recorded. Four hybridization types have been reported with *Paphiopedilum* as the female parent and *Phragmipedium* as the male parent: *P. dayanum* (♀)×*P. sedenii* (♂) (Zeng et al., 2010), *P. bellatulum* (♀)×*P. schlimii* (♂) (Zeng et al., 2010), *P. stonei* (♀)×*P. albopurpureum* (♂) (Zeng et al., 2010), and *P. harrisianum* (♀)×*P. schlimii* (♂) (Zeng et al., 2010). There are also four hybridization types with *Paphiopedilum* as the male parent and *Phragmipedium* as the female parent: *P. longifolium* (♀)×*P. henryanum* (♂) (Zeng et al., 2010), *P. grande* (♀)×*P. memoria* J. H. Walker (♂) (Zeng et al., 2010), *P. schlimii* (♀)×*P. micranthum* (♂) (Zeng et al., 2010), and *P. Bel Royal* (♀)×*P. micranthum* (♂) (Zeng et al., 2010).

In 1917, Kajanus reported interspecific hybridization between Brassica rapeseed (*B. napus*) and turnip (*B. rapa*). Research was then performed on distant hybridization between *Brassica* and *Raphanus*, and interspecific hybridization in *Sinapis*, *Diplotaxis*, and *Brassica* (Peterka et al., 2004; Lelivelt and Krens, 1992; Xing et al., 1988; Lin et al., 2007), From these combinations a series of intraspecies hybrids were obtained, including turnip (*Raphanus sativus*, ♀)×cabbage (*Brassica oleracea*, ♂) (Du and Nikolaĭ, 1974), rocket salad (*Eruca sativa*, ♀)×cabbage (*B. oleracea*, ♂) (Nagaharu et al., 1937), swede type rape (*Brassica napus*, ♀)×*Rorippa indica* (♂) (Dai et al., 2001), and *Brassica campestris* (♀)×turnip (*R. sativus*, ♂) (Huang et al., 2001).

Examples of intergeneric hybrids in dicotyledonous plants also include: *Sorbus aucuparia* (♀)×*Crataegus sanguinea* (♂) (Li, 1955), *Malus pumila* (♀)×*Pyrus pyrifolia* (♂) (Zhang et al., 1991), and longan (*Dimocarpus longgana*, ♀)×leechee (*Litchi chinensis*, ♂) (Zhao et al., 2008). In 1761, Koelreuter conducted hybridization experiments with rustic tobacco *Nicotiana rustica* (♀)×*Nicotiana paniculata* (♂) (Gai, 1997). Nikolaev obtained 12 high-yield varieties of hybrid offspring among *Mentha sachalinensis* (♀)×*M. incana* (♂), with increased content of essential oils and menthol (Nikolaev and Bang, 1976). Examples of interspecific hybridization include: apricot (*Prunus armeniaca*, ♀)×plum (*Prunus salicina*, ♂) (Ruud, 1959), *Actinidia chinensis* (♀)×*Actinidia eriantha* (♂) (Wang et al., 1994), amur grape (*Vitis amurensis*, ♀)×grape (*Vitis vinifera*, ♂) (Song et al., 1998), plum (*P. salicina*, ♀)×apricot (*P. armeniaca*, ♂) (Zeng et al., 2000), *Cerasus avium* (♀)×*Cerasus pseudocerasus* (♂) (Chen et al., 2004), *Rubus idaeus* (♀)×*Rubus crataegifoliu* (♂) (Zhang et al., 2009), red bayberry (*Myrica rubra*, ♀)×*Myrica nana*, ♂) (Xie et al., 2009), *Eriobotrya prinoides* (♀)×*E. japonica* (♂) (Qiao et al., 2010).

General overview of distant hybridization in animals

Distant hybridization of invertebrates

According to a new report, in the invertebrate phylum *Echinodermata*, *Strongylocentrotus purpuratus* eggs can accept *Asterias ochracea* sperm, and the appearance of the hybrid larvae is similar to that of the female parent (Loeb, 1903). Separate crosses of sea hedgehog (*Echinocardium cordatum*, ♀) with limpet (*Acmaea nanshaensis*, ♂) and californianus (*Mytilus edulis*, ♂) and annelid (*Archiannelida protodrilus*, ♂) revealed that these three hybrid larvae are similar to *E. cordatum* larvae. Although sperm from the male parent is introduced into the egg, nuclear fission between distant males and females is difficult to achieve. This is because the male chromosomes are gradually degraded, and are not incorporated into the nucleus of subsequent generations (Kupelwieser, 1909; Zhu, 1961). In contrast, Godlewski combined the eggs of sea urchin with the sperm of comatulid and found that the surface of the hybrid larvae resembled that of the female parent, indicating true fusion of the nucleus and a positive role of sperm cells in mitosis (Godlewski, 1906; Shearer et al., 1913). F_1 hybrids resulting from distant hybridization between *Chlamys farreri* (♀)×*Chlamys nobilis* (♂) exhibit chromosomal polymorphism (Liu et al., 2006). The fertilization cytology of hybridization between *Patinopecten yessoensi*×*Chlamys farreri* showed that sperm can normally enter an egg regardless of whether they are orthogonally or reciprocally crossed. Furthermore, during the normal fertilization process, heterologous sperm plays a role in egg activation and is also involved in the composition of the genetic material (Yang et al., 2002a).

There was large variation in the hybrid progeny of distant hybridization between atlas silkworm (*Attacus atlas*, ♀) collected from the yield, and costor silkworm (*Attacus cynthia*, ♂), and their characteristics were intermediate between those of the parents (Chen, 2000). All generations of offspring derived from the hybridization of giant silkworm (*Antheraea yamamai*, ♀)×*Antheraea polyphemus* (♂) (Zhu and Li, 2002) were able to reproduce, regardless of whether mating occurred between moths, with moths from different area, or backcrossing. Under natural conditions, *Anoplophora glabripennis* and *A. nobilis* can mate with each another. Elytra of the offspring of *A. nobilis* (♀)×*A. glabripennis* (♂) exhibits white, macular, and pale yellow spots, and the offspring of *A. glabripennis* (♀)×*A. nobilis* (♂) exhibits macular and pale yellow spots in their hair (Gao et al., 2000).

Distant hybridization of vertebrates

Distant hybridization of mammals. Some cases of hybridization have been reported in mammals. Including distant hybridization between babby (*Felis catus*, ♀) and serval (*Leptailurus serval*, ♂), which produces a tall, thin hybrid savannah cat resembling a serval. In 1985, hybridization between bottle-nosed dolphin (*Tursiops truncatus*, ♀) and *Pseudorca crassidens* (♂) generated a veritable hybrid wholphin with 66 teeth, compared with the 44 teeth of *P. crassidens* and the 88 teeth of *T. truncates*. In France in 1984, a living hybrid was obtained from a hybridization between goat (*Capra hircus*, ♀) and sheep (*Ovis aries*, ♂) (McGovern, 1973). Since 1953, Bulgarian breeders have been producing viable sheep and goat hybrids. The hybrid ewes have borne a second generation; however, the hybrid rams are sterile (Zhang et al., 2014). A hybrid camel produced by hybridization between camel (*Camelus ferus*, ♀) and llama (*Lama glama*, ♂), via artificial fertilization possessed ears that were intermediate in length between those of its parents. It had a long tail and strong legs that were adapted for desert travel, similar to those of the camel, but lacked a hump and had fluffy fur similar to that of its llama parent.

There are numerous examples of interspecific hybridization in mammals. Sika deer (*Cervus nippon*), red deer (*C. elaphus*), white-lipped deer (*C. albirostris*) and sambar (*Rusa unicolor*) are different *Cervus* species . The hybrid fawn obtained from sambar (*R. unicolor*, ♀)×sika deer (*C. nippon*, ♂) is large and grows rapidly. Hybridization between sika deer (*C. nippon*, ♀)×*C. elaphus xanthopygus* (♂) is widespread, and several hybrids have been obtained. Male and female F_1 hybrids can reproduce, and female deer become pregnant easily. Other types of interspecific hybridization include *C. albirostris* (♀)×*C. nippon* (♂), *R. unicolor* (♀)×*C. elaphus* (♂), and *C. chinensis* (♀)×*C. north America* (♂) (Mi et al., 2014). Following interspecific hybridization among horses, F_1 offspring can be obtained from the hybridization of horse (*Equus caballus*, ♀)×donkey (*Equus asinus*, ♂), very few female mules can cross with male horses or male donkey (Zong et al., 1985). A quagga is the hybrid offspring of donkey (*E. asinus*, ♀)×zebra (*Equus zebra*, ♂). The appearance and hair of a quagga resemble those of a donkey, but its body and limbs feature the black and white stripes of a zebra. The offspring of zebra (*E. zebra*, ♀)×horse (*E. caballus*, ♂) resemble *E. zebra*, and is therefore the reciprocal offspring (Zhang et al., 2014). One example of an interspecific bovine hybrid is the dzo, which is a hybrid between yak (*Bos grunniens*, ♀) and cattle (*Bos taurus*, ♂). Male dzo hybrids are infertile. Males of different hybrid cattle varieties and female dzo are allowed to interbreed freely. Ideal dual-purpose milk and meat offspring have been obtained through the breeding of hybrid progeny (Zhang et al., 2014). Natural mating of the Chinese red stepper, which was bred from the short horn bull and Mongolia cow, with Gannan Yak resulted in clear Red steppe-Yak heterosis, with heavier cubs that had rapid growth and development (Yang et al., 2007). The most representative example of sheep interspecific hybridization is that of *Ovis ammon* and *Ovis aries*. In addition, hybridization between *O. musimon* and *O. aries* has long been practiced in the former Soviet Union, and *O. ammon* arkal has been crossed with *Ovis merino* to create new varieties (Bunch et al., 1976). Examples of interspecific hybridization in other mammals include: lion (*Panthera leo*, ♀)×tiger (*Panthera tigris*, ♂), which produces offspring called tigons, and the mating of *P. tigris* (♀)×*P. leo* (♂), yielding the liger (Gray, 1954). A leopon is the offspring of *P. leo* (♀)×leopard (*P. pardus*, ♂) (Zhang et al., 2014). A grolar bear is the hybrid offspring of polar bear (*Ursus maritimus*, ♀)×silvertip (*Ursus arctos*, ♂) (Zhang et al., 2014).

Distant hybridization of birds. In 1960, Olsen found that the hybrid eggs obtained using the semen of turkey (*Meleagris gallopavo*) and inseminated chickens (*Gus gallus*), resulted in 60% developing to embryos, with 23 hatching, and after 19 weeks of hatching, four individuals weighed up to eight pounds (Olsen, 1960). Examples of intergeneric and genus hybrids in birds include:chicken (*G. gallus*, ♀)×pheasant (*Phasianus colchicus*, ♂) (Zhu, 1961), chicken (*G. gallus*, ♀)×*peacock* (*Pavo cristatus*, ♂) (Zhu, 1961), puinea hen (*Numida meleagris*, ♀)×*peacock* (*P. cristatus*, ♂) (Zhu, 1961), silkie (*Gallus domesticus*, ♀)×quail (*Coturnix coturnix*, ♂) (Zhang et al., 2014), *Tetrao urogallus* (♀)×*Lyrurus tetrix* (♂) (Zhu, 1961), puinea hen (*N. meleagris*, ♀)×chicken (*G. gallus*, ♀) (Zhu, 1961), silkie (*G. domesticus*, ♀)×puinea hen (*N. meleagris*, ♂) (Che and Wang, 2007), muscovy duck (*Cairina moschata*, ♀)×duck (*Anas domestica*, ♂) (Gong et al., 2005), Cherry Valley ducks (♀)×Mandarin duck (♂) (Gong et al., 2005), *Anas platyrhyncha domestica* (♀)×*M. duck* (♂) (Gong et al., 2005), Peking duck (♀)×*C. moschata* (♂) (Huang et al., 1997), and Silver King Pigeon (♀)×*Columba oenas* (♂) (Zhang et al., 2012).

Distant hybridization of reptiles. The hybridization between china terrapin animal and turtle was first appeared in the early 1990s, while it has not aroused people's concern. With the development of turtle breeding around the year 2000, a growing number of hybrid turtles have been identified. To date, no cases of interspecific and intergeneric hybridization have been reported, and no cases of interfamily hybridization have been found. Examples of distant hybridization in turtles include: tortoise (*Mauremys reevesii*, ♀)×*M. sinens* (♂) (Zhou and Li, 2013), *M. sinens* (♀)×*M. reevesii* (♂), *M. sinens* (♀)×*Mauremys mutic* (♂) (Zhou and Li, 2013), *Palea steindachneri* (♀)×*Pelodiscus sinensis* (♂) (Zhou and Li, 2013), *M. mutica* (♀)×*Cuora trifasciata* (♂) (Pan et al., 2009).

Distant hybridization of amphibians. Within amphibians, a few of the hybrids resulting from the cross between hylid (*Hyla arborea*, ♀)×spadefoot toad (*Pelobates cultripes*, ♂) can undergo metamorphosis, and all resemble *H. arborea* (Zhu, 1934). The male chromosomes of the hybrid offspring from hylid (*H. arborea*, ♀)×bufonid (*Bufo calamita*, ♂) were eliminated, and did not participate in embryonic development (Zhu, 1934). In contrast, most of the embryos obtained with bufonid (*B. calamita*, ♀)×hylid (*H. arborea*, ♂) died during the blastocyst and gastrula stages, with only a handful of female tadpoles developing to metamorphosis (Zhu, 1961).

Various cases of interspecific hybridization have been reported in amphibians, including direct and reciprocal crosses between *Rana nigromaculata*×*R. Plancyi*, which can yield small frogs (Ding, 1956). Healthy progeny are obtained from the reciprocal cross of *Microhyla major*×*M. ornata* (Zhu, 1934), while only a few tadpoles are generated from the cross of *Rana guentheri* (♀)×*Rana rugulosa* (♂) (Zhu, 1934). Hybrid offspring from *Rana hubeiensis* (♀)×*R. nigromaculata* (♂) can develop into tadpoles and metamorphose into adult frogs (Liu et al., 1990).

Distant hybridization of fish. There are 32,000 species of fish in nature, representing the largest number of species in vertebrates, thus providing a solid foundation for distant hybridization in fish (Liu, 2014; Liu, 2010; Zhang et al., 2014).

Examples of hybridization between different orders in fishes include: *Megalobrama amblycephala* (Cypriniformes, ♀)×*Siniperca chuatsi* (Perciformes, ♂) (Liu, 2014) and *Hypophthalmichthys molitrix* (Cypriniformes, ♀)×*Pagrosomus major* (Perciformes, ♂) (Zhang et al., 2014).

Inter-familial hybridization has been reported between *Oreochromis aureus* (Perciform Cichlidae, ♀) and *Siniperca chuatsi* (♂), with fingerling survival rates of 0.3%–0.5% (Yang et al., 2004). Examples of hybridization between different carp subfamilies: *Aristichthy nobilis* (♀)×*M. amblycephala* (♂) and its reciprocal cross (Liu, 2014), *A. nobilis* (♀)×*Ctenopharyngodon idellus* (♂) and its reciprocal cross (Guo et al., 1966), *C. idellus* (♀)×*M. amblycephala* (♂) (He et al., 2013b), *C. idellus* (♀)×*H. molitrix* (♂) and its reciprocal cross (Zhang et al., 2014), *C. idellus* (♀)×*C. carpio* (♂) (Ye et al., 1989), *C. idellus* (♀)×*Megalobrama terminalis* (♂) (Liu, 1987), *Mylopharyngodon piceus* (♀)×*M. terminalis*

(♂) (Liu et al., 1981; Chen, 1984), *C. carpio* (♀)×*C. idellus* (♂) (Li, 1991), *H. molitrix* (♀)×*M. amblycephala* (♂) and its reciprocal cross (Pan, 1987; Zhu et al., 1993), *H. molitrix* (♀)×*Xenocypris davidi* (♂) (The Yangtze River Fisheries Research Institute, 1975), and *C. carpio* (♀)×*H. molitrix* (♂) and its reciprocal cross (Gui et al., 1993; Wang and Liu, 1986). No formation lines (formed continuous hybrid lines of F_2 or above) were found in fish crosses. In our laboratory, *C. auratus* red var. (♀)×*M. amblycephala* (♂) (Liu et al., 2007), as well as *M. amblycephala* (♀)×*X. davidi* (♂) (Hu et al., 2012) were obtained as distant hybridization strains. Autotetraploid fish strains (F_2–F_{12}) with genetic variation in characteristics were obtained from the hybrid of *C. auratus* (♀)×*M. amblycephala* (♂) (Qin et al., 2014).

