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Evidence for an Ancient Whole-Genome Duplication Event in Rice and Other Cereals

TIAN Chao-Guang[1,2,*], XIONG Yu-Qing[1,2,*], LIU Tie-Yan[1,2], SUN Shou-Hong[1], CHEN Liang-Biao[1], CHEN Ming-Sheng[1,①]

(1. *Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing* 100101, *China*;
2. *Graduate School, Chinese Academy of Sciences, Beijing* 100039, *China*)

Abstract: Gene duplication has been proposed as an accelerator of evolution. Ancient genome duplication events have been identified in diverse organisms, such as yeast, vertebrates, and *Arabidopsis*. Here, we have identified a whole genome duplication event (WGD) in the rice genome, which took place prior to the divergence of grasses about 70 million years ago (mya). A total of 117 duplicated blocks were detected, which are distributed on all 12 chromosomes and cover about 60% of the rice genome. About 20% genes on these duplicated segments are retained as duplicate pairs. In contrast, 60% of the transcription factor genes are retained as duplicates. The identification of a WGD in the ancestral grass genome will impact the study of grass genome evolution, and suggest that polyploidization and subsequent gene losses and chromosomal rearrangements have played an important role in the diversification of grasses.

Key words: genome duplication; genome evolution; polyploidization

水稻和其他禾本科植物基因组多倍体起源的证据

田朝光[1,2,*], 熊煜青[1,2,*], 刘铁燕[1,2], 孙守红[1], 陈良标[1], 陈明生[1,①]

(1. 中国科学院遗传与发育生物学研究所, 北京 100101;
2. 中国科学院研究生院, 北京 100039)

摘 要: 基因加倍(Gene duplication)被认为是进化的加速器。古老的基因组加倍事件已经在多个物种中被确定,包括酵母、脊椎动物以及拟南芥等。本研究发现水稻基因组同样存在全基因组加倍事件,大概发生在禾谷类作物分化之前,距今约 7 000 万年。在水稻基因组中,共找到 117 个加倍区段(Duplicated block),分布在水稻的全部 12 条染色体,覆盖约 60% 的水稻基因组。在加倍区段,大约有 20% 的基因保留了加倍后的姊妹基因对(Duplicated pairs)。与此形成鲜明对照的是加倍区段的转录因子保留了 60% 的姊妹基因。禾本科植物全基因组加倍事件的确定对研究禾本科植物基因组的进化具有重要影响,暗示了多倍体化及随后的基因丢失、染色体重排等在禾谷类物种分化中扮演了重要角色。

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* 表示同为第一作者

作者简介: 田朝光(1973-),男,博士生

① 通讯作者。E-mail: mschen@genetics.ac.cn; Tel: 010-64837087

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Gene duplication has been proposed as the major force of evolution, as duplicated genes can supply the genetic raw material for the creation of novel functions through mutation and natural selection[1]. WGD (whole genome duplication) is particularly intriguing, which was usually followed by diploidization with extensive loss of duplicated genes and genomic rearrangements[2~4]. There is evidence for segmental/genome-wide duplications in the vertebrates[5], including human[6,7], mouse[8] and fish[9]. The yeast (*Saccharomyces cerevisiae*) was also shown to be an ancient tetraploid[10~14]. In plants, polyploidy is ubiquitous[15], and recent studies based on the complete genome sequencing information have also hypothesized that the small crucifer *Arabidopsis* (*Arabidopsis thaliana*) is an ancient polyploid[3,16~20].

