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# Macromolecular Crystallography

Deciphering the Structure, Function and  
Dynamics of Biological Molecules

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## Chapter 14

# ***Proteopedia*: Exciting Advances in the 3D Encyclopedia of Biomolecular Structure**

Jaime Prilusky, Eran Hodis, and Joel L. Sussman

**Abstract** *Proteopedia* is a collaborative, 3D web-encyclopedia of protein, nucleic acid and other structures. *Proteopedia* (<http://www.proteopedia.org>) presents 3D biomolecule structures in a broadly accessible manner to a diverse scientific audience through easy-to-use molecular visualization tools integrated into a wiki environment that anyone with a user account can edit. We describe recent advances in the web resource in the areas of content and software. In terms of content, we describe a large growth in user-added content as well as improvements in automatically-generated content for all PDB entry pages in the resource. In terms of software, we describe new features ranging from the capability to create pages hidden from public view to the capability to export pages for offline viewing. New software features also include an improved file-handling system and availability of biological assemblies of protein structures alongside their asymmetric units.

**Keywords** Structural biology • Communication • 3D • Dissemination • Wiki • *Proteopedia* • Education • Instruction • Collaboration • Encyclopedia • Web resource • Jmol • PDB

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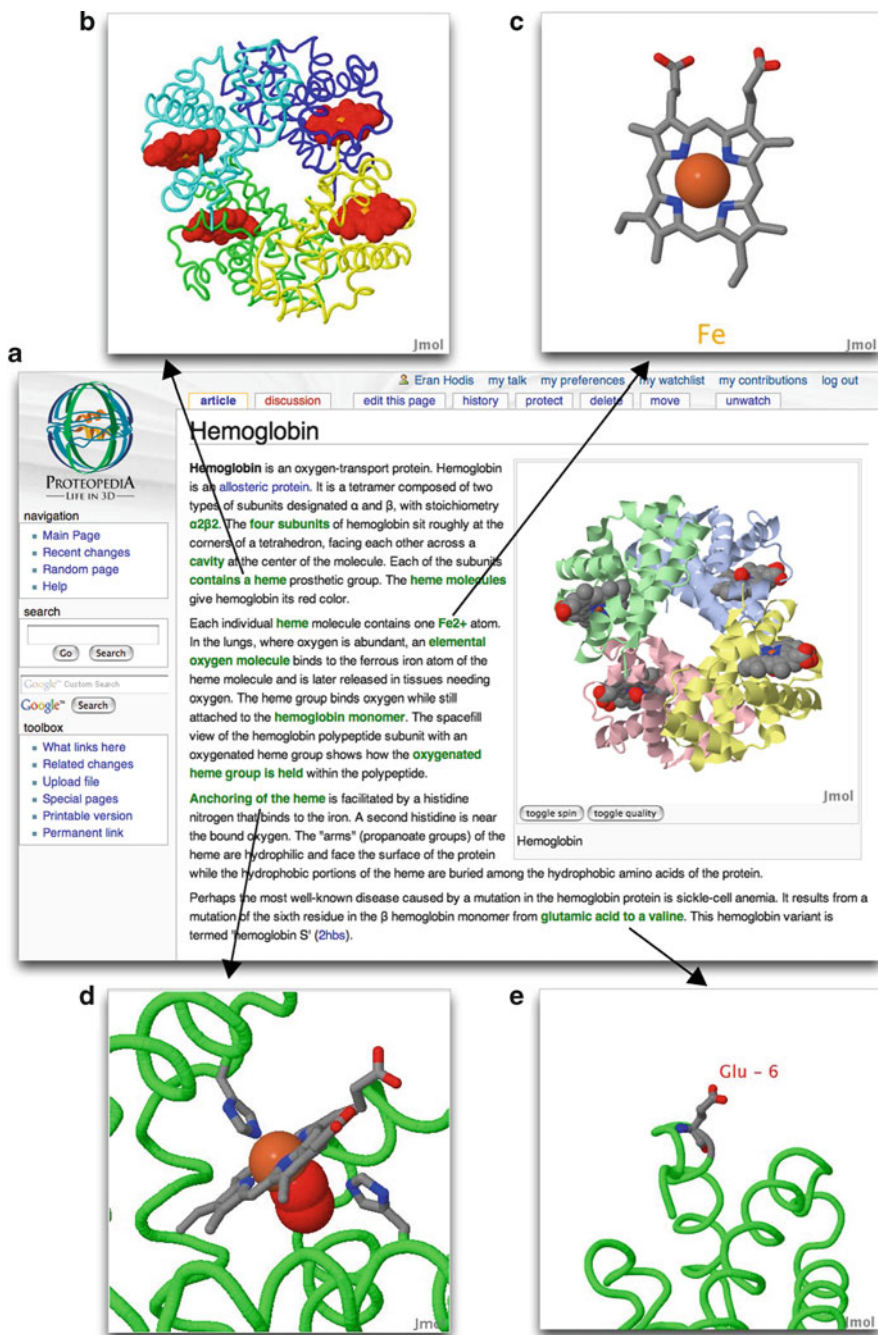
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## 14.1 Introduction