Examples of hybridization between fish genera include: *C. auratus* red var. (♀)×*C. carpio* (♂) (Liu, 2010; Liu et al., 2001), *C. auratus gibelio* (♀)×*C. carpio var. singguoensis* (♂) (Jiang et al., 1983), *H. molitrix* (♀)×*A. nobilis* (♂) (Zhang et al., 1979b) and its reciprocal cross, *Parabramis pekinensis* (♀)×*M. terminalis* (♂) (Yin et al., 1974), *M. amblycephala* (♀)×*P. pekinensis* (♂) (Lin, 1984), *M. piceus* (♀)×*C. idellus* (♂) (The Breeding Room of the Yangtze River Fisheries Research Institute, 1975), *Rhabodosargus sarba* (♀)×*P. major* (♂) (Qu et al., 2000), *Sparus latus* (♀)×*R. sarba* (♂) (Zhang et al., 1990), *R. sarba* (♀)×*Sparus macrocephlus* (♂) (Zhang et al., 1990), *Plagiognathops microlepis* (♀)×*X. davidi* (♂) (Fisheries Research Institute of Guangxi for Chamber dace Group, 1980), *Cirrhinus molitorella* (♀)×*Sinilabeo decorus* (♂) (Zhang et al., 1984), *O. niloticus* (♀)×*Sarotherodon melanotheron* (♂) and its reciprocal cross (Li et al., 2008). In our laboratory, we obtained F_2 hybrids and subsequent generations from distant hybridization of *C. auratus* red var. (♀)×*C. carpio* (♂) (Liu, 2010; Liu et al., 2001), *C. carpio* (♀)×*C. auratus* red var. (♂) (Liu, 2014), *M. amblycephala* (♀)×*Erythroculter ilishaeformis* (♂) (Liu, 2010), *E. ilishaeformis* (♀)×*M. amblycephala* (♂) (Liu, 2014), allotetraploid (4*n*AT) hybrid lineages (F_3–F_{26}) were obtained from the hybrid of *C. auratus* red var. (♀)×*C. carpio* (♂) (Liu, 2010; Liu et al., 2001).

Examples of interspecific hybridization include: *C. carpio yuankiang* (♀)×*Cpellegrini pellegrin* (♂) (Zhang et al., 1979a), *Oreochromis mossambicus* (♀)×*Tilapia nilotica* (♂) and its reciprocal cross (Liu et al., 1985; Wan et al., 1987), *Silurusmeri dionalis* (♀)×*Silurusmeri asotus* (♂) (Wang et al., 2004), *M. terminalis* (♀)×*M. amblycephala* (♂) and its reciprocal cross (Yang et al., 2002b), *Siniperca kneri* (♀)×*S. chuatsi* (♂) (Lu et al., 2013).

BARRIERS AND SOLUTIONS OF ANIMALS AND PLANTS DISTANT HYBRIDIZATION

Distant hybridization and reproductive isolation

Distant hybridization is often difficult to achieve due to different degrees of reproductive isolation among species (Deng et al., 2010a; Deng et al., 2010b; Wolff and Peters-van Rijn, 1993). Successful distant hybridization of plants is dependent on pollination and fertilization, which occur in a series of events from the germination of pollen grains to pollen tube growth, and from double fertilization to zygote and endosperm development. However, various factors are associated with reproductive isolation in natural hybrids of animals (e.g., mating season, place, time, and pheromone secretion), and any factor occurring out of order will directly result in hybridization failure (McClure and Franklin-Tong, 2006; Frédéric, 2008; Raghavan, 2007). The reproductive isolation of distant hybridization between species typically involves a variety of mechanisms acting in concert, and depending on the time-period, reproductive isolation in the distant hybridization of animals and plants can be divided into pre- and post-zygotic reproductive isolation.

Pre-zygotic reproductive isolation

Pre-zygotic isolation, or segregation occurring before fertilization, is a barrier usually encountered in the distant hybridization of species under natural conditions. Under ecological and habitat isolation, two species that are able to produce healthy fertile offspring, but are not in different areas or different ecological niches, can achieve distant hybridization. For instance, differences in meteorological factors affecting *P. yunnanensis* and *P. densata* within a suitable living area result in flowering asynchronism, thus hindering the exchange of genes between the two species and resulting in isolation (Song et al., 2002). Work by Knowlton showed that geographical isolation resulting from the uplift of the Panama isthmus approximately 3-million-years-ago led to speciation on both sides of the isthmus. For example, seven pairs of *Alpheus* species from the Caribbean and Pacific exist on both sides of the bridge, with strong reproductive isolation between these pairs (Knowlton, 1993). Diet selection and reproductive isolation tests revealed that the offspring of the different hybridized populations were all male (*Panonchus citri* is parthenogenetic and androgenetic), suggesting that these two species have undergone reproductive isolation due to long-term host plant selection pressures (Liu et al., 2004).

Under seasonal and temporal isolation, organisms generally have a certain reproductive season and time (e.g., estrus and mating in animals, and flowering and pollination in plants). If the growing season or time of the same population is different, seasonal or temporal isolation will prevent the exchange of genes. When seasonal or temporal isolation occurs, distant hybridization cannot proceed smoothly between many plants. For example, sugarcane (*Saccharum officinarum*) is a late-flowering tropical species that typically blooms in December, *S. spontaneum* blooms in September to January of the following year, and *S. arundinaceum* flowers in November to December; such different flowering seasons spur the development of reproductive isolation (Sun et al., 2010). Wood frog (*R. Amurensis*), *R. pipiens*, and *R. clamitans* live in the same pond in North America. When the temperature of the water reaches 7°C (in February), *R. amurensis* begins to spawn, followed by *R. pipiens*, which spawns when water temperature reaches 12°C (in early March). *R. clamitans* starts to spawn when water temperatures reach 16°C (at the end of March). These differing breeding seasons lead to reproductive isolation (Chen, 1999).

Gametic isolation refers to the failure of fertilization due to a physiological lack of coordination after pollination or mating. For organisms undergoing *in vitro* fertilization, the male and female gametes may not attract one another. In cases of internal fertilization, the gamete or gametocyte of one species may not survive in the genital ducts of the other. For example, female rabbits (*Oryctolagus cuniculus*) begin to ovulate when male rabbit sperm reaches the oviducts 6-hours later. While conspecific sperm can live for approximately 38 h in the reproductive tract, heterogeneous sperm can only survive 3–4 h in the unaccommodating environment, thus preventing fertilization (Liu, 1982). Recent studies have shown that gamete affinity is related to oxidase activity in species. Beach et al. suggested that immune-mediated inhibition may maintain reproductive isolation between different species. Some scholars have speculated that during the process of recognition between pollen and pistil, an inhibitory factor may hinder the attachment and germination of pollen in stigma and induce the deposition of callose so that the pollen tube does not cross the stigma and enter the ovary. Genetic differences between distant hybridization parents hinder the mutual recognition of pollen and stigma to control incompatibility between distant species and plant development (Van Tuyl et al., 1991).

Post-zygotic reproductive isolation

Post-zygotic reproductive isolation occurs when the gametes of two species are capable of fertilization but a stable population cannot be formed for various reasons. Types of hybrid inviability or weakness include situtations when a zygote is performed but the zygote cannot survive; those when a zygote can survive but the embryo develops to a certain stage and dies, and those when larvae do not live to maturity, thus leaving no offspring. For example, in distant hybridization between *Linum austriacum* (♀) and *L. Perenne* (♂), the embryo of the hybrid cannot fully develop, because the embryo and endosperm are not coordinated. Alternatively, if the embryo and endosperm are more closely coordinated, hybrid embryos can develop fully but cannot pierce the female parent seed coat, and thus the resulting seeds cannot germinate and hybridization cannot occur. The internal mechanism of this disorder remains unclear (Chen, 1999). The "mechanistic model theory" has been postulated to explain the abnormal growth of maternal tissue (e.g., dysplasia in integument tapetum), which mechanically limits the growth of the embryo and endosperm, thus hindering the development of the embryo and endosperm and resulting in abortion (Van Tuyl et al., 1991; Gutierrez-Marcos et al., 2003). The nutritional deficiency hypothesis suggests that a lack of nutrition leads to the degradation of hybrid embryos, and that when a degraded endosperm cannot provide the nutrients required by the embryo, its development will decline further. Endosperm development is believed to be abnormal due to a lack of coordination between the immature embryo and endosperm tissue, or between the embryo, endosperm, and maternal tissues (e.g., integumentary tapetum) (Deng et al., 2010b; Raghavan, 2007; Gutierrez-Marcos et al., 2003). Some researchers also believe that the genetic imprinting of the parent determines disharmony between the embryo, endosperm, and parent tissue, causing development to appear abnormal (Gutierrez-Marcos et al., 2003).

Hybrid sterility occurs when hybridization between different species results in homozygous mature F_1 hybrids that cannot produce offspring. For example, mules, which arise by crossing a horse and a donkey, cannot reproduce because horses possess 64 chromosomes and donkeys have 63. Thus, mules have 63 meaning that when a mule forms germ cells, its chromosomes cannot form pairs (due to synapsis) and cannot achieve meiotic division or form normal gametes, resulting in infertility (Zhang et al., 2014). Attempts by the Institute of Oceanography of the Chinese Academy of Sciences to achieve interspecific hybridization between *Argopecten irradians* and *A. purpuratus* have revealed that no reproductive isolation exists between these two hybrid species, bidirectional fertilization can be realized, and the offspring hatch normally and live to adulthood. Internally transcribed spacer 1 (ITS1) markers have also verified the success of this form of hybridization. HE (Hematoxylin, H; Eosin, E) staining of paraffin sections of mature heterozygous gonads from F_1 development to sex maturity revealed that male gonads are significantly degraded and cannot produce healthy sperm, whereas female gonads develop further and can form normal eggs but cannot backcross with the parent, resulting in typical post-zygotic isolation: heterozygous male sterility (Zhang et al., 2012).

An important pathway to male sterility in plants involves distant hybridization. According to Kaul, approximately 10% of nuclear male sterile material and at least 70% of cytoplasmic male sterile material result from interspecific or intergeneric hybridization (Kaul, 1988). In a sterile male plant line, female reproductive organs are normal, but male reproductive organs are infertile and cannot produce functional pollen plants. There are two main forms of male sterility: nuclear male sterility (NMS) and cytoplasmic male sterility (CMS). Nuclear male sterility refers to the presence of sterile genes in the cell nuclei of the offspring. Genic male sterility can take two forms (single gene control and multigene interaction), which are mostly controlled by the recessive gene. Single gene-controlled dominant nuclear male sterility is typically due to gene mutations, such as FS-6 and Taigu genic male-sterile wheat. The main form of sterility occurring through gene interactions involves the interaction between dominant male sterile genes and restoring fertile epistatic genes. Male sterility has only been observed when dominant male sterile genes are present. Thus, fertility occurs when the two co-exist. CMS is mainly controlled by genetic material in the cytoplasm, while cytoplasmic physiology and biochemistry are shaped by the nuclear gene regulation of nuclear gene interactions produced by the infertility type (Tang et al., 1994). The abortive gene of plant CMS is present in mitochondria. Nuclear-cytoplasmic types of genic male sterile genes originating from plant distant hybridization mainly exist in distant hybrid parents, while the restorer gene is present in the close hybridization parent of the cytoplasmic donor. The cell nucleus of the cytoplasmic donor can restore nuclear replacement and fertility, indicating that distant hybridization does not cause cytoplasmic mutation. In contrast, the interaction between the new nuclear genotype and the coordinated cytoplasm may lead to male sterility due to nuclear-nuclear interactions between distant parents (Liu and Guan, 1995).

Hybrid weakness and interspecific hybridization can form fertile F_1 individuals; however, for F_2 or backcross progenies, the vast majority of recombinant genotypes are inharmonious and thus cannot adapt or survive. For example, for the spotted mutant of *Gossypium hirsutum,* as a female parent hybridized with *G. tomentosum*, the F_1 offspring survived and were fertile. However, among 106 F_2 seeds of the F_1 plant, seven grain embryos were small and did not germinate, and 32 grains appeared normal but did not germinate. Nine grains pierced the seed coat, but the cotyledons did not spread. Twenty-two seeds grew into seedlings, but died soon thereafter. A total of 116 seeds grew into weak seedlings that lived for only three weeks. Among 20 grains that grew into seedlings that lived for more than three weeks, subsequent development was abnormal. These results reveal a mechanism of hybrid decline in the F_2 genetic recombination gene, which is unable to withstand natural selection pressures, ultimately leading to its failure to survive (Chen, 1999).

This form of distant hybridization incompatibility in animals and plants has been attributed to three factors: first, the quantities or karyotypes of the two parent chromosomes can differ. In biology, all genetic phenomena and their regulation, are dependent on the stability of the morphology, structure, and number of chromosomes. When the number of chromosomes in the female parent is less than that in the male parent, forming viable offspring is difficult. Differences in the number of chromosomes results in differences in the quantity and nature of the genome, thus leading to the disordering of alleles in heterozygous individuals, the development of metabolic disorders, the underdevelopment of heterozygous individuals, and even death. Long-term laboratory studies have revealed that the survival rate of offspring derived through distant hybridization in fish is related to the number of chromosomes in the parent (Liu, 2014). When the number of chromosomes in the female parent is greater than or equal to that in the male parent, viable offspring are easily formed. When the number of chromosomes in the female parent is greater than that in the male parent, allotriploid and autodiploid fish can form (natural diploid gynogenetic fish) in hybrid F_1, autotetraploid fish can be bred from the self-bred progeny of allotetraploid fish, and continuous selfing can form autotetraploid fish strains. When the number of chromosomes in the female parent is equal to that in the male parent, allodiploid fish can form in the hybrid F_1, allotetraploid fish can be bred from the self-bred progeny of allodiploid fish, and allotetraploid fish strains can form through continuous selfing (Liu, 2014). Successful distant hybridization in the author's laboratory indicates that it is easier to obtain outcrossing species when the karyotypes of the parents are similar (Table 1). Our data indicate that it is also easier to obtain surviving distant plant and animal hybrids when the parents have a similar number of chromosomes (Tables 1–3). In a distant hybridization test of *C. idellus* ($2n$=48, ♀) and common carp ($2n$=100, ♂), the number of chromosomes in the female parent was less than that in the male parent, resulting in diploid hybrids that rarely survive in the resulting F_1 hybrids (Ye et al., 1989). Some hybrids carry the same number of chromosomes as their parents, but their karyotypes differ, or the sperm and egg pairs cannot survive due to disordered allelic expression in their offspring.

Second, differences in the gene locus or in the temporal order of enzyme expression can occur. When the genetic relationship between hybrid parents is distant, the temporal ordering of allelic gene expression may not be synchronized or mutually inhibited. Enzyme incompatibility can lead to spatiotemporal disorders in the induction of hybrid embryonic tissue and organ formation, resulting in malformations or premature death. For example, in the hybridization of birds, with a significant distance between the parent species, Levine and Haley observed that the activation of enzyme-encoding genes of maternal inheritance was prioritized (Levine and Haley, 1975). However, no antidiuretic hormone (ADH) was observed in hybrid chicken and quails, and following the embryonic development of hybrid bird for 13 days, ADH disappeared gradually, indicating that the maternal inheritance of ADH was restrained. Peter showed that genes encoding LDH in the embryos of hybrid poultry were activated within 12 h between fertilization and spawning. The pattern of inheritance in hybrid poultry embryos that prioritized maternal genetic isoenzymes was converted to one of paternal inheritance in different tissues of the adult hybrid birds, following trends in isozyme evolution similar to those in rooster (Meyerhof and Haley, 1975). This may explain the large number of deaths among chicken and quail hybrids.

