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The Tree of Life Web Project*

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Abstract

The Tree of Life Web Project (ToL) provides information on the Internet about our current knowledge of the evolutionary tree of life and associated information about characteristics and diversity of life on Earth. Development of this open-access, database-driven system began in 1994; its official release was in 1996. Core scientific content in the project is compiled collaboratively by more than 540 biologists, all experts in particular groups of organisms, from over 35 countries. Additional learning materials are contributed by over 200 students, teachers, and amateur scientists, while images, movies, and sounds are contributed by both of these groups and over 200 media-only contributors. Administration of the project follows a hierarchical, community-based model, with authors for different parts of the ToL chosen by the scientists working in that particular field. The goals of the project are to document all species on Earth, as well as all significant clades; to provide basic information about the phylogeny of life; to share this information with other databases and analytical tools; and to encourage understanding and appreciation for biodiversity, evolution, and the interrelationships of Earth's wealth of species. Here we provide an outline of the goals and history of the project; the current content, administration, architecture, contributors, and audience, the challenges we have faced, and the future of the project.

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Key words: tolweb.org, Tree of Life, Linnaeus, phylogeny, evolutionary tree, genetic history, biodiversity, online collaboration, digital dissemination

Introduction

About 250 years ago Carl Linnaeus defined the principles by which organisms have been subsequently named and grouped. The classification he built, and which taxonomists have continued to refine and expand, serves as the data structure that organizes our knowledge of the living world. In a very real sense, Linnaeus founded Bioinformatics.

A taxonomist does not, however, merely name and group; these activities on their own are barren of biology. A taxonomist describes, and thus taxonomy has provided biology with its first glimpses of the features of hundreds of thousands of species. And taxonomy's biological content does not end with descriptions. Today, though not in Linnaeus's time, we see the classification's species delimitations as conveying genetic interchange or descent, and grouping as conveying phylogeny. Linnaeus chose a nested classification, though he did not mean it to be phylogenetic. Whether he chose it by luck, based on a human need for nested categories, or not, based on patterns in nature, this choice simplified Darwin's task: Darwin merely needed to breathe evolutionary life into the static hierarchy as a means to convey perhaps the most profound metaphor in biology:

> The affinities of all the beings of the same class have sometimes been represented by a great tree... As buds give rise by growth to fresh buds, and these if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications. (Darwin 1859)

We now see all life on Earth as intimately connected in a single tree-like structure of flowing nucleotide sequences, housed in the bodies of organisms they help build. This tree is billions of years in age, with myriad branches, and millions of extant leaves. The existence of this tree, and that each of us is part of one of its leaves, is one of the most profound realizations that we as a species have achieved.

The dialog between Linnaeus's austere structure (taxonomy) and Darwin's romantic vision (evolutionary biology) gave rise to the New Synthesis in the mid-20th century, and to a more richly historical (phylogenetic) approach to evolution by the end of the century (Bowler 1996, Cracraft & Donoghue 2004). At the same time, digital bioinformatics arose, and so the dream Linnaeus might have envisaged could be achieved: a taxonomy with fundamental (biological) meaning that could organize, at the speed of light, our understanding of life.

There are by now many projects that represent taxonomy, phylogeny and biological diversity in the electronic world. In this paper we will not summarize them all, but focus on one, the Tree of Life Web Project, in the hope that our description of its goals, challenges and solutions may illuminate how Linnaeus's legacy can prosper into the digital future.

The Tree of Life Web Project

The Tree of Life Web Project (ToL) (Maddison & Maddison 1996; Maddison & Schulz 2007) is an Internet presentation of biological diversity and the phylogenetic tree on which it arose. Its goals are:

- To present information (text, pictures, video, sounds) about every species and significant clade on Earth, living and extinct, authored by experts in each group

- To display a current, established view of the phylogeny of all species, as synthesized by experts in each group
- To share information with other databases, and to link information from other databases through phylogeny
- To provide data to analytical tools
- To encourage an appreciation for the beauty and richness of biological diversity
- To encourage understanding about evolution, phylogeny, and biodiversity at all educational levels

We will begin by describing the importance of a phylogenetic perspective in the ToL, and then discuss its history, current content, challenges and solutions.

Conveying a Phylogenetic Perspective

The ToL does not present biodiversity as a collection of arbitrarily organized objects; rather, the project explicitly seeks to facilitate the casual and systematic exploration of organismal diversity from a phylogenetic perspective. Far from being simply an academic exercise, this approach promotes a deeper appreciation of the diversity and history of life, and it provides for a more profound understanding of biological patterns and processes. We hope it also provides a sense of wonder about the existence of the several-billion-year old tree that has produced all organisms on Earth, including *Homo sapiens* Linnaeus.

Phylogenetic research is emerging as one of the most significant endeavors in modern biology. The great explanatory potential of the tree of life is now widely recognized, and phylogenetic approaches are permeating research in all life sciences (Cracraft et al. 2000, Hillis 2004). Consequently, an understanding of phylogenetic concepts will be indispensable not only for future generations of biologists but for all citizens.

A phylogenetic hypothesis is abstract, a logical structure of nodes and branches. Many people learning biology find it difficult to understand and describe a phylogenetic tree (Baum et al. 2005, Tree Thinking Group 2004). Even trained biologists took more than 100 years to grasp fully what now seem simple phylogenetic concepts—one could argue, for instance, that Hennig's (1966) work was influential largely because he clarified some basic consequences of phylogenetic hypotheses.

The content and user interface of the ToL support "tree-thinking" in several different ways. The pages of the ToL contain diagrams of phylogenetic trees, and the text of many pages discusses aspects of the tree, while the glossary explains phylogenetic terms in context. However, perhaps ToL's most important assistance to tree-thinking is the navigational structure: the user's navigation through the tree follows the flow of evolutionary descent. Each step in navigating reinforces in the user's mind a sense of lineage, of connection, between ancestor and descendant. As well, each page is a clade (with a very few exceptions). Each time a user visits a page and pauses to think, "to what does this page refer?", the answer is: "a clade". Each time a user holds the cursor over a link and pauses to think "where will this take me?" the answer is "along a lineage of descent". Branching descent is reinforced subliminally, intuitively, as the user moves through the tree.

History

The idea to have a complete, digital phylogenetic tree of all life, adorned with information about organisms, occurred to DRM around 1988, but in a different context than the Internet. With the goal of introducing to students the extent of the Tree of Life, modifications to MacClade (Maddison & Maddison 2005) were planned that would embed hypertext links on trees in MacClade's tree window. Inspired by Apple's HyperCard™, the plan was to allow taxon names in a displayed tree to be hyperlinked to another MacClade file containing information about that taxon; the user could then navigate between files using hypertext links, and thus wander through an evolutionary tree of life. This feature was never implemented in a release version of MacClade, and the plan was dormant for six years.

In 1994, the year WPM joined the effort, the obvious medium in which to present such linked information was no longer MacClade, but the World Wide Web. Significant progress was made that summer when MacClade was modified to allow it to be used as a compiler to produce linked HTML pages from the information stored in NEXUS files, which were edited by MacClade's graphical editors. With this custom version of MacClade, the first prototype version of the Tree of Life (ToL) was put online on 16 November 1994.

The content within the ToL grew significantly in 1995, both within the groups we study (carabid beetles and salticid spiders) and, more importantly, in branches that are curated by others. The first branch authored by another contributor, Keith Crandall, was added to the growing tree on 1 June 1995 (Crandall 1995). This branch, about Astacidea (freshwater crayfish), was housed at the University of Texas at Austin, and was the first piece housed on a remote server. Over the next seven months, 16 additional branches were added by other authors; these covered eukaryotes as a whole, various vertebrate groups, scorpions, beetles, and aphids.

On 5 January 1996, when the Tree of Life project was first formally announced, the Tree itself contained 948 pages, which were housed in seven computers on two continents (Morell, 1996, Maddison & Maddison, 1996).

The connection of phylogenetic trees with hypertext links was not unique to the Tree of Life Web Project, and a number of other projects used the same format. Two significant projects in the early 1990's had similar interfaces: LifeMap, a CDROM produced in 1992 by the California Academy of Sciences, and the University of California at Berkeley's Phylogeny of Life (now the "History of life through time", http://www.ucmp.berkeley.edu/exhibits/historyoflife.php).

From 1996 to 1999 the ToL project had a total of $16,000 of direct funding, and growth was due primarily to the good efforts of the community of systematists who were contributing their time and energy to building pages. KSS joined the project as a volunteer assistant, and through time became managing editor.