*Proteopedia* [1] (<http://www.proteopedia.org>) is a collaborative, 3D web-encyclopedia of biomolecular structures. While structures of proteins, nucleic acids and other biomolecules are often conveyed using two dimensional images in journal articles, textbooks and even in lectures, such images can often be difficult to comprehend because they flatten a 3D structure into two dimensions. Structural biologists and chemists utilize a wide array of molecular visualization programs to navigate biomolecular structures in 3D, but these programs are generally inaccessible to those scientists and students without a background in structural biology. *Proteopedia* presents 3D biomolecular structures in a broadly accessible manner to a diverse scientific audience through easy-to-use molecular visualization tools (mostly Jmol [2], some Kinemage [3]) integrated into a wiki environment that anyone with a user account can edit. Structural information is intuitively communicated through rotatable and zoomable 3D structures displayed on *Proteopedia* pages adjacent to descriptive text containing links called 'scene-links' that when clicked elicit a change in the view, colors, and representation of the 3D structure, highlighting a point made in the text (Fig. 14.1).

*Proteopedia's* strength lies in the ease with which a user can both explore a protein structure as well as contribute his or her own description and structural annotation using *Proteopedia's* "Scene Authoring Tools" to create 'scene-links'. Additional features of the website complement this strength. For instance, in order to appeal to the scientific community, pages in *Proteopedia* are editable only by registered users, who register for free user accounts using their full real names and with biographical information about their scientific background. At the bottom of every *Proteopedia* page is an automatically generated list of the users who have edited that page, giving both credit and responsibility to *Proteopedia* users, as well as providing a measure of the reliability of the page. Each user has an area where he or she can create pages that only he or she can edit, to allow for the creation of tutorials for the classroom or of material for projection during a lecture, over which the user would understandably need complete control. While the focus is on user-added pages, each entry in the PDB (over 65,000) has a *Proteopedia* page automatically generated for it, seeded with relevant information and primed for expansion by *Proteopedia* users. Such automatically seeded PDB entry pages typically contain a rotatable, zoomable 3D structure next to the abstract from the publication describing the structure, along with 'scene-links' highlighting ligands or functional sites, structural and functional annotation aggregated from various resources, links to view the PDB entry in various useful resources and links to download the PDB entry. These and other *Proteopedia* features have been described in detail previously [1], but *Proteopedia* is constantly evolving with pages added and edited daily, as well as frequent improvements to the website's software. In this chapter we discuss several advances in *Proteopedia* content and software.

In terms of content, *Proteopedia* has advanced both in the number and quality of user-added pages as well as in the automatically generated information provided on



**Fig. 14.1** Green links change from one easily-authored molecular scene to another. Thus, text discussing and describing the structure and function is reinforced by immediate and significant visual input (Reproduced from Hodis et al. [1])

each page describing a PDB entry. When *Proteopedia* was first presented to the international scientific community at the 40th Crystallographic Meeting at Erice “From Molecules to Medicine” (2008), the resource’s informational value stemmed mostly from the automatically generated pages for each entry in the PDB, rather than from the tens of user-added pages that existed at that point.

Since then, *Proteopedia* user-added pages have gone from tens of pages to well over two hundred pages. While some of these pages are of higher quality than others, the growth in the number of contributions and in the use of the site are promising and inviting. The types of pages that have been added span from encyclopedic pages on particular protein structures, through tutorial pages for use in classroom settings to supplementary material pages accompanying publications in scientific journals. *Proteopedia*’s automatically generated pages for each entry in the PDB have benefitted from a collaboration with the ConSurf Team, and now each such *Proteopedia* page offers a view of the 3D structure with each residue colored by its level of evolutionary conservation [4, 5].