The grass family Poaceae is one of the largest families of angiosperms, including approximately 10 000 species that diverged from a common ancestor 50 to 70 mya[21]. It has been proposed that most grass species are of polyploid origin[22,23]. For example, bread wheat (*Triticum aestivum*) is an allohexaploid and has conserved homoeologous chromosomes[24,25]. However, maize (*Zea mays*) represents an older tetraploidization event, which lost its homoeologous chromosomes by reassembling homoeologous segments on newly formed chromosomes[26]. In contrast to maize and wheat, rice (*Oryza sativa*) and sorghum (*Sorghum bicolor*) are regarded as a diploid although tetraploid versions exist, where homoeologous chromosomes like in wheat are preserved. Homoeologous chromosomal regions derived from ancestral chromosomes of the progenitors of the grass family have been demonstrated using genetically mapped markers. In such a comparison, orthologous markers have shown that while maize falls into two subgenomes, rice and sorghum are represented by a single subgenome[27]. Segmental duplications in the rice genome were reported previously[28,29], but analysis of whole genome sequence data has provided unprecedented opportunities for identifying ancient genome duplication events, similar to those in yeast and *Arabidopsis*[3]. After the draft sequencing of the rice genome, genome-wide duplications were also proposed for the rice genome. But the nature and origin of these genomic duplications remained controversial [30~33]. Over 2 000 duplicated cDNAs were plotted by chromosomal regions, and the extent of genome duplications were defined[30]. However, most of the duplicated segments identified were small, except for a large segment shared by chromosomes 11 and 12. Dating on the basis of amino acid substitution rate revealed that a WGD occurred in rice some 40 to 50 mya[30]. However, another study claims that rice is an ancient aneuploid that has experienced the duplication of one or a large part of one chromosome about 70 mya, predating the divergence of most cereals[31]. By using transcription factor genes as anchor points, we have identified genome-wide duplications in the rice genome (Xiong *et al.*, submitted). In this manuscript, we have used the map-based complete sequence of the rice genome to provide evidence that a WGD took place in the ancestor of rice about 70 mya, predating the divergence of grasses, suggesting that gene duplications, insertions, and deletions have occurred over long period of time in the evolution of the grasses.

1 Material and Methods

1.1 Dataset

A total of 56 056 predicted rice genes (both nucleotide and amino acid sequence data) were retrieved from the TIGR database (http://www.

tigr. org). Retrotransposon-like sequences were removed by searching with BLASTP[34] to known retrotransposon sequences. The remaining dataset includes 42 688 gene models. The *Arabidopsis* data were downloaded from the TAIR database (http ://www. arabidopsis. org). The Moss EST data were downloaded from the NIBB PHYSCObase (http ://moss. nibb. ac. jp/)[35]. The data for maize, wheat, barley, and sorghum were selected from the SWISS-PROT protein database (http ://www. ebi. ac. uk/swissprot/) and the National Center for Biotechnology Information (NCBI) UniGene collection (http ://www. ncbi. nlm. nih. gov/Genbank/index. html).

1.2 Detection of duplicated blocks in the rice genome

The detection of duplicated blocks was initially performed using transcription factor genes of rice (Xiong *et al.*, submitted). We have expanded those duplicated regions by three steps. First, we identified all gene pairs in each pair of sister regions. We used the BLASTP program to search for all the predicted genes on each pair of duplicated chromosomes or segments of chromosomes. An e-value less than 1e-10, an overlapping region of more than 150 amino acids, and an identity of no less than 30% were used to identify the reciprocal best hits[31]. Second, the anchor points were identified based on the order and distance of each pair of genes. Small inversions were allowed in our analysis. The intervening region between two neighboring anchors contains no more than 30 genes on both strands[17]. Third, duplicated blocks were identified based on the number and order of anchors. The blocks identified contain at least three anchors in an appropriate order and orientation.

1.3 Phylogenetic analysis of duplicated genes

The homologs in maize, sorghum, barley, wheat, *Arabidopsis* or moss were detected using the BLASTP program. An e-value less than 1e-10, an overlapping region of more than 150 amino acids, and an identity of no less than 30% were used to identify the reciprocal best hits. The phylogenetic tree was constructed with the neighbor-joining method using the ClustalW program for alignment[36]. Each group contains four proteins: two rice duplicate pairs, the best homolog from an organism under comparison, and the best homolog from outgroup. The final rooted trees with less than 70% bootstrap support were not included for further analysis.

1.4 Asymmetric divergence of duplicate genes

A total of 608 maize homologs were used to detect rice duplicates with asymmetric divergence in these 608 pairs of rice duplicate genes. The phylogenetic tree was constructed with the neighbor-joining method using the ClustalW program for alignment[36]. The evolution rate of duplicate genes was derived from the tree branch length[11]. If one duplicate evolved 50% faster than the other one, asymmetric evolution was inferred for these duplicates[11].

