



# Article Cloning of Three Cytokinin Oxidase/Dehydrogenase Genes in Bambusa oldhamii

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**Abstract:** Cytokinin oxidase/dehydrogenase (CKX) catalyzes the irreversible breakdown of active cytokinins, which are a class of plant hormones that regulate cell division. According to conserved sequences of *CKX* genes from monocotyledons, PCR primers were designed to synthesize a probe for screening a bamboo genomic library. Cloned results of three genes encoding cytokinin oxidase were named as follows: *BoCKX1*, *BoCKX2*, and *BoCKX3*. In comparing the exon-intron structures among the above three genes, there are three exons and two introns in *BoCKX1* and *BoCKX3* genes, whereas *BoCKX2* contains four exons and three introns. The amino acid sequence of BoCKX2 protein shares 78% and 79% identity with BoCKX1 and BoCKX3 proteins, respectively. *BoCKX1* and *BoCKX3* genes are particularly closely related given that the amino acid and nucleotide sequence identities are more than 90%. These three BoCKX proteins carried putative signal peptide sequences typical of secretion pathway, and a GHS-motif was found at N-terminal flavin adenine dinucleotide (FAD) binding domain, suggesting that BoCKX proteins might covalently conjugate with an FAD cofactor through a predicted histidine residue.

Keywords: Bambusa oldhamii; cytokinin oxidase/dehydrogenase; genomic DNA library



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# 1. Introduction

Cytokinin is a phytohormone of plant growth regulators, playing an important role in the control of plant division. Many developmental events, such as shoot and root branching, leaf development, delay of senescence, and chloroplast ripening are directly regulated by the physiological functions of cytokinins [1–5]. In plants, the homeostasis of cytokinins is balanced in many aspects [6], including rate of de novo synthesis by isopentenyl transferase enzyme [7], rate of interconversion and transport [8], and rate of cytokinin turnover, mainly by cytokinin oxidase/dehydrogenase [9].

The *CKX* gene-encoded cytokinin oxidase/dehydrogenase enzyme (CKX, EC 1.5.99.12) catalyzes the turnover of the cytokinins, isopentenyl-adenine, zeatin, and their ribosides by a unique enzymatic reaction by cleaving and oxidizing its side chain for converting isopentenyladenine to unsaturated 3-methyl-2-butenal and adenine [2,10]. CKX enzyme activity was initially identified by Pačes and coworkers in 1971 [11] and named by Whitty and Hall in 1974 [12]. After nearly three decades, *ZmCKX1* was the first *CKX* gene independently cloned by two research groups in maize *Zea mays* [13,14]. CKX proteins are usually encoded by homologous genes in plants, such as *Arabidopsis thaliana* [15,16], *Hordeum vulgare* [17,18], *Jatropha curcas* [19], *Oryza sativa* [9,20,21], *Zea mays* [22,23], and so on. Recently, 23 *BnCKX* genes were identified in *Brassica napus* [24]. Therefore, CKX enzyme activity largely governs the utilization of cytokinins in plant cells.

Elevated cytokinin levels were linked with increased cytokinin degradation by CKX enzyme in many plants, such as *Zea mays* [25], *Triticum aestivum* [26], and *Brassica napus* [24,27], suggesting that *CKX* gene expression is manipulated by endogenous cytokinin extents [5]. Overexpression of the *AtCKX3* [28] and *OsCKX2* [9] are associated with reduced

flower numbers and grain numbers, respectively. Expression of the *AtCKX1* in *Nicotiana tabacum* enhances drought and heat stress tolerance, indicating that cytokinin levels may have a positive effect on plant stress responses [29–31]. Under salinity condition, rice yield penalty is reduced by knockdown of the *OsCKX2* gene as well as increased inflorescence meristem cytokinin extent [32].

Alternation in CKX enzymatic activity changes cytokinin concentrations in cells and tissues. CKX enzymes play key roles in contributing to the regulation of cytokinin-dependent processes and in controlling local cytokinin level [33]. Functions of CKX proteins can be regulated by several post-translational modifications, e.g., glycosylation, and contain FAD as a cofactor [21,34]. CKX proteins are widely detected in various subcellular compartments, such as chloroplast, mitochondria, and so on [35]. Most CKX enzymes are localized in the apoplast, e.g., ZmCKX1 [23], or vacuole, e.g., AtCKX1 and AtCKX3 [36]. Some CKX proteins are shown to be cytosolic enzymes, such as AtCKX7 [37] and ZmCKX10 [23]. AtCKX1 protein is recently reported to be an endoplasmic reticulum (ER) membrane protein [16].

*Bambusa oldhamii*, green bamboo, is a perennial plant in the tropics and subtropics, and bamboo shoot is an economic vegetable in far-eastern Asia [38–44]. Bamboo is one of the fast-growth timber plants, which are controlled by plant hormones, especially cytokinins [45]. Bamboo cytokinin biosynthesis by the BoAIPT1 isopentenyltransferase enzyme [7] and cytokinin degradation by the BoCKX enzymes may play equally important roles for fine-tuning cytokinin levels in the rapid-dividing tissues. In this study, we cloned and reported three completely sequenced *CKX* genes, including all exon-intron conformations and partial upstream promoter regions. Sequence analysis of the BoCKX1–3 predicts multiple asparagine residues as putative target sites of glycosylation. In addition, several *cis*-acting elements were discovered from the promoters regions of three *BoCKX* genes.

#### 2. Materials and Methods

#### 2.1. Plant Material

Edible fresh green bamboo shoot mainly harvested between April and September from Mucha mountain areas, Taipei City, Taiwan. Samples were divided into inedible shell and edible shoot and were frozen and stored at -80 °C freezer.

#### 2.2. Reagents

DNA ladders and iProof DNA polymerase were obtained from Bio-Rad, Hercules, CA, USA. PrimeStar DNA polymerase mixture was purchased from Takara, Kusatsu, Shiga, Japan. T4 DNA ligase and restriction endonucleases were purchased from New England Biolabs, Ipswich, MA, USA. SeaKem<sup>®</sup> LE Agarose was obtained from Lonza, Basel, Switzerland. Gel extraction/PCR cleanup kit was purchased from Biotools, New Taipei City, Taiwan. Plasmid mini-prep kit was obtained from Geneaid, New Taipei City, Taiwan. Oligonucleotides synthesis and DNA sequencing services were provided by Tri-I Biotech, New Taipei City, Taiwan.

#### 2.3. Total RNA Extraction, cDNA Synthesis, and DIG Labeled Probe Preparation

TRIZOL reagents (Invitrogen, Waltham, MA, USA) were used to extract total RNA from bamboo etiolated shoots and utilized as materials for complementary DNA (cDNA) synthesis using MMLV reverse transcriptase (Invitrogen, Waltham, MA, USA), and used as PCR template. Degenerate primers CKX-F (5'-GGGAGATGGTGACGTGCTCCAA-3') and CKX-R (5'-CAGCGACACSRMGTAGAACAC-3') were designed according to the conserved regions of the *OsCKX1* and *OsCKX2* genes from *Oryza sativa* [4]. PCR reaction was carried out at 94 °C for 30 s, 60 °C for 30 s, and 72 °C for 1 min, and then repeated for 30 cycle-reaction. The 900 bp *BoCKX* fragment (Figure S1) was confirmed by DNA sequencing (Tri-I Biotech, New Taipei City, Taiwan). DIG-labeled probe was synthesized by PCR reaction using DIG DNA labeling kit supplied by Roche, Basel, Switzerland.

# 2.4. Genomic Library Screening, Phage DNA Preparation, and DNA Sequencing by Chromosome Walking

A genomic library of green bamboo was previously constructed by Lambda FIX<sup>®</sup> II/*Xho*I Partial Fill-In Vector Kit (Strategene, San Diego, CA, USA) [7]. Nine to twenty-three kb bamboo genomic DNA fragments were conjugated with a 41.9 kb Lambda FIX<sup>®</sup> II vector, and the overall phage DNA constructed were between 50 and 65 kb [7]. The DIG-labeled *BoCKX* probe was used to screen the bamboo genomic DNA library. Plaques of phages were transferred onto a Hybond-H<sup>+</sup> hybridization membrane (MilliporeSigma, Burlington, MA, USA). The processes of hybridization and detection were based on the instructions of the manufacturer (Roche, Basel, Switzerland). Phage DNA was purified from *E. coli* XL1-Blue MRA (P2) by traditional method [46] and digested by *Not*I restriction endonuclease. Phage DNA isolated from positive clones (Lambda midi kit, Qiagene, Hilden, Germany) were further confirmed by DNA sequencing (Tri-I Biotech, New Taipei City, Taiwan), and chromosome walking method was used to obtain complete genomic sequences of the three *BoCKX* genes.

