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The Range of *Cryptobranchus bishopi* and Remarks on the Distribution of the Genus *Cryptobranchus**

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Since the publication of the description of *Cryptobranchus bishopi* Grohman (1943: 6) with the statement that this form is restricted to tributary streams of the upper Black River system in south-central Missouri and north-central Arkansas, one new record has appeared that necessitates re-examination of the geographic range pattern of this species. Mention of a specimen of *Cryptobranchus bishopi* (Univ. Kansas Mus. No. 16143) from Greene Springs, Vernon County, Missouri, is made by Hall and Smith (1947) in their report of the surprising occurrence in Kansas of *Cryptobranchus alleganiensis* from the Neosho and Spring rivers of the Arkansas River system. These authors state further that despite the proximity of these localities in eastern Kansas and western Missouri, and the distant known records for *alleganiensis*, the Kansas specimens cannot be considered as assignable to *bishopi* but are tentatively regarded as typical *alleganiensis*.

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The appearance of *C. bishopi* in Vernon County, Missouri, seems problematical, since Greene Springs is located in the vicinity of the upper reaches of the Osage River tributaries (Clear Creek, Dry Wood Creek and Marmaton River), a part of the Missouri River drainage and well within the assignable range of *alleganiensis*. Grohman (loc. cit., map, p. 7) records *alleganiensis* from a tributary of the Osage River and also in the adjacent Gasconade River. The admixture of two forms of *Cryptobranchus* within the same Missouri River system would lead one to suspect intergradation despite the fact that Grohman regarded *bishopi* as a full species. Upon careful examination and comparison of the "Vernon County" specimen with the paratype series I came to the conclusion that it is wholly typical of *bishopi* (the ratio between the diameter of the branchial opening and the interbranchial distance is 5:1.2). Suspicion was immediately focussed on the validity of the locality data. The Kansas University specimen was collected by B. C. Marshall (a professional collector who sold his specimens to various museums) at, according to the catalogue and jar label, Greene Springs, Vernon County, Missouri,

* Contribution from the Museum of Natural History of the University of Illinois, Urbana, Illinois.

on July 23, 1928. At the American Museum of Natural History Grobman's paratypes (A.M.N.H. nos. 23053-54) were examined and it was noted that these were also collected by Marshall July 23, 1928, at Greer Springs, Oregon County, Missouri. A further check of other specimens deposited at the American Museum by Marshall, disclosed that all the localities visited during the month of July centered in the Oregon County sector. Through the kindness of Dr. James Oliver, I was able to examine Marshall's itinerary for July, 1928, kept on file in the Department of Amphibians and Reptiles, American Museum. The exact collecting dates and localities were as follows: July 9, Lawrence County, Arkansas; July 12, Wright County, Missouri; July 13, Douglas County; July 14-15, Shannon County; July 23, Greer Springs, Oregon County; July 25, Greer, Oregon County. It seems fairly obvious therefore, that the Kansas University specimen is merely one of the same series designated as paratypes. It is unlikely that Marshall, at this time, made a journey to Vernon County, some 200 miles distant. I therefore suspect that the University of Kansas Museum locality is in error, and that during the process of transcription, "Greer" was misinterpreted as "Greene" and thus followed the designation of the specimen as Vernon County.

More recently another record of *bishopi* has come to light. This specimen (Univ. Kansas Mus. No. 27814) was collected in Spring Creek (a tributary of the White River), 19.7 miles WNW of West Plains, Douglas County, Missouri, by Dr. A. B. Leonard on August 22, 1948. It was first discovered under a rock in the swift flowing waters of the stream and although many other rocks in the vicinity were overturned, no other specimens were obtained. This individual measures 308 mm. from snout to vent. The branchial openings are typically reduced, 2.8 mm. in diameter on the right side and 5.0 mm. on the left, and thus well within the ascribed limits of *bishopi*. The body has the typical large blotches of this species.

The range of *C. bishopi* is now known to include Black River tributaries such as Current River, Greer Springs and Eleven Point River, and Spring Creek of the White River drainage system. Black and Dellinger (1938) reported *Cryptobranchus* from Spring River in Arkansas (Mammoth Spring, Fulton County), but no specimens are actually available. Dr. Dellinger told the author (in 1946) that several other specimens from this locality in the Black River system have come to his attention since that publication, and that they represent *bishopi*. The State Fish Hatchery at Mammoth Spring exhibit one or two examples occasionally, and fishermen in the area report having obtained the salamander on their lines. *C. bishopi* undoubtedly occurs in other streams in the central Missouri-Arkansas Ozark area. Fishermen claim that they are common in the upper Black River and possibly they may inhabit the St. Francis River which flows directly into the Mississippi River.

It is appropriate to remark upon the mode of speciation exemplified by the Cryptobranchidae. The family as a whole shows extreme conservatism, and there is little tendency toward the production of genotypic or phenotypic novel-

ties. The differences between *Cryptobranchur* and the Asiatic *Megalobatrachus* are minor and neither genus is very distinct from the fossil *Andrias rreuchzeri* from the Oligocene of Europe (Schmidt, 1946: 149). This group of derotreme salamanders shows little evidence of a phylogenetic sequence of differentiation. Rather, all morphological differences, e.g. the number of epibranchials on the hyobranchium and the closure of the branchial fenestrae, that form the bases for generic designations, rest on the level of metamorphosis attained.