In 2000, with the project's first major funding, DRM and KSS led a major transition: changing the architecture of the project into a database-driven, dynamically created web site, through the efforts of programmers Travis Wheeler, Danny Mandel, and most recently Andrew Lenards. The first databased version of the ToL replaced the older version in February of 2002. All branches of the project were returned to the home site at the University of Arizona, with no remaining remote branches. While the electronic files were no longer physically distributed, the effort to create them was still distributed among biologists around the world.

From late 2000 until mid-2004 we discouraged biologists from contributing to the project while we replaced the technology underlying the website and content editing. Regrowth resumed in 2004 once the MacClade/NEXUS content-editing system was replaced by TreeGrow, a cross-platform application that edits the ToL database content directly. During this time the National Science Foundation's Assembling the Tree of Life (ATOL) initiative was born, and to more clearly differentiate the two, and to highlight the independent origins and different natures of these efforts, we changed the name of the Tree of Life Project to the Tree of Life Web Project.

The rebirth of scientific core content was followed by a renewed growth in content for learners of all ages, primarily in the form of treehouses. Treehouses are special pages that provide resources for teachers as well as collections of stories, exercises, images, and other learning materials designed to appeal to a younger audience. Teachers, students, and amateur scientists were also invited to contribute to the project either as treehouse or media contributors (Leslie 2005).

Current Content

The primary scientific content in the ToL is displayed in three different kinds of web pages: branch pages, leaf pages, and other articles/notes. Branch pages display information about groups of species, and contain the navigational tree or list of subgroups. They contain pictures of the group, an introduction, a description of the group's characteristics, a discussion of phylogenetic relationships, references about the group, links to other information on the Internet, as well as other taxon-specific sections (Figs. 1, 2). Some examples of diverse branch pages are shown in Fig. 3. Leaf pages are similar to branch pages, but are terminal, and will not have descendants; in general leaf pages describe species (Fig. 4). Other articles and notes contain additional information that is too voluminous or specialized to be contained on the main branch and leaf pages (Fig. 5). These are attached through hyperlinks to the branch or leaf page of the taxon to which they apply.

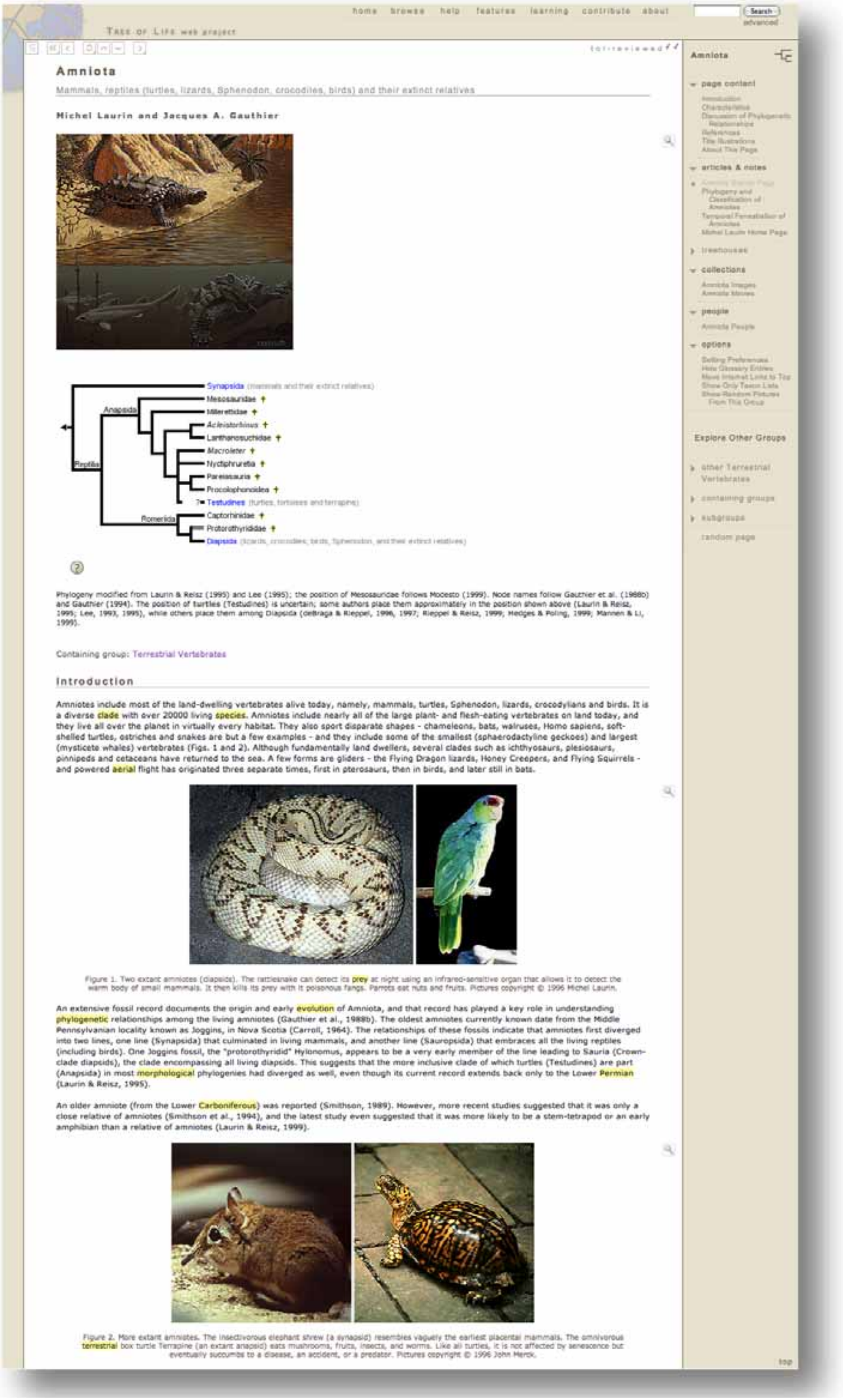
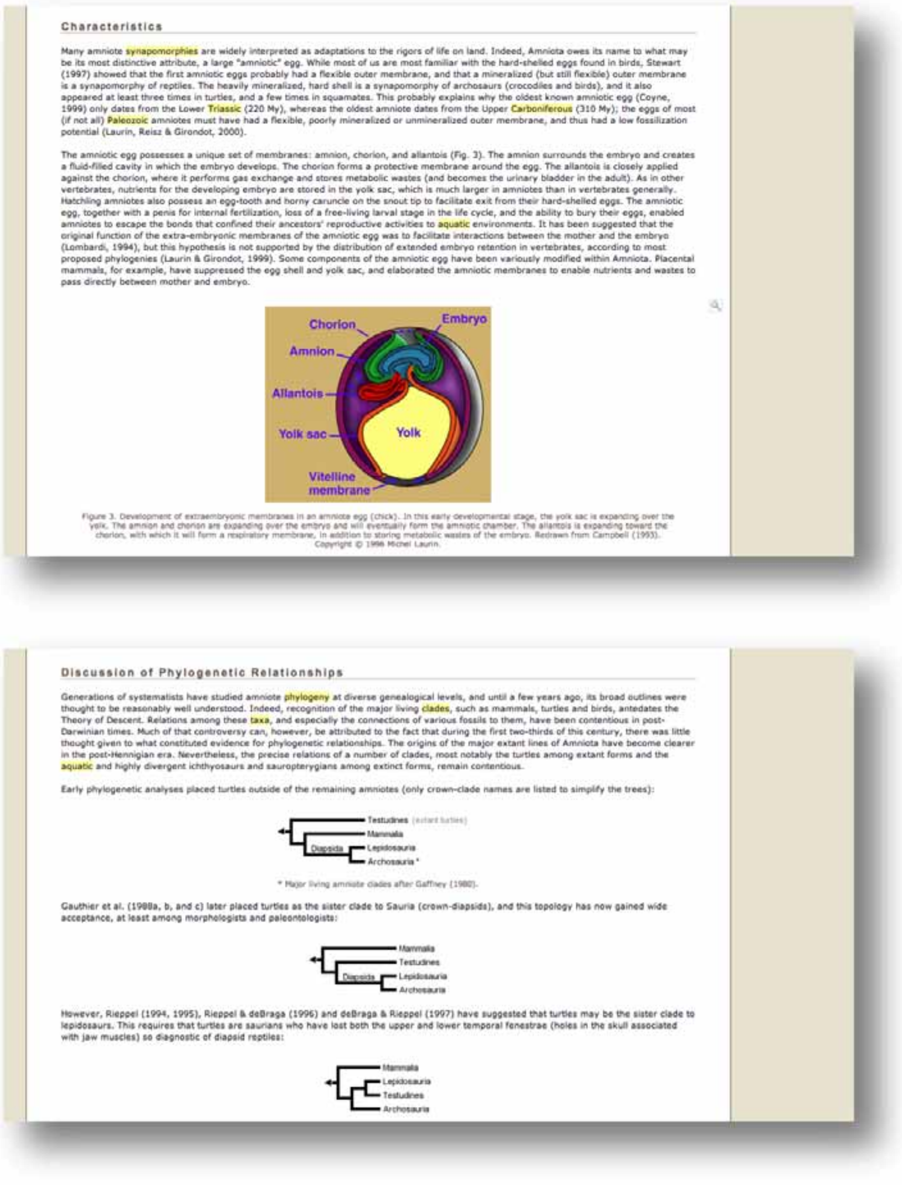


FIGURE 1. The start of a branch page in the ToL (Laurin & Gauthier, 1996), on amniotes, showing the navigational center (the tree), links which take one to subgroups or larger groups, and the Introduction.



