

Sea Urchin Acrosome Reaction and Sperm Binding

In sea urchins, the acrosome reaction is initiated by fucose sulfate-containing glycoproteins in the egg jelly that bind to specific receptors located directly above the acrosomal vesicle on the sperm cell membrane (Hirohashi et al 2008). Their large molecular weight (around a million Da) keeps these glycoproteins close to the vitelline layer. These polysaccharides are often highly species-specific, and egg jelly factors from one species of sea urchin generally fail to activate the acrosome reaction even in closely related species (Hirohashi and Vacquier 2002a; Hirohashi et al. 2002; Vilela-Silva et al. 2008). The binding of these glycoproteins to the sperm is thought to allow the calcium ions that have been stored in the sperm (probably in the acrosomal vesicle) to be released into the cytoplasm. Here, they facilitate the fusion of the acrosomal vesicle with the cell membrane (Hirohashi and Vacquier 2003; Granados-Gonzales et al 2005).

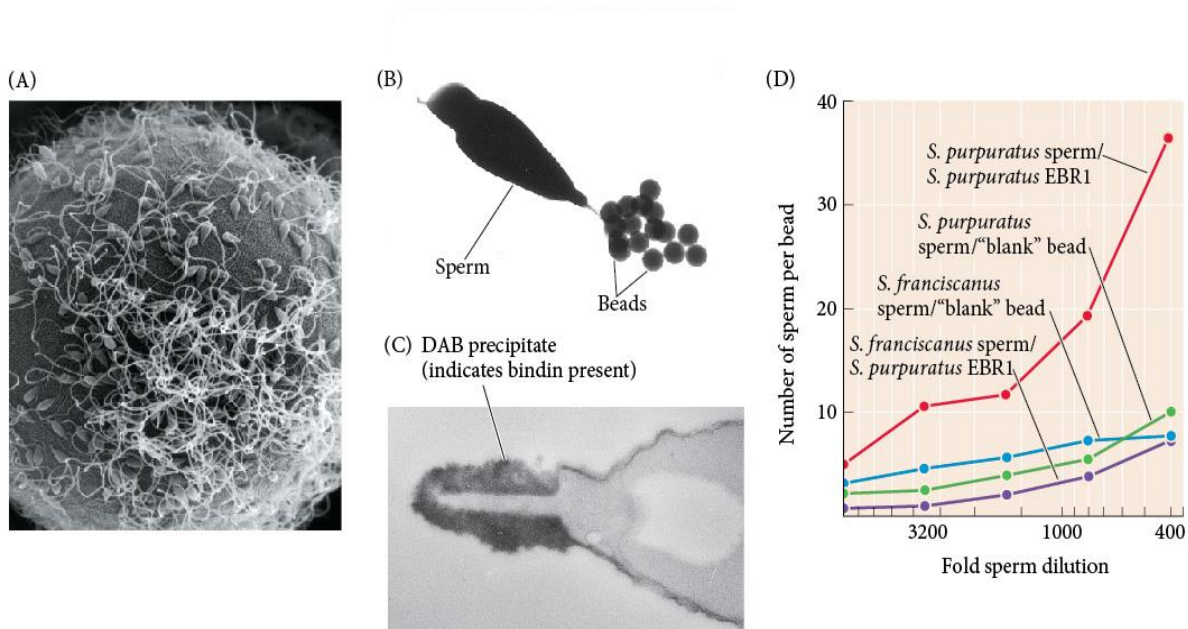
In *Strongylocentrotus purpuratus*, the acrosome reaction is initiated by a repeating polymer of fucose sulfate. When this sulfated polysaccharide binds to its receptor on the sperm, the receptor activates three sperm membrane proteins: (1) a calcium transport channel that allows Ca^{2+} to enter the sperm head; (2) a sodium-hydrogen exchanger that pumps sodium ions (Na^+) into the sperm as it pumps hydrogen ions (H^+) out; and (3) a phospholipase enzyme that makes another second messenger, the phospholipid inositol 1,4,5-trisphosphate (IP_3 , of which we will hear much more later in the chapter). IP_3 is able to release Ca^{2+} from *inside* the sperm, probably from within the acrosome itself (Domino and Garbers 1988; Domino et al. 1989; Hirohashi and Vacquier 2003). The elevated Ca^{2+} level in a relatively basic cytoplasm triggers the fusion of the acrosomal membrane with the adjacent sperm cell membrane, releasing enzymes that can lyse a path through the egg jelly to the vitelline envelope.