## 2.5. Bioinformatics and Promoter Analysis

Protein sequence alignment was analyzed by Vector NTI Suite 10 Sequence Software (Invitrogen, Waltham, MA, USA). Phosphorylation and glycosylation sites were predicted by NetNGly (http://www.cbs.dtu.dk/servies/NetNGly/, accessed on 15 March 2020) [47] and NetPhos (http://www.cbs.dtu.dk/services/NetPhos/, accessed on 15 March 2020) [48], respectively. The putative *cis*-acting elements and the transcriptional start site were predicted by PlantPAN (retrieved from: http://PlantPAN.itps.ncku.edu.tw, accessed on 25 May 2020) [49] and PlantProm (retrieved from: http://mendel.cs.rhul.ac.uk, accessed on 25 May 2020) [50].

#### 3. Results

#### 3.1. Cloning of Three BoCKXs Genes by Screening a Bamboo Genomic DNA Library

A Lambda FIX<sup>®</sup> II genomic library constructed genomic DNA was hybridized and screened by a DIG labeled *BoCKX* probe (Figure S1) [38]. Sequence alignment results showed a high similarity of 64% between the deduced amino acid sequence of the BoCKX probe and ZmCKX1 proteins (Figure S1). Phage DNAs were isolated from positive clones and digested by *Not*I restriction enzyme (Figure 1), followed by DNA sequencing. Three different digestion patterns from four positive clones were observed, indicating that three different *BoCKX* genes were identified. Chromosome walking methodology was performed to obtain the total sequence information of these positive clones. Luckily, three full-length *BoCKX* genes with partial promoter regions were obtained, namely *BoCKX1* (Figure 1A, lane 1), *BoCKX2* (Figure 1B, lanes 1 and 2), and *BoCKX3* (Figure 1A, lane 2). Gene names, *BoCKX1–3*, were designated in the order of DNA sequencing accomplished. These genomic DNA sequences had been deposited at GenBank (Bethesda, MD, USA) with accession numbers, GU263785, GU263786, and GU263787, respectively.

#### 3.2. Genomic Organization of the Three BoCKXs Genes

Phage DNA containing bamboo *CKX* genes were completely sequenced by chromosome walking method, and exon-intron structures of the three *BoCKX* genes were plotted in Figure 2A. The intron-exon organizations of various *CKX* genes in plants were compared and shown in Figure 2B. *BoCKX1* contained a 1578 bp open-reading frame (ORF) and encoded a 525 amino acid polypeptide or a 57.0 kDa protein (Figure 2A). *BoCKX2* contained a 1572 bp ORF and encoded a 523 amino acid polypeptide or a 57.4 kDa protein (Figure 2A). *BoCKX3* contained a 1569 bp ORF and encoded a 522 amino acid polypeptide or a 56.6 kDa protein (Figure 2A).



**Figure 1.** Three *CKX* genes were isolated by screening a bamboo genomic DNA Library. *BoCKX1* (**A**, lane 1), *BoCKX2* (**B**, lanes 1 and 2), and *BoCKX3* (**A**, lane 2) phagemids were purified and then digested by *Not*I. The size of the Lambda FIX II vector (41.9 kb) was indicated.



**Figure 2.** Exon-intron organization of Bamboo *CKX* genes. Introns (lines) and exons (rectangles) were graphed to scale, along with the number of base pairs (bp). Sequences compared (**A**) were isolated from *Bambusa oldhamii* (*BoCKX1*, GU263785; *BoCKX2*, GU263786; and *BoCKX3*, GU263787). Exon-intron structures of the *CKX* genes were compared among different species (**B**).

*BoCKX1* and *BoCKX3* were composed of three exons and two introns (Figure 2A,B), as also observed in other CKX genes, such as *OsCKX1* [4] and *ZmCKX1* [13,14]. Unlike *BoCKX1* and *BoCKX3*, the exon 2 of *BoCKX2* was divided into exons 2a and 2b (Figure 2A,B).

As a result, *BoCKX2* possessed four exons and three introns, similar to *Dendrobium sonia DsCKX1* [51] and *OsCKX2* (Figure 2B) [4]. *AtCKX1–6* genes all consisted of four introns and five exons (Figure 2B) [15].

# 3.3. Protein Similarity of CKXs Proteins

Protein sequence alignment research revealed that BoCKX proteins had 71–92% identities, with BoCKX1 protein being the most similar to BoCKX3 protein (92% identity; Figure 3 and Table 1).