Characteristics

Many amniote synapomorphies are widely interpreted as adaptations to the rigors of life on land. Indeed, Amniota owes its name to what may be its most distinctive attribute, a large "amniotic" egg. While most of us are most familiar with the hard-shelled eggs found in birds, Stewart (1997) showed that the first amniotic eggs probably had a flexible outer membrane, and that a mineralized (but still flexible) outer membrane is a synapomorphy of reptiles. The heavily mineralized, hard shell is a synapomorphy of archosaurs (crocodiles and birds), and it also appeared at least three times in turtles, and a few times in squamates. This probably explains why the oldest known amniotic egg (Coyne, 1999) only dates from the Lower Triassic (220 My), whereas the oldest amniote dates from the Upper Carboniferous (310 My); the eggs of most (if not all) Paleozoic amniotes must have had a flexible, poorly mineralized or unmineralized outer membrane, and thus had a low fossilization potential (Laurin, Reisz & Girondot, 2000).

The amniotic egg possesses a unique set of membranes: amnion, chorion, and allantois (Fig. 3). The amnion surrounds the embryo and creates a fluid-filled cavity in which the embryo develops. The chorion forms a protective membrane around the egg. The allantois is closely applied against the chorion, where it performs gas exchange and stores metabolic wastes (and becomes the urinary bladder in the adult). As in other vertebrates, nutrients for the developing embryo are stored in the yolk sac, which is much larger in amniotes than in vertebrates generally. Hatchling amniotes also possess an egg-tooth and horny caruncle on the snout tip to facilitate exit from their hard-shelled eggs. The amniotic egg, together with a penis for internal fertilization, loss of a free-living larval stage in the life cycle, and the ability to bury their eggs, enabled amniotes to escape the bonds that confined their ancestors' reproductive activities to aquatic environments. It has been suggested that the original function of the extra-embryonic membranes of the amniotic egg was to facilitate interactions between the mother and the embryo (Lombardi, 1994), but this hypothesis is not supported by the distribution of extended embryo retention in vertebrates, according to most proposed phylogenies (Laurin & Girondot, 1999). Some components of the amniotic egg have been variously modified within Amniota. Placental mammals, for example, have suppressed the egg shell and yolk sac, and elaborated the amniotic membranes to enable nutrients and wastes to pass directly between mother and embryo.

Figure 3. Development of extraembryonic membranes in an amniote egg (chick). In this early developmental stage, the yolk sac is expanding over the yolk. The amnion and chorion are expanding over the embryo and will eventually form the amniotic chamber. The allantois is expanding toward the chorion, with which it will form a respiratory membrane, in addition to storing metabolic wastes of the embryo. Redrawn from Campbell (1993).
Copyright © 1996 Michel Laurin.

Discussion of Phylogenetic Relationships

Generations of systematists have studied amniote phylogeny at diverse genealogical levels, and until a few years ago, its broad outlines were thought to be reasonably well understood. Indeed, recognition of the major living clades, such as mammals, turtles and birds, antedates the Theory of Descent. Relations among these taxa, and especially the connections of various fossils to them, have been contentious in post-Darwinian times. Much of that controversy can, however, be attributed to the fact that during the first two-thirds of this century, there was little thought given to what constituted evidence for phylogenetic relationships. The origins of the major extant lines of Amniota have become clearer in the post-Hennigian era. Nevertheless, the precise relations of a number of clades, most notably the turtles among extant forms and the aquatic and highly divergent ichthyosaurs and sauropterygians among extinct forms, remain contentious.

Early phylogenetic analyses placed turtles outside of the remaining amniotes (only crown-clade names are listed to simplify the trees):

* Major living amniote clades after Gaffney (1980).

Gauthier et al. (1988a, b, and c) later placed turtles as the sister clade to Sauria (crown-diapsids), and this topology has now gained wide acceptance, at least among morphologists and paleontologists:

However, Rieppel (1994, 1995), Rieppel & deBraga (1996) and deBraga & Rieppel (1997) have suggested that turtles may be the sister clade to lepidosaurs. This requires that turtles are saurians who have lost both the upper and lower temporal fenestrae (holes in the skull associated with jaw muscles) so diagnostic of diapsid reptiles:

FIGURE 2. Parts of two typical sections on a ToL branch page, the Characteristics section and the Discussion of Phylogenetic Relationships section.

In the current (October 2007), public ToL database, there are over 5000 branch pages, and nearly 3000 leaf pages. These are distributed non-randomly throughout the tree (Fig. 6). Most pages (approximately 96%) are of animals. Reflecting the nature of taxonomy as a continual work in progress, only about 3% of published ToL pages are considered complete; approximately 37% feature significant content but are still "under construction." The remaining 60% of pages provide a temporary skeleton, with tree diagrams or taxon lists, references, and some preliminary content. There are approximately 8000 additional pages that are being written but are not yet public. About 550 other articles and notes written by biologists have been published and are linked to branch and leaf pages throughout the ToL.

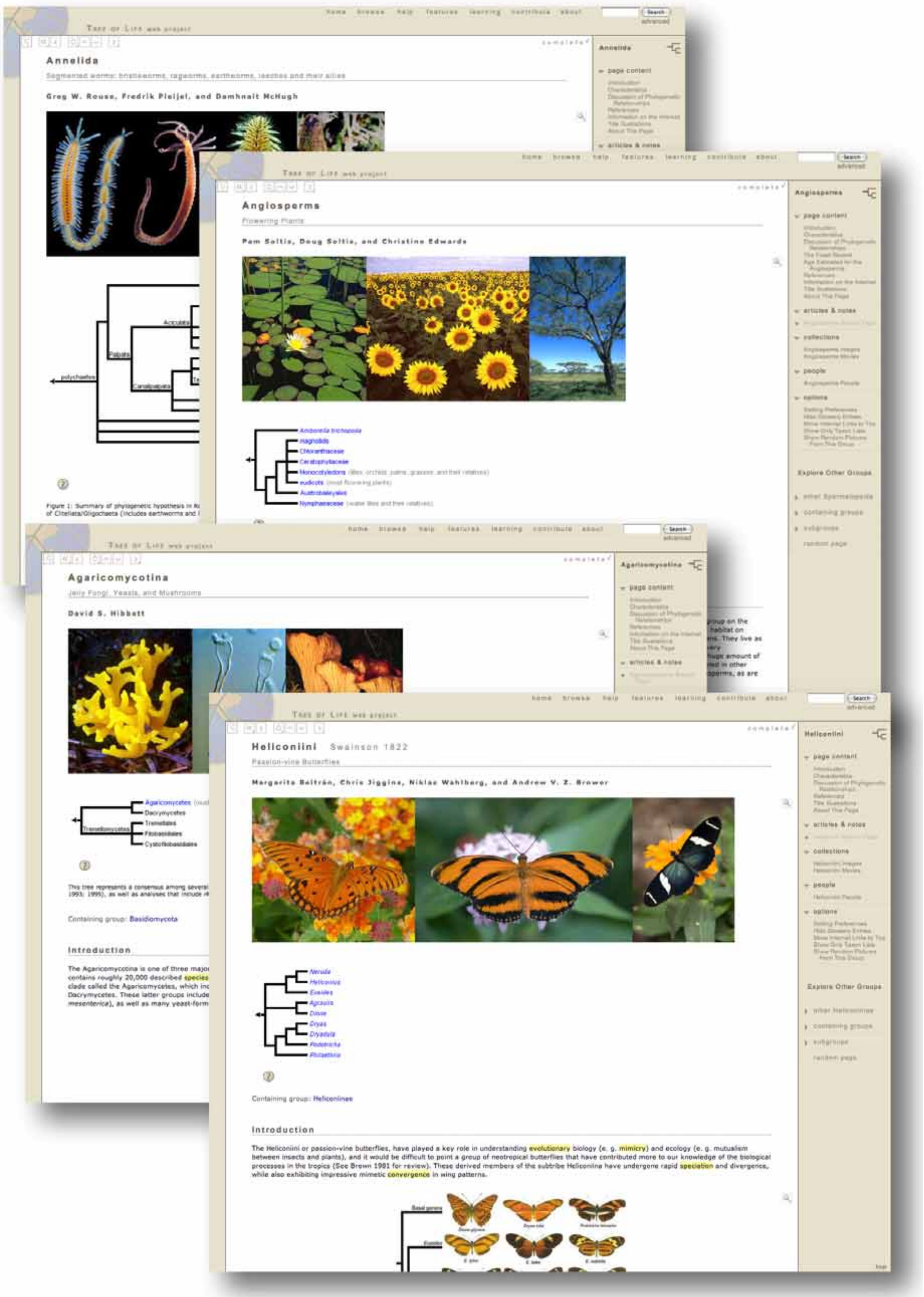


FIGURE 3. First sections of some example branch pages. From top to bottom, they are: Annelida (Rouse et al., 2002); Angiosperms (Soltis et al., 2005), Agaricomycotina (Hibbett, 2007a), and Heliconiini (Beltrán et al., 2007).

