

Evolution and functionalization of *Vitellogenin* genes in the termite *Reticulitermes speratus*

Short running title: Evolution of *Vitellogenin* genes in termites

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23 Abstract

24

25 Eusociality has been commonly observed in distinct animal lineages. The reproductive division of
26 labour is a particular feature, achieved by the coordination between fertile and sterile castes within the
27 same nest. The sociogenomic approach in social hymenopteran insects indicates that *vitellogenin* (*Vg*)
28 has undergone neo-functionalisation in sterile castes. Here, to know whether *Vgs* have distinct roles in
29 non-reproductive castes in termites, we investigated the unique characteristics of *Vgs* in the
30 rhinotermitid termite *Reticulitermes speratus*. The four *Vgs* were identified from *R. speratus* (*RsVg1-*
31 *4*), and *RsVg3* sequences were newly identified using the RACE method. Molecular phylogenetic
32 analysis supported the monophyly of the four termite *Vgs*. Moreover, the termites *Vg1-3* and *Vg4* were
33 positioned in two different clades. The *dN / dS* ratios indicated that the branch leading to the common
34 ancestor of termite *Vg4* was under weak purifying selection. Expression analyses among castes
35 (reproductives, workers, and soldiers) and females (nymphs, winged alates, and queens) showed that
36 *RsVg1-3* were highly expressed in fertile queens. In contrast, *RsVg4* was highly expressed in workers
37 and female non-reproductives (nymphs and winged adults). Localisation of *RsVg4* mRNA was
38 confirmed in the fat body of worker heads and abdomens. These results suggest that *Vg* genes are
39 functionalised after gene duplication during termite eusocial transition and that *Vg4* is involved in non-

40 reproductive roles in termites.

41

42 Keywords

43 eusocial insects, reproductive division of labour, vitellogenin, molecular evolution, gene expression

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46 Introduction

47

48 Eusociality is primarily characterised by the reproductive division of labour between fertile and sterile
49 castes within the same nest (Wilson, 2000). It has repeatedly evolved in several lineages, including
50 those of ants, bees, wasps, and termites. Reproduction is generally monopolised by one or a few fertile
51 individuals, whereas other tasks are performed by sterile individuals without activated gonads. The
52 genetic background is fundamentally shared among individuals in a nest, and phenotypic plasticity
53 leads to evolutionary success that accompanies their task specialisation for colony survival and growth
54 (e.g. O'Shea-Wheller *et al.*, 2021). Importantly, sterile castes are assumed to be evolutionary novelties
55 derived during the process of eusocial evolution from the solitary ancestor (Korb and Heinze, 2004).
56 Therefore, understanding the molecular mechanisms of the altruistic roles of sterile castes is a
57 fundamental research goal in evolutionary biology. In social Hymenoptera, important regulators
58 involved in social behaviours and caste differentiation were identified based on genomic and
59 transcriptomic analyses. These studies suggest that conserved genes have different functions from their
60 original roles during social evolution (Toth and Rehan, 2017). One of the best-studied genes with these
61 features is *vitellogenin* (Richards, 2019), which is a socially pleiotropic gene with different functions
62 in the reproductive and non-reproductive castes (see below).

63

64 Vitellogenin (Vg) is a major yolk precursor in most oviparous animals and is involved in ovary

65 development (Wahli, 1988; Raikhel and Dhadialla, 1992). In insects, *Vg* genes are generally expressed
66 in the fat body of adult females, and the related proteins are transported into the oocytes for storage
67 (Tufail and Takeda, 2008). Another feature is that behavioural transitions (e.g. nurses to foragers) are
68 mediated by the difference in *Vg* expression patterns with worker age in the honey bee *Apis mellifera*
69 and the harvester ant *Pogonomyrmex barbatus* (Amdam *et al.*, 2004; Nelson *et al.*, 2007; Corona *et*
70 *al.*, 2013). These studies suggest that *Vg* is a crucial regulator of worker-specific behaviours as well
71 as the reproductive maturity of queens among social hymenopteran insects. Based on the inferred
72 molecular phylogeny, *Vg* may be duplicated within formicid ant lineages (Corona *et al.*, 2013). The
73 duplicated genes have been shown to be differentially expressed between queens and workers in *P.*
74 *barbatus* and the fire ant *Solenopsis invicta* (Wurm *et al.*, 2011; Corona *et al.*, 2013). In ants and honey
75 bees, three *Vg* homologs (*Vg-like-A*, *-B*, and *-C*), which may be important for worker-specific
76 behaviour and physiology, were also identified (Kohlmeier *et al.* 2018; Miyazaki *et al.* 2021; Morandin
77 *et al.*, 2014; Morandin *et al.*, 2019; Salmela *et al.*, 2016). The expression patterns of *Vg-like-A* and *-B*
78 were different between castes in each of seven *Formica* species, but those of *Vg-like-C* were
79 consistently highly expressed in workers (Morandin *et al.*, 2014). The existence of multiple *Vg*
80 homologs, some of which lost an ancestral function and acquired a new function, may be essential for
81 the evolution of highly sophisticated social organisation in ants (Friedman and Gordon, 2016). In other
82 eusocial lineages, including termites, however, little is known about whether the particular *Vg* gene
83 plays an important role in sterile castes.

85 Termites are hemimetabolous insects that evolved from a cockroach-like ancestor (e.g. Lo *et al.*, 2000;
86 Inward *et al.*, 2007). Contrary to social hymenopterans, termite primary reproductives (queen and king)
87 are adult individuals, but sterile castes, including soldiers and workers, are immature individuals
88 (Thorne, 1997). High *Vg* expression in female reproductives has been observed in several termite
89 species (reviewed in Korb, 2016). For example, *Vg* gene expression is positively correlated with
90 ovarian development in primary queens of the rhinotermitid termite *Reticulitermes speratus* (Ishitani
91 and Maekawa, 2010; Maekawa *et al.*, 2010). The *Vg* gene was also highly expressed in secondary
92 reproductives (differentiated from immature stages and succeeded in the reproductive role from
93 primary reproductives; Fig. S1) of *R. speratus* and the dry-wood termite *Cryptotermes secundus* (Weil
94 *et al.*, 2007; Saiki and Maekawa, 2011). The first termite species whose genome has been sequenced
95 is the damp-wood termite *Zootermopsis nevadensis*, in which the presence of four *Vg* genes have been
96 reported (Terrapon *et al.*, 2014). Three *Vgs* were highly expressed in female reproductives, and one
97 was moderately expressed in non-reproductive individuals (Terrapon *et al.*, 2014). This suggests the
98 different functions of *Vg* genes in different castes. Therefore, it is possible that termite *Vgs* have
99 alternative roles not only in reproductive regulation but also in non-reproductive traits. However,
100 further information is required to understand the molecular evolution and function of termite *Vg* genes;
101 for example, precise phylogenetic relationships and expression pattern/localisation should be
102 identified.

103

104 In the present study, to obtain additional information on termite *Vg* genes, we focused on *R. speratus*,
105 for which whole genome sequences have recently been made available (NCBI Submission
106 DRA010978; BioProject Accession PRJDB2984, Shigenobu *et al.*, 2022). First, the *Vg* genes of *R.*
107 *speratus* (*RsVgs*) were identified from the genome, and a precise molecular phylogenetic tree was
108 constructed to determine the evolutionary relationships among multiple *RsVgs* with other
109 termite/insect *Vgs*. Second, the expression levels of *RsVgs* were investigated using RNA-seq data from
110 reproductive, worker, and soldier castes (NCBI BioProject Accession PRJDB5589, Shigenobu *et al.*,
111 2022). Third, to determine whether there were any relationships between *RsVgs* expression and
112 reproductive cycle in *R. speratus* queens, colony development was observed, and expression levels
113 were examined by real-time quantitative PCR. Finally, to localise the mRNA of *RsVg1* and *RsVg4*, *in*
114 *situ* hybridisation was performed in queens and workers. Based on the results obtained, we suggest
115 that termite *Vgs* are functionalised after gene duplication and *RsVg4* is involved in non-reproductive
116 role in *R. speratus*.

117

118 Materials and Methods

119

120 Termites

121

122 Mature colonies of *R. speratus* were collected in Toyama Prefecture, Japan, from 2015 to 2017. The
123 collected colonies were maintained in plastic boxes and kept at 25 °C in constant darkness. This species
124 has terminal workers (wingless immature), which occasionally differentiate into soldiers via
125 presoldiers and secondary reproductives (Roisin, 2000). Secondary reproductives are differentiated
126 from workers and nymphs (Fig. S1), and succeeded in the reproductive role when the primary
127 reproductives die or become senescent (Thorne, 1997; Roisin, 2000). The nymphs (winged immature)
128 can differentiate into winged alates and become the primary reproductives, and sometimes, secondary
129 reproductives (Roisin, 2000; Saiki and Maekawa, 2011) (Fig. S1). It was impossible to collect all
130 individuals from colonies with the constant social environment and resource availability. Workers,
131 soldiers, and nymphs were sampled from mature colonies. Primary reproductives (queens and kings)
132 were collected from the incipient colonies, which were established using alates (winged adults) derived
133 from different mature colonies in accordance with previous studies (Maekawa *et al.*, 2010; Shimada
134 and Maekawa, 2010; Miyazaki *et al.*, 2014) (see below). The sampled individuals were classified into
135 W4 workers (6th instar, Fig. S1), W5 workers (7th instar), N6 nymphs (8th instar), alates, and primary
136 reproductives, and separated into sex based on genital plates (Weesner, 1969).

137
138 Identification of vitellogenin (Vg) gene from *R. speratus* genome

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140 The Vg amino acid sequences were obtained from *Z. nevadensis* (Terrapon *et al.*, 2014) and other

141 insect protein databases. The similarity search was performed by blastP (evalue < 1.0E-05) using the
142 sequences obtained from the *R. speratus* protein database (Rspe OGS 1.0; Shigenobu *et al.*, 2022). Of
143 the *Vg* sequences identified, *RsVg3* (gene ID: RS013977) mRNA was determined by 3'-rapid
144 amplification of cDNA ends (3'-RACE) because the fragment of *RsVg3* (RS013977; 2217 bp) was
145 incomplete at the 3' site (see Results). The primer sequences were designed from the obtained *RsVg3*
146 sequence using the web interface Primer3Plus (Untergasser *et al.*, 2007) to determine the sequence of
147 the full-length *RsVg3* (Table S1). Total RNA was extracted from the whole body of a female secondary
148 reproductive collected from mature colonies using ISOGEN II (Nippon Gene, Tokyo, Japan). The
149 extracted RNA was purified using DNase I treatment to remove genomic DNA. The quality and
150 quantity of purified RNA were measured using a NanoVue spectrophotometer (GE Healthcare Bio-
151 Sciences, Tokyo, Japan). The cDNA was synthesised using the SMARTer™ RACE cDNA
152 Amplification kit (Clontech Laboratories, Mountain View, CA, USA) in accordance with a previous
153 study (Hojo *et al.*, 2011). The obtained 3' RACE products were purified using the QIAquick Gel
154 Extraction Kit (Qiagen, Tokyo, Japan), subcloned into a pGEM easy T-vector (Promega, Madison, WI,
155 USA), and transfected into *Escherichia coli* XL1-blue. Plasmids, including DNA fragments, were
156 extracted from a single colony of *E. coli* using the SIGMA GelElute™ Plasmid Miniprep Kit (Sigma-
157 Aldrich, St Louis, MO, USA). The inserted DNA sequence was determined using the BigDye
158 Terminator v3.1 Cycle Sequencing kit (Applied Biosystems, Foster City, CA, USA) with an automatic
159 DNA Sequencer 3130 Genetic Analyzer (Applied Biosystems). The obtained sequence was confirmed

160 by a BLAST search and deposited in the DDBJ/EMBL/GenBank databases (accession no. LC621340).