-	(1)	1	10	20	30	40	50	60	70	80	90	100	110
AtGKX1	(1)	MGLTSSLR	HRQNNET	GIFMI	LVLSCIFGE	RTNLCSNHSVST	PKELPSSNPSDI	RSSLVSLDL	EGYISFDDVH	INVARDEGNES	IQLPP	LAILHPR	SVEDISS
BOCKX1	(1)		AVV	VIEVAL	IASCHARG	GGGHPWPAPS	SLPGDLG	ALAVAG	KLRTDPNATV	PASMDFGNI	TALP	TAVLLPA	SPGDVAA
B-CKV2	(1)			a company	- SSSRAVAA	DNPWIL	PLOGENA	VLAAAG	KLEND FNATV	PASIDEGRU	DALF	AAVL PL	SPUDVAA
D-CKV1	(1)		MANT N	AMPDE	NDERLIT	G-DREWETSG	TOTNET	THOTOT	VIDED STOT	PASIDEGRI		ANVLS PA	OPODIAA
HyCkX2	(1)		MPOTITO	TETT	CICLUTAR	HUIKH	DELMEL DI	TARICTON	DCHESEHDIS	12 2 2 MD FCNT			SUNDIAL
O=CKX1	(1)		MAATY	TTTZAT	TASSHATAS	HCACCCUPIAN	A DT. PFPG	013396	ELETDENATU	PASMORGNI	1117 0		SPODUAE
OsCKX2	(1)			MAUL	LNCEVENT	APPPWPPSASS	ASFLDDLG	DIGIAP	LEADEASTA	BASADEGNUS	VAGVGAPRLA	AAAAULYPE	RPADIAA
OsCKX3	(1)	)	EVANVCTR	WN LI	LSLCSPYE	FIOS		PMDF	GPLNLLPTTT	TASSOFGRI	LFHS	SAVLKPC	APRDISL
ZmCKX1	(1)		MANNY	LLLAG	TACSHALAZ	GTPALGDDRGR	PWPASEA		ELET DENATA	AASTDEGNIT	SALP	AAVLNPS	STODLVA
Consensus	(1)		MLV Y	LLLV L	I SSHA AZ	Y	PL	LALAG	KLR D NAT	ASTDEGNI	SALP	AAVLEPS	SPGDIAA
100000000000000000000000000000000000000	1.1			0.7-00.007	71 VE 01100/010	1.0		0.000000000			0.0000000000000000000000000000000000000		22.020000
1	11.15	111	120	120	140	150	160	170	180	190	200	210	220
APCKY1/	103	MMEHTUHI	ST SNI TUS	2 P CH		HOGUNT ENE ST. P.	PDTPTVK	FOR	ACCETTIN	PETERSCER	ROWTHIN	UCCTI SNLC	TROPER
BoCKX1	(83)	TTPAAVET	C-XPETUS	PROTON	THEOREAL	CUUUHMI ST S	RAL	RADCP VUDA	SCENT TOUL	DATTEDCUA	PRETOVINI	UCCTI SNAC	USCOLED
BoCKX2	(80)	TERAHAY	APTTVA	FREESH	WMGONT N	COUVENESMO	AA APRTNU	SADGSYUDA	GGEOLEADVI	RASTARCUN	PATEDVIRI	UGGTI SNAG	USGOAFR
BoCKX3	(82)	TRAUVAT	C-WPFTUS	PROPERT	WMGON FN	CCUVUHMD8T.9	AORTNU	SADGRYVDA	SCEOL TOVI	PATTENCUL	TRATOVINI	UGGTISNAG	RECAPE
DsCKX1	(82)	TRISHES	HSETVS	ARGIGH	TREOLOAR	COTVINMPS.DO	G	STREMEVDA	GARONTIDUT	RETIRNELT	RSTOYLEL	GGTLAN	TAGONET.
HyCKX2	(78)	TVRHVELMO	EHSALTVA	ARGEGH	YGOBOAZ	GELVERME SLRS	VEMOVHP	ASP	SGGELWINVL	NETLENGLA	RSWIDTLHLT	VGGTLSNAG	VSGOTER
OsCKX1	(84)	LIRAAYAA	G-RPFTVS	FRGEGH	THOOALAP	A GGVVVHMQSMG	GGAPRINT	SADGAYVDA	GGEQL	RAALARGVA	RSWIDYLHLT	VGGTLSNAG	WSGOTYR
OsCKX2	(88)	LLRASCAR	APPAVS	ARGO GH	STHGOASA	D <mark>g V V V DMA S L</mark> GH	RLQGGGARRLAT	SVEGRYVDA	GGEQLWWDVL	RASMANGLT	VSWTDYLHLT	VGGTLSNAG	ISGOAFR
OsCKX3	(71)	LLSFLSAS	-LGKVIVA	ARGI GH	THEQAQAI	LD <mark>g IVV</mark> EMS <mark>SI</mark> PS	EIEFYRRG	E GDVS YADV	GGGIMWIEL	EQSIKLGLA	PRSWTDYLYLI	GGTLSNAG	ISGQTER
ZmCKX1	(84)	LLSAANST	G-WPYTIA	FRGEGH	SINGQAFAI	<mark>PGGVVVNMASL</mark> GI	DAAAPPRINT	SADGRYVDA	GGEQVWIDVI	RASLARGVA	PRSWNDYLYLI	GGTLSNAG	ISGQAFR
Consensus (	111)	LLRAAYAT	PFTVA	FRGEGH	SVMGQA AN	PGGVVV M SL S	B A RINV	SADG YVDA	GGEQLWIDVI	RATL HGLAN	PRSWTDYLHLT	VGGTLSNAG	ISGQAFR
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		G	HS F	AD-	ainding	n site							
		0	110.11		Jinding	gone							
(	221)	221	230	240	250	260	270	280	290	300	310	320	230
AtCKX1 (	208)	HGPQINNV	LEIVTER	GEVVIC	SEKRNSEL	FFSVLGGLGQFG	ITRARISLEPA	PHMURNER	LYSDFSAFSR	DOE YL IS	KE KT	FDYVEGFVI	IN
BoCKX1(	189)	HGPQISNV	ELDVITGY	GEMVIC	SKALNSDLE	DAVLGGLGQFG	TITRARIALE PA	PERARAVEL	VYTDFAVETA	DOERLIAPES	PDGSFE	MSYVEGSVY	VN
BoCKX2(	185)	HGPQIANV	ELDVITCK	GEMVTC	SERVESELS	PDAVLGGLGQFG	VITRARIAMDPA	PMRTRWERL	TYTDVASFTA	DQERLAVPGE	R <mark>DG</mark> VLG	P <mark>VSYVEG</mark> SVY	VN
BoCKX3(	186)	HGPQISNV	ELDVI <mark>TG</mark> Y	GGMVTC	SKALNSDLE	FDATLGGLGQFG	TTRARIKLEPA	PARARAVEL	VYTDFATFTA	DOERLVAPRE	PDGEFGI	MSYVEGSVY	VN
DsCKX1(	183)	HGPQISNV	HELDIVTER	GEMVIC	SESNNPDLE	FEVLGGLGQFG	ITRARIALEK.	POSVRWMRL	MYTDFELFTR	DQELLISIK?	AEGEGWI	KLN <mark>YVEG</mark> SLI	MEH
Hv CKX2 (	183)	HGPQISNVI	ELEIVIGR	GDIVIC	SPEQNSDLE	FRAALGGLGQFG	ITRARIALEPA	POMURWIRV	LYLDFMSLTE	DQEMLIS	AEKT	FD <mark>YIEGFV</mark> I	IN
OsCKX1(	190)	HGPQISNVI	.ELDVI <mark>TG</mark> H	GETVIC	SKAVNSDLE	DAVLGGLGQFG	ITRARVAVE PA	PARARWVRL	VYADFAAFSA	DOERLVAAR	P <mark>DG</mark> SH <mark>G</mark> I	PWSYVEGAVY	LAG
OsCKX2(	(194)	HGPQISNVI	. <mark>eldvi</mark> tgv	GEMVIC	SKEKAPDLE	PDAVLGGLGQFG	ITRARIFLAP	PARAR WVRF	VYTTAA AMTA	DQERLIAVDE	RA <mark>G</mark> GAGAVG <mark>G</mark> I	L <mark>M</mark> D <mark>YVEG</mark> SVH	LNQGLVE
OsCKX(3)	(177)	HGPQISNVI	LQLEVVIGR	GEIVIC	SPIKAL	FN <mark>AV</mark> LGGLGQFG	ITRARILLQEA	PORVEWVRA	FYDDFATFTK	DQELLVS	MPV1	L <mark>VDYVEGFI</mark> V	101 <mark></mark>
ZmCKX1/	191)	HGPOISNUE	PHOTTON	GEMUTC	SKOUNADLE	DAVLGGLGOFG	TTPAPTAWEDE	PARARWURF	THERESSER	DOFRITED	DECE-JOR	MAYNEGAUE	and the second second
							CARACEDES		VII DI AAL DA	DAPERT I VERI	Receedance		VN
Consensus (	221)	HGPQISNV	ELDVITGE	GEMVIC	SK LNSDLE	FDAVLGGLGQFG	VITRARIALE PA	PARARWVRL	VYTDFAAFTA	DQERLIA R	DG G	MSYVEGSVY	VN
Consensus (	221)	HGPQISNV	ELDVITGE	GEMVIC	SK LNSDLE	FDAVLGGLGQFG	/ITRARIALEPA	PARARWVRL	VYTDFAAFTA	DQERLIA R	DG G	MSYVEGSVY	VN
Consensus (	221) 331)	HGPQISNV 331	240	GEMVTC	SK LNSDLI 360	FDAVLGGLGQFGV 370	JITRARIALE PA	APARARWVRL 390	VYTDFAAFTA 400	ADQERLIA R	DG G	MSYVEGSVY 430	VN 440
Consensus( ( AtCKX1 (	221) 331) 304)	HGPQISNV 231 RTI	240 OLLNNWR <mark>38</mark>	GEMVTC 250 <b>F3</b> PN	SK LNSDLI 360 DSTQASRFI	FDAVLGGLGQFGV 370 K <mark>8</mark> D <mark>G</mark> KT <mark>LYCL</mark> F	VITRARIALE PA 380 VVKY <mark>F</mark> NPEEA	390	VYTDFAAFTA 400 MDQETGKLLS	410 ELNTIPSTL	ASSEVPYTE FI	MSYVEGSVY 430 DRVHIAERF	VN 440 LRAK <mark>GLW</mark>
