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Cortical alveoli in oocytes of freshwater neotropical teleost fish

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ABSTRACT

Depending on the species, the teleost cortical alveolus (CA) has from one to several layers of small to large cortical vesicles forming a continuous or discontinuous collar in the peripheral ooplasm. The histochemical composition of the CA, which also varies among species, is made of neutral glycoprotein, carboxylated glycoconjugate, neutral glycoprotein plus carboxylated glycoconjugate, sulfated glycoconjugate, neutral glycoprotein plus sialic acid-rich glycoprotein. The CA was sudanophobic in all species analyzed. The morphology and contents of the CA seem to express common characters among many of the groups studied. Variations in the morphology and contents of the CA may be related to different mechanisms of polyspermy blockade.

KEY WORDS: Neotropical teleosts - Oocytes - Cortical alveoli.

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INTRODUCTION

The cortical vesicles (CV), or cortical alveoli (CA), are the first conspicuous cytoplasmic structures of teleost oocytes visible under light microscopy (Selman & Wallace, 1989). They have been given several names, most frequently being called yolk vesicles. However, this term is inappropriate because these vesicles do not form yolk, in the strict sense of the word. Rather, they are analogous to the cortical granules of other vertebrates and invertebrates.

Ultrastructural studies (Selman *et al.*, 1986) and electrophoresis and autoradiography (Korfsmeier, 1966; Tesoriero, 1980; Selman *et al.*, 1986, 1988) have demonstrated that the CA contents are endogenously synthesized, involving endoplasmic reticulum and Golgi complex.

Determination of the CV chemical composition is essential for understanding their role in fertilization and early embryonic development (Hart, 1990). Histochemical studies have shown that CV contain carbohydrates and proteins (Selman *et al.*, 1986; Mayer *et al.*, 1988). The chemical nature of the carbohydrates contained in the CA is discussed by Tesoriero (1980), Selman *et al.* (1988), Verma & Thakur (1988) and Bazzoli & Rizzo (1990). The CA of several fishes have lectins with bond properties specific to sugars (Krajhanzl *et al.*, 1984), but the function of these lectins is unknown. Antibodies produced against purified ovarian lectins (Nosck, 1984) and CA glycoconjugates (Masuda *et al.*, 1986; Selman *et al.*, 1988) show that CV and CA are identical in structure and contents. To date, there have been no studies on the CA of neotropical fish. The present study analyzes the morphology and histochemical composition of the CA of 102 neotropical freshwater teleost species.

MATERIALS AND METHODS

Fishes, with maturing ovaries, belonging to 102 species in 21 families were captured in several Brazilian hydrographic basins (Table I).

Ovary fragments from one to five fishes of each species were fixed in Bouin's fluid, embedded in paraffin, and cut into section (4-7 μ m thick) for histological study and for histochemical demonstration of carbohydrates and proteins. The sections were stained with hematoxylin-eosin, Gomori's trichrome and Mallory's trichrome. The histological study was performed in well preserved and spherical oocytes sectioned through the nucleus.

Analyses of carbohydrates and proteins in the cortical vesicles (alveoli) were performed using the following histochemical techniques, from Pearse (1985): periodic acid-Schiff (PAS), for carbohydrates with 1:2 glycol groups (glycogen, neutral glycoproteins and sialomucins); salivary amylase (30 min at 37°C), for extraction of glycogen, followed by PAS; Alcian blue (AB) at pH 2.5, for sulfated and carboxylated acid glycoconjugates including sialomucins; AB at pH 0.5, for sulfated glycoconjugates; AB at pH 2.5 plus PAS, for neutral and acid glycoconjugates; ninhydrin-Schiff, for proteins with NH_2 group; hydrolyse with 0.1 N HCl (8 h at 60°C), for extraction of sialic acid, followed by PAS and AB pH 2.5 (Quintarelli *et al.*, 1961); and the combined method of Alcian yellow (AY) pH 2.5 plus AB pH 0.5, for identification of different acidic groups (Ravetto, 1964).

TABLE I - Histological characteristics and contents of cortical alveoli in 102 species of neotropical freshwater teleost fish (arranged according to the phylogenetic classification of Lauder & Liem, 1983).

