DISCUSSION

It has long been known that oviducts of amphibians secrete their glycoproteins to coat the outermost layer, so called "jelly layer" of the ovulated eggs. The production and secretion of these glycoproteins is under the hormonal regulation, mainly progesterone (Thornton, 1972; Vitaioli *et al*., 1990) and to a lesser extent hCG (Thornton, 1972). However, the information on the characterization of carbohydrate moieties on such glycoprotein secreted from a given part of oviduct, especially in the Thai rice field frog, *R. tigerina*, is still very limited. Specifically, the influence of progesterone hormone on the pattern of post-translationally modified proteins, which may in turn affect the deposition of glycoproteins on egg's jelly layer, has never been reported and would be an interesting issues for discussion in this study.

Jelly substances are reported to be produced in part by epithelial lining cells of pars recta (PR) and to a major extent by mucosal glands (MG) which are extensively increased in size during the active phase of jelly accumulation in the oviduct. In this study, we further asked the question whether each part of oviduct contributes any different glycoprotein components to the oviductal secretion. It was also interesting to know if the cells in the epithelial ridges (particularly of PCs) or mucosal glands, chiefly contributed to the glycosylated products of oviductal secretion. To demonstrate which epithelial cells were involved in producing oviductal glycoproteins, lectin histochemistry was performed. Our results revealed that basal lining epithelial cells, the NCC, of the PR region were intensely reactive with all lectins used in this study including, BSL-I (recognizing α-GalNAc and α-Gal), ConA (α-D-Man and α-D-Glu), LCA (α-D-Man and α-D-Glu), RCA-I (α-Gal and β-Gal), UEA-I (fucose), and WGA (GlcNAc and sialic acid). The results suggested that these NCC cells were actively involved in secreting glycosylated proteins containing many sugar moieties into oviductal secretion. In epithelial folds of the PC regions, recognition of lectins was divided into those stained NCC or CC cells or both. Lectins ConA and UEA-I were specific to CC cells while lectins RCA-I and WGA were specific to NCC cells. Although lectins BSA-I and LCA recognized both NCC and CC cells, BSA-I tended to be more specific to NCC than CC while LCA had relatively low reactivity to both cell

types. Despite the fact that LCA and ConA are lectins that are known to have similar sugar recognition, i.e., α-D-Man and α-D-Glu, it is unclear to us to explain the discrepancy in the staining results of these two lectins on the the oviductal tissues.

Regardless of the source producing these glycosylated proteins, the end-product of oviductal secretion detected in the lumen of oviducts in *R. tigerina* was enriched in many types of carbohydrate moieties with α-D-Man or α-D-Glu being the most prominent sugar residues. This interpretation was deduced from the lectin streptavidin blotting indicating the broadest reactivity of ConA among other lectins in the blots of secretory proteins. The obtaining results herein was greatly contradictory to the results of carbohydrate profiles reported in the toads *Bufo arenarum*, demonstrating that the oviductal secretions of *B. arenarum* contained no mannose residues but was rather enriched in galactoses, GalNAc, and fucoses (Silvia *et al*., 1997). This discrepancy between two species of amphibians would probably reflect the species-specific modification of carbohydrates which may in turn play a crucial role in species-specific regulation in the certain event, especially those during fertilization processes. Furthermore, it has generally been believed that the similar glycoprotein components in the oviductal secretions would be gradually accumulated from the early part (i.e., PR) up to the ended part (i.e., PC) of the oviduct (Low *et al*., 1967). In fact, our results in this study have provided a significant finding revealing that different parts of oviduct contributed different sets of glycoproteins which had the same carbohydrate composition into the oviductal secretions. Giving some example for glycoproteins enriched in α-Gal and α-GalNAc (recognized by BSL-I), PR secreted 180 and 150 kDa glycoproteins containing Gal or GalNAc while PC2 secreted 130 kDa glycoproteins and PC3 and PC4 specifically secreted the medium ranged (70 kDa) glycoproteins (Figure17). Our findings also added a new role of PC epithelial ridge in contributing a significant amount of glycoproteins, not only mucin or mucopolysaccharides as has been reported previously (Prachaney, 1996), into oviductal secretions. The significance of these PC-derived glycoproteins in any steps of fertilization, apart from those derived from PR region, would rather be an interesting issue to be investigated and would also be considered as a novel role for PC oviductal epithelium.

