THE HELLBENDERS

By

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and

Charles Edwin Mays

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THE HELLBENDERS: NORTH AMERICAN "GIANT SALAMANDERS"

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INTRODUCTION

The primary purposes of this publication are twofold: first, to bring together the scattered information concerning hellbenders; secondly, to present original information which we have obtained during the last few years primarily studying animals from the Ozark region of Missouri.

Originally, we had planned to survey all specimens within major museum collections. However, a move by the senior author and a time limit placed on publication funding has precluded this accomplishment. This has also greatly reduced collaboration during the writing of the manuscript. The junior author wrote most of the sections on reproduction, development, and blood cells, while the senior author assumed responsibility for the remainder of the text.

The recent influx of information concerning salamanders has prompted this work. It is hoped that this volume will aid those researchers interested in the biology of *Cryptobranchus* and in comparative studies of salamanders in general.

Even as we go to press there are many other researchers involved in studies utilizing *Cryptobranchus*. These include: Dr. Stevan Arnold, University of California, Santa Barbara (behavior); Dr. Bill Brodie, Wesleyan College, Macon, Georgia (ecology); Dr. Thomas Dietz, Louisiana State University, Baton Rouge (renal physiology); Dr. Victor Hutchison, University of Oklahoma, Norman (ecological physiology); Dr. Charles Melton, University of Pittsburgh (blood chemistry); Dr. F. Taketa, Medical College of Wisconsin, Milwaukee and the senior author (hemoglobin biochemistry); Dr. Wilmer Tanner, Brigham Young University, Provo, Utah (myology); Dr. Daniel Toews, Acadia University, Wolfville, Nova Scotia (circulation); Dr. Robert Wilkinson, Southwest Missouri State University, Springfield (ecology); John Colowit, Clarion State College, Pennsylvania (ecology); and Donald Merkle, Miami University of Ohio (systematics and genetics).

ACKNOWLEDGMENTS

We thank Dr. Harvey Barton, Ronald Austin, Rebecca Cooper, Bruce Dietsche, Bill Hamilton, Michael Selby, Charles Selman and Richard and Diane Spieler for their assistance in field work.

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Dr. F. Taketa, Dr. Charles Melton, Dr. Robert Wilkinson, Rebecca Cooper, Ronald Houp, David P. Jerrett, Gary Jesmok, Guy Johnson, Robert Manis, James Pyland, John Stone and J. W. Edward Wortham, Jr. kindly supplied us with data from their studies.

Dr. George Harp, Joan Jass, Guy Johnson and Edward Petuch aided in invertebrate identification. Dr. Leon Richards and David Kopitzke made many plant identifications. Gary McGrew assisted in calcium and magnesium serum determinations. Illustrations were provided by Robert Frankowiak, Mary T. Carton, Kenneth Kratz, Leo Johnson, Janice Mahlberg and the authors. Adrian Czajka, Robert Henderson, Kenneth Kureck, Gerald Ludwig, Michael McCoid, Gregory Roth and Donald Tills assisted in the field and made valuable comments concerning our studies and this manuscript. We thank Drs. Margaret Kaser and Albert E. Reynolds for criticism of this manuscript. Susan Pleskatcheck patiently typed and corrected many drafts of this manuscript. Librarians James Klessig, Joan Nelson, John Lundstrom and the Herpetological Information Search Systems staff greatly aided our procurement of reference material. Karl W. Schmidt assisted in too many ways to enumerate.

We thank Carolyn and Cheryl Anne Nickerson; Judy, Kristine and Steven Mays for their understanding during our studies.

Funding for our hellbender studies was supplied through Arkansas State University Faculty Research Grants (511-619 and 511-619 supplement), Max Allen's Zoological Gardens (RE 1971), Frederick L. Ott Research Fund, Friends of the Museum [to Nickerson] and DePauw University and Indiana Academy of Science [to Mays]. Publication funding was provided by the Milwaukee Public Museum.

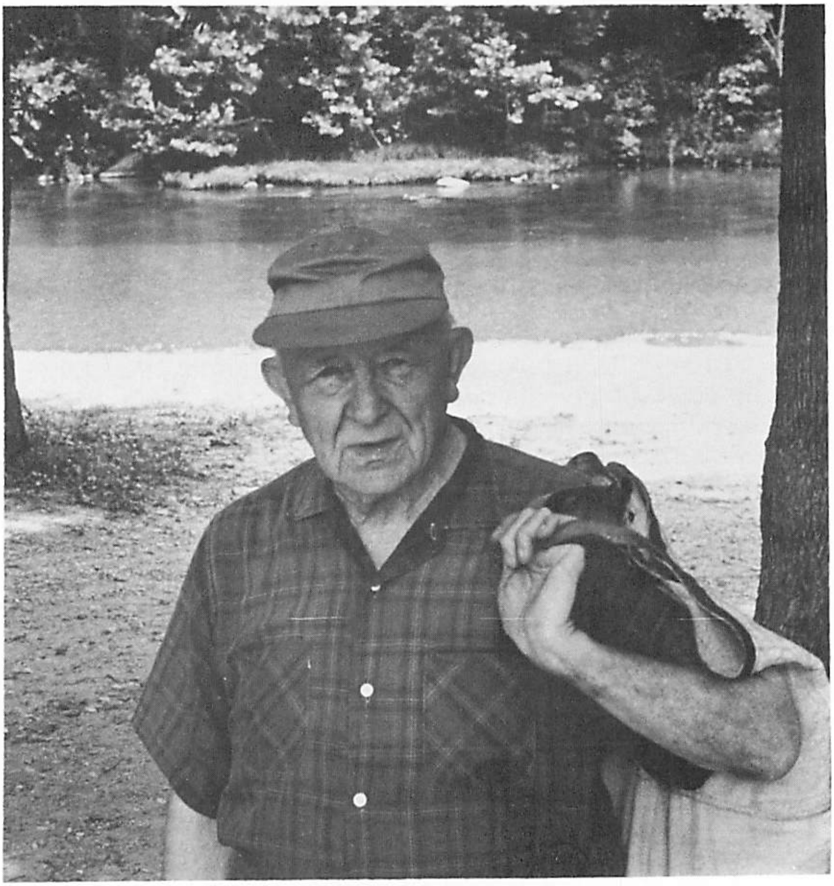

Figure 1. We dedicate this publication to Karl W. Schmidt, a gentlemen whose fine mind, land and equipment were so generously offered and utilized during our studies. His friendship will always be treasured.

THE HELLBENDERS:

NORTH AMERICAN "GIANT SALAMANDERS"

I. CLASSIFICATION AND DISTRIBUTION

Family Cryptobranchidae

The family contains two extant genera of salamanders; i.e., *Andrias* which occurs in the Orient, and *Cryptobranchus* in the central and eastern U.S.

Genus *Cryptobranchus* Leuckart

Diagnosis — Large, partially paedomorphic salamanders with reported lengths to 740 mm having, with rare exceptions, a single pair of gill openings as adults. Larvae are gilled and reach 13 cm total length. Lungs are present, but adult respiration is primarily cutaneous. Adults have four epibranchials. The body is greatly flattened dorso-ventrally, and the tail is oar-like. Eyes are proportionately diminutive and eyelids are absent. Lateral-lines are well developed, and highly vascularized lateral folds are present. The skull is semilarval; postparietals, supratemporals, lacrimal and septomaxillary bones are absent. Vertebrae are amphicoelous.

Reproduction occurs during late summer or fall, and fertilization is external.

Cryptobranchus Leuckart, 1821:260.
Salamandra Daudin, 1803.
Necturus Rafinesque, 1820:4.
Urotropis Rafinesque, 1822:3.
Protonopsis LeConte, 1824:57.
Abranchus Harlan, 1825:233.
Menopoma Harlan, 1825:270.
Salamandrops Wagler, 1830:209.

The genus *Cryptobranchus* is monotypic, *C. alleganiensis*, and only two subspecies are described. The hellbender was first described as "la salamandre des monts Alleganis" by Sonnini (Sonnini and Latreille, 1801) and later by Bosc (1803) using the same common name (Harper, 1940).

Cryptobranchus alleganiensis (Daudin)

Salamandra alleganiensis Daudin, 1803:231. Type-locality, as noted by Daudin, is the Allegheny Mountains in Virginia. However, Harper (1940) restricts the type locality to the North Toe River, Mitchell County, North Carolina in the vicinity of Davenport's Plantation (ca. four miles ENE of Spruce Pine). There is no known holotype. See Harper (1940) and Dundee (1971).

Salamandra horrida Barton, 1808:7-8.
Salamandra gigantea Barton, 1808:8.
Salamandra maxima Barton, 1808:8.
Molge gigantea Merrem, 1820: 187.
Cryptobranchus salamandroides Leuckart, 1821:260.
Urotropis mucronata Rafinesque, 1822:3.
Abranchus alleghaniensis van der Hoeven, 1837:384.
Protonopsis horrida Barnes, 1826:278.
Salamandrops gigantea Wagler, 1830.
Eurycea mucronata Rafinesque, 1832:121.
Cryptobranchus fuscus Cope, 1889:43.
Cryptobranchus alleghaniensis Cope, 1889:43.
Cryptobranchus terrasodactylus Wellborn, 1936:63.
Cryptobranchus bishopi Grobman, 1943:6.

Hellbender *Cryptobranchus a. alleganiensis* (Daudin).

Diagnosis — A race of *Cryptobranchus alleganiensis* occupying the entire species range except those streams draining the southern slopes of the Salem Plateau; i.e., the North Fork of the White River and the Black River system. The dorsum is characteristically spotted. The lower labium is usually uniformly colored. Spiracular openings are comparatively large with a diameter about half of the internarial distance. They may reach 74 cm total length. The lateral-line canals of the pectoral region have papillate elevations.

Salamandra alleganiensis Daudin, 1803, 8:231.
Cryptobranchus salamandroides Leuckart, 1821:260.
Cryptobranchus alleganiensis Stejneger and Barbour, 1917:3.
Cryptobranchus alleganiensis alleganiensis Schmidt, 1953:11.

Ozark Hellbender *Cryptobranchus a. bishopi* Grobman

Diagnosis — A race of *Cryptobranchus alleganiensis* occupying sections of the Black River drainage and the North Fork of the White River drainage in Missouri and Arkansas. *C. a. bishopi* differs from *C. a. alleganiensis* in: (1) typically having dorsal blotching versus spotting; (2) increased chin mottling; (3) having a smooth surfaced lateral-line system in the pectoral region on non-larval forms; and (4) with reduced spiracular openings; i.e., the diameter averaging 26 per cent of the internarial distance. They may reach 62.0 cm, total length.

Cryptobranchus bishopi Grobman, 1943:6. Type-locality is the Current River at Big Spring Park, Carter County, Missouri. The holotype was collected 25 August 1930 by E. P. Creaser and is maintained within the University of Michigan Museum of Zoology 68930.

Cryptobranchus alleganiensis bishopi Schmidt, 1953:12.

