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Affinity chromatography of a binder of 1-methyladenine, the maturation-inducing hormone for starfish oocytes

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ABSTRACT

Starfish oocytes are arrested at the prophase stage of the first meiotic division in the ovary. They resume meiosis by the stimulus of 1-methyladenine (1-MeAde), the maturation-inducing hormone for starfish oocytes. Putative 1-MeAde receptors have been suggested to be present on the oocyte surface, but not yet been characterized biochemically. As reported recently (T. Toraya, T. Kida, A. Kuyama, S. Matsuda, S. Tanaka, Y. Komatsu, T. Tsurukai, Biochem. Biophys. Res. Commun. 485 (2017) 41–46), it became possible to detect unknown 1-MeAde binders of starfish oocytes by immunophotoaffinity labeling, *i.e.*, photoaffinity labeling combined with immunochemical detection. We designed and synthesized water-soluble and insoluble polymer-bound 1-MeAde derivatives. A water-soluble polymer-bound 1-MeAde derivative, in which 1-MeAde is bound to dextran through an N^6-substituent, triggered the germinal-vesicle breakdown toward follicle-free oocytes, dejellied oocytes, and denuded oocytes. This is consistent with the idea that putative 1-MeAde receptors are located on the cell surface of starfish oocytes. A water-insoluble polymer-bound 1-MeAde derivative, in which 1-MeAde is bound to Sepharose 4B through an N^6-substituent, served as an effective affinity adsorbent for the partial purification of a 1-MeAde binder with M_r of 47.5 K that might be a possible candidate of the maturation-inducing hormone receptors of starfish oocytes.

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1. Introduction

Fully grown oocytes in the starfish ovary remain arrested at the prophase stage of the first meiotic division. Reinitiation of meiosis is triggered by 1-MeAde, the oocyte maturation-inducing hormone (MIH) of starfish (Fig. 1A) [1], which is produced and released by the ovarian follicle cells in response to the gonad-stimulating substance, a peptide hormone excreted from the radial nerve [1]. The gonad-stimulating substance is closely related to the vertebrate relaxin [2].

Upon exposure of oocytes to 1-MeAde, the maturation-promoting factor (MPF) is activated in the cytoplasm and induces oocyte maturation [3]. An MPF was identified as the complex of Cdk1 (Cdc2) kinase with cyclin B [4,5]. Thereafter, various protein kinases and protein phosphatases have been identified as regulators of cell division and its check points [6,7]. Greatwall kinase originally identified as Scant (Scott of the Antarctic) in a fruit fly [8] is a nuclear protein that is required for proper chromosome condensation and mitotic progression in *Drosophila* [9]. Recently, Hara et al. reported that Greatwall kinase serves as the other critical component of MPF by suppressing the protein phosphatase 2A-B55 that opposes Cdk1-cyclin B [10]. 1-MeAde-induced oocyte maturation is inhibited by the microinjection of pertussis toxin, suggesting that a pertussis toxin-sensitive G-protein is involved in the signal transduction pathway [11]. A starfish G-protein that serves as

Abbreviations: Adsorbent I, 1-MeAde-Sepharose 4B; Adsorbent II, adenine-Sepharose 4B; AH-Sepharose, aminohexyl-Sepharose 4B; Analog I, N^6-(6-aminohexyl)carboxamidomethyl-1-methyladenine; ASW, modified van't Hoff's artificial seawater; CaFASW, Ca^{2+}-free artificial seawater; CBB, Coomassie Brilliant Blue R-250; EC_{50}, 50%-effective concentration; EGTA, *O*,*O*′-bis(2-aminoethyl)ethyleneglycol-*N*,*N*,*N*′,*N*′-tetraacetic acid; GVBD, germinal-vesicle breakdown; HB, homogenizing buffer or 20 mM HEPES buffer (pH 7.4) containing 5 mM EGTA and 5 mM $MgCl_2$; HEPES, 2-[4-(2-hydroxyethyl)-1-piperazinyl]ethanesulfonic acid; 1-MeAde, 1-methyladenine; MIH, maturation-inducing hormone; MPF, maturation-promoting factor; PAGE, polyacrylamide gel electrophoresis; PMSF, phenylmethanesulfonyl fluoride; Reagent I, N^6-[6-(5-azido-2-nitrobenzoyl)aminohexyl]carboxamidomethyl-1-methyladenine; SDS, sodium dodecyl sulfate.

