CRUSTACEAN VITELLOGENIN: A SYSTEMATIC AND EXPERIMENTAL ANALYSIS OF THEIR GENES, GENOMES, MRNAS AND PROTEINS; AND PERSPECTIVE TO NEXT GENERATION SEQUENCING

BY

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ABSTRACT

Crustacean vitellogenesis is a process that involves Vitellin, produced via endoproteolysis of its precursor, which is designated as Vitellogenin (Vtg). The *Vtg* gene, mRNA and protein regulation involve several environmental factors and physiological processes, including gonadal maturation and moult stages, among others. Once the *Vtg* gene, mRNAs and protein are obtained, it is possible to establish the relationship between the elements that participate in their regulation, which could either be species-specific, or tissue-specific. This work is a systematic analysis that compares the similarities and differences of *Vtg* genes, mRNA and Vtg between the crustacean species reported in databases with respect to that obtained from the transcriptome of *Callinectes arcuatus*, *C. toxotes*, *Penaeus stylirostris* and *P. vannamei* obtained with MiSeq sequencing technology from Illumina. Those analyses confirm that the *Vtg* obtained from selected species will serve to understand the process of vitellogenesis in crustaceans that is important for fisheries and aquaculture.

RESUMEN

La vitelogénesis de los crustáceos es un proceso que involucra la vitelina, producida a través de la endoproteólisis de su precursor llamado Vitelogenina (Vtg). La regulación del gen *Vtg*, los ARNm y la Vtg involucra factores ambientales y procesos fisiológicos, incluyendo: maduración gonadal, etapas de muda, entre otros. Con el gen *Vtg*, los ARNm y la proteína obtenidos, es posible correlacionar los elementos que participan en su regulación, pudiendo ser especie-específicos o tejido-específicos. Este trabajo es un análisis sistemático que compara las similitudes y diferencias

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en los genes *Vtg*, mRNA y Vtg entre especies de crustáceos reportadas en bases de datos contra las obtenidas a partir del transcriptoma de *Callinectes arcuatus*, *C. toxotes*, *Penaeus stylirostris* y *P. vannamei* mediante la tecnología de secuenciación MiSeq de Illumina. Estos análisis confirman la importancia de los estudios de la vitelogénesis en especies de crustáceos de importancia pesquera y acuícola.

INTRODUCTION

Crustacea have different sexual systems, each aimed at achieving maximum reproduction efficiency in their specific situation. In oviparous species, ovary maturation comprises the synthesis of yolk protein denoted as Vitellin (Vn), which is the most important source of energy and nutrients for embryo development (Boulangé-Lecomte et al., 2017). Vn is produced through the endoproteolysis of its precursor Vitellogenin (Vtg), and both proteins are immunologically similar (Avarre et al., 2003; Zmora et al., 2007; Xie et al., 2009). The process of Vtg biosynthesis and its accumulation in the ovary is named “vitellogenesis”, and it is essential for ovarian maturation (Thongda et al., 2015). According to species, Vtg biosynthesis occurs in the ovary and/or hepatopancreas (Shen et al., 2014).

Before the 1990s, most studies focused on ovarian Vtg synthesis; thereafter, crustacean extra-ovarian Vtg synthesis has been well analysed (Jayasankar et al., 2002; Bae et al., 2017). Among species, there are differences between ovarian and extra-ovarian Vtg synthesis (Phiriyangkul et al., 2007). Some proposals to explain this pattern have been established, including applied methodologies, molecular concentration, source of the organisms, among others. The procedures to establish *Vtg* mRNA concentration in any physiological condition request a correct hybridization between mRNA and the antisense molecule, such as oligonucleotides, complementary DNA (cDNA), or an adequate primer to DNA polymerization. Therefore, the *Vtg* gen, cDNA and protein sequence are fundamental for a molecular probe design to quantify the mRNA from the genes' expression that participate in crustacean vitellogenesis.

Nowadays, to obtain DNA or RNA sequences quickly in a specific physiological condition, Next Generation Sequencing (NGS) technologies are the better option. They often produce in the order of thousands or hundreds of thousands of sequences, in shorter times and at significantly lower costs (Jimenez-Gutierrez et al., 2016). NGS has been performed in several species of crustaceans; some works have focused on reproduction-involved tissues (He et al., 2012; Gao et al., 2014; Shen et al., 2014), and few of them have yielded physiological implications (Tarrant et al., 2014; Peng et al., 2015; Lee et al., 2017; Das et al., 2018; Uengwetwanit et al., 2018; Wang et al., 2019). In this way, since NGS technologies give new options to identify genes and mRNAs, among which the various *Vtg*

transcripts (Shen et al., 2014; Tarrant et al., 2014), NGS is another option to establish the *Vtg* mRNA expression between maturity stages and sexes (Liu et al., 2015), whose sequences are published in public data bases such as GenBank.

From the available information, most of the *Vtg* mRNA characterizations from ovary or hepatopancreas were carried out under laboratory conditions. Even though cultured species do not face dramatic climatic changes, many metabolic pathways are circadian-rhythm dependent. In both wild and cultured organisms, many clock genes are strongly related with ovarian development (Tarrant et al., 2014; Chen et al., 2017). Therefore, there currently exists a lack of integration of *Vtg* mRNAs from crustacean species from fishery, as well as information integration among the different species of crustaceans.

In this work, *Vtg* mRNAs from the most important crustacean species for the Eastern Pacific fishery (i.e., *Callinectes arcuatus* Ordway, 1863, *C. toxotes* Ordway, 1863 and *Penaeus stylirostris* Stimpson, 1871, and cultured *Penaeus vannamei* Boone, 1931), were determined with MiSeq Illumina Sequencing Technology. This work sought to deepen the understanding of the different molecules involved in crustacean vitellogenesis, for their use in the evaluation of reproductive periods, and their regulation in different crustacean species of commercial importance.

MATERIAL AND METHODS

Crustacean genomes, *Vtg* genes mRNA and *Vtg* identification in the National Center for Biotechnology Information (NCBI)

To identify the crustacean genomes in the Genome Database from NCBI, the keyword “crustacean” was used. Then, the *Vtg* gene sequences were identified using the keyword “Vitellogenin” in Genomedata Base whereas the mRNAs were determined from the “GenBank Database” using the same keywords (Benson et al., 2005). To construct the *Vtg* and *Vtg* crustacean database, the complete open reading frame (ORF) sequences were used, and partial sequences were discarded.

To corroborate the complete *Vtg* genes mRNAs and protein sequences reported in the respective databases, a Basic Local Alignment Search Tool (BLAST; Altschul et al., 1990) in the NCBI database was made with an Expected Threshold of 100, a Match/Mismatch of 1-2 and 20 000 Max Target Sequences. Furthermore, a multiple alignment among *Vtg* Selected was performed with software Kalign 2.0 (Lopez, 2008; Lassmann et al., 2009; Chojnacki et al., 2017). The alignment parameters were similar to those proposed by the lost DNA model (Martínez-Pérez et al., 2005): output format Clustal W, gap open penalty of 9.0, gap extension penalty 0.2, terminal gap penalties 0.45, and bonus score 0.0.

The identification of the introns and exons of the reported *Vtg* genes was done according to the reported GenBank sequence and from the respective paper. Furthermore, data from mRNA and ORF of each *Vtg* sequence were corroborated with the alignment among the genomic sequence with the aforementioned parameters. The codons of each exon were established with corresponding amino acids obtained from the ORF translation with the software EXPASY Translate tool (SIB, 2016).

Vitellogenin mRNA phylogenetic tree, and *Vtg* domains

Determination of the phylogenetic relationships among the sequences of the *Vtg* mRNA was made by Bayesian inference with Mr Bayes software (Ronquist et al., 2012), in 2 runs with 4 Markov-Monte Carlo chains and with a maximum of 30 million generations and sampling every 3000 generations. The *Vtg* domain identification from each species was done following the protein report from GenBank.

Animal collection

Wild animals including *Callinectes arcuatus*, *C. toxotes* and *Penaeus stylirostris* were obtained from a fishing boat in the East Pacific (23°20'N 106°30'W), while cultured *P. vannamei* were obtained from an aquaculture farm in Mazatlán, Sinaloa, Mexico (23°1'N 106°12'W). From the wild animals, a stock from both *Vtg* synthesis tissues (ovary and hepatopancreas) was used to obtain the transcriptome that represents all maturity stages, the capture season and the circadian rhythm for each species. For the cultured organisms, a stock from each *Vtg* synthesis tissue (ovary and hepatopancreas), was used to obtain the transcriptome that represents all maturity stages and the circadian rhythm. The details are indicated in table I.