161

162 Molecular phylogenetic analyses of *Vg* genes

163

164 The amino acid sequences of *Vg*, *Vg*-like apolipocrustacein (*ApoCr*) and insect apolipophorin II/I

165 (*apoLp-II/I*) were obtained from NCBI, in accordance with previous studies (Avarre *et al.*, 2007; Tufail

166 and Takeda, 2008; Hayward *et al.*, 2010; Morandin *et al.*, 2014; Roy-Zokan *et al.*, 2015; Salmela *et*

167 *al.*, 2016; Shang *et al.*, 2017). According to these reports (Avarre *et al.*, 2007; Hayward *et al.*, 2010),

168 the *ApoCr* and *apoLp-II/I* sequences were used as outgroups. The DNA and/or amino acid sequences

169 were obtained from the appropriate databases and related references (Table S2). The obtained

170 sequences (286-3380 aa) were aligned using MAFFT with the option ‘auto’ (FFT-NS-i strategy) (Katoh

171 and Standley, 2013). The aligned sequence sets (Supplementary data) were processed using trimAl

172 v1.2 rev59 with the option ‘automated1’ (Capella-Gutierrez *et al.*, 2009). The molecular phylogenetic

173 tree and branch support values were estimated using two different methods. The neighbor-joining

174 method (Saitou and Nei, 1987) was used to construct the phylogenetic tree using MEGA7 (bootstrap

175 values: 5000, JTT model, pairwise deletion) (Kumar *et al.*, 2016). RAxML (Stamatakis, 2014) was

176 used for tree construction by the maximum likelihood method (bootstrap values: 1000). The amino

177 acid substitution models were estimated using MEGA7, and the LG + G model was selected (BIC,

178 26782.8213097696; lnL, -12549.156785332). The accession number or gene ID of each sequence is

179 shown in Table S2.

180

181 Molecular evolution of termite *Vg* genes

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183 To investigate the selection pressure at play on *Vg* genes in termites, each *Vg* gene from all termite
184 species and *C. punctulatus*, serving as an outgroup, were independently aligned. Termite *Vg1* (see
185 Results) alignment was missing *C. formosanus* species as *Vg1* was not present in this species, and
186 termite *Vg3* (see Results) was completely excluded since it was only present in termites and the use of
187 a cockroach outgroup was therefore impossible. To estimate overall dN/dS (ω) ratios of each *Vg* genes
188 in the termite clade, the null model (M0) from codeml in PAML (v4.9j) was used (Yang 2007). To
189 assume an independent ω ratio for each branch and to evaluate variation of ω ratio between the branch
190 of the termite most recent common ancestor and the other branches, a branch test was used. The branch
191 test from codeml consists of a log-likelihood ratio test following a χ^2 distribution of the null model
192 M0 with two models, a free-ratio model M1 and a two-ratio model M2.

193

194 *RsVg* gene expression analysis using RNA-seq data

195

196 RNA-seq data were used to compare the expression levels of *RsVgs* among three castes (workers,
197 soldiers, and reproductives), two body parts (heads and the remaining parts), and two sexes (biological

triplicates; Shigenobu *et al.*, 2022). Briefly, older workers (W4–5) and soldiers were sampled from natal colonies in accordance with their external morphology, and primary reproductives were sampled from incipient colonies established by female–male pairs. RNA-seq analyses were performed with 12 categories (castes \times sexes \times body parts) with three biological replicates (in total 36 libraries). Detailed procedures for the trimmed mean of M-values (TMM) normalization, reads per kilobase of exon per million mapped sequence reads (RPKM) calculation were based on a previous analysis (Shigenobu *et al.*, 2022). To examine differential expression among castes and between sexes, we modelled TMM-normalized counts per million (CPM) for each gene using a generalized linear mix model (GLMM) in which caste, sex and their interaction are treated as fixed effects and individual sample as random effects, using the R package glmmSeq v0.1.0 (<https://github.com/KatrionaGoldmann/glmmSeq>). A false discovery rate (FDR) of 0.05 was used as a threshold for statistical significance.

Measurements of egg numbers during incipient colony development

Incipient colonies were identified according to previous studies (Maekawa *et al.*, 2010; Shimada and Maekawa, 2010; Miyazaki *et al.*, 2014). Alates were collected from multiple mature colonies, and then the individuals were separated into sexes based on abdominal sternites (Weesner, 1969). Female and male de-winged individuals from different colonies were paired. Each pair was placed in a 20 mL glass vial with mixed sawdust food (Mitani, Ibaraki, Japan) and maintained at 25 °C in constant darkness.

217 Colonies were sampled after 0.5, 1.5, 2.5, 3.5, 4.5, 5.5, 6.5 and 7.5 months (9–60 colonies at each
218 point). The number of eggs produced by queens was counted from the sampled colonies at each time
219 point. The number of eggs was compared among the periods during colony development using the
220 Kruskal-Wallis test followed by the Steel-Dwass test (based on the results of Levene's test) with R
221 v.3.4.0 (R Core Team, 2017). The number of eggs during colony development was described with the
222 polynomial regression equation, and the degree was statistically compared by the analysis of variance
223 (ANOVA) among the constructed polynomial regression models using R v.4.0.3 (R core team, 2020).

224

225 *RsVg* gene expression analysis in queens during incipient colony development

226

227 Gene-specific primers were designed against the obtained *RsVg* sequences using Primer3Plus
228 (Untergasser *et al.*, 2007) for real-time quantitative PCR (Table S1). Total RNA was extracted from 3
229 different individuals (except for the head parts) and biological triplicates were prepared for each
230 developmental stage. Extracted RNA were purified by DNase treatment using the method described
231 previously. cDNA was synthesised from the purified RNA using a High-Capacity cDNA Reverse
232 Transcription Kit (Applied Biosystems). Expression analyses of *Vg* genes were performed using
233 Thunderbird SYBR qPCR Mix (Toyobo, Osaka, Japan) and Mx3005P Real-Time QPCR System
234 (Agilent Technologies, Santa Clara, CA, USA). To determine a sustainable internal control gene, the
235 suitability of six reference genes (Table S3), *EFl-alfa* (accession no. AB602838), *NADH-dh* (no.

236 AB602837), *β-actin* (no. AB520714), *GstD1* (gene ID: RS001168), *EIF-1* (RS005199), and *RPS18*
237 (RS015150) were used and evaluated using GeNorm (Vandesompele *et al.*, 2002) and NormFinder
238 (Andersen *et al.*, 2004) software. All gene-specific primers used in this analysis (Table S1) were
239 confirmed to amplify a single PCR product using the dissociation curves and product sizes. The
240 expression levels of *RsVgs* were statistically analysed using one-way ANOVA followed by Tukey's
241 multiple comparison test (based on the results of Levene's test) with R v.3.4.0. The expression levels
242 of *RsVgs* were described with the polynomial regression equation, and the degree was statistically
243 compared by ANOVA among the constructed polynomial regression models using R v.4.0.3.

244
245 Localisation of *RsVg1* mRNA in queens and *RsVg4* mRNA in workers

246
247 Gene-specific primers were designed against the obtained *RsVg1* and *RsVg4* sequences using
248 Primer3Plus (Untergasser *et al.*, 2007) for RNA probe synthesis (Table S1). The probe for *in situ*
249 hybridisation was prepared according to a previous study (Hojo *et al.* 2011). Total RNA was extracted
250 from whole bodies of five workers using ISOGEN II, and purified as described previously. cDNA was
251 synthesised as the method shown above and used for the amplification of *RsVg4* fragment. cDNA was
252 synthesised from the total RNA extracted from female secondary reproductives (see above), and used
253 for the amplification of *RsVg1* fragment. The amplified *RsVgs* fragment was subcloned, and inserted
254 DNA sequence was determined as described previously. The obtained sequence was confirmed to be

255 the target sequence of *RsVgs* by BLAST search. The digoxigenin (DIG)-labelled RNA probes of
256 *RsVg1* and *RsVg4* were prepared from plasmids containing *RsVgs* fragments using a DIG RNA
257 Labeling Kit (Roche, Basel, Switzerland). Three workers were separated into heads and bodies (thorax
258 and abdomen) by dissection, and each part was fixed with 4% paraformaldehyde and cryoprotected in
259 sucrose solution. A queen was collected 5.5 months after the incipient colonies were constructed, and
260 the body separated from the head was fixed and cryoprotected. The fixed samples were embedded in
261 OCT compound (Sakura Finetek USA Inc., Torrance, CA, USA) and sliced to prepare 14 µm thick
262 parasagittal cryosections with a CM1510S cryostat (Leica, Tokyo, Japan). After the sections were
263 hybridised with DIG-labelled antisense probe (or sense RNA probe for control), the slides were washed
264 using an ISHR Starting Kit (Nippon Gene) in accordance with the manufacturer's instructions.
265 Detection of DIG-labelled RNA was performed with an alkaline phosphatase-conjugated anti-DIG
266 antibody with nitro-blue tetrazolium/ 5-bromo-4-chloro-3-indolyl-phosphate (NBT/BCIP) as a
267 substrate, using a DIG Nucleic Acid Detection Kit (Roche). Images were captured using a Biozero
268 microscope (Keyence, Tokyo, Japan).

269

270 Results

271

272 Identification of four *RsVg* genes

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274 Similarity searches were conducted to determine the number of *Vg* genes in the *R. speratus* genome.
275 There are four *Vg* genes in the genome, similar to those in *Z. nevadensis* (Terrapon *et al.*, 2014). The
276 lengths of the four *Vg* genes (*RsVg1*, 2, 3, and 4) were predicted to be 6048 bp (*RS000616*), 6042 bp
277 (*RS000610*), 2217 bp (*RS013977*), and 4269 bp (*RS011073*), respectively. The predicted CDS length
278 of *RsVg3* (*RS013977*) was less than that of other *RsVg* sequences and incomplete at the 3' site (with
279 no stop codon). Moreover, the deduced amino acid sequences possessed a conserved Lipid transport
280 protein, N-terminal (Lipid_transpt_N) (IPR001747), but the von Willebrand factor, type D domain
281 (VWD) (IPR001846) could not be identified in *RsVg3* (*RS013977*). Consequently, we performed 3'-
282 RACE and obtained the full length of *RsVg3* (5310 bp), which possessed these three domains. These
283 results indicated that the four *RsVgs* identified were homologous genes with three conserved domains,
284 Lipid_transpt_N, Vitellinogen, open beta-sheet, and VWD (Fig. S3).

