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Review

Egg serpins: The chicken and/or the egg dilemma

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ABSTRACT

Twenty-seven serpins belonging to clade A, B, C, D, E, F, G, H and I serpins are currently referenced in chicken genome databases. Phylogenetic analysis of chicken serpins revealed that ovalbumin (Serpinb14) and its paralogs ovalbumin-related protein Y (Serpinb14b) and ovalbumin-related protein X (Serpinb14c) are found in bird species. These clade B serpins are specifically expressed in reproductive tissues and exported in the egg where they constitute major protein components. These data suggest that these three paralogs have probably appeared in birds to face new environments and ensure the extra-uterine development of an embryo in a shell egg. Twelve other serpins have been identified in the newly produced egg, some of them having a specific distribution in the respective egg structures (eggshell, egg white, vitelline membrane and egg yolk). The physiological role of these egg serpins remain largely unexplored, but there is increasing evidence in literature or by homologies with their mammalian counterparts, that some of them participate in cell proliferation, tissue remodeling and/or angiogenesis associated with folliculogenesis and development of extraembryonic structures, eggshell biomineralization, egg defense and nutrition of the embryo. A better knowledge of the phylogenetic evolution of these 15 serpins in other oviparous species, on their egg distribution, on their regulation during embryonic development (activation/degradation/transfer) and on their functional specificity, is needed to better appreciate their role and their bird-specificity. These review shed light on the multiple possibilities that offer the avian egg model to study the role of serpins in reproduction and developmental biology.

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Abbreviations: ACC, amorphous calcium carbonate; CAM, chorioallantoic membrane; ESM, eggshell membrane; OVAX, ovalbumin-related protein X; OVAY, ovalbumin-related protein Y.

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1. Evolution and distribution of egg serpins

Systematic analysis of National Center for Biotechnology Information and chicken Ensembl databases for identifying serpins in chicken species revealed the presence of 27 members of this family (Table 1, Fig. 1). Among these, 16 serpins are still predicted and have been referenced in databases by automated computational analysis of genomic chicken sequences annotated using gene prediction methods, which sometimes can lead to discrepancies between gene and protein names (as an example, *Serpinb2* gene corresponds to a predicted Serpinb10 protein, Table 1). However, the relevance of 5 of them have been recently validated, as serpins a8, c1, d1 and f1 were unambiguously identified in the egg (see §1.2). Thus, 11 of the serpins identified to date from genome analysis, need further validation and the information available about their physiological functions is therefore very partial, even inexistent. Surprisingly enough, Serpine1 was not identified in this analysis. To investigate whether *Serpine1* exists as a pseudogene in chicken or whether it was not annotated correctly in databases, Serpine1 was searched in the chicken genome using reciprocal tBLASTn. The serpin was not found and the closest gene identified by reciprocal tBLASTn against human genome referred to *SERPINE2*, which was actually identified in both Pubmed and Ensembl databases and referenced in Table 1. Thus, to date, we cannot ascertain that this gene is absent due to errors in genome annotation or whether it actually disappeared in chickens during evolution. Chicken ov-serpins are largely represented as 10 clade B serpins could be identified [1,2]. These ov-serpins are clustered on a 150 kb locus chromosome 2q (Fig. 1B) and comprise *Serpinb1*, *Serpinb2*, *Serpinb5*, *Serpinb6*, two *Serpinb10* homologs (*Serpinb10*, *Serpinb10b/MENT*), *Serpinb12* and *Serpinb14*, *Serpinb14b* and *Serpinb14c* namely ovalbumin and its related genes Y (OVAY) and X (OVAX). Another cluster on chromosome 5 was identified containing 7 members of the *Serpina* family (Fig. 1E). This cluster includes 5 homologs of alpha1-antitrypsin/alpha1-proteinase inhibitors, *Serpina1*, *Serpina3*, *Serpina4*, *Serpina5*, *Serpina9*, which correspond to human antitrypsin, alpha1-antichymotrypsin, kallistatin, Protein C inhibitor, and SERPINA9, respectively. Out of these 27 serpins, only 15 are actually recovered in the chicken egg in which the biological significance and biological activity intimately depends on the process of egg formation and on their subsequent localization (eggshell/egg white/vitelline membrane/yolk). This first part will review the evolution of these chicken serpins in vertebrate species and their distribution in the various egg compartments.