1.5 Age estimation of duplicated blocks

The values of dS (synonymous substitution rate) were calculated with the PAML software[37]. The synonymous substitution rate was considered to be 6.03×10^{-9} synonymous base substitutions per site per year[38].

2 Results and Discussion

2.1 Detection of duplicated segments

Previously, we detected 12 pairs of large intragenomic duplicated segments in the rice genome by phylogenetic analysis of transcription factor genes (Xiong *et al.*, submitted). We have extended those studies with more stringent criteria (see Material and Methods), and identified 117

duplicated blocks, which contain 1 934 anchors and about 20 000 gene models, with at least three anchor points within each block (Fig. 1, Table 1). Except for genes on chromosomes 11-12, the average identity of duplicated genes in the rice genome is about 62%, which is similar to 63% found in yeast[39]. However, the average identity of duplicated genes on chromosomes11-12 is about 76%, suggesting that the segmental duplication on chromosomes 11-12 is a more recent event.

Continuous duplicated blocks on a chromosome likely represent one large duplicated region, although they do not satisfy our criteria for one duplicated block (see Material and Methods) (Fig. 1). Our 117 blocks could compose 12 duplicated segments, including chr1-5 (short arm and long arm), 2-4, 2-6 (short arm and long arm), 3-7 (short arm and long arm), 3-10, 3-12, 4-8, 8-9, and 11-12. The duplicated regions cover 26 000 gene models and 61. 1% of the rice genome, which is similar to 61. 9% reported earlier by Paterson *et al.*[40].

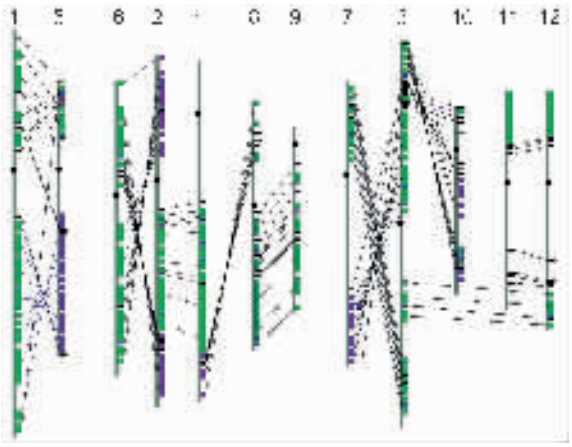

Fig. 1 Duplicated blocks in the rice genome

Sister duplicated segments are connected with a single line. The duplicated segments that have the same orientation are marked with the same color; the duplicated segments that have different orientations are labeled with different colors. The centromeres of chromosomes are marked as black dots.

Table 1 Summary of rice duplicated blocks

	Small blocks[a]		Large blocks[a]			Total blocks	Total anchors
	No. of Blocks	No. of anchors	No. of Blocks	No. of anchors	Mean of dS[b]		
Chr1-5	7	29	14	441	0.82	21	470
Chr2-4	3	13	8	250	0.79	11	263
Chr2-6	4	17	12	268	0.84	16	285
Chr3-7	5	17	14	207	0.86	19	224
Chr3-10	8	36	10	119	0.84	18	155
Chr8-9	8	30	6	153	0.79	14	183
Chr11-12	7	21	1	245	0.25	8	266
Chr3-12	1	4	3	42	0.86	4	46
Chr4-8	3	16	3	26	0.92	6	42
Total	46	183	71	1751	0.75	117	1934

a: Small blocks refer to those bocks with 3-6 anchors, and large blocks with no less than seven anchors. b: The mean of dS was calculated based on large blocks only.

71 duplicated blocks contain at least 7 anchors within each block. In total, these duplicated blocks contain 1 751 anchors and 18 000 gene models, and cover about 42% of the entire genome. The following analyses were based mainly on these 71 duplicated blocks. In these 71 duplicated blocks, 20% of the genes are retained as duplicate pairs, compared to only 12% in yeast[11] and 28% in *Arabidopsis* for the recent duplication[17]. In contrasting, about 60% of the transcription factor genes are retained as duplicate pairs on these blocks (Xiong *et al.*, submitted), which could be due to the potential of regulatory genes to evolve new functions and hence be retained in the genome[41,42]. In *Arabidopsis*, genes involved in signal transduction and transcription were also preferentially retained after WGD and subsequent gene losses[43].