In terms of software, *Proteopedia* has added many new capabilities: A ‘Workbench’ area now allows users to create pages that are hidden from public view or shared with a select group of users. An ‘Export’ feature allows a user to save a page to his or her computer for offline viewing. ‘Scene-links’ have now been optimized and protected against future PDB remediations that have in the past, have been disruptive. The *Proteopedia* Scene Authoring Tools (SAT) now include “Undo” and “Redo” buttons and tooltips for several of the SAT buttons, as well as the option to color a protein’s residues based on their level of evolutionary conservation according to ConSurf [4, 5]. Citing of scientific publications within the body of a *Proteopedia* page has been simplified and users can simply indicate a publication’s PubMed ID to have the full reference appear in the page’s ‘References’ section. Visualization advances include a ‘Pop-up’ button to allow for expansion of any *Proteopedia* Jmol applet and the beginnings of color-keys associated with ‘scene-links’. The addition of a semi-automatic mechanism for users to reserve blocks of many ‘Sandbox’ pages aids educators in cordoning off pages for use in workshops or for class projects. Biological assemblies are more functionally relevant than asymmetric units, and they are now available in *Proteopedia* [6, 7]. Finally, a translator from PyMOL [8] to Jmol allows a user to create ‘scene-links’ in *Proteopedia* using PyMOL “.pse” session files (in preparation for publication).

## 14.2 Advances in Content

### 14.2.1 User-Added Content

The over 800 registered *Proteopedia* users have created a variety of pages on the web resource, from pages describing a particular protein structure to pages serving as tutorials for university courses. Many of these pages have been organized into

the *Proteopedia* Table of Contents [9], accessible via a link on the left-hand side of any *Proteopedia* page. Although because the Table of Contents is manually curated, and *Proteopedia* is a growing resource, new pages may have yet to be added to the Table of Contents.

A page describing the ribosome is currently featured on the Main Page of *Proteopedia* [10, 11] and previously featured articles include ‘Swine Flu, Neuraminidase & Tamiflu’ and ‘Poly-A Polymerase’ [12]. Other new additions include pages on DNA [13], Lac Repressor [14], Mechanosensitive Channels [15] and HIV-1 Protease [16] and others (see What’s New [17] and Topic Pages [18]).

Tutorials created by one educator are often useful for other educators, and *Proteopedia* users are encouraged to share and adapt tutorials on the site. Examples of new tutorials include a tutorial on Serine Proteases [19] and a tutorial on Structural Templates [20]. Other tutorials and pages created by educators for teaching are listed on the site as well [21].

Educators have also assigned class projects involving the creation of *Proteopedia* pages. Courses and programs making use of *Proteopedia* range from the high-school level [22] to the undergraduate level (see GFP [23] and Proteins involved in cancer [24], in particular the pages linked to from that page are all created by undergraduate students) to the graduate level (see Triose\_Phosphate\_Isomerase [25] and CBI\_Molecules [26]).

Structural biologists have also created pages in *Proteopedia* as supplementary material for publications in scientific journals. The page ‘3btp’ describes the crystal structure of *Agrobacterium tumefaciens* VirE2 in complex with its chaperone VirE1 [27] and serves as supplementary material for an article in *PNAS* [28]. Another page describes engineered mutants of *B. cereus* HlyIIR, a member of the TetR family of dimeric transcriptional regulators [29], and serves as supplementary material for a recent article in *Proteins* [30].

### ***14.2.2 Coloring by Evolutionary Conservation for all PDB Entries (ConSurf)***

Of tantamount importance to a biologist examining a solved protein structure is how that protein’s function relates to its structure. Biochemical and molecular biology studies best illuminate a protein’s structure-function relationship, but computational analysis can also be informative, especially when the more laborious experimental work has yet to be carried out.

Evolutionary conservation of specific protein residues can often indicate functional importance. If certain residues have been protected from change over millions of years of evolution, there is a good chance that they are crucial for protein folding or difficult to comprehend function or protein folding. Almost all *Proteopedia* pages titled for a PDB entry (for example ‘1h88’) now have a link underneath the 3D structure titled “Evolutionary conservation [show]”. Clicking on “[show]” colors the residues of the rotating 3D structure by their level of evolutionary conservation