RNA isolation and illumina sequencing

Total RNA from each tissue stock was obtained with the following protocol: Total RNA was isolated from 100-150 mg of the tissue stock with the Pure Link RNA Mini Kit (Invitrogen / Thermo Fisher Scientific, Waltham, MA) following the manufacturer's instructions and resuspended in 90 μ l free RNase water. A second round of purification was conducted as follows: a volume of Trizol reagent and 40 μ l of chloroform were added, then the mixture was vortexed for 10 s and incubated for 10 min. at 4°C. The phases were obtained by centrifugation at 13 000 g for 45 min. at 4°C to obtain the supernatant. The RNA was precipitated with 90 μ l of isopropyl alcohol and 10 μ l of high salt buffer (0.8 M sodium citrate and 1.2 M NaCl) and then incubated over night at -20°C. The RNA was

TABLE I
Sources of collection of the species of Crustacea studied herein

Species	Tissue	Maturity stages	Collection_date	Day/night	Source
<i>Penaeus vannamei</i> Boone, 1931	Ov	I to V	Nov 2018	Circadian rhythm	Aquaculture
<i>Penaeus vannamei</i>	Hp	I to V	Nov 2018	Circadian rhythm	Aquaculture
<i>Penaeus stylirostris</i> Stimpson, 1871	Ov/Hp	I to V	Jan 2018-Jan 2019	Undetermined	Fisheries
<i>Callinectes arcuatus</i> Ordway, 1863	Ov/Hp	I to V	Jan 2018-Jan 2019	Day	Fisheries
<i>Callinectes toxotes</i> Ordway, 1863	Ov/Hp	I to V	Jan 2018-Jan 2019	Day	Fisheries

Ov, Ovary; Hp, Hepatopancreas.

concentrated by centrifugation at 13 000 g for 55 min. at 4°C. The pellet was washed two times as follows: 200 μ l of 70% ethanol with DEPC water (0.1% diethyl pyrocarbonate in Type 1 Water) were used and recovered at the previous speed and temperature centrifugation for 15 min. The RNA was dried off at room temperature and hydrated with 30 μ l of DEPC water.

Ovarian and hepatopancreas transcriptomic illumina sequencing

All RNA samples were submitted to Genoma Mayor, Universidad Mayor in Chile (Santiago de Chile). The RNA concentration of each sample was determined with QuantiFluor® dsDNA System (Promega, Madison, WI) and the Integrity with Bioanalyzer 2100 RNA 6000 Nano Kit (Agilent Technologies, Santa Clara, CA). The library construction was done using TruSeq Stranded mRNA (Illumina, San Diego, CA). The purity library and size fragments were determined as previously described for total RNA extraction, and the library was sequenced in Illumina MiSeq instrument according to the manufacturer's procedure.

De novo assembly and Vtg analysis

To obtain each transcriptome, the adapter sequences from each read and low-quality reads were first eliminated with the software Trim-galore, from http://www.bioinformatics.babraham.ac.uk/projects/trim_galore/. The normalization was done with Trinity version 2.6.6 (Haas et al., 2013) with the function: <insilico_read_normalization.pl>. The de novo assembled was carried out with the software SPAdes version 3.12.0 at <http://cab.spbu.ru/files/release3.12.0/>. Finally, to establish the correlation between the sequences assembled and their function, a BLAST alignment

was done with software Diamond version 0.9.22 versus the “Nucleotide collection” database from NCBI. From these results, the putative *Vtg* sequences of each species were corroborated with a second BLAST alignment.

RESULTS

Until November 2018, 27 crustacean genome projects had been reported by the NCBI (see Supplementary Material A-I). From these, six corresponded to the class Branchiopoda, mainly comprising species of the families Triopsidae and Daphniidae. In contrast, the genome of eight of the nine families of the class Hexanauplia had been sequenced. The rest of the genomic projects reported in the NCBI corresponded to species of Malacostraca; however, the majority of these were still under construction.

From the available information, two main *Vtg* genes had been determined. Both genes, *Vtg1* and *Vtg2*, from *Daphnia magna* Straus, 1820 have 16 introns and 17 exons, whereas in species of Decapoda, such as *Metapenaeus ensis* (De Haan, 1844), and *Scylla paramamosain* Estampador, 1950, the *Vtg1* gene has 14 introns and 15 exons, and the *Vtg2* gene has fewer than 12 introns and 13 exons (Supplementary Material A-II). The length of the nucleotide sequence of *Vtg* in the GenBank database ranges from 5000 to 6000 bp in classes such as Branchiopoda and Hexanauplia; meanwhile, in the class Malacostraca, the *Vtg* sequences range from 7782 to 8518 bp. Those genes code for *Vtgs* varying from 2534 to 2592 amino acids in length (Supplementary Material A-III).

The phylogenetic relationships determined based on nucleotide *Vtg* sequences of crustacean species showed, that the analysed Decapoda share a common ancestor (fig. 1). There were three main clades: one from the suborder Dendrobranchiata, another for the infraorder Caridea, and the third for the infraorder Brachyura. The evaluated sequences were not separated by tissue of origin, but were catalogued by the species to which they belong. Despite some previously reported transcriptomes that show up to 20 transcripts per species that encode *Vtg* (Supplementary Material A-IV), in some species, different results with respect to *Vtg* expression had been reported depending upon the methodology applied (Supplementary Material A-V).

On international databases, the reported *Vtg* molecular weights range from 200 to 500 kDa, according to the species. *Vtg* from the classes Branchiopoda and Hexanauplia contain less than those from the class Malacostraca. *Vtg* has conserved regions among the species, especially in their amino terminus, where the Vitellogenin-N domain is located. In this sense, seven domains have been found in species of crustaceans, at least three of which are found in all crustacean species: the domains Vitellogenin-N, Von Willebrand factor type D (VWD), and the

Fig. 1. Phylogenetic tree based on Vtg sequences from species of Crustacea. The nucleotide sequences were aligned with Clustal W software, with the parameters proposed in the DNA loss model (Martinez-Perez, 2005). The phylogeny with Bayesian inference was obtained with MrBayes software with 2 runs, and 4 Markov-Monte Carlo chains, with *Daphnia pulex* Leydig, 1860, as an outgroup. Numbers above the nodes indicate nonparametric bootstrap values (30 million generations, sampling the chains every 3000 generations). Sequences that specify the tissue of origin are marked with the suffixes Hp, Hepatopancreas; Ov, Ovary; Ts, Testicle. The access numbers are indicated in the table Supplementary Material A-II.

Fig. 2. Domain locations from crustacean Vtg sequences reported in GenBank. Each region is indicated in its respective colour. The positions of each domain are indicated in the table Supplementary Material A-VI. Sources: Genom, Genomic; CoOrg, Complete Organism; Hp, Hepatopancreas; Ov, Ovary; Ts, Testicle; HP OV, Hepatopancreas & Ovary; Ov Ts, Ovary & Testicle; ND, Not Determined.

Domain of Unknown Function (DUF) DUF1943 (fig. 2; Supplementary Material A-VI). Other domains that are exclusively present in Malacostraca are the Ferritin-like domain, the C8 domain, and the VWD domain.

Some publications related to Vtg synthesis show more than one Vtg; however, in the GenBank database one Vtg sequence is exclusively reported for most

TABLE II

The similarity of *Vtg* sequences from hepatopancreas and ovary from several species of decapod Crustacea

Species	Accession numbers		Similarity (%)
	Ovary	Hepatopancreas	
<i>Penaeus merguensis</i> (De Man, 1888)	AAR88442.2	ACV32381.1	99
<i>Penaeus vannamei</i> Boone, 1931*	AAP76571.2	AGX26044.1	99
<i>Penaeus vannamei</i> **	MN105877	MN105878	69
<i>Callinectes sapidus</i> Rathbun, 1896	AEI59132.1	ABC41925.1	98
<i>Cherax quadricarinatus</i> (Von Martens, 1868)**	AAS68191.1	AAG17936.1	54
<i>Metapenaeus ensis</i> (De Haan, 1844)*	AAN40700.1	AAN86120.1	42

* *Vtg* sequence from the hepatopancreas (HP) is incomplete.

** *Vtg* sequence from the ovary (OV) is incomplete.

crustaceans, with an exception for species such as *Penaeus merguensis* (De Man, 1888), *P. vannamei*, *M. ensis*, *Cherax quadricarinatus* (Von Martens, 1868), and *Callinectes sapidus* Rathbun, 1896, which have *Vtg* sequences reported from both tissues (hepatopancreas and ovary). Complete *Vtg* sequences from both tissues are almost identical. However, for some of these sequences, at least one is incomplete. In the specific case of previously reported *P. vannamei*, the partial *Vtg* sequence was from the amino-terminal region, which is the most conserved region. In our results, the partial ovary *Vtg* sequence carboxyl-terminal region has a similarity of 69% with hepatopancreas *Vtg*. In contrast, for *C. quadricarinatus* and *M. ensis*, the partial sequences were from the carboxyl-terminal region, which is why the similarity of the sequences that could be checked drops to 54% and 42%, respectively (table II).

