

Current Range Distribution of Cryptobranchid Salamanders Examined Using Biogeographic Methods

REBECCA POLICH



WRITER'S COMMENT: Since I was a little girl, reptiles and amphibians have fascinated me. To this day, I love to chase these creatures across fields and over walls, I marvel at their beautiful colors and patterns, and I adore the cocky looks they throw back over their shoulders after they successfully evade me. When Professor Shapiro announced that there would be a research paper assigned for EVE 147, I immediately looked for a chance to write about reptiles or amphibians. I was lucky in that Dr. Shapiro made this term paper a rather open-ended assignment; the only collar on the creativity of the student was that the assignment had to relate to biogeography in some way. It was up to the students to pick a topic and to follow through with the research. I looked at this research paper as a great opportunity to follow through with a question that had been plaguing me since the following spring when I took Dr. Shaffer's herpetology class: why is it that out of three species of extant Cryptobranchid salamanders, two are found in relatively close locations (southeastern China and Japan), but the third is found in the American southeast? Thanks to this research paper, I was afforded the opportunity to research this question that had for so long enthralled me (without even feeling bad about taking time away from my studies!). I believe that I have answered this question very well considering the available research on these charismatic salamanders. I hope you enjoy reading this paper as much as I enjoyed writing it.

I am grateful to Dr. Shapiro for assigning this research paper, as well as for letting me follow this topic even though he worried that I wouldn't be able to find enough original research papers. I am also eternally grateful to my parents; I was lucky enough to have grown up with loving parents who encouraged my budding affection for these creatures. They helped me collect California slender salamanders after their emergence from their burrows in my backyard following rain, and my father and I would often chase after Western fence lizards in the foothills of the Santa Monica Mountains. I believe it is due to their encouragement of my "unladylike" tendencies to endlessly chase lizards in my backyard that in my adult life I have completed

a B.S. in biological sciences and next fall will begin a PhD in ecology and conservation biology. I am also grateful to Prized Writing for publishing this original piece of my own making. I hope that in the reading of this essay some of the wonder that I have for these animals will be passed on to the readers.

INSTRUCTOR'S COMMENT: Why are organisms found where they are? In a nutshell, that's what the science of Biogeography is about. Evolution and Ecology 147 explores this complex and difficult subject. Distributions result from both contemporary ecological factors (organisms can only live in certain places due to the distribution and availability of their necessary resources) and historical ones (organisms can only live in a place if they have had access to it and have been able to colonize and persist there). Disentangling the two is often difficult. Furthermore, historical access can result from either changes in the distribution of land and sea (plate tectonics) and of climates -- taken together, such processes are known as "vicariance"--or by long-distance colonization across geographic barriers, familiarly known as "dispersal." Until recently, trying to reconstruct the origins of distributions was mostly a matter of logic and scenario-spinning, aided by the fossil record when one existed. But the molecular genetic revolution has, for the first time, made such efforts rigorously testable and hence scientific in the strict sense. Students in EVE 147 demonstrate their mastery of this highly synthetic subject by writing long term papers, typically on the biogeography of a particular taxon (group of organisms). In this paper Rebecca Polich takes on the mudpuppies and hellbenders, a small, ugly-but-charismatic, "primitive-looking" group of aquatic salamanders disjunctly distributed in eastern North America and eastern Asia. Her work is a fine example of what biogeographers do and how they do it.

—Arthur Shapiro, Evolution and Ecology

Introduction

The family Cryptobranchidae contains some of the most enigmatic species of any family of salamander. Worldwide, these salamanders are renowned for the immense sizes that they have been known to attain, with the Chinese giant salamander routinely growing to lengths of nearly five feet and weighing in at over 100 pounds. The interest with which these creatures are regarded can be seen in the names that they are given by the humans who live alongside them. For example, the American *Cryptobranchus alleganiensis* is known vernacularly as the hellbender. The etymological roots of this name are uncertain, but it has been suggested that “it was named by settlers who thought ‘it was a creature from hell where it’s bent on returning.’ Another rendition says the undulating skin of a hellbender reminded observers of ‘horrible tortures of the infernal regions’” (Johnson and Briggler, 2004, p. 1).

