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Nuclear receptor FTZ: partial cloning and expression pattern in fat body of the American cockroach *Periplaneta americana* (Linnaeus, 1758) during vitellogensis

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ABSTRACT

The aim of the present study was to understand the importance of the nuclear receptor Fushi tarazu factor 1 (FTZ-F1) in relation to vitellogenin genes expression in the fat body of *Periplaneta mericana* during the first vitellogenic cycle. Initially, a 342 bp fragment was cloned from the female fat body through degenerate primer RT-PCR method. Its sequence analysis revealed high homology with other insects and animals FTZ-F1. In order to find the relation between the *P. americana* FTZ and vitellogenins, we analyzed the expression pattern of the latter in the fat body during vitellogensis. The PamFTZ transcript was detected during all stages of vitellogenesis in the fat body with a little increase in day 5, preceding the bulk of vitellogenin genes expression. We assumed that nuclear protein FTZ in the hemimetabolous insect, *P. americana* might functions as a competence factor that facilitates juvenile hormonal activation of gene expression as in holometabolous insect, *Drosophila melanogaster*.

Keywords: Nuclear receptor FTZ, *Periplaneta americana*, Vitellogenesis, Female fat body, Expression pattern.

INTRODUCTION

In oviparous animals, vitellogenesis is a key event in egg maturation, which involves the production of yolk protein precursors by the fat body (an insect metabolic tissue analogous to vertebrate liver) then their uptake by developing oocytes (Raikhel, 1992; Tufail and Takeda 2008). The two primary insect hormones governing vitellogenesis are the sesquiterpenoid juvenile hormone III (JH III) and the steroid 20-hydroxyecdysone (20E). As stated previously, JH III promotes the acquisition of competence in the fat body during the pevitellogenic development. The previtellogenic development showed nuclear enlargement and DNA replication in some species such as *L. migratoria* and *A. aegypti* (Nair *et al.*, 1981; Irvine and Brasch, 1981 and Ditmann *et al.*, 1998). It also showed proliferation of endoplasmic reticulum in some species such as *L. maderae* and *A. aegypti* (della-Cippa and Engelmann, 1984; Raikel and Lea, 1990). Finally, it showed the synthesis of specific proteins that are prerequisites for adult vitellogensis such as transcription factors. Members of the nuclear receptor superfamily are key regulators of physiology and represent the classical model of intracellular regulation of gene expression. Nuclear receptors directly alter gene expression by entering the nucleus and binding to DNA response elements in the presence of ligand. In vertebrates, nearly 50 receptors have been identified, and many have been associated with a wide range of small, lipophilic ligands (Dubrovsky *et al.*, 2011). *Drosophila* represents a much

simpler system, with only 18 nuclear receptor genes in the genome and only two known physiologically active lipophilic hormones, ecdysone and juvenile hormone (King-Jones and Thummel, 2005).

The molecular mechanism of 20E action has been dissected in detail in *A. aegypti* vitellogensis (Cruz *et al*., 2009) which influences a set of genes, including hormonal receptor HR3, HR4, HR39, E75, E78 and fushi tarazu transcription factor 1 (FTZ-F1). Subsequently, the products of these genes alone, or in combination with other factors, activate late effector genes that control downstream physiological responses for the promotion of vitellogenesis (Zhu *et al*., 2003; 2006). Fushi tarazu factor 1 (FTZ-F1) is an orphan nuclear receptor (Ueda and Hirose, 1990) that was initially identified as an activator of a pair-ruled homeobox gene involved in the segmentation of *Drosophila* (Lavorgna *et al*.,1991). Since then, numerous FTZ-F1 homologues have been recognized in several species. Zhu *et al*. (2003) stated that FTZ-F1 is indeed the factor defining the acquisition of competence to 20E in the mosquito fat body. Moreover, this is achieved through JH III-mediated post transcriptional control of FTZ-F1 (Zhu *et al*., 2006).