Third, nuclear-cytoplasmic incompatibility can occur. The

Table 1 Distant hybridization combinations in fish from our laboratory

Phylogenetic relationship		Hybridized combination	Karyotype combination	Genetic algebra
Intergeneric	With identical chromosome numbers	*Carassius auratus* red var. (♀)×*Cyprinus carpio* (♂) (2n=100)×(2n=100)	22m+34sm+22st+22t×22m+34sm+22st+22t	F_1–F_{26}
		Cyprinus carpio Koi (♀)×*Carassius auratus* red var. (♂) (2n=100)×(2n=100)	22m+34sm+22st+22t×22m+34sm+22st+22t	F_1–F_2
		Megalobrama amblycephala (♀)×*Erythroculter ilishaeformis* (♂) (2n=48)×(2n=48)	18m+22sm+8st×18m+22sm+8st	F_1–F_4
		Erythroculter ilishaeformis (♀)×*Megalobrama amblycephala* (♂) (2n=48)×(2n=48)	18m+22sm+8st×18m+22sm+8st	F_1–F_4
Subfamily	With identical chromosome numbers	*Ctenopharyngodon idellus* (♀)×*Megalobrama amblycephala* (♂) (2n=48)×(2n=48)	18m+24sm+6st×18m+26sm+4st	F_1
		Megalobrama amblycephala (♀)×*Xenocypris davidi* (♂) (2n=48)×(2n=48)	18m+26sm+4st×18m+26sm+4st	F_1–F_2
		Xenocypris davidi (♀)×*Megalobrama amblycephala* (♂) (2n=48)×(2n=48)	18m+26sm+4st×18m+26sm+4st	F_1
		Xenocypris davidi (♀)×*Erythroculter ilishaeformis* (♂) (2n=48)×(2n=48)	18m+26sm+4st×18m+22sm+8st	F_1
		Erythroculter ilishaeformis (♀)×*Xenocypris davidi* (♂) (2n=48)×(2n=48)	18m+22sm+8st×18m+26sm+4st	F_1
		Megalobrama amblycephala (♀)×*Elopichthys bambusa* (♂) (2n=48)×(2n=48)	To be measured	F_1
	With different chromosome numbers	*Carassius auratus* red var. (♀)×*Megalobrama amblycephala* (♂) (2n=100)×(2n=48)	22m+34sm+22st+22t×18m+22sm+8st	F_1–F_{12}
		Carassius auratus red var. (♀)×*Xenocypris davidi* (♂) (2n=100)×(2n=48)	22m+34sm+22st+22t×18m+26sm+4st	F_1
		Carassius auratus red var. (♀)×*Erythroculter ilishaeformis* (♂) (2n=100)×(2n=48)	22m+34sm+22st+22t×18m+22sm+8st	F_1
Subfamily	With different chromosome numbers	*Carassius auratus* red var. (♀)×*Elopichthys bambusa* (♂) (2n=100)×(2n=48)	To be measured	F_1

egg cytoplasm controls the retardation or acceleration of gene expression in hybrid embryos. When the cytoplasm of an egg cannot coordinate with the DNA of the sperm nucleus, gene expression will be blocked or accelerated, and thus the embryo will not develop normally, and will subsequently die (Lou and Li, 2006). Whitt studied generic hybridization between Cichlidae fish and showed that the hybrid offspring of *Lepomis cyanellus* (♀) and *Micropterus salmoides* (♂) can grow and develop normally, while those of *M. salmoides* (♀) and *L. cyanellus* (♂) are malformed at the embryonic stage and fail to hatch (Whitt, 1981). Those results show that the offspring of reciprocal crosses cannot survive; this is not due to a difference in the number of chromosomes and karyotypes, but rather because the sperm chromosome of *L. cyanellus* does not show a strong connection to the egg cytoplasm of *M. salmoides*. This also occurs in the offspring of reciprocal crosses of cyprinoid and crucian, and of grass carp and *M. terminalis* (Liu, 1993).

In both plants or animals, the degree of reproductive isolation in distant hybridization is often asymmetric, meaning that the egg of one species and the sperm of another can be fertilized, but the reverse cannot occur (Mallet, 2008). For example, hybridization experiments performed in our laboratory on red carp and *M. amblycephala* generated diploid, triploid, and tetraploid offspring from red carp female parents and *M. amblycephala* male parents, whereas no live off-

Table 2 Distant hybridization combinations in aniamls and plants

Phylogenetic relationship			Hybridized combination	Group
Interspecific	With identical chromosome numbers	Plants	*Laminaria japonica* (♀)×*Laminaria saccharina* (♂) (Jin et al., 2009) $(2n=62)\times(2n=62)$	Phytocomycetes
			Prunus armeniaca (♀)×*Prunus salicina* (♂) (Ruud, 1959) $(2n=16)\times(2n=16)$	Angiosperms
			Actinidia chinensis (♀)×*Actinidia eriantha* (♂) (Wang et al., 1994) $(2n=58)\times(2n=58)$	Angiosperms
			Vitis amurensis (♀)×*Vitis vinifera* (♂) (Song et al., 1998) $(2n=38)\times(2n=38)$	Angiosperms
			Prunus salicina Lindl. (♀)×*Prunus armeniaca* (♂) (Zeng et al., 2000) $(2n=16)\times(2n=16)$	Angiosperms
			Cerasus avium (♀)×*Cerasus pseudocerasus* (♂) (Chen et al., 2004) $(2n=16)\times(2n=16)$	Angiosperms
			Rubus idaeus (♀)×*R. crataegifoliu* (♂) (Zhang et al., 2009) $(2n=14)\times(2n=14)$	Angiosperms
			Myrica rubra (♀)×*M. nana* (♂) (Xie et al., 2009) $(2n=16)\times(2n=16)$	Angiosperms
			Eriobotrya prinoides (♀)×*E. japonica* (♂) (Qiao et al., 2010) $(2n=34)\times(2n=34)$	Angiosperms
		Animals	*Cervus albirostris* (♀)×*Cervus nippon* (♂) (Mi et al., 2014) $(2n=66)\times(2n=66)$	Mammals
			The red deer (♀)×*North American deer* (♂) (Mi et al., 2014) $(2n=68)\times(2n=68)$	Mammals
			B. taurus (♀)×*Bos grunniens* (♂) (Zhang et al., 2014) $(2n=60)\times(2n=60)$	Mammals
			Shorthorn (♀)×*Mongolia cow* (♂) (Yang et al., 2007) $(2n=60)\times(2n=60)$	Mammals
			Panthera leo (♀)×*P. tigri* (♂) (Gray, 1954) $(2n=38)\times(2n=38)$	Mammals
			P. tigris (♀)×*Panthera leo* (♂) (Gray, 1954) $(2n=38)\times(2n=38)$	Mammals
			Panthera leo (♀)×*Panthera pardus* (♂) (Zhang et al., 2014) $(2n=38)\times(2n=38)$	Mammals
			Ursus arctos (♀)×*Ursus maritimus* (♂) (Zhang et al., 2014) $(2n=74)\times(2n=74)$	Mammals
			Mauremys reevesii (♀)×*M. sinens* (♂) (Zhou and Li, 2013) $(2n=52)\times(n=52)$	Reptilia
			M. sinens (♀)×*Mauremys reevesii* (♂) (Zhou and Li, 2013) $(2n=52)\times(2n=52)$	Reptilia
			M. sinens (♀)×*M. mutic* (♂) (Zhou and Li, 2013) $(2n=52)\times(2n=52)$	Reptilia
			Rana nigromaculata (♀)×*R. plancyi* (♂) (Ding, 1956) $(2n=26)\times(2n=26)$	Amphibians
			R. plancyi (♀)×*Rana nigromaculata* (♂) (Ding, 1956) $(2n=26)\times(2n=26)$	Amphibians
			R. guentheri (♀)×*R. rugulosa* (♂) (Zhu, 1934) $(2n=26)\times(2n=26)$	Amphibians
			Microhyla major (♀)×*M. ornata* (♂) (Zhu, 1934) $(2n=24)\times(2n=24)$	Amphibians
			M. ornata (♀)×*Microhyla major* (♂) (Zhu, 1934) $(2n=24)\times(2n=24)$	Amphibians
			Rana hubeinensis (♀)×*Rana nigromaculata* (♂) (Liu et al., 1990) $(2n=26)\times(2n=26)$	Amphibians

(*To be continued on the next page*)

(*Continued*)

Phylogenetic relationship			Hybridized combination	Group
Interspecific	With different chromosome numbers	Plants	*Asplenium azoricum* (♀)×*A. scolopendrium* (♂) (Rumsey et al., 2004) $(4n=144)\times(2n=72)$	Pteridophyta
			A. onopteris (♀)×*A. azoricum* (♂) (Rumsey et al., 2004) $(2n=72)\times(4n=144)$	Pteridophyta
			Taxodium distichum (♀)×*Taxodium ascendens* (♂) (Jiangsu Institute of Botany, 1975) $(2n=22)\times(2n=24)$	Gymnosperae
		Animals	*Chlamys farreri* (♀)×*C. nobilis* (♂) (Liu et al., 2006) $(2n=38)\times(2n=32)$	Invertebrate
			Antheraea yamamai (♀)×*A. polyphemus* (♂) (Zhu and Li, 2002) $(n=31)\times(n=30)$	Invertebrate
			Rusa unicolor (♀)×*Cervus nippon* (♂) (Mi et al., 2014) $(2n=62)\times(2n=66)$	Mammals
			Cervus nippon (♀)×*Cervus elaphus xanthopygus* (♂) (Mi et al., 2014) $(2n=66)\times(2n=68)$	Mammals
			Rusa unicolor (♀)×*C. elaphus* (♂) (Mi et al., 2014) $(2n=62)\times(2n=68)$	Mammals
			Equus caballus (♀)×*Equus asinus* (♂) (Zong et al., 1985) $(2n=64)\times(2n=62)$	Mammals
			Equus asinus (♀)×*Equus caballus* (♂) (Zong et al., 1985) $(2n=62)\times(2n=64)$	Mammals
			Equus asinus (♀)×*Equus quagga* (♂) (Zhang et al., 2014) $(2n=62)\times(2n=44)$	Mammals
			Equus quagga (♀)×*Equus caballus caballus* (♂) (Zhang et al., 2014) $(2n=44)\times(2n=64)$	Mammals
			Equus caballus caballus (♀)×*Equus quagga* (♂) (Zhang et al., 2014) $(2n=64)\times(2n=44)$	Mammals
			Ovis musimon (♀)×*Ovis aries* (♂) (Bunch et al., 1976) $(2n=60)\times(2n=54)$	Mammals
			Ovis ammon arcal (♀)×*Ovis merino* (♂) (Bunch et al., 1976) $(2n=58)\times(2n=54)$	Mammals
Intergeneric	With identical chromosome numbers	Plants	*Taxodium distichum* (♀)×*Cunninghamia lanceolata* (♂) (Jiangsu Institute of Botany, 1975) $(2n=22)\times(2n=22)$	Gymnosperae
			Raphanus sativus (♀)×*Brassica oleracea* (♂) (Du, 1974) $(2n=18)\times (2n=18)$	Angiosperms
			Sorbus aucuparia (♀)×*Crataegus sanguinea* (♂) (Li, 1955) $(2n=34)\times(2n=34)$	Angiosperms
			Malus pumila (♀)×*Pyrus pyrifolia* (♂) (Zhang et al., 1991) $(2n=34)\times(2n=34)$	Angiosperms
			Dimocarpus longgana (♀)×*Litchi chinensis* (♂) (Zhao et al., 2008) $(2n=30)\times(2n=30)$	Angiosperms
		Animals	*Patinopecten yessoensi* (♀)×*Chlamys farreri* (♂) (Yang et al., 2002a) $(2n=38)\times(2n=38)$	Invertebrate
			Chlamys farreri (♀)×*Patinopecten yessoensi* (♂) (Yang et al., 2002a) $(2n=38)\times(2n=38)$	Invertebrate
			Felis catus (♀)×*Leptailurus serval* (♂) $(2n=38)\times(2n=38)$	Mammals
			Camelus ferus (♀)×*Lama glama* (♂) (Zhang et al., 2014) $(2n=74)\times(2n=74)$	Mammals
			Gallus domesticus (♀)×*Coturnix coturnix* (♂) (Zhang et al., 2014) $(2n=78)\times(2n=78)$	Aves
			Cairina moschata (♀)×*Anas domestica* (♂) (Gong et al., 2005) $(2n=78)\times(2n=78)$	Aves
			Anas platyrhyncha domestica (♀)×*Mandarin duck* (♂) (Gong et al., 2005) $(2n=78)\times(2n=78)$	Aves
			Palea steindachneri (♀)×*Pelodiscus sinensis* (♂) (Zhou and Li, 2013) $(2n=66)\times(2n=66)$	Reptilia
			Mauremys mutica (♀)×*Cuora trifasciata* (♂) (Pan et al., 2009) $(2\mathrm{n}=52)\times(2\mathrm{n}=52)$	Reptilia

(*Continued*)

(*To be continued on the next page*)

Phylogenetic relationship			Hybridized combination	Group
Intergeneric	With different chromosome numbers	Plants	*Pleurotus ostreatus* (♀)×*Lentinus edodes* (♂) (Liu et al., 1991; Chen, 1996; Hua, 2004) $(n=9)\times(n=8)$	Phytocomycetes
			Taxodium ascendens (♀)×*Cunninghamia lanceolata* (♂) (Jiangsu Institute of Botany, 1975) $(2n=24)\times(2n=22)$	Gymnosperae
			Taxodium ascendens (♀)×*Cryptomeria fortunei* (♂) (Jiangsu Institute of Botany, 1975) $(2n=24)\times(2n=22)$	Gymnosperae
			Brassica napus L. (♀)×*Brassica rapa* (♂) (Peterka et al., 2004; Lelivelt, 1992; Xing et al., 1988; Lin et al., 2007) $(2n=38)\times(2n=20)$	Angiosperms
			Eruca sativa (♀)×*Brassica oleracea* (♂) (Nagaharu et al., 1937) $(2n=22)\times(2n=18)$	Angiosperms
			Brassica napus L. (♀)×*Rorippa indica* (♂) (Dai et al., 2001) $(2n=38)\times(2n=32)$	Angiosperms
			Brassica campestris (♀)×*Raphanus sativus* (♂) (Huang et al., 2001) $(2n=20)\times(2n=18)$	Angiosperms
		Animals	*Tursiops truncatus* (♀)×*Pseudorca crassidens* (♂) $(2n=44)\times(2n=48)$	Mammals
			Capra hircus (♀)×*Ovis aries* (♂) (McGovern, 1973) $(2n=60)\times(2n=54)$	Mammals
			Gus gallus (♀)×*Meleagris gallopavo* (♂) (Olsen, 1960) $(2n=78)\times(2n=82)$	Aves
			Gus gallus (♀)×*Phasianus colchicus* (♂) (Zhu, 1961) $(2n=78)\times(2n=82)$	Aves
			Vietnam chicken (♀)×*Pavo cristatus* (♂) (Zhu, 1961) $(2n=78)\times(2n=76)$	Aves
			Numida meleagris (♀)×*Pavo cristatus* (♂) (Zhu, 1961) $(2n=74)\times(2n=76)$	Aves
			Numida meleagris (♀)×*Gus gallus* (♂) (Zhu, 1961) $(2n=74)\times(2n=78)$	Aves
			Gallus domesticus (♀)×*Numida meleagris* (♂) (Che and Wang, 2007) $(2n=78)\times(2n=74)$	Aves
			Peking duck (♀)×*Cairina moschata* (♂) (Huang et al., 1997) $(2n=80)\times(2n=78)$	Aves
Inter-familial	With identical chromosome numbers	Plants	*Taxodium distichum* (♀)×*Cedrus deodara* (♂) (Jiangsu Institute of Botany, 1975) $(2n=22)\times(2n=22)$	Gymnosperae
	With different chromosome numbers	Plants	*Taxodium ascendens* (♀)×*Cedrus deodara* (♂) (Jiangsu Institute of Botany, 1975) $(2n=24)\times(2n=22)$	Gymnosperae
		Animals	*Hyla arborea* (♀)×*Pelobates cultripes* (♂) (Zhu, 1934) $(2n=24)\times(2n=26)$	Amphibians
			Hyla arborea (♀)×*Bufo calamita* (♂) (Zhu, 1934) $(2n=24)\times(2n=22)$	Amphibians
			Bufo calamita (♀)×*Hyla arborea* (♂) (Zhu, 1934) $(2n=22)\times(2n=24)$	Amphibians
Classes	With different chromosome numbers	Animals	*Strongyloceutrotus purpuratus* (♀)×*Asterias ochracea* (♂) (Loeb, 1903) $(2n=46)\times(2n=44)$	Invertebrate

spring were obtained in the reverse test group. This may have been related to differences in the genetic materials of the parents and the various mechanisms of reproduction isolation involved (Liu, 2014). Pre- and post-zygotic processes tend to decrease the fitness of the hybrid progeny, which is consistent with natural selection, and tends to ensure the independence of a species by eliminating hybrids. However, when heterozygotes encounter suitable ecological niches, new species can form due to the loss of reproductive isolation mechanisms. Therefore, reproductive isolation safeguards the biological evolution of a species, and overcoming reproductive isolation constitutes a key force underlying the creation of new species through biological evolution, and is a key factor affecting distant hybridization in artificial breeding.