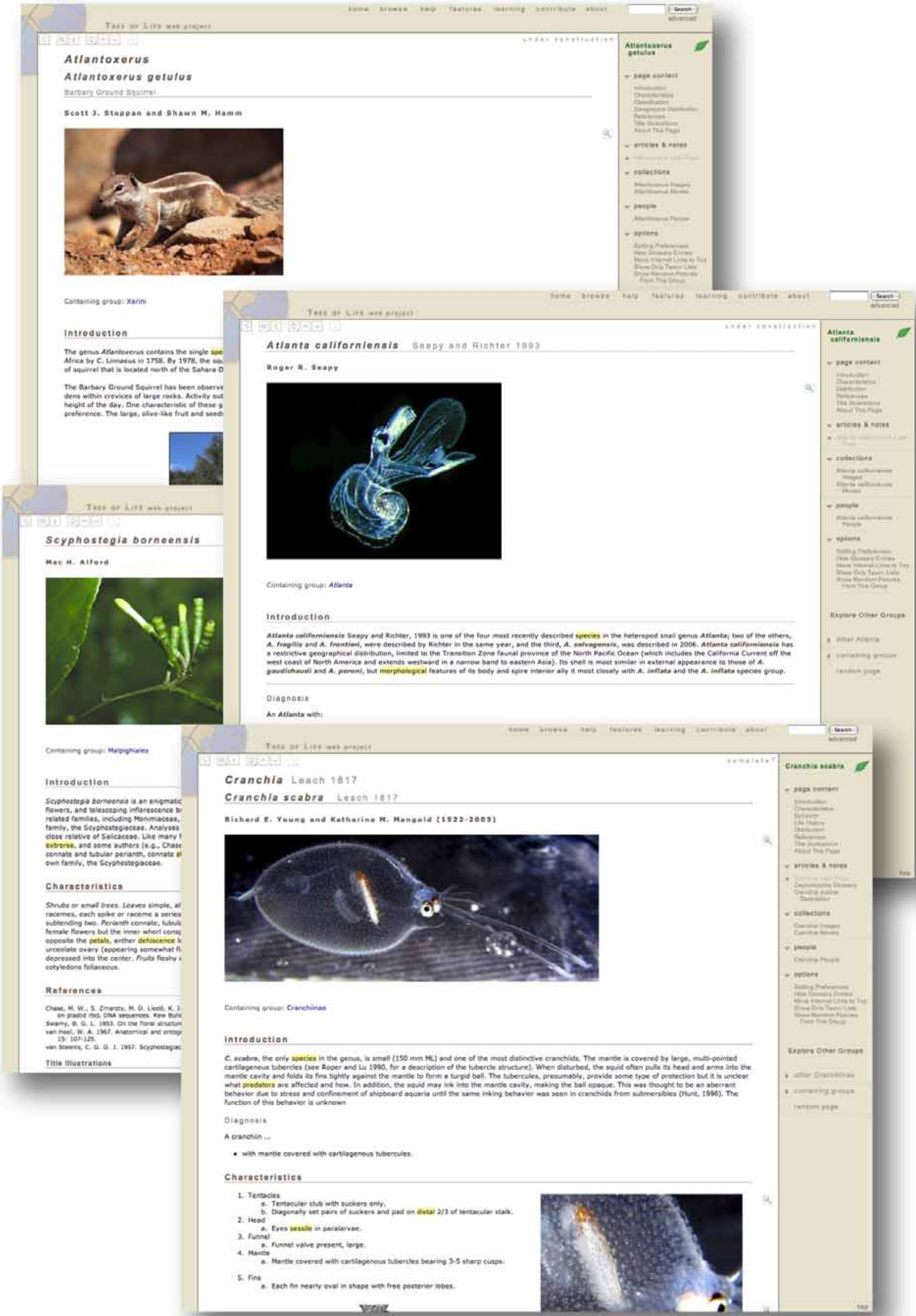


FIGURE 4. First sections of some example leaf pages. From top to bottom, they are: *Atlantoxerus getulus* (Steppan & Hamm, 2006), *Atlanta californiensis* (Seapy, 2005), *Scyphostegia borneensis* (Alford, 2007), and *Cranchia scabra* (Young & Mangold, 2007).

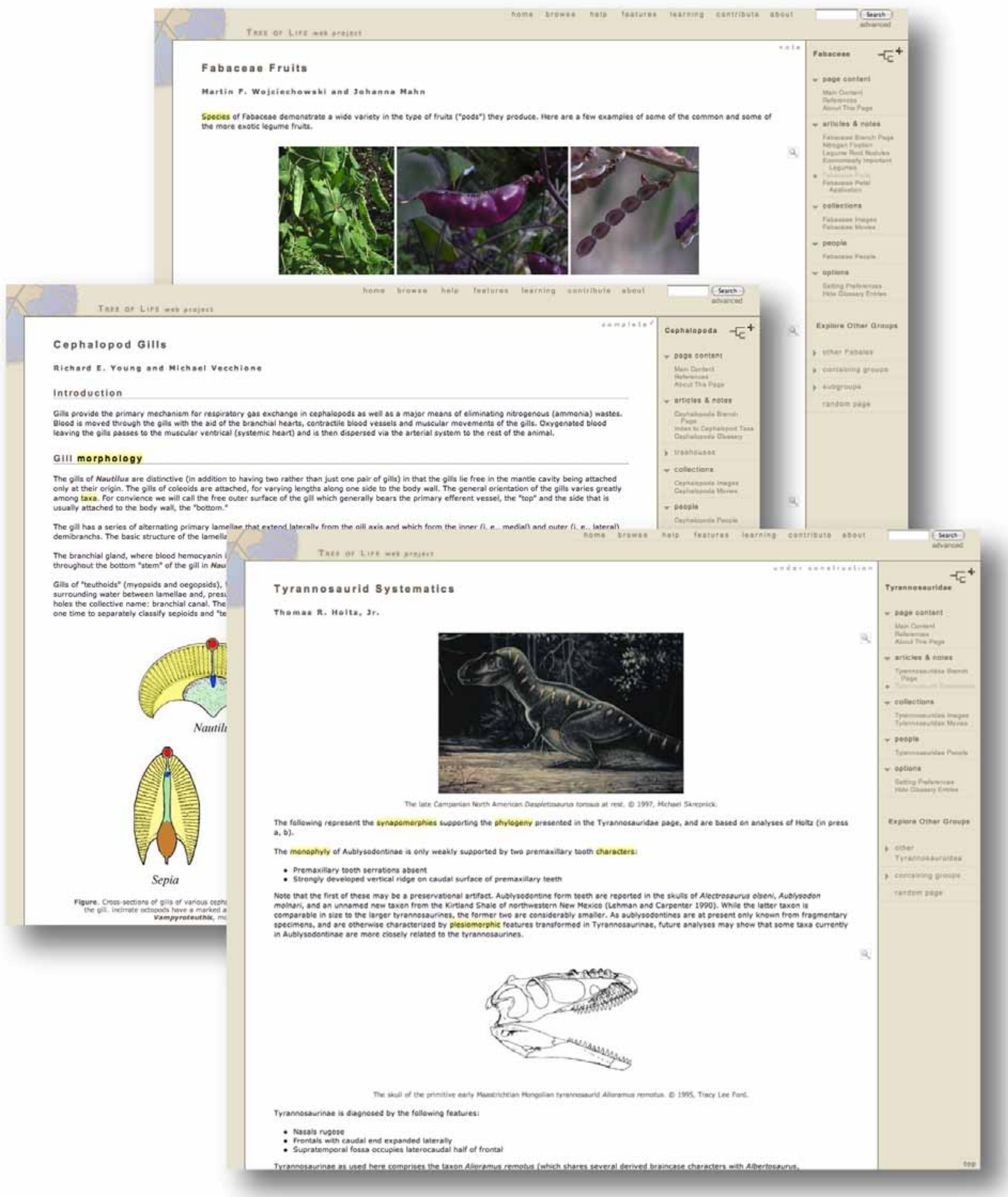


FIGURE 5. First sections of some articles and notes. From top to bottom, they are: "Fabaceae Fruits" (Wojciechowski & Mahn, 2006), attached to the Fabaceae page; "Cephalopod Gills" (Young & Vecchione, 2006), attached to the cephalopod page; "Tyrannosaurid Systematics" (Holtz, 2000), attached to the Tyrannosauridae page.