Species	River basin	Cortical alveoli	
		Type	Contents
OSTEOGLOSSIFORMES			
Arapaimidae			
<i>Arapaima gigas</i>	Amazonas	CMS	NEG-SIG
Osteoglossidae			
<i>Osteoglossum bicirrhosum</i>	idem	idem	idem
CHARACIFORMES			
Characidae			
<i>Cretochanes affinis</i>	São Francisco	CML	NEG-CAG
<i>Astyanax bimaculatus</i>	idem	CMS	idem
<i>Astyanax fasciatus</i>	Paraná	idem	idem
<i>Moenkhausia intermedia</i>	idem	idem	idem
<i>Tetragonopterus chalceus</i>	São Francisco	idem	idem
<i>Brycon lundii</i>	idem	DMS	CAG
<i>Brycon orbignyanus</i>	Paraná	idem	idem
<i>Triportheus guentheri</i>	São Francisco	DOS	NEG
<i>Roeboides paranensis</i>	Paraná	COL	NEG-CAG
<i>Charax gibbosus</i>	Paraguai	idem	idem
<i>Galeocharax knerii</i>	Paraná	DMS	CAG
<i>Acestrorhynchus britskii</i>	São Francisco	CML	NEG-CAG
<i>Acestrorhynchus lacustris</i>	Paraná/São Francisco	idem	idem
<i>Salminus brasiliensis</i>	São Francisco	CMS	CAG
<i>Salminus bilarii</i>	Paraná/São Francisco	idem	idem
<i>Salminus maxillosus</i>	Paraná	idem	idem
<i>Brachybalcinus franciscoensis</i>	São Francisco	DMS	idem
<i>Myleus micans</i>	São Francisco	CML	SAG
<i>Myleus tiete</i>	Paraná	idem	idem
<i>Myloplus levis</i>	idem	idem	idem
<i>Mylossoma orbignyanum</i>	idem	idem	idem
<i>Serrasalmus brandtii</i>	São Francisco	CML	SAG
<i>Serrasalmus marginatus</i>	Paraná	idem	idem
<i>Pygocentrus piraya</i>	São Francisco	idem	idem
<i>Serrasalmus spilopleura</i>	Paraná	idem	idem
<i>Pygocentrus nattereri</i>	idem	idem	idem
<i>Characidium cf. fasciatum</i>	Santa Maria Vitória	CMS	CAG
Erythrinidae			
<i>Hoplias cf. lacerdae</i>	Paraná/São Francisco	CMS	NEG-CAG
<i>Hoplias malabaricus</i>	idem	idem	idem
Anostomidae			
<i>Leporinus crassilabris</i>	Jequitinhonha	DMS	NEG
<i>Leporinus elongatus</i>	Paraná/São Francisco	idem	idem
<i>Leporinus friderici</i>	Paraná	idem	idem
<i>Leporinus reinhardti</i>	São Francisco	idem	idem
<i>Leporinus taeniatus</i>	idem	idem	idem
<i>Leporinus piau</i>	idem	idem	idem
<i>Leporinus obtusidens</i>	idem	idem	idem
<i>Leporinus striatus</i>	Paraná	idem	idem
<i>Leporellus vittatus</i>	idem	idem	idem
<i>Leporinus amblyrhynchus</i>	idem	CML	idem
<i>Leporinus octofasciatus</i>	idem	DML	idem
<i>Schizodon nasutus</i>	idem	idem	idem
<i>Schizodon knerii</i>	São Francisco	idem	NEG-CAG
Curimatidae			
<i>Steindachnerina elegans</i>	São Francisco	DOS	NEG
<i>Cyphocharax modestus</i>	Paraná	idem	idem
<i>Steindachnerina insculpta</i>	idem	idem	idem
<i>Cyphocharax nagelii</i>	idem	idem	NEG-CAG
<i>Cyphocharax cf. spilurus</i>	Paraguai	idem	idem

(continued)

(continued)

