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COMPARATIVE MORPHOLOGY OF THE YOLK NUCLEUS (BALBIANI BODY) IN FRESHWATER NEOTROPICAL TELEOST FISH

NILO BAZZOLI and HUGO PEREIRA GODINHO

Departamento de Morfologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Caixa Postal 2486 – 31270-901 Belo Horizonte, MG

(With 1 figure)

RESUMO

Morfologia Comparativa do Núcleo Vitelínico (Corpo de Balbiani) em Peixes Teleósteos Neotropicais de Água Doce

A morfologia do núcleo vitelínico (NV) ou corpo de Balbiani foi estudada em ovócitos pré-vitelogênicos de 107 espécies de teleósteos brasileiros pertencentes a 21 famílias. O NV sofre modificações morfológicas gradativas desde seu aparecimento na região justanuclear até seu desaparecimento no ooplasma periférico quando seu conteúdo fragmenta-se e dispersa-se de modo variado, dependendo da espécie, em uma das seguintes modalidades: grânulos finos ou grossos espalhados em todo ooplasma, grânulos finos ou grossos formando colar periférico e fragmentos dispersos no ooplasma. Em algumas espécies, o NV migra para a periferia do ovócito onde desaparece aparentemente sem fragmentar-se. O padrão de fragmentação e dispersão geralmente ocorre de maneira similar nos peixes de mesma família ou subfamília. Nossos achados morfológicos sugerem que, possivelmente, o NV destes teleósteos, possa atuar na formação de vesículas corticais (alvéolos).

Palavras-chave: peixes teleósteos neotropicais, fragmentação do núcleo vitelínico, dispersão do núcleo vitelínico.

ABSTRACT

The yolk nucleus (YN) or Balbiani body morphology was studied in previtellogenic oocytes of 107 Brazilian teleost fish belonging to 21 families. The YN goes through gradual morphological changes since its appearance in the justanuclear region until its disappearance in the peripheral ooplasm when its contents break and disperse in different ways, depending on the species: thick or thin granules scattered over the ooplasm; thick or thin granules forming a peripheral collar and into dispersed fragments in the ooplasm. In some species, the YN migrates to the periphery of the oocyte where it disappears without apparently breaking or dispersing. The pattern of fragmentation and dispersion generally is similar in fishes of same family or

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subfamily. Our morphological findings support the evidences that the YN of teleost may be related to the formation of cortical vesicles (alveoli).

Key words: neotropical teleost fish, yolk nucleus fragmentation, yolk nucleus dispersion.

INTRODUCTION

In the teleost fish oocytes, a basophilic and conspicuous structure in the cytoplasm, the yolk nucleus (YN) is often observed. Described for the first time in teleosts by Hubbard (1894) *in* Sahai and Bannatwala (1989), it also has other denominations, such as: Balbiani body, Balbiani's vitelline body, nucleolus-like bodies, cement, pallial substance, nuage, chromidia and cytocenter. At the ultrastructural level, the YN is formed by an aggregate of ribonucleoproteins associated to a heterogeneous population of cytoplasmic organelles, such as mitochondria, multivesicular bodies, endoplasmic reticulum, Golgi elements and annulate lamellae (Guraya, 1979; Selman and Wallace, 1989; Cruz-Hofling and Cruz-Landin, 1990).

Recently, Bazzoli and Rizzo (1990) studied the dynamics of the oogenesis in ten Brazilian teleost species and observed the occurence of YN in the previtellogenic oocytes of all of them. Cangussu-Mariani *et al.* (1991) described the YN morphology of *Astyanax bimaculatus* and stablished six stages of its development. Considering that there are no detailed comparative studies on fish YN, the present paper, basing on morphological evidences gathered from optical microscopy, proposes to analyze YN origin and fate in 107 freshwater Brazilian teleost species, belonging to 21 families.

MATERIAL AND METHODS

Fish with maturing oocytes, belonging to 107 species, were captured in various Brazilian hydrographic basins (Table I).

Ovary fragments of 1 to 5 fish of each species were fixed in Bouin's liquid, embedded in paraffin, cut at 4-7 μm of thickness and stained with haematoxilin-eosin, Gomori's trichrome and Mallory's trichrome.