Transcriptomes from cultured *P. vannamei* and wild *Penaeus stylirostris*, *Callinectes arcuatus* and *C. toxotes* allow to identify the *Vtg* sequences and their deduced proteins (table III). The *P. vannamei* complete *Vtg* from hepatopancreas shares 69% similarity with partial carboxyl-terminal ovary *Vtg*. In general, all *Vtg* sequences presented identities greater than 90% with those from previously reported species, including other species of the same genus. The effect of neuropeptides and physiological conditions on *Vtg* expression and synthesis in crustaceans is illustrated in Supplementary Material A-VII.

DISCUSSION

Traditional and NGS technologies can help to establish genomes and transcriptomes. From the available genomes, the number and arrangement of the introns/exons are species-specific (Martínez-Pérez et al., 2009). The numbers of *Vtg* introns

TABLE III

Vtg mRNA from *Penaeus vannamei* Boone, 1931, *P. stylirostris* Stimpson, 1871, *Callinectes arcuatus* Ordway, 1863, and *C. toxotes* Ordway, 1863, and their similarities with previously reported crustaceans, among which *Callinectes sapidus* Rathbun, 1896

Species	Tissue	<i>Vtg</i> accession number	Deduced protein similarity (%)	GenBank species
<i>Penaeus vannamei</i>	Ov	MN105877.1	99.4	<i>P. vannamei</i> ROT61469.1
<i>Penaeus vannamei</i>	Hp	MN105878.1	94	<i>P. vannamei</i> AAP76571.2
<i>Penaeus stylirostris</i>	Ov/Hp	MN105879.1	99	<i>P. vannamei</i> ROT61470.1
<i>Callinectes arcuatus</i>	Ov/Hp	MN105880.1	93.1	<i>C. sapidus</i> AEI59132.1
<i>Callinectes toxotes</i>	Ov/Hp	MN105881.1	91.7	<i>C. sapidus</i> AEI59132.1

Ov, ovary; Hp, hepatopancreas.

and exons from crustacean species are like those from other invertebrate and vertebrate species, suggesting a common ancestor (Kung et al., 2004). Nevertheless, the higher number of introns of Branchiopoda with respect to Malacostraca is directly related to their lower number of base pairs on *Vtg* sequences and to the higher specialization of *Vtg* of Malacostraca species.

Despite the presence of at least two *Vtg* sequences reported for several species, in the phylogenetic tree, the sequences are not separated according to the tissue of origin but according to species. This suggests a possible alternative splicing and punctual mutations within each species (Tarrant et al., 2014; Liu et al., 2015). Some authors have suggested a divergent evolutionary process (Tarrant et al., 2014; Liu et al., 2015).

The *Vtg* transcript of vertebrates is encoded by a multigene family (Tarrant et al., 2014). But in the invertebrates, only for *Procambarus clarkii* (Girard, 1852), 29 transcripts were reported that encode *Vtg* (Shen et al., 2014). Our results from each tissue, which agree with previous reports, suggest possible alternative mRNA splicing events (Mak et al., 2005) or an early gene duplication event, followed by rapid sequence divergence (Phiriyangkul et al., 2007), which represent phenomena that are not limited to the infraorder group and neither by their geographical distribution.

Most works have focused on differential tissue expression of *Vtg* in female crustaceans. For example, in the shrimp *Metapenaeus ensis*, *Vtg1* is expressed in ovary and hepatopancreas, whereas *Vtg2* is expressed exclusively in the hepatopancreas (Wong et al., 2008). However, a main point of discussion is which organ is the major site of synthesis. A major *Vtg* expression in the hepatopancreas has been reported for some crustacean species, such as the shrimps *Penaeus japonicus* Spence Bate, 1888 (cf. Okumura, 2007), *P. merguensis* (cf. Phiriyangkul et al., 2007), *P. vannamei* (cf. Raviv et al., 2006) and *M. ensis* (cf. Tsang et al., 2003; Tiu et al., 2006a), the freshwater crayfish *Procambarus clarkii*, and the blue swimming crab

Callinectes sapidus (cf. Shen et al., 2014; Thongda et al., 2015). Nonetheless, the results depend upon the methodologies applied.

With genome databases, *Vtg* genes, mRNA and *Vtg* proteins, in this work, the *Vtg* is confirmed in ovary/hepatopancreas transcriptomes from the wild-caught crustaceans *C. arcuatus*, *C. toxotes* and *P. stylirostris* in addition to the ovary and hepatopancreas transcriptomes from cultured *P. vannamei*. Even so, there are some previously published transcriptomes from *P. vannamei* with Illumina MiSeq technology, most of which do not have a reproductive focus (Zhang et al., 2016; Fan et al., 2019), and some of them are focused on eyestalk tissue (Wang et al., 2019) and changes in hepatopancreas after eyestalk ablation (Lee et al., 2017). Next to *Vtg*, some other mRNAs have been implicated in reproduction control, such as the *Vtg* receptor (*VtgR*; Shen et al., 2014), the Gonadotropin-Releasing Hormone (GnRH) signalling pathway (among them: *GnRH receptor* and *epidermal growth factor receptor*), *Torso-like*, and *Vigillin*, among others (Tarrant et al., 2014; Uengwetwanit et al., 2018).

Preliminary transcriptomic results from *P. vannamei*, *P. stylirostris*, *C. arcuatus* and *C. toxotes* help to find some reproduction-related genes such as *VtgR*, *vitelline membrane outer protein*, *vitellogenin carboxipeptidase*, *ecdysone receptor (EcR)*, *ecdysteroid-regulated protein*, *ecdysone-induced protein*, *progesterone-like protein*, *progesterone-induced-blocking factor*, *progesterone receptor*, *crustacean female sex hormone ovarian isoform*, *lutropin-choriogonadotropic hormone receptor*, *ovarian peritrophin*, *ovary development related protein*, *ovigerous-hair stripping substance*, *ovoinhibitor*, *ovarian killer protein*, *ecdysteroid receptor*, *ecdysteroid-regulated protein*, *ecdysone-induced protein*, *voltage-dependent calcium channel*, *FEM-1*, and *insulin growth factor*, among others.

Most of these could serve as molecular markers of maturity stages, as well as to study the interactions in the induction and repression of reproduction. However, further studies are necessary to understand the role of each one on the reproduction of crustaceans.

Despite the substantial amount of information generated from NGS, there remains a large number of unknown genes and functions, because organisms have phenotypic plasticity, i.e., the ability to express different phenotypes from the same genotype due to changes in environmental conditions (An et al., 2018). Also, the complete genome of most crustaceans is unknown, and there is a limited number of non-redundant sequences in the international databases for some species.

Vtg synthesis

Vtg is a member of a family of lipid transfer proteins (Smolenaars et al., 2007). The classes Branchiopoda and Hexanauplia have fewer amino acids as compared

to the class Malacostraca. The fact that Malacostraca species present more domains implies a higher level of regulation and more possible functions for Vtg. The Vitellogenin-N domain is the core of the protein, and transfers cholesterol and triglycerides to Vtg (Bai et al., 2015). The Ferritin-like domain stores iron in a biologically available form. The GL/ICG motifs from the C8 and VWD domains are necessary for the oligomerization of the protein (Bai et al., 2015; Wu et al., 2018). In addition to these domains from crustacean Vtg, some motifs, such as R-K.XXR, KLSR, KCYR, and KFSR, are found in mammals, insects, and crustaceans (Xie et al., 2009). These have been proposed as processing motifs for the subtilisin-like protease family (Tseng et al., 2001).

Vtg is composed of two subunits in the early stages of vitellogenesis and of four subunits in the late stages of vitellogenesis, which is congruent with Western blot immunopositive signals concentrated on the lower-molecular-weight fraction of the ovarian polypeptide (Okuno et al., 2002; Zmora et al., 2007). Vtg subunits have been detected by ELISA assays in the ovary, haemolymph, and hepatopancreas; however, in some crustacean species, Vtg was not found in the hepatopancreas, despite the presence of the *Vtg* transcript (Auttarat et al., 2006). In some species, Vtg levels in the hepatopancreas at any stage are low or undetectable by Western blot (Auttarat et al., 2006; Phiriyangkul et al., 2007).