Two vitellogenin genes Vg1 and Vg2 were previously cloned and sequenced from the female fat body of the American cockroach *P. americana* (Tufail *et al*., 2000, 2001). Both expression profile and level of Vg1 and Vg2 are found to be synchronous and up-regulated by the hemolymph JH titer and suppressed by hemolymph ecdysteroid titer during vitellogenesis (Weaver and Partt, 1977; Weaver *et al*., 1984; Elgendy *et al*., 2009). The present work aimed to clone and detect the expression pattern of *P. americana* FTZ, PamFTZ nuclear receptor in relation to vitellogenic cycle influenced by both 20E and JH III action. This study will open the way for better understanding of the vitellogenin gene hormonal regulation on the molecular level, which is very important for the future development of integrated pest management.

MATERIALS AND METHODS

Animals

Colonies of *P. americana* were maintained under constant dark, feeding on artificial diet MF (Oriental Yeast Co. Ltd. Tokyo) and water ad libitum. White female roaches were collected daily and kept separately. The fat bodies were sampled in different developmental times, from day 1 to day 9 for studying the expression profile. Fat body tissues were isolated in phosphate-buffered saline (PBS 19: 2 mM KH_2PO_4, 137 mM NaCl, 10 mM Na_2HPO_4, 2.7 mM KCl, pH 7.4), frozen immediately in liquid nitrogen and stored at -80^{o}C until required.

RNA Extraction and cDNA Construction

Total RNA was extracted from the above samples using Isogen reagent (Nacalai tesque, Kyoto, Japan) according to the manufacturer's instructions. Poly (A) RNA was purified from total RNA using mRNA purification kit (Amersham-Pharmacia, Piscataway, NJ, USA). A total of 2 µg of mRNA was used to generate ds cDNA using Avian Myelobastosis Virus (AMV) reverse transcriptase (20 units) and an oligo (dT) primer [a cDNA synthesis primer (10 µM)] with the dNTP mixture (10 mM) from the Marathon cDNA amplification kit (Clontech, Palo Alto, CA, USA). This ds cDNA was then used as a template for the cloning of the DNA binding doman of the nuclear receptor fushi tarazu factor from *P.americana* (PamFTZ).

Cloning of DBD of nuclear receptor FTZ

The cDNAs prepared from adult female fat body degenerate primers based on the conserved DNA binding doman

(DBD) and F box of the *Blattella germanica* FTZ-F1 (Cruz *et al*., 2008) were used to obtain PamFTZ homolog cDNA fragment. Briefly, the degenerate primers designed were as follows: forward primer 5ʻ-AARGARGGNATHG ARGA-3ʻ and reverse primer.5ʻ-GTYTG NACNGCDATYTC-3ʻ. Amplification conditions employed were heating to 94^{o}C for 2 min, followed by 35 cycles of 94^{o}C for 30 s, 50^{o}C for 30 s, and 65^{o}C for 1 min. The amplified fragment using cDNA from the fat body (342 bp) was sub-cloned into pT7Blue vector (Novagen) and sequenced.

Structural comparison of DBD of nuclear receptor FTZ

PamFTZ (DBD) sequence (GenBank accession number: AB862966) was compared with other insect FTZ, DBD sequences and homology was predicted using Genytex Programme. Sequences used for the homolgy analysis were (accession number in parentheses): *Bombyx mori* (AB649122), *Blattella germanica* (FM163377), *Spodoptera litura* (ADT91626).

Quantitative real time PCR (QRT-PCR)

Fat bodies from adult females were sampled during days of oogenesis (days 1 to 9), frozen immediately in liquid nitrogen and kept at -80°C until use. Total RNA was extracted by Isogen reagent (Nacalai tesque, Kyoto, Japan) according to the manufacturer's instructions. Contaminating genomic DNA was removed by treatment with RNase-free DNaseI (Invitrogen). One µg DNase-treated total RNA were reverse transcribed using ReverTra Ace (Toyobo Co., Osaka, Japan) and poly dT primer according to the manufacture's instructions. Primers set for FTZ genes (DBD region), [PamFTZ-F(GGCTACC ACTACGGGCTCTT, from 49 to 68) and PamFTZ-R (CTTCTGGAAGCGGCAA TATG,182 from to 201)] in addition to, the housekeeping gene, Actin,[Actin-F (TGACTGAGCGTGGTTACAGC, from 330 to 394 bp) and Actin-R (CAGGAA GGAAGGTTGGAACA, from 534 to 553 bp)] were designed using Primer Express Version 1.5 (Applied Biosystem) and tested to ensure amplification of a single band using RT-PCR. The real time PCR amplification was performed on ABI700 Sequence Detection System (Applied Biosystem) by using SYBR GreenI MasterMix Plus (Eurogentec, Seraing, Belgium). Each reaction was contained 2.5µl of cDNA template and 50 nM primers in a final volume of 25 µl. Cycling parameters were 95°C for 10 min to activate DNA polymerase, and then 40 cycles of 95°C for 15 sec and 60°C for 1min. Melting curves were drawn using Dissociation Curves software (Applied Biosystems) to ensure that only a single product was amplified for each gene. Each cDNA was run four times and the average used for analysis. The value of PamFTZ mRNA were measured relative to those of Actin as housekeeping gene at each time point and expressed as a relative (FTZ/ Actin) ratio.