RESULTS

In the previtellogenic oocytes of all species investigated in the present paper, the yolk nucleus (YN) occurs as a singular and basophilic structure with varied morphology. It appears surrounded by a clear halo and it is frequently found adjacent to the nucleus (Fig. 1). It migrates towards the peripheral ooplasm during oocyte development while the clear halo is being filled up with fine granular material (Fig. 2). As the previtellogenic oocyte grows, the contents of the YN break and disperse in one of the following patterns (Table I): thin (Figs. 3 and 4) or thick (Fig. 5) granules, forming a peripheral collar; thin (Fig. 6) or thick (Fig. 7) granules which disperse throughout the ooplasm and, finally, as fragments spreaded in the ooplasm (Fig. 8). In some species, the YN migrates to the peripheric ooplasm without breaking or dispersing (Figs. 9 and 10). Cortical vesicles (alveoli) are frequently observed in the vicinity of the dispersed YN (Fig. 4). As the number of these vesicles increases, the contents of the YN tend to disappear (Fig. 10). In the majority of the species, the contents of the YN break and disperse as thin (40%) or thick (39%) granules throughout the ooplasm whereas the other patterns are less frequent: dispersed fragments in the ooplasm (8%) and without fragmentation and dispersion (13%).

Previtellogenic oocytes stained with haematoxilin-eosin showing the morphology and development of the YN. Fig. 1 — Connection of the YN with the oocyte nucleus – *Serrassalmus brandtii* – 150X; Fig. 2 — Finely granular material filling the clear halo around the YN – *Prochilodus argenteus* – 450X; Fig. 3 — Dispersed YN, forming a peripheral collar of narrow collar of thin granules – *Prochilodus argenteus* – 260X; Fig. 4 — Cortical vesicles (alveoli) in close contact with the contents of the YN after its dispersion – *Prochilodus argenteus* – 510X; Fig. 5 — Dispersed YN, forming a peripheral collar of thick granules – *Astyanax bimaculatus lacustris* – 260X; Fig. 6 — Dispersed YN, originating thin granules throughout the ooplasm – *Salminus hilarii* – 160X; Fig. 7 — Dispersed YN, originating thick granules throughout the ooplasm – *Pimelodus fur* – 260X; Fig. 8 — YN fragments spreaded in the ooplasm – *Leporinus crassilabris* – 320X; Fig. 9 — *Myleus micans* YN migrating to the peripheral ooplasm without dispersing its contents – 160X; Fig. 10 — Cortical vesicles (alveoli) appearing close to the YN (without dispersion) of *Serrasalmus spilopleura* – 230X.

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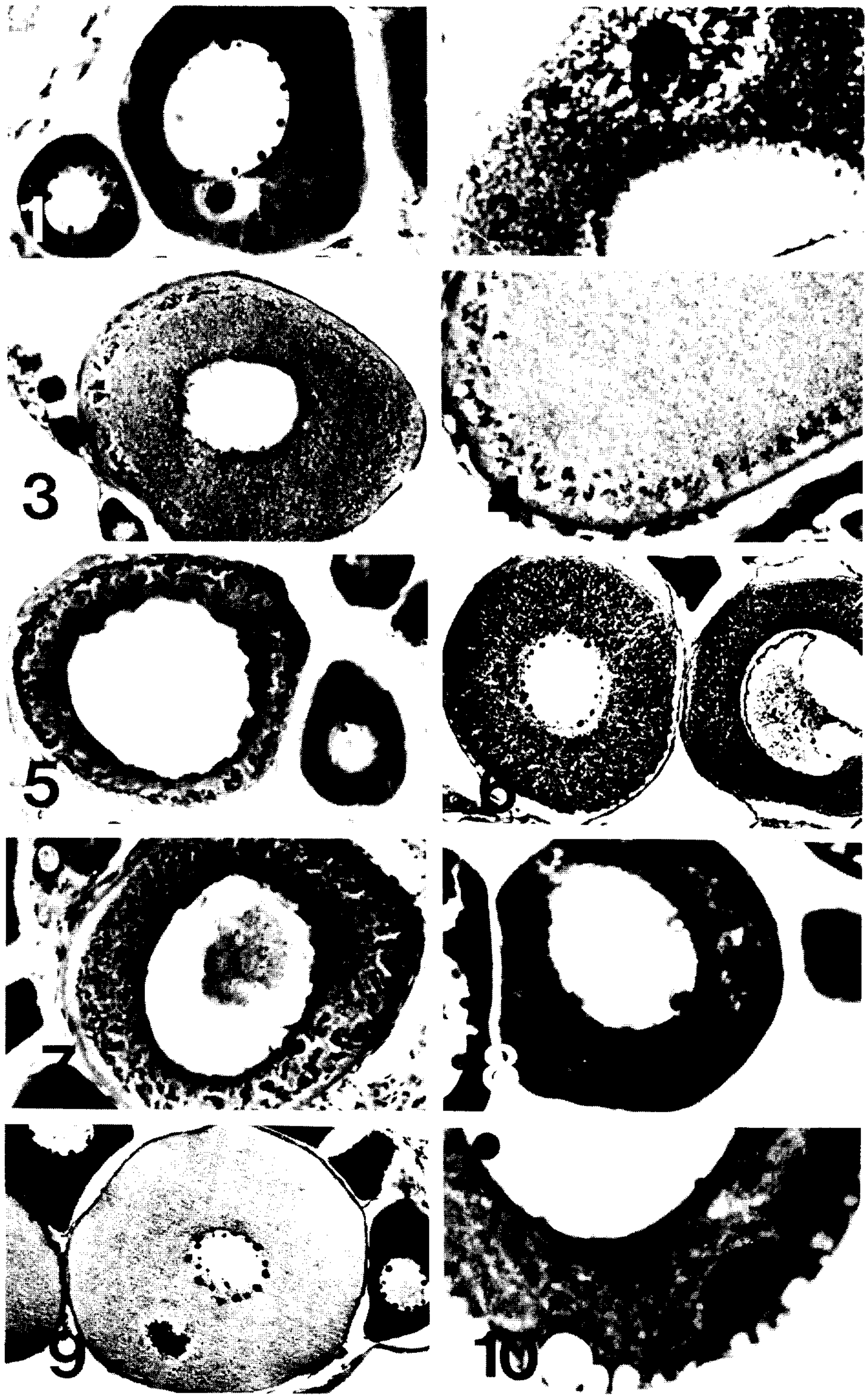