The Chinese and Japanese giant salamanders (*Andrias japonicus* and *Andrias davidanus*) are also fondly regarded in their countries of origin. The Chinese name for *A. davidanus* literally means “baby fish,” because some of its vocalizations reminded locals of crying infants (Xinhua News Agency, 2006). Similarly, the Japanese giant salamander has been celebrated in traditional Japanese paintings, popular literature, and a Japanese cultural festival that takes place every year in the Okayama Prefecture (AmphibiaWeb, 2011; AltJapan, 2008). The Japanese giant salamander has even been featured in a bizarre science fiction book entitled *War With the Newts*, by Czech author Karel Capek, which describes the hostile takeover of the planet by an intelligent species of salamander (Wingrove, 1984, p. 117).

However, the family cryptobranchidae is not interesting simply because of the impact its species have had on human culture. What is perhaps most interesting about these salamanders is the bizarre range distribution of the extant members of this family. There are only three recognized extant species of cryptobranchid salamander: the American hellbender (*Cryptobranchus alleganiensis*), the Japanese giant salamander (*Andreas japonicus*), and the Chinese giant salamander (*Andreas davidanus*). The two Asian salamanders are found relatively close to one another, with *A. japonicus* being located in southern Japan and *A. davidanus* being located in southeaster China. However, the American hellbender is located on the other side of the world in the American

southeast (AmphibiaWeb, 2011). There are no living cryptobranchid salamanders to be found in between these two isolated populations. This bizarre fact begs the question, where was the center of origin for cryptobranchid salamanders, and how is it that the last remaining living members of this family ended up in their current distributions? Through examining the literature on cryptobranchid salamander fossil records and phylogeny, I have attempted to answer these questions.

Diversity and Natural History

One of the most striking observations of the extant cryptobranchid salamanders is the amount of physical and behavioral similarities that they share. Often they are described as being “ancestral,” that is, possessing traits that resemble those of ancestral salamanders. They are a highly unmodified species and have looked largely the same for thousands of years. The Hellbender of North America, *Cryptobranchus alleghaniensis*, is the largest amphibian in North America. It can reach sizes of up to 74cm total length, nearly two and a half feet long! This salamander is entirely aquatic and is characterized by a dorso-ventrally flattened appearance, small eyes, and very baggy skin. Individuals of the species usually have greenish to yellowy brown skin (Petranka, 1998 p. 140-141).

The larger Asian cryptobranchid salamanders are remarkably similar in appearance to their American cousin. Both the Japanese giant salamander, *A. japonicus*, and the Chinese giant salamander, *A. davidanus*, are also dorso-ventrally flattened and characterized by greenish to yellow brown skin. They are mainly distinguishable from the Hellbender due to the presence of tubercles and marbling in their color patterns (Kawachimi and Ueda, 1998, p. 133; Lui and Lui, 1998, p. 30-33). Also, they are notably larger. The Chinese giant salamander is the largest recorded living amphibian, with adults reaching a total length of around 100cm (Lui, 1950, p. 32). Adult Japanese giant salamanders usually only reach lengths of 30-70cm, though adults have been found that are as large as 102cm (Kawachimi and Ueda, 1998, p. 133).

In addition to the physical similarities that these salamanders share, they also are adapted to very similar habitats. They are all adapted to streams with flowing water, though there are slight differences in optimal habitat. Hellbenders require the cold water of fast flowing streams and rivers. They seem to prefer larger streams and rivers. They also require many rocks and boulders in their habitat because they use them as shelter

and for breeding sites (Petranka, 1998, p. 143-144). Japanese giant salamanders also require cool water, but they are more flexible as to the size of the streams and rivers that they inhabit. They can be found in relatively large rivers (20-50 m wide) as well as small tributaries (1-4 m wide). They also tend to inhabit only streams with rocky bottoms, though unlike Hellbenders, they are generally found in rocky caverns or burrows on the edges of the submerged river banks, rather than under the rocks themselves (Okada et al., 2008, p. 192, 199-200). Chinese giant salamanders also are more likely to be found in submerged cavities on the banks of the river rather than under rocks. There is no reported preference for rivers of a certain size; however, they only inhabit rivers less than 1500 meters above sea level (Lui and Lui, 1998, p. 30-33).

The breeding behaviors and life histories of these salamanders are also remarkably similar. For example, both the Hellbender and the Asian giant salamanders are nocturnal predators that prey upon small fish and fresh water arthropods (Petranka, 1998, p. 143-144; Xinhua News Agency, 2006). In all three species, the breeding season occurs in the fall from August to September, and the eggs are fertilized externally and guarded by the male until they hatch (Kawachimi and Ueda, 1998, p. 135; Petranka, 1998, p. 143-144). Also, aggressive behaviors by male salamanders against conspecifics during breeding season have been recorded in both Hellbenders and the Japanese giant salamander (Kawachimi and Ueda, 1998, p. 135; Petranka, 1998, p. 143-144). Although no such behavior has been observed in the Chinese giant salamander, it is possible that this behavior exists, but that it has not yet been recorded. The similarities between these species across both appearance, behavior, and ecology indicate that these creatures have remained largely the same since their initial evolution, and potentially that they have experienced very low levels of genetic differentiation since that event.