285

286 Molecular phylogenetic analyses

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288 To resolve the phylogenetic positions of *RsVgs*, molecular phylogenetic analyses were performed using
289 maximum likelihood and neighbor-joining methods. Four monophyletic groups, including *Vg* genes
290 obtained from termites (*R. speratus*, *Z. nevadensis*, *C. formosanus*, *C. secundus*, and *M. natalensis*)
291 and cockroaches (*C. punctulatus* and/or *B. germanica*) were highly supported by both methods (99–
292 100% bootstrap values) (Fig. 1). The extant copies were orthologous relationships among termite

species, and we named these clades the termites *Vg1-4*. The termite *Vg1-3* were closely related to conventional *Vg* and *Vg-like-C* homologs, although the precise phylogenetic relationships among each clade were not identified because of low bootstrap values (Fig. 1). In contrast, the termite *Vg4* was closely related to the *Vg-like B* genes of social hymenopteran insects (Fig. 1). Note that we found 2 *Vg4* sequences in *C. secundus* (XP_023710404-5), but based on the position of their locus (LOC111866074), we concluded that they were splicing variants, and one of them (OTU No. [63]) was used for molecular phylogenetic analyses. Although the precise numbers of *Vg* genes in cockroaches and termites are still ambiguous [for example, no termite *Vg1* gene in the current gene model of *C. formosanus* (Itakura et al. 2020)], no homologous termite *Vg3* genes were identified in cockroaches. However, homologous termite *Vg4* genes were observed both in *C. punctulatus* (OTU No. [64]) and *B. germanica* [65].

304

305 Molecular evolution of three termite *Vgs*

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The estimated dN/dS (ω) ratios were much less than 1 in all focal branches observed in three *Vgs* (Fig. S2, Table S4). The ω ratio observed in the branch leading to the common ancestor of termites was not significantly different from those in other branches in the conventional termite *Vg1-2* (Table S4). In termite *Vg4*, however, the ω ratio in the focal branch was significantly different from those in other branches (Table S4), although an independent ω ratio obtained from a free-ratio model M1 was not

312 strongly lower or higher than those of the other branches (Fig. S2c).

313

314 Expression analyses among castes using RNA-seq data

315

316 A GLMM analysis for the RNA-seq expression data showed that the expression levels of *RsVg1-3*
317 genes were significantly different among castes and sexes (GLMM: FDR < 0.05, Fig. 2, TableS5) with
318 higher expression in female reproductives (queens) compared to males and sterile castes, both in heads
319 (Fig. 2a) and bodies (thoraxes + abdomens) (Fig. 2b), except for *RsVg3* in heads. The expression levels
320 of *RsVg4* genes were also significantly different among castes (FDR < 0.05) in heads (Fig. 2a) and
321 bodies (Fig. 2b). However, the *RsVg4* gene expression levels of workers were higher than those of
322 other castes, and no differences were observed between female and male individuals. We found no
323 significant interaction between caste and sex in all GLMM analyses. Note that because RNA-seq
324 libraries were prepared from pools of multiple tissues, and only three biological replications were
325 analyzed, the differences of gene expression levels may include confounded effects such as allometric
326 differences and/or other ecological factors (e.g. social context, colony size).

327

328 Measurements of egg production numbers during incipient colony development

329

330 The number of eggs was measured during incipient colony development, and the reproductive cycles

331 of queens were clearly observed (Fig. 3), as shown in a previous study (Maekawa *et al.*, 2010). The
332 number of eggs changed significantly during the period of colony development (Kruskal-Wallis test,
333 $df = 7$, $\chi^2 = 84.44$, $p = 1.71\text{e-}15$; Steel-Dwass test, $p < 0.05$). The onset of egg production occurred
334 during the initial periods of colony development (within 3.5 months of colony establishment). The
335 diapause periods were observed from 3.5 to 6.5 months, and the restart of egg production occurred 7.5
336 months after colony establishment. The polynomial regression analyses indicated that the changes of
337 egg numbers were significantly fitted by cubic equations during colony developments (Fig. S4a, Table
338 S6).

339

340 Gene expression analyses of queens during incipient colony development

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342 Expression analyses of *RsVg* genes in female individuals were performed using real-time qPCR. The
343 *RsGstD1* gene was selected as an endogenous control based on a comparison with five other reference
344 genes examined in this study (Table S3). The expression levels were compared among several time
345 points during incipient colony development. The expression levels of *RsVg1* were higher in the female
346 reproductives (queens) at 1.5 months after colony establishment but extremely low at 3.5 and 4.5
347 months, and then increased at 6.5 and 7.5 months (Fig. 4a; one-way ANOVA, $df = 10$, $F = 2.9585$, $p =$
348 0.01624 ; Tukey's test, $p < 0.05$). The expression patterns of *RsVg2* and *RsVg3* were essentially similar
349 to those of *RsVg1*, whereas no significant differences were found between the periods (Fig. 4bc; one-

way ANOVA, $df=10$, $F=2.4151$, $p=0.04069$ (*RsVg2*) and $df=10$, $F=2.3005$, $p=0.04967$ (*RsVg3*);
Tukey's test, $p < 0.05$). Note that the lack of significance might be due to a lack of power from our
data as the number of biological replicates is low and no technical replicates have been performed. In
contrast, the expression levels of *RsVg4* were significantly higher in the periods before colony
establishment (N6 nymphs and alates) (Fig. 4d; one-way ANOVA, $df=10$, $F=4.4846$, $p=0.00161$;
Tukey's test, $p < 0.05$). The polynomial regression analyses indicated that the expression patterns of
RsVg1-3 were significantly fitted by cubic equations (Fig. S4b-d, Table S6), whereas those of *RsVg4*
were significantly fitted in quadratic equations (Fig. S4e, Table S6).

358

Localisation of *RsVg* mRNA

360

RsVg4 mRNA localisation was examined by *in situ* hybridisation using worker heads and bodies from
mature colonies (Fig. 5). The results showed that *RsVg4* mRNA signals were localised in the fat body
of worker heads and bodies (Fig. 5ac). Specific signals were not observed in sections treated with the
sense probe (Fig. 5bd). Similarly, *RsVg1* mRNA signals were observed in the fat body of a queen
thorax and abdomen (Fig. 5e), and no signals were detected in the sections treated with the sense probe
(Fig. 5f).

367

Discussion

369

370 Phylogenetic relationships of termite *Vitellogenin* genes

371

372 In the present study, four *Vg* genes were identified in the genome of *R. speratus*. Generally, in
373 oviparous animals, Vg is distinguished from other large lipid transfer proteins (LLTP) by having three
374 conserved domains (Avarre *et al.*, 2007). A conserved domain, Vitellinogen open β -sheet (IPR015255)
375 also known as a DUF1943 (PF09172), was lacking in the *Vg* genes within the clade containing *Vg*-
376 *like-B* of social hymenoptera insects (OTU No. [66]–[71] in Fig. 1) and those of Hemiptera (No. [72]–
377 [74]) (Shang *et al.*, 2017), however, all termite *Vg4* genes except *C. formosanus* homolog (No. [62])
378 possessed this domain. Although the relevance of the Vitellinogen open β -sheet domain is currently
379 unclear, its loss may occur independently in several lineages. The molecular phylogenetic tree showed
380 that the termite *Vg1-2* were positioned at a conventional insect *Vg* clade, and termite *Vg3* was most
381 closely related to this clade, whereas the termite *Vg4* was closely related to the hymenopteran *Vg-like*-
382 *B* clade (Fig. 1). Phylogenetic relationships shown in Fig. 1 were essentially similar to those inferred
383 in Kohlmeier *et al.* (2018), for example *Vg-like-A* and *Vg-like-B* were closely related to each other. We
384 found that *RsVg3* possessed all three conserved domains (Fig. S3), whereas previous studies showed
385 that the hymenopteran *Vg-like-C* had incomplete domain structure (Morandin *et al.*, 2014; Salmela *et*
386 *al.*, 2016). There were no cockroach homologs for termite *Vg3*, suggesting that it had appeared only
387 in termites. However, there were cockroach homologs for termite *Vg4*, and it might have been already

388 present in the most recent common ancestor between termites and cockroaches. The dN / dS ratios
389 indicated that the branch leading to the common ancestor of termite *Vg4* was relatively under weak
390 purifying selection but not in termite *Vg1-2* clades (Fig. S2, Table S4). This is not contradicted with
391 the evidence in the bumble bee genus *Bombus*, which indicated that *Vg-like* genes showed a general
392 tendency of relaxation of purifying selection (Zhao *et al.*, 2021). Considering the inferred phylogenetic
393 relationships of insect *Vg* genes, it is possible that termite *Vg4* has diverged less from the outgroups
394 compared to the other termite *Vg1-3* genes.

395

396 Different *Vg* gene expression patterns in females between reproductive and non-reproductive periods

397

398 Novel *Vg* roles may have been acquired to regulate caste-specific physiological and behavioural traits
399 during the course of hymenopteran social evolution (Robinson *et al.*, 2005; Smith *et al.*, 2008). The *P.*
400 *barbatus* and *S. invicta* genomes possess two and four *Vg* genes, respectively (Wurm *et al.*, 2011;
401 Corona *et al.*, 2013), suggesting that there were several duplication events that produced multiple *Vg*
402 genes in ants (Corona *et al.*, 2013). Moreover, caste-specific *Vg* gene expression was associated with
403 the tasks performed by a queen and workers in honey bees and ants (Amdam *et al.*, 2003; Corona *et*
404 *al.*, 2013). The present study showed that the expression levels of *RsVg1-3* genes were particularly
405 high in female reproductives (queens) (Fig. 2). Furthermore, the expression patterns of *RsVg1-3* and
406 *RsVg4* were clearly different, and non-linear regressions observed in *RsVg1-3* were similar to the

407 reproductive cycles of queens (Fig. S4). In a previous study, the expression patterns of the *RsVg* gene
408 (*RsVg1* in this study) were related to the number of eggs in each colony and juvenile hormone (JH)
409 titre changes in queens at each period (i.e. the 'stages I–V' shown in Maekawa *et al.*, 2010). JH-related
410 *RsVg1* expression has also been observed during the differentiation of secondary reproductives in *R.*
411 *speratus* (Saiki *et al.*, 2015). However, the expression levels of *RsVg4* were higher in workers than in
412 reproductives (Fig. 2). In addition, *RsVg4* was highly expressed in nymphs and alates compared to
413 fertile queens (Fig. 4d). Since low JH levels are required for alate differentiation in termites (Cornette
414 *et al.*, 2008; Oguchi *et al.*, 2021), similar JH-related *RsVg4* expression changes are unlikely. In
415 summary, the present results suggest that *RsVg1-3* are involved in the regulation of female
416 vitellogenesis, while *RsVg4* has a distinct role in non-reproductive individuals (see below). Further
417 analysis is required to determine whether the *RsVg1-3* genes have different subfunctions for
418 vitellogenesis in termites. Recently, Elsner *et al.* (2021) discovered that three queen-biased *Vgs* were
419 highly expressed in builders compared to foragers (all females) of the fungus-growing termite
420 *Macrotermes bellicosus*. To clarify the caste, sex and age specificity of termite *Vg1-3* gene expressions
421 should also be clarified in the future.