Species	River basin	Cortical alveoli	
		Type	Contents
<i>Curimatella lepidura</i>	São Francisco	DML	idem
Prochilodontidae			
<i>Prochilodus costatus</i>	São Francisco	DMS	CAG
<i>Prochilodus</i> cf. <i>bartii</i>	Jequitinhonha	idem	idem
<i>Prochilodus argenteus</i>	São Francisco		idem
<i>Prochilodus lineatus</i>	Paraná	idem	idem
Cynodontidae			
<i>Raphiodon vulpinus</i>	Paraná	DMS	NEG-SAG
Parodontidae			
<i>Parodon tortuosus</i>	Paraná	COS	CAG
SILURIFORMES			
Gymnotidae			
<i>Gymnotus carapo</i>	Not determined	DMS	
Sternopygidae			
<i>Eigenmannia virescens</i>	São Francisco	CML	NEG-CAG
Ramphichthyidae			
<i>Rhamphichthys rostratus</i>	Paraná	CMS	SAG
Doradidae			
<i>Franciscodoras marmoratus</i>	São Francisco	DOS	NEG
<i>Rbinodoras d'orbignyi</i>	Paraná	idem	idem
<i>Trachydoras paraguayensis</i>	idem	idem	idem
<i>Pterodoras granulatus</i>	idem	idem	idem
<i>Wertheimeria maculata</i>	Jequitinhonha	idem	idem
Auchenipteridae			
<i>Trachelyopterus galeatus</i>	São Francisco	CML	NEG
<i>Parauchenipterus</i> cf. <i>jequitinhonbae</i>	Jequitinhonha	idem	idem
<i>Trachelyopterus nuchalis</i>	Paraná	idem	idem
Ageneiosidae			
<i>Ageneiosus ucayalensis</i>	Paraná	DMS	CAG
<i>Ageneiosus valenciennesi</i>	idem	idem	idem
Pimelodidae			
<i>Bergiaria westermanni</i>	São Francisco	DMS	NEG
<i>Conorhynchus controstris</i>	idem	idem	idem
<i>Pimelodus fur</i>	Paraná	idem	idem
<i>Pimelodus maculatus</i>	idem	idem	idem
<i>Pimelodus paranaensis</i>	idem	idem	idem
<i>Pseudopimelodus zungaro</i>	idem	idem	idem
<i>Rhamdia</i> cf. <i>quelen</i>	idem	idem	idem
<i>Rhamdia bilarii</i>	idem	idem	idem
<i>Iberingichthys labrosus</i>	idem	idem	idem
<i>Hemisorubim platyrhynchus</i>	idem	idem	idem
<i>Sorubim</i> cf. <i>lima</i>	idem	idem	idem
<i>Pseudoplatystoma coruscans</i>	São Francisco	idem	NEG-CAG
<i>Steindachneridion amblyura</i>	Jequitinhonha	CMS	NEG
<i>Lophiosilurus alexandri</i>	São Francisco	COS	idem
Trichomycteridae			
<i>Trichomycterus</i> cf. <i>alternatu</i>	Santa Maria Vitória	DOS	NEG
Hypophthalmidae			
<i>Hypophthalmus marginatus</i>	Amazonas	DOS	NEG
Callichthyidae			
<i>Hoplosternum littorale</i>	Paraná	CML	CAG
Loricariidae			
<i>Hypostomus francisci</i>	São Francisco	CMS	CAG
<i>Rhinelepis aspera</i>		idem	idem

(continued)

(continued)

Species	River basin	Cortical alveoli	
		Type	Contents
<i>Loricaria lentiginosa</i>	Paraná	idem	idem
<i>Loricaria</i> sp.	idem	idem	idem
<i>Loricariichthys</i> sp.	idem	idem	idem
<i>Hypostomus</i> sp.	idem	idem	SAG
<i>Megalancistrus aculeatus</i>	idem	idem	idem
<i>Pterygoplichthys etentaculatus</i>	São Francisco	CML	CAG
<i>Hypostomus</i> aff. <i>albopunctatus</i>	Paraná	idem	idem
PERCIFORMES			
Cichlidae			
<i>Cichla ocellaris</i>	Paraná/São Francisco	COS	NEG-SIG
<i>Geophagus brasiliensis</i>	São Francisco	idem	idem
<i>Gymnogeophagus balzani</i>	Paraguai	idem	idem
<i>Geophagus</i> sp.	Jequitinhonha	idem	idem
Sciaenidae			
<i>Pachyurus francisci</i>	São Francisco	COS	NEG
<i>Pachyurus squamipinnis</i>	idem	idem	idem
<i>Plagioscion squamosissimus</i>	Amazonas/Paraná	idem	idem

Type of cortical alveoli: COL, continuous with one layer of large vesicles; COS, continuous with one layer of small vesicles; CML, continuous with multiple layers of large vesicles; CMS, continuous with multiple layers of small vesicles; DOS, discontinuous with one layer of small vesicles; DML, discontinuous with multiple layers of large vesicles; DMS, discontinuous with multiple layers of small vesicles.