Range

The hellbender *Cryptobranchus alleganiensis alleganiensis* ranges from southern and western New York southward to northern Georgia, Alabama, Mississippi and westward to central Missouri and possibly southeastern Kansas (Fig. 2).

The Ozark hellbender *Cryptobranchus alleganiensis bishopi* is restricted to a small portion of southeastern Missouri and northeastern Arkansas (Fig. 2). This includes portions of the Black River, North Fork of the White River and possibly St. Francis River drainages.

The Fossil Record

Estes (1964; 1965) studied skeletal material from *Scapherpeton* and *Lisserpton* and determined that they were "essentially cryptobranchids in many aspects of their skull structure". However, he placed *Scapherpeton* within a separate family, Scapherpetonidae (Suborder Cryptobranchoidea). Meszoely (1966) studied North American (Colorado and Nebraska) cryptobranchid fossils. He noted that *Andrias* has a closed spiracle, a hyoid arch, and two visceral arches of which only the second is ossified in adults; whereas *Cryptobranchus* has a spiracle, a hyoid arch, and four visceral arches with ossification occurring in the hyoid arch and the second and third visceral arches. The latter statement is in agreement with the findings of Reese (1906a) and Furbringer (1922). However, Westphal (1958) maintains that ossification may occur in all of the visceral arches.

The North American cryptobranchid material examined by Meszoely (1966) was fragmentary (maxillae, dentaries and vertebrae), while comparative European fossils and recent cryptobranchid skeletons were mostly complete. His conclusions were: (1) that North American cryptobranchid fossils from middle Miocene to Mio-Pliocene; i.e., *Plicagnathus matthewi* and *Cryptobranchus mccalli*, varied little in their maxillae and dentaries and should all be referred to *Andrias matthewi*; (2) a caudal vertebra of Pleistocene age from Frankstown Cave, Pennsylvania (CM 11149), which has been referred to as *Cryptobranchus* (Peterson, 1925) and a plethodontid (Richmond, 1964) is an ambystomatid.

Figure 2. The range of the hellbender, *Cryptobranchus alleganiensis alleganiensis* and the Ozark hellbender, *C. a. bishopi* (from Conant, 1971).

There are several recent records from archeological sites in western Pennsylvania (Guilday, 1961; Lang, 1968; and Buker, 1970).

II. A POPULATION OF OZARK HELLBENDERS

In the summer of 1969 we initiated studies of a population of *C. a. bishopi* within a stretch of the North Fork of the White River in Ozark County, Missouri. Before considering the results of these studies we will first attempt a description of the region in general and our research site in particular (Fig. 3).

Geologic History and Topography of the Area

The Ozark Plateau province of the Interior Highlands may be divided into three sections; i.e., Springfield Plateau, St. Francis Mountains, and the Salem Plateau (Thornbury, 1965). Our research area was on the southern slopes of the latter.

The Salem Plateau section was uplifted at least twice, at the end of both the Cretaceous and Tertiary. Following the former the Ozark region was worn down to a low and comparatively level plain and characterized by swamps and sluggish streams. The subsequent late Tertiary uplift was probably slow and lengthy (Steyermark, 1962). This presumably rejuvenated the streams and the cutting of new valleys.

Currently, local relief on the interfluve upland tracts of the Salem Plateau is rarely 100 ft., but adjacent to major streams; e.g., the White River may reach 500 ft. This deep and intricate dissection is a prime distinguishing feature of the Salem Plateau and is most characteristic of the southern side (Thornbury, 1965).

Bedrock throughout most of Missouri is Paleozoic in age, and Ordovician is the most prominent in the Ozark Highlands (Howe and Koenig, 1961). The widespread distribution of dolomites and limestones within rocks of the Salem Plateau coupled with the deep dissection is responsible for a marked development of large springs (Thornbury, 1965). Beckman and Hinchey (1944) noted seven springs with daily yields in excess of six million gallons, which flow into the North Fork of the White River drainage. Many of these springs are intimately associated with surface runoff.

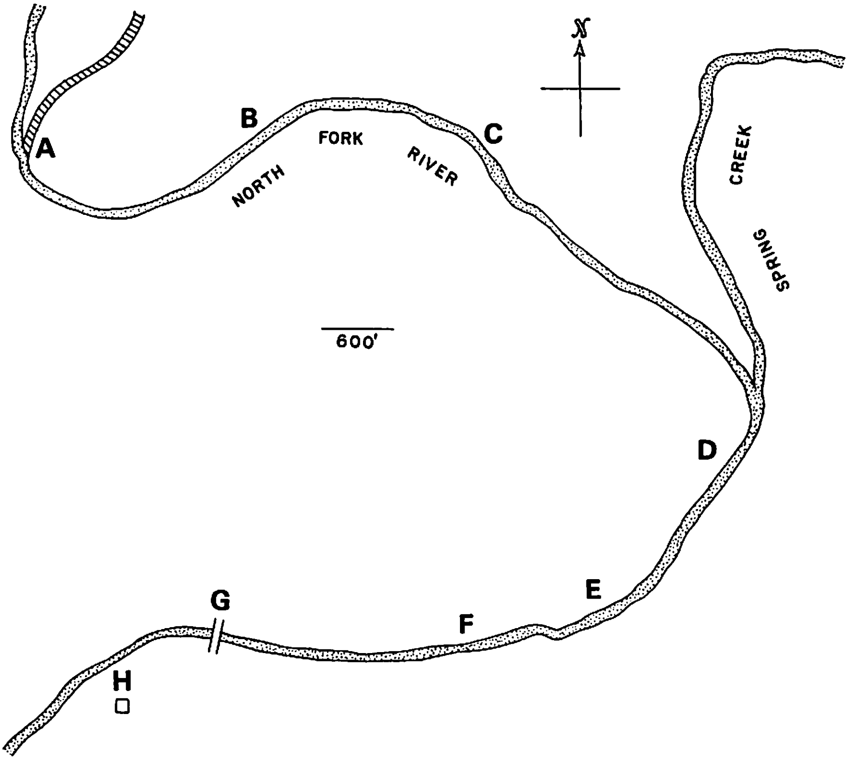

Figure 3. Landmarks and riffles along the North Fork of White River, Ozark County, Missouri research area. A. Blair's Ford. B. Riffle between stations 2 and 3. C. Riffle between stations 9 and 10. D. Riffle between stations 16 and 17. E. Riffle between stations 34 and 35. F. Riffle between stations 38 and 39. G. Patrick's Bridge. H. Campsite at Althea Spring near Karl Schmidt's residence.

This area has been above sea level since late Paleozoic times, and the nearest approach of Quaternary glaciation was almost 150 miles to the north. Thus, loess deposits are not characteristic (Howe and Koenig, 1961; Steyermark, 1962). The nearest major magnetic anomaly is some 30 miles distant (Hayes, 1967).

Meanders, especially incised meanders, are common features of Ozark streams, but rather poorly developed on the North Fork of the White River by comparison. From its headwaters the North Fork of the White River drains southward from the Salem Plateau cutting, often steeply, through dolomite, limestone and sandstone enroute to joining the White River in Arkansas.

The North Fork of the White River basin drains an area of 561 square miles or 1,157 square miles including Bryant Creek (Bolon, 1952; U.S. Geological Survey, 1969-1971). The average daily discharge (1944-1969) at the waterstage recorder about 2.0 miles downstream from our research section was 703 cubic feet per second. The recorded extremes are 30,600 cubic feet per second on 30 January 1969 and 187 cubic feet per second 14-18 September 1954 (U.S. Geological Survey, 1969-1971).

The study site is located between the headwaters, whose watershed is protected by Mark Twain National Forest, and that portion of the stream directly affected by damming; i.e., Norfork Lake.

The study section varies from white water riffles to lengthy sluggish pools which may be 2.5 meters deep (non-flood stage). Although flooding may add appreciably to this depth (six meters in 1969), runoff is rapid (Karl W. Schmidt, 1969). This may be noted by comparing days on either side of the record flooding of 1969 (Table 1). Additionally, stream clarity is remarkable and difficult to disrupt. In 1969 we were able to work the next day following a two inch rain.

The bottom is variable with sections featuring gravel beds, including chert or piles of dolomite, limestone and some sandstone rocks or even smooth waterswept beds of dolomite or limestone. Siltation is currently minimal and usually restricted to pools and stream margins. However, clearing via bulldozing has increased greatly along this watershed during our studies, and it could soon be greatly affected.

Water and benthic samples were taken (biweekly average) at one or more collecting sites (Cooper and Nickerson, 1971). Water quality data are presented in Table 2. The results of the benthic studies are incomplete.

Climate

Missouri has a continental type climate, and while extremes of heat and cold, drought and moisture have been recorded, they are not as pronounced as in more northern states. The winters are reasonably brisk, seldom severe, with occasional brief spells of cold. The average number of days during the year with minimal temperatures below 32° F is 65 days in the southeast. There is an average of three cold waves a season, and the mean duration of each is less than three days. Some of the southern counties receive as few as five inches of snowfall annually. Long rainy spells are unusual. Summer rains are frequently in the form of thunderstorms, occasionally severe with hail and strong winds (Moxom, 1941). The nearby weather recording station at Olden, Howell County has noted extremes of -29° and 106° F. The average date of killing frost in the spring is 17 April and the fall equivalent is 17 October. The mean temperature in January is 35.6° F and in July 76.3° F. Annual precipitation averages 43.92 inches with a peak of precipitation occurring in the spring (Moxom, 1941).

Vegetation

The prominent vegetation types of the watershed of the North Fork of the White River are oak-hickory and oak-pine. In 1840-1860 there were two extensive pine forests on this watershed, which covered 220 square miles. These were subsequently reduced yielding 80 to 90 foot logs, some 4 ft in diameter (Sauer, 1920). The short-leaf pine, *Pinus echinata*, is still prevalent there. The only other native conifers are the red cedar, *Juniperus virginiana* and Ashe's juniper, *J. Ashei*, which seem to have a proclivity for limestone bluffs and open glades.

Oaks are the most prominent and diverse of the dedicuous trees and *Quercus alba*, *Q. falcata*, *Q. macrocarpa*, *Q. marilandica*, *Q. palustris*, *Q. prinoides*, *Q. rubra*, *Q. Shumardii*, *Q. stellata* and *Q. velutina* are all present. Others include *Carya cordiformis*, *C. ovata*, *C. tomentosa*, hickories; *C. illinoensis*, pecan; *Acer negùndo*, *A. rubrum*, *A. saccharinum*, *A. saccharum*, maples; *Ulmus alata*, *U. americana*, *U. rubra*, elms; *Salix caroliniana*, *S. humilis*, *S. interior*, *S. nigra*, *S. rigida*, willows; *Populus deltoides*, cottonwood; *Juglans nigra*, black walnut; *Juglans cinerea*, butternut; *Aesculus glabra*, Ohio buckeye; *Sapindus Drummondii*, soapberry and *Magnolia acuminata*, cucumber tree make up most of the remaining tree flora.