Evidently, as Noble (1927, 1929) has shown, a very small genetic factor is responsible for this type of variation in metamorphosis. A desensitization of specific tissues to thyroid extracts (the metamorphosis-inducing endocrine hormone) has evolved, and if it were not for this small mutation, cryptobranchids could normally transform completely since the thyroid gland is functional. "Change" in this respect should not be considered as a phylogenetic shift of position. Thus it would be very difficult indeed to attempt to analyze the evolution of the cryptobranchids in the light of primitive-versus-modern components. It may be stated only in this fashion: *Megalobatrachus* is further along in total development toward adulthood than is *Cryptobranchu*, *alleganiensis*, which is somewhat "retarded" and represents a lower stage in the ontogenetic development of the family. *C. bishopi* may be placed somewhere between these two extremes. The species composing the genus *Cryptobranchus* represent then, merely a reshuffling of evidently one genetically controlled factor; *bishopi* showing a definite "advancement" toward a completed metamorphosis because of the tendency toward the closure of the branchial fenestrae.

In the light of the above remarks it is doubtful if *C. bishopi* differentiated altogether by mere isolation and the consequential genetic shift and stabilization of characters. Rather, *bishopi* represents an attainment of a certain "stage" or "degree" in the ontogenetic development of the species as a whole. A mutation threshold in the developmental series is reached by the influence of internal factors (considering of course that external factors are here regarded as fairly constant in the phylogeny of the group) and this identical threshold of development theoretically may be crossed again and again (presumably from any direction) in the speciation of the group. This periodical recurrent mutational type from the same stock ("iteration" of Beurlen, 1929) may give rise to isochronous convergence. If this be possible then polyphyletic speciation may occur. Potentially the "*bishopi*" phenotype may erupt within any part of the range of the genus since this species represents only a functional stage of development. In this species, stabilization by genetic inheritance and perhaps the effect of environmental selection (although this last point is doubtful) enhances to a degree the maintenance of the "thyroid immunity." Such a physiological action manifested itself in profound morphological effects that formed the basis for the recognition of distinct species. This change is latent in every *Cryptobranchus* and merely needs "stimulus" for its expression.

To repeat the thesis explored above, it may be postulated in this case that

speciation and differentiation have been the result of change in the "reactivity" of tissues and its morphogenetic effect. The raising and the lowering of the threshold level of tissue sensitivity to thyroid hormone has resulted in arrested ontogenetic development and in complete metamorphosis. The adult of the theoretical ancestor may be pictured as a hynobiid salamander, probably of a swift-water habitus.

It is difficult to determine which of the species of *Cryptobranchus* represents the basal stock in North America. The point of contact between the two probably occurred in the Black River watershed. Previous to glaciation in North America, cryptobranchids evidently enjoyed a wide distribution. A fossil genus, *Plicognathus*, is known from the Lower Pliocene of Nebraska. With the advent of glaciation, the representatives of this family of salamanders withdrew to a specialized area in the unglaciated portion of the country, which presented optimum conditions for their existence. Two areas were available at this time: the Ozarkian and the Appalachian Uplifts.

The distributional pattern of *Cryptobranchus* in the Ozarks shows that speciation within the North American group was accomplished forcibly by a head-water stream capture localized to the Black River system. This conception of limiting the differentiation of *Cryptobranchus* to this area is strengthened by an examination of the distribution of the striped shiner, *Notropis anatus*. Hubbs and Moore (1940) indicate that the range of the subspecies *N. anatus* includes adjacent tributaries of both the Missouri River drainage and the Black River, whereas the White River and tributaries and adjacent Missouri River streams show a marked faunistic break between them, with *N. pilsbryi* occupying the former and *N. anatus* the latter streams. The occurrence of *Cryptobranchus bishopi* in Spring Creek of the White River drainage apparently represents an emigration from the original localized population of the Black River drainage. The occurrence of *alleganiensis* in Spring River of the Neosho River system illustrates, in all probability, a more recent stream and faunal capture from the Missouri River basin. It is interesting to note that *bishopi* and this population of *alleganiensis* have remained localized, and are restricted by the upper steep gradient areas of their respective streams. These animals have not been able to move down to the lower valleys. The Missouri River, on the other hand, has a lower gradient by comparison, and *alleganiensis* has become dispersed from this area to the Mississippi River and its valley. Except for a small isolated population in Iowa,* dispersal has been eastward.

The invasion of the Appalachian Uplands by the Cryptobranchidae seems to be of recent origin, the Ohio River forming the pathway to the east. In this highland area there are many instances of the spread of this species by means of stream capture. Coastal streams of Georgia and North Carolina are occu-

* Bishop (1943) mentions Iowa but no specimens are available. Mr. Lowell S. Miller of Parsons College, Fairfield, Iowa, relates that his Zoology students have obtained this species in Skunk River, in south-eastern Iowa.

plied only in their upper headwater regions. The Tennessee River evidently received its population through stream capture involving its upper tributaries (French Broad Creek, *etc.*). The lowest station on the Tennessee River where this species has been found is at Florence, Alabama (Univ. Mich. Mus. No. 66760). The Susquehanna River system, in turn, also received a *Cryptobranchus* population by stream capture in its western headwaters involving the Allegheny River system to the west (Netting, 1932: 174). Not all of the river systems in the Appalachians are occupied, however, which leads one to believe that this area did not form the original site for the dispersal of the genus. *C. alleganiensis*, for instance, is recorded from the upper Youghiogheny River of the Ohio River system but not from the adjacent eastward flowing north branch of the Potomac River.

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