This suggests that the demand for Vtg from the ovary is greater than the rate of synthesis from the hepatopancreas (Auttarat et al., 2006), whereas in the ovaries the concentrations of Vtg during ovarian maturation are lower than those of Vn (Auttarat et al., 2006; Wong et al., 2008). This is likely because Vtg may be excreted from the hepatopancreas immediately after synthesis and/or due to the great number of proteases already present in this organ (Phiriyangkul & Utarabhand, 2006; Zmora et al., 2009). In some cases, the presence of small Vtg peptides depends upon the accurate preservation of the sample, because even under a congelation point, RNases and proteases have activity (Auttarat et al., 2006).

Ovary development and maturation

Regardless of the presence of one or two *Vtg* transcripts, their expression is strictly related to the oogenic cycle (Raviv et al., 2006), and Vtg levels in the haemolymph are often indicative of ovarian development (Thongda et al., 2015). For most crustacean species, ovarian development is separated into four stages (Nguyen et al., 2018) and external conditions are intimately connected with ovarian maturation, depending mostly on the season of the year, with maximum reproduction peaks in seasons with higher temperatures (Thongda et al., 2015).

Previous reports show a species-specific *Vtg* expression pattern. For most crustaceans, both *Vtg* transcription and yolk volume increase in parallel to ovarian

maturation (Kung et al., 2004). For the shrimps *Penaeus merguensis*, *P. indicus* H. Milne Edwards, 1837 and *P. vannamei*, the *Vtg* expression levels are higher in the ovary than in the hepatopancreas at all evaluated stages (Phiriyangkul & Utarabhand, 2006; Raviv et al., 2006), whereas for the shrimp *P. japonicus*, the expression pattern is the opposite (Tsutsui et al., 2000). The highest *Vtg* mRNA levels from the ovarian tissue of *P. merguensis* were observed in the early vitellogenic stage, and these decrease in advanced stages, with an opposite expression pattern in the hepatopancreas (Phiriyangkul et al., 2007). However, in some reports for *P. japonicus* (cf. Okumura, 2007), and *Scylla paramamosain* (cf. Jia et al., 2013), a constant increase occurs from the primary vitellogenic stage to final maturation, with a decrease after oviposition.

In some species of decapods, such as the mud crab *S. paramamosain* (cf. Gong et al., 2015) and the prawn *Macrobrachium rosenbergii* (De Man, 1879) (cf. Okuno et al., 2002), the ovary is only known as a site for *Vtg* uptake and accumulation during ovarian development (Gong et al., 2015), synthesizing only small amounts of *Vtg* (Tiu et al., 2006b). In other species, such as the ridgeback prawn *Sicyonia ingentis* (Burkenroad, 1938), the shrimp *P. japonicus* and the swimming crab *Callinectes sapidus* (cf. Tsukimura, 2001; Okumura, 2007; Thongda et al., 2007; Zmora et al., 2007), *Vtg* synthesis occurs in both tissues. We have found *Vtg* transcripts in both tissues from adult females of the Pacific blue swimming crab *C. arcuatus* and also in the hepatopancreas of subadult females of *P. stylirostris* (without developed gonads), whereas in subadult females of *P. vannamei*, *Vtg* transcripts were absent.

It is important to highlight these physiological differences and the species-specific regulation level, because in tropical countries, fishery management is generalized for all members of the same crustacean family (e.g., in the families Penaeidae and Portunidae; NOM-039-PESC, 2003; NOM-002-SAG/PESC, 2013), despite differences in the regulation of their reproduction. In this sense, *Vtg* sequences for species that are not cultured commercially, such as the shrimp *P. stylirostris* and the crabs *C. arcuatus* and *C. toxotes*, among others, are less studied and were absent in the GenBank databases until this work.

All of the abovementioned studies suggest a perfectly coordinated process among the hepatopancreas and ovary, where the genes *Vtg*, *VtgR* and *EcR*, among others, could be potential markers for evaluating ovarian maturation in each species. However, *Vtg* expression and *Vtg* synthesis patterns are not the same for all infraorders from the subphylum Crustacea, not even among members of the same genus. Evaluations must be standardized by each species, and by each habitat, without neglecting the evolutionary history of each gene. An understanding of all of these physiological processes can be used to assay the crustacean reproduction process in both aquaculture and fisheries.

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SUPPLEMENTARY MATERIAL

The seven tables presented in Supplementary Material as well as the corresponding references, follow below.

TABLE A-I
Genome: Crustaceans with complete genome available on GenBank database

No.	Nuc acid	Class	Family	Organism	Common name	Genome ID	Reference
1	Genome	Branchiopoda	Daphniidae	<i>Daphnia manga</i>	Common water fleas	10953	Orsini et al. (2016)
2	Genome	Branchiopoda	Daphniidae	<i>Daphnia pulex</i>	Common water fleas	288	Colbourne et al. (2011)
3	Genome	Branchiopoda	Limnadiidae	<i>Eulimnadia texana</i>	Clam Shrimp	66591	Baldwin-Brown et al. (2018)
4	Genome	Branchiopoda	Triopsidae	<i>Lepidurus arcticus</i>	Tadpole shrimps	ND	Savojardo et al. (2019)
5	Genome	Branchiopoda	Triopsidae	<i>Lepidurus apus lubbocki</i>	Tadpole shrimps	ND	Savojardo et al. (2019)
6	Genome	Branchiopoda	Triopsidae	<i>Triops cancriformis</i>	Tadpole shrimp	7259	Ikeda et al. (2015)
1	Genome	Hexanauplia	Archaeobalanidae	<i>Semibalanus balanoides</i>	Northern acorn barnacle	73714	Nunez et al. (2018)
2	Genome	Hexanauplia	Acartiidae	<i>Acartia tonsa</i>	Copepod	66903	Jørgensen, (2017)*
3	Genome	Hexanauplia	Calanidae	<i>Calanus glacialis</i>	Copepod	64149	Weydmann et al. (2017)
4	Genome	Hexanauplia	Calanidae	<i>Calanus finmarchicus</i>	Copepod	10995	Weydmann et al. (2018)
5	Genome	Hexanauplia	Caligidae	<i>Caligus rogercrescevi</i>	Sea louse	38161	Leong et al. (2015)*
6	Genome	Hexanauplia	Harpacticidae	<i>Tigriopus kingsejongensis</i>	Antarctic-endemic copepod	ND	Kang et al. (2017)
7	Genome	Hexanauplia	Triopsidae	<i>Lepeophtheirus salmonis</i>	Salmon louse	2713	Tjensvoll et al. (2005)
8	Genome	Hexanauplia	Oithonidae	<i>Oithona nana</i>	Copepod of ocean Indo-West Pacific	53058	Regster and William, (2017)*
9	Genome	Hexanauplia	Temoridae	<i>Eurytemora affinis</i>	A calanoid copepod	17731	Regier et al. (2010)
1	Genome	Malacostraca	Armadillididae	<i>Armadillidium vulgare</i>	Pillbug	50510	Leclercq et al. (2016)
2	Genome	Malacostraca	Atyidae	<i>Caridina multidentata</i>	Amano Shrimp	54074	Sasaki et al. (2017)
3	Genome	Malacostraca	Atyidae	<i>Neocaridina deniculata</i>	Japanese swamp shrimp	ND	Kenny et al. (2014)

TABLE A-I
(Continued)

No.	Nuc acid	Class	Family	Organism	Common name	Genome ID	Reference
4	Genome	Malacostraca	Cambaridae	<i>Procambarus virginalis</i>	Marbled crayfish	66438	Gutekunst et al.(2018)
5	Genome	Malacostraca	Hyalidae	<i>Hyalella azteca</i>	Amphipod	16496	Lowe and Eddy (1997)
6	Genome	Malacostraca	Hyalidae	<i>Parhyale hawaiensis</i>	Amphipod crustacean	15533	Kao et al. (2016)
7	Genome	Malacostraca	Ligiidae	<i>Ligia exotica</i>	Sea roach or wharf roach	54073	Sasaki et al. (2017)
8	Genome	Malacostraca	Palaemonidae	<i>Palaemon carinicauda</i>	Shrimp	ND	Yuan et al. (2017)
9	Genome	Malacostraca	Penaeidae	<i>Penaeus vannamei</i>	Pacific shrimp	ND	Yu et al. (2015)
10	Genome	Malacostraca	Penaeidae	<i>Penaeus japonicus</i>	Shrimp	24063	Yamauchi et al. (2004)
11	Genome	Malacostraca	Penaeidae	<i>Penaeus monodon</i>	Shrimp	1(2027	Wilson et al. (2000)
12	Genome	Malacostraca	Varunidae	<i>Eriocheir sinensis</i>	Chinese mitten crab	12268	Sun et al. (2005)

Data are organized by class. Genome ID is the NCBI access code for the genome.