The Ozark region is known to have Missouri's most diversified flora. This is most evident in the numbers of aquatic and marginal plants of the North Fork of the White River, its springs and tributaries. These species include: *Isoetes Butleri*, quillwort; *Sparganium americanum*, bur-reed; *Potamogeton amplifolius, P. diversifolius, P. foliosus* and *P. illinoensis*, pondweeds; *Zannichellia palustris*, horned pondweed; *Alisma Plantago-aquatica*, water plantain; *Sagittaria latifolia* and *S. rigida*, arrowheads; *Anacharis Nuttallii*, waterweed; *Agrostis perennans; Bromus purgans; Cinna arundinacea; Diarrhena americana; Digitaria Ischaemum, D. sanguinalis; Echinochloa muricata; Elymus glaucus, E. riparius, E. virginicus; Eragrostis Frankii, E. hirsuta, E. hypnoides, E. pilosa, E. trichodes; Festuca obtusa; Glyceria striata; Leersia oryzoides, L. virginica; Muhlenbergia brachyphylla, M. frondosa, M. Schreberi, M. sylvatica, M. tenuiflora; Panicum agrostoides, P. anceps, P. capillare, P. dichotomiflorum, P. languinosum, P. latifolium, P. laxiflorum, P. virgatum; Poa sylvestris, P. Wolfii; Paspalum laeve, P. pubiflorum; Triplasis purpurea;* and *Uniola latifolia*, grasses; *Carex amphibola, C. Emoryi, C. granularis, C. lurida* and *C. vulpinoidea; Cyperus acuminatus,* C. *ovularis, C. refractus, C. strigosus* and *C. tenuifolius; Eleocharis acicularis; Fuirena simplex; Rhynchospora capillacea; Scirpus americanus, S. atrovirens, S. lineatus,* and *S. validus*, sedges; *Spirodela polyrhiza*, big duckweed; *Wolffia papulifera*, watermeal; *Heteranthera dubia*, water star grass; *Juncus acuminatus, J. brachycarpus, J. diffusissimus, J. Dudleyi* and *J. Torreyi*, rushes; *Saururus cernuus*, lizard's tail; *Polygonum aviculare, P. erectum, P. Hydropiper, P. hydropiperoides, P. pensylvanicum, P. Persicaria* and *P. punctatum*, smartweeds and knotweeds; *Ceratophyllum demersum*, coontail; *Nuphar luteum*, yellow pond lily; *Nelumbo lutea*, American lotus; *Ranunculus abortivus, R. longirostris* and *R. recurvatus*, buttercups (crowfoot); *Cardamine bulbosa* and *C. pensylvanica*, bitter cress; *Nasturtium officinale*, water cress; *Callitriche heterophylla*, water starwort; *Ludwigia palustris*, water purslane; *Myriophyllum heterophyllum* and *M. pinnatum*, water milfoil; *Hydrocotyle verticillata*, water pennywort; *Amsonia ciliata* and *A. illustris*, blue stars; *Veronica comosa*, water speedwell; *Utricularia gibba*, bladderwort; and *Justicia americana*, water willow (Steyermark, 1940; 1941; 1963; and our collections). Algae and mosses are incompletely surveyed and not included herein.

A large number of the plant species of the North Fork of the White River valley have affinities for calcareous soils and bluff or bluff-side microhabitats. Many others are dependent on springs and the spring-fed stream habitat.

The damming of the North Fork of the White River with the resulting formation of Norfork Lake has greatly affected the bluff and alluvial habitat. This has destroyed (inundated) many species downstream; e.g., cucumber trees *Magnolia acuminata* and cane *Arundinaria gigantea* (Steyermark, 1962).

Our Tag-Recapture Studies

During the summer of 1969 a 4.6 km section of the North Fork of the White River was marked off in 92 meter segments (50 stations). Utilizing skin diving gear (Fig. 4) Ozark hellbenders were collected from 9:00 A.M. to 5:00 P.M., tail or leg-tagged with Turtox mammalian ear tags, weighed, measured and released at the capture site along 2.67 km of stream bed. Population estimates were made by the Peterson Index Method (Overton and Davis, 1969). The population estimate was 428 "taggable sized" hellbenders/km of stream-bed with 95 per cent confidence limits of 341-573 hellbenders/km of stream-bed. The mean weight of 435 hellbenders was 365 grams. Biomass estimates were 156 kg/km with 95 per cent confidence limits of 124.5-210 kg/km of stream-bed (Nickerson and Mays, 1973).

Figure 4. The skin diving gear, used during the study, protects the diver from cold and abrasion.

In 1970 a population estimate for a riffle known to have a high population was undertaken. The salamanders were tail--tagged with Floy T-tags (Fig. 5). The riffle measured 92 x 50 meters (4,600 m^2) and varied in depth from a few centimeters to slightly more than one meter. The bottom was chert with scattered large rocks. The current varied from slight to 7.0 km/hr (none flood stage). Approximately 50-60 per cent of this riffle was suitable "diurnal habitat for taggable sized hellbenders" or one hellbender/8-10 m^2 with 95 per cent confidence limits of one hellbender/6-7 to one per 13-16 m^2. The riffle biomass estimate was 98.2 kg with 95 per cent confidence limits of 61.3-144.5 kg.

The Bottom Substrate and Population Structure

Numerous authors have noted the importance of rocks and logs as hellbender reproductive sites (Alexander, 1927; Bishop, 1941). Our studies indicate that the characteristics of the stream bottom greatly affect the Ozark hellbender's population structure. During 1969 and 1970 adult sized Ozark hellbenders could be found in any part of the 26 km surveyed section of the North Fork of the White River.

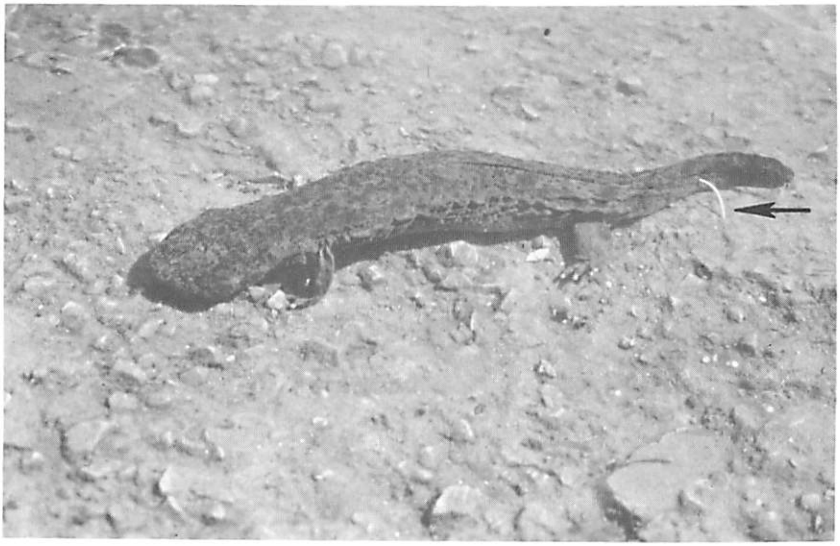

Figure 5. The use of Floy T-tags proved successful.

Density in most sections appeared to relate directly to the number of suitable large rocks for shelter. Piles of dolomite, limestone and sandstone "rocks" inevitably produced numerous Ozark hellbenders while smooth water-swept beds of dolomite, etc., were unproductive except where fragmentation had occurred. Greatest diversity in population structure occurred in rock piles on chert-gravel beds. This is shown by comparing the population structure of the riffle between stations 2-3 with that between stations 26-28, or that of the entire 2.67 km tagging section (Figs. 6-9). Larvae and other small Ozark hellbenders typically utilize small stones and chert. They were seldom taken in areas without this type of habitat diversity.

This microhabitat is teeming with small invertebrate food items and should provide maximum protection from predation. Interstices of gravel are known to be important for other salamanders (Dundee, 1973). One larval *C. a. bishopi* was reportedly collected by children 4 July 1969 from interstices of gravel in an area of subsurface percolation along the Eleven Point River, Oregon County, Missouri. A similar habitat has been reported for some riffle fishes (Stegman and Minckley, 1959).

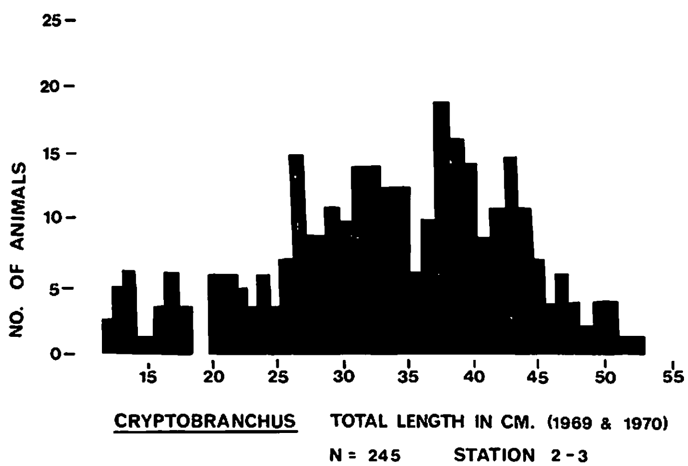

Figure 6. Ozark hellbender population structure in riffle between stations 2 and 3.

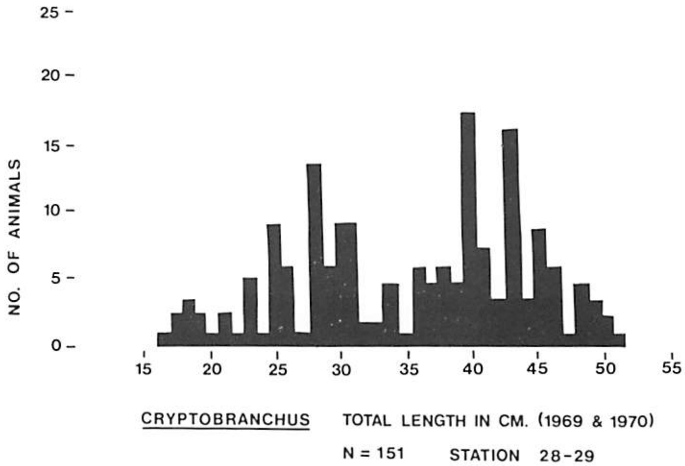

Figure 7. Ozark hellbender population structure in pool between stations 26-28.

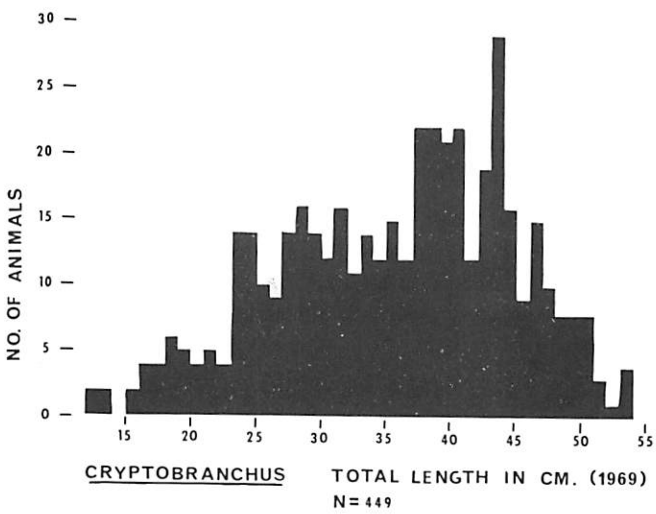

Figure 8. Ozark hellbender population structure for the 2.67 km tagging section. Numbers of individuals plotted by length.