Table 3 Distant hybridization combinations in fish described in this paper

Phylogenetic relationship		Num	Hybridized combination
Interspecific	With identical chromosome numbers	1	*Cyprinus carpio* (♀)×*Cpellegrini pellegrini* (♂) (Zhang et al., 1979a) $(2n=100)\times(2n=100)$
		2	*O. mossambicus* (♀)×*Tilapia nilotica* (♂) (Liu et al., 1985; Wan et al., 1987) $(2n=44)\times(2n=44)$
		3	*Tilapia nilotica* (♀)×*O. mossambicus* (♂) (Liu et al., 1985; Wan et al., 1987) $(2n=44)\times(2n=44)$
		4	*Silurusmeri dionalis* (♀)×*S. asotus* (♂) (Wang et al., 2004) $(2n=58)\times(2n=58)$
		5	*M. terminalis* (♀)×*Megalobrama amblycephala* (♂) (Yang et al., 2002b) $(2n=48)\times(2n=48)$
		6	*Megalobrama amblycephala* (♀)×*M. terminalis* (♂) (Yang et al., 2002b) $(2n=48)\times(2n=48)$
		7	*S. kneri* (♀)×*Siniperca chuatsi* (♂) (Lu et al., 2013) $(2n=48)\times(2n=48)$
Intergeneric	With identical chromosome numbers	1	*Hypophthalmichthys molitrix* (♀)×*Aristichthy nobilis* (♂) (Zhang et al., 1979b) $(2n=48)\times(2n=48)$
		2	*Aristichthy nobilis* (♀)×*Hypophthalmichthys molitrix* (♂) (Zhang et al., 1979b) $(2n=48)\times(2n=48)$
		3	*Parabramis pekinensis* (♀)×*M. terminalis* (♂) (Yin et al., 1974) $(2n=48)\times(2n=48)$
		4	*Megalobrama amblycephala* (♀)×*Parabramis pekinensis* (♂) (Lin, 1984) $(2n=48)\times(2n=48)$
		5	*Mylopharyngodon piceus* (♀)×*Ctenopharyngodon idellus* (♂) (The Breeding Room of the Yangtze River Fisheries Research Institute, 1975) $(2n=48)\times(2n=48)$
		6	*Rhabodosargus sarba* (♀)×*Pagrosomus major* (♂) (Qu et al., 2000) $(2n=48)\times(2n=48)$
		7	*Sparus latus* (♀)×*Rhabodosargus sarba* (♂) (Zhang et al., 1990) $(2n=48)\times(2n=48)$
		8	*Rhabodosargus sarba* (♀)×*Acanthopagrus schlegeli* (♂) (Zhang et al., 1990) $(2n=48)\times(2n=48)$
		9	*Plagiognathops microlepis* (♀)×*Xenocypris davidi* (♂) (Fisheries Research Institute of Guangxi for chamber dace group, 1980) $(2n=48)\times(2n=48)$
		10	*Cirrhinus molitorella* (♀)×*Sinilabeo decorus* (♂) (Zhang et al., 1984) $(2n=50)\times(2n=50)$
		11	*O. niloticus* (♀)×*Sarotherodon melanotheron* (♂) (Li et al., 2008) $(2n=44)\times(2n=44)$
	With different chromosome numbers	1	*Carassius auratus gibelio* (♀)×*Cyprinus carpio singuonensis* (♂) (Jiang et al., 1983) $(2n=156)\times(2n=100)$
Subfamily	With identical chromosome numbers	1	*Aristichthy nobilis* (♀)×*Megalobrama amblycephala* (♂) (Liu, 2014) $(2n=48)\times(2n=48)$
		2	*Megalobrama amblycephala* (♀)×*Aristichthy nobilis* (♂) (Liu, 2014) $(2n=48)\times(2n=48)$
		3	*Aristichthy nobilis* (♀)×*Ctenopharyngodon idellus* (♂) (Guo et al., 1966) $(2n=48)\times(2n=48)$
		4	*Ctenopharyngodon idellus* (♀)×*Aristichthy nobilis* (♂) (Guo et al., 1966) $(2n=48)\times(2n=48)$
		5	*Ctenopharyngodon idellus* (♀)×*Hypophthalmichthys molitrix* (♂) (Zhang et al., 2014) $(2n=48)\times(2n=48)$
		6	*Hypophthalmichthys molitrix* (♀)×*Ctenopharyngodon idellus* (♂) (Zhang et al., 2014) $(2n=48)\times(2n=48)$

(*To be continued on the next page*)

(*Continued*)

Phylogenetic relationship		Num	Hybridized combination
Subfamily	With identical chromosome numbers	7	*Ctenopharyngodon idellus* (♀)×*M. terminalis* (♂) (Liu, 1987) $(2n=48)\times(2n=48)$
		8	*Mylopharyngodon piceus* (♀)×*M. terminalis* (♂) (Liu et al., 1981; Chen, 1984) $(2n=48)\times(2n=48)$
		9	*Hypophthalmichthys molitrix* (♀)×*Megalobrama amblycephala* (♂) (Pan, 1987; Zhu et al., 1993) $(2n=48)\times(2n=48)$
		10	*Megalobrama amblycephala* (♀)×*Hypophthalmichthys molitrix* (♂) (Pan, 1987; Zhu et al., 1993) $(2n=48)\times(2n=48)$
		11	*Hypophthalmichthys molitrix* (♀)×*Xenocypris davidi*(♂) (The Yangtze river fisheries research institute, 1975) $(2n=48)\times(2n=48)$
	With different chromosome numbers	1	*Ctenopharyngodon idellus* (♀)×*Cyprinus carpio* (♂) (Ye et al., 1989) $(2n=48)\times(2n=100)$
		2	*Cyprinus carpio singuonensis* (♀)×*Ctenopharyngodon idellus* (♂) (Li, 1991) $(2n=100)\times(2n=48)$
		3	*Cyprinus carpio* (♀)×*Hypophthalmichthys molitrix* (♂) (Gui et al., 1993; Wang and Liu, 1986) $(2n=100)\times(2n=48)$
		4	*Hypophthalmichthys molitrix* (♀)×*Cyprinus carpio* (♂) (Gui et al., 1993; Wang and Liu, 1986) $(2n=48)\times(2n=100)$
Inter-familial	With different chromosome numbers	1	*Oreochromis aureus* (♀)×*Siniperca chuatsi* (♂) (Yang et al., 2004) $(2n=44)\times(2n=48)$
Orders	With identical chromosome numbers	1	*Megalobrama amblycephala* (♀)×*Siniperca chuatsi* (♂) (Liu, 2014) $(2n=48)\times(2n=48)$
		2	*Hypophthalmichthys molitrix* (♀)×*Pagrosomus major* (♂) (Zhang et al., 2014) $(2n=48)\times(2n=48)$

Overcoming reproductive barriers to the distant hybridization of animals and plants

Many experiments on distant hybridization have shown that selecting appropriate parents and considering reciprocal crosses is vital to the success of distant hybridization in animals and plants. Statistical observations show that cross combinations in plants and animals where the number of chromosomes in the female parent is greater than or equal to the number in the male parent easily produce live offspring (Tables 1–3). Barriers to distant animal hybridization mainly pertain to early embryo death, heterogeneous reproductive cells that are not easily fertilized, hybrid sterility, and extreme imbalances in sex ratios in interspecific and generic hybrids. Scholars have studied this issue from several angles, through the use of histomorphology, reproductive physiology, histochemistry, and chromosome genetics (Feng et al., 2009). Abnormal chromosome pairing, abnormal protein expression, organ differentiation, and abnormal expression of relevant genes strongly impact on embryo survival rates, and most scholars believe that variations in the chromosomes and genetic structures of distant hybridization are the main causes of hybrid sterility. For the distant hybridization of animals, parent selection plays a key role in overcoming reproductive obstacles and forming a fertile line of hybrid offspring. When performing experiments on distant hybridization in fish, such as those, conducted in our laboratory, we must consider the correlation between the number of chromosomes of distant hybrid parents, phylogenetic relationships, reproductive characteristics, appearance, feeding patterns, growth rates, resistance levels, and other factors according to different cross combinations that are expected to produce various fish offspring traits to develop different types of fish strains via selection (Liu, 2014; Liu, 2010; Zhang et al., 2014). Regarding the distant hybridization of plants, selected maternal plants in a given species show broad genetic variations compared with male gametes and egg nuclei, and the nuclei of different species differ considerably in terms of their convergence abilities. When using high numbers of chromosomes, the selection of high levels of chromosome ploidy, or the first flowering of young hybrid seedlings as female parents, and choosing male parents that show strong oxidase activity, the osmotic pressure of the pollen is slightly larger than the osmotic pressure of the stigma, thus supporting cross success (Li et al., 2003).

Second, promoting fertilization by overcoming pre-fertilization barriers is necessary to obtain distant hybrid offspring of animals and plants. In plants, physical processing of the pollen and stylet before pollination is necessary to improve the rate of fertilization. The pollen can be managed through suitable heating, electromagnetic radiation, ultraviolet rays, and gamma-ray irradiation, or by mixing pollen and duplicating pollination to promote fertilization. Alternatively, artificial pollination of the ovary after removing the stigma, or reducing the length of the stylet, can prevent the non-release of gametes, because the pollen tube is not long enough to reach the embryo sac (Li et al., 2003). In animal studies, researchers have obtained a sheep (♀)×goat (♂) hybrid cross through mixed insemination, repeated fertilization, and miscarriage prevention measures, and through the use of hyperthermia-inactivated sheep semen to preserve goat semen. Mixed semen followed by goat blood was injected into a pregnant ewe to prevent miscarriages and improve physiological differences, and 12 sheep-goat hybrids were obtained. Using the activity of sperm enzymes in the same semen, and goat semen to inject foreign blood compositions to moderate physiological incompatibility during pregnancy supports fertilization and embryonic development (Liu, 1982).

Third, in plants, embryo rescue techniques are some of the most effective means of overcoming embryo abortion after fertilization. Based on the differences between the cultivation objects, embryo rescue involves an ovule, ovary, and embryo culture. This method has been widely used in field and horticultural crops. A newly formed embryo has numerous nutrition and environmental requirements, and occupies a fully heterotrophic state. An embryo occupying the terminal stage of development is easily degraded, and thus embryo rescue should be performed as late as possible prior to degradation. In addition, this approach can improve the affinity of distant hybridization through preliminary vegetative approaches, intermediary agent method, tissue culture methods, *in vitro* fertilization, and somatic cell fusion (Li et al., 2003). Researchers often improve nutrition levels to maintain normal embryo development in animals. The physiological development, living habits and breeding condition requirements of distant hybrids differ greatly from those of the parents, and the conditions required for hybrid development can be fully satisfied, it might be possible to promote the normal development of physiological function and even regain fertility. When dzo is physiologically developed to a certain stage, supplying abundant nutrition and improving the quality of phosphorus-containing feed promotes the normal development of reproductive functions and restores fertility.

In some cases, even when numerous measures have been taken to effectively overcome pre-fertilization barriers and embryo abortion, hybrid sterility or genital dysplasia may still occur after fertilization and successful distant hybridization. In plants, because the parents of distant diploid hybrids often have distant relatives, chromosomes cannot pair normally during meiosis, and therefore cannot produce energetic gametes, increasing the likelihood of hybrid sterility. In such cases, chemical reagents such as colchicine can be used in the early stages of seed germination, or at the seedling stage, to double the chromosome number and form an allotetraploid (i.e., amphidiploid) during meiosis, with each amphidiploid chromosome having a corresponding homologous chromosome for pairing and synapsis. This, in turn, generates dynamic gametes and greatly improves the ripening rate. For animals, some unisexual sterility hybrids can be improved, or their fertility can be recovered through backcrossing with one of the fertile parents after several backcrosses. The effect of third-party hybridization (ternary hybrid) can also be observed (Liu, 1982).

As the formation of viable strains through distant hybridization requires reproductive isolation, the formation of fertile strains serves as a strong research model for research on ways to overcome reproductive isolation. Research in our laboratory has shown that a common feature links the artificial distant hybridization of 4*n*AT (F_3–F_{26}), autotetraploid carp (F_2–F_{12}), 2*n*BT (F_1–F_4), and homologous diploid strains of red carp (F_1–F_{12}). Furthermore, these strains not only inherit the genome of the maternal parent, but also the genetic material of the male parent, albeit to a different extent. An analysis of large DNA fragments from a BAC (bacterial artificial chromosome) library of allotetraploids revealed that mosaic genes in allotetraploid strains are composed of genetic material from the parents (Wang et al., 2015). The results of collaborative research between our laboratory and that of Zhang (Liu et al., 2016) and others have shown that the proportion of mosaic genes is 9.67%–11.06% at the transcription level. We found a similarly large number of mosaic genes in 2*n*BT strains (F_1–F_4). At the DNA level, genetic material from both parents takes the form of chimeric genes, which in turn, benefits diploid strains. Diploids constitute an important genetic base for overcoming reproductive barriers. In addition, we identified DNA fragments from the original parents of distant hybrids of autotetraploid carp and diploid red carp. These inserted DNA fragments also facilitated the diploidization of these strains. This form of diploidization also constitutes an important genetic base for overcoming reproductive obstacles.

THE DIVERSITY OF DISTANT HYBRIDIZATION OFFSPRING

Three combinations of genetic materials can be identified in the distant hybridization between plants and animals. First, when heterologous female gametes are combined with male gametes, the heterologous female gamete chromosomes gradually disappear before or after fertilization, and this disappearance mainly depends on the development of the male's genetic material (androgenesis). After fertilization, heterologous male gametes only activate female gametes, and mainly rely on the genetic material of the developed female gamete (gynogenesis). Second, heterozygous female gametes and male gametes are amphiprotically fused to produce hybrid diploid progenies. Finally, when early cleavage is blocked, retention of the second polar body and generation of an unreduced number of gametes leads to the formation of polyploid organisms.

Distant hybridization generates androgenetic offspring

It is effective to induce etheogenesis by producing androgenetic offspring through distant hybridization between different species. In plants, Kostoff carried out interspecific hybridization between South's tobacco (*N. langsdorffii*, ♂), which has 18 chromosomes, and big leaf tobacco (♀), which has 72 chromosomes (Kostoff, 1934). One of the 1,000 offspring carried no traits of the female parent and had nine chromosomes; it was speculated that it was likely generated from a male gamete of South's tobacco (Kostoff, 1934). Interspecific hybrids include *Oenothera*, *Youngia*, and *Rhododendron*, whose male gametes can penetrate nuclear-free or degenerated egg cells to form embryos (Hu, 1982).