Because over 80% of the genes have been

lost since the WGD event, extensive gene deletion and chromosome rearrangement must have taken place. In the yeast genome, gene loss in duplicated blocks occurred by many small deletions (the average size of a lost segment is two genes), and was typically balanced between the two sister regions (average balance between 57% to 43%)[11]. In the rice genome, of the 71 larger duplicated blocks, gene loss was also generally balanced between the two sister regions (average balance between 61% to 39%). The average size of a lost segment is five genes.

The largest duplication block lies on chromosomes 11-12, which contains 245 anchors and a size of about 4 Mb. The average size of duplicated blocks is more than 1 Mb, which contains 25 anchors and about 130 genes. The distribution of duplicated blocks on all 12 chromosomes is not entirely random. For example, except the large duplicated segments on the short arms of chromosomes 11 and 12, which have a very recent origin, very few additional duplicated segments were identified on these two chromosomes (Fig. 1). No duplicated block was identified in the centromeric regions, which is similar to the situation in *Arabidopsis*[17].

2.2 Dating of duplication events

Phylogenetic analysis provides an opportunity to assess the temporal order of duplication events and can be used to infer whether the duplication occurred before speciation[11,14,18,40,44]. However, a major handicap for the analysis of the rice genome is the absence of data from a descendent of a progenitor that did not undergo a WGD like in the comparison of *Kluyveromyces waltii* and *Saccharomyces cerevisiae*[11] or *Sorghum bicolor* and *Zea mays*[26]. Therefore, we can not establish orthology for all genes, two genes derived from the same ancestral chromosome, and have to base our phylogenetic analysis for each pair of duplicated genes on homologs from *Arabidopsis*, wheat, barley, sorghum and maize. On the other hand, if a homolog from another species matches more gene copies in rice than the two aligned pairs, it is assumed that the one that has formed after speciation is a paralogous sequence (Fig. 2). The ratio of internal trees for all cereal species tested is between 52% ~ 57% (Table 2). However, the ratio of internal trees for Arabidopsis is 5%. We estimated the duplication time by calculating the dS values assuming a molecular clock[17,30,40,45,20]. Based on these calculations a major duplication event occurred 73 mya ago before cereal species diverged from a common ancestor, but after the divergence of monocots and eudicots. The duplication on the short arms of chromosomes 11 and 12 is of very recent origin, and was estimated to have occurred 8 mya.

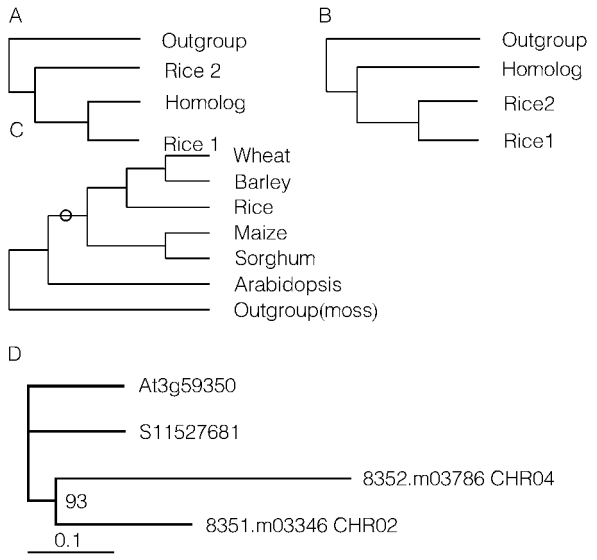

Fig. 2 Phylogenetic analysis of duplicated genes

A :Internal tree, the topology of which means that the duplication occurred before species divergence. B :External tree, the topology of which means that the duplication occurred after species divergence. C :Phylogenetic tree of cereals. A whole genome duplication event took place right before the divergence of cereals as indicated by the open circle. D :A pseudo-external tree of a pair of rice duplicate genes with their maize homolog. 8352. m03786 and 8351. m03346 are two rice duplicates. S11527681 is the maize homolog. At3g59350 is the outgroup from *Arabidopsis*. The number at the node (93) is the bootstrap value. The number above the line represents 0.1 substitutions per site.