Contents of the cortical alveoli: NEG, neutral glycoproteins; CAG, carboxylated acid glycoconjugates; SAG, sulfated acid glycoconjugates; SIG, sialic acid-rich glycoproteins.

For lipid demonstration, the following species were used: *Astyanax bimaculatus*, *Tetragonopterus chalcus*, *Tripottheus guentheri*, *Acestrorhynchus britskii*, *Acestrorhynchus lacustris*, *Salminus hilarii*, *Serrasalmus brandtii*, *Pygocentrus piraya*, *Hoplias* cf. *lacerdae*, *Leporinus piau*, *Leporinus reinhardtii*, *Leporinus taeniatus*, *Schizodon knerii*, *Steindachnerina elegans*, *Curimatella lepidura*, *Eigenmannia virescens*, *Hypostomus francisci*, *Cichla ocellaris* and *Plagioscion squamosissimus*. Ovary fragments were fixed either in formalin or formol-calcium, cut on cryostat into sections (10-12 μ m thick) and submitted to the following histochemical techniques, from Lison (1960) and Pearse (1985): Sudan black B, for lipids in general; Nile blue sulfate, for neutral and acidic lipids; and Sudan III and oil red O, for neutral lipids.

RESULTS

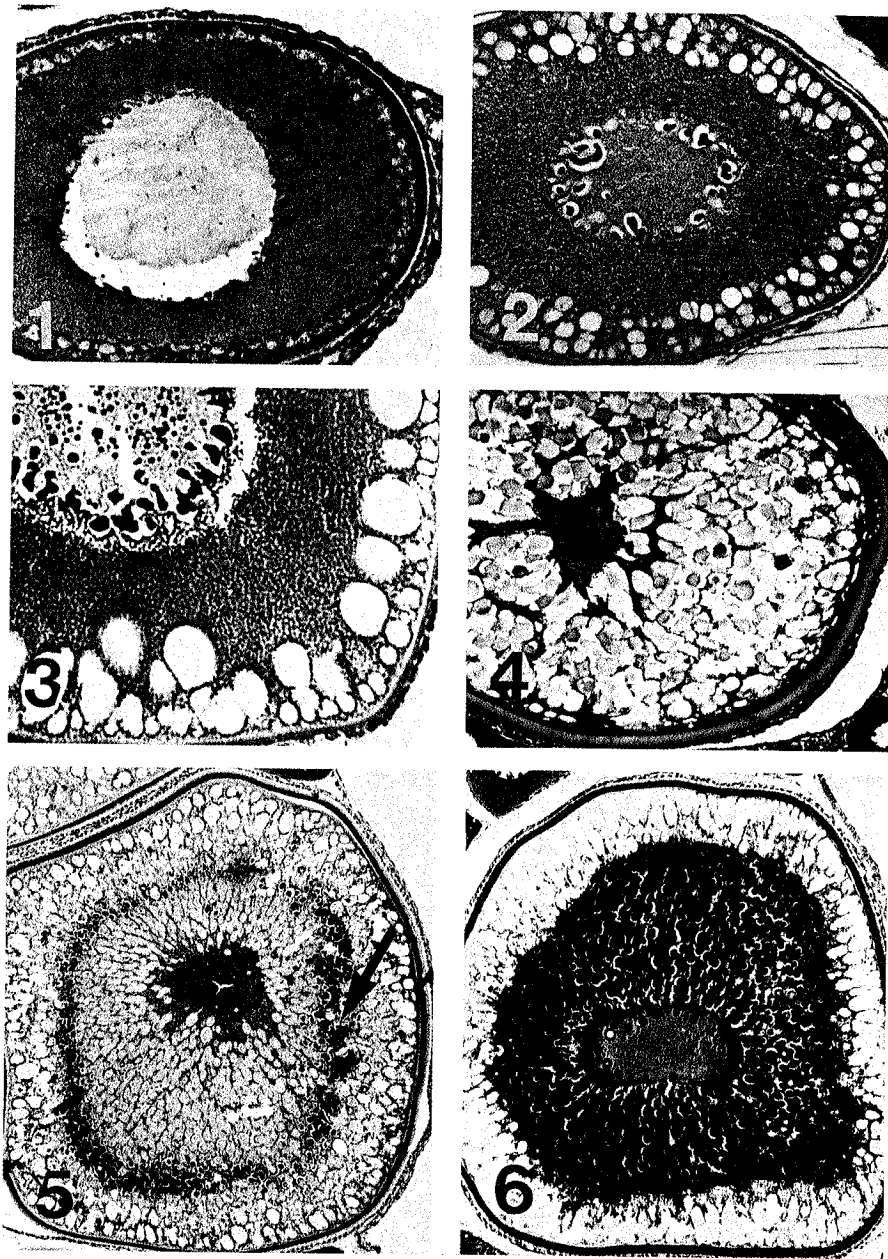
After routine histological preparations, the CV of the species under study occur as non-stained or slightly basophilic vacuolated structures. Frequently, clear CV are observed alongside others containing stained nucleoid in the same oocyte (Fig. 7). The cortical vesicles of all species first appear surrounding the peripheral ooplasm (Fig. 1) and gradually increase in number and volume (Figs 2 and 3) until they almost fill the oocyte cytoplasm (Fig. 4). Afterwards, they move to the peripheral ooplasm due to deposition of the proteinic yolk (yolk globules), which accumulates centripetally (Fig. 5). Thus, the CV are arranged in the periphery of the