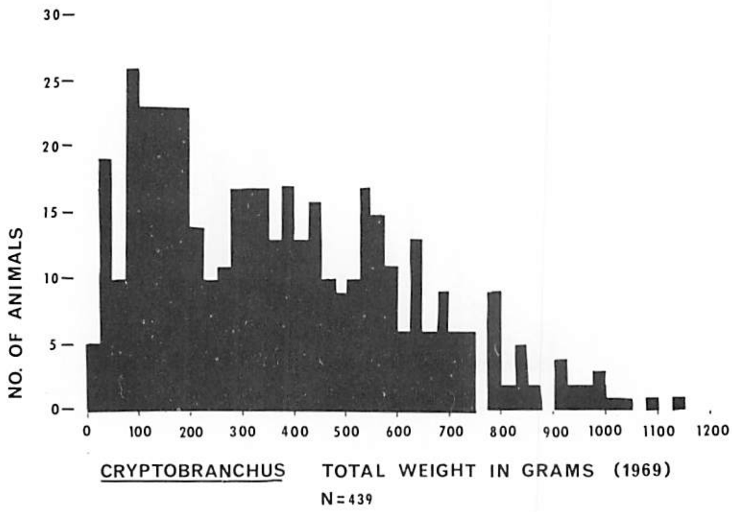

Figure 9. Ozark hellbender population structure for the 2.67 km tagging section. Numbers of individuals plotted by weight.

III. BEHAVIOR, PHYSIOLOGY AND MORE HELLBENDER ECOLOGY

Migration and Individual Movement

According to Alexander (1927) some hellbenders move many miles to reach their breeding grounds in the fall. The "greater males" supposedly begin their trek in mid-August. Green (1933) stated that in the summer they move to deep holes "to find the cooler water", while Oliver (1957) merely indicated movement from one area of a stream or lake to another. However, Bogert (1961) commented that nobody knew whether hellbenders migrated up and down streams seasonally or otherwise.

Hillis and Bellis (1971) conducted a toe-clip and recapture study and determined a mean activity radius (MAR) of 10.5 meters for a Pennsylvania population. They presented good evidence for homing upstream and downstream and noted an average home range size of 346.4 square meters. Seventy-three of 81 displaced hellbenders were recaptured with 40 being found less than one MAR from the initial capture site, and six were under the rock of initial capture. The maximum inter-capture distance was 160 meters. There was no difference in movement between hellbenders of size or sex.

In our study of the Ozark hellbender only three of 74 recaptures were found further than 90 meters from the tagging site. Eighty per cent of the recaptures were less than 30 meters from the tagging site and 37 per cent were found at the tagging station. A few were recaptured under the initial capture rock. As our studies were carried out largely in June and July, sexes were not usually distinguishable. The greatest unidirectional movement was 990 meters. Homing from some distance was indicated by one Ozark hellbender, which made a round trip of at least 1,050 meters (Table 3).

A Food Study of Ozark Hellbenders

Forty *C. a. bishopi* were taken near Althea Springs and Blair's Ford for analysis of stomach and intestinal contents (Nickerson and Selby, 1969). Ten specimens were collected each day on 18, 25 July, 1, and 8 August 1969. As these salamanders are typically nocturnal during this time period, all specimens were collected prior to 11:00 A.M., usually within an hour's time. Specimens were preserved immediately after capture by injection with a 10 per cent formalin solution. The data from this study appear in Table 4.

Crayfish were the most frequently encountered ingested material and easily represented the greatest volume of food. *Orconectes neglectus* and *O. propinquis* are present in the North Fork of the White River and both were identifiably evident within stomach contents or regurgitant. The number of crayfish in most specimens was one or two with a maximum of four encountered in two specimens. Snails were usually found in low numbers. However, one female *C. a. bishopi* (total length 39 cm) had 38 snails present within its intestines. In most instances this might essentially prove selective feeding upon these gastropods, but this section of the North Fork of the White River is endowed with amazingly dense snail populations. The high frequency of occurrence and the numbers of small rocks present in these samples would suggest a great amount of incidental ingestion, as would sand deposits and probably leaves. Ozark hellbenders often regurgitated during transport, prolonged storage in crowded containers, and continual handling (Fig. 10). Crayfish were consistently present in the regurgitant, but the only new food items noted were fish, *Cottus bairdi* and *Percina caproides*.

Figure 10. Ozark hellbender in the process of regurgitating crayfish.

Previous Studies

The food habits of *C. a. alleganiensis* are well established and parallel those of *C. a. bishopi*. Crayfish are the most frequently cited food item and Netting (1929) recorded 41 *Cambarus* sp. removed from the stomach of three Carnegie Museum specimens. Green (1935) sampled the stomach contents of 34 hellbenders collected between 8:00 P.M. and midnight on 21 June (Table 4). He noted crayfish chelae had penetrated the stomach wall of two specimens. Of 72 Pennsylvania specimens examined, only eight had empty stomachs, and again crayfish were the principle dietary item. Older references mention "shellfish" and "crabs" as food items (Harlan, 1825; Holbrook, 1842). Other invertebrates in their diet are aquatic insect larvae, insects, worms including earthworms, and mollusks (Reese, 1903; Morse, 1904; Surface, 1913; Alexander, 1927; Bishop, 1941). Fishes are the most common vertebrates in their diet, especially suckers and minnows including *Notropis* sp., *Notemigonus* sp. and *Campostoma anomalum* (Alexander, 1927; Netting, 1929; Ferguson, 1961). They have fed on lamprey, fish eggs, hellbender eggs, other hellbenders, tadpoles, a toad, aquatic reptiles and a small mammal (Reese, 1903; Smith, 1907; Surface, 1913; Alexander, 1927; King, 1939; Bishop, 1941; Beck, 1965; Houp, 1970; Wilkinson, 1972 and Brode, 1972).

Grote (1877) found a captive hellbender apparently in the act of swallowing its shed skin. Beck (1965) observed a 2 ft hellbender grab a "spotted water snake" mid-body and roll over and over, in alligator fashion, until they disappeared under a rock in deeper water.

In addition to their role as carnivores, hellbenders also scavenge, as evidenced by the consumption of numerous bait items offered by fishermen and animal parts taken in captivity (Reese, 1903; Bishop, 1941; Beck, 1965). Many postulate hellbenders will eat almost anything (Barnes, 1836; Hay, 1891; Cochran, 1961; Barbour, 1971).

Locating and Capturing Food

Presumably hellbenders utilize visual, chemical and tactile stimuli to locate and capture their food. Morse (1904) mentions accelerated movements during their search for food. Many authors attest to their response to carrion and dead baits (Townsend, 1882; Surface, 1913; Beck, 1965). The importance of visualization is indicated by their being caught on artificial lures (Green, 1933; Beck, 1965). Green (1933) observed that the hellbender "seizes its food with a sidewise jerk of its head snapping at it as it passes". Furthermore, "if the morsel does not yield, it will jerk and pull as if tearing off a bite". Brode (1972) has observed *Cryptobranchus* feeding upon live fish. The hellbender moved with one to four inches of a fish and then "snapped its mouth open and literally sucked the fish into his jaws".

One Ozark hellbender was discovered feeding upon a crayfish, when a rock was overturned. The crayfish was being swallowed tail first with the chelae protruding from the corners of the salamanders' mouth (Fig. 11).

Fasting and Fluctuations in Body Weight

Alexander (1927) and Beck (1965) have stated or implied that hellbenders fast during the winter. According to Surface (1913), when they are captured in early spring, when there is still ice, and late fall they are always ready to eat. Ozark hellbenders, from the North Fork of the White River, had food present within their digestive tracts year round. Hellbenders may fast for great lengths of time; e.g., five weeks (Townsend, 1882),

Figure 11. An Ozark hellbender eating a crayfish.

five or six months (Beck, 1965), or three months (Green, 1933). Two Ozark hellbenders collected 11 October 1969 were maintained at about 75^0 F and without food until their release 7 March 1970. Weight changes were from 181.5 to 95.5 g in a 30.5 cm salamander and 578.5 to 332 g for a 44.5 cm salamander. Both animals appeared vigorous when released.

Color Pattern

The dorsal ground color of *C. a. alleganiensis* may vary from grayish-black to brown, rufous, and olive-green (Hay, 1891; Rhoads, 1895; Surface, 1913; Alexander, 1927). Superimposed upon this ground color is a dorsal mottling or spotting which is characteristically black (Green, 1933; Conant, 1958). We have observed several with almost no spotting. The ventrum is sparingly marked and lighter in color.

The ground color of *C. a. bishopi* is similar to *C. a. alleganiensis*, but is characterized by dorsal blotching instead of spotting and more heavily pigmented lower lips (Grobman, 1943; Dundee and Dundee, 1965). Grobman (1943) viewed the greater extension of the dorsal pigmentation in *bishopi* as a juvenile character. The presence of reddish spots on the dorsum of *C. a. bishopi*, as described by Ratcliff (1965), is doubtful. We have examined hundreds of specimens from Spring River, Fulton County, Arkansas and found no evidence to support this description.

Dundee and Dundee (1965) noted that 75 per cent of the Arkansas and Missouri *C. a. bishopi* could be distinguished from *C. a. alleganiensis* on the basis of dorsal blotching instead of spotting. However, some populations are problematical. Johnson (1958) reported eastern Tennessee specimens which showed *bishopi* characteristics, including pigmentation. Barbour (1971) observed more abundant, larger and darker spots in western Kentucky specimens than those in eastern Kentucky. Mount (1971) has observed the *bishopi* pattern in Alabama *Cryptobranchus*. We have seen considerable variation in samples from various Missouri and Arkansas streams. However, our samples would support the findings of Dundee and Dundee (1965).

Color Change and Abnormal Coloration

Green (1933) believed that the hellbender's color varied with age and possibly food and water quality. We found that at least some Ozark hellbenders were capable of rather dramatic color change from an olive-brown ground color to a rather bright orange. Factors, which we have observed, apparently affecting the latter include temperature and light.

Of perhaps 2,000 *C. a. bishopi* from the North Fork of the White River, two animals were collected which maintained atypical ground colors. One was slate gray, the other bright orange. One of 83 *C. a. alleganiensis* taken from the Niangua River, Dallas County, Missouri, also maintained the orange ground color. On 29 October 1972 John Stone and Dr. Robert Wilkinson collected an adult albino *C. a. alleganiensis* in the Niangua River, with a total length 395 mm; weighing 323 g. This was the only abnormally colored specimen of about 1,200 examined. The notorious red *Cryptobranchus;* i.e., *C. fuscus*, which Holbrook (1842) believed to be a separate species, was perhaps similar to one of these Niangua River specimens. Grote (1877) believed it to be a color variant, while Reese (1903) thought females became red to attract males during mating season.