Table 2 Phylogenetic dating of the genomic duplication in rice

Species	*Arabid-opsis*	Maize	Sorghum	Barley	Wheat
Total number of trees	359	608	252	401	516
Number of internal trees	17	319	130	212	292
Percent of internal trees	5%	53%	52%	53%	57%

Note: The *Arabidopsis* sequences were subject to phylogenetic analysis using moss as outgroup. The maize, sorghum, barley and wheat sequences were subject to phylogenetic analysis using the *Arabidopsis* sequences as outgroup.

The age estimation of duplicated blocks suggested that either the whole genome duplicated as a single event or as massive duplications before the divergence of grasses. If independent duplication events might have taken place prior to the divergence of grasses, one might expect to find examples of triplications besides duplications. One could argue that, based on the Poisson distribution, 71 successive duplications would be expected to result in about 10 triplicated regions (duplicates of duplicates)[10]. However, we observed only one triplicated region in these 71 blocks. The expected number of triplicated regions for 117 duplicated blocks is 16; however, we observed only two. As described above, we calculated the dS values for all duplicated pairs. The distribution of these values indicates that most duplicated genes have duplicated at a similar time (Fig. 3). These results support that a WGD occurred about 70 mya predating the divergence of grasses.

The phylogenetic analysis of the duplicated genes could suffer from long branch attraction[10,14,39]. Further, comparison of paralogs between two species could also shift results significantly. For instance, when we examined our data using the maize homologs as examples, we find that out of 608 maize-rice trees, 133 (22%) show asymmetric evolution for the two rice duplicates. This ratio is similar to that in yeast (21% ~ 27%)[46] and *Arabidopsis* (21%)[43]. Twenty-three of these 133 trees show erroneous topology, mainly because one duplicate evolved faster than the other one. For example, 8351. m03346, 8352. m03786 and the maize homolog form a pseudo-external tree (Fig. 2, D).

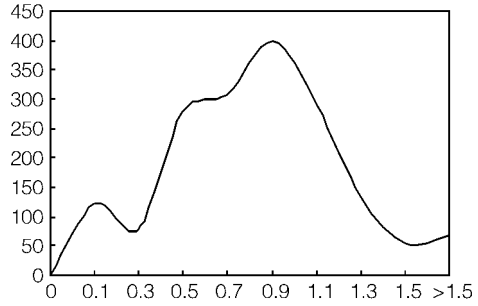

Fig. 3 Distribution of dS values for duplicated rice genes

The horizontal axis represents the values of dS. The vertical axis represents the number of duplicated pairs. The left shoulder represents the duplicated segment on the short arms of chromosomes 11 and 12.

2.3 Asymmetric evolution of duplicate genes

WGD (polyploidization) has been proposed as an accelerator of evolution[22,47]. In yeast, genome duplication played a direct role in the adaptation of the S. cerevisiae lineage towards fermentation[10,14,39]. Ohnologs (paralogs derived from whole genome duplication)[3,39] have evolved novel functions and show different spatial and temporal expression patterns or respond differently to environmental cues. About 20% of the ohnologs show asymmetric evolution, as one ohnolog evolved faster than the other one[11,46]. In *Arabidopsis*, 57% of the recent duplicated pairs and 73% ancient duplicated pairs have diverged in their expression patterns[43]. In *Arabidopsis*, 21% of the recent duplicates show asymmetric evolution in *Arabidopsis*[43].

In order to find out which genes have played important roles in the rice genome evolution, we analyzed the 133 asymmetrically evolved duplicates derived from the phylogenetic analysis of the rice duplicates with their maize homologs. We classified these 133 duplicate pairs into different

function categories based on Gene Ontology[48] (Table 3). Genes that encode enzymes involved in metabolism form the largest group, suggesting that the modification of metabolism might be important for species divergence and adaptation to the environment. For example, the ohnologs for hexokinases that are involved in glucose metabolic pathway have asymmetric divergence in yeast[39,49]. In rice, one duplicate pair, which encodes putative hexokinase, also has asymmetric evolution. Another group of genes that show asymmetric divergence are genes involved in regulatory network (mainly transcription factor genes). Thirteen transcription factor genes show asymmetric evolution, and are distributed in 8 gene families, including MADS-box, MYB, bZIP, WRKY, RAV2, AP2/ERF, BHLH, and E2F/DP.