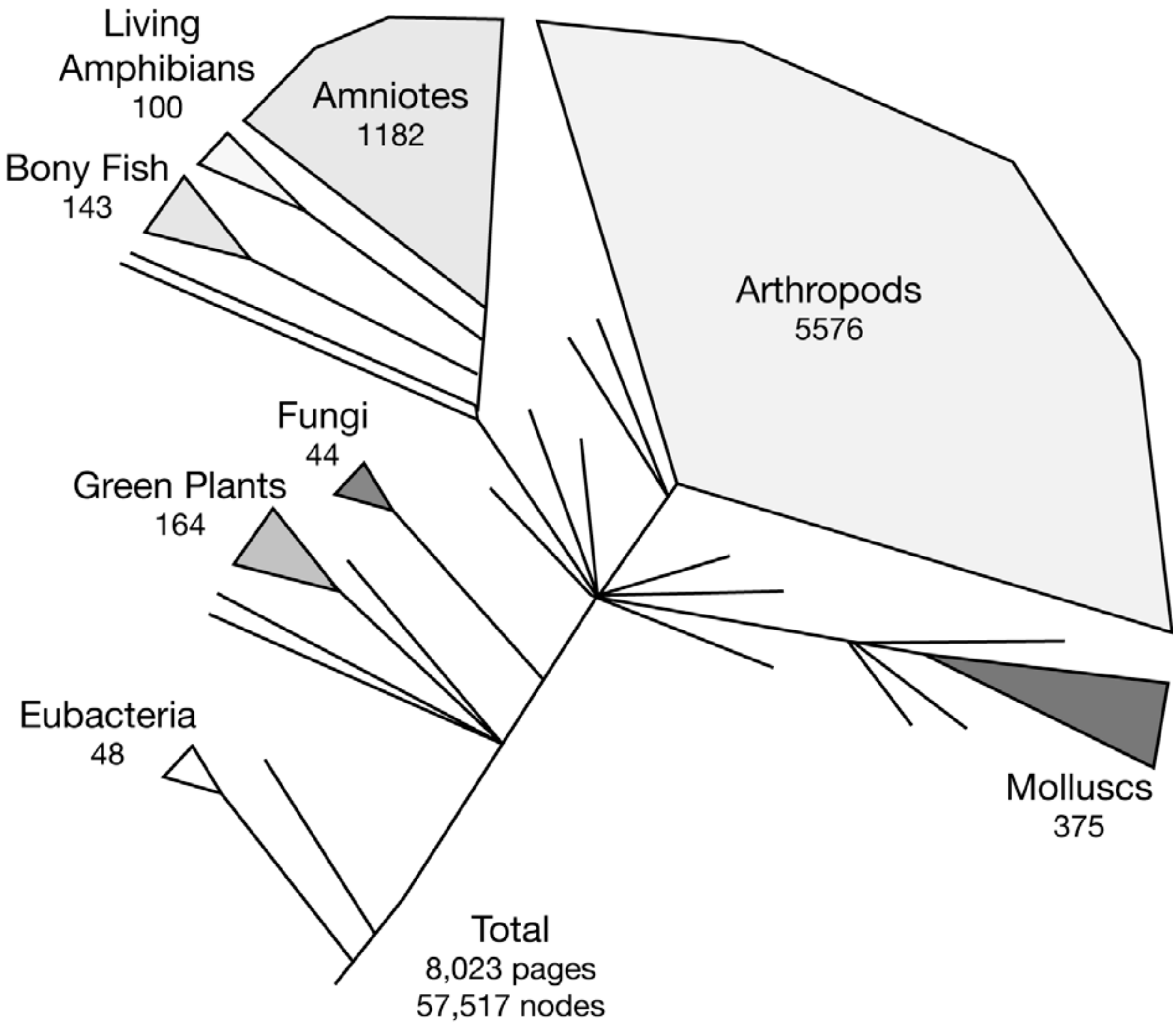


FIGURE 6. Schematic of the Tree of Life Web Project showing the groups best represented, with areas approximately proportional to number of pages, and darkness approximately proportional to fraction of pages that are completed.

Because ToL content development relies entirely on the initiative of research communities and individual scientists, the growth of the project has been punctuated, and coverage across different groups of organisms is uneven. Some branches of the tree, for example, cephalopods and salamanders, are very well developed, with most branches extending to the species level and featuring a number of pages with rich content. Other branches, such as fungi and angiosperms, have relatively few pages, but many of them are complete and of very high quality (e.g., Hibbett 2007b, Johnson 2004, Soltis et al. 2005, Spatafora 2007). On the other hand, several prominent groups such as bacteria, most mammals, and birds are still very much under construction, with most pages providing little more than a tree diagram, pictures, references, and internet links.

Within invertebrates, the cephalopods constitute one of the most active branches. With leadership from coordinators Richard Young, Michael Vecchione, and Katharina Mangold (now deceased), over 20 cephalopod workers from 13 different countries have published more than 700 pages so far (Young et al. 1996), with more than 350 descendent branch and leaf pages, and more than 350 articles and notes. Many of these pages feature detailed content, are richly illustrated, and regularly updated. The success of this branch as a community effort is due in great part to Richard Young's initiative as branch coordinator. For over a decade, he has been active acquiring new materials and recruiting other researchers as ToL contributors.

The ToL insect branch is generally well developed and features important contributions from many entomologists (e. g., Ashe 1998 on Aleocharinae, Caterino 2002 on Histeridae, Contreras-Ramos 1997 on Megaloptera, Engel 2005 on Zoraptera, Holzenthal et al. 1997 on Trichoptera, Kathirithamby 2002 on Strepsiptera, Nelson 1996 on Plecoptera, Pellmyr 1997 on Prodoxidae, Sikes et al. 2005 on Silphidae, Smith & Page 1997 on Phthiraptera, Trueman & Rowe 2001 on Odonata). Several endopterygote groups benefit from the stewardship of NSF-ATOL (Assembling the Tree of Life) groups: Coleoptera (e. g., Short 2007), Diptera (e. g., Bayless 2007, Lonsdale & Marshall 2004, Skevington 2005), Hymenoptera (e. g., Aguiar 2005, Deans & Jennings 2006, Shaw 2007, Yoder 2004), and Lepidoptera (e. g., Beltrán et al. 2007, Wahlberg & Brower 2007). As these research efforts progress, we expect a significant increase in high quality content for these branches. Early ToL development efforts by Keith Crandall in crustaceans and Wayne Maddison in spiders are also currently extended through collaboration with the decapod crustacean and spider ATOL groups.

Coverage of other invertebrates outside of cephalopods and arthropods is generally sparse, but there are some significant clusters of content-rich pages in the Annelida (e. g, Rouse et al. 2002), Cnidaria (e. g., Fautin & Romano 1997, 2000, Fautin et al. 2000), Echinodermata (e. g., Ausich & Messing 1998, Kerr 2000, Knott 2004, Primus 2005, Wray 1999), Gastropoda (e. g., Seapy 2007), and Platyhelminthes (e. g., Rohde 1998a,b).

The ToL archives significant revisions of branch and leaf pages and provides version-specific URLs in the recommended citation for each page. For example, as of October 2007, the page for Fungi exists in the ToL as two versions. The one displayed by default is the 13 July 2007 version (http://tolweb.org/Fungi/2377/2007.07.13), but the previous version, from 14 February 2005 (http://tolweb.org/Fungi/2377/2005.02.14), can be accessed through a link on the bottom of the current Fungi page. This allows for content to be continuously updated without compromising the relevance of references to older versions of a page.