*Sequence without published paper

TABLE A-II
Genes: Characterization of form of *Vtg* gene: number of introns, exons, RNA length, and the number of amino acids from the deduced protein

No.	Class	Family	Organism	Common name	Tissue	mRNA	<i>Vtg</i> Gen	Gen bp	Introns	Exons	mRNA bp	ORF bp	AA bp	Access Nuc	Access AA	Reference
	Branchiopoda	Daphniidae	<i>Daphnia magna</i>	Common water fleas	Genome		dmagvtg1	ND	16	17	6335	6335	2001	AB114859	BAD05137	Tokishita et al. (2006)
1	Malacostraca	Palaemonidae	<i>Macrobrachium lanchesteri</i>	Prawn	Genome		ND	10432	14	15	7614	7614	2537	KX154220.1	AQX37249.1	Ngernsiri et al. (2017)
2	Malacostraca	Palaemonidae	<i>Metapenaeus ensis</i>	Shrimp	Ovary		Meg1	10900	14	15	8012	7779	2592	AF548364.1	AAN40701.1	Tsang et al. (2003)
3	Malacostraca	Penaeidae	<i>Penaeus monodon</i>	Black tiger shrimp	Hepatopancreas and ovary		PmVtg1	ND	14	15	7948	7755	2583	DQ288843.1	ABB89953.1	Teseng et al. (2001); Tiu et al. (2006b)
4	Malacostraca	Nephropidae	<i>Homarus americanus</i>	Lobster	Hepatopancreas		HaVtg1	ND	14	15	ND	7755	2583	EF422415.1	ABO09863.1	Tiu et al. (2009)
5	Malacostraca	Portunidae	<i>Charybdis feriata</i>	Crucifix crab	Ovary		Vtg1		14	15	8032	77400	2579	AY724676.1	AAU93694	Mak et al. (2005)
1	Branchiopoda	Daphniidae	<i>Daphnia magna</i>	Common water fleas	Genome		dmagvtg2	ND	16	17	6229	6009	2001	AB252738	BAE94324	Tokishita et al. (2006)
2	Malacostraca	Palaemonidae	<i>Metapenaeus ensis</i>	Shrimp	Hepatopancreas		Meg2	ND	12	13	7898	7883	2560	AY530205	AAT01139.1	Kung et al. (2004)
3	Malacostraca	Portunidae	<i>Scylla paramamosain</i>	Mud Crab	Testis		Vtg2	10329	11	12	7071	7071	2356	KU987908.1	ARI46323.1	Yang et al. (2016)

Vtg Gen, name assigned to the Vitellogenin gene; Gen bp, size in base pairs of genes described for Vitellogenin; Introns, number of introns reported; Exons, number of exons reported; mRNA bp, Messenger RNA base pairs; ORF bp, Open reading frame base pairs; AA bp, number of amino acids; Access Nuc, NCBI accession code for nucleic acids; Access AA, NCBI accession code for amino acids.

TABLE A-III
Vtg mRNA: mRNA length, ORF, number of amino acids from the deduced protein, and the tissue of origin

No.	Nuc acid	Class	Family	Organism	Common name	Tissue	mRNA pb	ORF	pb	AA	pb	Access Nuc	Access AA	Reference
1	Genome	Branchiopoda	Daphniidae	<i>Daphnia magna</i>	<i>Vtg1</i> Common water fleas	Genome	ND	ND	2000	ND	UniProtKB—Q766D3 (Q766D3_9CRUS)	UniProtKB—Q766D3 (Q766D3_9CRUS)	Tokishita et al. (2006)	
2	Genome	Branchiopoda	Daphniidae	<i>Daphnia magna</i>	<i>Vtg2</i> Common water fleas	Genome	6029	6009	2002	6009	BAE94324.1 UniProtKB—Q1JUB0. EDB	BAE94324.1 UniProtKB—Q1JUB0. EDB	Tokishita et al. (2007)	
3	Genome	Branchiopoda	Daphniidae	<i>Daphnia pulex</i>	<i>Vtg1</i> Common water fleas	Genome	6000	6000	1999	6000	GL733346 EFX62844	GL733346 EFX62844	Colbourne et al. (2011)	
1	mRNA	Hexanauplia	Temoridae	<i>Tigriopus japonicus</i>	Copepod	mRNA TSNR	5692	5529	1842	5529	EU416312.1 ABZ91537.1	EU416312.1 ABZ91537.1	Lee et al. (2008)	
2	mRNA	Hexanauplia	Temoridae	<i>Eurytemora affinis</i>	Copepod	mRNA TSNR	5419	5310	1769	5310	JX402134.1 AGH68974.1	JX402134.1 AGH68974.1	Xuereb et al. (2012)	
3	mRNA	Hexanauplia	Cyclopoidae	<i>Paracyclops nana</i> <i>Vtg 1</i>	Cyclopoid copepod	Complete organism	5889	5718	1905	5718	GQ205415.1 ADD73551.1	GQ205415.1 ADD73551.1	Hwang et al. (2010)	
4	mRNA	Hexanauplia	Cyclopoidae	<i>Paracyclops nana</i> <i>Vtg 2</i>	Cyclopoid copepod	Complete organism	5590	5442	1813	5442	GQ205416.1 ADD73552	GQ205416.1 ADD73552	Hwang et al. (2010)	
5	Genome	Hexanauplia	Harpacticidae	<i>Tigriopus kingsejongensis</i> <i>Vtg 1</i>	Antarctic-copepod endemic	mRNA TSNR	5698	5568	1855	5568	KT367518.1 ALO75636.1	KT367518.1 ALO75636.1	Kang et al. (2017)	
6	mRNA	Hexanauplia	Harpacticidae	<i>Tigriopus kingsejongensis</i> <i>Vtg 2</i>	Antarctic-copepod endemic	mRNA TSNR	5520	5388	1795	5388	KT367519.1 ALO75637.1	KT367519.1 ALO75637.1	Kang et al. (2017)	
7	mRNA	Hexanauplia	Caligidae	<i>Lepeophtheirus salmonis</i> <i>Vtg 1</i>	Salmon louse	Complete organism	6093	5898	1965	5898	EF490954.1 ABU41134.1	EF490954.1 ABU41134.1	Eichner et al. (2008)	
8	mRNA	Hexanauplia	Caligidae	<i>Lepeophtheirus salmonis</i> <i>Vtg 2</i>	Salmon louse	Complete organism	5948	5712	1903	5712	EF490955.1 ABU41135.1	EF490955.1 ABU41135.1	Eichner et al. (2008)	
1	mRNA	Malacostraca	Penaeidae	<i>Penaeus merguensis</i>	Banana shrimp	Ovary	7961	7761	2586	7761	AY499620.2 AAR88442.2	AY499620.2 AAR88442.2	Phiriyangkul et al. (2007)	
2	mRNA	Malacostraca	Penaeidae	<i>Penaeus merguensis</i>	Banana shrimp	Hepatopancreas	7958	7764	2587	7764	F1644568.1 ACV32381.1	F1644568.1 ACV32381.1	Puengyam and Utarabhand (2009)*	
3	mRNA	Malacostraca	Penaeidae	<i>Penaeus semisulcatus</i>	Green tiger prawn	Ovary	7920	7764	2587	7764	AY051318.3 AAL12620.3	AY051318.3 AAL12620.3	Averre et al. (2003)	
4	mRNA	Malacostraca	Penaeidae	<i>Penaeus chinensis</i>	Chinese white shrimp	Hepatopancreas and Ovary	7956	7764	2587	7764	DQ354690.1 ABC86571.1	DQ354690.1 ABC86571.1	Xie et al. (2009)	
5	mRNA	Malacostraca	Penaeidae	<i>Penaeus vannamei</i>	Pacific White Shrimp	Hepatopancreas and Ovary	7970	7764	2587	7764	AY321153.2 AAP76571.2	AY321153.2 AAP76571.2	Raviv et al (2006)	
6	mRNA	Malacostraca	Penaeidae	<i>Penaeus japonicus</i>	Kuruma prawn	Hepatopancreas	7931	7764	2584	7764	AB176641.1 BAD98732.1	AB176641.1 BAD98732.1	Tsutsui et al. (2005)	

TABLE A-III
(Continued)