The promising role of progesterone in provoking oviductal protein production and secretion has been anticipated across many amphibian species, including *Bufo arenarum*, *Rana esculenta* and *Rana dybowskii* (Thornton, 1972; Fernández *et al*., 1997; Bandyopadhyay *et al*., 1998). As shown in this study, oviduct of *R. tigerina* was also actively stimulated upon administration with a single dose of progesterone. The overall increase in oviductal mass and circumference could be generally observed. Histologically, the changes in lectin staining patterns when compared the patterns in the seasonal breeders with those of hormonal administrative animals could be noticed. One of the most prominent effects was the enhanced staining in both CC and NCC cells in the epithelial ridges of the progesterone injected animals. The higher staining intensity of lectins UEA-I (recognizing Fuc residues) and RCA-I was predominant in the NCC and CC cells of the early part of oviduct. This suggested that production of fucose- and galactose-based glycoproteins was highly enhanced upon treating the animals with progesterone. Our results also elaborated the effect of progesterone on generally and selectively enhancing the release of the specific glycoproteins into oviductal contents. Examples of glycoproteins generally enhanced by progesterone in all parts of oviducts were glycoproteins recognizable by BSL-I and RCA-I. To our surprise, progesterone also showed the inhibitory effect on the secretion of some glycoproteins baring Fuc and GlcNAc or sialic acid residues recognizable by UEA and WGA, respectively. In addition, for LCA recognizable carbohydrates, it was found that progesterone enhanced the secretion of Man/Glu containing glycoproteins in the ended parts of oviduct (PC3 and PC4), on the other hand, the hormone seemed to inhibit secretion of the same glycoproteins in the early part of oviduct (PR and PC1). At present, it is still unclear how the same hormone could exert both enhancing effect and the reversal effect on different types of glycoproteins' secretion in the entire length of the oviduct as well as the differential secretion of the same glycoprotein in the early and ended parts of the oviduct.

Production of glycoproteins along the entire parts of oviduct is highly specific to the cells lining the oviductal epithelium rather than in the glandular tissue itself. This implication was drawn from the results of lectin histochemistry revealing that substances in the mucosal glands were non-reactive to slightly reactive with many types of lectins while the epithelial cells were moderately to highly reactive with lectins. One reason that may explain this finding was that the mucosal glands' substances could possibly contain different carbohydrate moieties from those of epithelial cells which were not recognized by lectins used in this study. In addition, carbohydrate compositions of the mucosal glands may be highly modified sugars by cationic molecules with the most well characterized ones being sulfated groups. This modification rendered the glandular contents highly negatively charged macromolecules which may not recognized by most of the lectins. It is also well documented that these highly charged polymers, for instance chondroitin sulfates and dermatan sulfates, have also been known to have a higher ordered arrangement to form a tightly packed structure appearing as a "bottle brush" or "feathery" structure such that reported for glucosaminoglycans. With the major reasons of highly charged effect and the packed structural organization, the substances of mucosal glands were thus poorly reactive with most lectins used in this study. Our results also indicated that glycoprotein substances from the epithelial cells were not secreted for storing purpose in the mucosal glands but were rather secreted directly into oviductal lumen as part of the jelly substances. In addition, as we could detect the glycoproteins specific for both CC and NCC cells (see preceding paragraph) in the oviductal secretions, it therefore remained to be investigated whether both CC and NCC cells (rather than only NCC cells) could secrete their glycoprotein products to be associated with other jelly compositions.

Many previous studies have laid the background on the physiological functions of substances derived from oviductal jelly. This includes the modification sperm binding ligand on the eggs. In this regard, one of the well studied examples is the conversion of glycoprotein in the egg coat of *X. laevis* by the secretory granules of PR and was later termed "oviductin" according to its origin (Hardy and Hedrick, 1992). The glycoprotein with the molecular mass of 43 (gp 43) in the coelomic envelope (CE)

is proteolytically converted into small glycoprotein (gp41) component of VE when the eggs pass through the early part of oviduct (Gerton and Hedrick, 1986). On the other study, the diffusible components of the jelly substances prepared by incubation the ovulated eggs in the high salt buffer has been claimed to promote the sperm's ability to fertilize dejellied eggs. These diffusible proteins are in the broad spectrum containing proteins smaller than 50 kDa which are proven to be self aggregated and required during sperm binding to the eggs. Other functions of jelly components include initiation of sperm capacitation, induction of the sperm acrosome reaction as well as the protective function for developing embryos (Glabe and Vacquier, 1978). In *R. tigerina,* all of these functions of jelly substances are not yet well understood. The information obtained in this study would be significant and considerable as a high impact ground work to link between histochemical findings and physiological functions of oviductal secretion in the future.