In addition to the scientific core content, the ToL also has a media collection featuring over 20,000 images, more than 400 movies, and about 100 sounds. Contribution to the media collection is open to the public. A grant from the NSF National Science Digital Library (NSDL) program has also allowed us to initiate the collection of learning materials and teacher resources, spearheaded by our learning materials editor, Lisa Schwartz, which are presented in the form of treehouses (Fig. 7). Treehouses may be authored by students, teachers, or amateur scientists, and links to these pages are available on branch and leaf pages of relevant organisms throughout the ToL hierarchy.

The ToL and Taxon Rank

In 1996, after the ToL had been formally announced, we began receiving queries from children urging us to add the nomenclatorial rank of the taxonomic names in the ToL: they needed this information for schoolwork that required their giving the full classification of an organism, with rank information for each level. When building the ToL, we had never thought about explicitly storing ranks of taxa. It had not been needed in constructing the content, as the hierarchy showing the nesting of groups was evident from, and implicit in, the tree structure.

In a collaborative effort such as the ToL, people will differ in their opinions about ranks. With different people in charge of different pieces of the tree, it is difficult to enforce the application of taxon names that follow a coherent Linnaean ranking. For example, the coordinators for a given group may consider their taxon to be of generic rank and give their group a generic name, while the authors of a descendent clade may consider their group to be of family rank and give their group a family name. The ToL can accommodate such conflicting ranks; however, the resulting nomenclature embodied in the ToL will lack "Linnaean integrity".

The ToL remains neutral as to whether or not taxa are ranked at all. The ToL has chosen not to require any explicit statements about ranks, and to leave nomenclature up to the expert coordinators for a given branch of the tree. In fact, the ToL can, and does, accommodate a mixture of ranked and rankless names for taxa. For example, in Core Malvales (Smith & Baum 2003) there are several explicitly rankless taxa.

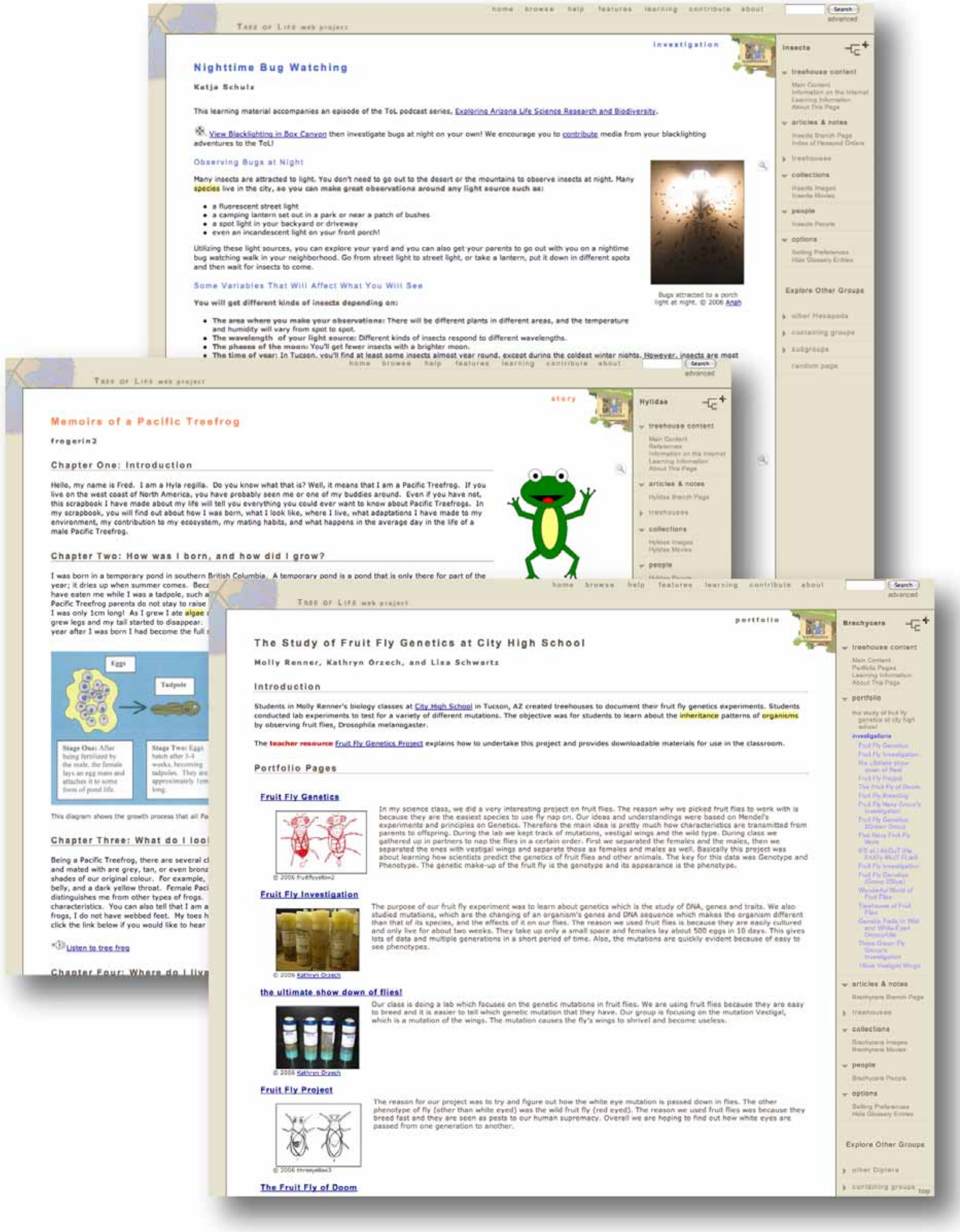


FIGURE 7. First sections of some example treehouse pages. From top to bottom, they are: "Nighttime Bug Watching", by Katja Schulz; "Memoirs of a Pacific Treefrog", by a student at Havergal College, a secondary school in Toronto, and "The Study of Fruit Fly Genetics at City High School", by Molly Renner, Kathryn Orzech, and Lisa Schwartz.

Content Contributors

Content in the Tree of Life Web Project is contributed by three overlapping groups of people: the scientific contributors, who write the primary branch and leaf pages, other articles and notes; treehouse contributors, who author learning materials; and media contributors, who donate images, videos, and sounds to the project.

Contribution is not self-organized as in an anonymous or weakly-filtered Wiki system, but rather is organized by editors who coordinate the contributions. In this sense, the ToL is like an edited book with each chapter a clade, except that editing can be hierarchically delegated for subclades. The filtering by editors is of variable stringency, with some pages made public even though still under construction, and others not only complete but also peer-reviewed (and marked as such).

As of October 2007, there were about 540 registered scientific contributors (those who have or will author content on the core branch and leaf pages) from 35 countries. 355 of the scientific contributors are from the United States, 40 from Canada, with the United Kingdom, Australia, Germany, and Sweden each having more than 10 registered contributors. Thirteen contributors are from Asia, ten from South America, and six from Africa. Because of the hierarchical coordination of the project, there are undoubtedly future contributors known to the communities curating a particular branch who have not yet registered, and thus 540 is an underestimate of the biologists working on the ToL.

Since the inception of the Tree of Life Treehouse program (http://treehouses.tolweb.org) in 2004, more than 200 students, teachers, and amateur scientists have published learning materials and teacher resources on the ToL. Over 80% of treehouse builders are pre-college students participating in formal classroom projects at middle and high schools in the United States (Arizona, California, New Jersey, New York) and Canada (Ontario).

Most of the images, movies, and sounds in the ToL media collection have been uploaded by scientific contributors However, many treehouse builders also contribute media files, and there are over 200 registered media-only contributors.

Audience and Use

The ToL was originally conceived as a tool for researchers and advanced students who turn to the site for current hypotheses of phylogenetic relationships and descriptions and illustrations of the characteristics of different groups of organisms. The ToL also provides references to the primary literature and links to other web sites and databases offering information and tools of interest to the research community. Early in the development of the web site, frequent inquiries from school-children, teachers, and amateur science enthusiasts made it apparent that the project also had a large audience of non-specialists. In response to this demand, the ToL has expanded its content development efforts to serve diverse audiences.

In 2006, there were over 2,500,000 unique visitors to the ToL, from 198 countries and independent states. The largest number of pages were served to the U.S.A., Germany, Singapore, Canada, and The Netherlands. The most frequently visited branch page on the site is the root page, followed by Fungi, Eukaryotes, and Animals.