oocyte to constitute the CA (Fig. 6).

The CA morphology varies according to the species (Table I), i.e., continuous with one layer of large (Fig. 8; 2% of the species) or small vesicles (Fig. 9; 4%), continuous with multiple layers of large (Figs 6 and 7; 19%) or small vesicles (Fig. 10; 21%), discontinuous with one layer of small vesicles (Fig. 11; 13%), and discontinuous with multiple layers of large (Fig. 12; 4%) or small vesicles (Fig. 13; 37%). Discontinuous CA with one layer of large vesicles was not observed.

The results on the histochemical reactions for CA carbohydrates and proteins are reported in Table II and Figures 14-16. Cortical alveoli probably have polysaccharides that form glycoconjugates or glycoproteins, because the ninhydrin-Schiff reaction, although weak, was positive in the CA of all species analyzed. The following glycoproteins and glycoconjugates were detected: neutral glycoproteins (35% of the species), carboxylated glycoconjugates (28%), neutral glycoproteins plus carboxylated glycoconjugates (18%), sulfated glycoconjugates (12%), neutral glycoproteins plus sialic acid-rich glycoproteins (6%), and neutral glycoproteins plus sulfated glycoconjugates (1%).

The PAS reaction remained unmodified after previous treatment with salivary amylase, showing that no glycogen occurred in the CA in the species studied. The CA are sudanophobic, as demonstrated by the Sudan



Figs 1-6 - **Fig. 1** - Cortical vesicles (CV) forming in the oocyte periphery of *Franciscodoras marmoratus* - HE - $\times 210$. **Fig. 2** - CV increasing in number and volume in the peripheral ooplasm - *Pygocentrus piraya* - HE - $\times 150$. **Fig. 3** - CV coalescing in the oocyte of *Myleus tiete* - HE - $\times 320$. **Fig. 4** - CV filling up the entire ooplasm - *Eigenmannia virescens* - HE - $\times 140$. **Fig. 5** - Deposition of yolk globules (arrow) in oocyte filled with CV - *Pygocentrus piraya* Gomori's trichrome - $\times 90$. **Fig. 6** - Continuous cortical alveoli (CA) composed by several layers of large CV - *Serrasalmus spilopleura* - Gomori's trichrome - $\times 90$.

black B, oil red O, Sudan III, and Nile blue sulphate reactions.