CONCLUSION

Using lectin histochemistry and lectin blotting as major approaches in this study, we have obtained a considerable amount of the results that may be used as an important information for the future physiological studies. These included:

1. Histochemical approaches using 6 types of lectins in the oviductal tissues collected during breeding period indicated that the staining of lectins RCA-I and WGA was highly specific to the NCC while the staining of lectins ConA and UEA was rather specific to the CC.

2. It was apparent that the staining of most lectins in the oviductal tissues generally decreased during non-breeding period.

3. Staining of all lectins was detected in a much greater extent in the epithelial folds or ridges than in the mucous glands, implicating that small glycoproteins found in the oviductal secretions were mainly derived from epithelial cells, not from the mucous glands.

4. In the different parts of oviduct, different molecular weight of the same glycoproteins could be seen. This could be due to differential production of the given glycoproteins from each part of the oviduct or due to selective absorption of certain glycoproteins by the oviductal epithelium.

5. Progesterone administration during non-breeding period had both enhancing and inhibitory effects on the cellular production (as gauged by lectin histochemistry) and the secretion of glycoproteins into the oviductal gelatinous components (gauged by lectin blotting).

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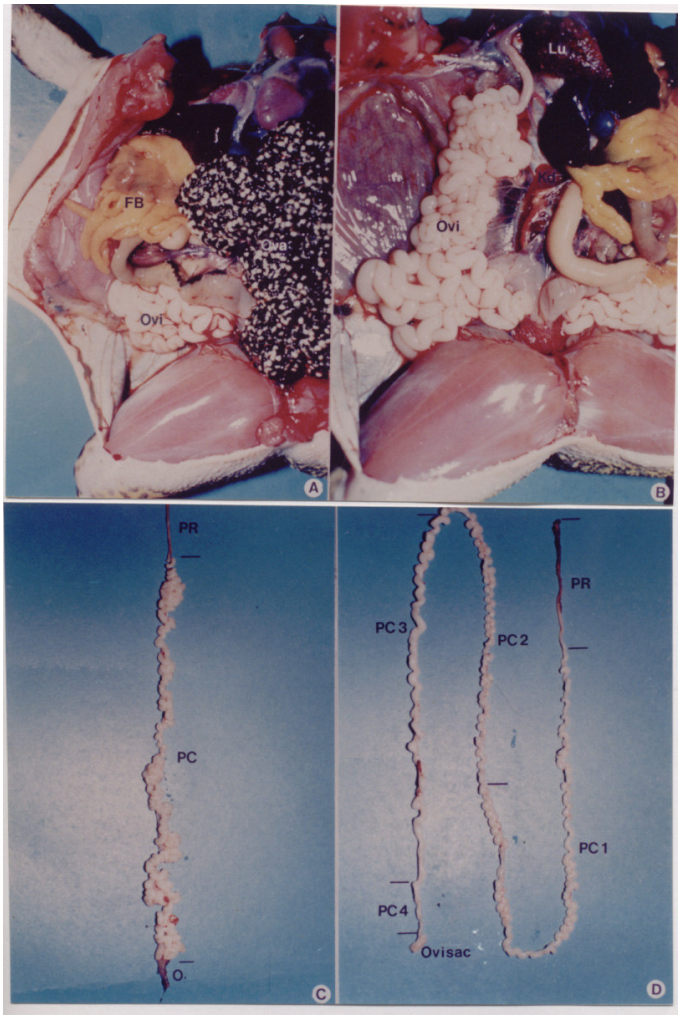
Appendix

Appendix Figure 1 **Mature female frog (*Rana tigerina*).**



Appendix Figure 2 **The internal organs of mature female frog.**

A: Ovary (Ova), Oviduct (Ovi) and Fat body (FB)

B: The position of oviducts (Ovi) in abdominal cavity.

Lu = lung, Kd = kidney

C,D: Oviducts showing pars recta (PR) and pars convolute (PC) as subdivided into PC1, PC2, PC3 and PC4. O = ovisac

Appendix Table 1 Lectin sources and their sugar specificity.