Adaptive Coloration

The dorsal pattern of the Ozark hellbender is well adapted for inconspicuousness on chert strewn stream bottoms. However, most striking is how difficult they are to detect among oak leaves in the fall. These leaves become splotched with black and accumulate in sections of Salem Plateau streams in which *C. a. bishopi* occur (Fig. 12). This is, of course, the time when these salamanders are reproductively active and when observed diurnal activity is at its peak. It is tempting to speculate that *Cryptobranchus* populations in streams with more visually homologous bottom substrate and reduced water clarity would exhibit less dorsal pigmentation.

Predators

There are a large number of potential predators of hellbenders, their eggs, and larvae. Since compiling such a list seems futile, we will restrict our comments primarily to known predators.

Fishes implicated in predation include northern pike, *Esox lucius;* muskellunge, *Esox masquinongy;* "shovelhead catfish" and large catfish (Beck, 1965; Barbour, 1971; Minton, 1972). During 1969 we checked the stomach contents of 20 fish (15 channel catfish, *Ictalurus punctatus*, 4 smallmouth bass, *Micropterus dolomieui* and 1 rock bass, *Ambloplites rupestris)* and found no evidence of their consumption of Ozark hellbenders. A food study of several hundred *Cottus bairdi* and *C. carolinae* has yet to yield *Cryptobranchus* eggs or larvae as a food item (Cooper and Nickerson, 1971).

Figure 12. The Ozark hellbender's pattern blends well with gravel and blotched leaves.

The fact that hellbenders are cannibalistic and often consume their eggs and each other is well known (see food section). We have observed cannibalism many times in our laboratories and have suggested that this may be an important factor in maintaining population stability (Mays and Nickerson, 1972). This belief is shared by other workers (Wilkinson, 1972).

Turtles and watersnakes, including *Natrix sipedon*, are known to feed on hellbenders (Rhoads, 1895; Surface, 1913). Man is, of course, a significant predator, and there is evidence to indicate commercial collecting has greatly diminished their populations in some areas (Swanson, 1948).

Defense

Hellbenders often remain motionless when uncovered. Their pattern and coloration is often so cryptic that they are overlooked by man and presumably other predators, even in clear water. They are capable of short spurts of "rapid swimming". However, they appear to tire easily and usually seek cover under a submerged object after transversing short distances. Their bite is not dangerous to man or other large vertebrates. Although hellbenders are usually reluctant to bite, large ones may tear the skin causing blood loss and some pain. Many people believe their bite is venomous, but it is innocuous. But, the skin secretions are noxious. We have observed dogs exhibit repulsive behavior after biting them. This reaction was immediate and lasted for several moments. Brodie (1971) has shown that their skin is not toxic to chickens when ingested but was repulsive to human taste.

Parasites

Fungi

Smith (1911) lost five hellbenders to "nitrogen disease" and had one infected by the water-mold *Saprolegnia.* This fungus infected the hind legs and tail of the salamander. The soft tissues of part of the tail and one leg were destroyed, leaving exposed bone, before they were sloughed off. Healing was well progressed after three months. Nickerson and Hutchison (1971) obtained no isolates of the facultative parasite *Basidiobolus ranarum* from *C. a. bishopi.*

Protozoans

Rankin (1937) found *Prowazekella longifilis* and *Tritrichomonas augusta* in the rectum (cloaca) of a North Carolina (implied) *Cryptobranchus*, and Malewitz (1956) found intestinal flagellates in *C. a. bishopi* feces, which were assumed to belong to the family Trichomonadidae and either the genus *Trichomonas* or *Tritrichomonas. Proteromonas* and *Trypanosoma* have also been isolated from hellbenders (Walton, 1942).

Nematodes

Mr. Robert Manis (1971) found a large number of nematodes in the lower portion of the small intestine and throughout the large intestines of several *C. a. bishopi* harvested from the North Fork of the White River 11 October 1969. Nematodes which infect *C. alleganiensis* include *Filaria cingula* (species sedis incertae), *Spiroxys allegheniensis, Spironoura cryptobranchi, S. mackini* and *Zanclophorus variabilis* (Krecker, 1916; Walton, 1930, 1935, 1936, 1941, 1942; Malewitz, 1956; Yamaguti, 1961).

Spironoura wardi and *Z. variabilis* are recorded from Ozark hellbenders (Spring River, Mammoth Springs, Arkansas) by Malewitz (1956). They were numerous within the intestines from 8 mm posterior to the stomach to 5 mm anterior to the anus (cloacal opening). Malewitz (1956) suggests a correlation of life cycles; i.e.,*C. a. bishopi* with *Spironoura. Zanclophorus variabilis* has also beeh found in *C. alleganiensis* (Walton, 1936; Dyer and Brandon, 1973). Johnson (1971) found roundworm cysts on the "outer wall" of a hellbender's small intestine. Many Indiana specimens were parasitized by dracunculoid worms which embed just under the skin (Minton, 1972).

Trematodes

Apparently *Telorchis (Cercorchis) cryptobranchi* is the only trematode reported from hellbenders (McMullen and Roudabush, 1936; Wharton, 1940; Walton, 1942).

Cestodes

The tapeworms *Crepidobothrium cryptobranchi* and *Ophiotaenia cryptobranchi* are parasites of *Cryptobranchus* (LaRue, 1914; Walton, 1942; Dyer and Brandon, 1973).

Acanthocephalans

Recently Dyer and Brandon (1973) discovered *Acanthocephalus aculatus* parasitizing Missouri hellbenders.

Annelids

Leeches (Hirudinea: Glossiphoniidae: apparently an undescribed species) were found on most Ozark hellbenders in the North Fork of the White River (Fig. 12). These are presumably the same or closely related to those mentioned by Dundee and Dundee (1965) from Spring River in Arkansas. Although the Spring River leech may be a new species, Dr. Marvin C. Meyer (1972) notes no further systematic work. Mr. Guy Johnson (Milwaukee Public Museum) is currently studying those from the North Fork of the White River.

On 24 September 1972 a survey of leech placement was initiated utilizing 56 *C. a. bishopi* collected within or near our North Fork of the White River study section. Leeches were found on most areas of the body surface, but were usually concentrated around the spiracles (Fig. 13), on the ventral surface of the head, in the axillae, and on and between the toes. Leeches were found singly on most areas of the body, but in areas of concentration, clusters of 6-8 individuals were typical. The number of leeches per host ranged from 0 to 48. There appeared to be little correlation between the number of leeches on the host and the size of the host. The leeches produced lesions on the skin of the host at the point of attachment, often causing large sores in areas of heavy leech concentration (Johnson, 1972).

Pough (1971) discovered a leech-repellent property of *Notophthalmus viridescens.* We note that *Placobdella parasitica,* a leech which often parasitises map turtles, *Graptemys geographica* and snapping turtles, *Chelydra serpentina* in Ozark hellbender streams, was not observed on any of perhaps 2,000 *Cryptobranchus* checked.

Excretion and Osmoregulation

Cryptobranchus has an opisthonephric kidney; i.e., an "adult kidney" which is assumed to incorporate both mesonephric and metanephric materials but be primarily of mesonephric origin. The anterior portion is partially modified in the male into an

Figure 13. Ozark hellbenders are often parasitized by leeches.

epididymis which connects with the testis. The nephric duct (mesonephros) of the male extends anteriorly and posteriorly from the epididymis and may be swollen and convuluted in the region of the epididymis. Posteriorly the nephric duct drains the enlarged and excretory portion of the opisthonephros. Ureters drain the posterior, excretory part of the kidney and enter the cloaca laterally to the rectum. The urinary bladder opens on the ventral surface of the cloaca (Branch, 1959; Jollie, 1962).

Virtually nothing is known about kidney function and water balance of most amphibians, expecially apodans and urodeles. In general even aquatic amphibians have competent excretory devices to assist them in avoiding hydration. They are not as physiologically adapted to arid environments. Furthermore, excessive gain or loss of osmolytes is not a problem for most amphibians. Few are adapted to brackish water, much less salt water (Deyrup, 1964). Harlan (1824) stated that he had killed a hellbender by placing it in slightly brackish river water at Baltimore. Recently Stone (1971) has shown that *C. a. alleganiensis* can regulate its body osmolality up to about 230 milliosmols. Then it becomes an osmoconformer up to about 260 milliosmols. He compared numerous physiological parameters for hellbenders in tap water (control) and the same animals in 266-273 milliosmol water (test). The blood urea nitrogen increased from a mean of 1.4mg/100 ml (control) to a mean of 33 mg/100 ml (test). The increase of serum sodium coupled with a decreased concentration of urine sodium indicated that the hellbender had some method of sodium retention. Furthermore, since the percentage of total nitrogen excreted as ammonia decreased as the water osmolality increased, a change from ammoniotelism to ureotelism is indicated (Stone, 1971).

Thorson (1964) estimated that 79 percent of the total body weight was fluid. Fifty seven percent of these fluids were intracellular and 22 percent extracellular. The interstitial fluids represented 18.5 percent while the plasma fluids accounted for only 3.5 percent of the total.

Respiration

Harlan (1825) briefly describes the lungs and part of the respiratory tract of hellbenders. He believed they never possessed gills and proposed the generic name *Abranchus* (without gills) for hellbenders. The young have gills, but these are lost early in the life of the hellbender (Bishop, 1941). The generic name *Cryptobranchus* (hidden gills) is misleading (Fig. 14). This has presumably led many authors, such as Surface (1913), Alexander (1927) and Bernstein (1953) to suggest these non-existent structures as functional respiratory organs.

The literature concerning lung size, development and utilization is quite contradictory. They have been described as simple sacs, poorly developed and small (Luckhardt and Carlson, 1921; Alexander, 1927; Hilton, 1952; Jollie, 1962). However, Reese (1903) and Bishop (1941) stated that they had well developed lungs. The former noted that hellbenders surfaced to respire every 15 minutes and could survive a week out of water (temperature and humidity not given). Furthermore, Bishop (1941) implied they utilized their lungs most in still water. But, Smith (1907) observed that they rarely surface in cold water, and Baker (1949) kept them submerged for days with no apparent effects. Both suggested significant buccopharyngeal and cutaneous respiration. Baker (1949) believed they utilized extensive buccopharyngeal respiration because of the arrangement of arteries to the pharynx and upper digestive tract. Gage and Gage (1886) and Willey (1920) were also advocates of buccopharyngeal respiration. Gage (1885a, 1885b, 1891) observed that the oral epithelium of *Cryptobranchus* was striated and nonciliated, similar to most amphibians which practice largely "aquatic respiration". He attributed little importance to the lungs as respiratory organs and believed the dominant form of respiration was cutaneous.