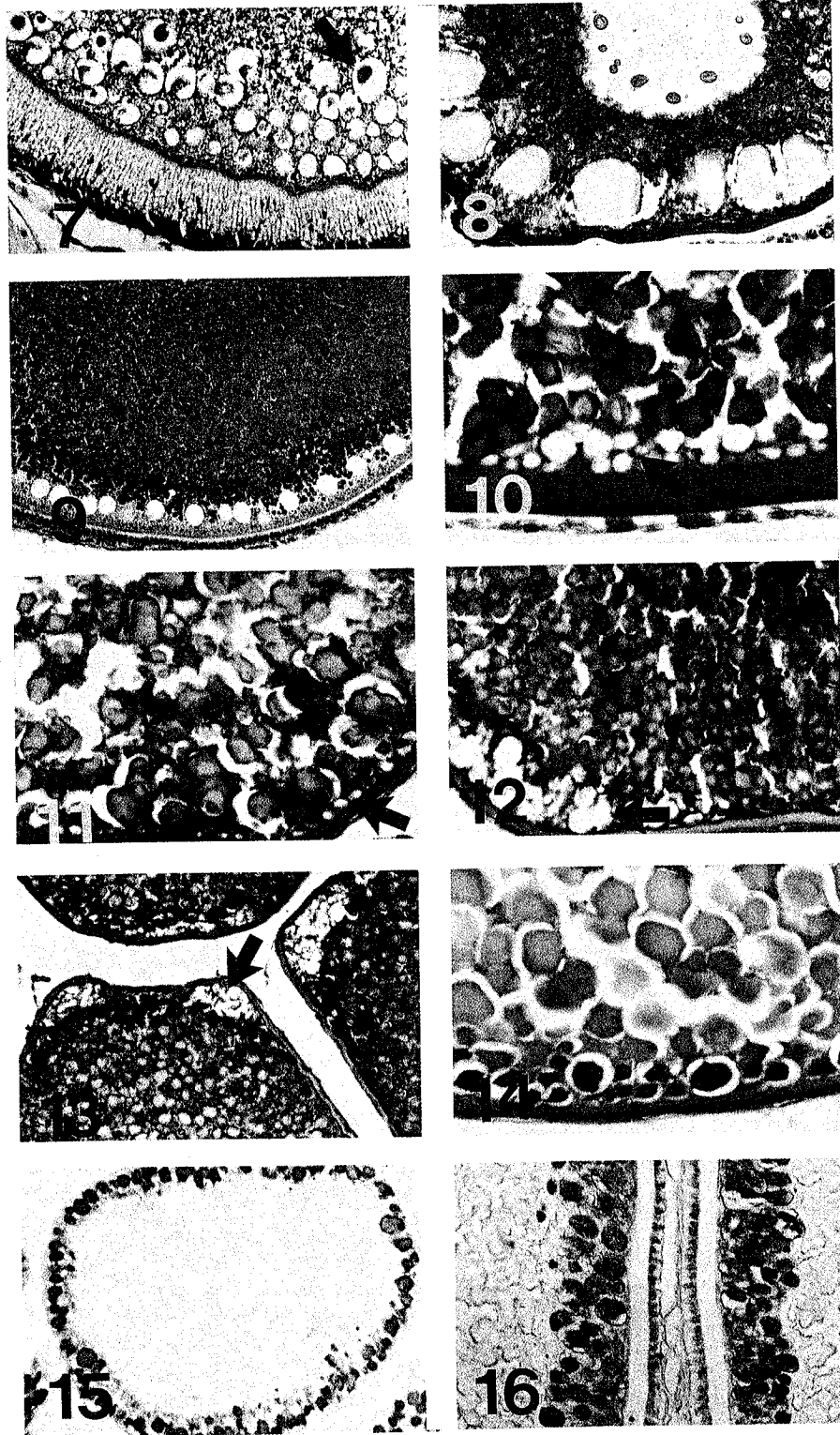
Morphology and contents of the CA seem to contain common characters within the members of a same genus, although some exceptions were noted (Table I).

DISCUSSION

A variety of CA morphology was observed in the present study. Previous works have also described

variations in the morphology of the CA, including small (Kobayashi, 1985), large (Selman *et al.*, 1988) or irregularly distributed CV in the cortical ooplasm (Hart & Donovan, 1983). Recently, oocytes of ten Brazilian teleost species were found to have either well or poorly developed CA (Bazzoli & Rizzo, 1990).