422

423 The potential roles of *RsVg4*

424

425 In insects, the *Vg* gene is mainly expressed in the female fat body for vitellogenesis (Tufail and Takeda,

2008). *RsVg1* mRNA was localised in the fat body of termite queens (Fig. 5). Similarly, *RsVg4* mRNA was localised in the fat body of workers, but no positive signals were observed in other tissues (Fig. 5). Although the function of *RsVg4* is still unclear, there are several related reports on *Vgs* within the *Vg-like-B* and closely related clades, which allow us to infer the function of *RsVg4*. For example, in *D. melanogaster*, *Crossveinless d* mRNA (OTU No. [75] in Fig. 1) was expressed in the fat body of larval stages in both sexes, and the product was transported into the wing tissues through haemolymph at pupal stages to regulate the development of the posterior cross vein (Chen *et al.*, 2012). However, it should be noted that rhinotermitid workers are completely wingless, and *RsVg4* may not have any developmental functions for wing formation. In the brown citrus aphid *A. citricidus*, *AcVg* (OTU No. [73]) was also expressed in the fat body of both adults and nymphs, and the silencing of *AcVg* expression resulted in a decrease in survival times and reproductive periods after alate emergence (Shang *et al.*, 2017). Moreover, the expression levels of the hymenopteran *Vg-like-B* were different among *Formica* species with queen-biased expression in *F. aquilonia* and worker-biased expression in *F. pratensis* (Morandin *et al.*, 2014). Although no functional analyses have been performed in any *Formica* species, *Vg-like-B* (OTU No. [71]) expression was upregulated in the fat body of honey bee *A. mellifera* workers to protect against oxidative stress induced by artificial paraquat treatments (Salmela *et al.*, 2016). Termite workers are likely more exposed to oxidative stress compared to other castes, because of the high oxygen concentration from the existence of gut symbionts (Brune *et al.*, 1995). Thus, one possible explanation for the role of *RsVg4* is protection from oxidative stress. To

445 further clarify the specific roles, RNA interference (RNAi) analysis should be performed in termites.

446

447 Conclusion

448

449 We clarified that different evolutionary trajectories could be found in *Vg* gene duplication and
450 functionalisation between termites and social hymenopterans. In social hymenopterans, particularly in
451 ants, *Vg* genes were duplicated and subsequently functionalised within a conventional clade. However,
452 in termites, *Vg* gene functionalisation after duplication might not have occurred within this clade (at
453 least between termite *Vg1* and *Vg2*). In contrast, termite *Vg4*, closely related to the *Vg-like-B* clade of
454 social hymenopterans, might have functionalised during the course of termite evolution. It might play
455 various crucial roles in termites, notwithstanding vitellogenesis of non-reproductive individuals.
456 Functional analyses should be conducted to determine whether hymenopteran *Vg-like-B* and termite
457 *Vg4* homologs contribute to social evolution in insects.

458

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470

471 Author contributions

472

473 HY and KM planned and designed the experiments. HY, YM, RHS and RS collected the samples. HY,
474 ShoS and NK performed the experiments. HY, YM, ShuS and YH analysed the data. HY, YM, ShuS
475 and KM wrote and revised the manuscript. All authors read and approved the final manuscript.

476

477 Conflict of interest

478

479 The authors declare that there are no conflict of interests.

480

481 Data availability statement

482

483 We deposited our raw sequence data to NCBI. Accession Numbers are stated in the manuscript.

484

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699

700 Figure captions

701

702 Fig. 1. Molecular phylogenetic tree of *Vg* genes in oviparous animals.

703 Phylogenetic tree inferred from *Vg* amino acid sequences (228-1070 aa) based on the maximum
704 likelihood (ML) analysis. Apolipocrustacein (ApoCr) and insect apolipophorin II/I (apoLp-II/I) were
705 used as outgroups, according to previous reports (Avarre *et al.*, 2007; Hayward *et al.*, 2010). Bootstrap
706 values (above 50%) from ML (1000 times) and neighbor-joining (NJ, 5000 times) analyses are shown
707 above and below the branches to indicate the level of support for each node, respectively. The asterisk
708 indicates a branch for which high bootstrap values could not be obtained (below 50%). The numbers
709 in parentheses after species names indicate the OTU numbers shown in Table S2.

710

711 Fig. 2. Expression values (the reads per kilobase of exon per million mapped sequence reads; RPKM)
712 of four *Vg* genes among castes in *R. speratus*.

713 The graphs indicate the expression values of *RsVg* genes in (a) heads and (b) bodies (including thoraxes
714 and abdomens). PR: primary reproductive; S: soldier; W: worker. Asterisks indicate genes with
715 significant differential expression (GLMM analysis, *FDR<0.05, **FDR<0.01). Statistical results
716 (GLMM) are shown in Table S5.

717

718 Fig. 3. Numbers of eggs observed in the colony at the periods during incipient colony development.
719 The boxes and whiskers represent the median, quartiles, and ranges, respectively. Numbers in
720 parentheses indicate the number of colonies examined. Non-parametric tests were fitted to these data
721 based on the results of Levene's test ($p = 4.438\text{e-}16$). Different letters over the boxes denote significant
722 differences (Kruskal-Wallis test followed by Steel-Dwass test, $p < 0.05$).

723

724 Fig. 4. Relative expression levels of four *RsVg* genes using biological triplicates in female N6 nymphs,
725 alates, and reproductives (0.5–7.5 months after colony foundation).

726 Each value was normalised to the expression level of the *glutathione S transferase D1* homolog
727 (*RsGstD1*) (Table S3). The boxes and whiskers mean median, quartiles and range, respectively.
728 Parametric tests were fitted to these data based on the results of Levene's test (*RsVg1*, $p = 0.1151$;
729 *RsVg2*, $p = 0.2338$; *RsVg3*, $p = 0.1316$; *RsVg4*, $p = 0.4887$). Different letters above the bars indicate

730 significant differences (one-way ANOVA followed by Tukey's test, $p < 0.05$). N6: the 6th-stage nymph
731 (Fig. S1), Before moult: N6 just before the moult into alates; Alate: winged adults; Reproductive:
732 female reproductives collected each month after incipient colony establishment.

733

734 Fig. 5. Localisation of *RsVg* mRNA in *R. speratus*.

735 Parasagittal cryosections of a worker head (a, b) and abdomen (c, d) subjected to *in situ* hybridisation
736 with antisense (a, c) and sense (b, d) DIG-labelled *RsVg4* mRNA probe. Parasagittal cryosections of a
737 queen body subjected to *in situ* hybridisation with antisense (e) and sense (f) DIG-labelled *RsVg1*
738 mRNA probe. The signals were only detected with antisense probe treatments (arrowheads). Scale bars
739 indicate 100 μm (a-d) and 50 μm (e, f). Br: brain. Sp: sternal plate.

740

741 Supplementary Figure 1. Caste differentiation pathway of *R. speratus*.

742 They have bifurcated developmental pathways. There are at least five worker stages in the apterous
743 line. The 4th-stage (W4) and 5th-stage (W5) workers are able to differentiate into soldiers via the
744 presoldier stage. There were six nymphal stages on the imaginal line. The 6th-stage (N6) nymphs
745 differentiate into winged alates, and de-winged females and males become primary reproductives
746 (queen and king). In both lines, W2–W5 workers and N3–N6 nymphs occasionally moult into
747 secondary reproductives.

748

749 Supplementary Figure 2. Molecular evolutionary analysis of *Vg* homologs by the PAML branch test in
750 (a) *Vg1*, (b) *Vg2*, and (c) *Vg4* clades of the phylogeny shown in Fig. 1. The focal branches are indicated
751 with a bold line, and an asterisk shows the significant difference with other branches in each clade (p
752 < 0.05 , Table S4). In the *Vg4* clade, the value above and below each node indicates an independent dN
753 $/ dS (\omega)$ ratio obtained from a free-ratio model M1.

754

755 Supplementary Figure 3. The domain architecture of four Vgs in the termite *R. speratus*.
756 Black rods indicate full Vg amino acid sequences. Three domains; lipid transport protein, N-terminal
757 (IPR001747), vitellinogen, open beta-sheet (IPR015255), and von Willebrand factor, type D domain
758 (IPR001846), are highlighted. Scaffold numbers of the gene model Rspe OGS1.0 (Shigenobu *et al.*,
759 2022) are indicated.

760

761 Supplementary Figure 4. Polynomial regression (orange line) of egg number changes and *RsVg* gene
762 expression patterns.

763 The changes of egg numbers are significantly fitted by cubic equations during colony developments
764 (a). Expression patterns of *RsVg1-3* are significantly fitted by cubic equations (b-d), whereas those of
765 *RsVg4* are significantly fitted in quadratic equations (e). Statistical results (ANOVAs) are shown in
766 Table S6.

767

768 Supplementary data. Alignment of amino acid sequences used for molecular phylogenetic analysis.

769

Table S1. Primer sequences used in this study.

	Gene name	Forward sequence (5' - 3')	Reverse sequence (5' - 3')
3' - RACE	<i>Rsvg3</i>	GTCTCAACGTGGTACGACCCAGCTT	-
	<i>Rsvg3_1</i>	GACGCCAACCACTGTACTA	AGCGTATTCGTGACTGTTCA
	<i>Rsvg3_2</i>	TGGACGTAGATATGCTGTAT	GGTAGTTGTCCAAGTTCAC
	<i>Rsvg3_3</i>	CGTATTACTCAACTACACGAC	GTAGGGTAACAACGAATAAC
	<i>Rsvg3_4</i>	CAGGAGCACATAAAAACGA	CTATGAGCGAATATGTGAAG
real-time qPCR	<i>Rsvg1</i>	CCTACATGCGTTGTTGATGG	TGACGACTATGCATCCAGC
	<i>Rsvg2</i>	GCGAAATGGAGAACCCTAAT	TCACTTCGTCGATTGCTGTA
	<i>Rsvg3</i>	ATGAGCTGATCCAGAGTTCG	ATGAGCGTATCGCGTCTTAG
	<i>Rsvg4</i>	AGAAGCCATGACACACCAAT	CTGCCTTCACAGACAGACCT
	<i>EF1</i>	GGTGATGCGGCTATTGTTAACC	GTGGTGGGAATTCTGAGAAAAGATT
	<i>β-Actin</i>	AGCGGGAATCGTCCGTGAC	CAATGGTGATGACCTGCCCAT
	<i>NADH-dh</i>	GCTGGGGGGTTATTCAATCCAT	GGCATACCACAAAGGCCAAAA
	<i>GstD1</i>	GCTGTTGGTGTGATTTGAA	GTATGCTGCGGGTTTCATCTT
	<i>EIF-1</i>	ATGGTAGGCTTGAAGCGATG	TTTGCACTCTGGTAGTCACG
	<i>RPS18</i>	ACTCTCAGCTCACATCCAGT	CCTCAGGCCCAATAATGTC
mRNA in situ hybridization	<i>Rsvg1</i>	ATCCAAAACCGAACCAAC	TACGAGCACCGCTACATT
	<i>Rsvg4</i>	TACGCTCACCAGATGCTGTA	GAGCCAGTGAGTGCAAAGTT

Table S2. The species used for the molecular phylogenetic analysis.