Naturally occurring androgenetic animals are rarein nature, but during the hybridization of fish, androgenetic offspring are occasionally observed. For example, Stanley observed diploid grass carp during male nuclear development in a carp (♀) and grass carp (♂) hybrid experiment, but with a low frequency, at approximately 0.02% (Stanley, 1976). Yu et al. used the eggs of crucian carp and normal sperm from crucian carp to initiate artificial insemination, and achieved approximately 5% male nuclear development that survived until maturity and produced sperm that could be used to fertilize female parent eggs to produce normal fry and fingerling offspring at 5.0%–8.0% (Yu et al., 2000).

Distant hybridization produces gynogenetic offspring

In plants and animals, the hybridization of different species or genera can also induce gynogenesis. In plants, distant pollen can remain unfertilized with female gametes, but can stimulate female gamete parthenogenesis. This method has been used to produce haploids in *Triticum*, *Nicotiana*, and *Solanum,* and approximately 39 species have been found in 73 cases. Unfertilized female gametes that develop into embryos can be haploids or diploids. Female gametes undergo endomitosis in the early stages of division and form haploids or diploids through chromosome duplication. When *S. luteum* pollen from morels (*S. nigrum*) was used, the pollen tube grew normally. However, sperm failed to fuse to the ovokaryon and disintegrated in the egg cytoplasm. The eggs still developed and formed haploid embryos (Vanbreukelen and Dong, 1984). Common wheat uses pollen pollination by *T. turgidum*, and the two homozygous diploids do not separate in the offspring. This is considered to involve parthenogenesis and nuclear chromosome duplication in the production of homozygous diploids (Hu, 1982). Hybridization with cultivated tetraploid potato (*S. tuberosum*) as the female parent, and diploid potato (*S. phureja)* as the male parent, can produce maternal double haploid offspring (Maheshwari, 1950).

Thus far, only fish and amphibians have been reported to naturally produce gynogenetic offspring, through distant hybridization between species and genera. Ding et al. performed hybridization experiments in Fujian tailless amphibians and observed that the hybrid of *R. limnacharis* (♀) and *Bufu melanostictus* (♂) can produce gynogenetic haploids of jersey frog (Wu, 1983). We used red carp as a female parent and *M. amblycephala* as a male parent in distant hybridization experiments between the subfamilies obtained from the natural gynogenesis of diploid red carp. Male and female ratios reached 1:1, and gonad development reflected that of ordinary red carp, with aged male and female individuals reaching sexual maturity. Further research revealed that the natural gynogenetic diploid involves a homologous diploid red carp and two sets of chromosomes from its original female red carp parent. As DNA fragments of the original male parent *M. amblycephala* could be detected in homologous diploid red carp, this type of homologous diploid red carp represents genetic variation. Distant hybridization experiments involving red carp as a female parent and *Xenocypri davidi* Bleeker as a male parent also resulted in natural gynogenesis of diploid red carp. The results of experiments involving *M. amblycephala* as a male parent (Liu, 2014) have produced similar results, and this natural gynogenesis of diploid red carp reflects that of the homologous diploid red carp.

Distant hybridization produces a heterologous diploid

Heterologous male and female gametes are commonly used to create harmonious gender relationships and to produce diploid hybrids for distant hybridization. This method is typically used to obtain new varieties that combine hermaphrodite types. Many distant hybrids are produced through natural, distant hybridization in plants. For example, *Pinus densata* is a natural diploid hybrid produced through the hybridization of *P. tabuliformis* and *P. yunnanensis*. This homoploid hybrid speciation occurs in a few species with parents that are not strictly reproductively isolated. The hybrid of Chinese cabbage ($2n$=20) and purple cabbage ($2n$=18) can produce 57 F_1 seedlings. The number of chromosomes in the root tip, and the pollen characteristics of the hybrid were investigated, with the formation of 47 chromosomes expected ($2n$=19). This true hybrid exhibited aborted pollen, and the comprehensive traits of the F_1 plants of the hybrid were intermediate between those of its parents (Qiao et al., 2012).

In animals, most offspring formed through distant hybridization between species are allodiploids. For example, we conducted distant hybridization experiments using red carp (♀) and *Cyrinus carpio* (♂) with bisexual fertility belonging to different genera and with 100-chromosome diploid fish. Hybrids of *C. auratus gibelio*×*Carprinus carpio*

F_1 and F_2 individuals are diploid hybrid fish with 100 chromosomes and a body shape reflecting the traits of the parents. The hybrid has two pairs of whiskers that are shorter than those of the male parent, and it grows faster than the female parent. It exhibits relatively strong levels of resistance. In our laboratory, we achieved generic hybridization of a hybrid of blunt snout bream (♀)×Topmouth culter (♂) (F_1 to F_4), and a hybrid of Topmouth culter (♀)×Blunt snout bream (♂) (F_1 to F_4) with hybrid diploid performance that can be passed down between generations. The characteristics measured included lateral line scales, scale rows above and below the lateral lines, body lengths/heights, and head lengths/heights. The shape characteristics were similar, to or different from those of the parents across the two hybrid diploid lines, revealing strong hybridity. The hybrid was a herbivore (Liu, 2014), rendering it useful for the study of relationships between *E. ilishaeformis* and grass carp.

Distant hybridization produces allopolyploids

When an early cleavage is blocked, the second polar body is retained, and an unreduced gamete is produced; thus, polyploids can form in distant hybridization offspring. Allopolyploids are produced through plant and animal distant hybridization by direct and indirect methods (Figure 1).

With respect to direct methods, we conducted subfamily hybridization tests with *C. auratus* red var. ($2n$=100, ♀)×*M. amblycephala* ($2n$=48, ♂) through the distant hybridization of animals. The F_1 offspring exhibited different ploidy features (Liu, 2014), including allotetraploid ($4n$=148), allotriploid ($3n$=124), and homologous diploid fish (also known as diploid natural gynogenetic fish) ($2n$=100). The obtained tetraploid possessed two sets of chromosomes from *C. auratus* red var. and two sets of chromosomes from *M. amblycephala*, and cleavage of the first fertilized egg was restrained. This method is used widely to obtain an allotetraploid in a single step. Heterologous and homologous diploid fish represent the second polar body of eggs blocked in the hybrid F_1 (Liu, 2014). In plants, interspecific hybridization between pickled cucumbers (*Cucumis hystrix*, $2n$=2X=24) and cultivated cucumbers (*C. sativus*, $2n$=2X=14) can generate offspring with different ploidy features, including allotetraploid ($2n$=4X=38), heterogeneous triploid ($2n$=3X=26), and allodiploid offspring ($2n$=2X=19) (Chen and Kirkbride, 2000). In plant studies, researchers also make use of natural, physical, chemical, and other factors to create autotetraploid hybrids and directly generate allotetraploid offspring. For example, the natural autotetraploid *A. thaliana* ($2n$=4X=20, ♀)×*A. arenosa* ($2n$=4X=32, ♂) can produce allotetraploid offspring ($2n$=4X=26) in *Arabidopsis*. However, artificially-induced chromosome doubling from autotetraploids and direct hybridization has also been widely applied to Brassica, rice, peanut (*Arachis hypogaea* L.), maize, and other crops (Wójcik et al., 2009).

When indirect methods are used, hybridity is a key factor that affects the frequency of $2n$ gametes. Our data indicate that the probability of forming hybrids that produce unreduced gametes (27.52%) is nearly 50-times higher than that of forming non-hybrids (0.56%) (Ramsey and Schemske, 1998). However, hybridity can promote the formation of unreduced gametes. The formation of hybrid organisms can produce unreduced gametes through distant hybridization, leading to chromosome doubling in their offspring. This method has been recognized as an efficient way to achieve polyploidy (Song et al., 2012). A polyploid is produced through unre-

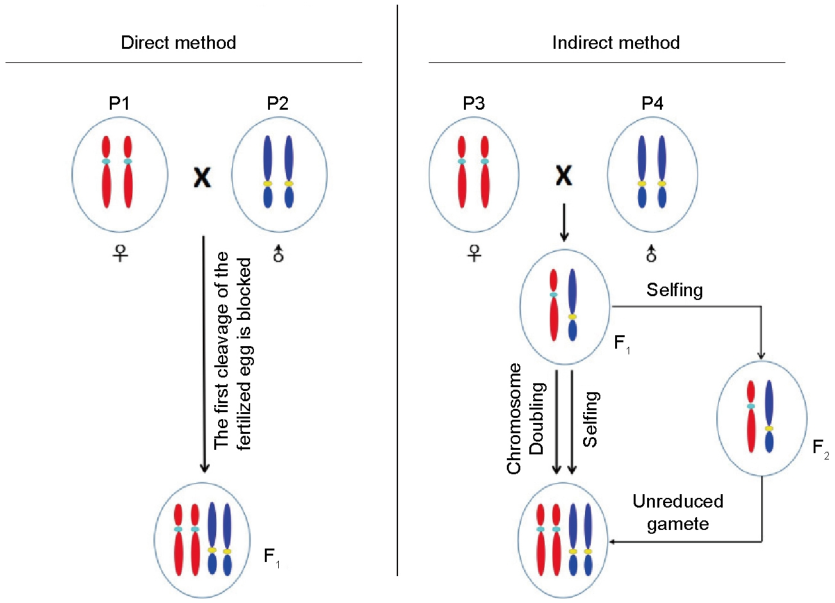

Figure 1 Diagram of distant hybridization formed by allotetraploids.

duced gamete fusion or through combination with a meiotic gamete. This is the most crucial requirement for polyploidy in plants and animals (Otto and Whitton, 2000). In 1876, Wilson obtained two sterile hybrid plants from offspring through hybridization between rye (*S. cereale*) ($2n$=2X=14) and common wheat ($2n$=6X=42). In 1891, Rimpo obtained seeds from sterile triticale hybrid plants and confirmed through cytological identification that the number of chromosomes in the cell was $2n$=8X=56, which is the sum of the chromosomes found in common wheat and rye. This represented the world's first artificially cultivated heterologous octoploid triticale (Huang and Sun, 1997). It is sometimes difficult to directly obtain allotetraploid offspring through distant hybridization. Researchers typically employ hybridization to obtain diploids, followed by the application of chemical or physical methods to obtain double chromosomes, or hybrid diploids to produce unreduced gametes, and by self-fertilization to indirectly obtain allotetraploid offspring. Our experiments on red carp (♀)×carp (♂) hybrids showed that female and male F_2 individuals can produce diploid eggs and diploid sperm, respectively, with no indication of reduction. These individuals formed female and male allotetraploid crucian carp populations in F_3 after fertilization (Liu, 2014). With respect to the evolutionary process of common wheat, researchers have speculated that distant hybridization between *T. monococcum* ($2n$=2X=14) and *Aegilops speltoides* ($2n$=2X=14) formed diploid hybrid offspring. Chromosome doubling also forms allotetraploid wild emmer wheat (*T. turgidum*, $2n$=4X=28). The distant hybridization of wild emmer wheat and *A. squarrosa* ($2n$=2X=14) produces triploid offspring, who form allohexaploid common wheat through chromosome doubling.

Plants can form incomplete allopolyploids composed of parent chromosomes. Common wheat is an allohexaploid (AABBDD) with 21 chromosomes whose gametes have three genomes (ABD). Diploid rye (RR), whose gametes have one genome (R), possesses seven chromosomes. Hybridization of common wheat and rye produces offspring with four genomes (ABDR), which exhibit disorders of synapsis and high sterility. The chromosome number of the offspring doubles in allopolyploid triticale (AABBDDRR), which is a complete allopolyploid (Huang and Sun, 1997). Octoploid tritielytrigia (AABBDDEE) is an incomplete allopolyploid formed from distant hybridization. It is a new species created through the hybridization of Thinopyrum (BBEEEE) and common wheat (AABBDD) that contains three groups of common wheat chromosomes and a set of Thinopyrum chromosomes (Guan, 1980). No report in animals have indicated how distant hybridization forms incomplete allopolyploids.

Chimeric embryos can also form in plant offspring produced through distant hybridization. The male gamete nucleus enters the egg (but does not fuse with the egg nucleus) and divides independently, forming chimeric male and female nuclei embryos with components from different sources. This can be viewed as a type of abnormal fertilization spurred by the incompatibility of male and female gametes. For example, the diploid egg of *Rudbeckia speciosa* splits several times after sperm entry; thus most cells in the egg of the chimera are diploids, with only a few haploid cells, which are frequently suspensor cells derived from sperm cells (Hu, 1982). In addition, in rain garlic, the haploid sperm divides in diploid eggs, and no more than two sperm cells form in source embryo cells. This phenomenon has also been observed in the distant hybridization of cocoa beans and cotton. Preliminary progress has been made in the application of semi-mating materials for breeding. The Shanxi Academy of Agricultural Sciences has applied distant hybridization and semigamy breeding to cotton cultivation, resulting in the cultivation of colored cotton varieties (Guo et al., 2005).

Polyploidy in animals can be obtained through distant hybridization. In distant hybridization lines of *C. auratus* red var. ($2n$=100, ♀)×*M. amblycephala* ($2n$=48, ♂), female and male F_1 allotetraploid fish (n=148) in, can produce unreduced diploid eggs ($2n$=100) and diploid sperm ($2n$=100). The heredity of these diploid gametes is derived from chromosomes of the original *C. auratus* red var. (♀), while the genetic material of the original *M. amblycephala* (♂) is lost during gametogenesis. These two types of diploid gametes form autotetraploid fish colonies with bisexual fertility ($4n$=200) in F_2 after fertilization (Liu, 2014). A tendency toward chromosome elimination (referring to polyploid or mixoploid tissue restored to the number of chromosomes, representing one of the diploid parents) may also occur through plant distant hybridization. The mechanism underlying this pattern is unclear. It is assumed that completing this process involves the formation of a multipolar spindle and the subsequent elimination of unbalanced cells. Following hybridization of cultivated barley (*Hordeum vulgare*) and its wild relative corm barley (*Hordeum bulbosum*), corm barley chromosomes in the embryos are lost during the first few rounds of mitosis, producing a cultivated barley haploid. When hybridization between other types of gramineae was used to eliminate haploid chromosomes, for some hybrid combinations, chromosome elimination caused the hybrid to include one parent haploid chromosome, whereas the other included the chromosomes of both parents. Genetic structures serve as good material to study single chromosomes (Riera-Lizarazu et al., 2000).

THE APPRAISAL OF OFFSPRING OBTAINED THROUGH DISTANT HYBRIDIZATION BETWEEN ANIMALS AND PLANTS

Morphological identification

The comparison of morphological characteristics between hybrid offspring and parents is the simplest way to confirm the authenticity of a distant hybrid. Because the hybrid body contains genetic material from both parents, the phenotype of the distant hybrid often tends to reflect both parents or one of the parents. In addition, as the genetic bases of the parents differ, the hybrid offspring will typically show certain variations. Therefore, true hybrids tend to exhibit some traits of their parents, as well as their own specific traits. It is possible to preliminarily identify the authenticity of hybrids through a comprehensive comparison of various traits.

The morphological identification of plant offspring derived from distant hybridization involves the examination of leaf shape, leaf color, leaf surface characteristics, flower organ coloring, size, plant height, degrees of extension, living habits, and other features through comparative studies. For example, in a study on the distant hybridization of pond cypress and cypress pine, angles, shapes, seedling heights, leaf shapes, and leaf arrangements of the hybrid were observed and compared (Jiangsu Institute of Botany, 1975). Animals are typically compared in terms of body coloring, body length, body weight, and other aspects. Studies comparing morphological characteristics between tetraploid crucian carp and the original parents in our laboratory showed that the length of the mouth of a tetraploid crucian carp falls between that of a common carp and red crucian carp. The standard allotetraploid carp body and head lengths/heights ranged between those of the original parent/length average, while the standard mean head length was smaller than that of the original parent. The vertebrae, gill, lateral line scale, and swallowing tooth quantities of allotetraploid carp fall between those of the original parents (Zhang et al., 2014).

Morphological identification is simple to apply and is cost-efficient, although applications of this method are restricted depending on similarities between the parental traits. Therefore, morphological identification can only be used as a preliminary method and must be combined with other more scientific and reliable methods.

