

Q

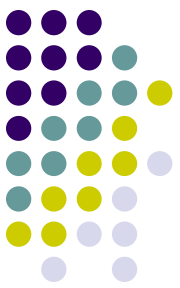
## Lens Proteins



*Lens Proteins* constitute what proportion of the lens by weight?

A

## Lens Proteins

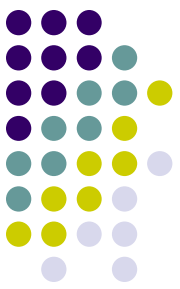


2

*Lens Proteins* constitute what proportion of the lens by weight? 1/3

Q

## Lens Proteins



3

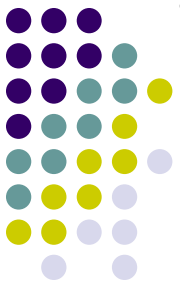
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4

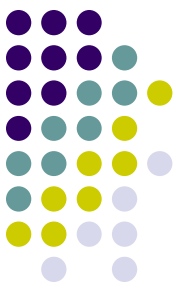
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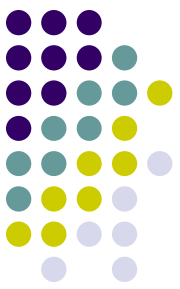
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*Alrighty then. Is it impressively high, or low?*  
High—no other tissue comes close (a content-by-weight of a third is **2 to 3 times** the protein content of most other tissues!)

Q

## Lens Proteins



7

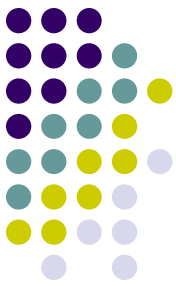
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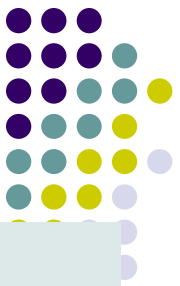
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## Lens Proteins



Briefly, what is the 'life cycle' of a lens fiber?

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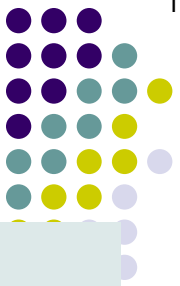
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The progenitor cells for lens fibers are the lens's   cells

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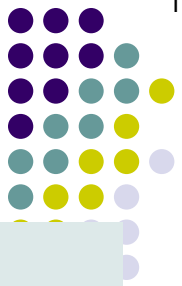
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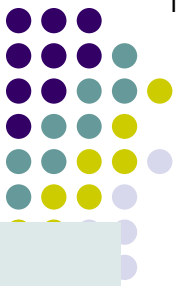
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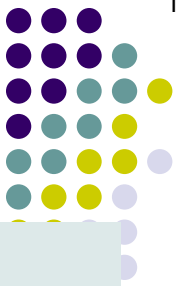
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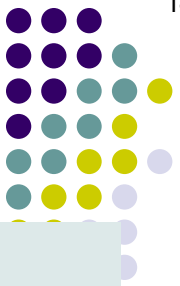
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The progenitor cells for lens fibers are the lens's epithelial cells, **which are found under the anterior and equatorial regions of the capsule**. Throughout life, epi cells migrate to a portion of the equatorial periphery called the **equatorial region**, where they elongate in circumferential fashion until reaching the anterior and polar poles, at which points they encounter and interdigitate with growing fibers from the *other* side of the lens.

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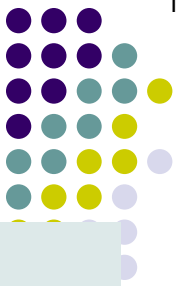
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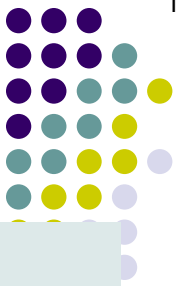
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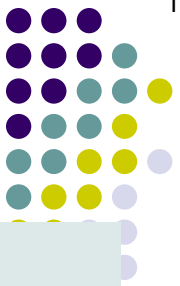
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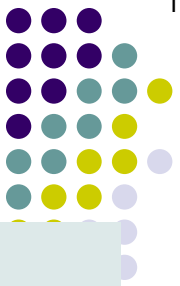
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The purpose is to render the lens's refractive index ( $n$ ) different enough from that of the aqueous and vitreous to make it (the lens) an effective and efficient refracting structure.

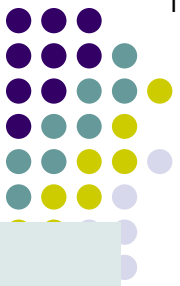
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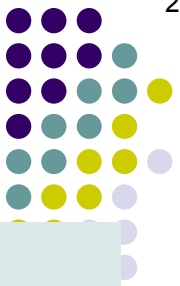
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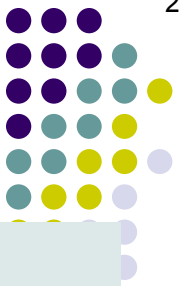
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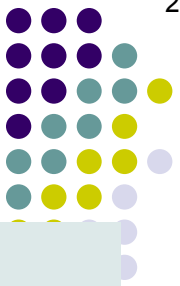
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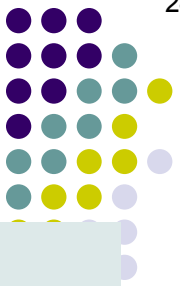
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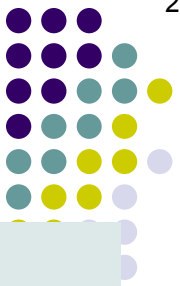
Here's where Snell's law comes into play. Snell's law tells us that the dioptric power produced at a refracting surface is

$$\frac{n' - n}{r}$$

where  $n'$  is the refractive index of the substance the light is heading into (the lens in this case),  $n$  is the refractive index of the substance the light is coming from (the aqueous), and  $r$  is the radius of curvature of the refracting surface (the anterior lens capsule).

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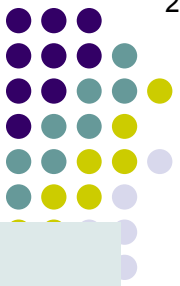
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You have probably anticipated the implications of all this for the composition of the intracellular space in lens fibers. If that space was filled with a liquid isotonic to aqueous, the refractive index of the lens would not differ appreciably from that of the aqueous itself. This would render the Snell's law numerator of the aqueous-lens interface essentially zero, meaning no refraction could occur there..

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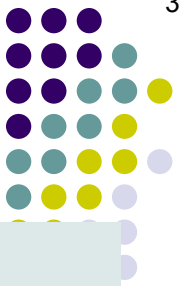
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## A

## Lens Proteins



OK, but what does all this have to do with the intracellular composition of lens fibers? The issue is one of refractive index. Look at Snell's law again, and note that the magnitude of the numerator is determined not by the values of the two refractive indices, but rather by the *difference* between the values. Thus, if there is little to no difference between the *ns* at an interface, there will be little to no refraction at it.

$$\frac{n' - n}{r}$$

You have probably anticipated the implications of all this for the composition of the intracellular space in lens fibers. If that space was filled with a liquid isotonic to aqueous, the refractive index of the lens would not differ appreciably from that of the aqueous itself. This would render the Snell's law numerator of the aqueous-lens interface essentially zero, meaning no refraction could occur there. **But the dense concentration of intracellular proteins gives the lens a refractive index of about 1.39, which differs enough from that of the aqueous ( 1.34 ) that meaningful refraction occurs.**

as an effective refracting structure. We will unpack this statement over the next several slides, but doing so requires we take a couple of steps back and review 1) lens-fiber development; and 2) **Snell's law of refraction.**

# Lens Proteins

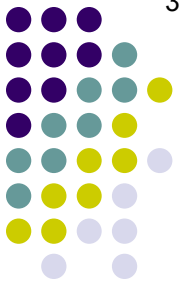
OK, but what does all this have to do with the intracellular composition of lens fibers? The issue is one of refractive index. Look at Snell's law again, and note that the magnitude of the numerator is determined not by the values of the two refractive indices, but rather by the *difference* between the values. Thus, if there is little to no difference between the *ns* at an interface, there will be little to no refraction at it.

Before we move on:

--If you're not grokking this whole *Snell's law* thing, review slide-set *BO17* (or better still, do the whole *Basic Optics* tutorial)

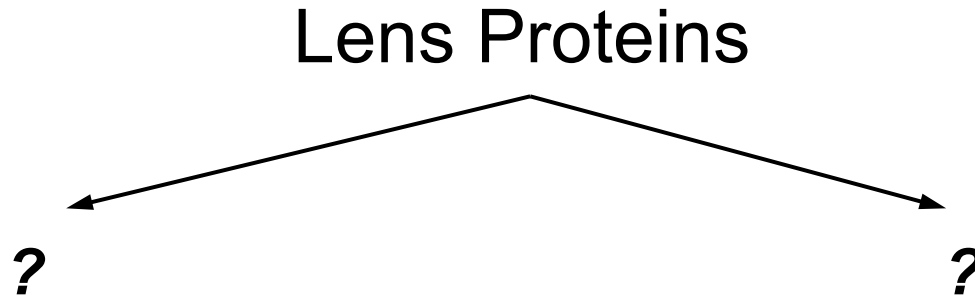
--For more details concerning lens fiber development, see set *L14*

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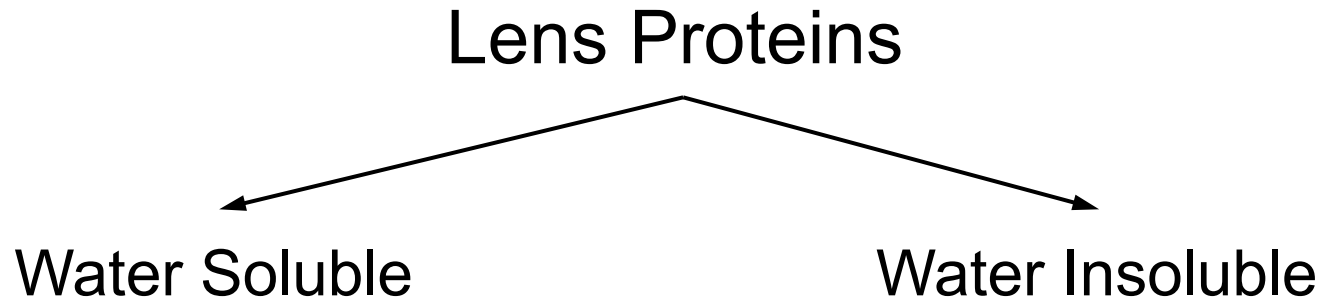
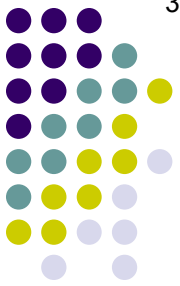
# Q

## Lens Proteins



*Lens proteins come in one of two basic types. What are they?  
(Hint: The types are divided on the basis of a physical property  
of the proteins.)*





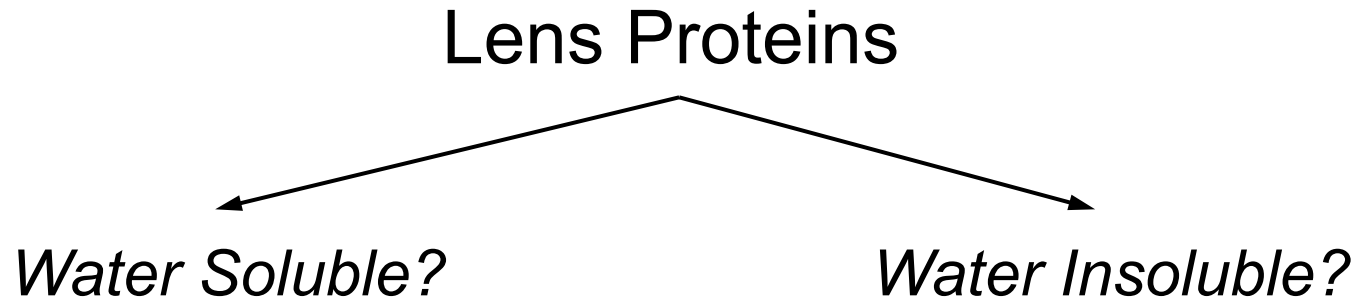
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Q