Phylogeny and Fossils as Evidence of Historic Range Distribution

The molecular relationships between the cryptobranchids and the other modern families of salamander used in conjunction with fossils have the potential to help inform where the family originated and how its members speciated and spread to inhabit their current ranges. Unfortunately, molecular evidence has historically been difficult to sort out in salamander families. Many different phylogenetic trees have been created that describe

different relationships between the salamander families. In 1993, Larson and Dimmick utilized 209 phylogenetically informative characters from each of the 10 extant salamander families to create a phylogenetic tree. These phylogenetically informative characters included 177 characters from rRNA, 20 characters from head and trunk morphology, and 12 characters from cloacae anatomy. The tree that they created placed the *Sirenidae* as the outgroup to the rest of the salamanders, with the cryptobranchids and hynobiids (*Cryptobranchoidea*) being the second group to diverge from the main salamander lineage (Larson and Dimmick, 1993, p. 85-87).

However, many phylogenetic trees created since then have placed the *Cryptobranchoidea* as the basal lineage to the rest of the salamander taxa. For example, in 2005 Weins et al. used a combination of RAG-1, nuclear ribosomal DNA, and morphological characters to draw this very conclusion. All but 13 of the nuclear ribosomal DNA characters were from the large subunit. The 13 that were not were from the small subunit. All told, 317 characters from 32 salamanders and three outgroups were analyzed. The DNA was analyzed using parsimony and Bayesian analysis (Wiens et al., 2005, p. 102-103). This phylogenetic tree agreed with a 2011 paper by Pyron and Weins. The 2011 paper was an enormous study that utilized genetic information from 2,871 amphibian species, representing 432 genera. The authors identified 12 loci that had been used successfully in the past for amphibian polygenetics. Nine of these loci were nuclear genes, while three were mitochondrial genes. The tree created in the Pyron and Weins study strongly supported the *Cryptobranchoidea* as the outgroup to other salamanders (Pyron and Weins, 2011, p. 546, 567, 570, 572-573, 575, 579). The multiple lines of genetic evidence from more recent research that utilized a wider variety of molecular characters indicate that the *Cryptobranchoidea* is the outgroup to all other salamanders. This information becomes important when examining the fossil record.

An important aspect of how the cryptobranchid salamanders came to have such divergent ranges involves determining where salamanders originated. In 2005, Zhang et al. used mitochondrial DNA to attempt to find the center of origin for salamanders, anurans, and caecilians. Their research indicates that salamanders likely originated in Eastern Asia in the mid-Carboniferous or early Permian period, with the cryptobranchidae evolving during the late Triassic through the mid-Jurassic period. Along with the hynobiids, they were the first extant salamander family to split

away from the main caudatan lineage (Zhang et al., 2005, p. 398-399). A 2007 study reported similar findings to those reported by Zhang et al. Using both mitochondrial and nuclear DNA, Roelants et al. created a evolutionary time tree that placed the origin of the caudata in the early Carboniferous period, with the cryptobranchidae evolving in the mid-Jurassic (Roelants et al., 2007, p. 888, 890). The theory proposed by both of these papers strongly supports the Laurasian pattern of distribution seen in modern salamanders.

However, Zhang et al. noted that an East Asian origin for salamanders is problematic because North America contains the highest number of extant salamander families. The authors decided upon an East Asian center of origin because the earliest salamander fossils have been found in China, and the high diversity of modern salamander families in North America could be due to continental vicariance during the Cretaceous when North America separated from Eurasia (Zhang et al., 2005, p. 398-399). A different paper adds a further line of evidence to the East Asian origin of salamanders in general and cryptobranchids in particular. This paper argues for an East Asian center of origin for cryptobranchid salamanders because cryptobranchids themselves are found in East Asia and southeastern America, while their sister clade, the hynobiids, are almost exclusively Asian in distribution. The paper argues that the most parsimonious explanation for these range patterns is that the most recent common ancestor to hynobiids and cryptobranchids evolved in East Asia, and later spread across Asia, and in the case of cryptobranchids, into North America (Gao and Shubin, 2003, p. 427-428).