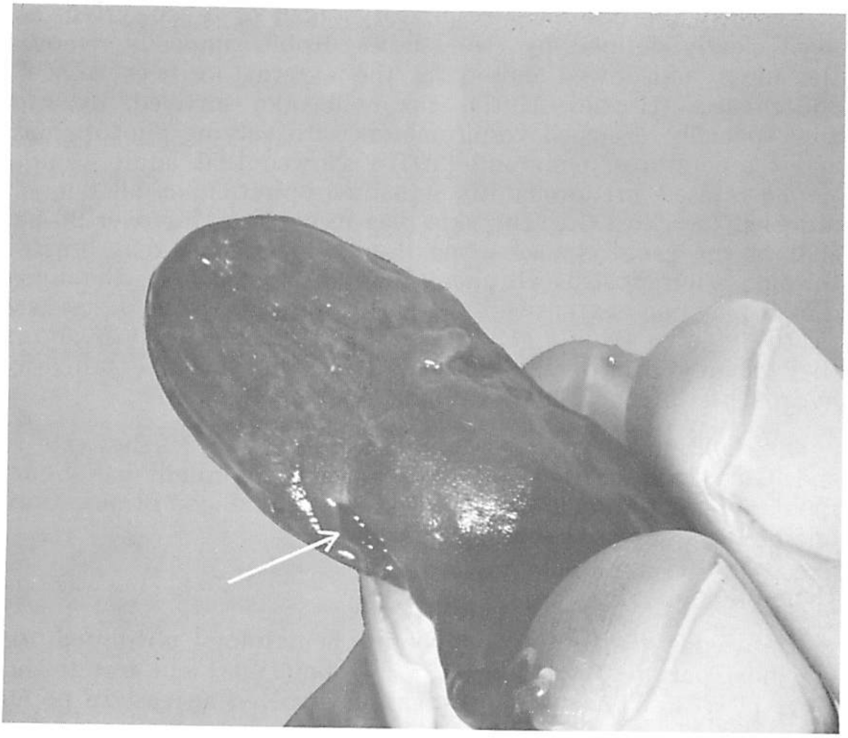

Figure 14. Ozark hellbender larvae have gills which are lost when they reach about 125 mm in total length.

Numerous authors mention the rocking or swaying behavior of *Cryptobranchus*. This "side to side" motion is characteristic of hellbenders in "still, poorly oxygenated and warm waters". Grote (1877) believed the swaying behavior was associated with skin shedding, sexual attraction, or some facet of the breeding period. Others observed that the rhythmic undulations of the lateral fold increase in rapidity as the environmental temperature increases and have linked this to cutaneous respiration (Bishop, 1941; Bernstein, 1953).

Comparative histological studies have added additional information. Noble (1925) showed *Cryptobranchus* to have a highly vascular integument with a reasonably thick epidermis. The lateral folds "are so richly supplied with capillaries that they form veritable lungs" (Noble, 1925). Bernstein (1953) observed vascularized dermal papillae invaginating the epidermal layers of the lateral body folds as well as those of the legs. These were not found in sections of the integument from the dorsal and ventral surfaces.

Recently the dominant respiratory organ or organ-system has been clearly defined by two studies. Robin surgically removed the lungs and sewed closed all the external orifices of a *C. alleganiensis* (Hughes, 1967). The hellbender survived. By utilizing specially designed respirometers with varying photoperiods and temperatures, Guimond (1970) showed that adult *C. alleganiensis* used predominantly aquatic respiration at all temperatures (5° – 25° C). The skin was responsible for over 90 per cent of the gas exchange. Even though hellbenders may breathe through their nostrils (Bruner, 1914; Foxon, 1964), the lungs don't play an extensive role in respiration. The lungs are relatively large (Noble, 1925), and radiographic analysis shows they occupy considerable volume. Thus, they may be primarily hydrostatic in function (Guimond, 1970).

Our field studies merely support the studies of Hughes (1967) and Guimond (1970). During the several thousand man hours spent studying *Cryptobranchus*, under natural conditions, only one hellbender was observed surfacing.

Hematology

Knowledge concerning hellbender hematology is limited for the most part to the studies of Wintrobe (1933) and Jerrett and Mays (1973). Wintrobe's investigation involved an eastern population of *C. a. alleganiensis*, while that of Jerrett and Mays compared the hematology of *C. a. alleganiensis* from the Niangua River, Dallas County, Missouri with that of *C. a. bishopi* from the North Fork of the White River, Ozark County, Missouri. A summary of the two studies is presented in Table 5. The general morphology of *Cryptobranchus* blood cells is shown in Fig. 15. Seifriz (1930) noted that the nuclei of *Cryptobranchus* erythrocytes were "composed of alveoli which are often clear, defined and about 1.2 μ in size". We know of no documentation of this by electronmicroscopy. A study of the quantitative relationship between *C. a. bishopi* erythrocyte volume and cellular DNA content is in progress (Melton, 1972).

Blood Chemistry

Hemoglobins

McCutcheon and Hall (1937) compared the hemoglobin-oxygen dissociation curves of numerous amphibians including *C. alleganiensis.* The hellbender's curve showed an "atypical" sigmoid shape. Both *C. a. bishopi* and *C. a. alleganiensis* had a single hemoglobin component (Taketa and Nickerson,

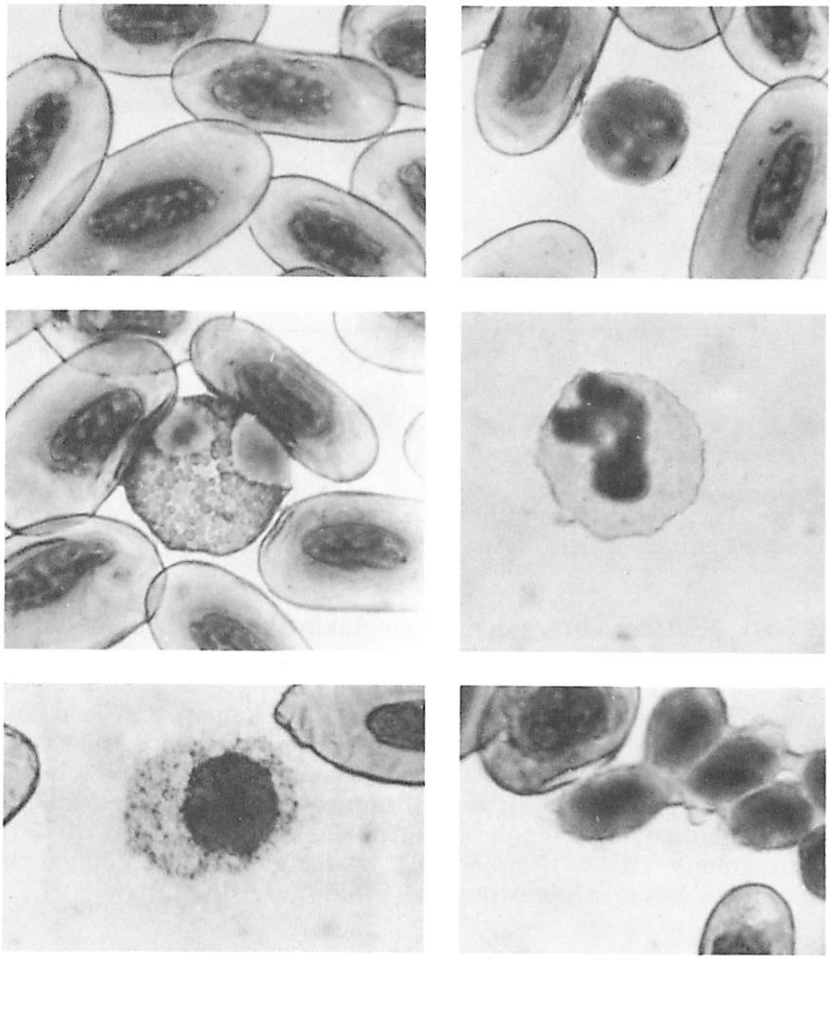

Figure 15. *Cryptobranchus* blood cells. Top left: erythrocytes. Top right: lymphocyte. Middle left: eosinophil. Middle right: neutrophil. Bottom left: monocyte. Bottom right: thrombocytes. 245 X.

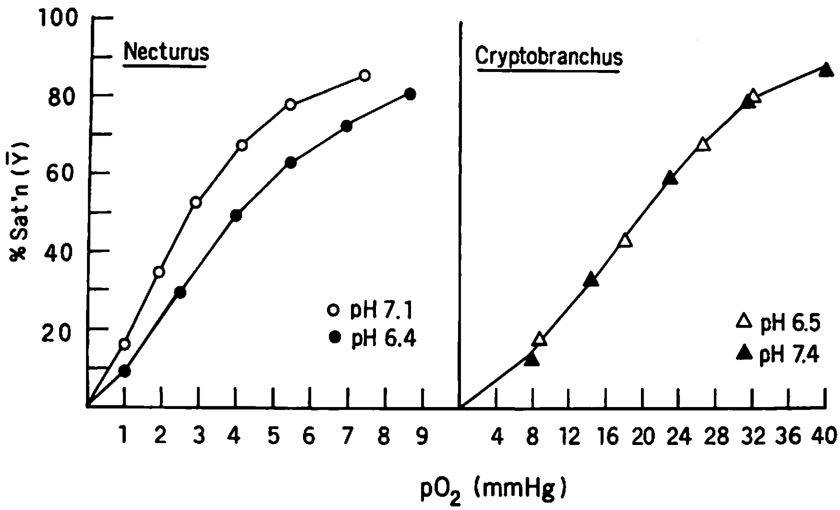

Figure 16, Oxygen equilibrium curves of *Cryptobranchus alleganiensis* and *Necturus maculosus* hemoglobins.

1973a). Furthermore, this hemoglobin had a sedimentation coefficient of 4.8S, exhibited a relatively low oxygen affinity (Fig. 16), a Hill Constant of 2.7 and an absence of a Bohr effect at a pH of near neutrality (Taketa and Nickerson, 1973a). Data from ultracentrifugation and tryptic peptide maps suggest a tetrameric molecule. Additionally, the effects of some organic phosphates on oxygen affinity are much less pronounced than in most mammalian hemoglobins (Taketa and Nickerson, 1973b). Thus, many of this molecule's characteristics are similar to amphibian larvae while others resemble those of adults.

Plasma Proteins, Serum Proteins and Other Blood Constituents

A comparison of the plasma proteins of *Cryptobranchus* with other large U.S. paedomorphic salamander genera revealed little serological correspondence (Boyden and Noble, 1933). Dessauer and Fox (1964) presented plasma protein profiles for numerous amphibians and reptiles. *Cryptobranchus* had the only salamander profile which could not be differentiated from other amphibians and reptiles. It was also the only salamander with a plasma fraction whose mobility was comparable to that of human albumin.