No.	Nuc acid	Class	Family	Organism	Common name	Tissue	mRNA pb	ORF pb	AA pb	Access Nuc	Access AA	Reference
7	mRNA	Malacostraca	Penaeidae	<i>Penaeus japonicus</i>	Kuruma prawn	Hepatopancreas and Ovary	7970	7764	2597	AB033719.1	BAB01568.1	Tsutsui et al. (2006)
8	mRNA	Malacostraca	Penaeidae	<i>Penaeus monodon</i>	Black tiger shrimp	Hepatopancreas and ovary	7948	7755	2584	DQ288843.1	ABB89953.1	Tiu et al. (2006b)
9	Gene	Malacostraca	Penaeidae	<i>Metapenaeus ensis</i>	Greasyback shrimp	Ovary	7980	7779	2592	AF548363.1	AAN40700.1	Tsang et al. (2003)
10	mRNA	Malacostraca	Penaeidae	<i>Metapenaeus ensis</i> Vig 1A	Greasyback shrimp	Ovary	8012	7779	2592	AF548364.1	AAN40701.1	Tsang et al. (2003)
11	mRNA	Malacostraca	Penaeidae	<i>Metapenaeus ensis</i> Vig 1	Greasyback shrimp	Vig 1 TSNR	7967	7752	2583	AY103478.1	AAM48287.1	Tsang et al. (2003); Kung et al. (2004)
12	mRNA	Malacostraca	Penaeidae	<i>Metapenaeus ensis</i> Vig2	Greasyback shrimp	Hepatopancreas	7898	7683	2560	AY530205.1	AAT01139.1	Kung et al. (2004)
13	mRNA	Malacostraca	Palaemonidae	<i>Macrobracon nipponense</i>	Greasyback shrimp	Ovary and Testis	7808	7611	2536	KJ768657.1	AJP60219.1	Bai et al. (2005)
14	mRNA	Malacostraca	Palaemonidae	<i>Macrobracon nipponense</i>	Giant freshwater prawn	Hepatopancreas	7782	7614	2537	AB056458.1	BAB69831.1	Yang et al. (2000)
15	Gene	Malacostraca	Palaemonidae	<i>rosenbergii lancesteri</i>	Prawn	Genome	7614	7614	2537	KX154220.1	AQX37249.1	Ngernsiri et al. (2017)
16	mRNA	Malacostraca	Palaemonidae	<i>carinicauda</i>	Shrimp	mRNA TSNR	7841	7632	2543	JQ319034.1	AFM82474.1	Liang et al. (2011)
17	mRNA	Malacostraca	Pandalidae	<i>Pandalus hypsinotus</i>	Coon-striped shrimp	Hepatopancreas	7827	7605	2534	AB117524.1	BAD11098.1	Tsutsui et al. (2004)
18	mRNA	Malacostraca	Pandalidae	<i>Pandalopsis japonica</i> Vig 1	Shrimp	mRNA TSNR	7791	7710	2533	GQ476736.2	ACU51164.1	Lee et al. (2008)
19	mRNA	Malacostraca	Pandalidae	<i>Pandalopsis japonica</i> Vig 2	Shrimp	Hepatopancreas	7792	7614	2537	KF731996.1	AHD26978.1	Jeon et al. (2010)
20	mRNA	Malacostraca	Parastacidae	<i>Cherax quadricarinatus</i>	Australian red claw crayfish	Hepatopancreas	7944	7755	2584	AF306784.1	AAG17936.1	Abdu et al. (2002)
21	mRNA	Malacostraca	Nephropidae	<i>Homarus americanus</i>	American lobster	Hepatopancreas	8518	7752	2583	EF422415.1	ABO09863.1	Tiu et al. (2009)
22	mRNA	Malacostraca	Upogebiidae	<i>Upogebia major</i>	Mud shrimp	Hepatopancreas	7799	7707	2568	AB365125.1	BAF91417.1	Kang et al. (2008)
23	mRNA	Malacostraca	Portunidae	<i>Callinectes sapidus</i>	Blue crab	Hepatopancreas	7833	7692	2563	DQ314748.1	ABC41925.1	Zmora et al. (2007)

TABLE A-III
(Continued)

No.	Nuc acid	Class	Family	Organism	Common name	Tissue	mRNA pb	ORF pb	AA pb	Acces Nuc	Acces AA	Reference
24	mRNA	Malacostraca	Portunidae	<i>Callinectes sapidus</i>	Blue crab	Ovary	7881	7695	2564	JF719908.1	AEI59132.1	Thongda et al. (2015)
25	mRNA	Malacostraca	Portunidae	<i>Scylla paramamosain</i>	Green mud crab	Spermatozoon	8316	7071	2356	KJ923433.1	AKB93368.1	Yang et al. (2016)
26	mRNA	Malacostraca	Portunidae	<i>Scylla paramamosain 1</i>	Green mud crab	Spermatozoon	7816	7683	2560	FJ812090.1	ACO36035.1	Yang et al. (2016)
27	mRNA	Malacostraca	Portunidae	<i>Scylla paramamosain2</i>	Green mud crab	mRNA TSNR	7809	7683	2560	KC734559.1	AGN96208.1	Yang et al. (2016)
28	Gene	Malacostraca	Portunidae	<i>Scylla paramamosain</i> Vtg 2	Mud Crab	Testis	7071	7071	2356	KU987908.1	ARI46323.1	Yang et al. (2016)
29	mRNA	Malacostraca	Varunidae	<i>Eriocheir sinensis</i>	Chinese mitten crab	mRNA TSNR	7921	7689	2562	KC699915.1	AGM75775.1	Qiu et al. (2013)
30	mRNA	Malacostraca	Portunidae	<i>Charybdis feriatus</i>	Red crab	Hepatopancreas	8032	7740	2579	AY724676.1	AAU93694.1	Mak et al. (2005)
31	mRNA	Malacostraca	Potamidae	<i>Longopotamon honanense</i>	Crab	Ovary	7764	7701	2566	KP319023.1	AKI23633.1	Yang and Liu (2014)
32	mRNA	Malacostraca	Portunidae	<i>Portunus trituberculatus</i>	Swimming crab	Hepatopancreas	7846	7683	2560	DQ000638.1	AAX94762.1	Yang et al. (2005)
33	mRNA	Malacostraca	Varunidae	<i>Eriocheir sinensis</i>	Chinese mitten crab	Hepatopancreas and Ovary	7939	7707	2568	MF043589.1	ASW18692.1	Le et al. (2017)
34	mRNA	Malacostraca	Squillidae	<i>Oratosquilla oratoria</i>	Mantis shrimp	mRNA TSNR	7686	7521	2506	KR422400.1	ALI16501.1	Zhang (2015)

Data are organized by class. mRNA bp, messenger RNA base pairs; mRNA TSNR, mRNA tissue not reported or published; Vtg 1 TSNR, Vitellogenin 1 tissue not reported or published; ORF bp, open reading frame base pairs; AA pb, amino acid base pairs; Acces Nuc, NCBI accession code for nucleic acids; Acces AA, NCBI accession code for amino acids.
* Sequence without published paper.

TABLE A-IV

Transcriptome: Available transcriptomes from different decapod species; tissue of the transcriptome and the technology applied to obtain it

No.	Class	Family	Organism	Emb	Lv	Ad	HpF	HpM	Ov	Ts	Next generation sequence	Reference
1	Branchiopoda	Daphniidae	<i>Daphnia magna</i>	*	–	–	–	–	–	–	Illumina MiSeq	Lai et al. (2016)
2	Branchiopoda	Daphniidae	<i>Daphnia magna</i>	–	–	–	–	–	*	–	Microarray	Toyota et al. (2016)
3	Hexanauplia	Balanidae	<i>Balanus amphitrite</i>	–	*	*	–	–	–	–	454 pyrosequencing	Chen et al. (2011)
4	Hexanauplia	Caligidae	<i>Caligus rogercresseyi</i>	–	–	Vg1-Vg2	–	–	–	–	Illumina Seq Platforms	Chávez-Mardones et al. (2015)
5	Malacostraca	Varunidae	<i>Eriocheir sinensis</i>	–	–	Mal>Fem	–	–	–	–	Ion Proton Sequencer	Liu et al. (2015)
6	Malacostraca	Penaeidae	<i>Penaeus vannamei</i>	–	–	–	–	–	*	–	454 pyrosequencing	Ventura-López et al. (2017)
7	Malacostraca	Palaemonidae	<i>Palaemonetes pugio</i>	–	–	–	–	–	–	–	Microarray	Li et al. (2013)
8	Malacostraca	Cambaridae	<i>Procambarus clarkii</i>	–	–	–	–	–	5	3	454 GS FLX system	Jiang et al., 2014)
9	Malacostraca	Cambaridae	<i>Procambarus clarkii</i>	–	–	–	14	–	6	–	Illumina HiSeq2000	Shen et al. (2014)
10	Malacostraca	Gammaridae	<i>Echinogammarus marinus</i>	–	–	–	Vg1	Vg1	Vg1-Vg2	454 GS-Flx titanium	–	Short et al. (2014)
11	Malacostraca	Nephropidae	<i>Nephrops norvegicus</i>	–	–	–	8	–	*	–	Illumina NextSeq 500	Rotllant et al. (2017)
12	Malacostraca	Portunidae	<i>Portunus trituberculatus</i>	–	–	–	9 AlSp	–	*	–	Illumina HiSeq2000	Yang et al. (2015)

Data are organized by class. Emb, embryo; Lv, larva; Ad, adult, HpF, hepatopancreas female; HpM, hepatopancreas male; Ov, ovary; Ts, testis; –, undetermined; Vg1, Vitellogenin 1 mRNA; Vg2, Vitellogenin 2 mRNA; Mal>Fem, Vtg mRNA is greater in males Vs to females; 9 AlSp, amount of Vitellogenin mRNA identified with alternative splicing; 8, number of Vitellogenin transcripts identified by tissue.