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TABLE I

List of species (related according to the phylogenetic classification of Lauder and Liem, 1983) and respective fragmentation and dispersion patterns of YN.

Family/Subfamily/Species	River basin	Fragmentation and dispersion patterns of YN
Osteoglossidae		
Arapaima gigas	Amazonas	thin granules throughout the ooplasm
Osteoglossum bicirrhosum	idem	idem
Characidae		
Tetragonopterinae		
Creatochanes affinis (*)	São Francisco	thick granules throughout the ooplasm
Astyanax bimaculatus lacustris	idem	thick granules forming a peripheral collar
Astyanax fasciatus	Paraná	idem
Moenkhausia intermedia	idem	idem
Tetragonopterus chalceus	São Francisco	idem
Bryconinae		
Brycon lundii	São Francisco	thin granules throughout the ooplasm
Brycon orbignyanus	Paraná	idem
Triportheinae		
Triportheus guentheri	São Francisco	dispersed fragments in the ooplasm
Characinae		
Roeboides paranensis	Paraná	thin granules throughout the ooplasm
Charax gibbosus	Paraguai	idem
Cynopotaminae		
Galeocharax knerii	Paraná	thin granules forming a peripheral collar
Acestrorhynchinae		
Acestrorhynchus britskii	São Francisco	thin granules throughout the ooplasm
Acestrorhynchus lacustris	Paraná/São Francisco	idem
Salmininae		
Salminus brasiliensis	São Francisco	thin granules throughout the ooplasm
Salminus hilarii	Paraná/São Francisco	idem
Salminus maxillosus	idem	idem
Stethaprioninae		
Brachychalcinus franciscoensis	São Francisco	thick granules throughout the ooplasm
Myleinae		
Myleus micans	São Francisco	without fragmentation and dispersion
Myleus tiete	Paraná	idem
Myloplus levis	idem	idem
Mylossoma orbignyanum	idem	idem
Piaractus mesoptamicus	idem	idem
Serrasalminae		
Serrasalmus brandtii	São Francisco	without fragmentation and dispersion
Serrasalmus marginatus	Paraná	idem
Pygocentrus nattereri	idem	idem
Pygocentrus piraya	São Francisco	idem
Serrasalmus spilopleura	Paraná	idem

(to be continue)

TABLE I (Continuation)