Wortham (1970) compared the serum protein patterns of populations of *C. a. bishopi* and *C. a. alleganiensis* using polyacrylamide gel disc electrophoresis. The total number of bands varied from five to eight. No observable differences were noted between sexes or size. However, there appeared to be slight migration differences between the serum patterns of most *C. a. bishopi* and those of *C. a. alleganiensis* (Wortham and Nickerson, 1971).

Although Thorson (1964) estimated the percentage of plasma fluid, the quantitative values for almost all serum constituents were lacking until Stone (1971) studied the effects of hypertonic media upon serum and urine constituents (Table 6). He found mean increases of serum sodium and serum osmolality but no significant change in serum potassium concentrations associated with hypertonic media (266-273 milliosmol water versus tap water control). Additionally, the serum proteins were larval; i.e., there was no change in the ratio of albumin as compared to globulins. McMillian and Wilkinson (1972) reported lower glucose readings for 11 *C. a. alleganiensis* from the same population sampled by Stone (1971). The mean blood glucose level was 28.5 mg per cent with a range of 15-55 mg per cent. Samples from *C. a. bishopi* and *C. a. alleganiensis* showed sexual differences in serum calcium but relatively little variation in serum magnesium (Wortham and Nickerson, 1970; Figs. 17-20).

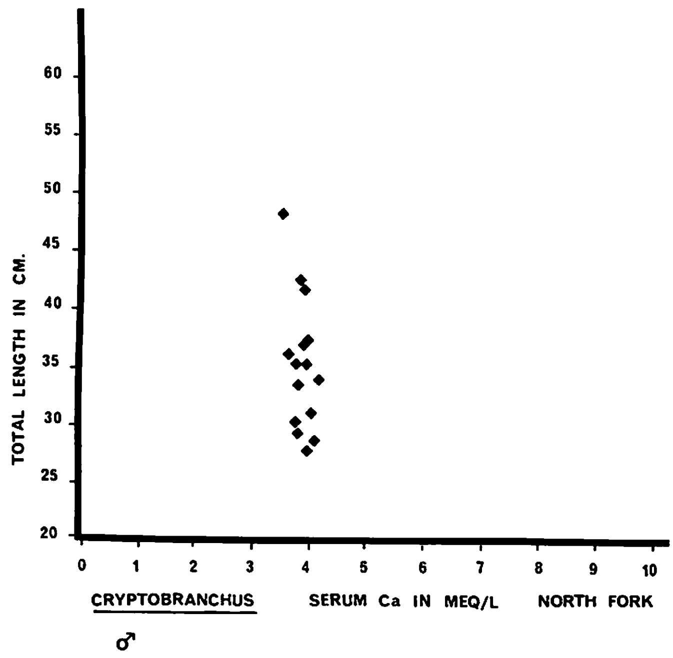

Figure 17. Serum calcium levels in male Ozark hellbenders.

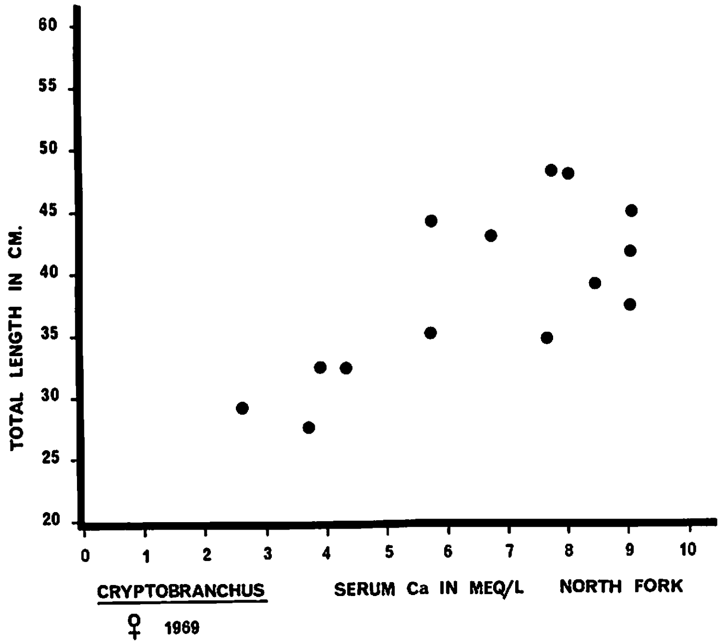

Figure 18. Serum calcium levels in female Ozark hellbenders.

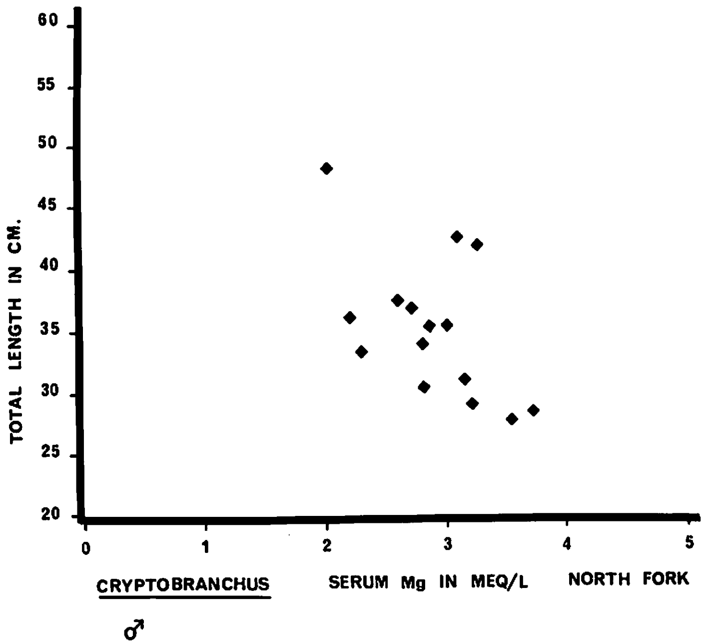

Figure 19. Serum magnesium levels in male Ozark hellbenders.

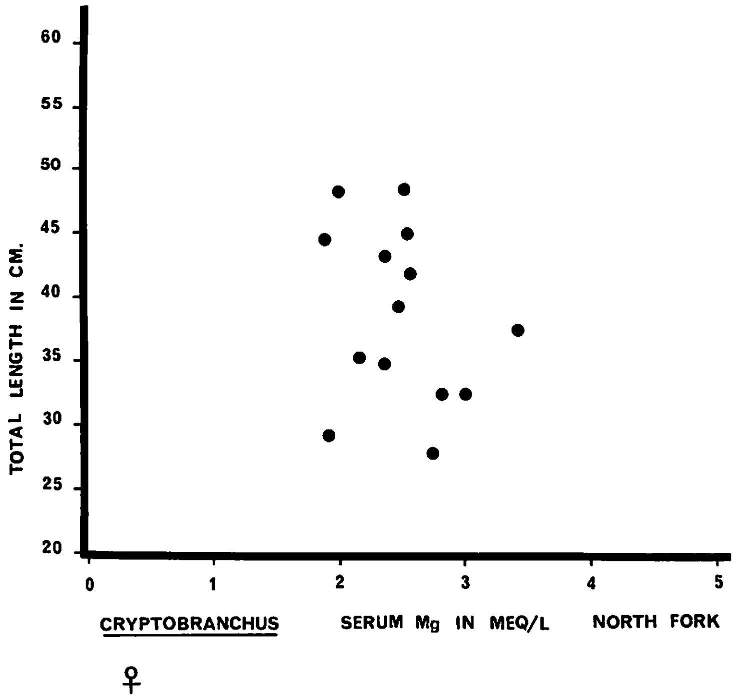

Figure 20. Serum magnesium levels in female Ozark hellbenders.

Skin Secretions

The literature is full of direct and indirect references to hellbender skin secretions. Green's (1933) comments essentially summarize many of the early references; i.e., "the salamander is covered with slime, which makes it slippery . . . when annoyed or when dying, it threshes around, covering itself with a thick, white slime very sticky and disagreeable". Barton (1812) believed the greatest quantity was secreted by the head.

We have observed great individual variation in the amount of skin secretions evidenced at the time of capture. Some produced copious quantities of a primarily whitish mucous material. This material can be compressed into "balls", which have elasticity and will actually bounce when propelled against a solid surface. Some of the secretion is water soluble and produces a frothy, "soapy" foam. Its presence is often demonstrable when freshly caught Ozark hellbenders are grouped in small containers of water (Fig. 21).

On 19 June 1969 we placed three live channel catfish *Ictalurus punctatus* (each weighing about 0.5 kg) in a 5-gallon cooler of water (70-75° F), which contained numerous freshly

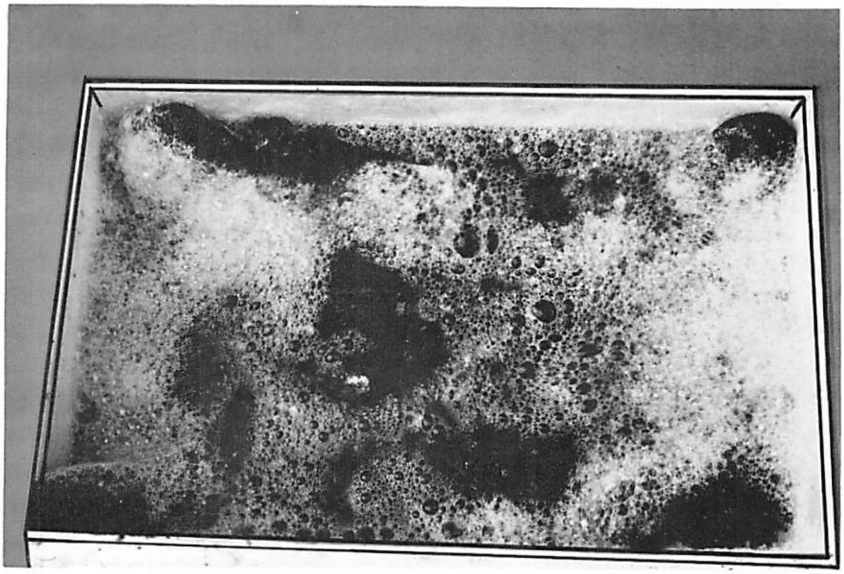

Figure 21. "Suds" produced by Ozark hellbender skin secretions.

C. a. bishopi. Shortly thereafter, the catfish rolled and thrashed vigorously. We removed the fish, placed them in fresh water alone (similar temp.), and the thrashing stopped. We repeated the process again with the same results. This indicated the possible presence of an irritant, presumably a skin secretion produced by *C. a. bishopi.* Similar reactions under similar conditions have been observed with other fishes including *Noturus albater*, *Cottus carolinae*, *C. bairdii* and *Ambloplites rupestris.*

Some early authors and numerous laymen believed the hellbender was poisonous. The skin of *Cryptobranchus* has been shown toxic to white mice when injected, but not lethal when ingested by white mice or chickens (Brodie, 1971). The only ingestion of *C. a. bishopi* we observed, under natural conditions, was by a smallmouth bass, *(Micropterus dolomieui).* We observed a dog grab an Ozark hellbender in its mouth. It quickly dropped the salamander and exhibited a repulsive response. Brodie (1971) tasted the secretion and observed that it was very bitter and caused a drying sensation, but did not burn. He thought that it would be effective in repelling would-be predators. A burning sensation occurs when these secretions come in contact with an open wound (Smith, 1907).