Cytology identification

The study of chromosome characteristics and ploidy levels is a reliable way of identifying distant hybrids. Studies have shown that most parent F_1 plants have an average number of chromosomes. Two main methods are used to identify chromosome ploidy in hybrid offspring. The somatic chromosome count assay is the simplest and most accurate method. Preparation of plant chromosome specimens involves more manual pressure and heating of hypotonic flaking cell wall, permeability, and materials such as roots and stem tips typically contain strong splinter cell sites. Indirect assays mainly involve flow cytometry and the determination of cell size through morphological analysis. Flow cytometry can be used to accurately determine the nuclear DNA content by comparing reliable identifications of the ploidy. This method can be used to quickly measure, analyze, and test a large number of samples over a short period and to identify sexual chimeras. When applying methods for cellular and morphological analyses to allotetraploid carp strains and autotetraploid carp strains, the number of chromosomes in the original parent red carp variety, with red carp including 100 chromosomes, and the allotetraploid strain and autotetraploid including 200. As the numbers of tetraploid, triploid, and diploid fish increase, the number of red blood cells and lymphocytes, and the diameters of nuclei and cells increase. The allotetraploid of the crucian carp red nucleus exhibits a dumbbell pattern. In plants, the chromosome counting method can be used for identification, and stomatal guard cells and the chloroplast assay method can be used for the identification of distant hybridization progeny. He et al. used the perimeter of stomatal guard cells and chloroplast number to study rapeseed hybrids. They observed a perimeter of less than 58.90 microns for cabbage rape, a circumference of 58.90–75.83 microns for hybrid F_1, and a perimeter greater than 75.83 microns for a mustard variety of *B. napus rape* (He et al., 2013a). Ten-to-twelve chloroplasts were found in cabbage rape, approximately 14–16 were found in hybrid F_1, and approximately 18–19 were found in mustard varieties of *B. napus rape.*

Identification by molecular cytology

With advances in molecular and cellular biology, and molecular genetics in recent years, molecular biology technologies, namely, chromosome *in situ* hybridization (CISH), have played an increasingly important role in the identification of offspring obtained by distant hybridization. Fluorescence *in situ* hybridization (FISH) with fluorescent tags has replaced isotope labeling and emerged as a new method of *in situ* hybridization. Genomic *in situ* hybridization (GISH) involves the use of genomic DNA from heterologous species as a probe. The use of both these methods in combination has proven accurate (at the molecular level) and intuitive (as identification results show). For example, Zhou used this approach to distinguish Oriental lily and Asian lily hybrids are from different parents of the genome and to detect pollen mother cells in the exchange of genome chromosomes during meiosis (Zhou, 2003).

We used FISH to analyse tetraploid carp strains. Near-centromere unique repetitive sequences were used as probes for red carp, *M. amblycephala*, allotetraploid $F_1(4nF_1)$ and autotetraploid $F_2(4nF_2)$ chromosome metaphase split phases in a FISH study. We found that all red carp chromosomes emitted the fluorescent signal, *M. amblycephala* chromosomes were not marked by the fluorescent signal, and chromosomes derived from red carp with 100 $4nF_1$ were marked by the fluorescent signal. While 200 chromosomes in $4nF_2$ were expected to emit a fluorescent signal, only 100 chromosomes were marked; thus, it is likely that the 100 chromosomes not marked with a fluorescent signal contained genetic mutations

(Liu, 2014).

Isozyme identification

Isozymes are enzymes that have a similar function but different structure. Isozyme markers are codominant and exhibit polymorphic responses at the protein level; therefore, with regard to parent and offspring isozyme (Peroxidase, esterase.) enzyme spectrum analyses can be used to identify the characteristics of the hybrid material for identification. Luo et al. used isozyme technology to accurately identify cultivated cucumber in Changchun (Luo et al., 2006). and dense spines and authenticity of cucumber hybrids. Chen et al. studied the mechanisms underlying two characteristics of offspring resulting from the hybridization of *M. piceus* (♀)×*M. terminalis* by investigating biochemical genetics (Chen et al., 1987). The authors used polypropylene gel disc electrophoresis with phthalein amine staining and CS910 double wavelength scanners to evaluate the organization of seven lactate dehydrogenase (LDH) isozymes in *M. piceus*, *M. terminalis*, and the first generation. LDH isozymes were observed in all types of *M. piceus* configurations and *M. terminalis* and its initial generation exhibited tissue specificity and the LDH isozyme spectrum between parents varied considerably across the two spectra. Some fish with female parent characteristics formed first, and the LDH isoenzyme spectra of these fish and of the female parent were almost identical. Other first-generation fish exhibited features of the parents, with LDH isoenzyme levels similar to those of the male parent. The spectrum significantly increased relative to that of *M. piceus*.

Molecular marker identification

The application of molecular biology technologies can be used to identify distant hybrids. A variety of molecular techniques are used for identification, including randomly amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), and inter-simple sequence repeat (ISSR). RAPD uses total genomic DNA as a template and random primers to amplify polymorphic DNA fragments by PCR. Then, the polymorphic fragments are detected by electrophoresis to determine the inner gene arrangements and external trait laws of performance. Li et al. used RAPD technologies to identify interspecific hybrids of chrysanthemum and obtained reliable results (Li et al., 2009).

ISSR and AFLP are two molecular marker technologies that can be used to amplify DNA sequences using primers. These methods boast high detection rates and high levels of repeatability and stability. To understand the evolution of bisexual fertile genetic stable allotetraploid genomes, ISSR and AFLP molecular marker analyses showed that in addition to the new DNA bands not present in the parent, DNA bands also disappeared in the original parents, and the disappearance of bands tended to be higher for the paternal genome in the allotetraploid genome. Based on amplification results from ISSR and AFLP, the average genetic distance between the two groups and the average genetic distance between the original parents and red crucian and common carp were calculated (Liu et al., 2009).

APPLICATION OF DISTANT HYBRIDIZATION IN ANIMALS AND PLANTS

Genetic breeding involves selecting and developing an individual and population from stable lines and cultivating a stable product line from a variable group. Distant hybridization processes have been studied through research and exploration to develop individual and population variations, genetically stable strains, and new species (Liu, 2014). For example, the formation of a tetraploid fish by distant hybridization in the laboratory can provide evidence for vertebrate evolution. The number of genes increases as the number of chromosomes doubles, providing a basis for gene mutation and for the production of new genes. Gene duplication can, in turn, lead to the mutation and creation of genes. Jurg stated that allopolyploids have greater potential than autopolyploids to evolve (Jurg, 1997). Bisexual fertile allotetraploid fish and genetic stability help to explore the mechanism of polyploid formation in natural fish for fish polyploid breeding. Our laboratory has successfully developed important hybrid fish lines with a variety of features, such as allotetraploid crucian carp lines (F_3–F_{26}) and autotetraploid fish strains derived from the distant hybridization of grass bream (F_2–F_{12}), diploid bream culter (F_1–F_4), strains of bream *Culter Alburnus*, bream strains (F_1–F_4), crucian carp strains (F_1–F_2), and bream *M. amblycephala* (♀)×*X. davidi* (♂) (F_1–F_2) 2007 strains (Table 1) (Liu, 2014). In turn, these hybrid strains promote breeding, resulting in significant economic, social, and ecological benefits. Fish and bream backcross hybrid strains of bream culter create rapidly growing lines that maintain high levels of resistance and quality, and present other advantages common to *Culter* bream varieties (Liu, 2014). Based on the developed homology and allotetraploid fish populations, various diploid fish exhibiting sterility, rapid growth, strong resistance, and other advantages of triploid fish were produced, with potentially broad application.

In animals, castration is an important method used to individual infertility. As early as 2000 years ago, castration technology was widely used in poultry livestock (He and He, 2013). This technology is not only used in male animals, but also in for female livestock castration, in which the male or female gonads are removed. At present, castration technology is widely used in chicken, cattle, and pigs. For example, this technology is used to excise the rooster testes to remove their desire and ability for sex; with the disappearance of this male feature, the temperament of the rooster becomes meek, and the meat quality improves (Li and Luo, 2012).

Distant hybridization is an important method in genetic breeding. For example, the mule, which is a cross between a horse and an ass, is sterile. The offspring of interspecific hybridization between *A. irradians* and *A. purpuratus* are also sterile (Zhang et al., 2012). In addition, our laboratory has successfully developed allotetraploid fish and autotetraploid fish through distant hybridization. The hybridization of allotetraploid and autotetraploid fish has resulted in the development of a variety of infertile triploid fish. The infertility triploid fish groups usually have high economic value, and exhibit high quality, rapid growth, strong resistance, high production, as well as other advantages (Benfey, 1999).

The growth speed and meat quality of the sterile offsprings improved, and these were produced through distant hybridization or traditional castration technology. In terms of safety and operation, some problems still exist even though with the progress of castration technology, for example, with physical castration, the individual would bleed easily or get infected with bacteria such as staphylococcus and mildew slurry disease. Additionally, continuous eating causes accident which due to drug residues of chemical castration (Liu et al., 1959). These problems would be solved with the use of distant hybridization technology. At the same time, various animals would enhance disease resistance and immunity under long-term natural selection, and enhance the ability to cope with poor weather conditions, such as high temperature, cold, and drought. Thus, the ability to resist disease and cold resistance would be improved when related genes are imported into the offspring of distant hybridization. Furthermore, parthenogenesis can be induced by distant hybridization to improve the quality, production, and nutrition of the breed, and research into the creation of new species and the evolution of existing species would be accelerated with the application of distant hybridization. With the successful development of genetically modified fish in recent years, concerns over the effects of genetically modified fish in natural water bodies on fish germplasm resources have been raised. As sterile triploids are unable to produce offspring, they are ideal transgenic fish carriers, thus mitigating ecological safety concerns related to transgenic fish, the development of which has become a major area of fisheries research (Xu et al., 2015; Wu et al., 2013).

Male plant sterility is a common trait in higher plants. In the initial stage of heterosis utilization, the use of male sterile lines can simplify seed production processes and enable the breeding of new varieties with independent intellectual property rights and excellent traits. Sterile male plant lines can be obtained through distant hybridization and backcrossing. For example, wild abortive plants have been used for distant hybridization to breed male sterile rice lines. First, excellent male parent and wild abortive hybrids must be selected from maintainer strains of wild abortive sterile plants. Through continuous backcrossing, nucleocytoplasmic exchange can be completed, and an excellent sterile line can in turn be cultivated (Wang, 2006). Maize inbred and restorer lines were firstly applied for sexual hybridization with conventional male sterile lines of hybrid rice. Then, using the F_1 generation, continuous backcrossing with maize inbred and restorer lines was conducted to breed sterile, maintainer, and restorer maize rice lines. Male sterile and restorer lines can be crossed with any conventional hybrid rice restorer line and male sterile line, and the resulting combination of varieties exhibits excellent traits (i.e., stress, drought, and cold temperature resistance) (Zhang et al., 2015). The creation of heterochromatin systems through distant hybridization can be used to import alien chromosomes or fragments to create additional lines (by adding another species with one or two pairs of chromosomes to a species group of normal chromosome genes, resulting in the formation of a new type). This approach, which forms a basis for creating heterologous substitution and translocation lines, can be used for homologous chromosome pairing in plant cells, genetic map construction, molecular markers, gene cloning, and genome interaction research, and expression. The approach constitutes an important means of genetic research and chromosome engineering in breeding as well as a method for studying effective ways to transfer genes and genome structures (Peterka et al., 2004; Lelivelt and Krens, 1992; Xing et al., 1988; Lin et al., 2007).

Compliance and ethics *The author(s) declare that they have no conflict of interest.*

Acknowledgements *This work was supported by National Natural Science Foundation of China (31430088, 31210103918, 91331105), National High Technology Research and Development Program of China (2011AA100403), the Cooperative Innovation Center of Engineering and New Products for Developmental Biology of Hunan Province (20134486), Project supported by the Specialized Research Fund for the Doctoral Program of Higher Education of China (20114306130001), Educational Commission of Hunan Province (14B115), National Key Disciplines of Developmental Biology and Key Discipline Construction Project Funding for Developmental Biology of Hunan Province.*

Benfey, T.J. (1999). The physiology and behavior of triploid fishes. Rev Fish Sci 7, 39–67.

Bennert, H.W., and Fischer, G. (1993). Systematics and evolution of the *Asplenium trichomanes* complex. Webbia 48, 743–760.

Bennert, H.W., Sermolli, P., Rodolfo, E.G., Rasbach, H., Rasbach, K., and Reichstein, T. (1989). *Asplenium×helli Lusina*, the valid name for the hybrids between *A. ptrarchae* (Guerin) DC. and *A. trichomanes* L. (Aspleniaceae, Pteridophyta) II. Detailed description and illustrations. Webbia 43, 311–337.

Bennert, H.W., Sermolli, P., Rodolfo, E.G., Rasbach, H., Rasbach, K., and Reichstein, T. (1988). *Asplenium×helli Lusina*, the valid name for the hybrids between *A. petrarchae* (Guerin) DC. and *A. trichomanes* L. (Aspleniaceae, Pteridophyta) I. Nomenclatural notes. Bauhinia 9, 103–106.

Bunch, T.D., Foote, W.C., and Juan Spillett, J. (1976). Sheep-goat hybrid karyotypes. Theriogenology 6, 379–385.

Che, Q., and Wang, K. (2007). Embryo brain stem structure observation of hy-brid offspring between black bone chickens and guinea fowl (*Numida meleagris*) and measurement of its morphological indexes (in Chinese). J Anhui Agri Sci 35, 11104–11120.

Chen, J.F., and Kirkbride, J.H. (2000). A new synthetic species of Cucumis (Cucurbitaceae) from interspecific hybridization and chromosome doubling. Brittonia 52, 315–319.

Chen, S. (1984). Investigation on the inter-subfamily hybridization *Mylopharyngodon piceus* (♀)×*Megalobrama terminalis* (♂) I. Comparative cytogenetic study on *Mylopharyngodon piceus* (♀)×*Megalobrama terminalis* (♂) and their F_1 generation (in Chinese). J Nat Sci Hunan Nor Univ 7, 71–80.

Chen, S., Li, W., Tang, H., and Pan, D. (1987). Investigation on the inter-subfamily hybridization (*Mylopharyngodon piceus* R. ♀×*Megalobrama terminalis* R. ♂) Ⅱ. Comparative studies on lactate dehydrogenase isozymes of *Mylopharyngodon piceus* R. ♀, *Megalobrama terminalis* R. ♂ and their F_1 generation. J Nat Sci Hunan Nor Univ 10, 75–81.

Chen, X., Yang, H., Liu, H., Li, Y., and Feng, B. (2004). Employing distant hybridization to create new germplasm of stone fruit trees. Deciduous Fruits 36, 4–7.

Chen, Y. (1999). Analysis of reproductive isolation. Bull Biol 34, 20–21.

Chen, Z. (1996). Tries on the sexual distant hybridization of *Edible fungi* (sequel). Edible Fungi Zhejiang 4, 3–4.

Chen, Z. (2000). Study on distant hybridization of *Attacus cynthia* ricini dovonan and *Attacus atlas* linnaeus. Guangdong Sericult 3, 27–30.

Chen, Z., and Lin, R. (1998). Studies on interspecific hybridization of Pleurotus. Acta Edulis Fungi 5, 8–12.

Dai, X., Cheng, C., Pan, B., and Xiong, D. (2001). Preliminary study on compatibility of distant hybridization between rape (*Brassica napus*) and *Rorippa indica*. Agri Jiangxi 13, 60–61.

Deng, Y., Chen, S., Lu, A., Chen, F., Tang, F., Guan, Z., and Teng, N. (2010a). Production and characterisation of the intergeneric hybrids between *Dendranthema morifolium* and *Artemisia vulgaris* exhibiting enhanced resistance to chrysanthemum aphid (*Macrosiphoniella sanbourni*). Planta 231, 693–703.

Deng, Y., Teng, N., Chen, S., Chen, F., Guan, Z., Song, A., and Chang, Q. (2010b). Reproductive barriers in the intergeneric hybridization between *Chrysanthemum grandiflorum* (Ramat.) Kitam. and *Ajania przewalskii* Poljak (Asteraceae). Euphytica 174, 41–50.

Ding, H. (1956). Hybridization experiments of *Peking Anurans* (in Chinese). J Fujian Nor Univ 2, 1–7.

Du, B.N., and Nikolaĭ, P. (1974). Genetic Principles of Plant Breeding. (Beijing: Science Press).