The changes in PamFTZ expressions were analyzed by one-way ANOVA followed by Student t-test using SPSS 16.0 program.

RESULTS

Partial cloning and structural homology of PamFTZ (DBD and F1 box):

cDNAs were cloned by a RT-PCR approach using degenerate primers designed on the bases of the conserved sequences of the DBD from *B. germanica*. Using a fat body cDNA, a partial clone of 342 bp encoding the *P. americana* (PamFTZ) was cloned and analyzed (Fig. 1). The sequence was submitted to GenBank with accession number: AB862966. The predicted amino acids sequence (114 amino acides) shows high similarity to the DBD and characteristic F box from B. germanica (98%) and two lepidopteran species, S. litura and B. mori (95%) (Fig. 2).

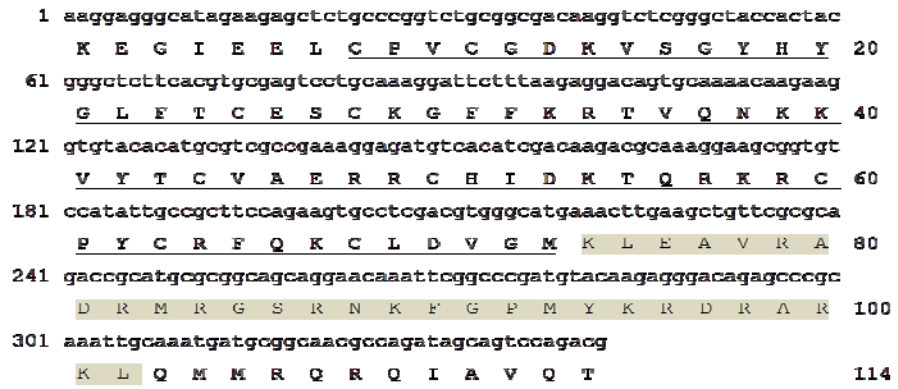

Fig. 1: Nucleotides and deduced amino acid sequences of the *Periplaneta americana* FTZ-F1 (PamFTZ-F1) (GenBank accession number: AB862966). The left numbers indicate nucleotide length and the right numbers indicate the amino acids. The DNA binding domain is underlined. The FTZ-F1 box is shaded in grey colour.

Fig. 2: Comparison of the FTZ-F1 (DBD and F1 box) amino acids sequence of *P. americana* with other species. The PamFTZ is aligned with the homologous region of *B. germanica*, *B. mori* and *S. litura*. Conserved sequences are boxed.

The comparison of PamFTZ (DBD) with FTZ-F1 proteins from other insects, crustaceans, nematodes, and the two closest human homologs, steroidogenic factor 1 (SF-1) and liver receptor homolog 1 (LRH-1), showed that the DBD and FTZ-F1 box are the highest conserved domains, with an overall 78–99% amino acid identity in the FTZ-F1 box and 80-98% in the DBD (Table 1).