* mRNA expression.

TABLE A-V
Vtg aporation: Tissue with greater contribution of Vtg of different species of crustaceans

No.	Class	Infraorder	Family	Species	Ov	Hp	Reference
1	Malacostraca	Dendrobranchiata (Suborder)	Penaeidae	<i>Penaeus japonicus</i>	*		Yano and Chinzei (1987)
2	Malacostraca	Dendrobranchiata (Suborder)	Penaeidae	<i>Penaeus merguensis</i>	*	*	Tsutsui et al. (2000) Okumura et al. (2007) Phiriyangkul et al. (2007)
3	Malacostraca	Dendrobranchiata (Suborder)	Penaeidae	<i>Penaeus vannamei</i>	*		Avarre et al. (2003)
4	Malacostraca	Dendrobranchiata (Suborder)	Penaeidae	<i>Penaeus monodon</i>	**	*	Raviv et al. (2006) Tiu et al. (2006b)
5	Malacostraca	Dendrobranchiata (Suborder)	Penaeidae	<i>Penaeus semisulcatus</i>	*		Tseng et al. (2001) Tseng et al. (2001)
6	Malacostraca	Dendrobranchiata (Suborder)	Penaeidae	<i>Metapenaeus ensis</i>	*	*	Tsang et al. (2003)
7	Malacostraca	Dendrobranchiata (Suborder)	Sicyoniidae	<i>Sicyonia ingentis</i>	**		Tsukimura (2001)
8	Malacostraca	Caridea	Palaemonoidae	<i>Macrobrachium rosenbergii</i>	*		Jayasankar et al. (2002)
9	Malacostraca	Caridea	Palaemonoidae	<i>Macrobrachium nipponense</i>	*		Bai et al. (2015)
10	Malacostraca	Caridea	Pandalidae	<i>Pandalus hypsinotus</i>		*	Tsutsui et al. (2004)
11	Malacostraca	Astacidea	Cambaridae	<i>Procambarus clarkii</i>		*	Wolin et al. (1973)
12	Malacostraca	Astacidea	Parastacidae	<i>Cherax quadricarinatus</i>		*	Serrano-Pinto et al. (2004)
13	Malacostraca	Brachyura	Epialtidae	<i>Libinia emarginata</i>		*	Wolin et al. (1973); Paulus and Laufer (1987)

TABLE A-V
(Continued)

No.	Class	Infraorder	Family	Species	Ov	Hp	Reference
14	Malacostraca	Brachyura	Portunidae	<i>Callinectes sapidus</i>	*	*	Zmora et al. (2007) Thongda et al. (2015)
15	Malacostraca	Brachyura	Portunidae	<i>Scylla serrata</i>		*	Warrier and Subramoniam (2002)
16	Malacostraca	Brachyura	Portunidae	<i>Scylla paramamosain</i>	**	*	Jia et al. (2013)
17	Malacostraca	Brachyura	Portunidae	<i>Charybdis feriata</i>		*	Mak et al. (2005)
18	Malacostraca	Brachyura	Portunidae	<i>Portunus trituberculatus</i>		*	Yang et al. (2005)
19	Malacostraca	Brachyura	Carcinidae	<i>Carcinus maenas</i>		*	Paulus and Laufer (1987)
20	Malacostraca	Brachyura	Ocypodidae	<i>Leptuca pugilator</i>		*	Wolin et al. (1973)
					*		Eastman-Reks and Fingerman (1985)
21	Malacostraca	Brachyura	Grapsidae	<i>Pachygrapsus crassipes</i>	*		Lui and O'Connor (1977)

* The major apportionment site.

** Equal contribution in both sites.

TABLE A-VI
Vtg domains: Positions of the different domains in each *Vtg* sequence available from crustacean species

No. Class	Family	Organism	Source	Vitellogenin_N	DUF1943	DUF1081	DUF445	Ferritin_like	VWD	C8	AA	Access No.	Reference
1	Branchiopoda Daphniidae	<i>Daphnia magna</i> Vtg1	Genome	253..961	998..1268	—	—	—	168..1895	—	2000	UniProtKB — Q766D3 (Q766D3_9CRUS)	Tokishita et al. (2006)
2	Branchiopoda Daphniidae	<i>Daphnia magna</i> Vtg2	Genome	254..962	999..1275	—	—	—	1684..1841	—	2002	UniProtKB — Q1UUB0.EDB	Tokishita et al. (2007)
3	Branchiopoda Daphniidae	<i>Daphnia pulex</i> Vtg1	Genome	251..959	996..1272	—	—	—	1681..1838	—	1999	EFX62844	Colbourne et al. (2011)
1	Hexanauplia Temoridae	<i>Eurytemora affinis</i> Vtg1	ND	20..696	745..992	—	—	—	1457..1618	—	1769	AGH68974.1	Xuerb et al. (2012)
2	Hexanauplia Temoridae	<i>Tigriopus japonicus</i>	ND	24..716	748..1028	—	—	—	1511..1677	—	1842	ABZ91537.1	Lee et al. (2008)
3	Hexanauplia Cyclopoidae	<i>Paracyclops</i> <i>nana</i> Vtg1	CoOrg	24..774	848..1086	—	—	—	1571..1739	—	1905	ADD73551.1	Hwang et al. (2010)
4	Hexanauplia Cyclopoidae	<i>Paracyclops</i> <i>nana</i> Vtg2	CoOrg	22..696	741..1036	—	—	—	1481..1657	—	1813	ADD73552	Hwang et al. (2010)
5	Hexanauplia Harpacticidae	<i>Tigriopus</i> <i>kingsejongensis</i> Vtg1	mRNA	24..725	757..1032	—	—	—	1517..1688	—	1855	ALO75636.1	Kang et al. (2017)
6	Hexanauplia Harpacticidae	<i>Tigriopus</i> <i>kingsejongensis</i> Vtg 2	mRNA	32..716	761..1046	—	—	—	1476..1629	—	1795	ALO75637.1	Kang et al. (2017)
7	Hexanauplia Caligidae	<i>Lepeophtheirus salmonis</i> Vtg 1	CoOrg	24..750	782..1069	—	—	—	1578..1771	—	1965	ABU41134.1	Eichner et al. (2008)
8	Hexanauplia Caligidae	<i>Lepeophtheirus salmonis</i> Vtg 2	CoOrg	22..713	758..1103	—	—	—	1551..1705	—	1903	ABU41135.1	Eichner et al. (2008)
1	Malacostraca Penaeidae	<i>Penaeus merguensis</i>	Ovary	42..585	617..925	949..1047	—	—	2356..2496	2532..2578	2586	AAR88442.2	Phiriyangkul et al. (2007)
2	Malacostraca Penaeidae	<i>Penaeus merguensis</i>	Hepat	42..585	618..926	950..1048	—	—	2348..2497	2533..2579	2587	ACV32381.1	Puengyam and Utairabhand (2009)*
3	Malacostraca Penaeidae	<i>Penaeus semisulcatus</i>	Ovary	42..585	618..926	949..1048	—	—	2357..2497	2533..2579	2587	AAL12620.3	Averre et al. (2003)
4	Malacostraca Penaeidae	<i>Penaeus chinensis</i>	Hepat Ovary	42..585	618..926	950..1048	—	—	2357..2497	—	2587	ABC86571.1	Xie et al. (2009)
5	Malacostraca Penaeidae	<i>Penaeus vannamei</i>	Hepat Ovary	42..585	618..926	947..1048	—	—	2351..2497	—	2587	AAP76571.2	Raviv et al. (2006)
6	Malacostraca Penaeidae	<i>Penaeus vannamei</i>	Ovary	42..585	618..926	947..1048	—	—	181..247	323..369	377 Partial	—	This study
7	Malacostraca Penaeidae	<i>Penaeus vannamei</i>	Hepat	42..585	618..920	—	—	—	—	—	2318 Partial	—	This study