Consensus ( ( AtCKX1 ( BoCKX1)	221) 331) 304) 290)	HGPQISNV 331 RTI 	240 DLLNNWR <mark>33</mark> AAG <mark>L</mark> K <mark>SA</mark> G	GEMVTC 350 <b>F3</b> PN - <b>F53DA</b>	SK LNSDLI 360 DSTQASRFI DVARIVAH2	FDAVLGGLGQFGV 370 KBDGKTLYCL ABERNATAVYSII	VITRARIALE PA 380 VVKYENPEEAS SATLNYDN <mark>A</mark> TAA	390 390	400 MDQETGKLLS	410 ELNYIPSTLE	DG G 420 TSSEVPYTEFT	MSYVEGSVY 420 DRVHIAERK DRVYGAEVA	VN 440 LRAKGLW LEKVGQW
Consensus ( AtCKX1 ( BoCKX1 ( BoCKX2 (	221) 331) 304) 290) 286)	HGPQISNV 231 RTI RSI	240 DLLNNWRSS AAGLKSAG	GEMVTC 350 F8PN -FF8DA -FF8DA	SK LNSDLH 360 DSTQASRFH DVARIVAH DVERIAALS	FDAVLGGLGQFGV 370 X8DGKTLYCL ARERNATAVYSIN AFRRNAA <mark>VYSIN</mark>	JITRARIALE PA 380 VVKYENPEEAS ATLNYDNATA SAAVHYNRITA (	390 390 3	400 MDQETGKLLS VDQELRSVIC VDQEVRALLE	410 ELNYIPSTI ELSYEEGFS	420 FSSEVFYIEFI TVRDABYVEFI FERDVFYVEFI	MSYVEGSVY 420 DRVHIAERE DRVYGAEVA	VN 440 LRAKGLW LERVGQW LEKAGLW
Consensus ( AtCKX1 ( BoCKX1) BoCKX2( BoCKX2)	221) 331) 304) 290) 286) 287)	HGPQISNV 231 RTI RSI RSI	240 DILNNWRSS AAGIKSAG ASGIKATA AAGIKSAG	350 FSPN -FFSDA -FFSDA -FFSDA	SK LNSDLN 360 DSTQASRFF DVARIVAH2 DVERIAAL2 DVARIVAL2	FDAVLGGLGQFGV 370 KØD <mark>G</mark> KTEYCE ABERNA TAVYSI AERNA A <mark>V</mark> VYSI A <mark>B</mark> ERNA TAVYSI	VITRARIALEP 380 VVKYENPEEA CATLNYDNATA CAAVHYNRTTA CAAVHYNRTA CATLNYDN <mark>A</mark> TA	390 390 9 9	400 MDQETGKLLS VDQELRSVID VDQEVRALLE VDQELRSVID	410 ELNVIPSTI ELSVEGTS ELSVEGTS	ACCONTRACTOR DG G 420 FSSEV PYTE FI VRDAE YVE FI FROV PYVE FI VRDAE YVE FI	MSYVEGSVY 430 DRVHIAERF DRVYGAEVA DRVHHELV DRVHHELV	VN 440 LRAKGLW LEKVGQW LEKAGLW LDRVGLW
Consensus ( AtCKX1 ( BoCKX1) BoCKX2( BoCKX2( DsCKX1)	221) 331) 304) 290) 286) 287) 285)	HGPQISNV 231 RTI RSI RSI 	240 DLLNNWRSS AAGLKSAG ASGLKATA AAGLKSAG BLKSNWRSP	GEMVTC 350 FSPN -FFSDA -FFSDA -FFSDA -FFSER	SK LNSDLN 360 DSTQASRFN DVARIVAHJ DVERIAALJ DVARIVAL2 DLKKIKKL3	FDAVLGGLGQFGV 370 KBDGKTLYCLF ABERNATAVYSII ABERNATAVYSII ABERNATAVYSII ABERNATAVYSII AS-GHEG <mark>VIYCL</mark> I	VITRARIALEP 380 2 VVKYENPEEA 2 ATLNYDNATA 2 AAVHYNRITA 2 A SFYYDYATA 2 A SFYYDYGHEM	390 390 8 8 8 9	400 MDQETGKLLS VDQELRSVID VDQEVRALLE VDQELKSVID MDQDIEELLR	410 ELNTIPSTLE ELSTERGEN ELSTEREN ELSTEREN ELSTEREN ELSTEREN	DG G <u>420</u> PSSEV PYLE P PVRDAS YVE P1 PVRDAS YVE P1 PVRDAS YVE P1 PRDVS YVE P1	430 430 DRVHIAERF DRVYGAEVA DRVHHELV DRVHGELV NRVHGGELF	440 LRAKGLW LEKNGQW LEKAGLW LDKVGLW LRAMGLW
Consensus ( AtCKX1 ( BoCKX1) BoCKX2( BoCKX3( DsCKX1) HVCKX2 ( PCCK2)	221) 331) 304) 290) 286) 287) 285) 279)	HGPQISNU 231 RT RS RS RS 	240 21LNNWR38 AAGLKBAG ASGLKATA AAGLKBAG 21LNNWR39 31LNNWR38	GEMVTC 350 - FSPN - FSDA - FFSDA - FFSDA - FFSDA - FFSDA	SK LNSDLE 260 DSTQASRFF DVARIVAH7 DVERIAAL7 DVERIAAL7 DVARIVAL7 DFERASRFF	270 370 RBDEKTLYCL ARENATAVYSI AERNATAVYSI AERNATAVYSI AERNATAVYSI AS-GNEGVIYCL ETDRKVLECL	VITRARIALEPS 380 VVKYENPEEA SATINYDNATA SATINYDNATA SATINYDNATA SAFYYDVGHEM MTKNENPEEA	350 350 350 35 35 35 35 35 35 35 35 35 35 35 35 35	400 MDQETGKLLS VDQEIRSVID VDQEVRALLE VDQELKSVLD MDQDIEELLR MEQEVHALLS	410 ELNVIPSTLE ELSVEGTS ELSVEGTS ELSVEGTS ELSVEGTS ELSPEKETA ELSPEKETA ELSPISE	DG G 420 PS EV PYLE P VRDASYVE PI FERDV PYLE PI FORDASYVE PI FRNDV SYMG PI FRNDV SYMG PI FRNDV SYMG PI	420 420 DRVHIAERK DRVHGAEVA DRVHHELV DRVHGELV NRVHGELK DRVHSSEMK	440 IRAKGLW LEEVGQW LEEAGLW LDEVGLW IRAMGLW IRAKGLW
Consensus ( AtCKX1 ( BoCKX1) BoCKX2( BoCKX3( DSCKX1) HVCKX2 ( OSCKX1)	221) 331) 304) 290) 286) 287) 285) 285) 279) 292)	HGPQISNV 231 RU RU 	240 DLLNNWR S AAGLKBAG ASGLKATA AAGLKBAG BLKSNWR S FILNNWR S AVALKS SG	GEMVTC 350 - FSPN - FSDA - FFSDA - FFSDA - FFSBA GFFSDA	SK LNSDL 360 DSTQASRFF DVARIVAH DVERIAL DVERIAL DVERIAL DEKKIKL DPERASRFF DAARVAL	270 270 KGDERTYCLM AERNATAVYSIN AERNATAVYSIN AERNATAVYSIN AG-GHEGVIYCLM TDREVLECLM AARNATAVYSIN	VITRARIALEP 380 VVKYENPEEAE ATLNYDNATA EAAVHYNRITA ASFYYDYGHEM MTKNFNPEEAE ATLNYAANATF	290 390 39	400 MDQETGKLS VDQETKSVID VDQELKSVID VDQELKSVID MDQDIEELLR MEQEVHALS VDAAVAAAG	410 ELNMIPSTL ELSTERER ELSTERER ELSTERER CLISTERERA ICLISTERERA ICLISTERERA ICLISTERERA ICLISTERERA	420 PSSEV PYLE PT VRDASYVE PT VRDASYVE PT VRDASYVE PT PRIDVSYME PT PRIDVSYME PT PSRDVE YEE PT	MSYVEGSVY 420 DRVH IAERR DRVYGAEVA DRVHEELV DRVHEELV DRVHGELR DRVHGELE DRVHGELE	440 IRAKGLW LEEVGQW LEEAGLW LDEVGLW IRAKGLW IRAKGLW LEEAGLW
Consensus( AtCKX1( BoCKX1( BoCKX2( BoCKX2( BoCKX2( DSCKX1( USCKX2( OSCKX2( OSCKX2( OSCKX2)	221) 331) 304) 290) 286) 287) 285) 287) 285) 279) 292) 304) 272)	HGPQISNV 321 RT RT 	240 DLLNNWR S AAGLKBAG AAGLKBAG AAGLKBAG BLKSNWR S FILNNWR S AVALKSSG BPSSS S BPSSS S	GEMVTC 350 - FSPN - FSDA - FSDA - FSDA - FSBR - FNPQ GFSDA SFFSDA	SK LNSDL 260 DSTQASRFF DVARIVAH DVARIVAL DVARIVAL DFRASRFF DARVAL DEARVAL DEARVAL	270 270 370 370 345 D G KT Y C H 45 - G KT Y C H 45 - G KT Y C H 47 - G K Y Y C H 5 D R Y Y C H 48 - G Y Y C H 48 - G Y Y C H 5 D R Y Y C H 5	VITRARIALEP 280 VVKY PNPEA SATINYDNATA SAAVHYNRITA CATINYDNATA MICH PNPEE MICH PNPEE SATINYAANAT SATINYGGAACE	290 3 3 3 3 3	400 MDQEIGKLS VDQEIRSVID VDQEIRSVID VDQEIRSVID MDQDIELSVID MDQDIELLS VDAVAAALS VDAVAALS	410 ELNVIPSTL ELSPERFAL ELSPERFAL ELSPERFAL ELSPERFAL ELSPERFAL ELSPERFAL ELSPERFAL	420 420 SSEVPYIE F1 VRDABYVE F1 VRDABYVE F1 VRDABYVE F1 VRDABYVE F1 SRDVTYE F1 SRDVTYE F1 AQDVAYAGF1	MSYVEGSVY 430 DRVHIAERM DRVYGAEVA DRVHEEIV DRVHEEVA NRVHGEIF DRVHSERM DRVYGEFF DRVHGEIF	440 LRAKGLW LEEVGQW LEEAGLW LRAMGLW LRAKGLW LRAKGLW LRAAGLW