Table1: Percent Amino Acids Identity among FTZ-F1 Homologs

Species	DBD	FTZ-F1 Box
Bellatella germanica	98	99
Tribolium castaneum	97	99
Apis mellifera	97	99
Drosophila melanogaster	97	99
Aedes agypti	95	99
Manduca sexta	95	99
Bombyxi mori	93	99
Spodoptera litura	93	99
Homo sapiens (SF-1)*	85	91
Homo sapiens (LRH-1)*	85	95
Caenorhabditis elegans	80	78

*SF-1 , steroidogenic factor

**LRH-1, liver receptor homology 1

Expression profile of PamFTZ gene in the fat body during vitellogensis:

The nuclear protein gene FTZ expression was measured using total RNAs isolated from female fat body during the first vitellogenic cycle. To determine the relative concentration of PamFTZ (DBD) expression related to the reference gene Actin, we applied real time PCR using a primer pair located within the DBD and SYBR - green I reagent. PamFTZ mRNA was present during all days of the first vitellogenic cycle. Detection of PamFTZ transcript started at day 1, then gradually increased and peak at day 5 of vitellogenic stage just preceding the peaks of Vg genes transcripts measured by Elgendy *et al*., 2009. After, day 5 PamFTZ mRNA level declined by the time ecdysteroid peak in hemolymph at the end of vitellogenic cycle (Edwared *et al*., 1984) (Fig. 3).

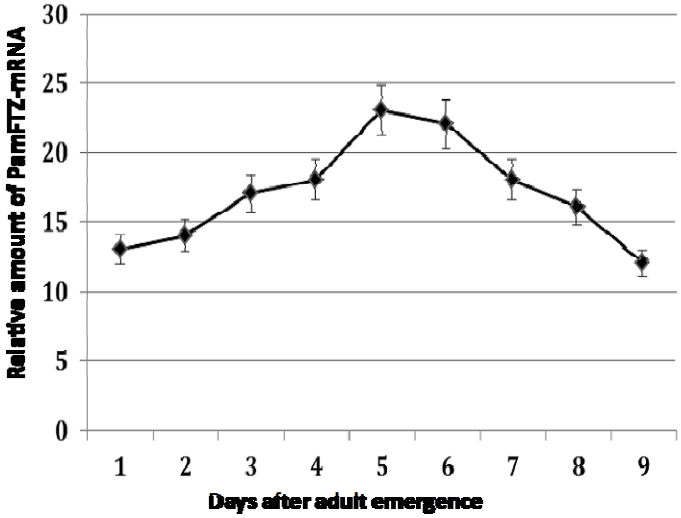

Fig. 3: The relative developmental expression patterns of PamFTZ in the fat body of adult female *P. americana* during vitellogenic period. FTZ gene expression was analyzed by Real-time PCR and was plotted relative to Actin gene expression. Representative data (mean ± SEM) from at least three independent experiments are shown.

DISCUSSION

One of the striking features of juvenile hormone (JH) is its wide range of effects on insect development and physiology (Wyatt and Davey, 1996). During pre-adult development, JH supports larval growth and, together with ecdysone, orchestrates molting and metamorphosis (Riddiford, 2008). In adults, JH regulates reproductive maturation and affects various aspects of insect behavior (Berger and Dubrovsky, 2005). The pleiotropic nature of JH creates certain difficulties for understanding the molecular mechanism of its action (Wheeler and Nijhout, 2003; Palli, 2009). However, the overall consensus is that JH acts through multiple pathways by utilizing more than one receptor. Nuclear protein FTZ has a very important role as competence factor for both 20E and JH III responsiveness. For better understanding of the molecular mechanisms influence the vitellogenin genes expression in the hemimetaboulous insect *P. americana*, we cloned and measured the expression of the nuclear protein FTZ.

Cloning and structural analysis of PamFTZ (DBD and F1 Box)

The initial isolation of a cDNA fragment encoding the american cockroach FTZ-F1 homolog was achieved through a PCR-based approach.

A pair of degenerate PCR primers used to amplify cDNA of the *P. americana* FTZ homolog is shown in Fig. 2. After a PCR fragment of the appropriate size, 342 bp, was sequenced and confirmed to encode a polypeptide of the expected sequence.

The conceptual translation of PamFTZ amino acid sequence revealed distinctly high similarity with its insect counterparts of *Belattella*, *Bombyx* and *Spodoptera* (Cruz *et al*., 2008; Lavorgna *et al*., 1991, 1993; Sun *et al*., 1994), particularly in the DBD and the adjacent stretch of 29 amino acids known as the FTZ-F1 box (Fig. 1). The DBD and F1 box of PamFTZ-F1 were highly conserved relative to the corresponding sequences in insect homologs (Fig. 2). In the case of BgFTZF1, the box is 99% conserved compared with those of other insect homologs, with the exception of that of *B. mori* (Table 1). The FTZ-F1 box extends the DNA binding site of the protein and hence increases the binding specificity (Ueda *et al*., 1992), and also contains putative nuclear localization signals (Li *et al*., 1999). Given the high conservation of the DBD and the FTZ-F1 box in BgFTZ-F1, it was not surprising that the cockroach nuclear receptor bound to the recognition element PyCAAGGPyCPu, as happens with other insect FTZ-F1 homologs (Li *et al*., 2000; Ueda *et al*., 1992).