ToL user feedback as well as numerous links on web sites of biology courses, libraries, and natural history museums indicate that the site is commonly used as a resource in formal and informal science education. The ToL is featured in major directories of online learning materials (e.g., The National Science Digital Library, NSDL, http://nsdl.org; Multimedia Educational Resource for Learning and Online Teaching, MERLOT, http://www.merlot.org; Digital Library for Earth System Education, DLESE, http://www.dlese.org), and it is cited by biology text books (e.g., Cooper & Hausman 2007, Freeman 2004, Starr 2006). In order to connect with educators across the United States, the ToL has participated in conferences including those of the National

Science Digital Library (NSDL), National Science Teachers Association (NSTA), National Association of Biology Teachers (NABT), International Society for Technology in Education (ISTE), and the Special Libraries Association (SLA). The project also collaborates with several other prominent bioscience outreach organizations including the University of California Museum of Paleontology, the BioQuest Curriculum Consortium, and the Education and Outreach Group at the National Evolutionary Synthesis Center (NESCent).

Architecture

The current ToL contains at its core a MySQL™ database containing the structure of a large, unadorned tree, which consists of a collection of interconnected nodes. The root node of this tree represents all of life; the terminal nodes, with no descendants, either represent leaf nodes (individual species, subspecies, or strains) or are branch nodes that have not yet been extended to the species level.

In addition to the set of connected nodes, the database contains numerous objects: paragraphs of text, images, videos, taxon names, and so on. These objects are attached to the nodes of the tree: nodes deep in the tree of life have objects attached that apply to large, more inclusive groups (e.g., eukaryotes, animals, beetles), while nodes higher up in the tree own objects that apply to less inclusive groups, up to the level of individual species and subspecies. Attaching objects to relevant nodes in the tree automatically organizes them according to phylogenetic hypotheses, and this architecture thus supports the retrieval of phylogenetically structured data about organisms. Because taxon names are just another class of objects attached to nodes, and objects automatically "follow" when a node is moved, the system easily accommodates changes in nomenclature and phylogenetic hypotheses.

ToL pages themselves are objects attached to nodes in the tree. ToL page objects contain information about the content to be presented in a web page should a user request to see the page for a particular group in the ToL. The ToL server, when such a request is made, creates the page by obtaining the text sections, images, and so on that are to be presented, at the same time creating an image map of the tree that is to be shown on the page, and sending the page to the user's web browser.

Because each page is created dynamically, it can be customized based on a user's preferences. There currently are options to add or delete certain features. For example, if a user so chooses, they can ask the pages to appear with a hidden glossary of scientific terms. Any word in the glossary will be highlighted on the page; a definition appears if the computer's cursor is moved over the word (Fig. 8).

The web pages presented in a user's web browser are only one possible view into the data. The ToL web site also lets visitors browse through a variety of phylogenetically structured collections of objects ranging from media files to people registered as contributors or enthusiasts for a given group of organisms. For example, on the root page of the project, the page for all Life on Earth, there is a link under the *collections* menu for *Life on Earth Images*. This collection features all images that are attached to any node in the tree. The *Lepidoptera Images* collection, linked from the Lepidoptera branch page, features all images that are attached to nodes in the Lepidoptera branch. In turn, the *Danaus plexippus Images* collection, linked from the *Danaus plexippus* leaf page, features only those images attached to the *Danaus plexippus* node.

In addition to display on the ToL web site, ToL data are also available via web services (http://webservices.tolweb.org) to other databases and to analytical tools, including Mesquite (Maddison & Maddison 2007), as will be discussed below.

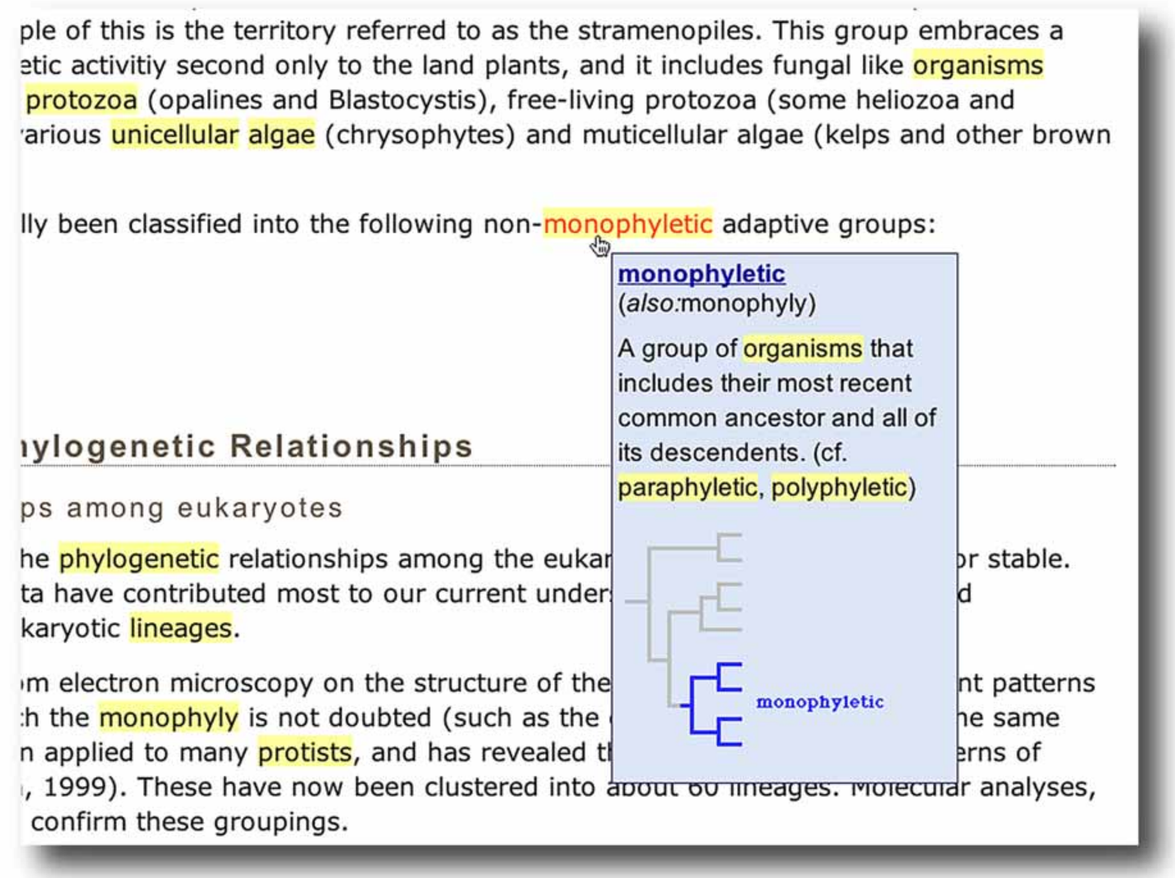


FIGURE 8. The glossary in the ToL in use. The user has moved the cursor over the highlighted word "monophyletic" and the definition is being shown.

Administration and Construction

The current administrative structure of the ToL has DRM as the editor and overall coordinator, with KSS as the managing editor.

The administration of branches of the ToL is handled hierarchically, with one or more experts in each group serving to help coordinate the efforts within that group, passing off coordination of subgroups as appropriate. For clades in which the community of systematists have organized themselves in an effort to research collaboratively the phylogeny and diversity within the clade, those communities are often the coordinating body. For example, a diverse array of mycologists began the Assembling the Fungal Tree of Life (AFTOL) project, and the group of people that lead AFTOL have also been designated the coordinators of the fungal branch of the ToL. Similar coordination arrangements have been made with several other Assembling the Tree of Life (ATOL) groups and Research Coordination Networks (RCN) including AmphibiaTree (amphibians), DeepFin (fish), BTOL (beetles), FLYTREE (flies), HymAToL (bees and wasps), LepTree (moths and butterflies).

While decisions about general aspects of the project reside with DRM, we view this stewardship of the project as only temporary, as the project belongs more directly to the community of systematists. ToL administration will change over the next year, as an advisory board is being established, with representatives of the communities of contributors and users of the project, and decisions about future directions will be passed into the hands of the advisory board.

Challenges of Resources and Collaboration

Many resources are needed to document the diversity of life on Earth. Funding for administration and programming is necessary to coordinate efforts, help contributors add data, ensure that the content is of high quality, and construct the database and other tools to allow for editing and sharing of content. But these are only a very small fraction of the need: the most valuable resource is knowledge about the organisms, and the limiting resource is time and funding of biologists needed to acquire that knowledge and make it available.

While extensive information about smaller, well-studied groups such as fish is available online (e.g., Fishbase, http://fishbase.org), very large, or less-well-studied groups, such as beetles, have much less information available. For many species, if there is any digital information available, it is only a name: pictures, textual descriptions of characters, natural history, etc., have not yet entered the electronic realm. For very diverse clades, a massive effort is needed to acquire basic pictures, write the relevant descriptions, and so on.