Morphological heterogeneity in CA has been attributed to fixation artifacts (Brummett & Dumont, 1981) or content extraction during histological preparation (Selman *et al.*, 1988). However, ultrastructural studies have recorded CV with an electron-dense core together with



Figs 7-16 - **Fig. 7** - CA of *Trachelyopterus galeatus* with electron-lucent CV and stained nucleoid (arrow) - HE - $\times 200$. **Fig. 8** - Continuous CA composed of a single layer of large CV - *Roeboides paranensis* - HE - $\times 210$. **Fig. 9** - Continuous CA with a single layer of small CV - *Lophiosilurus alexandri* - HE - $\times 230$. **Fig. 10** - Continuous CA with several layers of small CV (arrow) - *Salminus maxillosus* - HE - $\times 480$. **Fig. 11** - Discontinuous CA with a single layer of small CV (arrow) - *Steindachnerina elegans* - HE - $\times 480$. **Fig. 12** - Discontinuous CA with several layers of large CV (arrow) - *Curimatella lepidura* - HE - $\times 480$. **Fig. 13** - Discontinuous CA with several layers of small CV (arrow) - *Tetragonopterus chalceus* - HE $\times 200$. **Fig. 14** - PAS + CA - *Hoplias cf. lacerdae* - $\times 430$. **Fig. 15** - AB pH 2.5 + CA - *Acestorhynchus britskii* - $\times 110$. **Fig. 16** - AB pH 0.5 + CA - *Rhamplichthys rostratus* - $\times 190$.

TABLE II - Histochemical contents of the cortical alveoli in 102 species of neotropical freshwater teleosts, and respective reactions.

Contents of the cortical alveoli	Histochemical reactions					
	PAS	AB 2.5	AB 0.5	AY 2.5	NS	AH
Neutral glycoproteins	+	-	-	...	+	...
Carboxylated acid glycoconjugates	-	+	-	...	+	...
Neutral glycoproteins + carboxylated acid glycoconjugates	+	+	-	...	+	**
Sulfated acid glycoconjugates	-	+	+	-	+	...
Neutral glycoproteins + sialic acid-rich glycoproteins	+	+	-	...	+	*
Neutral glycoproteins + sulfated acid glycoconjugates	+	+	+	-	+	**

+, positive reaction; -, negative reaction; ..., not performed; PAS, periodic acid-Schiff; AB 2.5, Alcian blue pH 2.5; AB 0.5, Alcian blue pH 0.5; AY 2.5, Alcian yellow pH 2.5; NS, ninhydrin-Schiff; AH*, AB 2.5 and PAS reactions with diminished intensity after sialic acid hydrolysis; AH**, AB 2.5 and PAS reactions not modified after sialic acid hydrolysis.

homogeneous electron-lucent contents in the same oocyte (Inoue *et al.*, 1987; Ohta *et al.*, 1990). The significance of this heterogeneity in the CV populations is still unknown (Hart, 1990).

The weak ninhydrin-Schiff reaction in the CV of all species analyzed suggests the presence of reduced amounts of protein in these structures, similar to the report of Selman *et al.* (1986). The latter authors have found little, rough endoplasmic reticulum in oocytes in the CV stage of *Fundulus heteroclitus*. The substances detected in the CA of the 102 species analyzed coincide with those reported by Guraya (1986).

Some families analyzed in the present study tended to have similar CA morphology and chemical composition, independently of the habitat of the fishes. Despite these similarities, the histochemical and morphological patterns of the CA in the 102 species studied are apparently not related to phylogeny. According to Inoue *et al.* (1987), sialic acid-rich glycoproteins isolated from CA of fish oocytes representing few families seem to present different degrees of sialylation. On the basis of the diverse chemical nature of the polysaccharides, Yamamoto (1956) classified the CA into three types and suggested that the variations in the mucopolysaccharide chemical composition of the CV are related to the fish habitat: marine = neutral only, freshwater = acid only, and anadromous = neutral plus acid. These chemical patterns have been noted for several freshwater species in the present study.

In response to fertilization, the glycoprotein content of the CA is released into the perivitellinic space, blocking polyspermy (Kobayashi, 1985; Ohta *et al.*, 1990). It has been suggested that CA lectins of teleost species can also act in blocking polyspermy (Nosek, 1984), and substances released from the CA during the cortical reaction can take part in egg hardening (Hart, 1990). Therefore, variations in the morphology and chemical composition of the CA may express different mechanisms of polysper-

my blockade. In fact, Verma & Thakur (1988) suggested that the diversity of CV contents seems to be species-specific, thus enabling the performance of specific functions during fertilization.

In conclusion, the cortical alveoli, present in all species studied, showed similar pattern of development. Their form and arrangement varied among different species. They contained polysaccharides which formed glycoprotein and glycoconjugates. Although phylogenetic relationships could not be identified, morphological aspects and histochemical contents tended to be similar within members of a same genus.

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