Consensus( AtCK(1) BoCK(1) BoCK(2) BoCK(2) DSCK(1) DSCK(1) OSCK(2) OSCK(2) OSCK(2) OSCK(2) OSCK(2)	221) 331) 304) 290) 286) 287) 285) 279) 292) 304) 273) 273)	HGPQISNV 331 RT RT 	240 21 LNIWR 53 AAGIK54 G ASGIRATA AAGIK54 G SLKSIWR 5 JILNIWR 53 AVALK53 G SPSS535 - EQSLH 5	GEMVTC 350 FSPN -FFSDA -FFSDA -FFSDA -FFSEK -FNPQ GEFSDA SFFSDA SIAFPT	SK LNSDL <u>360</u> DSTQASRFF DVARIVAR DVARIVAL DVARIVAL DIKKIKL DFRASRFF DARVAL DEARVAL DEARVAL NVDFNPDF	270 270 28	280 280 2005 PREPAS ATEM DNATA AAFYNATA AAFYNATA AFYN DYRHA MTKN FNPEA ATEM YANAT ATEM YANAT GIYFGGAAGP FAWRDYQWN	250 3	VYTDFAAFTA 400 MDQETGKIIS VDQELRSVID VDQELRSVID VDQELKSVID MDQDIELLR MDQDIELLR VDAAVAALG VDAAVAALG VDAAVAALG VDARMDVIRR	ADORRLIA R 410 ELNVIPSTLI ELSTEKGFA ELSTEKGFA ULST	420 420 VRDA VET VRDA VET VET VRDA VET VET VET VET VET VET VET VET	MSYVEGSVY 420 DRVHIAERK DRVHGELV DRVHGELV DRVHGELF DRVHSERK DRVHGELF DRVHGELF NRVHGELF	440 LRAKGLW LEENGQW LEENGLW LEENGLW LRAKGLW LEENGLW LEENGLW LEENGLW LRANGLW
Consensus( AtCK01( BoCK01) BoCK02( BoCK02( DsCK01) HVCK02( OsCK01) OsCK02( OsCK02( OsCK03) ZmCK01( Cmccoccoccoccoccoccoccoccoccoccoccoccocco	221) 331) 304) 290) 286) 287) 285) 279) 292) 304) 273) 295) 291)	HGPQISNV 331 RB RB RB 	240 DILINWR S AAGLKBAG ASGLKATA AAGLKBAG SLKSNWR S DILINWR S DILINWR S DVALKSSG SPSSSSS -EQSLHS ATDIANTG	GEMVTC 250 - FSPN - FSPA - FSPA - FSPA - FSPA SFSDA SFSDA SIAFFT - FTDA	SK LNSDL 360 DSTQASRFF DVARIVAL DVARIVAL DVARIVAL DIKKIKKL DARVAL DARVAL DARVAL NVDFNPDF DVARIVAL DVARIVAL	270 270 CBDEKTLYCH ARENA TAVYSI ARENA TAVYSI ARENA TAVYSI C-DRKYSI CHORATAVYSI FARATAVYSI FARATAVYSI CKNIPKI CKNIPKI CHURYSI CHURYSI	VITRARIALEP 280 2005 PREEA 2015 P	290 290 290 290 290 290 290 290	400 MDQETGRLLS VDQELRSVLC VDQELRSVLC MDQDIELLS VDQELRSVLC MDQDIELLS VDANVAALS VDRNMUUER VDRNMUUER VDRNMUUER VDRNMUUER	410 ELNTIPSTI ELREREFA ELSTEGETA ELSTEGETA CLEVEGETA CLEVEGETA ELREREFA ELREREFA CLESTASIA	420 420 SEVENTE TI FERDE YVE T FERDE YVE T FERDE YVE T FERDE YVE T FERDE YVE T FERDE FE SEDE YFE SEDE YFE SEDE YFE SEDE YFE	432 430 BRVHIÄERF DRVYGAEVA DRVHGEEVA DRVHGEEVA DRVHGEEFF DRVHGEEFF DRVHGEEFF DRVHGEEVA	440 LRAKGLW LERAGLW LERAGLW LRAKGLW LRAKGLW LRAKGLW LRAKGLW LRAKGLW LRAKGLW LRAKGLW
Consensus ( AtCKX1 ( BoCKX1 ( BoCKX1 ( BoCKX2 ( BoCKX2 ( DSCKX1 ( OSCKX2 ( OSCKX2 ( OSCKX3 ( ZnCKX1 ( Consensus (	221) 331) 304) 290) 286) 287) 285) 285) 292) 304) 273) 295) 331)	HGPQISNV 331 R0 R0 R0 	240 DLLNNWRSS AAGLKSAG ASGLKATA AAGLKSAG DLKSNWRSP JLLNNWRSS AVALKSSG DFSSSSSS -EQSLHSS ATDLANTG A L SSS	GEMVTC 250 - FSPN - FSPA - FSPA - FSPA - FSPA SFSDA SFSDA SIAFFT - FFTDA FFSDA	SK LNSDL 260 DSTQASRFF DVARIVAH2 DVARIVAL2 DVARIVAL2 DARYVAL2 DEARVAL2 NVDFNPDFF DVARIVAL2 DVARIAL2	270 270 RS-DERTICEI ARENATAVYSI LERNAAVYSI ARENATAVYSI SCHENTYCI SCHENTYCI REAGYLYEI REAGYLYEI REAGYLYEI REAGYLYEI REAGYLYEI ARNA TYYSI ARNA VYYSI	280 200 200 200 200 200 200 200 200 200 200 200	250 350 35 35 35 35 35 35 35 35 35 35 35 35 35	400 HOETGELS VDCELSSVIC VDCELSSVIC VDCELSSVIC VDCELSSVIC VDCELSSVIC VDCELSSVIC VDCAVALS VDAVAALS VDAVAALS VDAVAALS VDCEVEVSS VDCEVSSVIC VDCEVSSVIC	ADORRLIA R 410 ELMUIPSTLI ELSTERGFA ELSTERGFA ELSTERGFA ULRTPASL ELHFEGFA ELHFEGFA ELHFEGFA ELHFEGFA ELSTE GFA	DG GY ASE 420 420 420 420 420 420 420 420	420 420 DRVHAERA DRVHELY DRVHELY DRVHELY DRVHELY DRVHELY DRVHELY DRVHELY DRVHELY DRVHELY DRVHELY DRVHELY	440 LRAKGLW LERVGQW LERAGLW LRAGLW LRAKGLW LRAKGLW LRAKGLW LRAAGLW LRAGLW LRAGLW LRNSCLW LNSCLW LNKGLW
Consensus ( AtCK11 BoCKX12 BoCKX22 BoCKX22 DsCKX11 OsCKX22 OsCKX12 OsCKX22 Consensus	221) 331) 304) 290) 286) 287) 285) 279) 292) 304) 273) 295) 331) 441	HGPQISNU 331 RU RU RU 	240 DLLNWRSS ASGLKATA ASGLKATA ASGLKATA ASGLKATA SGLKSINRS DLKSINRSS DLKSINRSS DLKSINRSS DLSS SSSSS ASGLKATS ASS ASS ASS ASS ASS	GEMVTC 350 FSPN -FSDA -FFSDA -FFSDA -FFSDA GFFSDA SIAFPT -FFTDA FFSDA	SK LNSDL <u>360</u> DVARIVAH DVERIAAL DVERIAAL DVERIAAL DVERIAAL DVERIAAL DERKSRE DARVAL DERKSRE DVARIAL DVARIAL	270 270 28DERTEYCH ARENNARAVSI ARENNARVSI ARENNARVSI -GHEGUIYU -GHEGUIYU ARANARAVSI TANHPRIYUCH ARANATVYSI AR NA VYJSI AR NA VYJSI	VITAR IALEP 280 VUKY INPERA ATALY DNATA AARHYNNITA AAFYI DYCHEN MIKNINPERA ATALY DYCHEN MIKNINPERA ATALY DYCHEN MIKNINPERA ATALY DYCHEN ATALY DY	2390 2390 2390 2390 2390 2390 2390 2390	400 MDOETGRILS VDQELRSVID VDQELRSVID MDQDIRSVID MDQDIELLR MDQDIELLR MDQDIELLR VDANVAALG VDANVAAL	ALO CELLA RALLA CONTRACTA	A CONTRACTOR OF A CONTRACT A CONT	MSYVEGSVY 120 DRVHIAERI DRVYGEVX DRVHELV DRVHELVX DRVHELV DRVHELS DRVHGEF D	440 LEARCLW LEENCLW LEENCLW LEENCLW LEENCLW LEARCLW LEARCLW LEARCLW LEARCLW LEARCLW LEARCLW LEARCLW LEARCLW LEARCLW