OTU no	Species	Database and reference	Accession number or gene ID
[1]	<i>Cryptotermes secundus</i>	Csec_1.0 (Harrison et al., 2018)	XP_023706879
[2]	<i>Zootermopsis nevadensis</i>	Znev OGS v2.2 (Terrapon et al., 2014)	Znev_07681
[3]	<i>Reticulitermes speratus</i>	Rspe OGS1.0 (Shigenobu et al., 2021)	RS000616
[4]	<i>Macrotermes natalensis</i>	Mnat_gene_v1.2 (Poulsen et al., 2014)	MN002567
[5]	<i>Cryptocercus punctulatus</i>	ESM1 (DRA004598, Hayashi et al., 2017)	comp77743_c0_seq1
[6]	<i>Macrotermes natalensis</i>	Mnat_gene_v1.2 (Poulsen et al., 2014)	MN002568
[7]	<i>Coptotermes formosanus</i>	CopFor1.0 (Itakura et al., 2020)	GFG39872
[8]	<i>Reticulitermes speratus</i>	Rspe OGS1.0 (Shigenobu et al., 2021)	RS000610
[9]	<i>Cryptotermes secundus</i>	Csec_1.0 (Harrison et al., 2018)	XP_023706896
[10]	<i>Zootermopsis nevadensis</i>	Znev OGS v2.2 (Terrapon et al., 2014)	Znev_07682
[11]	<i>Cryptocercus punctulatus</i>	ESM1 (DRA004598, Hayashi et al., 2017)	comp194989_c0_seq1
[12]	<i>Blattella germanica</i>	OrthoDB (Waterhouse et al., 2013)	BGER020452
[13]	<i>Rhyarobia maderae</i>	NCBI database	BAB19327
[14]	<i>Rhyarobia maderae</i>	NCBI database	BAD72597
[15]	<i>Periplaneta americana</i>	NCBI database	BAB32673
[16]	<i>Periplaneta americana</i>	NCBI database	BAA86656
[17]	<i>Blattella germanica</i>	OrthoDB (Waterhouse et al., 2013)	BGER000125
[18]	<i>Graptopsaltia nigrofusca</i>	NCBI database	BAA85987
[19]	<i>Pediculus humanus</i>	OrthoDB (Waterhouse et al., 2013)	PHUM524870
[20]	<i>Pediculus humanus</i>	OrthoDB (Waterhouse et al., 2013)	PHUM524850
[21]	<i>Anthonomus grandis</i>	NCBI database	AAA27740
[22]	<i>Nicrophorus vespilloides</i>	OrthoDB (Waterhouse et al., 2013)	XP_017778650
[23]	<i>Nicrophorus vespilloides</i>	OrthoDB (Waterhouse et al., 2013)	XP_017781017
[24]	<i>Riptortus clavatus</i>	NCBI database	AAB72001
[25]	<i>Plautia stali</i>	NCBI database	BAA88076
[26]	<i>Plautia stali</i>	NCBI database	BAA88075
[27]	<i>Plautia stali</i>	NCBI database	BAA88077
[28]	<i>Ephemera danica</i>	OrthoDB (Waterhouse et al., 2013)	EDAN008490
[29]	<i>Pimpla nipponica</i>	NCBI database	AAC32024
[30]	<i>Apis mellifera</i>	NCBI database	CAD56944
[31]	<i>Pogonomyrmex barbatus</i>	NCBI database	XP_025073621
[32]	<i>Solenopsis invicta</i>	Ensembl Metazoa database based on the genome sequence (W	XP_025987667
[33]	<i>Solenopsis invicta</i>	Ensembl Metazoa database based on the genome sequence (W	XP_025987667
[34]	<i>Harpegnathos saltator</i>	NCBI database	EFN86099
[35]	<i>Solenopsis invicta</i>	Ensembl Metazoa database based on the genome sequence (W	NP_001291514
[36]	<i>Solenopsis invicta</i>	Ensembl Metazoa database based on the genome sequence (W	NP_001291513
[37]	<i>Pogonomyrmex barbatus</i>	NCBI database	XP_025073621
[38]	<i>Formica exsecta</i>	NCBI database	AI196912
[39]	<i>Camponotus floridanus</i>	NCBI database	EFN64902
[40]	<i>Aedes aegypti</i>	NCBI database	AAA18221
[41]	<i>Lymantria dispar</i>	NCBI database	AAB03336
[42]	<i>Bombyx mori</i>	OrthoDB (Waterhouse et al., 2013)	NP_001037309
[43]	<i>Samia cynthia pryeri</i>	NCBI database	BAD91196
[44]	<i>Danaus plexippus</i>	NCBI database	OWR44310
[45]	<i>Coptotermes formosanus</i>	CopFor1.0 (Itakura et al., 2020)	GFG36045
[46]	<i>Macrotermes natalensis</i>	Mnat_gene_v1.2 (Poulsen et al., 2014)	MN000066
[47]	<i>Reticulitermes speratus</i>	Rspe OGS1.0 (Shigenobu et al., 2021)	RS013977
[48]	<i>Cryptotermes secundus</i>	Csec_1.0 (Harrison et al., 2018)	XP023712833
[49]	<i>Zootermopsis nevadensis</i>	Znev OGS v2.2 (Terrapon et al., 2014)	Znev_08605
[50]	<i>Apis mellifera</i>	NCBI database	XP_001122505
[51]	<i>Harpegnathos saltator</i>	NCBI database	EFN86751
[52]	<i>Camponotus floridanus</i>	NCBI database	EFN73216
[53]	<i>Formica exsecta</i>	NCBI database	AI196915
[54]	<i>Solenopsis invicta</i>	Ensembl Metazoa database based on the genome sequence (W	XP_011172130
[55]	<i>Pogonomyrmex barbatus</i>	NCBI database	XP_011631341
[56]	<i>Panaeus monodon</i>	NCBI database	ABW77320
[57]	<i>Panaeus monodon</i>	NCBI database	AAF19002
[58]	<i>Daphnia magna</i>	NCBI database	BAD05137
[59]	<i>Zootermopsis nevadensis</i>	Znev OGS v2.2 (Terrapon et al., 2014)	Znev_06771
[60]	<i>Macrotermes natalensis</i>	Mnat_gene_v1.2 (Poulsen et al., 2014)	MN000928
[61]	<i>Reticulitermes speratus</i>	Rspe OGS1.0 (Shigenobu et al., 2021)	RS011073
[62]	<i>Coptotermes formosanus</i>	CopFor1.0 (Itakura et al., 2020)	GFG34789
[63]	<i>Cryptotermes secundus</i>	Csec_1.0 (Harrison et al., 2018)	XP_023710404
[64]	<i>Cryptocercus punctulatus</i>	ESM1 (DRA004598, Hayashi et al., 2017)	comp89049_c0_seq6
[65]	<i>Blattella germanica</i>	OrthoDB (Waterhouse et al., 2013)	BGER006422
[66]	<i>Harpegnathos saltator</i>	NCBI database	EFN87799
[67]	<i>Solenopsis invicta</i>	Ensembl Metazoa database based on the genome sequence (W	XP_011162482

[68]	<i>Pogonomyrmex barbatus</i>	NCBI database	XP_011629719
[69]	<i>Camponotus floridanus</i>	NCBI database	EFN61573
[70]	<i>Formica exsecta</i>	NCBI database	AII96914
[71]	<i>Apis mellifera</i>	NCBI database	XP_006561178
[72]	<i>Diuraphis noxia</i>	NCBI database	XP_015366382
[73]	<i>Aphis citricidus</i>	NCBI database	AVP41182
[74]	<i>Aphis medicaginis</i>	NCBI database	AGC97434
[75]	<i>Drosophila melanogaster</i>	OrthoDB (Waterhouse et al., 2013)	NP_732076
[76]	<i>Nicrophorus vespilloides</i>	OrthoDB (Waterhouse et al., 2013)	XP_017777145
[77]	<i>Apis mellifera</i>	NCBI database	XP001121939
[78]	<i>Harpegnathos saltator</i>	NCBI database	EFN75537
[79]	<i>Formica exsecta</i>	NCBI database	AII96913
[80]	<i>Camponotus floridanus</i>	NCBI database	EFN69845
[81]	<i>Solenopsis invicta</i>	Ensembl Metazoa database based on the genome sequence (W	XP_011161539
[82]	<i>Pogonomyrmex barbatus</i>	NCBI database	XP_011644827
[83]	<i>Bombyx mori</i>	OrthoDB (Waterhouse et al., 2013)	XP_004926335
[84]	<i>Xenopus laevis</i>	NCBI database	P18709
[85]	<i>Gallus gallus</i>	NCBI database	P87498
[86]	<i>Caenorhabditis elegans</i>	NCBI database	CAA26849
[87]	<i>Caenorhabditis elegans</i>	NCBI database	CAA39669
[88]	<i>Caenorhabditis elegans</i>	NCBI database	CAA39670
[89]	<i>Locusta migratoria</i>	NCBI database	Q9U943
[90]	<i>Manduca sexta</i>	NCBI database	Q25490
[91]	<i>Anopheles gambiae</i>	NCBI database	XP_321226
[92]	<i>Panaeus monodon</i>	NCBI database	ABB89953
[93]	<i>Drosophila melanogaster</i>	NCBI database	Q9V496

Table S3. Stability values of reference genes in real-time qPCR analysis.

Gene symbol	Gene ID	Stability value	
		GeNorm	NormFinder
<i>EF1-alfa</i>	AB602838	0.883	0.340
<i>NADH-dh</i>	AB602837	1.059	0.534
<i>beta-actin</i>	AB520714	0.989	0.486
<i>GstD1</i> *	RS001168	0.850	0.286
<i>EIF-1</i>	RS005199	0.912	0.418
<i>RPS18</i>	RS015150	1.336	0.828

* *GstD1* was selected by GeNorm and NormFinder due to the lowest stability values among six genes analyzed.

Table S4. The estimated dN / dS ratios based on Model 0 and the results of χ^2 test.

		dN/dS ratio	$2\Delta\ln L$	d.f.	p value
Model 0 vs Model 1	Termite Vg1	0.3572	23.55872	7	0.001361654
	Termite Vg2	0.3910	31.607706	9	0.000232726
	Termite Vg4	0.3589	41.457698	9	4.12813E-06
Model 0 vs Model 2	Termite Vg1	0.3572	1.916162	1	0.166280377
	Termite Vg2	0.3910	0.382294	1	0.536378076
	Termite Vg4	0.3589	8.316270	1	0.003929152

Table S5. Summary of the results of the generalized linear mixed model (GLMM) analysis on RNA-seq data using the R package glmmSeq v0.1.0.