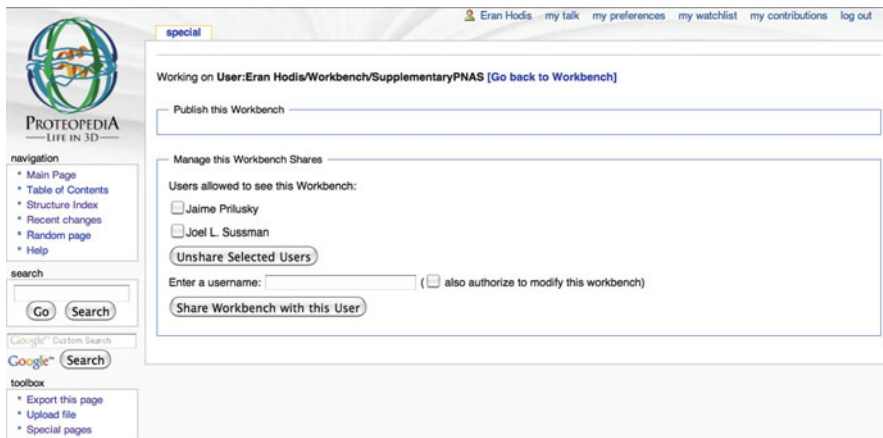
according to ConSurfDB [4, 5] (see: <http://consurfdb.tau.ac.il>), on a scale from 1 (Variable, teal-colored) to 5 (Average, white-colored) to 9 (Conserved, magenta-colored), with a color key explaining the coloring scheme. Briefly, ConSurfDB assigns conservation levels to a protein sequence by multiple sequence alignment to similar sequences followed by Bayesian analysis of the level of conservation of each residue (for a more detailed explanation see ConSurf-DB Process [31] or ConSurf [4, 5]). Residues for which there are insufficient data are colored yellow, and residues for which there are no data are colored grey. Clicking on “[show]” also expands a previously hidden “Evolutionary conservation display area” containing buttons for toggling the conservation colors on and off for different chains of the structure, allowing separate examination of individual chains separately. It should be noted that in *Proteopedia*'s coloring by evolutionary conservation, all the chains in the molecule are colored as such, but this can be misleading since ConSurf calculates evolutionary conservation independently for sequence-different chains, thus the scale of conservation may be different between chains, although the colors are the same (ConSurfDB avoids this problem by only displaying one chain at a time). Links in the “Evolutionary conservation display area” offer the user a page describing this and other caveats [32], a page with a detailed explanation of ConSurf in *Proteopedia* [33], and a page at ConSurfDB with complete results for the PDB entry being viewed (for example [34]).

## 14.3 Advances in Software and Development

### 14.3.1 Pages Hidden from Public View

While previously a user could create a page that only he or she could edit, that page would still be publicly visible. Public visibility of page content is problematic in certain cases, especially when developing a page for use as supplementary material to accompany a journal article submission.

A new feature in *Proteopedia* called the “Workbench” feature allows users to create hidden pages that they can either keep private or share with selected users. A Workbench page is created as a sub-page of a user's userpage. Each user has a userpage created in his or her name when he or she joins the site, for example ‘User:Eran Hodis’, and he or she can create subpages of that userpage such as ‘User:Eran Hodis/Hemoglobin’. The Workbench area is such a subpage: ‘User:Eran Hodis/Workbench’, and any subpage of the Workbench area is similarly protected: ‘User:Eran Hodis/Workbench/SupplementaryPNAS’. A page in the Workbench can be shared with selected users by clicking on the ‘Workbench’ tab near the top of the page and entering the usernames to whom the page should be also visible (Fig. 14.2). Different subpages in the Workbench area can be assigned to be visible to different users. Files, including images or PDB files, can be uploaded with the prefix ‘Workbench’ in order to similarly protect them from public viewing.



**Fig. 14.2** The “Workbench” interface allowing a user to choose with whom to share a Workbench page. In this case the user “Eran Hodis” has shared the page “User:Eran Hodis/Workbench/SupplementaryPNAS” with the users “Jaime Prilusky” and “Joel L. Sussman”

### 14.3.2 Save Pages for Offline Viewing

Online resources such as *Proteopedia* depend on the user having a working Internet connection in order to access content. Simple web pages that are composed only of text and HTML can easily be saved locally to a user’s computer for offline viewing, but *Proteopedia* pages contain complex content like Java applets used to run Jmol or Kinemage to visualize 3D structures on the page.

*Proteopedia*’s ‘Export’ feature allows a user to save a *Proteopedia* page, including visualizations of 3D structures, to his or her computer for offline viewing. Clicking on the “Export this page” link visible on the left hand side of any *Proteopedia* page (Fig. 14.3) brings up a dialog asking the user where he or she wants to save the page on his or her computer. The page is then scanned for all relevant Java applets, Javascript files, Jmol scripts, and other files necessary for reliable offline viewing, and these files are packaged and downloaded to the user’s computer into a folder with the same name as the *Proteopedia* page, along with the textual content of the page itself. Inside the downloaded folder, opening the file “index.html” provides an offline replica of the exported *Proteopedia* page.