Table 3 Classification of rice duplicate genes with asymmetric evolution

Molecular Function	Number	Biological process	Number
Chaperone	2	Cell communication	8
Catalytic activity	82	Cell growth and/or maintenance	21
Enzyme regulator	2	Cell cycle	5
Binding	64	Cell motility	0
Nucleic acid binding	33	Metabolism	87
Structural molecule	4	Response to stress	5
Motor	2	Transport	15
Transporter	11	Death	1
Transcriptional regulator	7	Development	4
Signal transductor	7	Physiological processes	101
Hypothetical/ unknown protein	4	Biological process unknown	2
Unclassified	14	Unclassified	11

Note :The genes were annotated and classified by GoPipe program (Chen L *et al.*, unpublished data). The same gene can be classified into different groups, so the sum can exceed the number of duplicates (133).

To conclude, we detected a WGD predating the divergence of cereal species but postdating the split of monocot-eudicot divergence. The duplicated regions cover about 50% ~60% of the rice genome. How about the remaining 40% of the rice genome? From the yeast study, we learned that some ohnologs have diverged beyond detection by BLAST search[39], so they cannot be easily recognized in our current searching algorithm. Discovery of many of the duplicated regions will await the complete sequencing of a reference genome, which diverged from the rice genome before the WGD[11,12] or other grasses, such as maize and sorghum[4,26].

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“2005 中国黑龙江国际农业生物技术峰会”

由中国黑龙江省农业科学院、英国皇家农业大学、中国生物工程学会和香港文汇报共同主办的“2005 中国黑龙江国际农业生物技术峰会”将于 2005 年 9 月在哈尔滨市举行。会议将邀请世界著名生物技术科学家到会做学术报告,共同探讨农业生物技术最新研究动态、前瞻技术及未来发展方向,引导产、学、研相结合,打造国际合作平台,共同推进农业生物技术的研究和产业开发。本次会议包括大会主题报告、分组报告研讨和生物技术博览三大模块。大会主题 :生物技术与现代农业。

会议包括以下内容:

1. 植物生物技术的研究与应用 ;2. 动物生物技术的研究与应用 ;3. 微生物生物技术的研究与应用 ;4. 生物、食品安全性评估及公众评价 ;5. 农业生物技术产业化论坛。

已邀请到的大会报告人

国外(按英文字母顺序排列) :1. Brain Heap 教授 2. Ganesh M, Kishore 博士 3. Lee Sing Kong 教授 4. Paul Davies 教授 5. Roger N. Beachy 博士

国内(按姓氏笔画顺序排列) :1. 王连铮 2. 任继周 3. 沈荣显 4. 杨胜利 5. 周 琪 6. 黎志康 7. 薛红卫

会议时间与地点

时间 :2005 年 9 月 6 ~10 日 ;地点 :哈尔滨国际会展中心

参会费用

国内与会代表每人缴纳注册费 980 元人民币,在读研究生(凭有效证件)500 元人民币,国外与会代表 380 美元。注册费包括会议交通、资料、用餐等费用,差旅费自理。

论文征集

1. 欢迎与会人员提交论文或论文摘要,内容应符合大会主题范围,近期未公开发表的研究论文或综述的英文电子版。论文按版面收费,每版 180 元人民币,为审阅稿件方便起见,在提交论文时应附中文摘要 ;另外,可单独提交英文论文摘要,每篇收费 300 元人民币,也须附中文摘要。会议论文将以《中国生物工程杂志》增刊形式正式出版。具体格式要求见网站 :www.iac2005.haas.cn

2. 投稿通过电子邮件报送,并请在电子邮件主题栏中注明所属内容。电子邮箱 :haas2005@vip.163.com 或 haas2005@126.com

3. 征文截止日期 :2005 年 7 月 15 日

联系方式

网 站 :www.iac2005.haas.cn 电子邮件 :haas2005@vip.163.com 或 haas2005@126.com

通信地址 :黑龙江省哈尔滨市学府路 368 号 黑龙江省农业科学院国际合作处 邮 编 :150086

电 话 :086-451-86677452 传 真 :086-451-86695508

联 系 人 :王 珣 :13351913218 李 铁 :13936133830 韩德贤 :13936042361