Consensus ( AtGK1 ( BoCKC1) BoCKC2( BoCKC2( BoCKC2) OsCKC1 ( OsCKC2 ( OsCKC2) Consensus ( ACCC1)	221) 331) 304) 290) 286) 286) 287) 292) 304) 273) 295) 331) 441) 441)	HGPQISNV 321 RT RT RT 	240 JLLNNWRB AGC IKSA AGC IKSA AGC IKSA AGC IKSA AGC IKSA JURSA AVAIKSS JULNWRB AVAIKSS AVAIKSS AVAIKSS ATDIAN G ATDIAN G ATDIAN G ATDIAN G	GEMVIC 250 FSDA -FFSDA -FFSDA -FFSDA -FFSDA SFFSDA SFFSDA SIAFPI -FFTDA FFSDA 460	SK LNSDL <u>360</u> DSTQASRFF DVARIVAH DVARIVAH DVARIVAL DERKIXKL DERKIXKL DERKALT DARVALT DERKALT DVARIVAL <u>470</u>	270 270 28-00 KT 0 C II ARE NA TAVYS II ARE NA TAVYS II ARE NA TAVYS II C 0 C 0 C 0 C II ARANA TAVYS II ARANA TAVYS II C 0 C NA TAVYS II ARANA TAVYS II	280 200 200 200 200 200 200 200 200 200 200 200	250 250 250 250 250 250 250 250 250 250	VYTDFAAFTA 400 MDOFFGFLIS VDCELRSVID VDCELRSVID VDCELSVID VDCELSVID VDCRVHALIS VDANVAALG VDCRVHOUTER VDCRVHUTER VDCRVLSF VDCELASVIC VDCEVLSF VDCELASVIC SII0	410 ELNTIPSTL ELSTEREGT ELSTEREGT ELSTEREGT ELSTEREGT ELSTEREGT ELSTERGT ELSTEGT ELSTEGT ELSTEGT	420 420 SEVEYIE FI VEDA YVE I VEDA YVE I VEDA YVE I VEDA YVE I VEDA YVE I SEVYIE FI SEVYIE	430 DRVH GAEVA DRVH GAEVA DRVH GAEVA DRVH GEVA DRVH GEVA DRVH GEVA DRVH GEVA DRVH GEVA DRVH GEVA DRVH GEVA DRVH EVA DRVH EVA	440 IRAKGLW LEKAGLW LEKAGLW LEKAGLW LEKAGLW IRAKGLW IRAKGLW IRAKGLW IRAKGLW IRAKGLW S50
Consensus( ( AtCX11 BoCKX2( BoCKX2( BoCKX2( DSCKX1) Consensus( ( AtCX11 AtCX11	221) 331) 304) 290) 286) 287) 285) 279) 292) 304) 273) 295) 331) 441) 396) 395)	HGPQISNY: 331 RT RS RS RS TWRTQPQS 	240 DULINNE 3 AC LESA AC LESA AC LESA AC LESA AC LESA AC LESA AC LESA POLINNE 3 AVALES 4 POLINNE 3 AVALES 4 AVALES 4 AVA	GEMVTC 250 FSDA -FFSDA -FFSDA -FFSDA SFFSDA SFFSDA SFFSDA SFFSDA SFFSDA 460 QFATE	SK LNSDLH 3600 DSTQASSFI DVARLVAHD DVERLAALD DVARLVAHD DFRASSFI DARVVALD DFRASSFI DARVVALD DFRASSFI DVARLVALD	270 270 270 28-05 KTE (21 28-05 KTE (21 28-05 KTE (21 27-05 KTE (21 27-05 KTE (21 27-05 KTE (21 27-05 KTE (21 27-05 KTE (21 28-05 KTE (21 28-0	280 VKY NPER ATAV DATA ATAV DATA ATAV DATA ATAV DATA ATAV DATA ATAV DATA ATAV DATA ATAV DATA ATAV DATA ATAV ANAT IYFGAAG9 FAMADQUKA ATAV ANATA ATAV ANATA ATAV ATAV ANATA ATAV ATAV ANATA ATAV ATAV ANATA ATAV ATAV ANATA ATAV ATAV ANATA ATAV	250 250 250 250 250 250 250 250	VITDFAAFTA 400 MDOETGFLLS VDOELRSVID VDOELRSVID MDOELRSVID MDOELSVID MDOELASVID VDOELASVID VDOELASVID VDOELASVID VDOELASVID VDOELASVID VDOELASVID VDOELASVID	AUGURALIA R 410 ELNMIPSTL ELSPECTA ELSPECTA ELSPECTA ELSPECTA ELSPECTA ELSPECTA ELSPECTA ELSPECTA ELSPECTA 520 AVFR35KIN	DG         G           420         SSEV PYTE PT           VRDAB YVE PT         FRVP PYVE PT           VRDAB YVE PT         FRVP PYVE PT           FRDVP YVE PT         FRVP PYVE PT           SRDVN YVE PT         SRDVN YVE PT           SVEV Y PPT         FRVP PYVE PT           SVEV Y PPT         FRVP PYVE PT           SVEV Y PPT         SSO           SVEV Y PT         SSO           SVEV Y PT         SSO           SSO         SSO           SSO         SSO           SSO         SSO	MSYVEGSVY 430 DRVHIAERN DRVHKELV DRVHGEVA DRVHGEVA DRVHGEVA DRVHGEFE DRVHGEFE DRVHGEFE DRVHGEVA DRVHGEVA DRVHEELA 540	440 IBAKCLW LENGCW LENGCW LENGCW IBAKCLW IBAKCLW IBAKCLW IBAKCLW IBACLW IBACLW IBACLW IBACLW IBACLW IBACLW IBACLW IBACLW IBACLW IBACLW
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Consensus ( ACCX1 BoCXX1 BoCXX2 BoCXX3 DoCXX1 VoCX2 OSCXX1 Consensus ( ACCX1 BoCXX1 BoCXX1 BoCXX1 BoCXX1 BoCXX1 BoCXX1 BoCXX1 Consensus ( ACCX1 BoCXX2 BoCXX3 DSCX1 Consensus ( ACCX1 BoCXX1 BoCXX1 BoCXX1 BoCXX1 Consensus ( ACCX1 BoCXX1 BoCXX1 BoCXX1 BoCXX1 BoCXX1 Consensus ( Consensus) ( Consensus ( Consensus) ( Cons	221) 331) 304) 2280) 2280) 2280) 2292) 2292) 2292) 2295) 3331) 3850) 3850) 3850) 3850) 3855) 3371) 5510) 5550) 5550) 5550) 5550) 5550) 5550) 5550) 5550) 5550) 5570) 2441) 2551) 2573) 2441) 2551) 2551) 2573) 2672) 2732) 2752)	HGPQISHT 311 RI RI RI 	ELLOVITOR ALLINNER ACLENSE ACLENSE ACLENSE ACLENSE ACLESSE CLES	GENVIC 250 	SK LNSDLI 360 DSTCASRF DVARLVALD DVARLVALD DVARLVALD DVARLVALD DFRASKT DARVALD DFRASKT DARVALD DFRASKT DARVALD DFRASKT DARVALD DFRASKT DARVALD DFRASKT DARVALD DFRASKT DFRASKT DFRAST DFF DFRAST DFF DFF DFF DFF DFF DFF DFF DF	270 270 270 270 270 270 270 270	280 VIKN NPEA ATM VNT NA ATM VNT A ATM VNT A ATM VNT A ATM VNT A ATM VNT A ATW VNT A A ATW VNT A A ATW VNT A A A A A A A A A A A A A A	PARARWVRL 350 3	VYT DPAAPTA 900 HD QE T GT L 1 VYD DE T GT L 1 VYD DE T GT L 1 NO QU Y RALD VYD QU Y RALD VYT AV HUT S VYT AV HUT S VYT AV GT S VYT AV S VYT	200         210           210         210           211         210           212         211           213         212           214         212           215         212           210         212           211         212           212         212           213         212           214         212           215         212           216         212           217         212           218         212           217         212           218         212           218         213           218         213           218         213           218         213           218         213           218         213           218         213           218         213           218         213           218         213           218         214           219         214           211         214           212         214           213         214           214	JG GLASI JG G 420 SSEV PYE 21 VE DA VE 21 SE DU YE 2	MSTVEGSY 420 DEVHIAERI DRVHCALPA DRVHCELW DRVHCELW DRVHCELW DRVHCELW DRVHCELW S40 TUHYCAAN	440 1RAR GLW LE RY GLW LY RY CHW LY RY GLW LY RY G