Lectin source	Lectin acronym	Sugar specificity
Bandeiraea simplicifilia	BSL-I	α-GalNAc and α-Gal
Canavalia ensiformis	ConA	α-Man > α-Gal > α-GlcNAc
Lens culinaris	LCA	α-Man > α-Glc > α-GlcNAc
Ricinus communis	RCA-I	β-Gal > α-Gal >> GalNAc
Ulex europaeus	UEA-I	α-L-Fuc
Triticum vulgare	WGA	GlcNAc > β- GlcNAc > Sialic acids

Source: Kiernan (1999)

Appendix Table 2 Some lectins used as histochemical reagents

Source of lectin (Name, where available)	Common abbreviation	Specific affinity
Group 1.Affinity for glucose and mannose		
Canavalia ensiformis (concanavalin A)	ConA	α-Man > α-Glc >α-GlcNAc
Galanthus nivalis (snowdrop lectin)	GNL	α-1→3-Man
Lens culinaris (lentil lectin)	LCA	α-Man > α-Glc >α-GlcNac
Narcissus pseudonarcissus (daffodil agglutinin)	NPA	α-1→6-Man-α-1→6-Man-α-1→6-Man
Pisum sativum (pea lectin)	PSA	α-Man > α-Glc >α-GlcNAc
Group 2.Affinity for *N*-acetylglucosamine		
Griffonia simplicifolia (*Bandeiraea simplicifolia*; Griffonia lectin II)	GSL-II or BSL-II	α-GlcNAc and β-GlcNAc
Lycopersicon esculentum (tomato lectin)	LEL or TL	GlcNAc oligomers GlcNAc-β-1→4-GlcNAc=
Phytolacca americana (pokeweed mitogen)	PAA or PWM	Gal-β-1→4-GlcNAc
Solanum tuberosum (potato lectin)	STA	GlcNAc-β-1→4-GlcNAc
Triticum vulgare (wheat germ agglutinin)	WGA	GlcNAc-β-1→4-GlcNAc>β-GlcNAc>Sialic acids
Group 3. Affinity for galactose and *N*-acetylgalactosamine		
Arachis Hypogaea (peanut agglutinin)	PNA	Gal-β-1→3-GalNAc>α- and β-Gal
Artocarpus integrifolia (jacalin, jackfruit lectin)	Jac	Gal-β-1→3-GalNAc
Bauhinia purpurea (Bauhinia lectin)	BPL	Gal-β-1→3-GalNAc> α-GalNAc
Dolochos biflorus (horse gram lectin)	DBA	GalNAc-α-1→3-GalNAc>> α-GalNAc
Glycine max (soybean agglutinin)	SBA	α- and β-GalNAc> α- and β-Gal
Griffonia simplicifolia (*Bandeiraea simplicifolia*; Griffonia lectin I)	GSL-I or BSL-I	α-GalNAc (isolectin A) and α-Gal (isolectin B)
Maclura pomifera (osage orange lectin)	MPA	α-GalNAc> α-Gal
Phaseolus vulgaris (kidney bean lectin)	PHA-E or PHA-L	Gal-β-1→4-GalNAc-β-1→2-Man
Ricinus communis (castor bean agglutinin I)	RCA-I or RCA_{120}	β-Gal>α-Gal>>GalNAc

Appendix Table 2 Some lectins used as histochemical reagents (continued)

Source of lectin (Name, where available)	Common abbreviation	Specific affinity
Vicia villosa (hairy vetch lectin)	VVA	(Protein)-α-GalNAc>Gal-α-1→3-GalNAc> β-GalNA
Group 4. Affinity for L-fucose		
Anguilla anguilla (eel lectin)	AAA	α-L-Fuc
Lotus tetragonobolus (*Tetragonobolus purpureus*; asparagus pea lectin)	LTA	α-L-Fuc
Ulex europaeus (gorse lectin I)	UEA-I	α-L-Fuc
Group 5. Affinity for sialic and uronic acids		
Aplysia depilans (Apysia gonad lectin)	AGL	Galacturonic acid>>D-Gal
Bovine or porcine lung, pancreas salivary glands (aprotinin; bovine trypsin inhibitor)		Uronic acid and sialic acids
Limax flavus (slug lectin)	LFA	N-Acetylneuraminic acid>N-glycolylneuraminic acid
Limulus polyphemus (limulin or horseshoe crab lectin)	LPA	N-Acetyl (or N-glycolyl)neuraminic acid-α-2→6-GalNAc
Sambucus nigra (elder bark lectin)	SNA	N-Acetylneuraminic acid-α-2→6-(Gal or GalNAc)
Tritrichomonas mobilensis	TML	Some sialic acids

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