## Lens Proteins



34



*One of these types predominates in the lens of a young person—  
which one?*

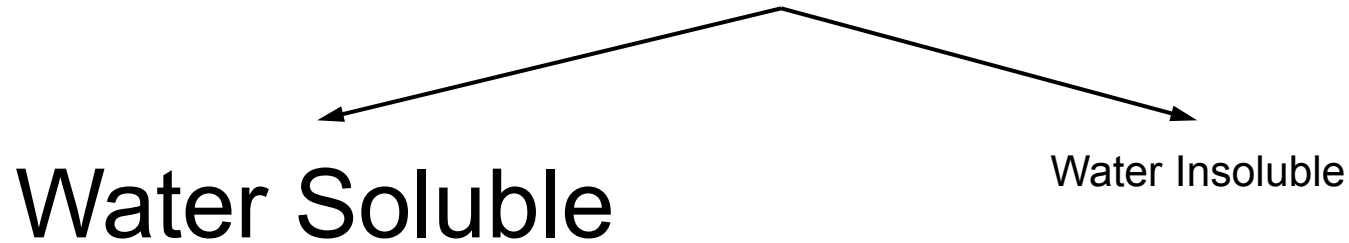
# A

## Lens Proteins



35

## Lens Proteins



*One of these types predominates in the lens of a young person—  
which one?*

Water soluble

Q

## Lens Proteins



36

### Lens Proteins

Water Soluble

Water Insoluble

*Water-soluble proteins comprise what percentage of proteins in the young lens?*

*One of these types predominates in the lens of a young person— which one?*

Water soluble

# A

## Lens Proteins



## Lens Proteins

Water Soluble

Water Insoluble

*Water-soluble proteins comprise what percentage of proteins in the young lens?*

80%

*One of these types predominates in the lens of a young person— which one?*

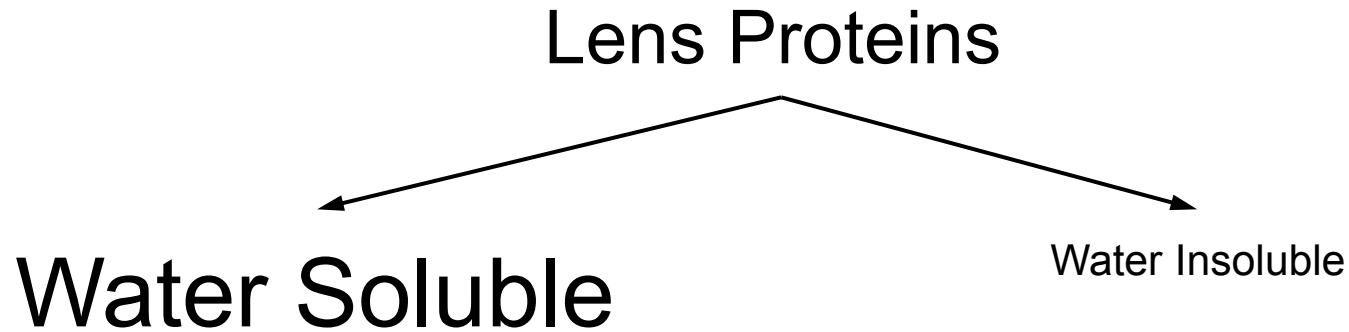
Water soluble

Q

## Lens Proteins



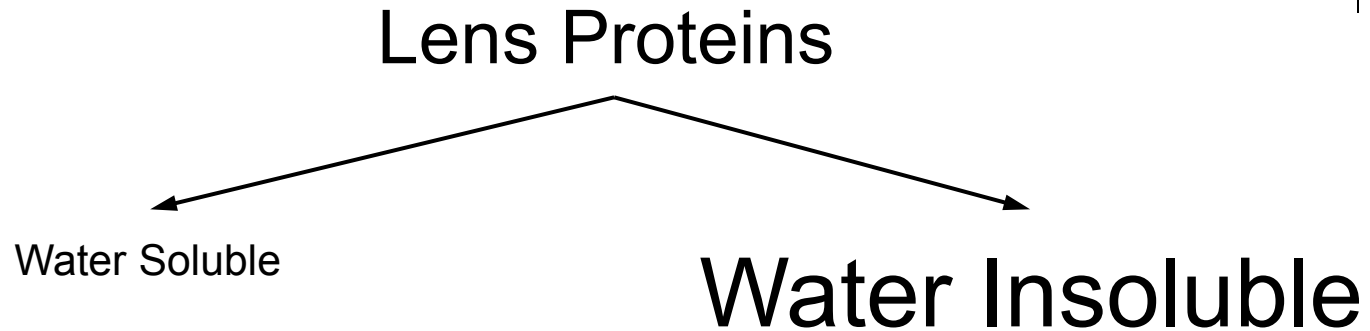
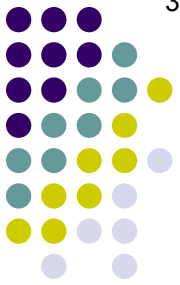
38



*One of these types predominates in the lens of a young person—  
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Water soluble

*What happens to the relative proportions of water soluble vs  
insoluble proteins as the person ages?*



*One of these types predominates in the lens of a young person—  
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Water soluble

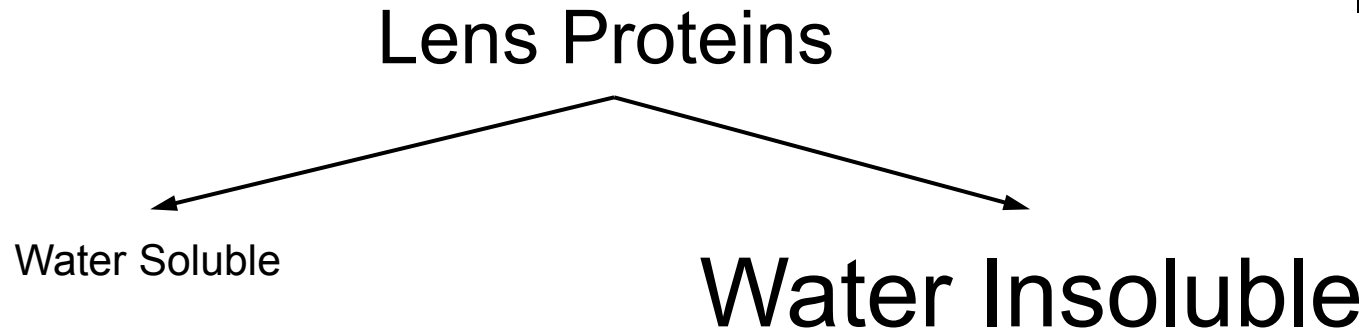
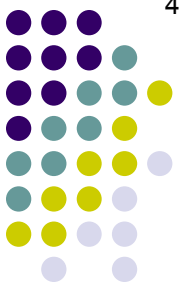
*What happens to the relative proportions of water soluble vs  
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It reverses—water *insoluble* predominates

Q

## Lens Proteins

40



*What accounts for this change in the proportion of water-soluble vs insoluble proteins?*

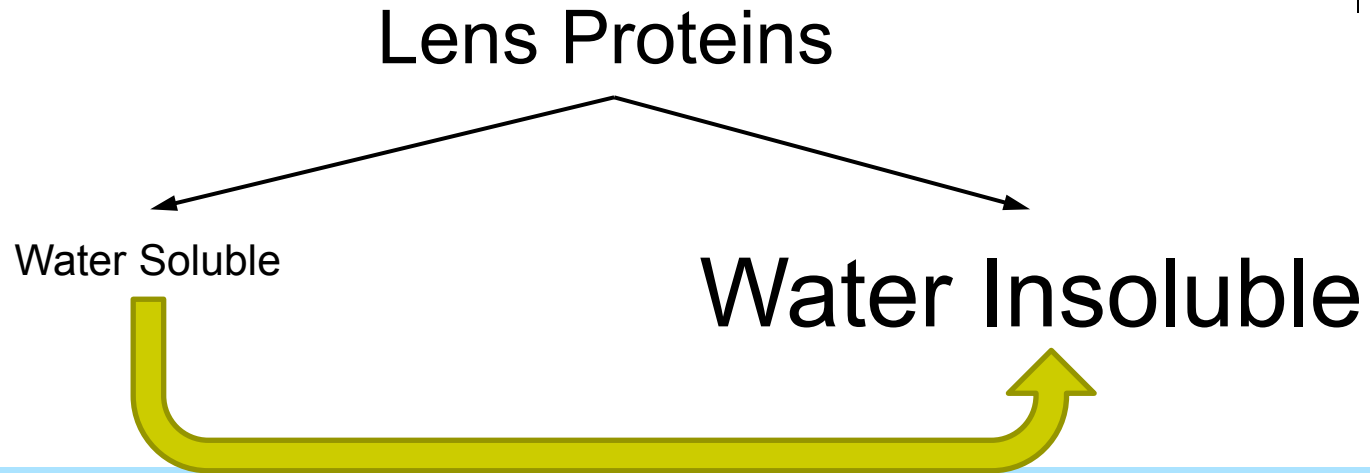
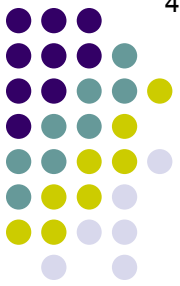
It reverses—water *insoluble* predominates



A

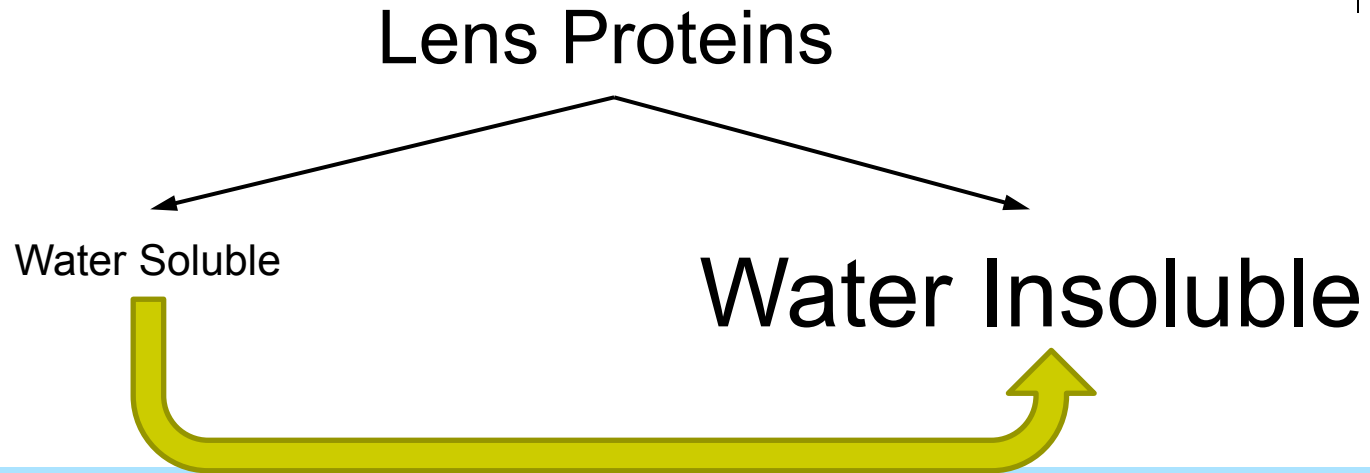
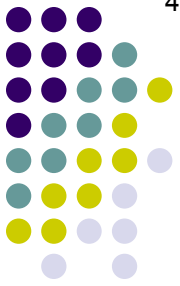
## Lens Proteins

41



*What accounts for this change in the proportion of water-soluble vs insoluble proteins?*  
It's very straightforward—as the lens ages, water-soluble proteins aggregate, in the process forming particles that are water-insoluble

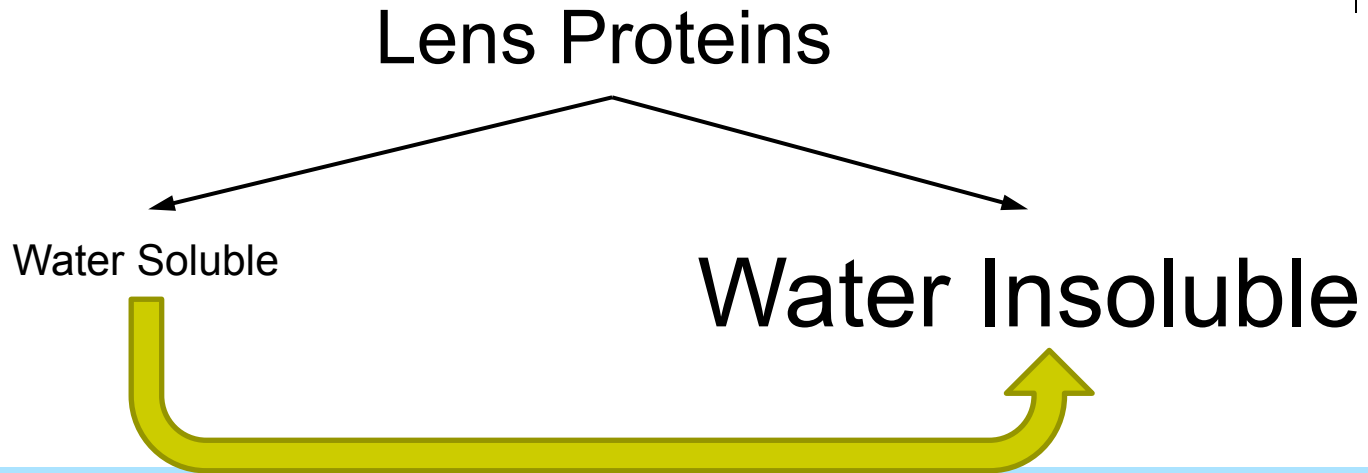
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*Is this fact of any clinical relevance, or are you just torturing me with minutiae?*

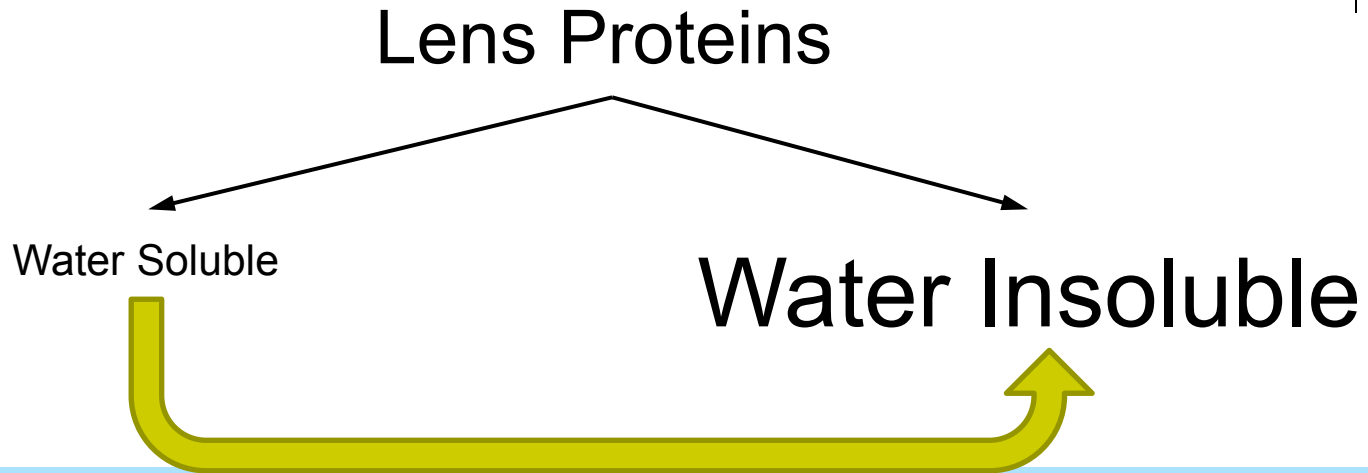
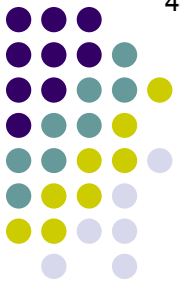
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Unlike much of the esoterica in this slide-set, a straight line can be drawn from this fact to the exam room. These water-insoluble aggregates are very large and scatter light, thereby reducing acuity.