Body parts using RNA-seq	Gene name	Gene ID	Dispersion	AIC	log ₂ lik	X Intercept	CasteSoldier	CasteWorker	SexMale	CasteSoldier SexMale	CasteWorker SexMale	China_Caste	China_Sex	China_Caste Sex	P_Caste	P_Sex	P_Caste Sex	q_Caste	q_Sex	q_Caste Sex
Head	<i>RuJg1</i>	RS000616	0.092440137	69.51950118	-26.75975059	4.965969005	-6.34088411	-5.926603221	-4.391977138	3.942252898	4.279011349	57.19614388	64.97947338	11.67740548	3.79783E-13	7.56823E-16	0.002912619	1.27813E-11	7.031E-12	0.999559864
	<i>RuJg2</i>	RS000610	0.100514652	92.00559702	-38.00279851	5.771083004	-6.437928421	-7.292815217	-2.363601615	2.326764304	2.846771777	121.7027727	64.20680678	6.522405011	3.74E-27	1.12E-15	0.038342264	3.17E-25	7.03E-12	0.999559864
	<i>RuJg3</i>	RS013977	0.2382322	38.43058185	-11.21523093	1.005628722	-3.085070264	-3.085070264	-2.571501349	2.571501349	2.571501349	4.701306416	2.093602091	1.430548039	0.095306887	0.147916949	0.489058082	0.300334409	0.999971164	0.999559864
	<i>RuJg4</i>	RS011073	0.070476537	107.0676508	-45.5338254	1.95707444	0.34112556	0.825785472	-0.117403573	0.158784943	0.03691925	11.19071702	0.158153901	0.190816692	0.003715067	0.690861893	0.309001672	0.023708815	0.999971164	0.999559864
	<i>RuJg1</i>	RS000616	0.110010039	76.48448157	-30.24224078	5.41988602	-7.126803232	-6.75412307	-3.946609407	4.050069343	3.926246224	61.11515542	93.12199129	9.890539181	3.36E-14	4.92E-22	0.007116996	1.74E-12	2.12E-18	0.272783076
	<i>RuJg2</i>	RS000610	0.131473795	105.0271683	-44.51358416	6.476783894	-7.451163839	-7.78011035	-2.078216518	2.52588054	2.699436784	158.9963222	40.0486997	7.090259579	2.98E-35	2.48E-10	0.028864876	7.43E-33	2.47E-07	0.617070078
Body (thorax and abdomen)	<i>RuJg3</i>	RS013977	0.085968109	53.25117632	-18.62558816	3.069389033	-5.148830574	-4.491129747	-2.456276696	2.456276696	1.798573868	25.97812646	22.194866024	1.724635074	2.29E-06	2.46E-06	0.422182524	2.37E-05	0.001063745	0.999559435
	<i>RuJg4</i>	RS011073	0.043817326	114.5213148	-49.26065724	2.338822098	0.189582119	0.72104712	0.1315356	0.14509626	-0.107433213	12.51501174	0.741346398	0.468774362	0.001916019	0.38822992	0.791055475	0.009629473	0.99982328	0.999559435

Table S6. Fitting polynomial models and comparison by ANOVAs.

	degree	Res.Df	RSS	Df	Sum of Sq	F	Pr (>F)
egg	1	135	626.98				
	2	134	560.67	1	66.318	24.2302	2.51E-06
	3	133	369.49	1	191.175	69.8485	7.79E-14
	4	132	361.28	1	8.207	2.9986	0.0857
<i>RsVg1</i>	1	31	2.3084				
	2	30	2.3083	1	0.00003	0.0005	0.9821
	3	29	1.958	1	0.3503	5.2397	0.0298
	4	28	1.8719	1	0.08612	1.2882	0.2660
<i>RsVg2</i>	1	31	1259.8				
	2	30	1214.85	1	44.948	1.2829	0.2670
	3	29	1017.23	1	197.625	5.6404	0.0246
	4	28	981.05	1	36.181	1.0326	0.3182
<i>RsVg3</i>	1	31	504.43				
	2	30	504.36	1	0.072	0.0049	0.9447
	3	29	421.37	1	82.99	5.6484	0.0246
	4	28	411.39	1	9.979	0.6792	0.4168
<i>RsVg4</i>	1	31	0.27563				
	2	30	0.22322	1	0.052408	7.1645	0.0121
	3	29	0.21214	1	0.011086	1.5154	0.2282