The implication of this data is that cryptobranchid salamanders used to be very widespread, and the species and their ranges that we see today are simply relics of what once was. However, it is impossible to definitively state that this must be the case if all we have to rely on is the current range of extant cryptobranchid salamanders and molecular evidence. This hypothesis will be strongly bolstered by the presence of fossil evidence. If the hypothesis is correct, then surely the huge amount of land that this taxa once covered contains some fossil remnants. In support of the hypothesis, fossil remnants of extinct cryptobranchids have indeed been found.

Currently, the oldest known fossil cryptobranchid is over 160 million years old. Its name, *Chunerpeton tianyiensis*, is a combination of Chinese and Greek words. *Chu* is Chinese for early, *herpeton* is Greek for creeping animal, and *tianyi* is an ancient name for Ningcheng, the

county where the creatures were discovered. This creature lived during the middle Jurassic period, and specimens have only been found in Inner Mongolia, China. The specimens share over eight derived characters with living cryptobranchids, including nasal passages that are much narrower than the distance between the eyes, presacral vertebrae bearing uncapitate ribs, and reduction in the number of rib-bearing anterior caudal vertebrae to two or three (Gao and Shubin, 2003, p. 425-426). This specimen helps root cryptobranchid origins in East Asia because it is the earliest known fossil of this taxon.

Other evidence for the East Asian origins of cryptobranchid salamanders is the fact that there are many fossils from this part of the world that are either clearly cryptobranchid salamanders or can be identified as stem caudates that share many features with cryptobranchids. For example, *Sinerpeton fengshanensis* is a neotenic salamander from the late Jurassic. It has been found in the Fengshan province of China, and it shares several derived features with cryptobranchids, such as rib structure, but is also distinct from them due to several other characteristics. These characters include presacral vertebra with laterally expanded zygapophores and a greatly expanded metacarpal II in the hand (Gao and Shubin, 2003, p. 427-428). Other late-Jurassic/early Cretaceous salamanders have been discovered that are similar to cryptobranchids and yet distinct, such as *Regalerpeton weichangensis* from the Huajiying province in China and *Jeholotriton paradoxus* from Inner Mongolia, China (Wang and Rose, 2005, p. 523). These salamanders all share features with cryptobranchids and yet lack the deterministic cryptobranchid features. It is difficult for scientists to assess what exactly they are, especially because many of them are known only from incomplete fossils. However, what these creatures do tell us is that cryptobranchids almost undoubtedly originated in East Asia, as this is the only part of the world in which such a diversity of early, extinct cryptobranchids and closely related species are found. Such a fossil record is what one would expect from the center of origin for a species.

The fossils that have been found outside of China are considerably younger than those found within. In 1732, Johan Schuechzer famously reported fossil cryptobranchid remains as being the remains of a dead human child that perished in the Biblical flood. He called these remains “Homo diluvii testis” or “Man, a witness of the deluge.” Cuvier later recognized these fossils as being non-human, and placed them within the order Urodela. In 1837, Tschudi described the specimen and gave it its

current name, *Andrias scheuchzeri*, in honor of its discoverer. Meszoely reports that the remains of *A. scheuchzeri* in Europe are only around 30 million years old. He has dated them to the mid Oligocene, which makes them around 70 million years younger than the early fossil cryptobranchids from China (Meszoely, 1966, p. 496, 514-515). Most fossil remains in North America are even more recent. Cryptobranchid remains from Nebraska and Colorado have been identified as the same species, and the different remains date from the mid-Miocene to the early Pliocene. This species has been placed in the family *Andrias* due to similarities between itself and the Asian cryptobranchids, including similarities between neural spines and the length and positioning of the maxilla. This specimen is today known as *Andrias matthewi* (Meszoely, 1966, p. 347-348).

Interestingly, cryptobranchid fossils have been found in North America that are older than those found in Europe. Naylor identified a species of cryptobranchid salamander that he referred to as *Cryptobranchus saskatchewanensis* after the province of Saskatchewan in Canada, where it was found. He dated this salamander to the early Paleocene, which at the time made it the oldest fossil cryptobranchid salamander known (the Chinese fossil cryptobranchids had not yet been discovered). He used this information to theorize that cryptobranchids actually originated in North America, though he admitted that this hypothesis was falsifiable with the discovery of new fossil cryptobranchids (Naylor, 1981, p. 81). Indeed, since this fossil salamander is around 90 million years younger than the earliest fossils found in China, it can safely be said that this salamander is not the first known cryptobranchid. Similarly, *Piceoerpeton willwoodensis* is a fossil cryptobranchid from the late Eocene. It has been found only in Wyoming, and is believed to be distinct from both *Andrias* and *Cryptobranchus*, though archaeologists believe it is most likely more closely related to *Cryptobranchus* (Meszoely, 1967, p. 346-347). This amphibian was also believed to represent the first known cryptobranchid salamander, but that assertion has now been disproved. It still serves a valuable role in defining the ancient range of this enigmatic family.