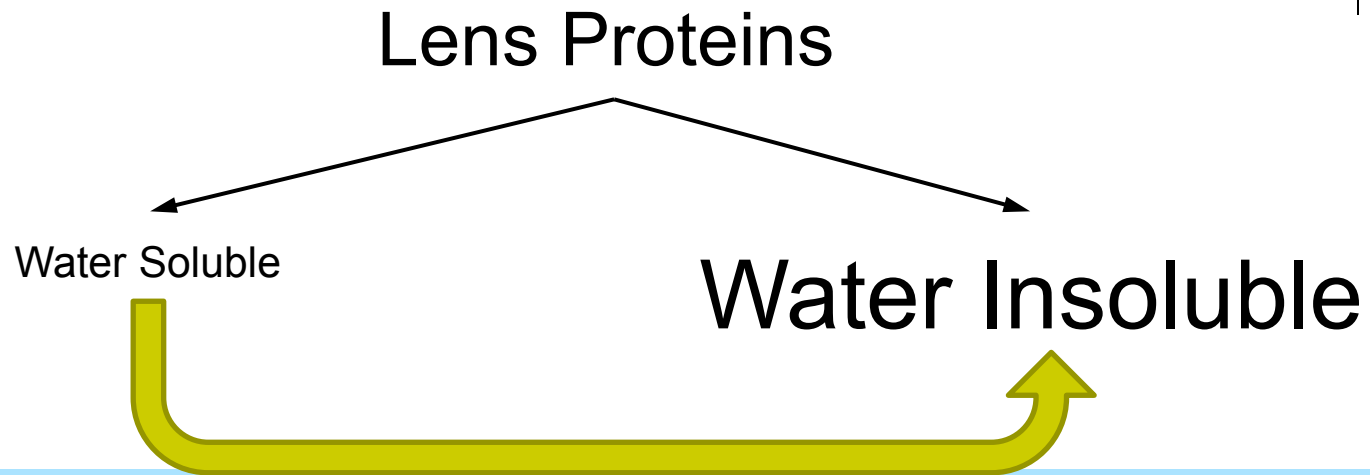
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Unlike much of the esoterica in this slide-set, a straight line can be drawn from this fact to the exam room. These water-insoluble aggregates are very large and scatter light, thereby reducing acuity. **Further, there is a direct correlation between the proportion of water-insoluble proteins and how brunescent a cataract is.**

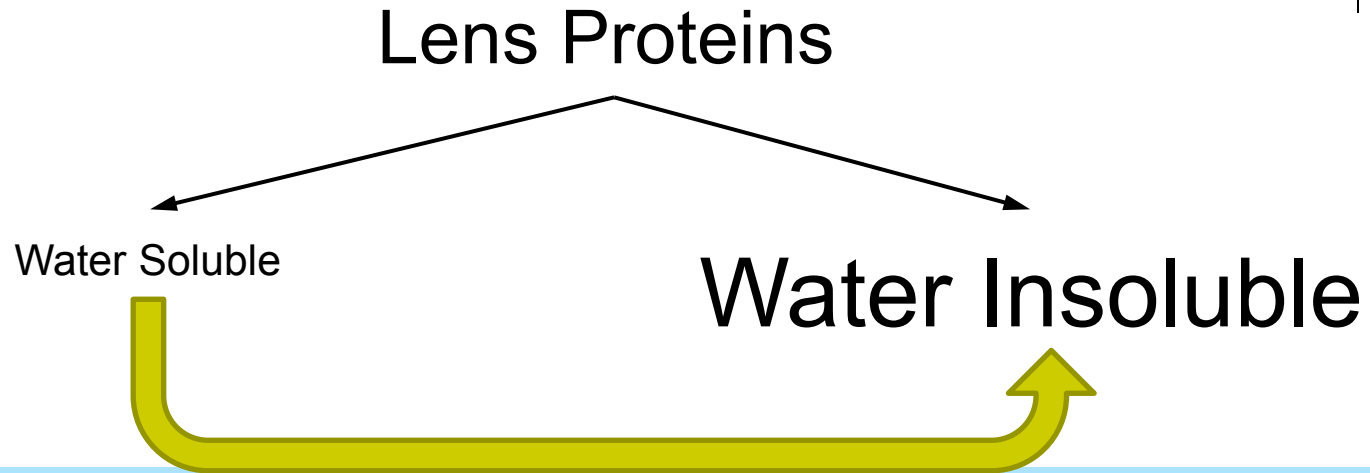
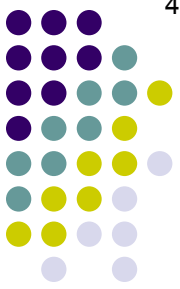
It reverses—water *insoluble* predominates



*Water-insoluble proteins comprise what percentage of proteins in an old, brunescent lens?*

Further, there is a direct correlation between the proportion of water-insoluble proteins and how brunescent a cataract is.

It reverses—water *insoluble* predominates



*Water-insoluble proteins comprise what percentage of proteins in an old, brunescent lens? It can be as high as 90%!*

change in the proportion of water-soluble vs insoluble proteins?  
—as the lens ages, water-soluble proteins aggregate, in the  
proportion of water-insoluble proteins increases  
Is there a relationship between the proportion of water-insoluble proteins and the degree of brunescence?  
Under the microscope, a straight line can be drawn from this fact to the fact that the water-insoluble aggregates are very large and scatter light, making the lens appear cloudy.  
Further, there is a direct correlation between the proportion of water-insoluble proteins and how brunescent a cataract is.

It reverses—water *insoluble* predominates

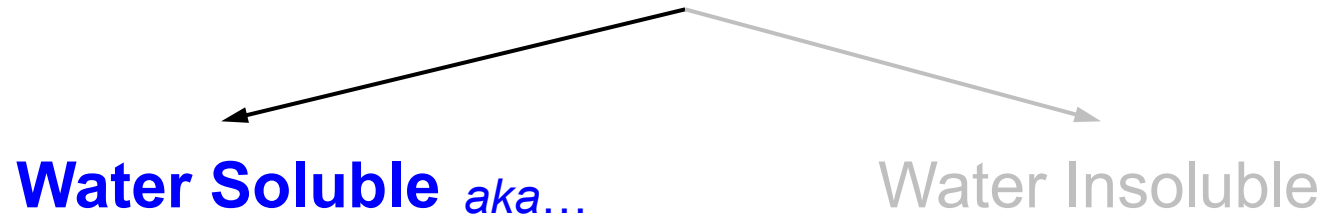
Q

## Lens Proteins



47

## Lens Proteins



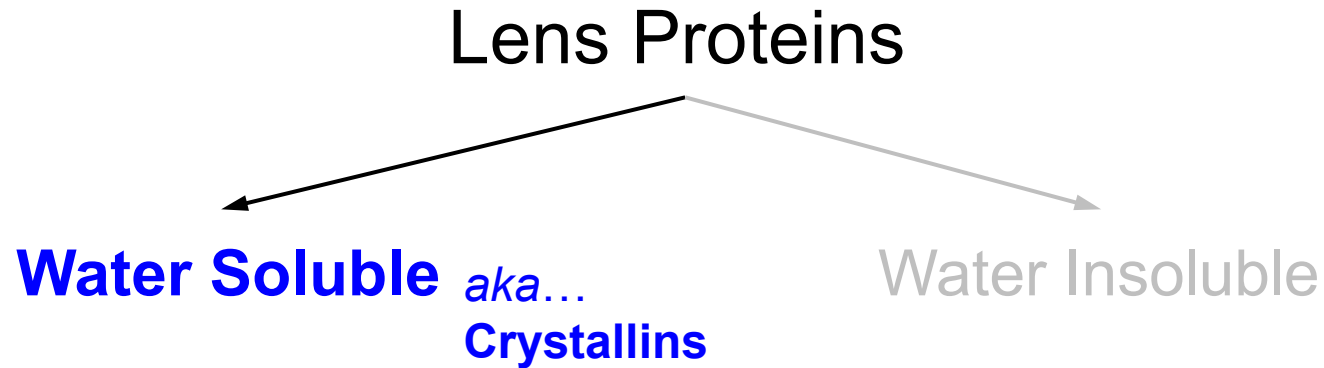
*By what other name are the water-soluble proteins known?*

A

## Lens Proteins



48



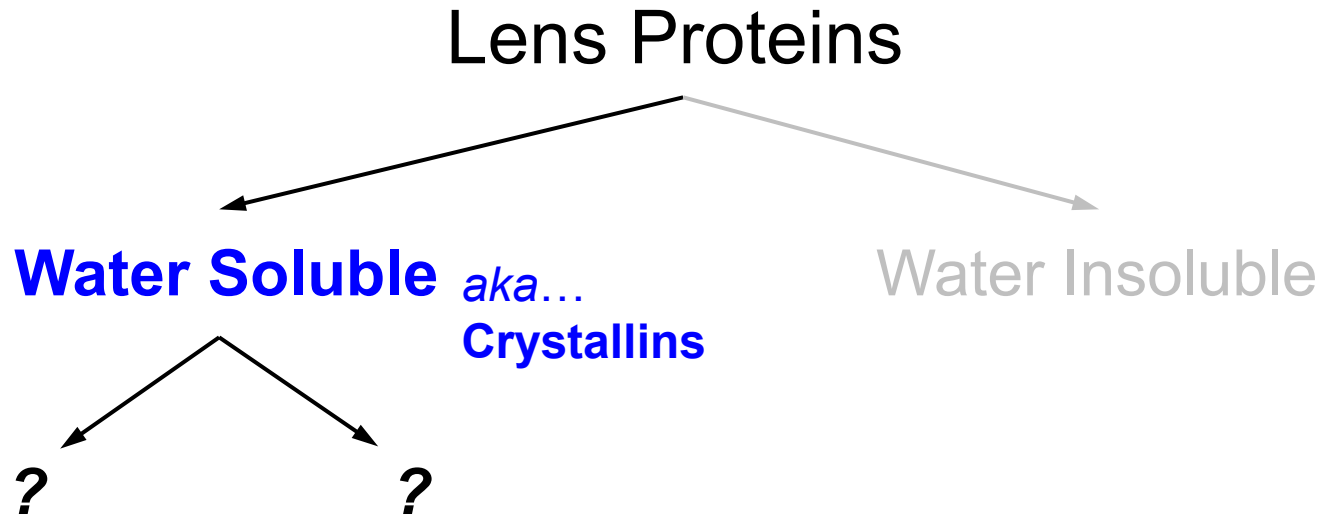
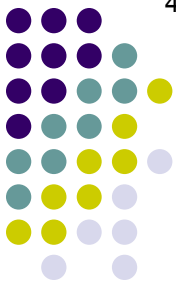
*By what other name are the water-soluble proteins known?*  
'Crystallins'



Q

## Lens Proteins

49



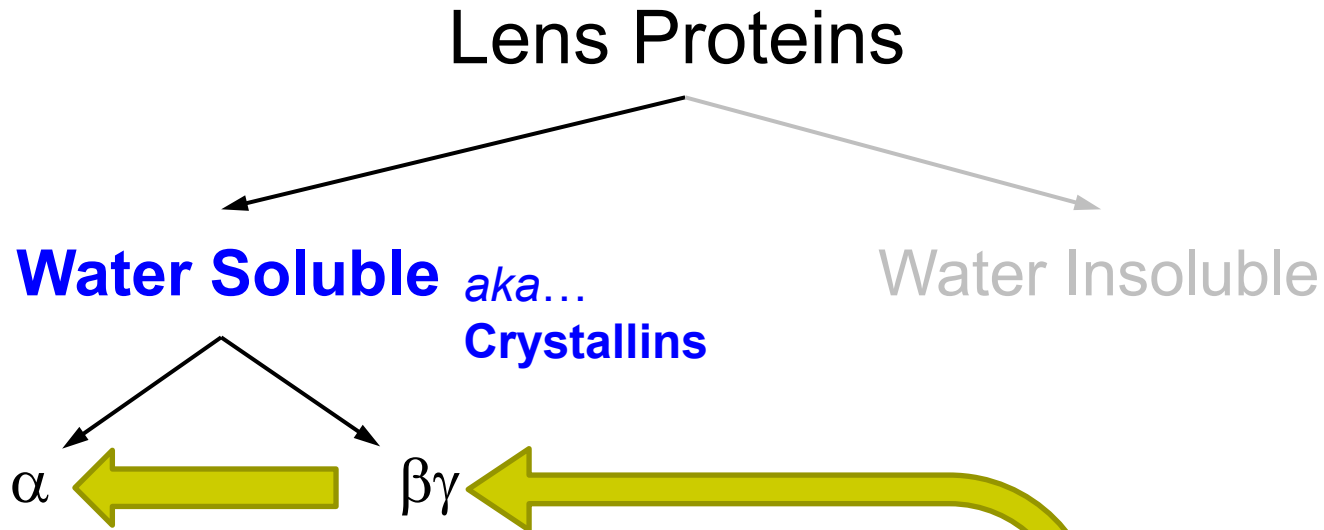
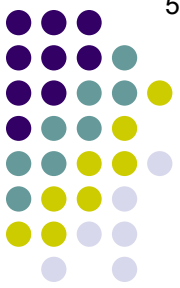
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*Crystallins come in three forms (two of which are grouped together). What are they?*

# A

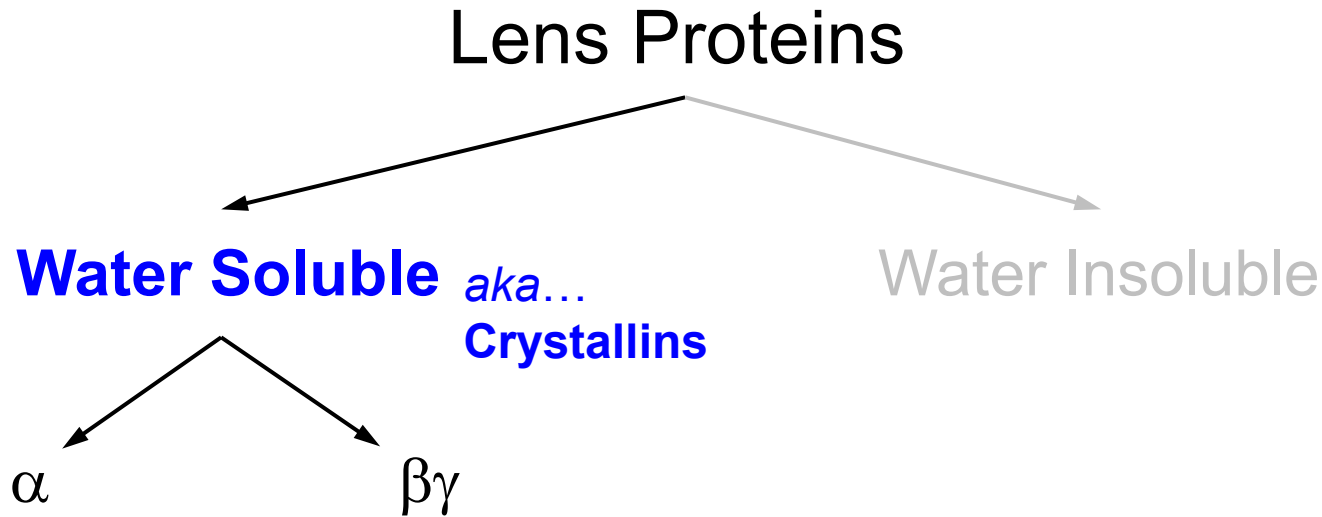
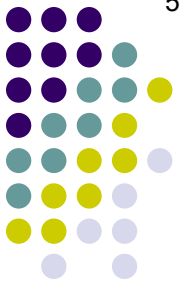
## Lens Proteins

