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Review

Egg carotenoproteins in neotropical Ampullariidae (Gastropoda: Arquitaenioglossa) ☆

H. Heras *, M.S. Dreon, S. Ituarte, R.J. Pollero

Instituto de Investigaciones Bioquímicas de La Plata, CONICET-UNLP, La Plata, Argentina, Facultad de Ciencias Médicas - La Plata, Argentina

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Abstract

Carotenoid-binding proteins are commonly found in invertebrates. Their carotenoids form non-covalent complexes with proteins giving tissues a variety of colors. In molluscs they have been described in only a few species. In particular, the egg perivitellin fluid of those Ampullariid species which deposit eggs above the waterline is provided with carotenoproteins playing several roles ranging from photoprotection, antioxidant or antitrypsin actions to nutrient provision for development. These molecules form complex glyco-lipo-carotenoproteins of high molecular weight where either free astaxanthin (3,3′-dihydroxy-β, β′-carotene- 4,4′dione) or astaxanthin esterified with fatty acids, occur more frequently. This review compiles the current knowledge on the biochemical composition and biophysical data on the chemical and thermal stability of egg carotenoproteins in ampullariid. In addition, recent data on their metabolism, their cellular site of biosynthesis during perivitellogenesis, as well as their carotenoid binding properties are reviewed, highlighting the physiological significance of carotenoproteins in the context of the reproductive biology of these molluscs.

Keywords: Antioxidant; *Asolene*; Apple snail; Carotenoid; Mollusca; Perivitellin; *Pomacea*; Ovorubin; Lipoprotein; Embryogenesis

Contents

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* Corresponding author. INIBIOLP (CONICET-UNLP), Facultad de Ciencias Médicas, 60 y 120 s/n, 1900 - La Plata, Argentina. Tel.: +54 221 4824894; fax: +54 221 4258988.
E-mail address: h-heras@atlas.med.unlp.edu.ar (H. Heras).

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1. Introduction

The family Ampullariidae has a worldwide distribution. Commonly referred to as “apple snails”, these freshwater arquitaenioglossa are exceptionally well adapted to both temperate regions, where thermal changes during the year are large (Albrecht et al., 1999, 2005) and to subtropical and tropical regions where periods of drought may alternate with periods of excessive rainfall (Pizani et al., 2005). These adaptations are reflected in their noteworthy anatomical, physiological and ecological features. Among them is the strategy of some ampullariid genera (Fig. 1) to deposit their eggs above the waterline in a calcareous, colored clutch. This remarkable egg-laying strategy, very unusual for an aquatic invertebrate, was probably developed to protect their eggs against predation by fish and other water inhabitants (Turner, 1998), but at the same time it exposes the eggs to sunlight and desiccation. To cope with these harsh conditions ampullariids have developed some fascinating mechanisms at the biochemical level, where carotenoid pigments forming complexes with proteins play a central role.

Many of the more than 700 carotenoids found in nature are present in invertebrate species that display colored tissues. They are usually non-covalently bound to proteins forming carotenoproteins that are primarily found in two body areas: adult surfaces (exoskeleton and epidermis) and reproductive structures (gonads and eggs) (Cheesman et al., 1967). The ovaries and egg yolk carotenoproteins usually form a water-soluble complex, and frequently, associated with sugars and lipids, forming glyco-lipo-carotenoprotein particles (Zagalsky, 1985). One particular carotenoid, astaxanthin (ASX; 3,3′-dihydroxy-β, β′-carotene-4,4′dione) is most usually isolated from invertebrate carotenoproteins, including Ampullariidae (Fig. 2). ASX is a good example of a carotenoid that can cover the complete visible absorption spectrum by forming complexes with different proteins that usually have no sequence homology among them. From an evolutionary point of view, it is remarkable that such complex coloration mechanism developed from the astaxanthin-protein interaction (Zagalsky, 1985).

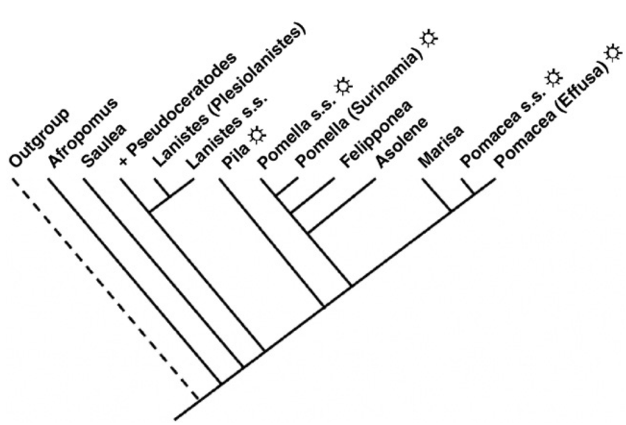

Fig. 1. Phylogenetic tree of the Ampullariidae (according to Berthold, 1989). ☼: Genus with aerial egg-laying.

Carotenoproteins have been studied in several invertebrate phyla, mostly Porifera, Cnidaria, Arthropoda and Echinodermata (Britton et al., 1982; Cheesman et al., 1967; Zagalsky, 1985; Zagalsky et al., 1990). Mollusca, however, have been given much less attention and except for ovorubin, the well studied carotenoprotein from *Pomacea canaliculata*, there are few reports on the presence of carotenoproteins in other molluscs, namely (a) Polyplacophora: the hemolymph of *Cryptochiton stelleri* (Allen, 1977), (b) Bivalvia: muscle of *Mytilus edulis* (Yang et al., 1994), extracts from whole body of *Unio pictorum* (Czeczuga, 1983), gonads of *Volsella modiolus* (Euler et al., 1934) and ovaries of *Pecten maximus* (Ceccaldi and Zagalsky, 1967; Zagalsky, 1972) and (c) Gastropoda: mantle of *Cerithidea californica* (Nakadal, 1960), ovary of *Patella vulgata* (Goodwin and Taha, 1950) and skin of *Flambellina iodinea* (Cheesman et al., 1967).

During vitellogenesis the main components of the egg vitellus such as lipids, proteins and carbohydrates are synthesised. Vitellus proteins are named vitellins (Wallace et al., 1967), and have different origins. In most vertebrates, they are usually synthesised in the liver, released to circulation as precursor particles called vitellogenins (Vg), taken up by the ovary and incorporated into the developing oocyte (heterosynthetic mechanism). In most insects and some crustaceans this mechanism is similar to that in vertebrates, while in other crustaceans and some fish it has been reported that the ovary is involved in this process (autosynthetic mechanism) though some may have both vitellogenic mechanisms (Fainzilber and Zlotkin, 1992; Kanost et al., 1990; Lubzens et al., 2003). In comparison, little is known about this process in molluscs. In cephalopods (de Jong-Brink et al., 1983) and some gastropods (Barre et al., 1991; Bride et al., 1992) heterosynthesis seems to