Family/Subfamily/Species	River basin	Fragmentation and dispersion patterns of YN
Characidiinae		
Characidium cf. *timbuiensis*	Santa Maria da Vitória	thin granules throughout the ooplasm
Erythrinidae		
Hoplias cf. *lacerdae*	Paraná/São Francisco	thick granules throughout the ooplasm
Hoplias malabaricus	idem	idem
Anostomidae		
Leporinus amblyrhynchus (*)	Paraná	thin granules throughout the ooplasm
Leporinus striatus (*)	idem	idem
Leporellus vittatus (*)	idem	idem
Schizodon knerii (*)	São Francisco	idem
Schizodon nasutus (*)	Paraná	idem
Leporinus crassilabris	Jequitinhonha	dispersed fragments in the ooplasm
Leporinus elongatus	Paraná/São Francisco	idem
Leporinus friderici	Paraná	idem
Leporinus obtusidens	São Francisco	idem
Leporinus octofasciatus	Paraná	idem
Leporinus piau	São Francisco	idem
Leporinus reinhardti	idem	idem
Leporinus taeniatus	idem	idem
Curimatidae		
Steindachnerina elegans	São Francisco	thin granules throughout the ooplasm
Steindachnerina insculpta	Paraná	idem
Cyphocharax nagelii	idem	idem
Cyphocharax modestus	idem	idem
Cyphocharax cf. *spilurus*	Paraguai	idem
Curimatella lepidura	São Francisco	idem
Prochilodontidae		
Prochilodus costatus	São Francisco	thin granules forming a peripheral collar
Prochilodus cf. *hartii*	Jequitinhonha	idem
Prochilodus argenteus	São Francisco	idem
Prochilodus lineatus	Paraná	idem
Cynodontidae		
Raphiodon vulpinus	Paraná	thin granules throughout the ooplasm
Parodontidae		
Apareiodon affinis	Paraná	thick granules forming a peripheral collar
Parodon tortuosus	idem	idem
Gymnotidae		
Gymnotus carapo	Not determined	thin granules throughout the ooplasm
Sternopygidae		
Eigenmannia virescens	São Francisco	thin granules throughout the ooplasm
Ramphichthyidae		
Rhamphichthys rostratus	Paraná	thick granules throughout the ooplasm

(to be continue)

TABLE I (Continuation)

Family/Subfamily/Species	River basin	Fragmentation and dispersion patterns of YN
Doradidae		
Franciscodoras marmoratus	São Francisco	thick granules throughout the ooplasm
Rhynodoras d'orbignyi	Paraná	idem
Trachydoras paraguayensis	idem	idem
Pterodoras granulosus	idem	idem
Wertheimeria maculata	Jequitinhonha	idem
Auchenipteridae		
Parauchenipterus galeatus	São Francisco	thin granules throughout the ooplasm
Parauchenipterus cf. *jequitinhonhae*	Jequitinhonha	idem
Auchenipterus nuchalis	Paraná	idem
Ageneiosidae		
Ageneiosus ucayalensis	Paraná	thick granules throughout the ooplasm
Ageneiosus valenciennesi	idem	idem
Pimelodidae		
Steindachneridion amblyura (*)	Jequitinhonha	thin granules throughout the ooplasm
Bergiaria westermani	São Francisco	thick granules throughout the ooplasm
Conorhynchus conirostris	idem	idem
Pimelodus fur	Paraná	idem
Pimelodus maculatus	idem	idem
Pimelodus paranaensis	idem	idem
Pseudopimelodus zungaro	idem	idem
Pseudoplatystoma coruscans	São Francisco	idem
Rhamdia cf. *quelen*	Paraná	idem
Rhamdia hilarii	idem	idem
Iheringichthys labrosus	idem	idem
Hemisorubim platyrhynchos	idem	idem
Paulicea luetkeni	idem	idem
Sorubim cf. *lima*	idem	idem
Lophiosilurus alexandri	São Francisco	idem
Trichomycteridae		
Trichomycterus cf. *alternatum*	Santa Maria da Vitória	thin granules throughout the ooplasm
Hypophthalmidae		
Hypophthalmus edentatus	Paraná	thick granules throughout the ooplasm
Hypophthalmus marginatus	Amazonas	idem
Callichthyidae		
Hoplosternum littorale	Paraná	thin granules throughout the ooplasm
Loricariidae		
Hypostomus aff. *albopunctatus*	Paraná	thin granules throughout the ooplasm
Hypostomus francisci	São Francisco	idem
Rhinelepis strigosa	Paraná	idem
Loricaria sp.	idem	idem
Loricariichthys sp.	idem	idem
Hypostomus sp.	idem	idem
Pterygoplichthys etentaculatus	São Francisco	idem
Loricaria lentiginosa	Paraná	idem
Rhinelepis aspera (*)	São Francisco	thick granules throughout the ooplasm
Megalancistrus aculeatus (*)	Paraná	idem

(to be continue)

TABLE I (Continuation)

Family/Subfamily/Species	River basin	Fragmentation and dispersion patterns of YN
Cichlidae		
Cichla ocellaris	Paraná/São Francisco	without fragmentation and dispersion
Geophagus brasiliensis	São Francisco	idem
Gymnogeophagus balzanii	Paraguai	idem
Geophagus sp.	Jequitinhonha	idem
Sciaenidae		
Pachyurus francisci	São Francisco	thick granules throughout the ooplasm
Pachyurus squamipinnis	idem	idem
Plagioscion squamosissimus	Amazonas/Paraná	idem

YN = yolk nucleus / (*) = species which have not followed the most frequent YN fragmentation and dispersion pattern of their respective family and/or subfamily.