50



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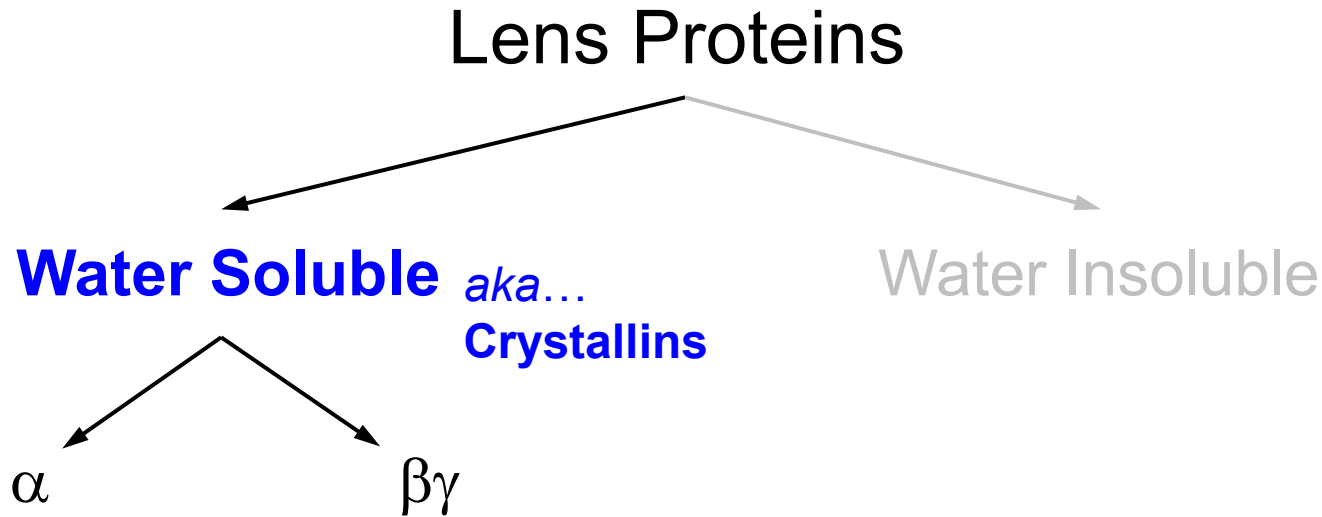
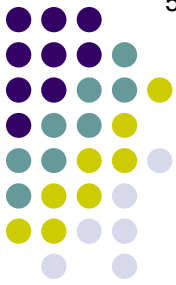
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*What vital role do crystallins play in lens function?*

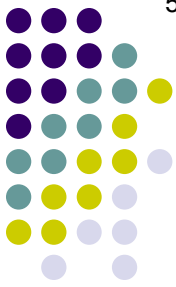


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*They are the proteins cranked out by elongating lens fibers that increase the lens's refractive index enough to render it a viable refracting structure*



## Lens Proteins

**Water Soluble** aka...  
**Crystallins**

Water Insoluble

$\alpha$

$\beta\gamma$

*By what other name are the water-soluble 'Crystallins'?*

*What might you be expected to remember about each of the crystallins?*

$\alpha$ : The largest vs smallest

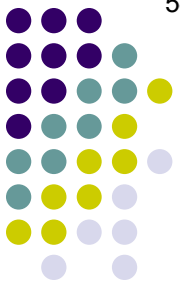
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By what other name are the water-soluble 'Crystallins'?

What might you be expected to remember about each of the crystallins?

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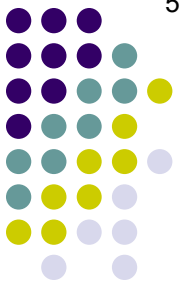
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By what other name are the water-soluble 'Crystallins'?

*What might you be expected to remember about each of the crystallins?*

$\alpha$ : The largest; also, it is a heat-shock protein

$\beta$

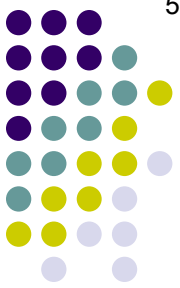
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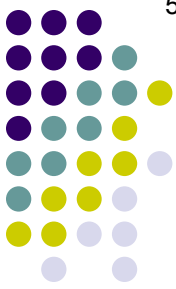
*By what other name are they known?  
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*In general, what is a heat-shock protein?*

*Crystallins come in three types (alpha, beta, and gamma). What are the functions of each?*

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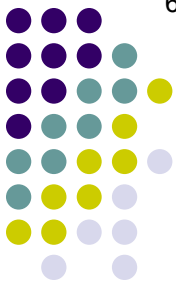
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*What role does  $\alpha$ -crystallin play in the lens in this regard?*  
Denatured lens proteins will aggregate (ie, glom together) to form large particles;  $\alpha$ -crystallin interdicts this process by binding to the denatured proteins

*What vital role do crystallins play in the lens?*  
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## Lens Proteins

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What vital role do crystallins play in the lens?  
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by binding to the denatured proteins

Is protein denaturation and aggregation a significant issue in the human lens?



## Lens Proteins

### Lens Proteins

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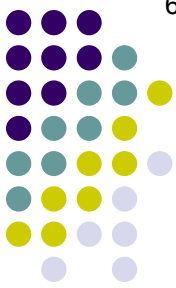
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Is protein denaturation and aggregation a significant issue in the human lens?

Indeed it is. The resulting particles contribute directly to **cataract** formation.



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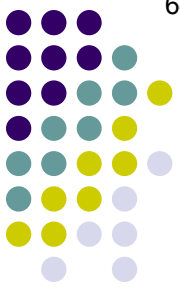
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By what other name are the water-soluble 'Crystallins'?

*What might you be expected to remember about each of the crystallins?*

$\alpha$ : The largest; also, it is a heat-shock protein

$\beta$ : The most v least common by weight

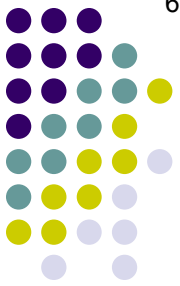
$\gamma$

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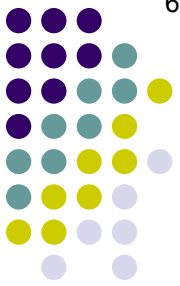
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*What might you be expected to remember about each of the crystallins?*

$\alpha$ : The largest ; also, it is a heat-shock protein

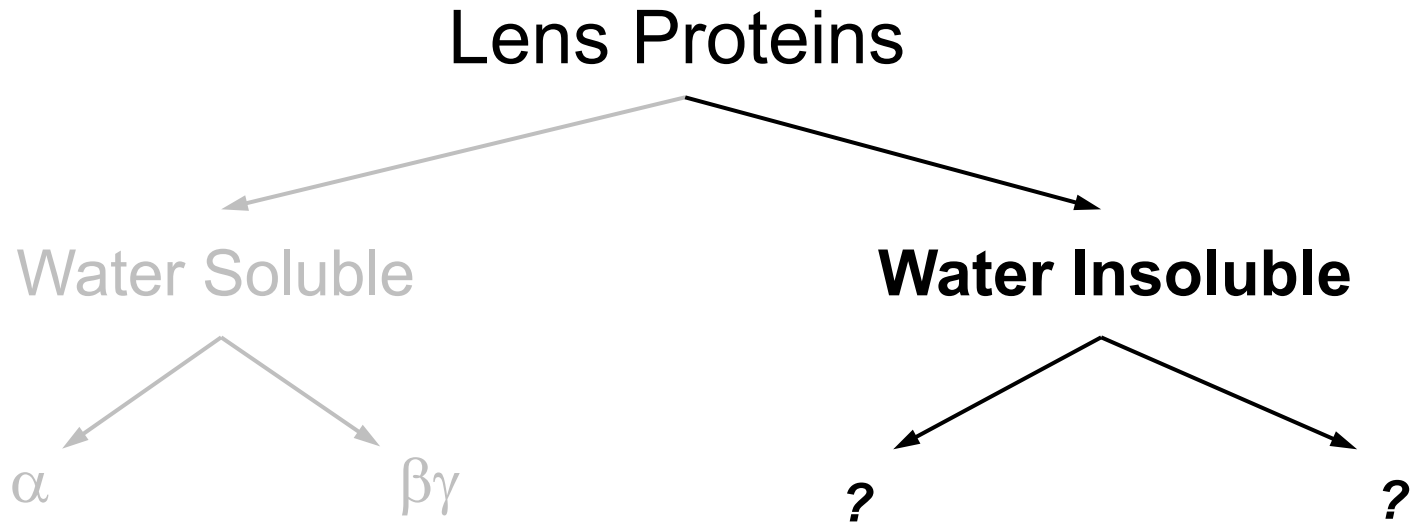
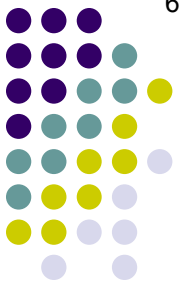
$\beta$ : The most common by weight

$\gamma$ : The smallest of the three

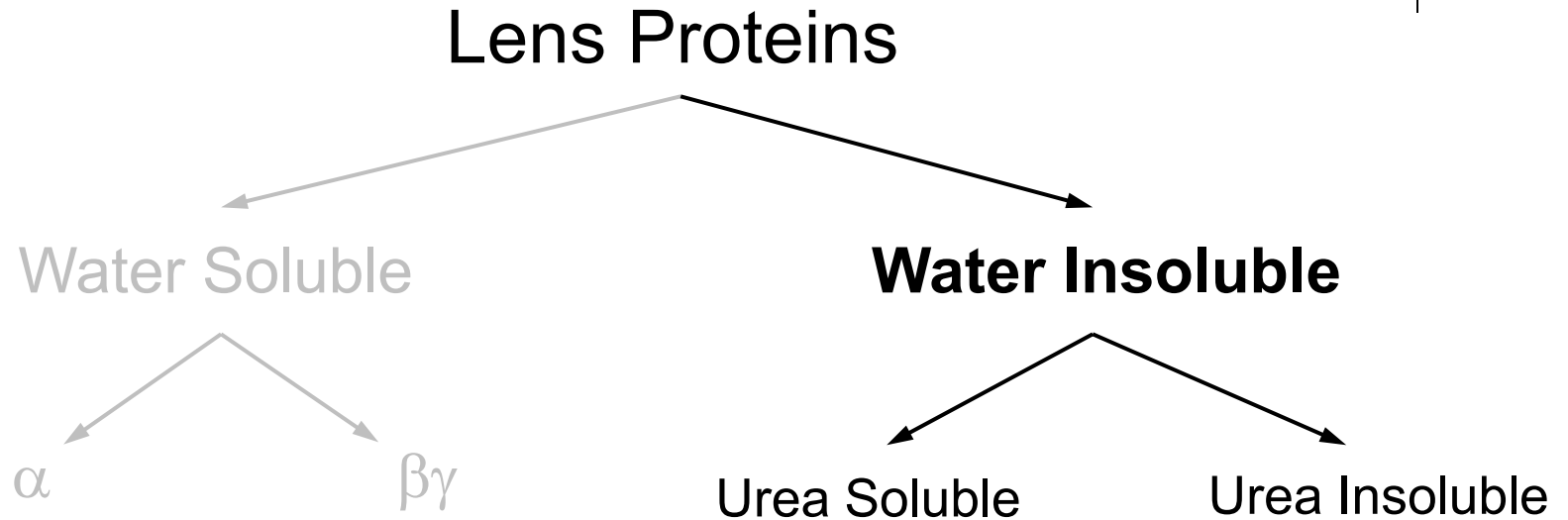
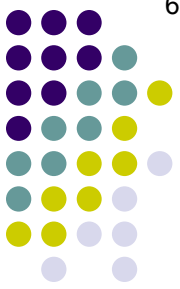
*Crystallins come in three forms (two of which are grouped together). What are they?*

*What vital role do crystallins play in lens function?*

They are the proteins cranked out by elongating lens fibers that increase the lens's refractive index enough to render it a viable refracting structure



*Water-insoluble proteins come two basic types. What are they?  
(Hint: The types are divided on the basis of a physical property  
of the proteins.)*

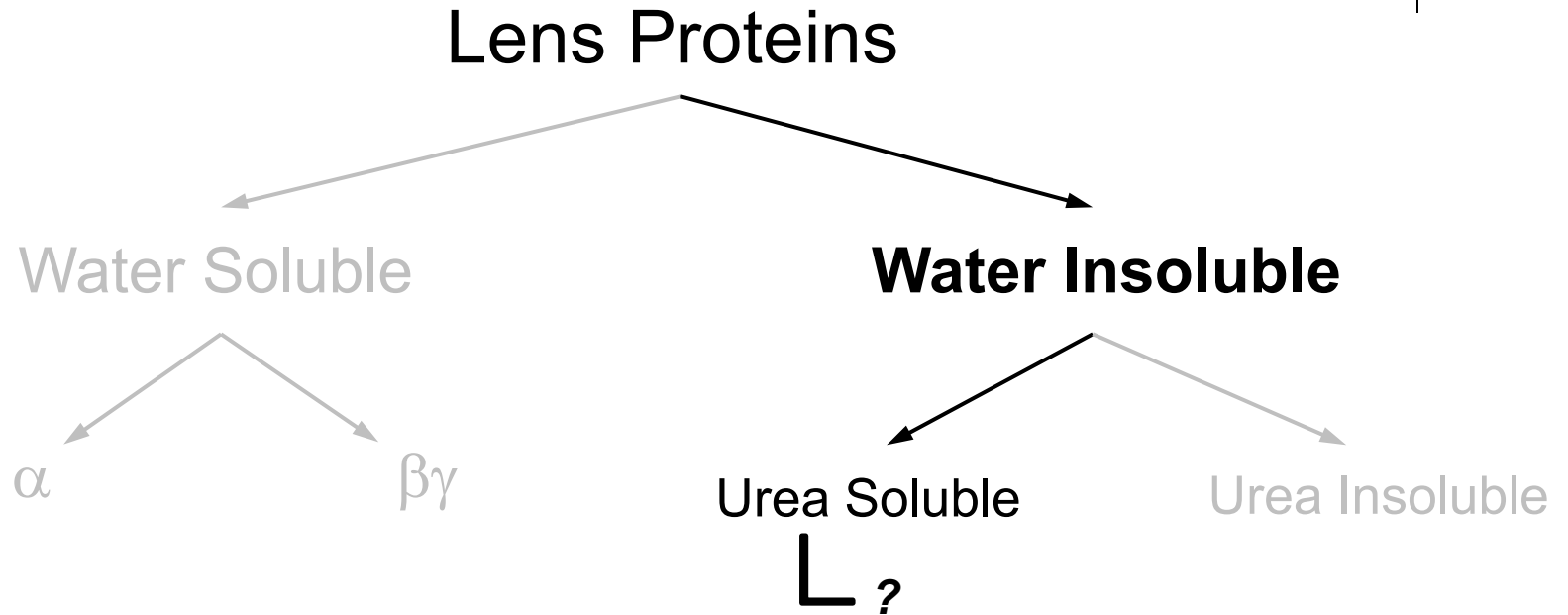


*Water-insoluble proteins come two basic types. What are they?  
(Hint: The types are divided on the basis of a physical property  
of the proteins.)*