Conclusions

The fossil and molecular evidence indicate that cryptobranchid salamanders originated in southeastern China in the mid Jurassic (Zhang et al., 2005, p. 398). This is evident from molecular evidence and the fact that the earliest known fossils of species belonging to the cryptobranchid family

have been found in China. After their initial evolution, the cryptobranchids dispersed across Asia into Europe, and then into North America. This was possible at the time because Europe and North America were connected as the super-continent of Laurasia, which formed around 200 million years ago (Zhang et al., 2007, p. 399). A Laurasian distribution of ancient cryptobranchids would explain how the cryptobranchids managed to find their way into North America. This is very important information, as cryptobranchids, being salamanders, are recognized as poor dispersers, especially across salt water. We know that by the Oligocene, ancient cryptobranchids had reached Europe (Meszoely, 1966, p. 496). However, it is likely that they were present before then, as cryptobranchid fossils have been found in North America that date to the Paleocene (Naylor, 1981, p. 81). However, they may have been present earlier. The fossil record for cryptobranchids is unfortunately sparse, evidence of which can be seen in the fact that the oldest known North American cryptobranchids predate the oldest known European cryptobranchids. This should not be possible, as at no point was North America in between Europe and Asia. Therefore, the most logical conclusion is that the older fossils from Europe have not yet been found or fossils were never preserved in the first place.

This lack of fossils leads to ignorance about the exact patterns of dispersal that the ancient cryptobranchids used as they disseminated out of China. This is an important area for further research, and it could yield promising information about dispersal patterns of cryptobranchids as they dispersed out of China. For example, in addition to continued searches for fossils, some idea of dispersal patterns can be derived from molecular studies of living salamanders. For example, in 1994, Routman et al. was able to create a rough outline of the dispersal of the American hellbender throughout North America. From mitochondrial DNA, they found that there are two subspecies of the American hellbender. One is *Cryptobranchus alleghaniensis alleghaniensis*, which is found from southern New York to northern Georgia, Alabama, Mississippi, the western parts of West Virginia, Virginia, the Carolinas, central and southern Missouri, and the northern Ozarks. The other subspecies is *Cryptobranchus alleghaniensis bishopi*, which is found in the southern Ozarks. Mitochondrial DNA has also revealed that *C. a. alleghaniensis* populations from the rivers that flow south into the Ohio River and the populations from rivers flowing north out of the Ozark Mountains are very similar genetically. This close relationship implies that the invasion of the Ozarks from the Ohio river

basin (or vice versa) was relatively recent. It is possible that the Pleistocene glaciation wiped out hellbender populations living in rivers north of the Ohio. After the glaciers receded, this area has gradually been colonized by hellbenders from the Ozarks. In addition, there are extremely low levels of genetic divergence among hellbenders from the northern Missouri Ozarks and populations of hellbenders from Pennsylvania, Indiana, and Illinois. This evidence suggests that this entire region was likely invaded after the Pleistocene glaciation by hellbenders that had persisted in a refugium in one of these areas (Routman et al., 1994, p. 1805-1806).

This molecular evidence is interesting, but incomplete. Mitochondrial DNA alone cannot be relied upon to re-create patterns of dispersal. Mitochondrial DNA can be inconsistent and reveal false patterns. For example, mtDNA inconsistencies in the *C. alleghaniensis* populations can be due to past geologic phenomenon, but they could also be due to random lineage extinction across a widespread ancestral population (Routman et al., 1994, p. 1808). Further studies utilizing multiple, alternate molecular evidence, need to be performed. In addition, molecular studies that attempt to identify patterns of dispersal have yet to be performed on either *A. japonicus* or *A. davidanus*. This is an important area of research that should receive more consideration. However, the sharp decreases in the Asian giant salamander populations in recent years would probably skew any molecular findings about historical distribution. Nonetheless, it is still valuable research that should be performed to help scientists determine a more complete history for the family *Cryptobranchidae*.