Developmental expression pattern of PamFTZ in the adult female fat body during vitellogenesis.

In order to examine the PamFTZ-F1 developmental profile in the vitellogenic fat body tissue in more detail, we used a more sensitive real time-PCR analysis (Fig. 3). The PamFTZ gene is constitutively expressed throughout vitellogenesis. PamFTZ transcript started at day 1, then gradually increased and peaked at day 5 of vitellogenic stage just preceding the peaks of Vg genes transcripts measured by Elgendy *et al*., 2009. After day 5 PamFTZ mRNA level decline by the time ecdysteroid peak in hemolymph given that the appearance of Bg-FTZ-F1. The mRNA coincides with the decline of the ecdysteroid pulse measured by Weaver *et al*. (1984). These results suggested that 20E has a modest inhibitory effect on PamFTZ expression similar to that observed in the in vitro study of previtellogenic fat bodies from the mosquito *A. aegypti* (Li *et al*., 2000; Zhu *et al*., 2006). Moreover the highest induction of PamFTZ was detected before the first JH III peak at day 2 just preceding the first appearance of Vg mRNA in the fat body (Weaver and Parott, 1977; Elgendy *et al*., 2009), which suggested that PamFTZ might play another role in the JH III gene induction. Similarly, the *D. melanogaster* FTZ-F1 mediate juvenile hormone activation of E75A gene expression through an intracellular pathway (Dubrovsky *et al*., 2011).

In summary, we have cloned the DBD and F1 box for the nuclear receptor FTZ from the hemimetabolous insect *P. americana*. The fat body developmental expression pattern of PamFTZ during vitellogenesis suggested that FTZ-F1 functions as a factor that facilitates JH III activation and or 20E suppression of Vgs gene expression. These data will help in the future investigations to understand both the ecdysteroid-dependent genetic hierarchy and JH mechanism controlling vitellogenesis in the American cockroach *P. americana.*

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ARABIC SUMMARY

استنساخ جزئى والتعبيرالنمطى للمستقبل النووى FTZ في الأجسام الدهنية للصرصور الأمريكى أثناء مرحلة تكوين المح

عزة محمد الجندى[1] و ماكيو تاكيدا[2]

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الهدف من هذه الدراسة هو اثبات اهمية المستقبل النووى للتعبير الجينى لجينات انتاج المح فى الأجسام الدهنية للصرصور الأمريكى أثناء دورة انتاج المح الأولى. وقد تم عزل شريط من الحامض النووى ال د.ن.ا لهذا المستقبل النووى بطول 342 زوج من القواعد فى الأجسام الدهنية لأنثى هذا الصرصور بطريقة البادئات المبنية على اساس تتابع الأحماض الأمينية بإستخدام تقنية تفاعل البلمرة المتسلسل للنسخ العكسى.، وقد دلت تحاليل تتابع الأحماض الأمينية على وجود نسبة عالية من التطابق مع جين لبعض الحشرات والحيوانات الأخرى.وكمحاولة لإيجاد العلاقة بين جين وعملية انتاج المح لهذا الصرصور فقد قمنا بتحليل التعبير الجينى له فى الأجسام الدهنية أثناء مرحلة انتاج المح. وقد دلت النتائج على وجود التعبير الجينى فى جميع مراحل تكوين المح مع وجود زيادة ملحوظة فى اليوم الخامس الذى يسبق الزيادة الهائلة فى التعبير الجينى لجينات المح. وقد تمكنا من خلال هذه الدراسة ان نفترض أن هذا المستقبل النووى فى الصرصور الأمريكى كحشرة ناقصة التحور يعمل بمثابة عامل الكفاءة الذي يسهل التنشيط الجينى للهرمونات كما هو الحال في حشرة الدروسوفيلا كحشرة كاملة التحور.