Q

## Lens Proteins

69



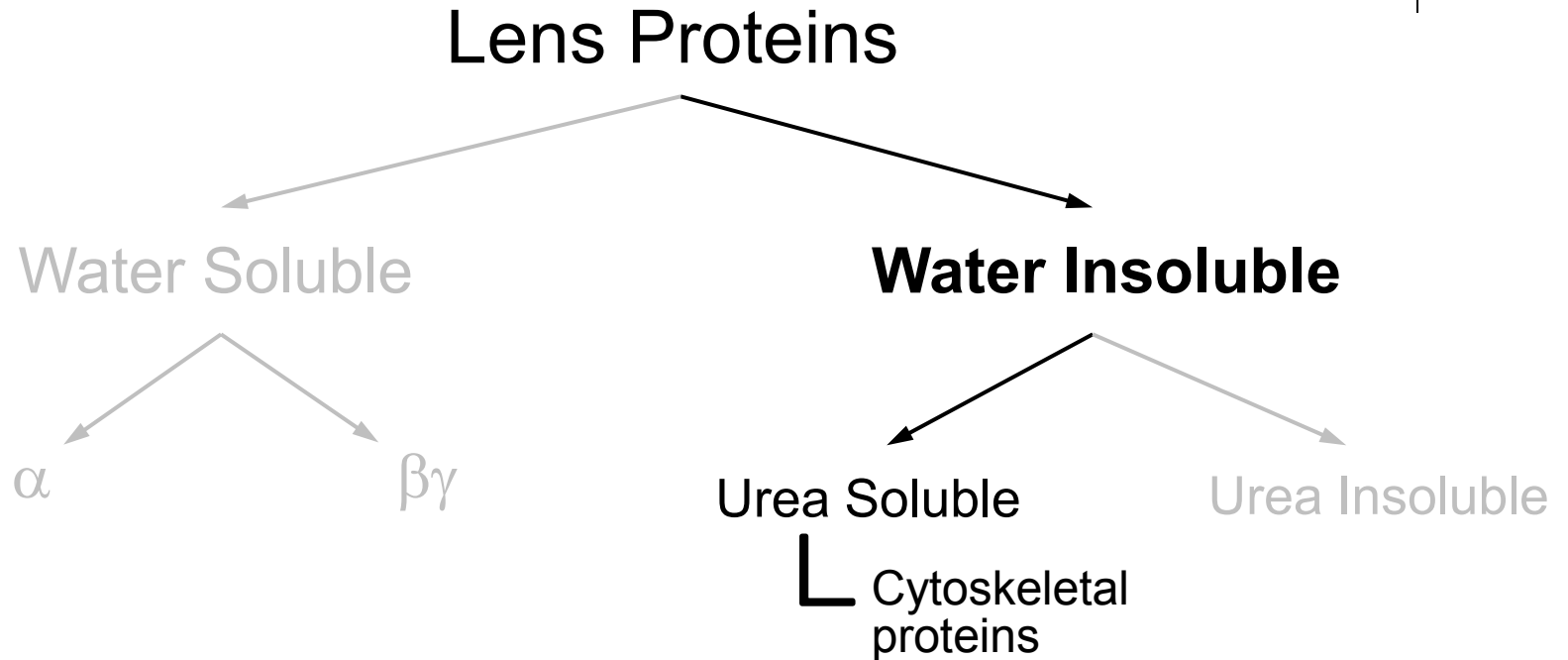
*What sort of protein comprises the majority of the urea-soluble fraction of the water-insoluble lens proteins?*

A

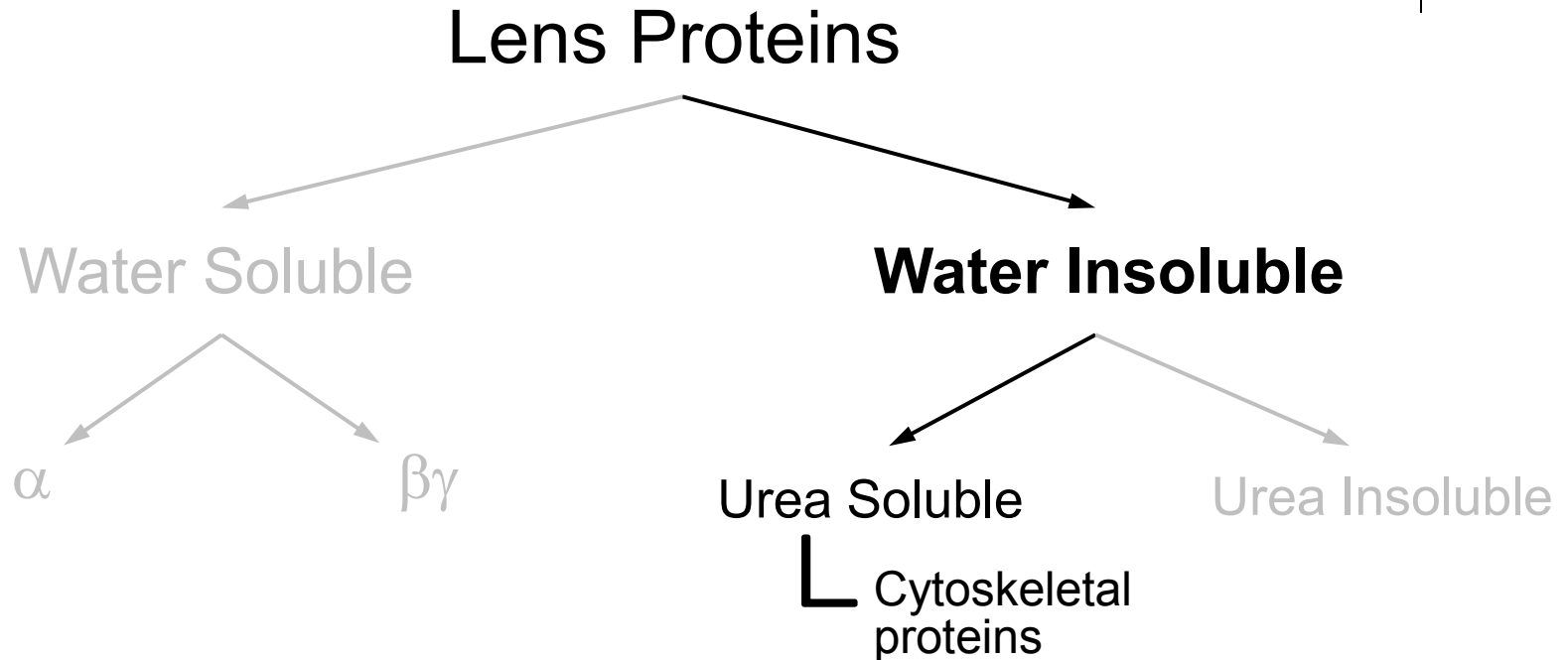
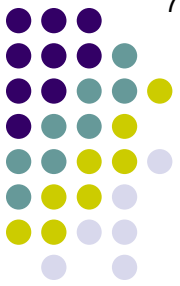
## Lens Proteins



70



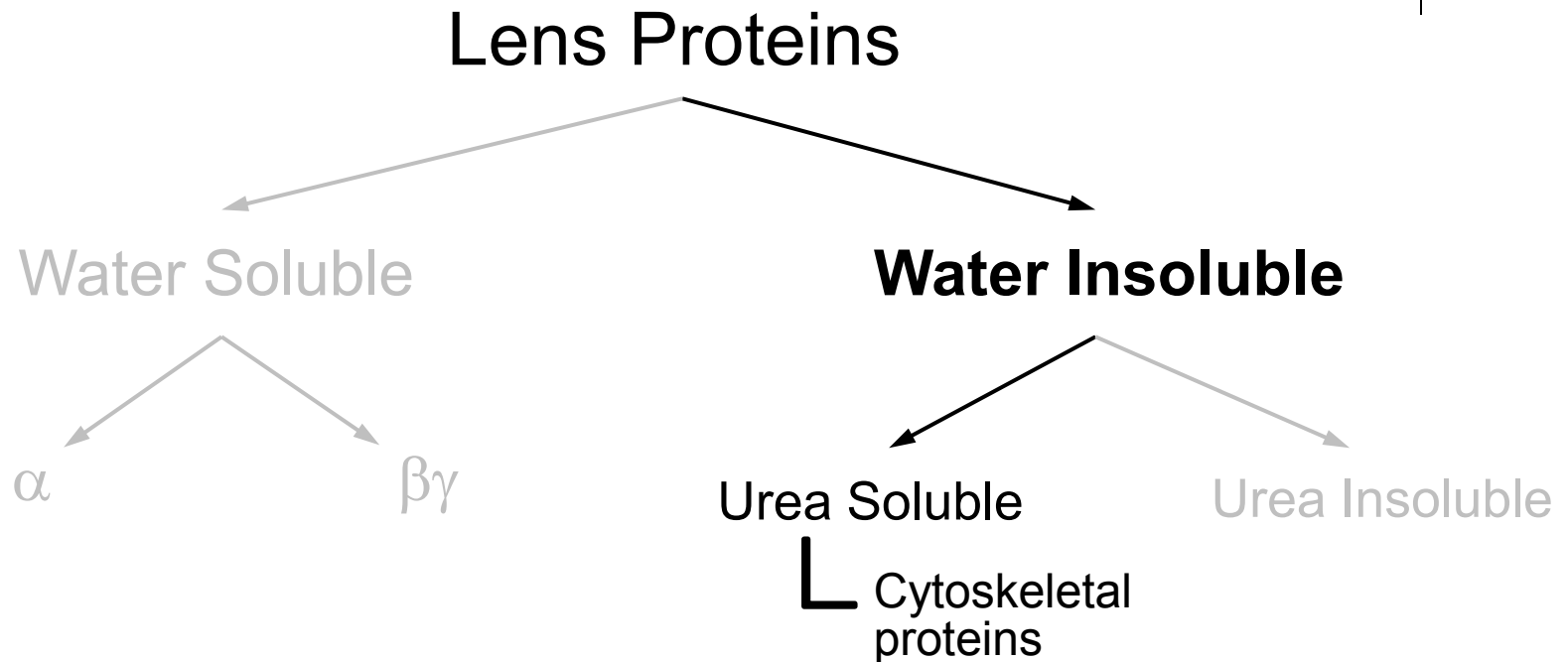
*What sort of protein comprises the majority of the urea-soluble fraction of the water-insoluble lens proteins?*  
Cytoskeletal proteins



*What sort of protein comprises the majority of the urea-soluble fraction of the water-insoluble lens proteins?*

Cytoskeletal proteins

*What function do cytoskeletal proteins serve?*



*What sort of protein comprises the majority of the urea-soluble fraction of the water-insoluble lens proteins?*

Cytoskeletal proteins

*What function do cytoskeletal proteins serve?*

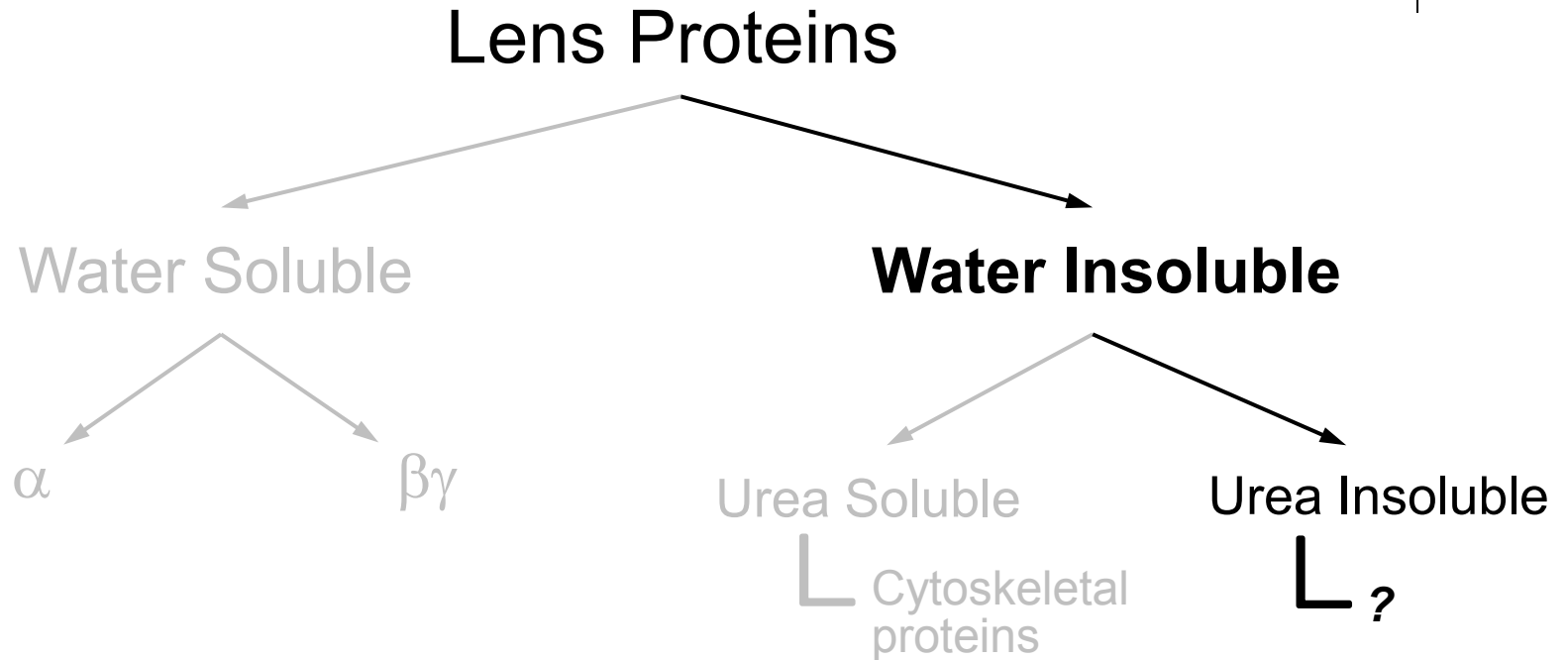
They are the primary component of the structural framework of lens cells