Feng, X., Liu, X., Yao, S., Yao, X., Miraguli, G., and Zhao, Z. (2009). Analysis of the possible mechanism of early death of hybrid embryos between chicken and quail. China Poult 31, 36–39.

Fisheries Research Institute of Guangxi for chamber dace group. (1980). Using hybrid inprove the cold resistance of dace (in Chinese). Freshwater Fisheries 6, 26.

Frédéric, B. (2008). Double-fertilization, from myths to reality. Sex Plant Reprod 21, 3–5.

Fu, J., Li, D., and Xie, B. (2008). Distant hybridization of *Pleurotus eryngii* and letinous edodes. Papers of Chinese mycology Fourth member Congress and the Seventh National Symposium on mycology 234–242.

Gai, J. (1997). The Theory of Crop Breeding. (Beijing: China Agriculture Press).

Gao, R., Wang, B., Li, G., Reardon, R., Wu, Y., and Yun, H. (2000). Report on the cross breeding between *Anoplophora glabripennis* (Motsch) and *A. nobilis* Ganglbauer (Coleoptera, Cerambycidae). J Beijing Forest Univ 22, 23–26.

Godlewski, E. (1906). Untersuchungen uber die Bastardierung der Echinideen- und Crinoideenfamilie. Archiv Für Entwicklungsmechanik Der Organismen 20, 579–643.

Gong, D., Zhang, J., Duan, X., Zhao, X., Chen, Z., and Yang, Y. (2005). Study on the growth performance and meat characteristics of differet crossing mule duck. J Yandzhou Univ 26, 27–30.

Grant, P.R., Grant, B.R., and Petren, K. (2005). Hybridization in the recent past. Am Natist 166, 56–67.

Gray, A.P. (1954). Mammalians Hybrids Commonwealth. (Cambridge: Cambridge University Press).

Guan, Q.L. (1980). Formation, meiotic stability and karyotype analysis of octoploid *Agrotriticum hybrids*. Acta Agron Sin 6, 129–138.

Gui, J., Liang, S., Zhu, L., Sun, J., and Jiang, Y. (1993). Cytogenetic analysis of developmental difference in hybrid embryos between reciprocal crosses in distant hybridization of fishes (in Chinese). Zool Res 14, 171–177.

Guo, B., Yang, F., Niu, Y., Huang, S., and Ji, L. (2005). Identification of interspecific hybrids in Dendranthema. Cotton Sci 17, 99–102.

Guo, H., Tu, F., Wang, B., and Xiao, S. (1966). Preliminary observation between grass carp and *Aristichthys nobilis* artificial hybridization and their generations. Chin J Zool 4, 188–189.

Gutierrez-Marcos, J.F., Pennington, P.D., Costa, L.M., and Dickinson, H.G. (2003). Imprinting in the endosperm: a possible role in preventing wide hybridization. Philos Trans R Soc B-Biol Sci 358, 1105–1111.

He, L., and He, H. (2013). Castration techniques of bulls. Chin Livestock Poult Breed 9, 59–60.

He, L., Sun, W., Zeng, X., Lou, Q., Qian, C., and Chen, J. (2013a). Interspecific hybrid identification of rapeseed using stomatal guard cel perimeterand chloroplast number. Acta Botan Boreali-Occidentalia Sin 33, 280–286.

He, W.G., Xie, L.H., Li, T.L., Liu, S.J, Xiao, J., Hu, J., Wang, J., Qin, Q.B., Liu, Y. (2013b). The formation of diploid and triploid hybrids of grass carp (♀)×blunt snout bream (♂) and their 5SrDNA analysis. BMC Genet 14, 110.

Hedderson, T.A. (1986). A naturally occurring moss hybrid between *Orthotrichum gymnostomum* and *O. obtusifolium* from Newfoundland, Canada. Bryologist 89, 165–167.

Hou, X., Wang, Z.R. (2000). A subspecific taxonomic study on *Asplenium trichomanes* L. from China. Acta Phytotaxonom Sin 38, 242–255.

Hu, S. (1982). Embryology of *Angiosperms*. (Beijing: Higher Education Press), pp. 216–225.

Hu, J., Liu, S., Xiao, J., Zhou, Y., You, C., He, W., Zhao, R., Song, C., and Liu, Y. (2012). Characteristics of diploid and triploid hybrids derived from female *Megalobrama amblycephala* Yih×male *Xenocypris davidi* Bleeker. Aquaculture 364-365, 157–164.

Hua, X. (2004). Breeding of sweet F1 at 001 strain. Edible Fungi, 12–13.

Huang, B., Chang, L., Ju, C., and Chen, J. (2001). Production and cytogenetics of intergeneric hybrids between Ogura CMS *Brassica campestris* var *purpuraria* and *Ruphanus sativus*. Acta Genet Sin 28, 556–561.

Huang, H., Xie, J., Wu, C., Xie, M., Liu, L., and Hu, Y. (1997). Study on screening performance of hybrid mule duck. Acta Agr Jiangxi 9, 20–24.

Huang, Q., and Sun, J. (1997). Prospect of plant polyploidy in crop breeding. Sci Technol Rev 7, 53–55.

Jiang, Y., Liang, S., Chen, B., Yu, H., Shan, S., Yang, D., Lin, S., and Shen, G. (1983). Biological effect of heterologous sperm on gynogenetic offspring in *Carassius auratus* gibelio (in Chinese). Acta Hydr Sin 8, 1–16.

Jiangsu Institute of Botany. (1975). Preliminary results of *Taxodium ascendens*×*T. distichum*. Hubei Forest Sci Technol 5, 19–20.

Jin, Z., Liu, Y., Zhang, J., Gong, Q., Cui, J., and Liu, T. (2009). Breeding actuality and developing direction of laminaria in China. Trans Oceanol Limnol 1, 141–150.

Jurg, S. (1997). Vertebrate evolution by interspecific hybridization-are we polyploidy? FEBS Lett 400, 2–8.

Kaul. (1988). Male Sterility in High Plants. (Berlin: Springer Verlag), pp. 2–5.

Knowlton, N. (1993). Sibling species in the sea. Annu Rev Ecol Syst 24, 189–216.

Kostoff, D. (1934). A haploid plant of *Nicotiana sylvestris*. Nature 133, 949–950.

Kupelwieser, H. (1909). Entwicklungserregung bei Seeigeleiern durch Molluskensperma. Archiv Für Entwicklungsmechanik Der Organismen 27, 434–462.

Lelivelt, C.L.C., and Krens, F.A. (1992). Transfer of resistance to the beet cyst nematode (*Heterodera schachtii* Schm.) into the *Brassica napus* L. gene pool through intergeneric somatic hybridization with *Raphanus sativus* L. Theoret Appl Genet 83, 887–894.

Levine, J.P., and Haley, L.E. (1975). Gene activation of alcohol dehydrogenase in Japanese quail and chicken-quail hybrid embryos. Biochem Genet 13, 7–8.

Li, C. (1991). Electrophoretic analysis on the serum protein of Xingguo red carp, grass carp and their hybrid F_1 (in Chinese). Freshwater Fisheries 6, 12–14.

Li, Q.W., and Luo, R. (2012). Technical advisor and prospect of capon. Breed Manag 12, 42–44.

Li, S., Yan, B., Cai, W., Li, T., Jia, J., and Zhang, Y. (2008). Evaluation of growth, salt tolereance and parents' heterosis contribution in reciprocal hybrids F_2 between *Oreochromis niloticus* and *Sarotherodon melanotheron*. J Fish China 32, 335–341.

Li, S.K. (1955). The Complete Works of Michurin (Vol. 2). (Beijing: Agriculture Press), pp. 123–124.

Li, Y., Chen, X., and Zheng, Z. (2003). Recent progress in the studies of distant hybridization breeding in fruit crops. J Shandong Agri Univ 34, 139–143.

Lin, C., Sun, P., Cheng, F., Wang, L., and Gao, J. (2007). Distant hybridization of Brassica plants. Shandong Agri Sci 4, 27–31.

Lin, Y. (1984). A comparative of the karyotypes in Chinese bream, herbivorous bream and their hybrid (in Chinese). Zool Res 5, 65–66.

Liu, C., Luo, C., and Chen, X. (1990). Hybridization experiments of four species of frogs (in Chinese). J Nat Sci Hunan Normal Univ 13, 286–288.

Liu, G., Bao, Z., Hu, J., Wang, S., Yao, B., and Zhan, A. (2006). ISSR analysis of two species of scallop (*Chlamys farreri*, *C. Nobilis*) and their intra and interspecies mating descendants. Period Ocean Univ China 36, 71–75.

Liu, H., Zhao, Z., Deng, Y., Deng, X., He, L., Wu, S., and Shuai, X. (2004). Host plant suitability and reproductive isolation of two *Schizotetranychus bambusae* populations from the bam-boo species *Phyllostachys pubescens* and *Neosinocalamus affini*. Chin J Appl Ecol 15, 299–302.

Liu, H. (1982). Questions about animal distant hybridization and hybrid sterility. China Yak 1, 15–20.

Liu, L., Yan, J., Liu, S., Liu, D., You, C., Zhong, H., Tao, M., and Liu, Y. (2009). Evolutionary analysis based on ISSR, AF1P molecular markers and cyclins gene cloning of the allotetraploid hybrid (4nAT). Chin Sci Bull 54, 2096–2107.

Liu, R., Wang, H., and Chen, J. (1985). Investigation on sexual difference com-position of serum protein of two tilapia and their hybrid (in Chinese). J Fish China 9, 265–273.

Liu, S. (2014). Fish Distant Hybridization. (Beijing: Science Press).

Liu, S.J. (2010). Distant hybridization leads to different ploidy fishes. Sci China Life Sci 53, 416–425.

Liu, S., Liu, Y., Zhou, G., Zhang, X., Luo, C., Feng, H., He, X., Zhu, G., and Yang, H. (2001). The formation of tetraploid stocks of red crucian carp×common carp hybrids as an effect of interspecific hybridization. Aquaculture 192, 171–186.

Liu, S., Luo, J., Chai, J., Ren, L., Zhou, Y., Huang, F., Liu, X., Chen, Y., Zhang, C., Tao, M., Lu, B., Zhou, W., Lin, G., Mai, C., Yuan, S., Wang, J., Li, T., Qin, Q., Feng, H., Luo, K., Xiao, J., Zhong, H., Zhao, R., Duan, W., Song, Z., Wang, Y., Wang, J., Zhong, L., Wang, L., Ding, Z., Du, Z., Lu, X., Gao, Y., Murphy, R.W., Liu, Y., Meyer, A., and Zhang, Y.P. (2016). Genomic incompatibilities in the diploid and tetraploid offspring of the goldfish×common carp cross. Proc Natl Acad Sci USA 113, 1327–1332.

Liu, S., Qin, Q., Xiao, J., Lu, W., Shen, J., Li, W., Liu, J., Duan, W., Zhang, C., Tao, M., Zhao, R., Yan, J., and Liu, Y. (2007). The formation of the polyploid hybrids from different subfamily fish crossings and its evolutionary significance. Genetics 176, 1023–1034.

Liu, S., Zhu, K., and Xu, Y. (1959). Fattening technology introduction of capon. Heilongjiang Animal Sci Veterin 5, 28–30.

Liu, S. (1987). Studies of insemination cytology in hybridization between grass carp and preshwater bream (in Chinese). J Fish China 11, 225–232.

Liu, Y. (1993). Reproductive Physiology of Cultured Fish in China. (Beijing: Agriculture Press).

Liu, Y., Chen, S., and Wang, Y. (1981). The fertilization cytology research of *Megalobrama terminalis* sperm and *Mylopharyngodon piceus* eggs (in Chinese). Acta Hydrobiol Sin 7, 329–340.

Liu, Z., Dong, Y., Tai, L., Pang, G., Zhao, S., and Xu, J. (1991). Studies on interspecific protoplast fusion of *P. sapidus* and *L. edodes*. J Genet Genom 18, 352–357.

Liu, Z., and Guan, C. (1995). On the genetic mechanism of male sterility in higher plants. Explor Nat, 80–87.

Loeb, J. (1903). On a method by which the eggs of a sea urchin (*Strougyloceutrotus purpuratus*) can be fertilized with the sperm of a starfish (*Asterias ochracea*). Univ Cal Pub 1, 1–3.

Lou, Y., and Li, X. (2006). Distant hybridization of fish and its application in aquaculture. China J Fish Sci China 13, 151–158.

Lovis, J.D. (1955). The problem of *Asplenium trichomanes*. In: Species Studies in the British F1ora, J. E. Lovsley. (London: Academic Press), pp. 99–103.

Lovis, J.D. (1964). The taxonomy of *Asplenium trichomanes* in Europe. Brit Fern Gaz 9, 147–160.

Lovis, J.D., Melzer, H., and Reichstein, T. (1965). *Asplenium×adulteriniforme hybr. Nov.*=diploides *Asplenium trichomanes* L.×*A. viride* Hudson. Bauhinia 2, 231–237, 315–321.

Lovis, J.D., and Reichstein, T. (1977). Asplenium azoricum and other Ferns of the *A. trichomanes* Group from the Azores. Am Fern J 67, 81–93.

Lu, X., Sun, J., Wang, H., Luo, D., Hou, X., Liu, L., and Li, G. (2013). Observations on embryonic development of reciprocal hybrids of *Siniperca kneri* Garman×*Siniperca chuatsi* Basilewsky and F_2 of *S. kneri* (♀)×*S. chuatsi* (♂) F_1 (in Chinese). J Fish Sci China 20, 975–981.

Luo, X.D., Dai, L.F., Liu, Q., Lou, Q.F., Qian, C.T., and Chen, J.F. (2006). Isozyme analysis of reciprocal interspecific hybrid F_1 between *Cucumis sativus* and its wild relative *C. hystrix*. Acta Phytotaxonom Sin 44, 488–493.

Maheshwari, P. (1950). An Introduction to the Embryology of Angiosperms. (New York: McGraw-Hill).

Mallet, J. (2005). Hybridization as an invasion of the genome. Trends Ecol Evol 20, 229–237.

Mallet, J. (2007). Hybrid speciation. Nature 446, 279–283.

Mallet, J. (2008). Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation. Philos Trans R Soc B-Biol Sci 363, 2971–2986.

Manton, L. (1950). Problems of Cytology and Evolution in the *Pteridophyta*. (Cambrige: Cambrige University Press), pp. 125–157.

McClure, B.A., and Franklin-Tong, V. (2006). Gametophytic self-incompatibility: understanding the cellular mechanisms involved in "self" pollen tube inhibition. Planta 224, 233–245.

McGovern, P.T. (1973). The effect of maternal immunity on the survival of goatxsheep hybrid embryos. Reproduction 34, 215–220.

Meyerhof, P.G., and Haley, L.E. (1975). Ontogeny of lactate dehydrogenase isozymes in chicken-quail hybrid embryos. Biochem Genet 13, 7–18.

Mi, D., Liu, S., and Li, H. (2014). Main hybrid types in the production of deer in China. Special Economic Animal Plant 17, 7–10.

Mitsumoto, S., Neushul, M., and Chen, J.X. (1983). Hybridization and genetic studies of brown algae. Foreign Fish Period 4, 8–10.

Mokry, F., Rasbach, H., and Reichatein, T. (1986). Asplenium adulterium Milde subsp. presolanense subsp. Nova (Aspleniaceae, Pteridophyta). Botanica Helvetica 96, 7–18.

Murakami, N., and Iwatsuki, K. (1999). Phylogeny of Aspleniaceae inferred from rbcL nucleotide sequences. Am Ern J 89, 232–243.

Nagaharu, U., Nagamastu, T., and Mizushima, U. (1937). A report on meiosis in the two hybrids, *Brassica alba* Rabh. (female)×*B. oleracea* L. (male) and *Eruca sativa* Lam. (female)×*B. oleracea* L. (male). Cytologia, Fujii Jubilee 12, 437–441.

Nikolaev, A.G., and Bang, B.T. (1976). The composition of the essential oil of mentha lavanduliodora. Chem Nat Compounds 10, 537.