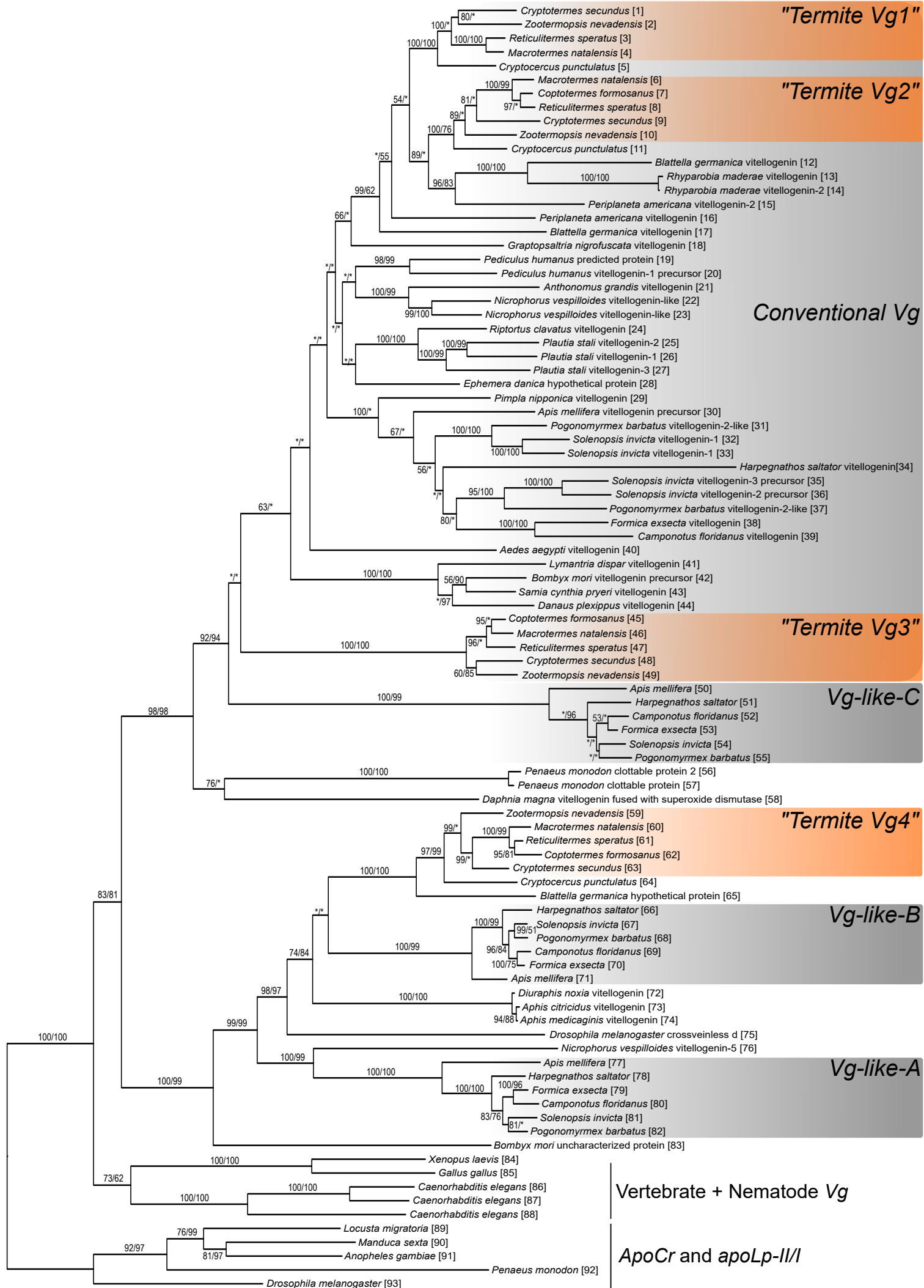


Figure 1

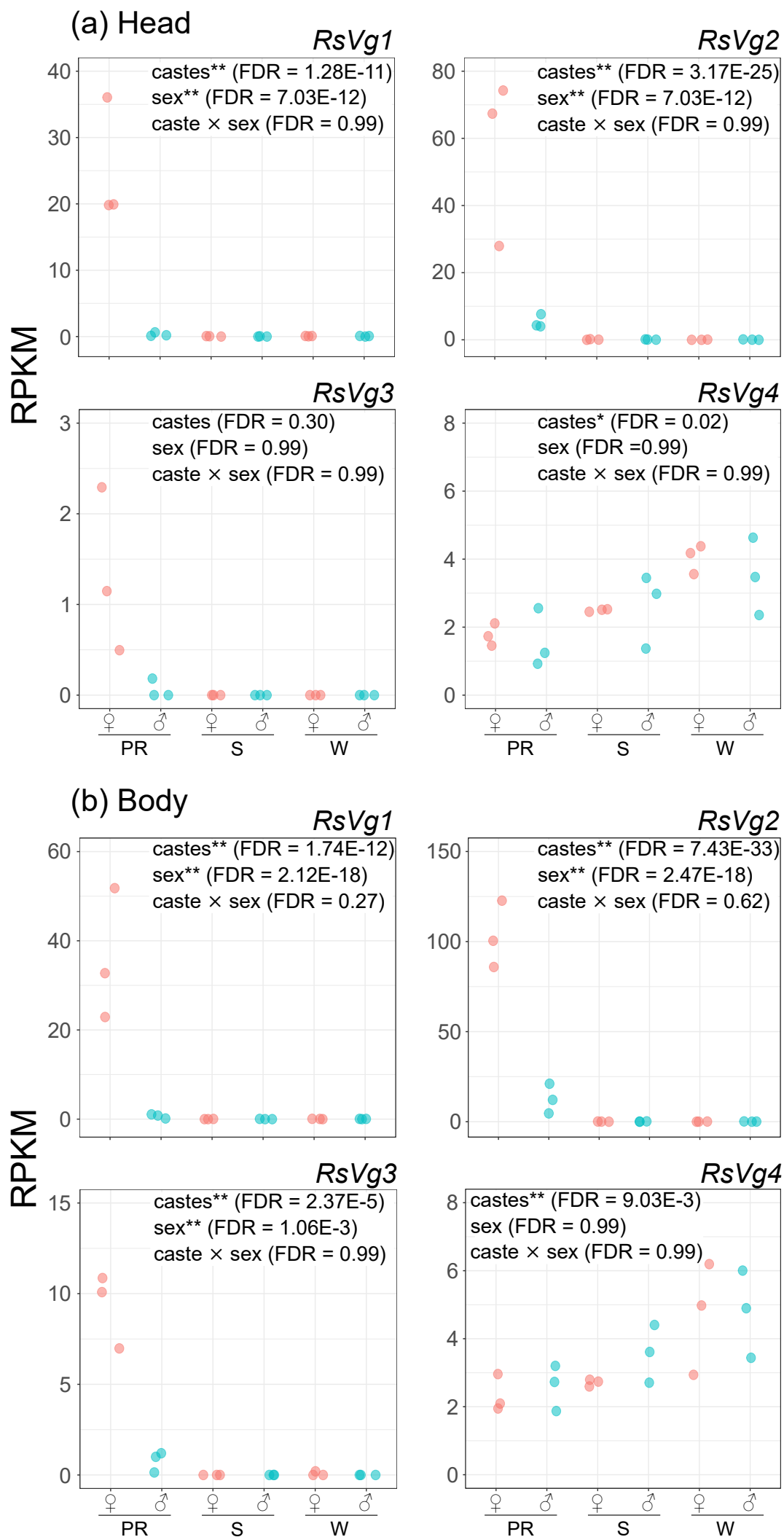


Figure 2

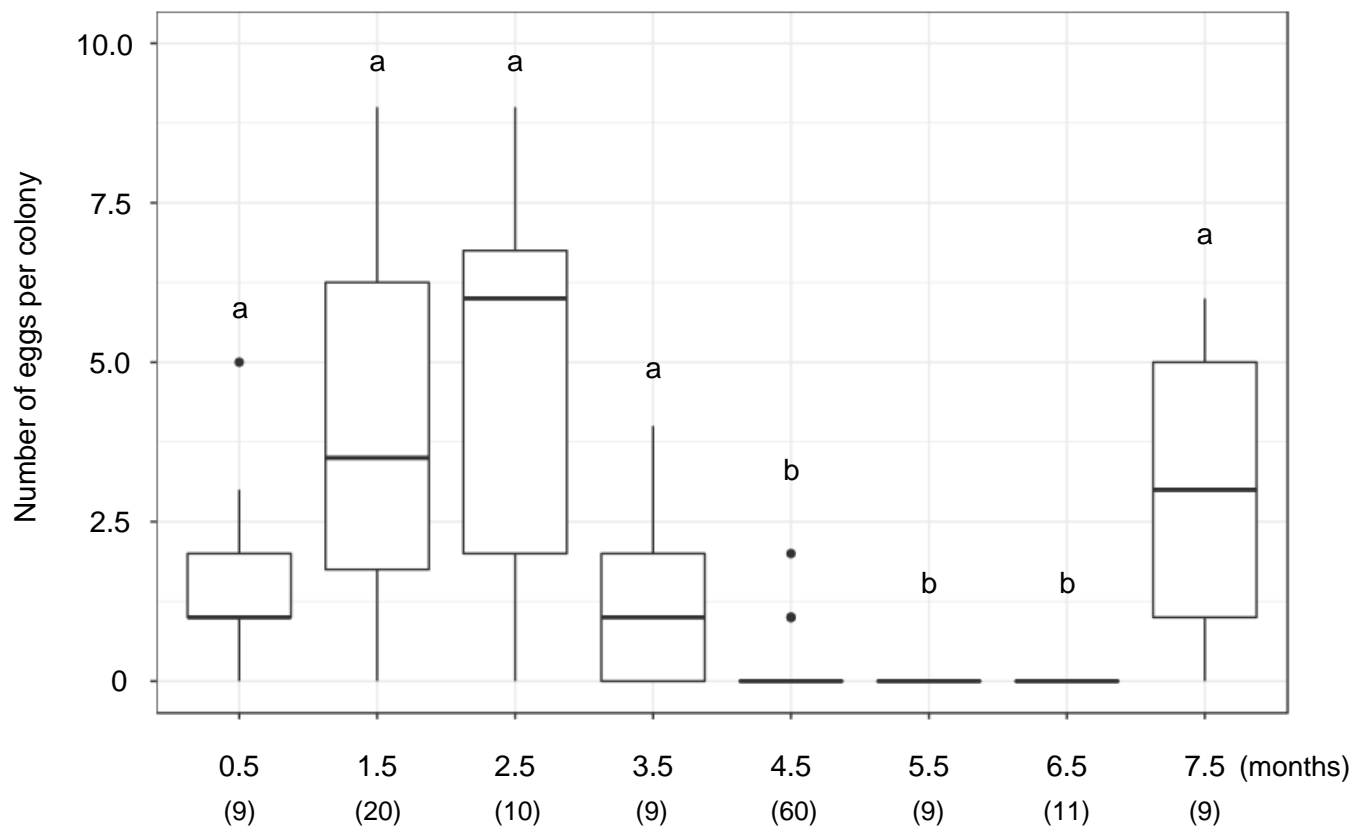


Figure 3

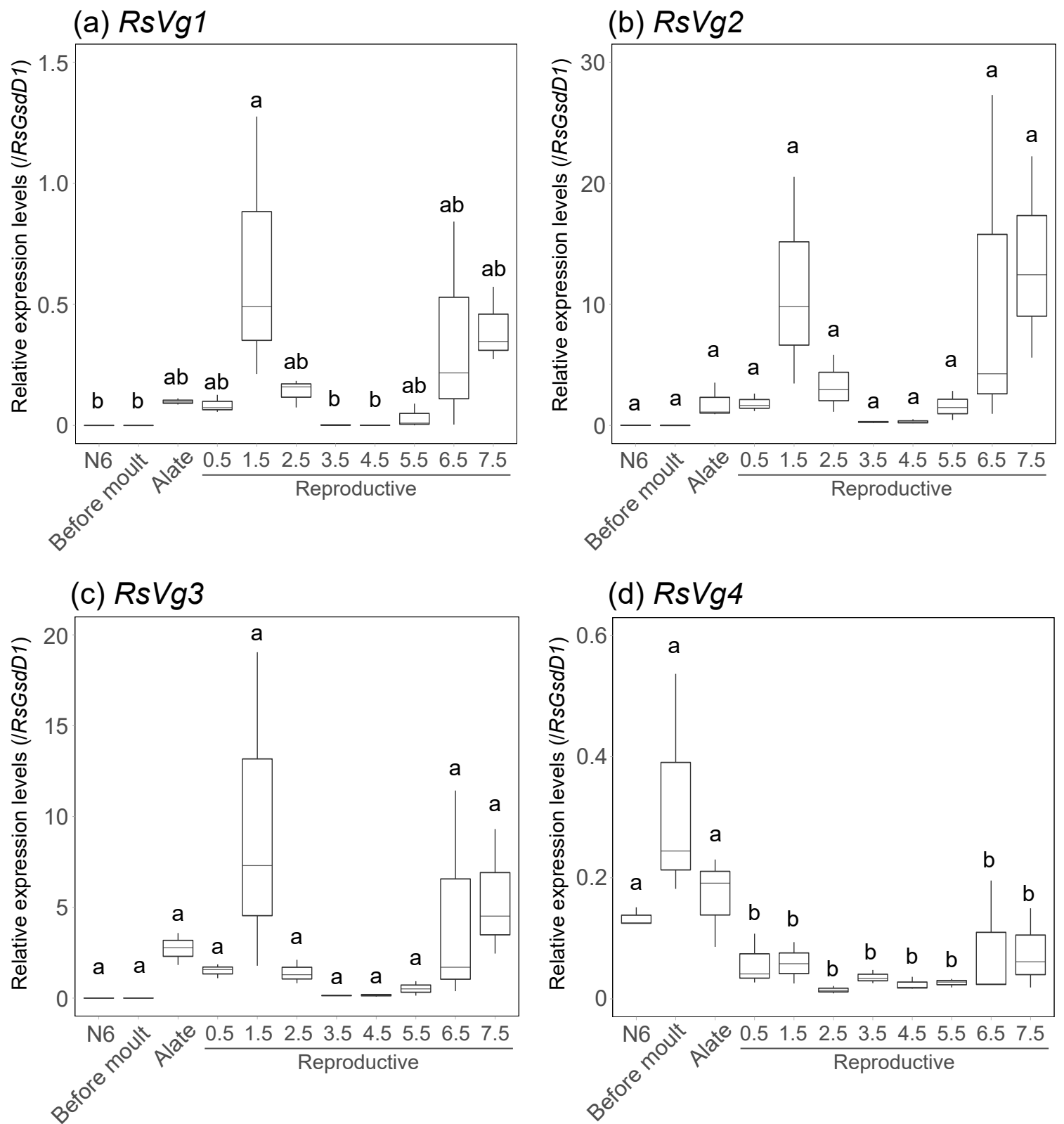


Figure 4

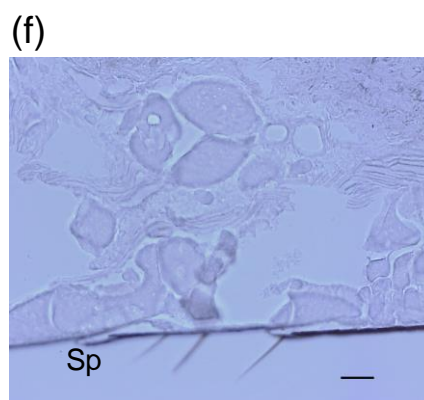
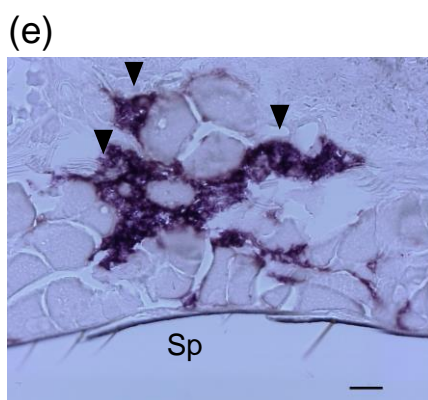
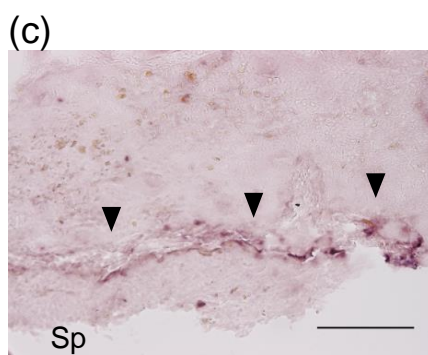
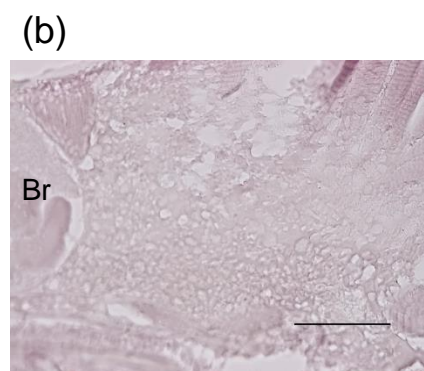
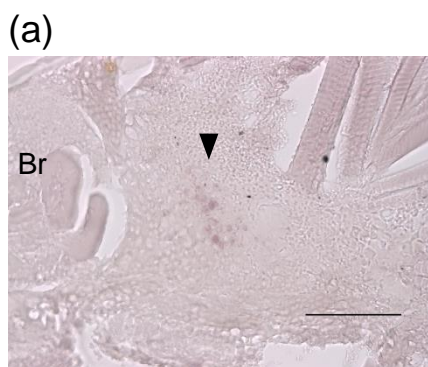
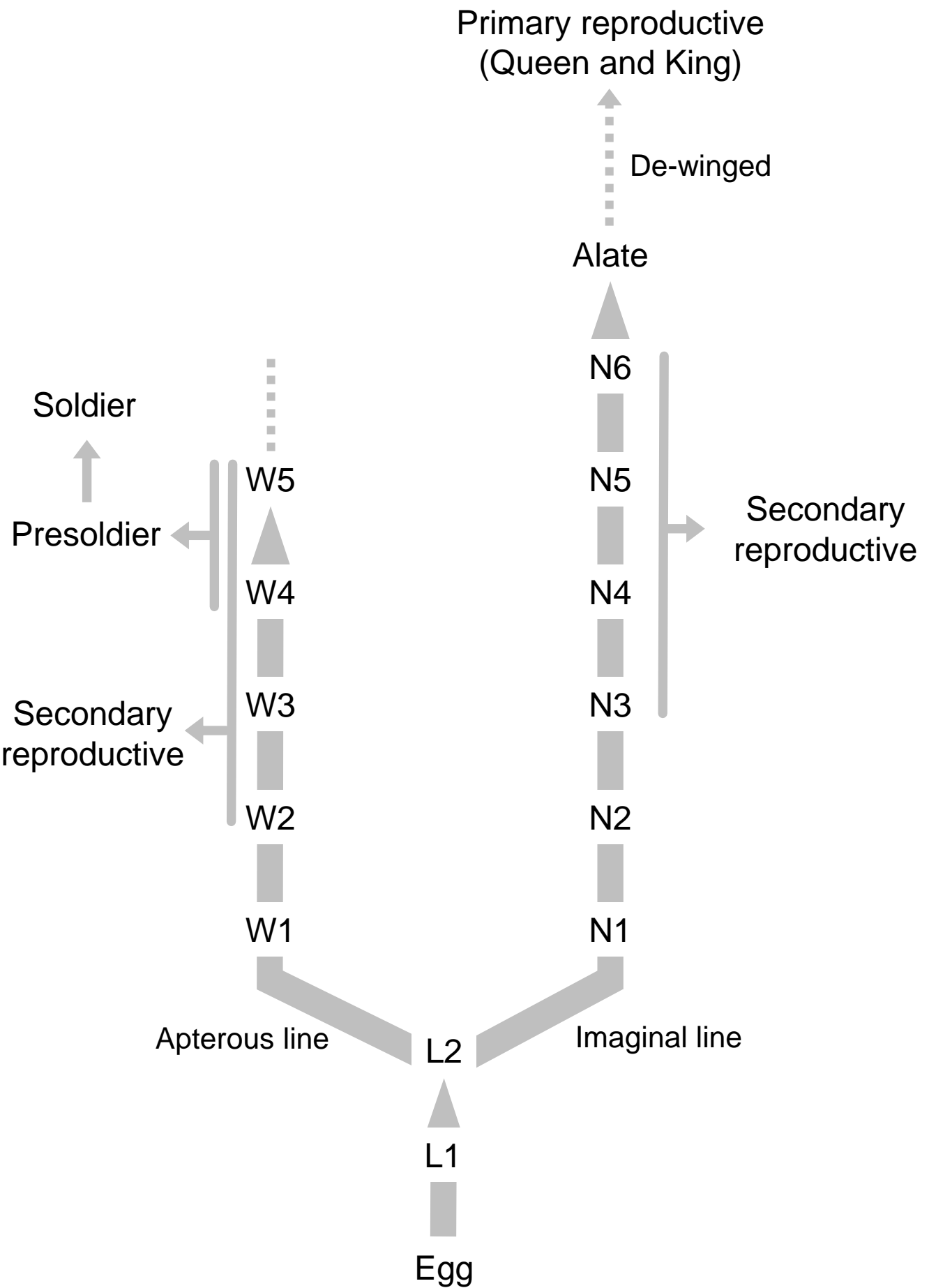
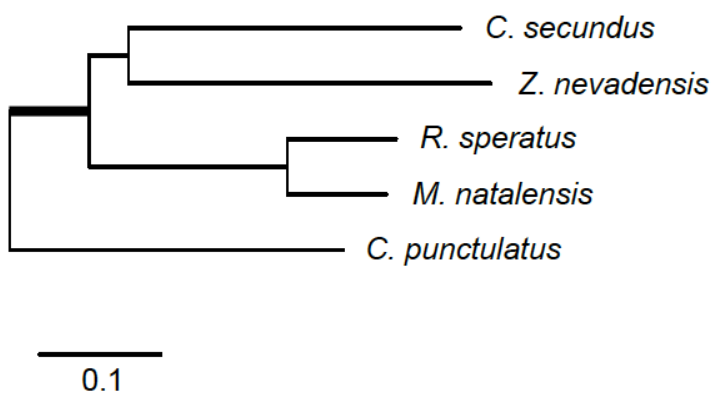


Figure 5

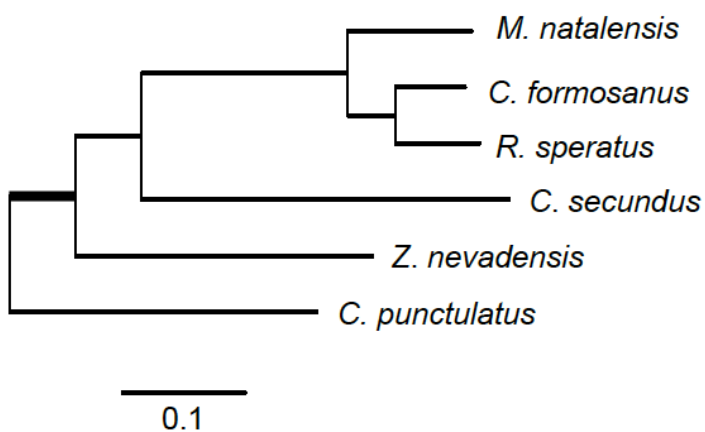


Supplementary Figure 1

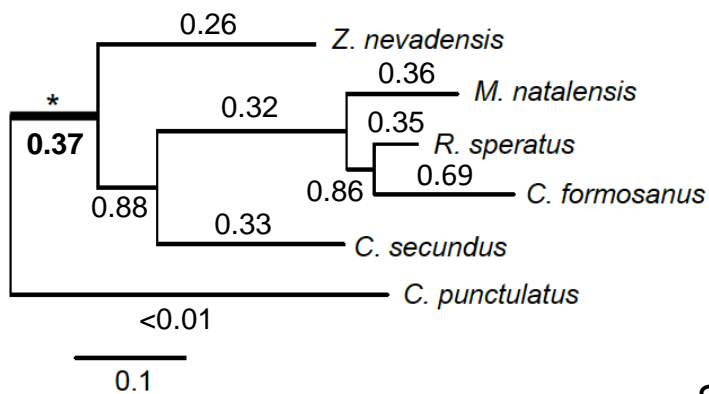
(a) *Vg1*



(b) *Vg2*



(c) *Vg4*



RsVg1 (RS000616), scaffold_101