Q

## Lens Proteins

73

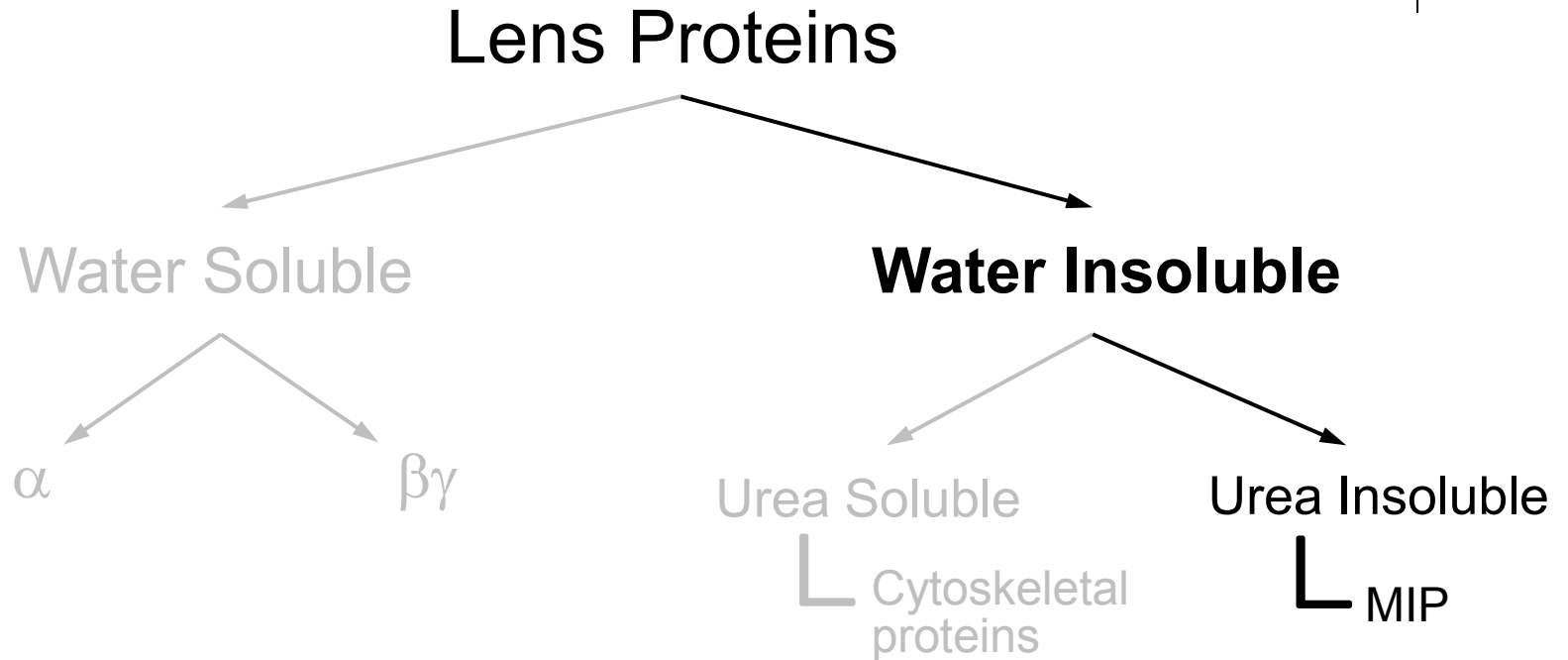
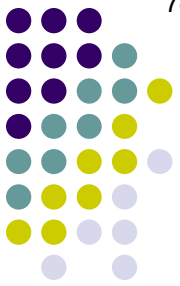


*What sort of protein comprises the majority of the urea-insoluble fraction of the water-insoluble lens proteins?*

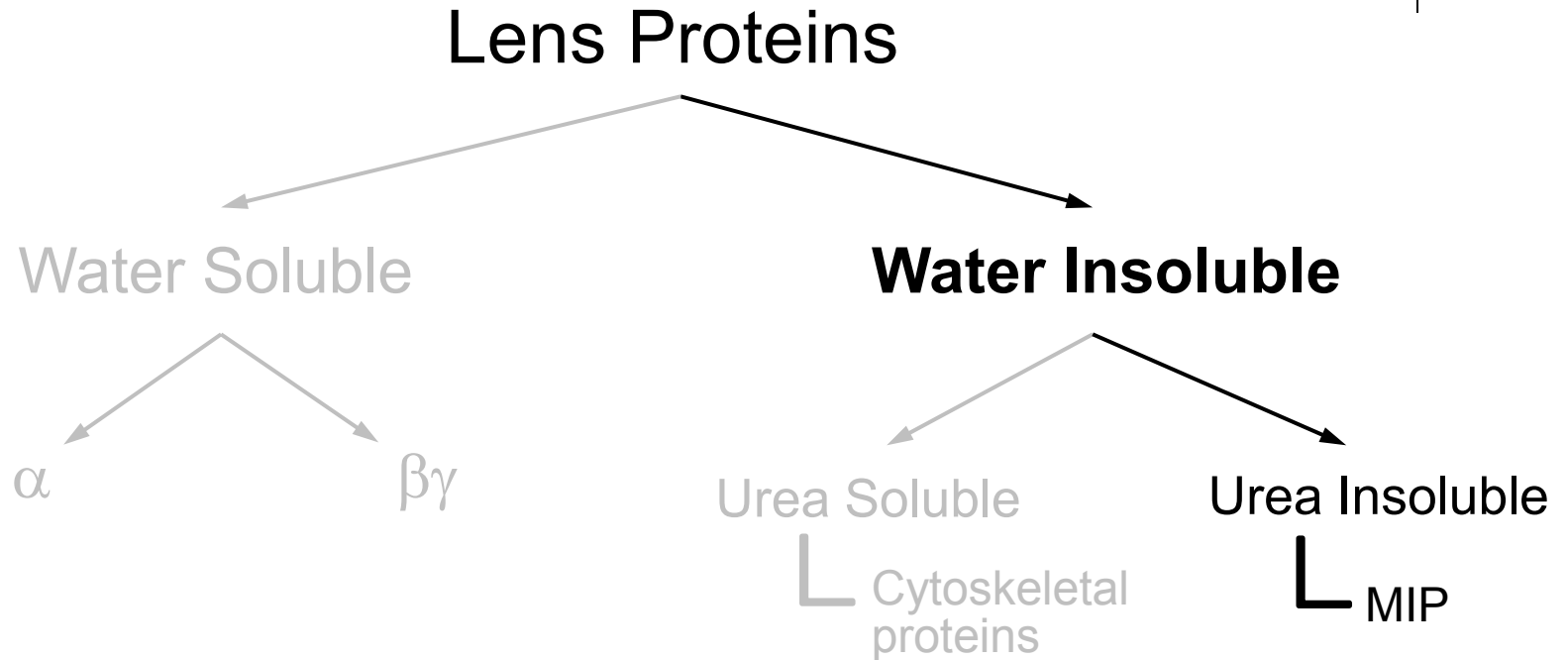
A

## Lens Proteins

74



*What sort of protein comprises the majority of the urea-insoluble fraction of the water-insoluble lens proteins?*  
Major intrinsic protein (MIP)



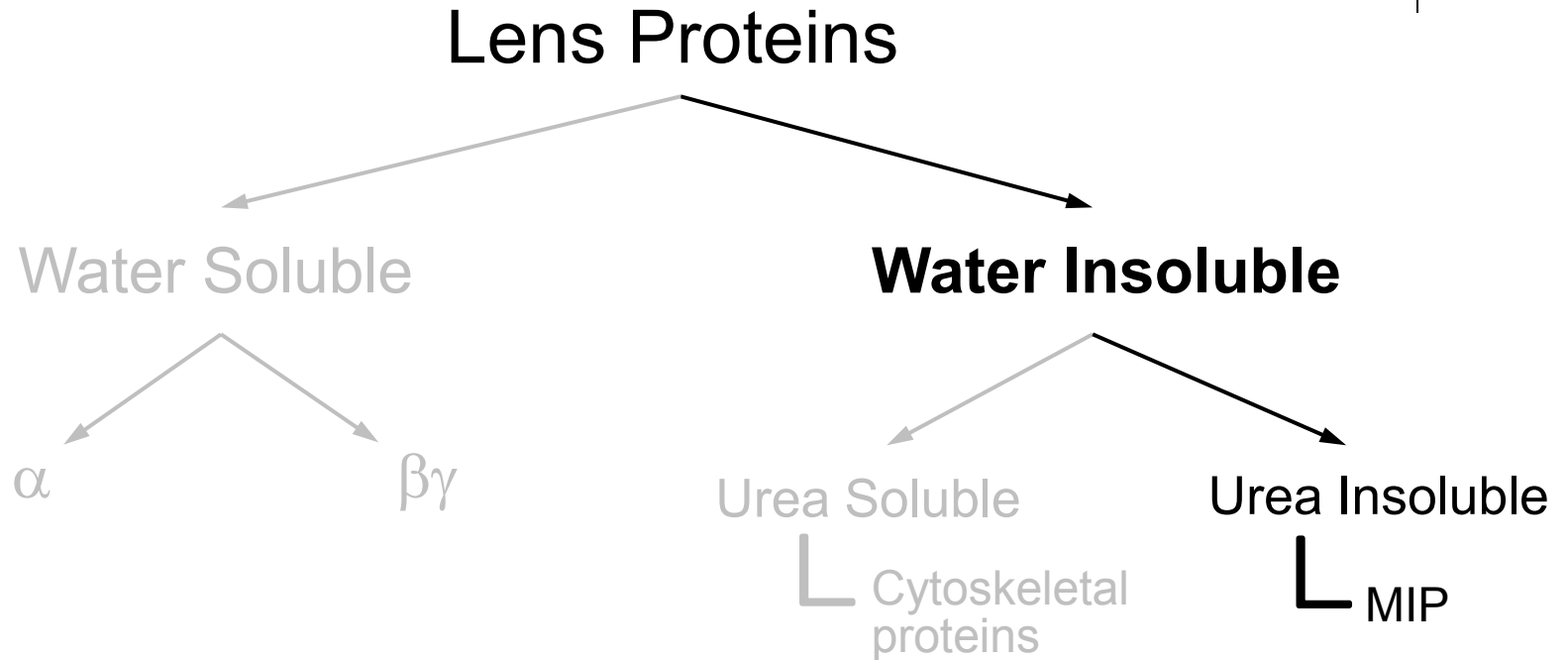
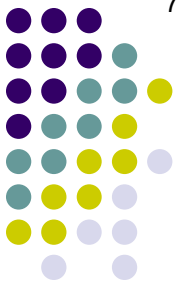
*What sort of protein comprises the majority of the urea-insoluble fraction of the water-insoluble lens proteins?*  
Major intrinsic protein (MIP)

*To what class of proteins do MIPs belong?*

A

## Lens Proteins

76



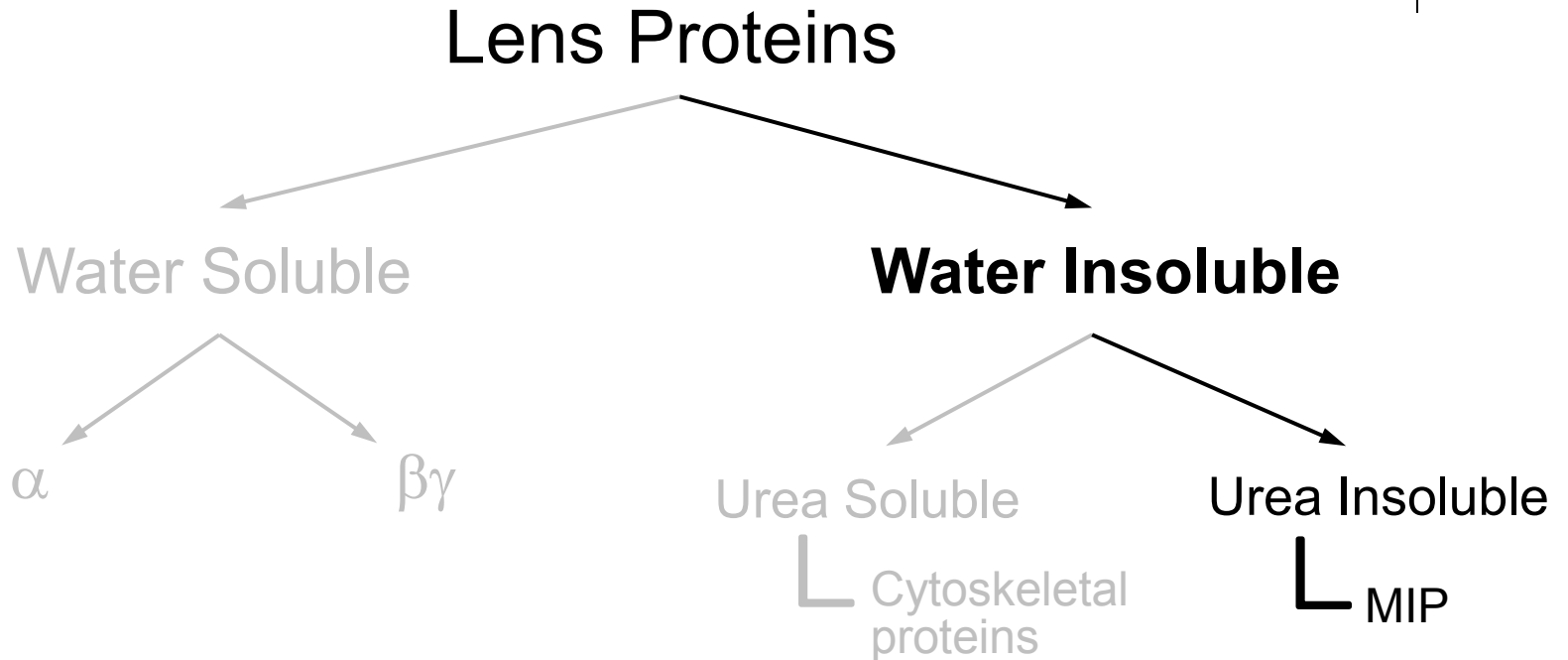
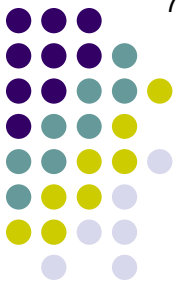
*What sort of protein comprises the majority of the urea-insoluble fraction of the water-insoluble lens proteins?*  
Major intrinsic protein (MIP)