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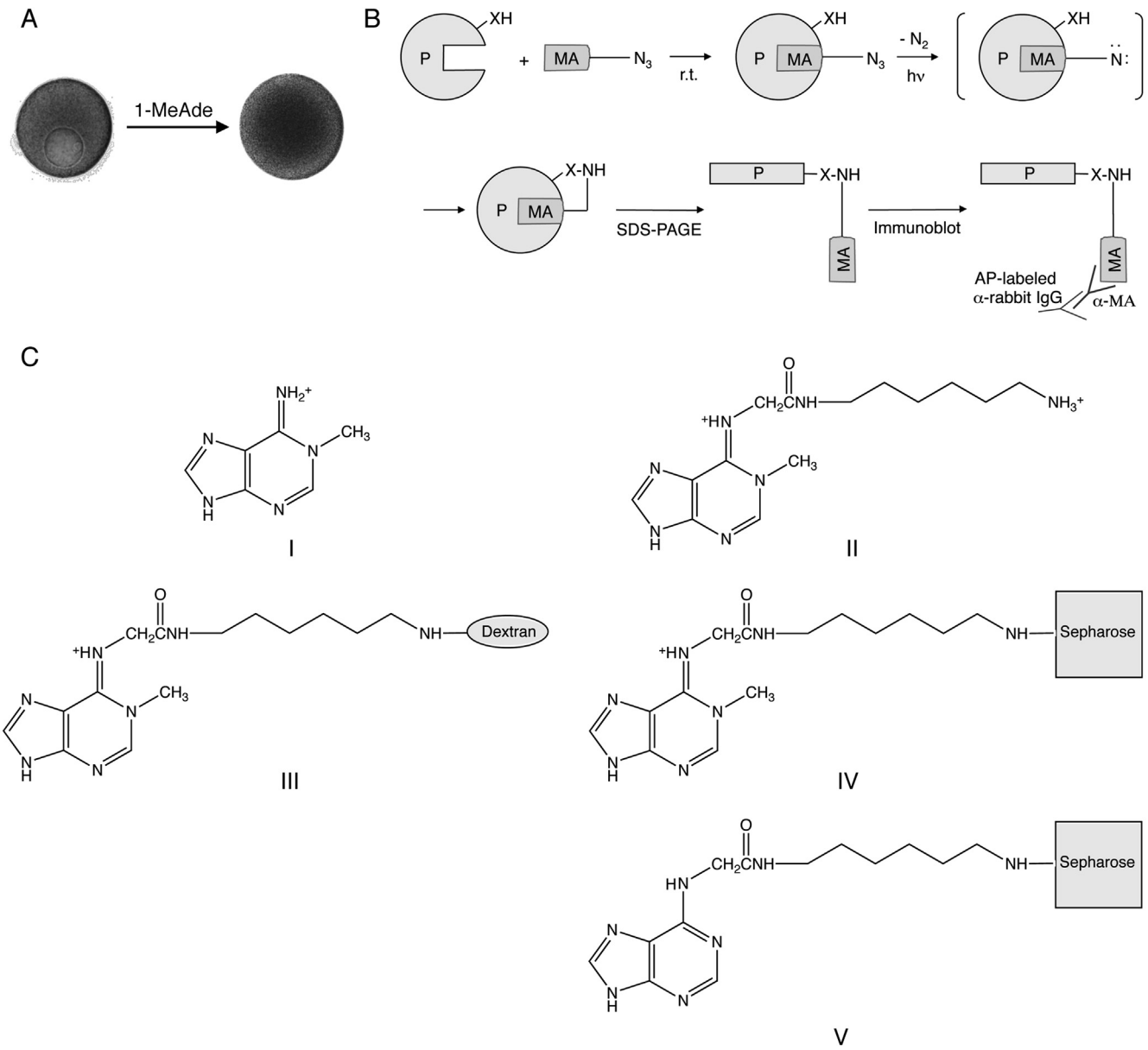

Fig. 1. Starfish oocyte maturation (A), the principle of immunophotoaffinity labeling of 1-MeAde binders in starfish oocytes (B), and the 1-MeAde derivatives used in this study (C). (A) *Left*, immature oocyte with germinal vesicle; *right*, mature oocyte. (B) MA, 1-MeAde; MA-N_3, 1-MeAde derivative containing an azide group; P, 1-MeAde binders including putative 1-MeAde receptors; -XH, generic functional group reactive with a nitrene; α-MA, anti-1-MeAde antibody; AP, alkaline phosphatase. (C) I, 1-MeAde; II, Analog I; III, 1-MeAde-dextran; IV, Adsorbent I or 1-MeAde-Sepharose 4B; V, Adsorbent II or adenine-Sepharose 4B.

a pertussis toxin substrate was purified from the oocyte plasma membranes [12]. The cDNA encoding its α subunit was cloned, and the deduced amino acid sequence was reported [13]. The βγ subunits of starfish G-protein were shown by Chiba et al. to induce oocyte maturation when injected into cytoplasm [14] and to coexist with cytokeratin filaments in starfish oocytes [15]. The involvements of phosphoinositide-3-kinase, phosphoinositide-dependent kinase (PDK) 1, Akt (protein kinase B), and Cdc25 phosphatase in starfish or other animal oocyte maturation were also suggested [16–20].

Putative 1-MeAde receptors have not yet been characterized biochemically, although the specific binding of 1-MeAde to the isolated cortices of starfish oocytes was reported independently by Yoshikuni et al. [21,22], Tadenuma et al. [23], and by ourselves [24]. Identification and characterization of 1-MeAde receptors would be necessary for understanding the entire signal transduction pathway from 1-MeAde to MPF in starfish oocytes. For this purpose, we have developed an immunophotoaffinity labeling method for 1-MeAde binders (Fig. 1B) [25].

In this study, we designed and synthesized dextran-bound and agarose-bound 1-MeAde derivatives (Fig. 1C). The hormonal activity of the former toward starfish oocytes and the use of the latter as an effective affinity adsorbent for the purification of an oocyte 1-MeAde binder are reported here.

2. Materials and methods

2.1. Materials

1-MeAde was obtained from Sigma. N^6-(6-aminohexyl)

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