References

- AltJapan. (2008). Hanzaki Matsuri Dakara. Retrieved November 20, 2011, from http://altjapan.typepad.com/my_weblog/2008/08/the-realm-of-the-salamander.html
- AmphibiaWeb: Information on amphibian biology and conservation. [web application]. (2011). Berkeley, California: AmphibiaWeb. Retrieved November 20, 2011, from <http://amphibiaweb.org/>.
- Biju, S.D., Bossuyt, F., Gower, D.T., Guillaume, K., Loader, S.P., Moriau, L., Roelants, K., and Wilkinson, M. (2007). Global Patterns of Diversification in the history of Modern Amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, 104(3): 887-892.
- Bonett, R.M., Chippindale, P.T., and Wiens, J.J. (2005). Ontogeny Discombobulates Phylogeny: Paedomorphosis and Higher-Level Salamander Relationships. *Systematic Biology*, 54(1): 91-110.
- Chen, Y., Zhou, H., Lui, Y., Zhang, P., and Qu, L. (2005). Mitogenomic Perspectives on the Origin and Phylogeny of Living Amphibians. *Systematic Biology*, 54(3): 391-400.
- Dimmick, W., and Larson, A. (1993). Phylogenetic Relationships of the Salamander Families: An Analysis of Congruence among Morphological and Molecular Characters. *Herpetological Monographs*, 7: 77-93.
- Evans, S.E., Jones, M.E.H., Wang, Y., Zhang, G. (2009). A new Early Cretaceous salamander (*Regalerpeton weichangensis* gen. et sp. nov.) from the Huajiyang Formation of northeastern China. *Cretaceous Research*, 30(3): 551-558.
- Gao, K., and Shubin, N.H. (2003). Earliest known crown-group salamanders. *Nature*, 422: 424-428.
- Johnson, T.R., Briggler, J. (2004). The Hellbender. *The Conservation Commission of the State of Missouri*. Retrieved November 18, 2011, from http://mdc.mo.gov/sites/default/files/resources/2010/05/5174_3015.pdf
- Kawamichi, T. and Ueda, H. (1998). Spawning at nests of extra-large males in the Giant Salamander *Andrias japonicus*. *Journal of Herpetology*, 32: 133-136.

*Current Range Distribution of Cryptobranchid Salamanders
Examined Using Biogeographic Methods*

- Liu, C.C. (1950). Amphibians of Western China. *Chicago Natural History Museum, Chicago*.
- Liu, G., and Liu, Q. (1998). *Andrias davidianus*. In Zhao, E. (Ed.), *China Red Data Book of Endangered Animals. Amphibia and Reptilia* (pp. 30-33). Beijing, China: Science Press.
- Meszoely, C. (1966). North American Fossil Cryptobranchid Salamanders. *American Midland Naturalist*, 75(2): 495-515.
- Meszoely, C. (1967). A New Cryptobranchid Salamander from the Early Eocene of Wyoming. *Copeia*, 67(2): 346-349.
- Naylor, B.G. (1981). Cryptobranchid Salamanders from the Paleocene and Miocene of Saskatchewan. *Copeia*, 1(1): 76-86.
- Okada, S., Utsunomiya, T., Okada, T., Felix, Z.I., and Ito, F. (2008). Characteristics of Japanese Giant Salamander (*Andrias japonicus*) populations in two small tributary streams in Hiroshima Prefecture, Western Honshu, Japan. *Herpetological Conservation and Biology*, 3: 192-202.
- Petranka, J. W. (1998). Salamanders of the United States and Canada. *Smithsonian Institution Press*.
- Pyron, A.R. and Weins, J.J. (2011). A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution*, 61(2): 543-583.
- Rose, C.S., Wang, Y. (2005). *JEHOLOTRITON PARADOXUS* (AMPHIBIA: CAUDATA) FROM THE LOWER CRETACEOUS OF SOUTHEASTERN INNER MONGOLIA, CHINA. *Journal of Vertebrate Paleontology*, 25(3): 523-532.
- Routman, E., Templeton, A.R., and Wu, R. (1994). Parsimony, Molecular Evolution, and Biogeography: The Case of the North American Giant Salamander. *Evolution*, 48(6): 1799-1809.
- Wingrove, D. (Ed.) (1984). The Science Fiction Source Book. England: Shuckburgh Reynolds.
- Xinhua News Agency. (2006). Retrieved November 18, 2011, from <http://www.china.org.cn/english/environment/178434.htm>