Who should perform this work may not be immediately obvious. It should not simply be professional systematists; there are many excellent students and amateurs, some of whom are the only experts in a particular clade. The ToL has left it to the community of systematists who study a group to decide who should contribute to their various branches, and both students and amateurs who have gained the respect of professional researchers have been invited to participate. Along the way we have considered alternative approaches, such as having some clades use a more Wiki-like approach, where editing of content is open to anyone. While this would undoubtedly increase the rate of content growth, and would yield some excellent content, it would change the fundamental nature of the ToL project and essentially duplicate the efforts of Wikipedia. The ToL scientific core content explicitly presents biodiversity from the point of view of experts. We focus our content development efforts on this community, because we believe that the perspective of professionals who have dedicated their career to the scientific study of a group of organisms is of unique value. Of course, there are great potential benefits in placing this expert content in the context of contributions from other communities. We have taken some steps in this direction with our treehouse and media contributor programs, and we hope to expand our activities in this area by collaborating with other projects that focus on alternative contributor communities.

Ensuring accuracy and quality of ToL content also requires resources. We carefully select experts as coordinators and authors, and have editorial mechanisms to check the content of contributions. The ToL has several levels of review of content, with the review mechanism indicated on each page. Some pages have only passed review by ToL editors (DRM or KSS), and are marked as "complete". Pages that are marked as ToL reviewed are reviewed by systematists who are ToL coordinators of that group. A few pages have undergone standard, anonymous peer-review, and can be so listed in a *curriculum vitae*. All of these reviews take time and effort on the part of biologists.

Documenting life on Earth is a collaborative enterprise, and as such, requires a social setting that encourages and rewards people for contributions. As in any social setting, there will be disagreement about scientific results, as well as social conflict, both of which will disrupt the effort. Making contributors feel welcome and valued is vital; their value is not only through contributions to their specific taxon, but also through the general ideas and inspiration they bring to the project. In turn, rewards contributors can gain come from multiple sources. For many, the sanctioning by their employers or their community of peers is critical, and so any effort of this nature should give credit where it is due, and ideally have mechanisms, such as peer review, or provision of information about the use of their content, to increase the importance of the product in the eyes of administrators. As important for many, though, is for the home of the data (the ToL or otherwise) to provide a high-quality environment in which biologists can share with the world information about the organisms that inspire them.

The rights of creators of the content must also be respected, and the ToL has taken the approach to let contributors specify to what extent their intellectual property can be reused and redistributed. We support a variety of licensing options, including all standard Creative Commons licenses.

Related Projects

There are now many excellent efforts to document in electronic form the diversity of life on Earth. Some of these cover all of life (e.g., the University of California at Berkeley's "History of life through time", http://www.ucmp.berkeley.edu/exhibits/historyoflife.php; The Catalogue of Life, http://www.sp2000.org; WikiSpecies, http://species.wikimedia.org), others specific clades, large (e.g., Animal Diversity Web, http://animaldiversity.ummz.umich.edu) or relatively small (e.g., FishBase http://fishbase.org; AmphibiaWeb http://amphibiaweb.org, Elateridae: Click Beetles of the Palearctic Region, http://www.elateridae.com).

Many of these projects began since the ToL has been operational, and the overlap in goals and content among efforts reflects the diverse interests and different approaches in the community of systematists. While the ToL has satisfied the needs of some systematists who want to contribute to the growing collection of diversity information on the Web, other researchers have sought alternative venues.

This fragmentation of projects was perhaps inevitable given the creativeness and independence of systematists. Undoubtedly, the information about organisms available online is richer and more diverse because a multitude of initiatives have experimented with different models of content development and have captured the imagination of content contributors in different ways. However, systematists seeking a platform for the dissemination of their research results are often hesitant to commit to a particular project, and the great fragmentation of online biodiversity documentation is a challenge for users in search of reliable, authoritative information about organisms. To alleviate these problems, the ToL is working with other projects to combine content development efforts. For example, AmphibiaWeb (http://amphibiaweb.org) will soon be the source of leaf page content within the amphibian branch of the ToL, and lepidopterists will soon be able to submit materials for ToL pages through the interactive web tools of the LepTree project (http://leptree.net/). In addition to these close collaborations between individual projects, the large number of web resources that present rich information about particular portions of life's diversity has also spawned the creation of sites that automatically aggregate content from multiple sources. Two notable examples are uBio (http://www.ubio.org/portal/) and iSpecies (http://iSpecies.org).

TreeBase (http://treebase.org) is a complementary project that houses the results of the primary phylogenetic literature: original data matrices, methods, and trees. This is the literature from which scientific contributors to the ToL synthesize the phylogenetic hypothesis that is presented therein. In the future, we hope to allow the ToL to display directly trees from TreeBase, including those derived from supertree or supermatrix analyses (Sanderson et al., 1998; Bininda-Emonds et al., 1999; Gatesy et al., 2002; Bininda-Emonds, 2004).

ToL and the Encyclopedia of Life—In May of 2007 a new effort, the Encyclopedia of Life (EOL; http://eol.org), was announced whose goals and basic nature matches those of the ToL: presentation of information about all species on Earth, as well as the branches of the evolutionary tree of life, for diverse audiences, authored by expert systematists in each group. The EOL has acquired significant funding and backing by major institutions, and will be a major force in the presentation of taxonomic information on the Web. Because of the almost-complete overlap in the two projects' goals, the ToL and EOL have agreed to collaborate in this effort, with the ToL focusing more on branch pages, serving that information to the EOL, and the EOL focusing more on species information, and serving those data to the ToL.

Future

Many changes lie ahead in the ToL, with a new administrative structure and governance plan and improvements in interface and content. Among the more vital alterations will be in the way the ToL interacts with other databases, including the Encyclopedia of Life.

Sharing content between the ToL and some of the many databases that now contain biodiversity information will be one of the primary efforts for the ToL over the next few years. Thorough sharing of information will require that the participating databases know that they are speaking about the same nodes in the tree of life. If a piece of text in the EOL is to be displayed on the appropriate page in the ToL, then a mechanism will need to be in place enabling the ToL to know to which node on its tree the EOL meant for the information to be attached. To do this, we will need not only phylogenetic definitions of taxa (deQueiroz & Gauthier 1990) and taxonomic name servers (Patterson et al. 2006), but phylogenetic definitions for the location of any objects (images, media, text, etc.) that might be attached to nodes in the trees. Developing these definitions will be a key part of the future of inter-database communication.

We have also been working on making the content of the ToL available to analytical programs. For example, modules in development for Mesquite (Maddison and Maddison 2007) can now access the tree structure contained within the ToL, and display it within Mesquite's tree windows. We will eventually build modules in Mesquite that will harvest the tree structure and allow it to be combined in a phylogenetic analysis with other data. If the appropriate taxonomic name servers and phylogenetic definition servers can be built, then such analytical programs could be designed to conduct phylogenetic analyses merging information from multiple databases.

As the number of clades and species within the ToL database grows, we will need to explore supplementary ways to visualize and navigate the tree of life in a web browser. The complete tree will be immense, comprising several million nodes representing known groups of organisms. The ToL currently features over 57,000 published nodes, and almost an equal number of new nodes have already been added to the ToL development database and are awaiting publication. Making it easy for people to explore content associated with this vast structure is a challenge of technical implementation and user interface design. In recent years progress has been made in the development of software for visualizing large trees (e.g., Bingham & Sudarsanam 2000, Hughes et al. 2004, Munzner et al. 2004), but efforts have generally focused on the development of desktop applications, and so far no satisfactory tool for web use has emerged. The Biodiversity Synthesis Group of the emerging Encyclopedia of Life (http://www.eol.org/biodiversity_synthesis.html) has recently set as one of its goals the development of a web-based, interactive visualization and navigation tool for large evolutionary trees. The ToL will participate in the working group that is being organized for this purpose. We hope that this initiative will result in an open-source tree viewer/navigator that can be ported to a variety of web-based systems. The tool should dynamically integrate links to web pages, images, and other content from a database, and it needs to be highly customizable for use in both research and outreach contexts.

Concluding Remarks

Our choice to design and coordinate the Tree of Life Web Project was not motivated only by the scientific mission to synthesize and describe; it was motivated also by the importance to us of that which is described: the Tree of Life itself — the lineages of genetic descent that remain on Earth. If our own line of genetic descent is to act so as to save the others, then there must first be a change in our species' perspectives on others. When we began the Tree of Life Web Project, we felt that a small role we could play was to enhance the public's esthetic appreciation of biodiversity, because with that appreciation might come a will to preserve. Biodiversity is a chest of jewels that so few open. For this reason we have sought from the start to adorn the Tree with rich depictions of organisms and their lives: images, compelling biological stories, other media. It is our hope that the project that Linnaeus began will, by making Earth's biotic richness known, eventually help to save it.

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