*To what class of proteins do MIPs belong?*  
Aquaporins

Q

## Lens Proteins

77

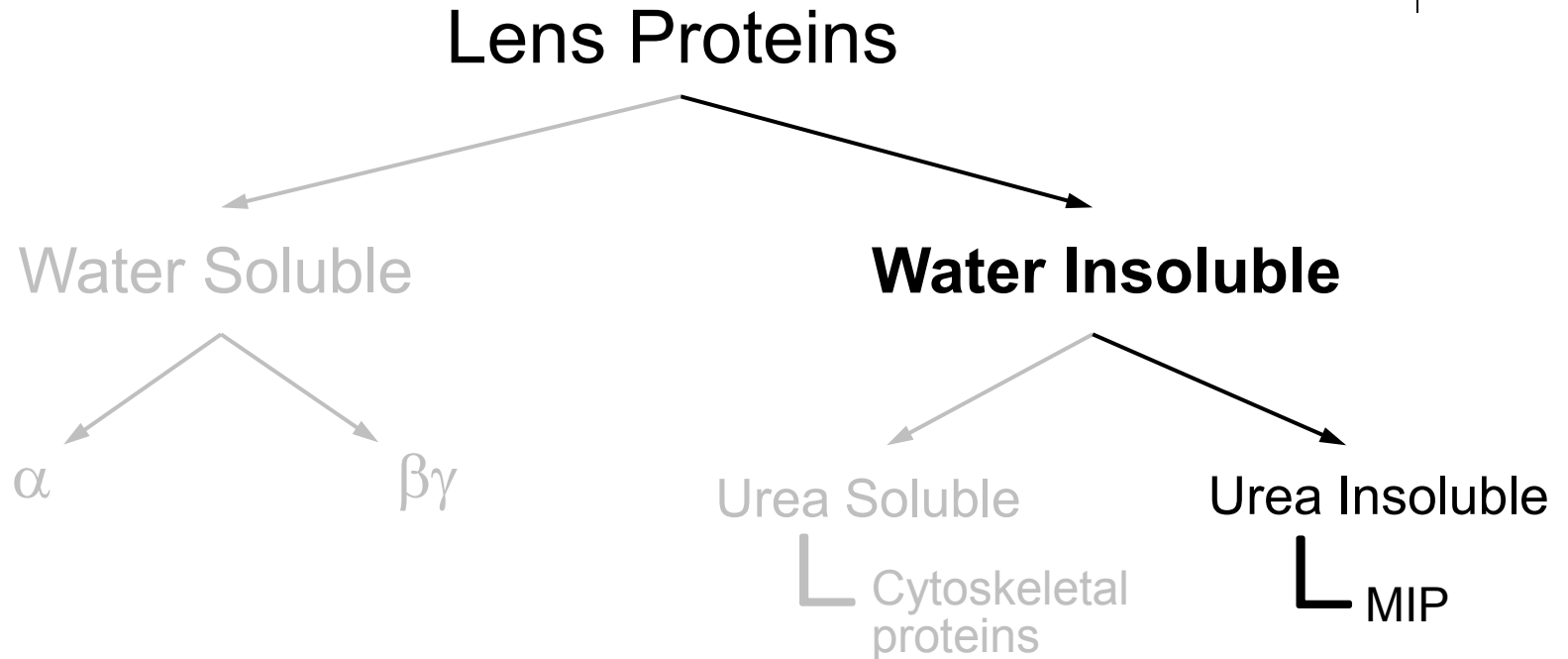


*What sort of protein comprises the majority of the urea-insoluble fraction of the water-insoluble lens proteins?*  
Major intrinsic protein (MIP)

*For what function are aquaporins known?*

*to which MIPs belong?*

**Aquaporins**



*What sort of protein comprises the majority of the urea-insoluble fraction of the water-insoluble lens proteins?*  
Major intrinsic protein (MIP)

*For what function are aquaporins known?*  
As   channels in cell membranes

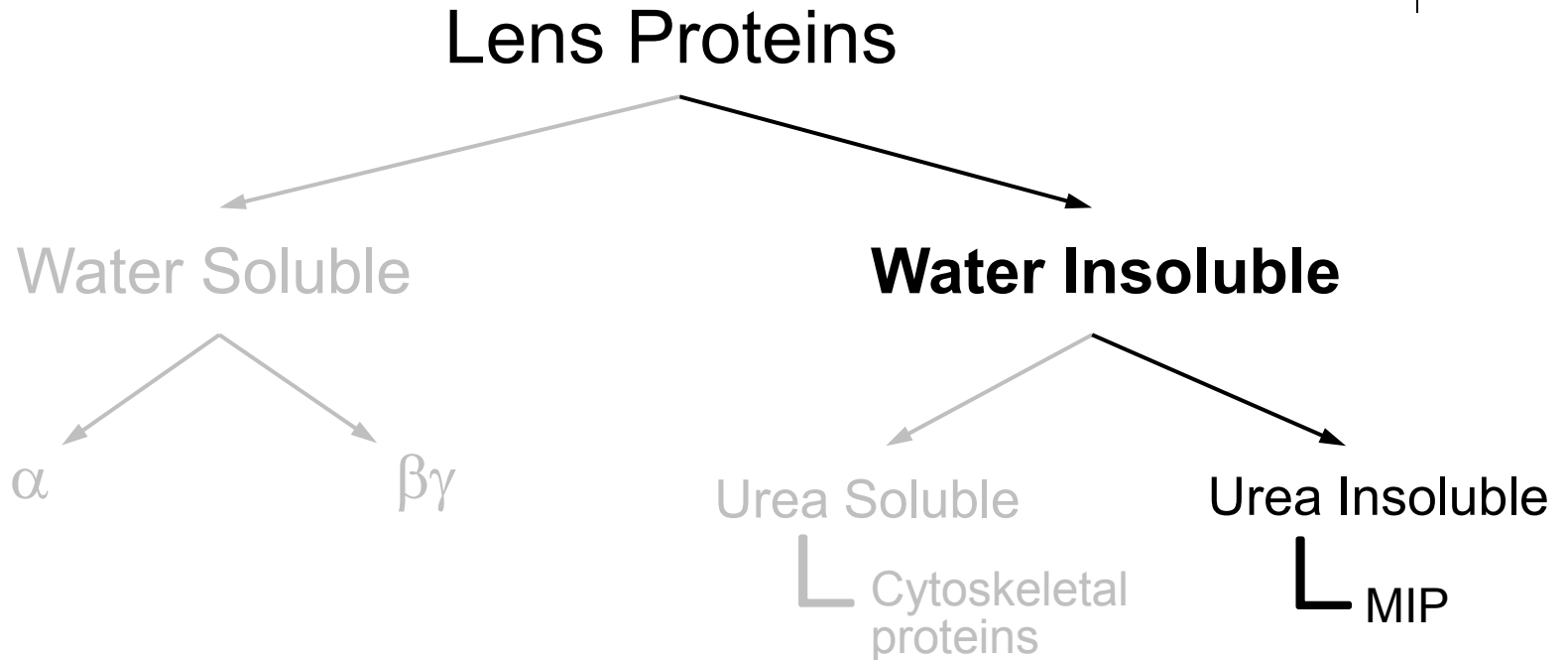
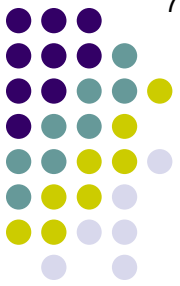
*to MIPs belong?*

**Aquaporins**

A

## Lens Proteins

79



*What sort of protein comprises the majority of the urea-insoluble fraction of the water-insoluble lens proteins?*  
Major intrinsic protein (MIP)

*For what function are aquaporins known?*  
As water channels in cell membranes

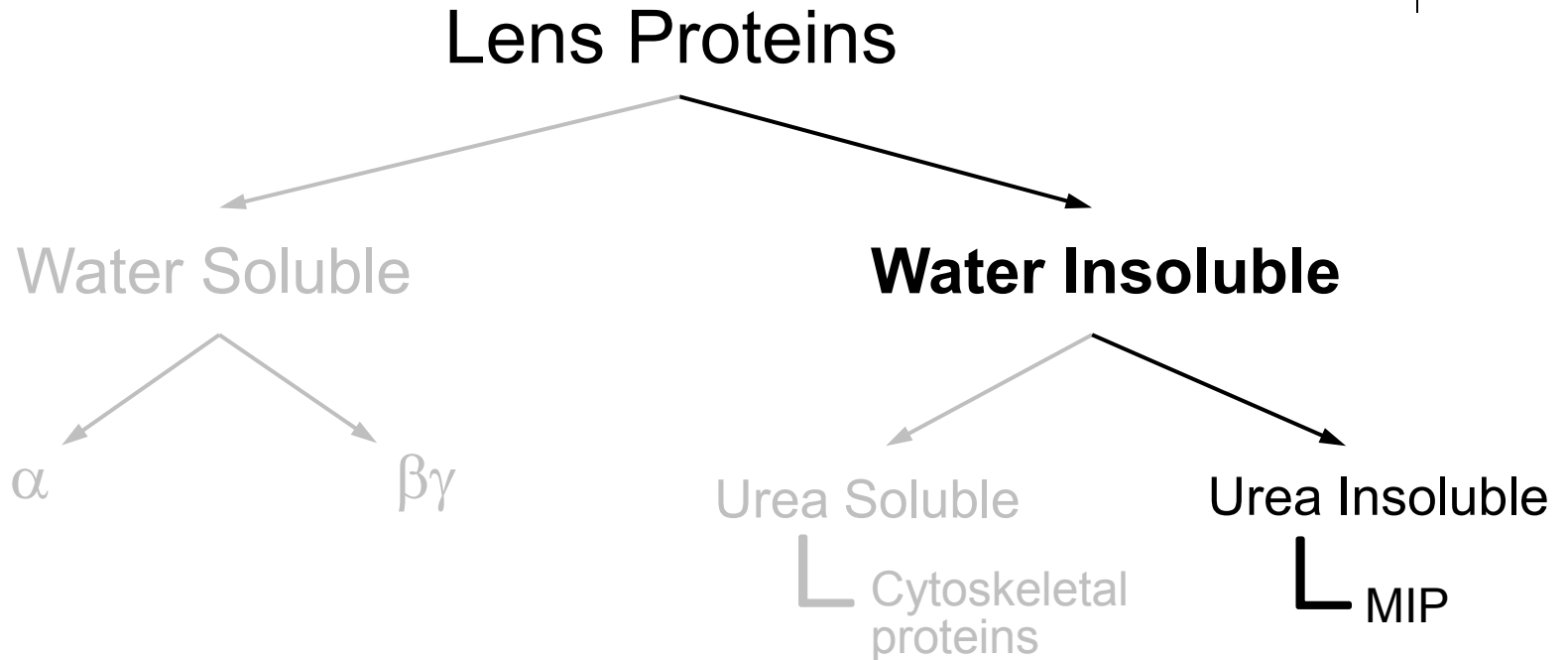
*to which MIPs belong?*

**Aquaporins**

A

## Lens Proteins

80



*What sort of protein comprises the majority of the urea-insoluble fraction of the water-insoluble lens proteins?*  
Major intrinsic protein (MIP)

*For what function are aquaporins known?*

As water channels in cell membranes (Note: The *Lens* book is not clear whether the MIP/aquaporin in lens cells serves this function)

*to MIPs belong?*

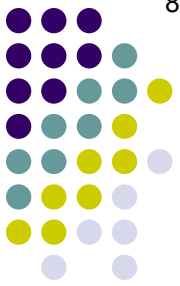
**Aquaporins**



Q

## Lens Proteins

81



### Lens Proteins

Water Soluble

**Water Insoluble**

$\alpha$

$\beta\gamma$

Urea Soluble

Urea Insoluble

└ MIP

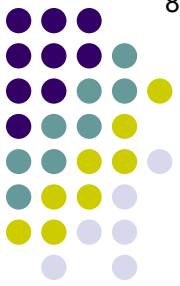
*The word 'aquaporin' rings a bell...In what ophthalmic condition does (dys)function of such channels play a role? (Note: The lens is in no way involved.)*

*of the urea-insoluble  
soluble lens proteins?  
intrinsic protein (MIP)*

*to MIPs belong?*

**Aquaporins**

*No water channels in cell membranes (Note: The lens book is not clear whether the MIP/aquaporin in lens cells serves this function)*



## Lens Proteins

Water Soluble

**Water Insoluble**

$\alpha$

$\beta\gamma$

Urea Soluble

Urea Insoluble

└ MIP

*The word 'aquaporin' rings a bell...In what ophthalmic condition does (dys)function of such channels play a role? (Note: The lens is in no way involved.)*

Neuromyelitis optica (NMO, aka **eponym** dz)

*of the urea-insoluble  
soluble lens proteins?  
intrinsic protein (MIP)*

*to MIPs belong?*

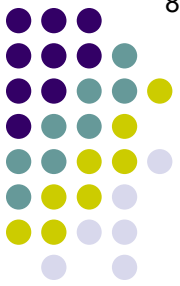
**Aquaporins**

*No water channels in cell membranes (Note: The lens book is not clear whether the MIP/aquaporin in lens cells serves this function)*

# A

## Lens Proteins

83



### Lens Proteins

Water Soluble

Water Insoluble

$\alpha$

$\beta\gamma$

Urea Soluble

Urea Insoluble

└ MIP

*The word 'aquaporin' rings a bell...In what ophthalmic condition does (dys)function of such channels play a role? (Note: The lens is in no way involved.)*

Neuromyelitis optica (NMO, aka *Devic's dz*)

*of the urea-insoluble  
soluble lens proteins?  
intrinsic protein (MIP)*

*to MIPs belong?*

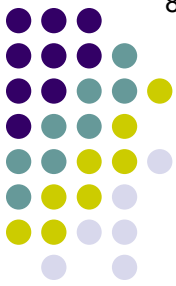
**Aquaporins**

*No water channels in cell membranes (Note: The lens book is not clear whether the MIP/aquaporin in lens cells serves this function)*

A

# Lens Proteins

84



## Lens Proteins

Water Soluble

**Water Insoluble**

$\alpha$

$\beta\gamma$

Urea Soluble

Urea Insoluble

└ MIP

*The word 'aquaporin' rings a bell...In what ophthalmic condition does (dys)function of such channels play a role? (Note: The lens is in no way involved.)*

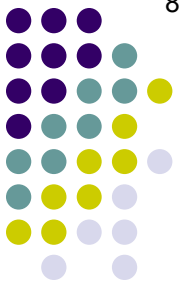
Neuromyelitis optica (NMO, aka *Devic's dz*) and neuromyelitis optica spectrum disorder (NMOSD)

of the urea-insoluble  
soluble lens proteins?  
intrinsic protein (MIP)

to MIPs belong?