RsVg2 (RS000610), scaffold_101




RsVg3 (RS013977, LC621340), scaffold_762



RsVg4 (RS011073), scaffold_500

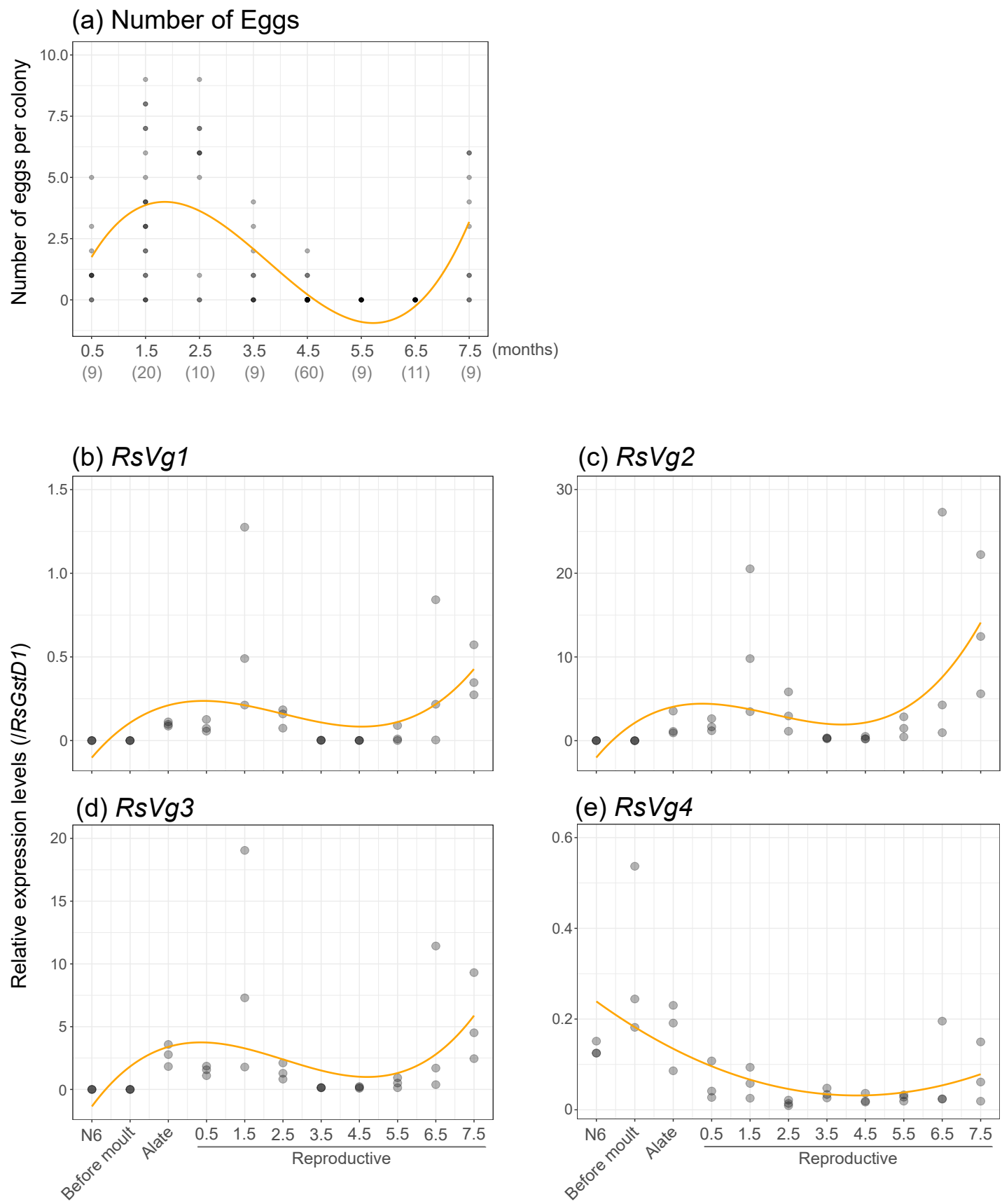


 Lipid transport protein, N-terminal (IPR001747)

 Vitellinogen, open beta-sheet (IPR015255)

 von Willebrand factor, type D domain (IPR001846)

Supplementary Figure 3



Supplementary Figure 4

>RsVg1_RS000616

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>EFN86099_Hsaltator

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>NP732076_Dmelanogaster

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>AVP41182_Acitricidus

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>CAA39670_Celegans

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