This ‘Export’ feature allows *Proteopedia* users to store pages offline, whether for perusal during times when an Internet connection is unavailable or for a backup in case of Internet failure when using *Proteopedia* pages in a lecture or presentation.

The screenshot shows the Proteopedia interface for the article 'Lac repressor'. At the top, there are navigation tabs: 'article', 'discussion', 'edit this page', 'history', 'protect', 'move', and 'watch'. The user 'Joel L. Suseman' is logged in, with links for 'my talk', 'my preferences', 'my watchlist', 'my contributions', and 'log out'. On the left, there is a 'navigation' menu with links to 'Main Page', 'Table of Contents', 'Recent changes', 'Random page', and 'Help'. Below that is a 'search' box with a 'Go' button. A 'Google' search box is also present. The 'toolbox' at the bottom left contains several options, with 'Export this page' highlighted in a red box. The main content area has a 'Contents' table of contents, a 3D molecular model of the lac repressor, and a section titled 'What is the lac repressor?' with an '[edit]' link. The text explains that repressors inhibit gene expression by binding to the operator sequence.

**Fig. 14.3** View of a page with the Export this page highlighted for the Lac repressor page in *Proteopedia* [14]

### 14.3.3 Scenes Optimized and Protected Against Changes in PDB Files

The PDB remediation, released on March 17, 2009, caused problems across many ‘scene-links’ on many *Proteopedia* pages. The root of the problem was that at the time *Proteopedia* ‘scene-links’ did not save the version of the PDB file that was used to create them. This meant that a ‘scene-link’ that loaded the nucleosome structure in PDB entry 1a0i simply loaded the latest version of PDB entry 1a0i before recalling the view, coloring, and representations stored in the scene script. When the latest version of a PDB entry changed in the remediation, records such as chain names might have changed in that file, but many commands in the scene script are chain-specific, and were not changed. Thus, the large-scale PDB remediation resulted in many ‘scene-links’ failing to properly recall their saved scene script.

*Proteopedia*’s solution to this problem, and to future remediations, is to save the files (PDB or otherwise) that each ‘scene-link’ loads, at the time that the scene is saved. This “freezes” the files in the state they were in when the scene was created, thus avoiding any future problems due to remediation. Before “freezing” a new file, *Proteopedia* first checks whether that same file has already been frozen, avoiding duplicates and ensuring that scenes that load the same file are aware of that fact. A smooth transition between ‘scene-links’ is crucial for *Proteopedia*’s intuitive feel, and by making sure that two scenes that load the same structure are aware of

this commonality, we prevent reloading of the same structure when transitioning between these two scenes, which would result in a choppy transition.

### **14.3.4 Improvements to the Scene Authoring Tools**

The *Proteopedia* Scene Authoring Tools (SAT) are central to *Proteopedia*'s collaborative features – they provide users with the ability to easily create, edit, and add 'scene-links' to any *Proteopedia* page in order to describe and annotate 3D protein structures. Several recent additions to the SAT merit mention: "Undo/Redo" buttons, explanatory "Tooltips", and the option to choose an evolutionary conservation color scheme, according to ConSurf.

The new "Undo" and "Redo" buttons in the SAT allow a user to undo and redo any changes they may have made to the scene they are currently creating using the SAT. In choosing the perfect view, colors, representations and labels for a particular scene, sometimes mistakes are made. Before the existence of an "Undo" button, mistakes may have sometimes been frustrating to fix. Now, all changes made to the scene displayed in the SAT Jmol applet are recorded and are undoable, regardless of whether they have been made using the SAT or using the Jmol console.

The SAT offers many options for creating a revealing scene of a biomolecule structure, but with a wealth of options comes confusion. Beginning with many of the buttons visible on the "colors" tab that allow the user to choose different coloring schemes, buttons and options in the SAT now can include explanatory tooltips that appear when the user hovers over them. These tooltips will slowly spread from the "colors" tab to other areas of the SAT and are editable by *Proteopedia* users, to allow for user improvement of SAT help features.