1.1. Phylogenetic analysis of chicken serpins

In serpin genes, some have shown a strong correlation between genomic organization, patterns of amino acids at specific sites, and insertion/deletion patterns, which contributed to identify serpin groups and to decipher vertebrate serpin evolution [3,4]. Serpin genes have rapidly evolved; a high sequence divergence is found between all serpin clades, the sequence identity varying from 22% to 29%.

Phylogenetic analysis of the 27 serpins found in the chicken genome shows that serpin genes have been originated and duplicated before the divergence of teleosteans. Another duplication event occurred after divergence between species, for example, the clade A of *Gallus gallus* encompasses seven *Serpina* genes with a sequence identity around 47%. The same phenomenon is observed for mammal and fish.

Using the phylogenetic trees available in Ensembl (http://www.ensembl.org), and because of the stringency of the method used, three serpins groups are distinguished. The first phylogenetic tree contains serpins from clade B, C, E and I (Fig. 2), the second refers to serpins from clade A, D, F, G and H (Fig. 3), and the last tree, contains only one clade A serpin, *Serpina8*.

The clade B serpin, present in the first tree, contains ovalbumin gene (*Serpinb14*) and its recently duplicated OVAY (*Serpinb14b*) and OVAX (*Serpinb14c*) [5–7]. OVAX, is not annotated in Ensembl but by using reciprocal tBLASTn alignment method (http://blast.ncbi.nlm.nih.gov/Blast.cgi), this gene could be easily identified as the closest neighbor of OVAY in chromosome 2 with a 73% of protein sequence identity as previously shown [1,2]. The evolution of clade B serpins starts before the split of bony fishes and tetrapods, 450 millions years ago, leading to at least six clade B serpin genes found in mammal and bird genomes. The *G. gallus* genome contains ten clade B serpin genes on chromosome 2 in the same syntenic locus (Figs. 1 and 2). Six of them could also be found in *Homo sapiens* genome (*SERPINB1, B2, B5, B6, B10, B12*). Chicken clade B serpins (Figs. 1 and 2) are syntenic with two loci on chromosome 6 and 18 in human and other mammalian genomes, which suggests a split resulting to a break of synteny in mammals [2]. Recent duplications events occurred independently in fishes, mammals and birds, after divergence between these species. Due to recent duplication, avian Serpinb14 (ovalbumin), Serpinb14b (OVAY) and Serpinb14c (OVAX), have no human or other mammalian species orthologues and seem to be specific to oviparous species [1,8,9]. Three orthologues to ovalbumin are referenced in duck, flycatcher and turkey in Ensembl database but information is lacking for other oviparous species. However, it is noteworthy that we found a potential orthologous of Serpinb14c in *Alligator mississippiensis* (A0A0Q3ZV65), sharing 56% protein sequence identity with the chicken homolog. These ovalbumin genes adapted to oviparous species, are supposed to have lost their protease inhibitor activity [1], and potentially acquired specific properties adapted to the development of an embryo in an egg exposed to terrestrial environments [8,9].

Clade A, D, F, G and H serpins are found in the second phylogenetic tree. As shown in Fig. 3, except clade A serpins, each of these serpins has an orthologue in both *G. gallus* and *Bos taurus*.

Similarly to clade B serpins, and for both species (*G. gallus*; *B. taurus*), duplication events led to the presence of several clade A serpins after species divergence (Fig. 4). Concerning *G. Gallus* genome, this duplication gave rise to Serpina1, a3, a4, a5, a9, a10 and a12. These serpins have similar peptidase inhibitor function and are essentially expressed by the liver. The synteny analysis (http://www.genomicus.biologie.ens.fr/) reveals that clade A genes are localized in a gene cluster in chicken chromosome 5 (Fig. 3). The same phenomenon is observed in *B. Taurus*, where all clade A serpins are localized in a unique gene cluster on chromosome 21. Clade A serpins show multiple recent duplications leading to ten

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