**Figure 3.** Sequence alignment of the primary structure of BoCKX proteins with CKXs proteins from other species. The sequences shown here were from *Arabidopsis thaliana* (AtCKX1), *Bambusa oldhamii* (BoCKX1–3), *Dendrobium sonia* (DsCKX1), *Hordeum vulgare* (HvCKX2), *Oryza sativa* (OsCKX1–3), and *Zea mays* (ZmCKX1). The conserved FAD-binding site, GHS motif, was indicated.

	BoCKX1	BoCKX2	BoCKX3
BoCKX1	100	78	92
BoCKX2		100	79
BoCKX3			100

**Table 1.** Amino acids identities (%) among the coding regions of the BoCKX1, BoCKX2, and BoCKX3 proteins.

The deduced amino acid sequences of CKXs from several plant species underwent phylogenetic analysis (Figure 4). All CKX protein sequences contained a conserved GHS motif as the FAD-binding site and the histidine residue within the GHS motif may be responsible for covalently conjugated with FAD cofactor [34]. OsCKX1 and ZmCKX1 proteins were the closest homolog to BoCKX1 (78% identity) and BoCKX3 (76% identity) proteins, and these genes contained similar exon-intron organization (Figure 2B, Figure 4). Although *BoCKX2* and *OsCKX2* shared identical genomic organization (Figure 2B, Figure 4), the amino acid similarity was only 52% identity.



**Figure 4.** Phylogenetic analysis of CKXs from other plant species by Vector NTI Suite 10 Sequence Software (Invitrogen, Waltham, MA, USA).

#### 3.4. Analysis of the cis-Acting Elements in BoCKX1

To better understand the potential transcriptional regulations, the upstream sequence of the *BoCKX1* was completely sequenced and limited promoter region (-262) was obtained (Figure 5). PlantProm [50] predicted the probable transcriptional start site (+1) of *BoCKX1*, which was situated 83 base pairs from the translational start codon (ATG, Figure 5). Promoter sequence analysis was obtained from PlantPAN [49], and a putative TATA box and an NGATT motif [52] were addressed at -27 and -235 positions, respectively (Figure 5).

gccgatcatttcgtctgagatagagattgctaaagtatgatatgaattcgtatacgtgtc	-203
caagtggacacatatgccgatctcgtctcggtttcattacctcttattactcttattcct	-143
tagcctatatatatgtatctttgtagtcacatatgtttttttgaatttttttcatattaa	-83
attttatcttctattctttcgatcttctattttatcgtacgttt tataactatatata	-23
TATA box	
tatagaggggtgcaagtgcagtgcaaacacaacaccttaattaa	+38
+1 -	
tctcttgcggattaagtggtcttaaagcgcttaaacgcgttgctaatggcggtggtttac	+98
M A V V Y -	

**Figure 5.** Promoter sequence analysis of the *BoCKX1* gene. The start codon of translation (ATG) was shaded. The predicted transcriptional start site was indicated as "+1". The putative functional TATA box and one NGATT element were indicated.

#### 3.5. Analysis of the cis-Acting Elements in BoCKX2

To better understand the potential transcriptional regulations, the upstream sequence of the *BoCKX2* was completely sequenced and over 1.4 kb promoter region was obtained (Figure 6). PlantProm [50] predicted the probable transcriptional start site (+1) of *BoCKX2*, which was situated 44 base pairs from the translational start codon (ATG, Figure 6). Promoter sequence analysis was performed by PlantPAN [49], and a putative TATA box and CAAT box were addressed at -27 and -40 positions, respectively (Figure 6). Among the promoter region, nine NGATT motifs [52] and one *as-1* like conserved site (-1289) [53] were identified (Figure 6).

${\tt gtctgcacgtgactggtgcatgcgaaattattaacccatgctttttttatgcataactt}$	-1385
$a {\tt ctaggttgagcctttcgtaagctttgcagtttgtagtgctttgcgtttgcgcttaagcc}$	-1325
taatctaggtgtgtaacgttttaactttttgtgacgtgtaacgttttaacttaagctatc	-1265
as-1 like	
tttacagcgcacatgctgagttacgttcagcccaaggatttcaaaaaaacgaacaaagaaa	-1205
${\tt cata attttga a a a atta a a a cgtttcgtt attgt attgt gttt a atttgt ttc atcttc$	-1155
tatgagcacaatatcaatattttcatagaattcatagaagcacctcttcctggcatgtcc	-1095
tagtgttgtgatgcacaatgacatgcatgtttgtttatggattgccttcctt	-1035
${\tt caaaggatatgcatacatgaaactgctcatttgaacaagtaacacattttgggcctgttt}$	-975
${\tt gggaccgctccgctctacgtttttcagctccgctctatgttttttagccaaacaggttca}$	-915
$\verb gctccacgcactctgttcgaggaaaaaaaggtggagttgtgagagcacctaaaggggtgc  $	-855
tccacaaactctaggttttttgtggagctgctccacggtagaattcgtggagcagagttt	-795
$gtggagcagtcccaaacacgccctttgtctccgacaaaacaatgaagtcatc \\ ggatt \\ tta$	-735
tttgaacagcttcaataagaaaattagtctattttttgaaaacagacag	-675
tt ctt gactta a at cat cct gg cgg tat a ca a g cct cat at ta a g a a a a ca cat tat g c g	-615
aggacagccgactgtcgcagtcatcttttgacttacaacaccgaggtcatggttggcaca	- 555
$\verb ccgttatggccgctatacagcagttgacaaattgcatcatgcacaggaattaatgttact  $	-495
$\underline{tttg} tctctaaagtctaaattcattggaca\underline{tgatt}ctttcccgcttgatcagacggttgt$	-435
$\underline{gatt} gtaacttatgttattctttttagttagaaggg\underline{tgatt}ttcaaccggtggttagtct$	-375
a at cagtg ctg ca att aga a ctt agtgg ctt a cg att a cg gtt tg a ctc ca a cta a cta cta cta cta cta ct	-315
aagccagtggggtttatcatgtggattcatctcagagaaaaaaaa	-255
${\tt gtttttgttgatggtttttaattttatgaatagtaataat$	-195
${\tt cagacagagagaaactcgcgtg} cgatt {\tt tagctatataaatgaaatcattatagtgtgta}$	-135
$ttataattaactagtacattct\overline{gtttt}aaaaaaatattttatttgaaagttaagtactta$	-75
aaaaactatttattatatagtttttagaagtcaatatgtcctataaatacggtccgaagt	-15
CAAT box TATA box	
ccgagcagacgtactaatcagaaaatacgcagtcgcacaaacagcgcaaacacactaata	; +46
+1 M	

**Figure 6.** Promoter sequence analysis of the *BoCKX2* gene. The start codon of translation was shaded. The predicted transcriptional start site was indicated as "+1". The putative functional TATA box, CAAT box, *as-1* like motif and ten NGATT elements were designated.