**Aquaporins**

No water channels in cell membranes (Note: The lens book is not clear whether the MIP/aquaporin in lens cells serves this function)



## Lens Proteins

Water Soluble

**Water Insoluble**

$\alpha$

$\beta\gamma$

Urea Soluble

Urea Insoluble

└ MIP

*The word 'aquaporin' rings a bell...In what ophthalmic condition does (dys)function of such channels play a role? (Note: The lens is in no way involved.)*

Neuromyelitis optica (NMO, aka *Devic's dz*) and neuromyelitis optica spectrum disorder (NMOSD)

*Which aquaporin is implicated in these conditions?*

*of the urea-insoluble  
soluble lens proteins?  
intrinsic protein (MIP)*

*to MIPs belong?*

**Aquaporins**

*As water channels in cell membranes (Note: The lens book is not clear whether the MIP/aquaporin in lens cells serves this function)*

A

## Lens Proteins



86

## Lens Proteins

Water Soluble

Water Insoluble

$\alpha$

$\beta\gamma$

Urea Soluble

Urea Insoluble

└ MIP

*The word 'aquaporin' rings a bell...In what ophthalmic condition does (dys)function of such channels play a role? (Note: The lens is in no way involved.)*

Neuromyelitis optica (NMO, aka *Devic's dz*) and neuromyelitis optica spectrum disorder (NMOSD)

*Which aquaporin is implicated in these conditions?*

Aquaporin 4 (AQP4)

*of the urea-insoluble  
soluble lens proteins?  
intrinsic protein (MIP)*

*to MIPs belong?*

**Aquaporins**

*As water channels in cell membranes (Note: The lens book is not clear whether the MIP/aquaporin in lens cells serves this function)*

Q

# Lens Proteins



87

## Lens Proteins

Water Soluble

Water Insoluble

$\alpha$

$\beta\gamma$

Urea Soluble

Urea Insoluble

L MIP

*The word 'aquaporin' rings a bell...In what ophthalmic condition does (dys)function of such channels play a role? (Note: The lens is in no way involved.)*

Neuromyelitis optica (NMO, aka *Devic's dz*) and neuromyelitis optica spectrum disorder (NMOSD)

*Is AQP4 the aquaporin found in the lens?*

*Which aquaporin is in the lens?*  
**Aquaporin 4 (AQP4)**

*What is the function of the urea-insoluble lens proteins?*  
Intrinsic protein (MIP)

*Do MIPs belong to the class of aquaporins?*

**Aquaporins**

*No water channels in cell membranes (Note: The lens book is not clear whether the MIP/aquaporin in lens cells serves this function)*

A

## Lens Proteins



88

## Lens Proteins

Water Soluble

Water Insoluble

$\alpha$

$\beta\gamma$

Urea Soluble

Urea Insoluble

L MIP

*The word 'aquaporin' rings a bell...In what ophthalmic condition does (dys)function of such channels play a role? (Note: The lens is in no way involved.)*

Neuromyelitis optica (NMO, aka *Devic's dz*) and neuromyelitis optica spectrum disorder (NMOSD)

*Which aquaporin is in the lens?*  
**Aquaporin 4 (AQP4)**

*Is AQP4 the aquaporin found in the lens?*  
No

*What is the function of the urea-insoluble lens proteins?*  
Intrinsic protein (MIP)

*Do MIPs belong?*

**Aquaporins**

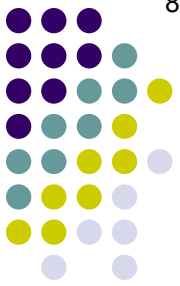
*No water channels in cell membranes (Note: The lens book is not clear whether the MIP/aquaporin in lens cells serves this function)*



Q

## Lens Proteins

89



## Lens Proteins

Water Soluble

Water Insoluble

$\alpha$

$\beta\gamma$

Urea Soluble

Urea Insoluble

L MIP

*The word 'aquaporin' rings a bell...In what ophthalmic condition does (dys)function of such channels play a role? (Note: The lens is in no way involved.)*

Neuromyelitis optica (NMO, aka *Devic's dz*) and neuromyelitis optica spectrum disorder (NMOSD)

*Which aquaporin is in*  
**Aquaporin 4 (AQP4)**

*Is AQP4 the aquaporin found in the lens?*

No

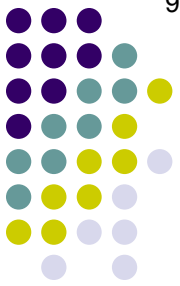
*Which aquaporin is found in lens cells?*

*of the urea-insoluble  
soluble lens proteins?  
intrinsic protein (MIP)*

*to MIPs belong?*

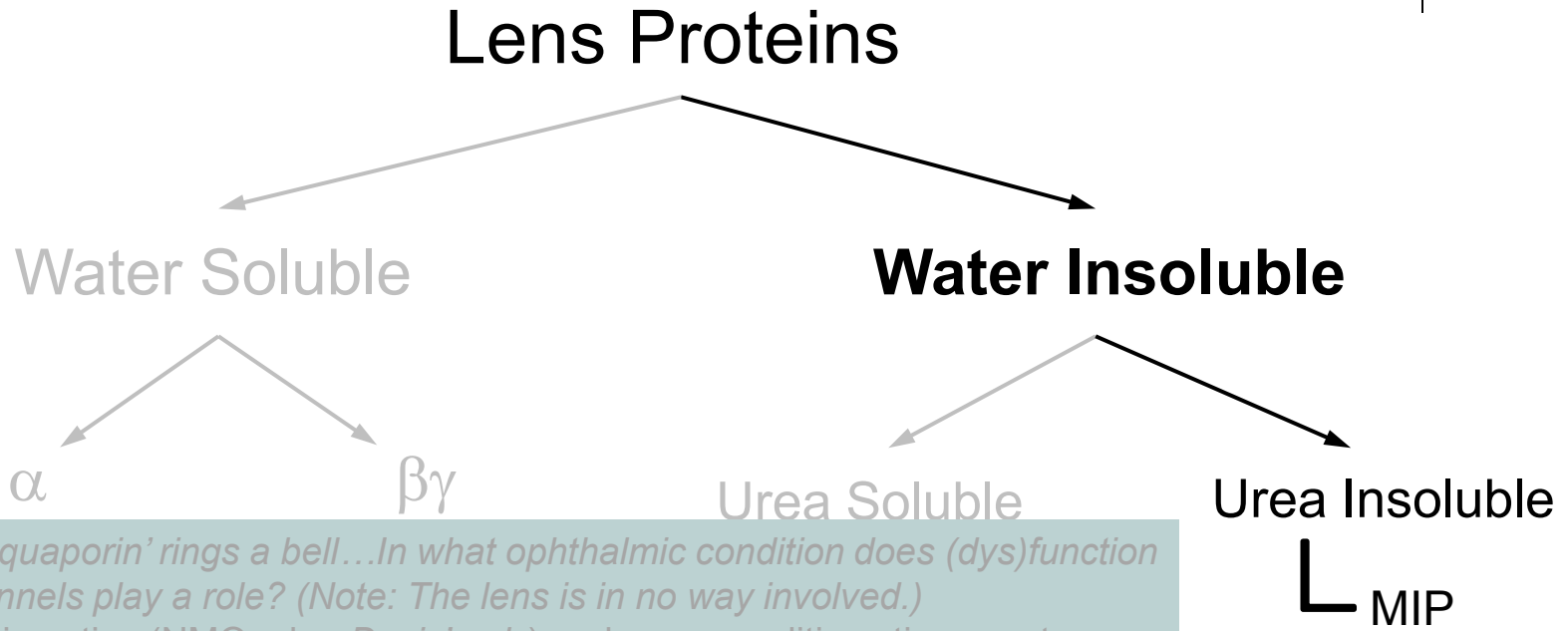
**Aquaporins**

*No water channels in cell membranes (Note: The lens book is not clear whether the MIP/aquaporin in lens cells serves this function)*



A

## Lens Proteins



*The word 'aquaporin' rings a bell...In what ophthalmic condition does (dys)function of such channels play a role? (Note: The lens is in no way involved.)*

Neuromyelitis optica (NMO, aka *Devic's dz*) and neuromyelitis optica spectrum disorder (NMOSD)

*Which aquaporin is in the lens?*  
**Aquaporin 4 (AQP4)**

*Is AQP4 the aquaporin found in the lens?*  
 No

*Which aquaporin is found in lens cells?*  
 Aquaporin 0

*What is the function of the urea-insoluble water-soluble lens proteins?*  
 Intrinsic protein (MIP)

*Do MIPs belong to aquaporins?*

**Aquaporins**

*No water channels in cell membranes (Note: The lens book is not clear whether the MIP/aquaporin in lens cells serves this function)*

Q

## Lens Proteins



91

## Lens Proteins

Water Soluble

**Water Insoluble**

$\alpha$

$\beta\gamma$

Urea Soluble

Urea Insoluble

└ MIP

*The word 'aquaporin' rings a bell...In what ophthalmic condition does (dys)function of such channels play a role? (Note: The lens is in no way involved.)*

Neuromyelitis optica (NMO, aka *Devic's dz*) and neuromyelitis optica spectrum disorder (NMOSD)

*Which aquaporin is implicated in these conditions?*

Aquaporin 4 (AQP4)

*What is the typical ophthalmic manifestation of NMO(SD)?*

*of the urea-insoluble soluble lens proteins?*  
intrinsic protein (MIP)

*to MIPs belong?*

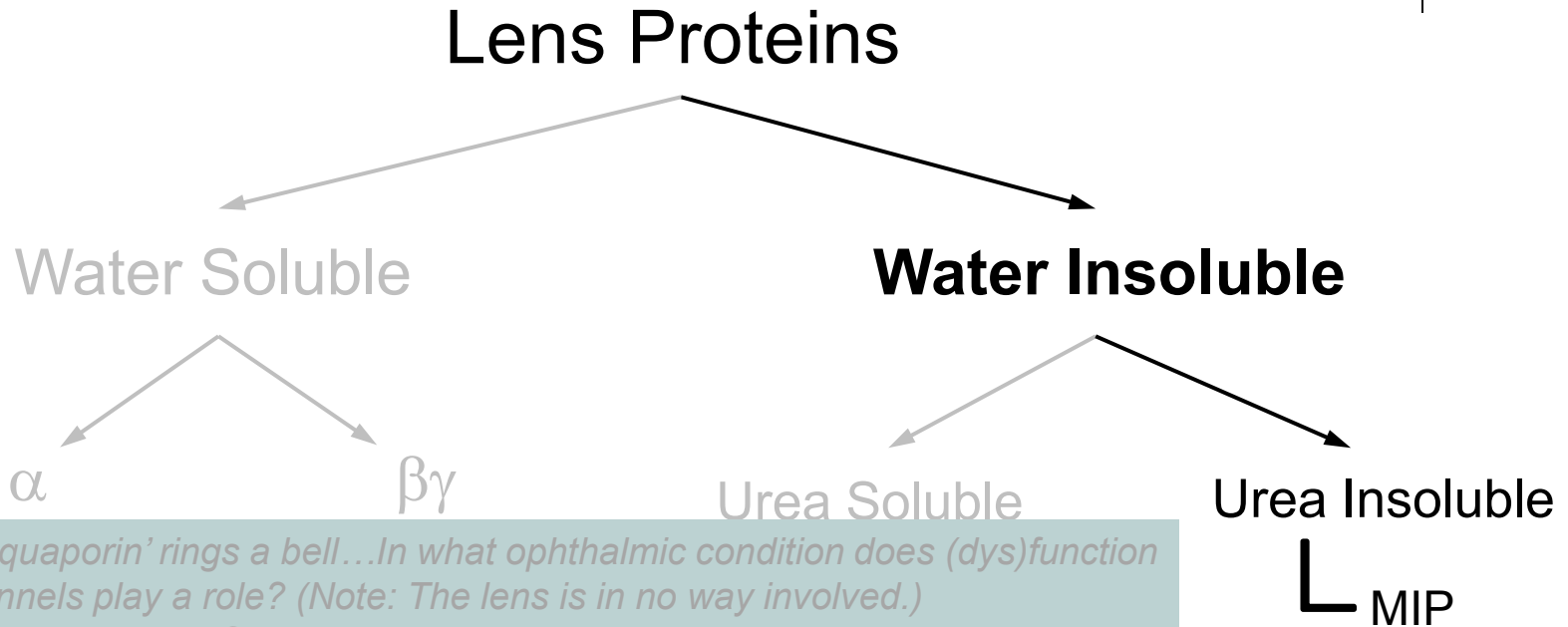
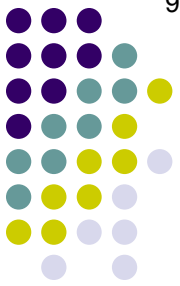
**Aquaporins**

*As water channels in cell membranes (Note: The lens book is not clear whether the MIP/aquaporin in lens cells serves this function)*

# A

## Lens Proteins

92



*The word 'aquaporin' rings a bell...In what ophthalmic condition does (dys)function of such channels play a role? (Note: The lens is in no way involved.)*

Neuromyelitis optica (NMO, aka *Devic's dz*) and neuromyelitis optica spectrum disorder (NMOSD)

*Which aquaporin is implicated in these conditions?*

Aquaporin 4 (AQP4)

*What is the typical ophthalmic manifestation of NMO(SD)?*

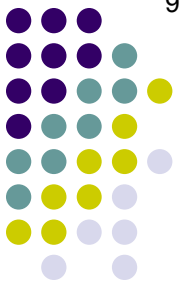
Optic neuritis

*of the urea-insoluble soluble lens proteins?*  
intrinsic protein (MIP)

*to MIPs belong?*

**Aquaporins**

*As water channels in cell membranes (Note: The lens book is not clear whether the MIP/aquaporin in lens cells serves this function)*



## Lens Proteins

### Lens Proteins

Water Soluble

Water Insoluble

***For more on AQP4 and NMO(SD), see slide-set N8***

$\alpha$

$\beta\gamma$

Urea Soluble

Urea Insoluble

└ MIP

*The word 'aquaporin' rings a bell...In what ophthalmic condition does (dys)function of such channels play a role? (Note: The lens is in no way involved.)*

Neuromyelitis optica (NMO, aka *Devic's dz*) and neuromyelitis optica spectrum disorder (NMOSD)

*Which aquaporin is implicated in these conditions?*

Aquaporin 4 (AQP4)

*What is the typical ophthalmic manifestation of NMO(SD)?*

Optic neuritis

*of the urea-insoluble soluble lens proteins?*  
Intrinsic protein (MIP)

*to MIPs belong?*

**Aquaporins**

*As water channels in cell membranes (Note: The lens book is not clear whether the MIP/aquaporin in lens cells serves this function)*