The second part of the acrosome reaction involves the extension of the acrosomal process by the

polymerization of globular actin molecules into actin microfilaments; Tilney et al. 1978). The influx of Ca^{2+} is thought to activate the protein RhoB in the acrosome and midpiece of the sperm (Castellano et al. 1997; de la Sancha et al. 2007). This GTP-binding protein helps organize the actin cytoskeleton in many types of cells and is thought to be active in polymerizing actin to make the acrosomal process.

Biochemical studies have confirmed that the bindins of closely related sea urchin species have different protein sequences. This finding implies the existence of species-specific bindin receptors on the egg vitelline envelope (Figure 1A). Indeed, two of them have been identified (Hirohashi and Lennarz, 1998; Vacquier 2012). First, there is a 350-kDa glycoprotein that displays the properties expected of a bindin receptor (Figure 1B; Kamei and Glabe 2003). These bindin receptors are thought to be aggregated into complexes on the vitelline envelope, and hundreds of such complexes may be needed to tether the sperm to the egg. The carbohydrate portion of this bindin receptor on the egg vitelline envelope appears to recognize the bindin protein on the acrosome (Figure 1C) in a species-specific manner. The second bindin receptor, EBR1, appears to bind to bindin through protein-protein interactions. Closely related species of sea urchins (i.e., different species in the same genus) have divergent bindin receptors, and eggs will adhere only to the bindin of their own species (Figure 1D). Thus, species-specific recognition of sea urchin gametes can occur at the levels of sperm attraction, sperm activation, the acrosome reaction, and sperm adhesion to the egg surface.

However, a recent new study (Limatola et al 2022) claims to find that the egg plasma membrane, and not the vitelline layer, is where species-specific recognition of the sea urchin gametes occurs. *Paracentrotus lividus* eggs were incubated in acidic seawater, which should remove the egg jelly. Under these conditions, the acrosome reaction should not occur. However, at variance with the prevailing view, these dejellied *P. lividus* eggs still interacted with sperm, albeit with altered calcium ion responses. Indeed, eggs deprived of the jelly and their vitelline layer reacted with multiple sperm. These results suggest that the plasma membrane, and not the vitelline layer, is the site of gamete recognition, and that the vitelline layer works in unfertilized eggs to prevent polyspermy. There may be multiple adhesion systems working here, as there is in mammalian fertilization.



(A) © Mia Tegner/SPL/Science Source; (B) from K. R. Foltz et al. 1993. *Science* 259: 1421–1425; (C) from G. W. Moy and V. D. Vacquier. 1979. *Curr Top Dev Biol* 13: 31–44, courtesy of V. Vacquier; (D) after N. Kamei and C. G. Glabe. 2003. *Genes Dev* 17: 2502–2507.

Figure 1 Bindin receptors on the sea urchin egg. (A) Scanning electron micrograph of sea urchin sperm bound to the vitelline envelope of an egg. Although this egg is saturated with sperm, there appears to be room on the surface for more sperm, implying the existence of a limited number of bindin receptors. (B) *Strongylocentrotus purpuratus* sperm bind to polystyrene beads that have been coated with purified bindin receptor protein. (C) Immunochemically labeled bindin (the label manifests as a dark precipitate of diaminobenzidine, DAB) is seen to be localized to the acrosomal process after the acrosome reaction. (D) Species-specific binding of sea urchin sperm to the bindin receptor EBR1. *S. purpuratus* sperm bound to beads coated with EBR1 bindin receptor purified from *S. purpuratus* eggs, but *S. franciscanus* sperm did not. Neither sperm bound to uncoated “blank” beads.

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