From Table I, it can be inferred that fragmentation and dispersion of the YN is a common character for the majority of the families and subfamilies analyzed (Osteoglossidae, Bryconinnae, Characinae, Acestrorhynchinae, Salmininae, Myleinae, Serrasalminae, Erythrinidae, Curimatidae, Prochilodontidae, Doradidae, Auchenipteridae, Ageneiosidae, Hypophthalmidae, Cichlidae, Sciaenidae). In the subfamily Tetragonopterinae and in the families Anostomidae, Pimelodidae and Loricaridae a common pattern was also observed for most of their species, although some exceptions were recorded.

DISCUSSION

There is no common agreement as to the terminology of the teleost YN. To Guraya (1979) the most appropriate term is Balbiani's vitelline body, being the term YN used to designate the basophilic, dense, spherical and central part of that body. The denomination "cement" refers to the "nuage" of nuclear origin associated with mitochondrial aggregates (Clerot, 1976; Cruz-Hofling and Cruz-Landim, 1990). The term YN is used in the present investigation since it is the most frequently used (Chowdhery *et al.*, 1979).

The relationship of the YN to the nucleus of the previtellogenic oocyte is indicated by the apparent connection of peripheral nucleoli to the internal wall of the nuclear envelope, suggesting a possible participation of these nucleoli in the YN formation. Alves and Godinho (1987) reported that peripheral nuclear material seems to flow towards the cytoplasm in oocytes of *Schizodon knerii*. Electron-microscopy and radioautographic studies show the passage of similar material through the pores of the nuclear envelope to constitute the YN (Azevedo, 1984; Cruz-Hofling and Cruz-Landim, 1990).

Several studies, to which our observations coincide, indicate the formation of the YN in the justanuclear region and its disappearance in the peripheral ooplasm when the first cortical vesicles are seen (Thomas and Sathyanesan, 1985; Sahai and Bannatwala, 1989). This dynamics has been confirmed by Begovac and Wallace (1988) in vitally stained oocytes.

Two patterns of fragmentation and dispersion of the YN in teleosts have been registered: (a) thick granules forming a peripheral collar (Chaudhry, 1952; Beams and Kessel, 1973; Mayer *et al.*, 1988; Cangussu-Mariani *et al.*, 1991) and (b) its disappearance in the peripheral ooplasm without fragmentation and dispersion (Nayyar, 1964; Guraya, 1963). YN fragments dispersed in the ooplasm observed in the present work are similar to those described by Guraya (1979) in the amphibian *Bufo woodhousii*. Nayyar (1964) studied the YN of 8 species of Cyprinid and Silurid fish and did not find any difference in their morphology and development.

Despite the universal occurence of YN, its functional significance has not been completely understood (Selman and Wallace, 1989). According to Guraya (1979), it is involved in an extensive production of organelles during the primary growth of the oocyte. Chowdhery *et al.* (1979) found no correlation between YN and yolk formation whereas Sahai and Bannatwala (1989) suggest its participation at the beginning of the yolk deposition. The close spacial relationship between dispersed YN material and cortical vesicles (alveoli) indicate that it may take part in the formation of those vesicles. This relationship is strengthened by ultrastructural studies which show YN organelles involved in processes of synthesis (Guraya, 1979; Selman and Wallace, 1989; Cruz-Hofling and Cruz-Landim, 1990). In *Syngnatus scovelli*, the multivesicular bodies present in YN may represent a precursor compartment for intracellular degradation of the vitelogenin which will form the yolk globules (Begovac and Wallace, 1988).

Fishes of same family and subfamily of the present study tend to show similar pattern of YN fragmentation and dispersion. From the 107 species analyzed, only 9 did not follow the pattern of their respective families or subfamilies. In spite of that, the pattern of YN fragmentation and dispersion of the species studied are not apparently related to phylogeny. Further studies are necessary for a better characterization of the YN in those families or subfamilies which had only one species analyzed in the present study.

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