One of the coloring schemes with a new tooltip of its own is the "evolutionary conservation" coloring scheme button offered on the SAT "colors" tab. Clicking on this button colors the residues of the current selection in the Jmol applet by their level of evolutionary conservation, according to ConSurf, on a scale from 1 (Variable, teal-colored) to 5 (Average, white-colored) to 9 (Conserved, magenta-colored). It is recommended that users include a color key in their *Proteopedia* page when including scenes with residues colored by evolutionary conservation.

### **14.3.5 Simple Citations Using PubMed ID Numbers**

Proper references are important to any scientific writing, but adding a reference longhand is a laborious process prone to error. A new mechanism in *Proteopedia* allows users to add references using their PubMed ID alone. For instance, to cite the 2005 ConSurf paper [5] in a *Proteopedia* page, whereas previously a user would have to type out the entire reference between reference tags like so:

```
<ref>Landau M., Mayrose I., Rosenberg Y., Glaser F., Martz E., Pupko T.  
and Ben-Tal N. 2005. ConSurf 2005: the projection of evolutionary  
conservation scores of residues on protein structures. Nucl. Acids Res.  
33:W299-W302.</ref>
```

Now using the PubMed ID in the following format suffices to add the same reference to the page:

```
<ref>PMID:15980475</ref>
```

Such references can be placed anywhere when editing a *Proteopedia* page, and they will show up properly numbered and aggregated at the bottom of the *Proteopedia* page, wherever the user places the wikitext “</references>”. Additional information on citing references in *Proteopedia* is available at [Help:Editing#Citing\\_Literature\\_References](#) [35].

### 14.3.6 Visualization Advances

Additional visualization advances include a “Pop-up” button underneath every *Proteopedia* Jmol applet, and a preliminary working version of “Color Keys” in *Proteopedia*.

The “Pop-up” button appears underneath every Jmol applet in *Proteopedia* and when clicked results in a large Jmol applet pop-up window. It provides a much larger view of the displayed structure and can be re-sized. Clicking on “refresh model” in the pop-up window results in the pop-up Jmol applet refreshing to emulate the display in the original Jmol applet.

“Color Keys” in *Proteopedia* are a way to provide a legend for each ‘scene-link’ since often each scene-link can highlight many complex structural elements with several different distinguishing colors. Users have been working around the lack of “Color Keys” in *Proteopedia* by using colored text next to the scene-link (for example Lac\_Repressor [14]), which is acceptable, but not ideal as too much colored text can confuse the reader. “Color Keys” will allow the user to specify a unique color key for each ‘scene-link’ at the time the user saves the ‘scene-link’ using the SAT. Then, as each ‘scene-link’ is clicked by the viewing user, the appropriate color key appears underneath the Jmol applet as the scene is loaded. This feature is still in development, but a preliminary test has been created publicly, here: for Gramicidin Channel in Lipid Bilayer [36].

### 14.3.7 *Semi-Automatic Reservation of Sandbox Pages for Courses*

Users can now semi-automatically reserve a block of continuous ‘Sandbox’ pages (e.g. ‘Sandbox 50’ through ‘Sandbox 100’) in *Proteopedia*. Sandbox pages are typically used as a place to experiment and create content without committing to its reliability. Educators and lecturers often need to reserve such a block of Sandbox pages for use by their students in workshops and class projects, but previous reservation was done by hand (*i.e.*, an educator would have to find out which pages are not being used, and edit these pages with a note indicating their now-reserved status). The new mechanism allows a registered user to reserve Sandbox pages by filling out a form including general information on the course, the number of Sandbox pages needed and the information that they would like to have appear on each Sandbox page. The process is referred to as semi-automatic because a *Proteopedia* Administrator must review and approve the request before it is filled. Future improvements would allow automatic approval of Sandbox reservation for a select group of trusted educators.

### 14.3.8 *Biological Assemblies vs Asymmetric Units*

The biological assembly of a protein represent its functional form, whereas the asymmetric unit of a protein crystal structure does not. The asymmetric unit may not be relevant at all to a non-structural biologist. With this in mind, *Proteopedia* has added the option to load or display a PDB entry’s biological assembly as well as its asymmetric unit [6, 7]. This option appears in the *Proteopedia* SAT for creating ‘scene-links’ using biological assemblies and will soon appear by default on all automatically seeded pages for PDB entries.

## 14.4 Conclusions

The advances in both content and software described here help *Proteopedia* to achieve its goal of making both structural information and its relationship to functional information accessible and understandable to a broad scientific audience. Future developments and improvements to the web resource will similarly be judged on their ability to help strive toward this goal.

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