TABLE A-VI
(Continued)

No. Class	Family	Organism	Source	Vitellogenin_N	DUF1943	DUF1081	DUF445	Ferritin_like	VWD	C8	AA	Access No.	Reference
8	Malacostraca Penaeidae	<i>Penaeus stylirostris</i>	Hepat Ovary	–	–	–	–	–	–	–	162 Partial		This study
9	Malacostraca Penaeidae	<i>Penaeus japonicus</i>	Hepat	42..585	618..926	–	–	–	2348..2497	2533..2579	2584	BAD98732.1	Tsutsui et al. (2005)
10	Malacostraca Penaeidae	<i>Penaeus japonicus</i>	Hepat Ovary	42..585	618..926	–	–	–	2358..2498	2533..2579	2597	BAB01568.1	Tsutsui et al. (2000)
11	Malacostraca Penaeidae	<i>Penaeus monodon</i>	Hepat Ovary	42..585	618..926	–	–	–	2354..2494	2530..2576	2584	ABB89953.1	Tiu et al. (2006b)
12	Malacostraca Penaeidae	<i>Metapenaeus ensis</i> Vtg 1	Hepat Ovary	42..585	620..926	948..1048	–	–	2357..2502	–	2592	AAN40701.1	Tsang et al. (2003)
13	Malacostraca Penaeidae	<i>Metapenaeus ensis</i> Vtg 2	ND	42..586	621..928	950..1050	–	–	2346..2491	–	2583	AAM48287.1	Tsang et al. (2003); Kung et al. (2004)
14	Malacostraca Penaeidae	<i>Metapenaeus ensis</i> Vtg 2	Hepat	42..586	619..928	–	–	–	2331..2470	–	2560	AAT01139.1	Kung et al. (2004)
15	Malacostraca Palaemonidae	<i>Macrobrachium nipponense</i>	Ovary- Testis	40..587	620..918	–	–	–	2304..2444	–	2536	AJP60219.1	Bai et al. (2005)
16	Malacostraca Palaemonidae	<i>Macrobrachium rosenbergii</i>	Hepat	41..588	621..919	–	–	–	2305..2445	–	2537	BAB69831.1	Yang et al. (2000)
17	Malacostraca Palaemonidae	<i>Macrobrachium lancesteri</i>	Genom	41..588	621..913	–	–	–	2305..2445	–	2537	AQX37249.1	Ngemsiiri et al. (2017)*
18	Malacostraca Palaemonidae	<i>Palaemon carinicauda</i>	ND	41..589	621..923	956..1038	–	–	2311..2451	–	2543	AFM82474.1	Liang et al. (2011)*
19	Malacostraca Pandalidae	<i>Pandulus hypsinotus</i>	Hepat	42..589	622..922	–	–	–	2302..2442	–	2534	BAD11098.1	Tsutsui et al. (2014)
21	Malacostraca Pandalidae	<i>Pandalopsis japonica</i> Vtg 2	Vtg2 Hepat	42..589	622..926	–	–	–	2302..2444	2483..2530	2537	AHD26978.1	Jeon et al. (2010)
22	Malacostraca Parastacidae	<i>Cherax quadricarinatus</i>	Hepat	42..585	617..932	954..1050	2049..2319	2095..2199	2345..2491	2530..2576	2584	AAG17936.1	Abdu et al. (2002)
23	Malacostraca Nephropidae	<i>Homarus americanus</i>	Hepat	42..588	621..930	955..1048	–	–	2351..2490	–	2583	ABO09863.1	Tiu et al. (2009)
24	Malacostraca Upogebiidae	<i>Upogebia major</i>	Hepat	41..582	615..922	–	–	–	2333..2475	–	2568	BAF91417.1	Kang et al. (2008)
25	Malacostraca Portunidae	<i>Callinectes sapidus</i>	Hepat	41..586	619..927	–	–	–	2332..2471	–	2563	ABC41925.1	Zmora et al. (2007)
26	Malacostraca Portunidae	<i>Callinectes sapidus</i>	Ovary	41..586	619..927	–	–	–	2333..2472	–	2564	AEI59132.1	Thongda et al. (2015)

TABLE A-VI
(Continued)

No.	Class	Family	Organism	Source	Vitellogenin_N	DUF1943	DUF1081	DUF445	Ferritin_like	VWD	C8	AA	Access No.	Reference
27	Malacostraca	Portunidae	<i>Callinectes toxotes</i>	Hepat Ovary	41..586	619..921	-	-	-	2329..2468	-	2560		This study
28	Malacostraca	Portunidae	<i>Callinectes arcuatus</i>	Hepat Ovary	41..587	619..922	-	-	-			1220 Partial		This study
29	Malacostraca	Portunidae	<i>Scylla paramamosain 1</i>	ND	40..585	618..919	-	-	-	2329..2468	-	2560	ACO36035.1	Yang et al. (2016)
30	Malacostraca	Portunidae	<i>Scylla paramamosain 2</i>	ND	40..585	618..919	-	-	-	2329..2468	-	2560	AGN96208.1	Yang et al. (2016)
31	Malacostraca	Portunidae	<i>Scylla paramamosain</i> Vtg 2	Testis	1..378	411..709	-	-	-	2125..2264	-	2356	ARI46323.1	Yang et al. (2016)
32	Malacostraca	Varunidae	<i>Eriocheir sinensis</i>	ND	41..587	620..926	-	-	-	2340..2471	-	2562	AGM75775.1	Qiu et al. (2013)*
33	Malacostraca	Portunidae	<i>Charybdis feritatus</i>	Hepat	40..585	618..923	-	-	-	2327..2487	-	2579	AAU93694.1	Mak et al. (2005)
34	Malacostraca	Potamidae	<i>Longopan</i>	Ovary	41..587	620..925	-	-	-	2335..2475	-	2566	AKI23633.1	Yang and Liu (2014)
35	Malacostraca	Portunidae	<i>honanense</i> <i>Portunus trituberculatus</i>	Hepat	41..584	617..925	-	-	-	2329..2469	-	2560	AAAX94762.1	Yang et al. (2005)
36	Malacostraca	Varunidae	<i>Eriocheir sinensis</i>	Hepat Ovary	41..587	620..920	-	-	-	2344..2477	-	2568	ASW18692.1	Li et al. (2017)
37	Malacostraca	Squillidae	<i>Oratosquilla oratoria</i>	ND	41..589	621..926	954..1052	-	-	2334..2488	-	2506	ALI16501.1	Zhang (2015)*

Data are organized by class. Vitellogenin_N, lipoprotein amino terminal region, pfam01347; DUF1943, domain of unknown function 1943, pfam09172; DUF1081, domain of unknown function 1081), pfam06448; DUF445, protein of unknown function 445, pfam04286; Ferritin_like, ferritin-like superfamily of diiron-containing four-helix-bundle proteins, cl00264; VWD, von Willebrand factor type D domain, cl02516; C8, C8 domain, pfam08742; AA pb, amino acid base pairs; Acces No., NCBI accession code for nucleic acids; CoOrg, complete organism; Hepat, hepatopancreas; ND, not determined; * Sequence without published paper.

TABLE A-VII

Vtg regulation: Physiological factors and responses in regulation of reproduction in crustacean species

Factor	Effect	Reference
Juvenile organism	Absence of <i>Vtg</i> and <i>VIH</i>	This study
Ovary development (I-IV)	Decreases <i>VIH</i> levels	Okumura (2007)
	Increase proportionally <i>Vtg</i> mRNA and <i>Vtg</i> synthesis	Kung et al. (2004); Thongda et al. (2007)
	Increase <i>MIH</i> levels, without significant changes in <i>MIH</i> expression	Zmora et al. (2009)
<i>VIH</i>	Affects <i>Vtg</i> expression depending on the ovarian-stage	This study; Bae et al. (2017)
Ecdysis (moult)	Does not occur at the same time as the reproduction	Zmora et al. (2009)
	Increase <i>Vtg</i> expression at initial maturation stages	Gong et al. (2015)
	Decrease <i>Vtg</i> expression days before the moult	Jayasankar et al. (2002)
Post-moult	Upregulation of <i>Vtg</i>	Avarre et al. (2003)
<i>MIH</i>	Negatively regulates ecdysteroidogenesis	Bae et al. (2017)
	Suppresses the Y organ	Zmora et al. (2009); Das et al. (2018)
High Ca ²⁺ concentrations	Abolish <i>MIH</i> effects, due to the enhanced degradation of cAMP.	Bae et al. (2017); Das et al. (2018)
Increasing <i>EcR</i> mRNA	Parallely increase <i>Vtg</i> levels until ovary stage III.	Gong et al. (2015)

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