#### 3.6. Analysis of the cis-Acting Elements in BoCKX3

To better understand the potential transcriptional regulations, the upstream sequence of the *BoCKX3* was completely sequenced and ~1.2 kb promoter region was obtained (Figure 7). PlantProm [50] predicted the probable transcriptional start site (+1) of *BoCKX2*, which was situated 79 base pairs from the translational start codon (ATG, Figure 7). Promoter sequence analysis was obtained by PlantPAN [49], a putative TATA box was addressed at -24 position, and five NGATT conserved regions [52] were boxed (Figure 7).

```
tcgcagtacgtcagtgcatcacggttagtcagaagtacatggcaatagagtaaggtcgt -1117
actgactgtagtacaaatgaattcgagctataattctacatgtgtattagacgagacatt
                                                         -997
                                                         -937
actgcagtgcagtactgcgcaaagacgtcgttcagcgtgatctcagtacgtgctctagag
cttcgatcgacagtgctctaaactaaacaaacgtgttataaagcgtaaaaaatagtagtg
                                                         -877
aagttactgaacgttcgtcaatgtgtgaagcggaaaattcctgtgaagaaacagacattt
                                                         -817
                                                         -757
gtatgtacgtacgttgactaacaccgtgtgccagtgtctgctgctgaggtggatccatgg
tcgtacatcaataggttcatcttttactgggaaaaaacgacgcaagcgtcaaactggacg
                                                         -697
t|tgatt|ttacttttactaaaat|ggatt|ggagaaattttgtcgtgaagacgcagacagaca
                                                         -637
cctcaatagttttcacagttaagcaaacatccttgcaaatatgcttgcctacattaaaca
                                                         - 577
taagggagtttctaggcatcatttggatgttttctttctaattatcatctaaatttatga\\
                                                         -517
ctcttggattaggatcaaggagccctttgtttttgagggggggagactttttgaaagggga
                                                         -457
ggggtagaattcaaggggaaagggagagaatttatgatcattggattttaattcaatag
                                                         -397
tcttaaatttgaatgatagttagaaaaaaaaacatctaagtggtgcctagacactcccaac\\
                                                         -337
                                                         -277
ataatactggtaggtgcacttcggttttgcttattaagaaacctgcacatttgcctcgaa
aatttgacatgcatgtacctcatctccctgcaactgattccgttcatttgcctcaggtaa
                                                         -217
atgaggcaattattgatcagtatatacgtcattttgtccaacgctgtttacgaattgtga
                                                          -157
                                                          -97
agatgaggtaaagtgacatgaaagctaaaaatatttgcagcctcgagttttctactaatt
                                                          -37
aagctttaattgcaacagacgtagacgttgttaacacacagtcacacgtagacgacgtt
+24
     TATA box
                                 +1
agtcacgcctcttttgcggattaagtggtattagcgtgcttaaacgcgttgctaatggcg
                                                          +84
                                                   M A
```

**Figure 7.** Promoter sequence analysis of the *BoCKX3* gene. The start codon of translation was shaded. The predicted transcriptional start site was indicated as "+1". The putative functional TATA box and five NGATT elements were designated.

#### 3.7. Comparison of Features in Plant CKX Proteins

CKX proteins had been reported to localize at different compartments [16,23,36,37], and some of them were secreted proteins [23]. All three BoCKX proteins were predicted to carry putative signal peptide sequences typical of secretion pathway (Table 2). Cytosolic and vacuolar forms of CKX were identified in other species [16,36], suggesting that there still may be some unknown *BoCKX* genes in *B. oldhamii*.

CKX functions are regulated by post-translational modifications, e.g., glycosylation. All CKX proteins were predicted to be glycoproteins (Table 2), and maize CKXs had been shown to be glycoproteins [14]. By using the NetNGly algorithms, BoCKX1, BoCKX2, and BoCKX3 had seven, five, and six putative glycosylation sites and at least five of them were more than 50% probability (Table 2), implying that BoCKX1–3 may be glycoproteins. In addition to glycosylation, many phosphorylation sites were predicted in BoCKX1–3 (Table 3); however, substantial results are needed.

Gene Name <sup>a</sup>	No. of Exons	Length (aa)	Mass (kDa) <sup>b</sup>	Subcellular Localization (PSORT) <sup>c</sup>	Glycosylation Sites <sup>d</sup>	Phosp	horylation Ser Thr Ty	Sites <sup>e</sup> r	Reference
BoCKX1	3	525	57.0	S <sup>f</sup>	7/6	11/8	4/1	6/3	This study
BoCKX2	4	523	57.4	S	5/5	14/8	5/3	8/3	This study
BoCKX3	3	522	56.6	S	6/5	11/8	3/1	8/4	This study
DsCKX1	4	536	60.4	S	2/2	h _	-	-	[51]
OsCKX1	3	558	59.1	S	2/1	-	-	-	[35]
OsCKX2	4	532	56.0	M <sup>g</sup>	6/5	-	-	-	[35]
OsCKX3	5	525	58.0	S	3/3	-	-	-	[35]
ZmCKX1	3	534	57.2	S	8/5	-	-	-	[22]

<b>Features of different CKX proteins from various plan</b>
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<sup>a</sup> Bo, Bambusa oldhamii; Ds, Dendrobium sonia; Os, Oryza sativa; Zm, Zea mays. <sup>b</sup> Molecular mass calculated with peptide-mass tool (http://ca.expasy.org/tool/peptide-mass.html accessed on 15 March 2020) [54]. <sup>c</sup> Subcellular localization predicted with PSORT (http://psort.nibb.ac.jp/ accessed on 15 March 2020) [55]. <sup>d</sup> All predicted N-glycosylation sites/predicted glycosylation sites with 50% probability were analyzed by NetNGly (http://www.cbs.dtu.dk/services/NetNGly/ accessed on 15 March 2020) [47]. <sup>e</sup> Phosphorylation site with 50% probability/predicted phosphorylation site with 90% probability was analyzed by NetPhos (http://www.cbs.dtu.dk/services/NetPhos/ accessed on 15 March 2020) [48]. <sup>f</sup> S: secretory pathway. <sup>g</sup> M: mitochondria. <sup>h</sup> -: non-determined.

Table 3. Predicted *cis*-acting elements of the *BoCKX* genes and its functions.

Cis-Element	<b>Consensus Sequence</b>	Function	References
TATA box	TATAAT	Core promoter <i>cis</i> -element of genes in eukaryotes	[50]
CAAT box	CAAT	The CAAT box is a conserved consensus sequence as the binding site of the RNA transcriptional factor	[50]
As-1 box	TGACG	Activation sequence 1 (as-1) is a salicylic acid (SA)- and auxin-responsive element	[53,56,57]
NGATT	N=G/A/C/T GATT	Arabidopsis cytokinin response regulators ARR1 binding element	[52,58,59]

#### 4. Discussion

A multi-gene family of CKX in plants has been reported previously [17,36]. In this study, we identified three cytokinin oxidase/dehydrogenase genes from green bamboo by screening a bamboo genomic DNA library (Figure 1). In the genomic DNA library construction, 9–23 kb bamboo genomic fragments were ligated with a phage vector [7]. Fortunately, four positive clones isolated contained three full coding regions as well as different sizes promoter regions (Figure 1). *BoCKX1* and *BoCKX3* genes had identical exonintron structures (Figure 2A) as well as 92% amino acid sequence identity (Table 1). The exon-intron structure of the *BoCKX2* was slightly different in comparison with the above two genes (Figure 2A). All three *BoCKX* genes showed similar exon-intron organizations between other *CKX* genes (Figure 2B). In theory, cytoplasmic, ER-membrane, or vascular-localized CKX should exist in green bamboo, and more screening of bamboo genomic DNA can be performed.

Several putative *cis*-acting elements were predicted from promoter regions of the *BoCKX1–3* genes (Figure 5, Figure 6, and Figure 7), and the functions of the motifs were listed in Table 3. All three *BoCKX* genes contained a conserved TATA box and a typical CAAT box was identified in the upstream site of TATA box of the *BoCKX2* [50]. *CKX* gene expression is induced by abiotic stress and plant hormones, such as abscisic acid and cytokinins [25]. As-1 box [53,56,57] and NGATT motif [52,58,59] were present in the 5'-flanking regions of *BoCKX* genes, suggesting that the *BoCKX* gene expressions may be affected by different plant hormones and cytokinin response regulator proteins.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/cimb45030123/s1, Figure S1: Alignment of the deduced amino acid sequences of *BoCKX*-specific probe and ZmCKX1.

Author Contributions: Methodology, C.-Y.H. and L.-S.H.; validation, L.-S.H.; investigation, C.-Y.H. and L.-S.H.; resources, C.-Y.H. and L.-S.H.; data curation, L.-S.H.; writing—original draft preparation, C.-Y.H. and L.-S.H.; writing—review and editing, L.-S.H.; supervision, L.-S.H.; project administration, L.-S.H.; funding acquisition, C.-Y.H. and L.-S.H. All authors have read and agreed to the published version of the manuscript.

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