Olsen, M.W. (1960). Turkey-chicken hybrids. Heredity 51, 69–73.

Otto, S.P., and Whitton, J. (2000). Polyploid incidence and evolution. Annu Rev Genet 34, 401–437.

Pan, D.B., Chen, K.C., Zhu, X.P., Zheng, G.M., Liu, Y.H., Chen, Y.L., and

Li, K.B. (2009). The morphologic characters of hybrid (*Mauremys mutica* ♀×*Cuora trifasciata* ♂) and comparison with their paren. Acta Hydr Sin 33, 620–626.

Pan, G.B. (1987). Preliminary studies on the hybrid between *Hypophthalmichthys molitrix* and *Megalobrama amblycephala* (in Chinese). Freshwater Fisheries 1, 17–19.

Peterka, H., Budahn, H., Schrader, O., Ahne, R., and Schütze, W. (2004). Transfer of resistance against the beet cyst nematode from radish (*Raphanus sativus*) to rape (*Brassica napus*) by monosomic chromosome addition. TAG Theor Appl Genet 109, 30–41.

Philibert, M.H. (1883). Un Orthotrich hybride. Rev Bryol 10, 8–13.

Qiao, H.Y., Li, F., Zhang, S.J., Zhang, S.F., Zhang, H., and Sun, R.F. (2012). Production and identification of interspecific hybrids between Chinese cabbage and purple cabbage. Plant Sci J 30, 407–414.

Qiao, Y., Lin, S., He, X., and Yang, X. (2010). Identification of intraspecific and interspecific hybridizations in Loquat (Eriobotrya) using RAPD molecular markers. J Fruit Sci 27, 385–390.

Qin, Q., Wang, Y., Wang, J., Dai, J., Xiao, J., Hu, F., Luo, K., Tao, M., Zhang, C., Liu, Y., and Liu, S. (2014). The autotetraploid fish derived from hybridization of *Carassius auratus* red var. (female)×*Megalobrama amblycephala* (male). Biol Reprod 93, 1–11.

Qu, Y., Li, J., and Zhou, H. (2000). Larval development and growth of intergeneric crossing of *Sparidae fishes* (in Chinese). J Fish Sci China 7, 110–112.

Raghavan, V. (2007). Double Fertilization, Embryo and Endosperm Development of Flowering Plants. (Beijing: Science Press).

Ramsey, J., and Schemske, D.W. (1998). Pathways, mechanisms, and rates of polyploid formation in flowering plants. Annu Rev Ecol Syst 29, 467–501.

Reichstein, T. (1981). Hybrids in European Aspleniaceae (Pteridophyta). Botanica Helvetica 91, 89–139.

Riera-Lizarazu, O., Vales, M.I., Ananiev, E.V., Rines, H.W., and Phillips, R.L. (2000). Production and characterization of maize chromosome 9 radiation hybrids derived from an oat-maize addition line. Genetics 156, 327–339.

Ruan, S., Ruan, X., Ruan, Z., Chen, J., Lai, W., Huang, Q., and Chen, Q. (2012). Pleurotus eryngii cultivation technology. Edible Med Mushrooms 20, 173–174.

Rumsey, F., Russell, S., Schäfer, H., and Rasbach, H. (2004). Distribution, ecology and cytology of *Asplenium azoricum* Lovis, Rasbach & Reichstein (*Aspleniaceae*, *Pteridophyta*) and its hybrids. Am Fern J 94, 113–125.

Rushing, A.E., and Snider, J.A. (1985). A natural hybrid between *Bruchia microspora* Nog. and *Trematodon longicollis* Michx. Monographs in Systematic Botany from the Missouri Botanical Garden 11, 121–132.

Ruud, B. (1959). How to cultivate plants services of human (Vol. 2). (Beijing: Science Press).

Schwartz, F.J. (1972). World literature to fish hybrids with an analysis by family, species, and hybrid. Pub Gulf Coast Res Lab Mus (Mississippi).

Schwartz, F.J. (1981). World literature to fish hybrids with an analysis by family, species and hybrid, supplement. NOAA Technical Report NMFS SSRF 2, 750.

Sharma, H.C., and Gill, B.S. (1983). Current status of wide hybridization in wheat. Euphytica 32, 17–31.

Shearer, C., Morgan, W.D., and Fuchs, H.M. (1913). On paternal characters in echinoid hybrids. Quarterly J Micro Sci 10, 282–284.

Sun, C., Chen, F., Fang, W., Liu, Z., and Teng, J. (2010). Advances in research on distant hybridization of Chrysanthemum. Sci Agri Sin 43, 2508–2517.

Song, B.H., Wang, X.Q., Wang, X.R., Sun, L.J., Hong, D.Y., and Peng, P.H. (2002). Maternal lineages of *Pinus densata*, a diploid hybrid. Mol Ecol 11, 1057–1063.

Song, C., Liu, S.J., Xiao, J., He, W.G., Zhou, Y., Qin, Q.B., Zhang, C., and Liu, Y. (2012). Polyploid organisms. Sci China Life Sci 55, 301–311.

Song, R., Lu, W., Wang, J., Shen, Y., Li, Y., and Lin, X. (1998). Ways for selection of brewing grape varieties from *Vitis amurensis* Rupr. interspecific hybridization and its effect. Sci Agri Sin 31, 48–55.

Stanley, J.G. (1976). Production of hybrid, androgenetic, and gynogenetic Grass Carp and Carp. Trans Am Fisheries Soc 105, 10–16.

Tang, Z., Liu, Z., and Su, Z. (1994). An analysis on the types of male sterility in plants. Biodiversity 2, 220–227.

The Breeding Room of the Yangtze River Fisheries Research Institute, Animal Biology Department of Wuhan University Teaching and Research Section. (1975). Preliminary study on several kinds of eco-nomic fish and the hybrid chromosome (in Chinese). Freshwater Fisheries 2, 11–13.

The Yangtze River fisheries research institute, Xiamen fisheries col-lege. (1975). Situation of freshwater fish breeding improved varieties breeding research and basic theory (in Chinese). Chin J Zool 1, 43–45.

Tree breeding group, College of Foresty, Nanjing Forestry University. (1973). Preliminary report on the experiment of hybrid breeding of trees. J Zhejiang Forestry Sci Technol 2, 81–90.

Ulychna, K.O. (1977). Hybrid sporogones in *Phascum cuspidatum*, Pottiaceae, Musci. Ukr Bot Zh 34, 155–158.

Vanbreukelen, E.W.M., and Dong, Y.Y. (1984). Rapidly determine of the competition between 2X and X pollen in living potato. Acta Valu Crop 3, 26–27.

Van Tuyl, J.M., Van Diën, M.P., Van Creij, M.G.M., Van Kleinwee, T.C.M., Franken, J., and Bino, R.J. (1991). Application of *in vitro* pollination, ovary culture, ovule culture and embryo rescue for overcoming incongruity barriers in interspecific *Lilium* crosses. Plant Sci 74, 115–126.

Wagner, F.S. (1987). Evidence for the origin of the hybrid cliff fern, *Woodsia*×*Abbeae* (Aspleniaceae: Athyrioideae). Systatic Bot 12, 116–124.

Wan, S., Huang, E., Qi, C., and Wei, Y. (1987). The comparison experiment of *Oreochromis mossambicus* and *Tilapia nilotica* reproduction performance (in Chinese). Freshwater Fishery 2, 15–16.

Wang, H., and Liu, R. (1986). The study of the hybridization of *Hypophthal-michthys molitrix* (♀) *Cyprinus carpio* (♂) species (in Chinese). J Nanjing Univ (Nat Sci) 22, 87–94.

Wang, J., Ye, L.H., Liu, Q.Z., Peng, L.Y., Liu, W., Yi, X.G., Wang, Y.D., Xiao, J., Xu, K., Hu, F.Z., Ren, L., Tao, M., Zhang, C., Liu, Y., Hong, Y.H., and Liu, S.J. (2015). Rapid genomic DNA changes in allotetraploid fish hybrids. Heredity 114, 601–609.

Wang, L.S. (2006). Plants of sterile lines breeding and hybrid breeding technology. J Anhui Agri Sci 34, 2362–2363.

Wang, S., Huang, R., Wu, X., and Kang, N. (1994). Studies on *Actinidia* breeding by species hybridization. J Fruit Sci 11, 23–26.

Wang, Z., Zou, G., Luo, X., Pan, G., Yang, G., and Zhu, C. (2004). A study on hybridization between *Silurus meridionalis* (♀)×*Silurusmeri asotus* (♂) (in Chinese). Freshwater Fishery 34, 41–43.

Whitt, G.S. (1981). Developmental genetics of fishes: isozymic analyses of differential gene expression. Am Zool 21, 549–572.

Wójcik, W., Jańczuk, B., and Bruque, J.M. (2009). The allotetraploid *Arabidopsis thaliana-Arabidopsis lyrata* subsp. petraea as an alternative model system for the study of polyploidy in plants. Mgg Mol Gener Genet 281, 421–435.

Wolff, K., and Peters-van Rijn, J. (1993). Rapid detection of genetic variability in chrysanthemum (*Dendranthema grandiflora* Tzvelev) using random primers. Heredity 71, 335–341.

Wu, H., Jiang, P., and Bai, J. (2013). Research advances in ecological safety of transgenic fish. Chin Agri Sci Bull 29, 39–43.

Wu, Z. (1983). A cytological study on the formation of the gynogenetic haploid of *Rana limnocharis*. Acta Zool Sin 29, 295–299.

Xie, X., Qiu, Y., Zheng, X., Qi, X., Qiu, L., Huang, Z., Wang, T., and Liang, S. (2009). Studies on the crossing between *Myrica rubra* and *M. nana* and embryo culture *in vitro* of its hybrid F_1. J Fruit Sci 26, 507–510.

Xing, G.M., Long M.H., and Tanaka, S. (1988). Clubroot resistance in *Brassica raphanus*. J Facul Agri Kyushu Univ 33, 189–194.

Xu, K., Duan, W., Xiao, J., Tao, M., Zhang, C., Liu, Y., and Liu, S.J. (2015). Development and application of biological technologies in fish genetic breeding. Sci China Life Sci 58, 187–201.

Yang, A.G., Wang, Q.Y., Liu, Z.H., Zhang, Y. (2002a). Cytological observation on cross fertilization of Chlamys farreri and *Patinopecten yessoensi* with fluorescent microscope (in Chinese). Progr Fish Sci 23, 1–4.

Yang, H., Xia, D., Liu, L., and Wu, T. (2004). Studies on hereditary relationship between *Oreochromis aurea* (♀), *Siniperca chuatsi* (♂) and their offspring. J Fish China 28, 594–598.

Yang, H., Li, S., and Zou, S. (2002b). A primary study on inheritance of mor-phological traits from *Megalobrarma amblycephala*, *Megalobrama terminalis* to their reciprocal hybrids (F_1) (in Chinese). J Shanghai Fish Univ 32, 3–5.

Yang, Q., Shi, H., Ma, D., Zhang, H., Wen, G., Mou, Y., Nian, M., Zhao, J., and Bao, F. (2007). Research of crossing between the Chinese red steppers and Gannan Yaks. China Cattle Sci 33, 1–5.

Ye, Y., Wu, Q., and Chen, R. (1989). Studies on cytology of crosses between grass carp and carp-asynchronization between nucleus and cytoplasm in distant hybridization of fishes (in Chinese). Acta Hydrobiol Sin 13, 234–239.

Yin, Y., Han, X., and Han, R. (1974). A preliminary study on *Parabramis pekinensis* and *Megalobrama terminalis* artificial hybridization (in Chinese). Genet Commun 3, 36–38.

Yu, H., Wu, J., Li, P., Guan, H., Xu, H., and Zhang, S. (2000). The androgenetic allogynogenetic silver crucian carp and its preliminary application. J Fish China 22, 17–21.

Zeng, S., Tian, R., and Chen, Z. (2010). Research progress on cross breeding of *Paphiopedilum*. J Trop Subtrop Bot 18, 459–468.

Zeng, Y., Mou, Y., Zeng, C., and Liu, Y. (2000). Studies on distant hybrid created and used from cross between plum and apricot. Northern Horticul 6, 22–23.

Zhang, H., Xu, S., Xin, W., Pu, Z., Tong, H., Xu, M., and Chen, W. (2012). Study on the F_1 carcass traits and hybrid heterosis of European Pigeons and Silver King Pigeons. Anim Breed Feed 6, 13–15.

Zhang, J., Ma, Z., and Wang, C. (1979a). Research and utilization of F_1 between *Cyprinus carpio rubrofuscus* (♀) and *Cpellegrini pellegrini* (♂) (in Chinese). Freshwater Fishery 2, 14–18.

Zhang, J., Liu, X., Wang, Z., and Jin, G. (1984). A comparative study on the karyotype among the hybrid fish (*Sinilabeo decorus* ♂×*Cirrhinus molitorella* ♀) and its parental fishes (in Chinese). Acta Hydrobiol Sin 8, 313–322.

Zhang, M., Chen, H., Wang, H., Shi, A., Hong, P., and Liu, K. (2015). States and prospect of plants' distant hybridization breeding. J Anhui Agri Sci 43, 11–17.

Zhang, S., Zhang, G., and Li, L. (2012). Reproductive isolation of inter-specific crosses between *Argopectehs irradias* and *Argopecten purpuratus*. Marine Sci 36, 9–14.

Zhang, X., Zhang, J., and Zhang, S. (1991). Breeding of Apple and Pear generic hybrid variety GanJin. J Fruit Sci 8, 65–70.

Zhang, Y., Dai, H., and Liu, Z. (2009). Interspecific hybridization among raspberry cultivars, *Rubus cratagifolius* and *Rubus parvifolius*. J Fruit Sci 26, 899–901.

Zhang, Y., Tan, Y., and Ou, Y. (1990). Chinese Pond Culture. (Beijing: Science Press), pp. 89–120.

Zhang, Z.H., Chen, J., Li, L., Tao, M., Zhang, C., Qin, Q.B., Xiao, J., Liu, Y., and Liu, S.J. (2014). Research advances in animal distant hybridization. Sci China Life Sci 57, 889–902.

Zhang, Z., Qiu, Q., Hu, M., and Lin, K. (1979b). Observations on the embryonic and larval development of the backcross hybrids of *Aristichthys nobi-lis* (♀)×(*Hypophthalmichthys molitrix* ♀×*Aristichthys nobilis* ♂) (♂) (in Chinese). Acta Zool Sin 25, 108–117.

Zhao, Y., Hu, Y., Guo, Y., Zhou, J., Fu, J., Liu, C., Zhu, J., and Zhang, M. (2008). Inter-generic hybrids obtained from cross between litchi and longan cultivars and their molecular identification. J Fruit Sci 25, 950–952.

Zhou, S. (2003). Discrimination of the genomes in BC1 progeny of Asiatic Lily and Oriental Lily using GISH. Acta Horticul Sin 30, 485–486.

Zhou, T., and Li, P. (2013). Chinese hybrid turtles and nomenclature. J Snake 25, 402–406.

Zhu, L., Gui, J., Liang, S., and Jiang, Y. (1993). Isozyme expression of distant hybridization offspring and artificial triploid in silver carp (*Hypophthalmichthys molitrix*) (in Chinese). Acta Hydrobiol Sin 17, 293–297.

Zhu, X. (1934). Research on Guangzhou frogs interbreed (in Chinese). Acta Scient Nat Univ Sunyatseni 6, 219–262.

Zhu, X. (1961). Discussion about the fertilization process of animal hybridization (in Chinese). Chin Sci Bull 7, 1–7.

Zhu, K. (1986). Study on the hybridization between the classes of higher plants. World Sci 1, 1–5.

Zhu, K. (1988). Super gate hybrid. World Sci 1, 2.

Zhu, Y., and Li, Q. (2002). Investigation on the fertility and chromosome of distant crossing hybrid of *A. yamamai* and *A. polyphemus*. Sci Sericul 28, 91–93.

Zong, E., Fan, G., Yin, H., Wang, B., Zhang, C., Sun, M., and Jiao, S. (1985). A study on the chromosomes of interspecific F_2 hybrids between horse and ass (in Chinese). Sci Agri Sin 1, 83–85.