Although perhaps all of the 540 *C. a. bishopi* tagged in 1969 rejected metal tags with subsequent prolonged tissue irritation, and many of perhaps 2,000 live *Cryptobranchus* examined had severe leech infestations, no infections by *Saprolegnia* or other pathological agents were observed. One of us (Nickerson) has maintained hellbenders with cutaneous lesions in the same aquaria containing *Necturus maculosus*, with lethal fungal infections, with no apparent effects on the hellbenders (Fig. 22). This led us to consider a possible antibiotic action of the skin secretions of hellbenders. Previous studies by Daniel and Simpson (1954) and Vial and Preib (1966, 1967) utilizing numerous species of Gram negative and positive bacteria, seven yeasts and two molds, showed no antibiotic activity for skin secretions from *Necturus maculosus*, *Ambystoma tigrinum*, *Triturus viridescens* and *Plethodon cinereus*. Nickerson et al. (1972) were unable to show any antibiotic activity of *C. a. bishopi* skin secretions against *Escherichia coli*, *Bacillus subtilis* and *Staphylococcus aureus*.

Numerous other functions have been attributed to skin secretions. Pattle has suggested that "one of the functions of mucus at respiratory surfaces may be to prevent excessive diffusion of water whilst allowing adequate diffusion of gases" (Robin and Murdaugh, 1967). Other potential functions of skin secretions include reducing friction to aid in aquatic locomotion (Rosen and Cornford, 1971) and sliding under rocks.

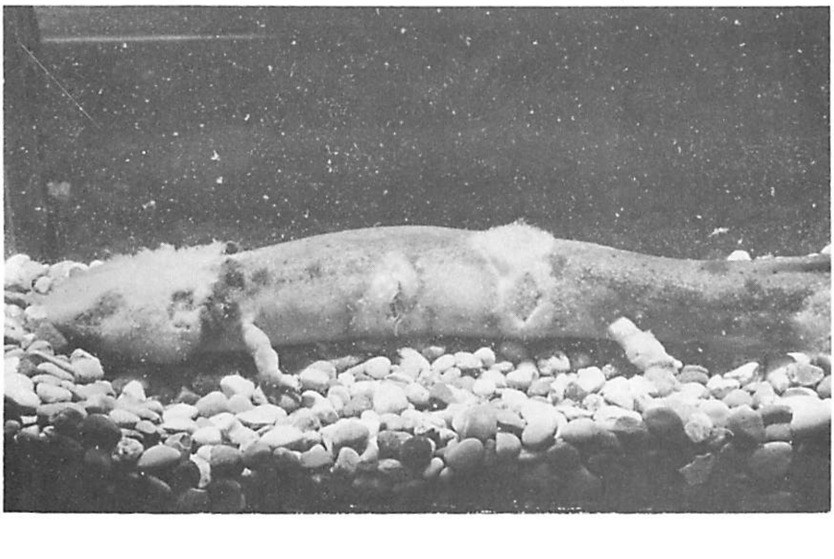

Figure 22. A *Necturus* with a lethal *Saprolegnia* infection.

Senses

Chemoreception

We know little about hellbender chemoreception. Numerous authors refer to taking or attracting them with dead bait. Both Townsend (1882) and Beck (1965) mention luring large numbers with dead fish and calf entrails, while Surface (1913) "counted 10 hellbenders coming upstream with their heads moving back and forth scenting blood" after he had shot a sucker upstream.

Photoreception

The eyes of *Cryptobranchus* are small, inconspicuous (Figs. 5, 23) and located so that there is no point in the visual field at which both eyes can focus on the same object (Walls, 1942; Oliver, 1955). Reese (1905b) studied *C. alleganiensis* eye histology and noted that the optic muscles were of considerable size even though the eye seemed to have almost no power of motion. But, the unusually large surface area of the retina may compensate for mobility. The cornea was flattened or depressed, similar to most aquatic amphibia, possibly affording less friction in swimming or protection against contact with rocks or other objects.

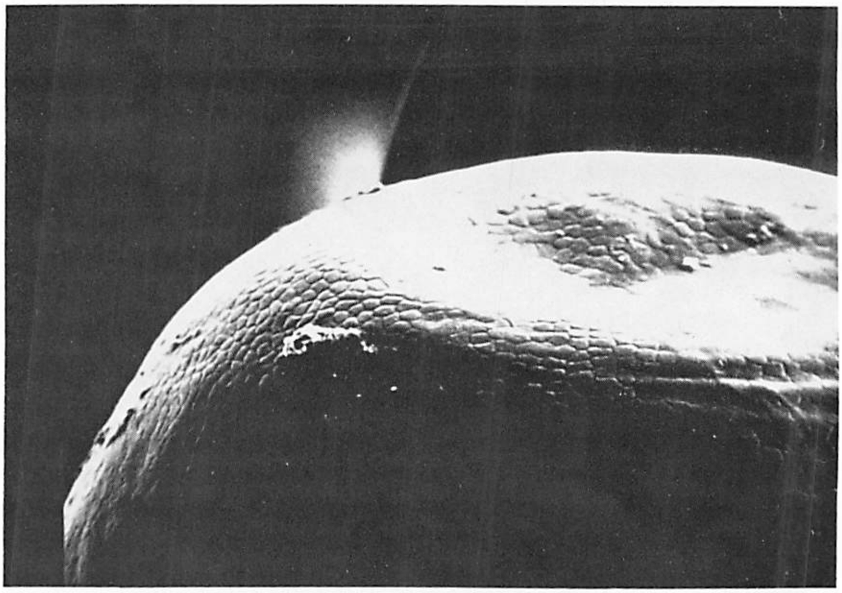

Figure 23. An electronscan photomicrograph of an Ozark hellbender's eye 90x.

The sclera is extremely thick and equal in thickness to the radius of the lens (Walls, 1942). Reese (1905) speculated that the spherical lens, which resembles teleosts, is particular adapted for short range vision and probably not keen even at short range. Furthermore, development of ciliary processes is slight, and no ciliary muscles were observed. Without these, focal accommodation would be limited. Walls (1942) described the hellbender eye as "extremely crude and disharmoniously developed, and its vision is no more than a mere directional light sense". But Green (1933) and Beck (1965) reported that hellbenders have been caught on subsurface artificial lures. This coupled with Smith's (1907) observations would indicate sight is important in feeding. More recently Riss et al. (1963) described hellbender optic pathways and related these to photoreception.

Reese (1906b) observed that all regions of the body were sensitive to white light but, based on response time, the tail was even more sensitive than the head. He related this to the hellbender's habit of concealment during daylight hours. Moreover, pure red light produced no response, which correlates with this animal's typically nocturnal habits. Dermal light sense was also studied by Pearse (1910). He agreed that the tail was the most light sensitive region and found most urodeles photonegative. The subject of dermal light sense was reviewed by Steven (1963).

Thermoreception and Tolerance

Early references to hellbender temperature tolerance are vague but colorful. According to Townsend (1882), one was carried behind him on horseback for six miles "under a blazing sun" and yet remained alive. Frear (1882) stated that one had "lain exposed to a summer sun for 48 hrs" and survived. Reese (1906b) exposed four *C. a. alleganiensis* to a variety of temperature gradients (Table 7). His data, at the upper limits, would appear to agree with Green (1933), who stated that they die quickly when exposed to warm water or air (40° C). Recently, Hutchison et al. (1973) have shown that the mean critical thermal maxima (CTM = the temperature at which organized locomotion is lost and they are unable to escape lethal conditions) of *C. a. bishopi* were 32.7° C at 5° C acclimation, 33.0° C at 15° C acclimation, and 36.6° C at 25° C acclimation.

While transporting hundreds of *C. a. bishopi* and *C. a. alleganiensis* we have observed that they can withstand great thermal change. They may be removed from streams (20° — 22°

C), plunged directly into ice water and maintained at 1° C for days. Our observations at lower temperature ranges differ from those of Reese (1906b). When transferring either *C. a. bishopi* or *C. a. alleganiensis* from streams at 18°-22° C into ice water, many individuals respond by vigorous thrashing and biting.

Sound Production, Phonoreception and Lateral-Line Organs

According to Shmal'gauzen (1964) sound transmission disappeared in hynobiid and cryptobranchid salamanders. However, both *C. a. alleganiensis* and *C. a. bishopi* do occasionally make noises when removed from the water. Minton (1972) stated that "when lifted from the water they may expel air with a distinct grunt and squirt a stream of water from each spiracular opening". Also, Evans (1972) has shown underwater vocalization in the hellbender's Chinese relative *Andrias davidianus* (Fig. 24). All of these underwater sounds were of short duration (0.1-0.3 seconds) and typically below 500 Hz, although some frequencies reached 1.5 KHz. These sounds were usually produced at night during prefight posturing, fighting and just prior to air gulping. Whether or not *Cryptobranchus* produced any similar sounds is not known.

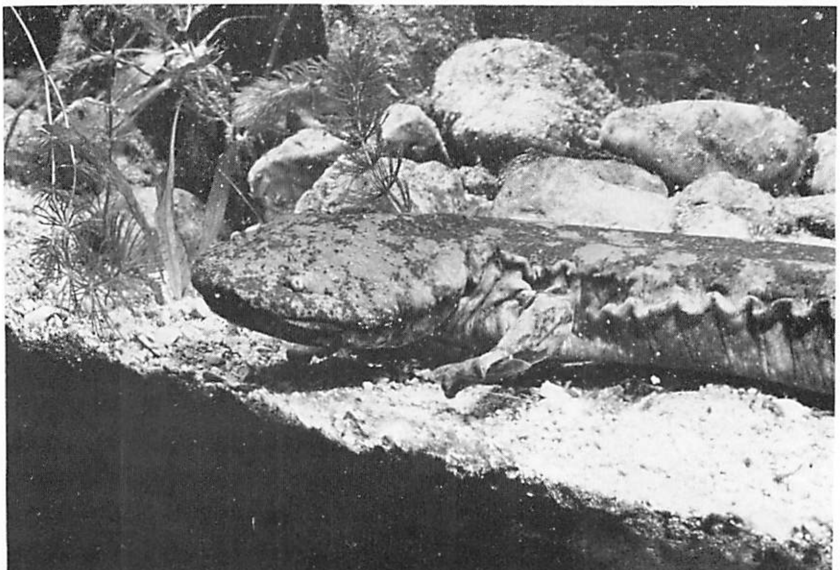

Figure 24. The Chinese "hellbender", *Andrias davidianus.*

Additionally, we know little about the importance of auditory reception in *Cryptobranchus*. They sometimes react to the shutter-release of some underwater cameras and contact between rocks and rocks and metal. Hellbenders frequently rest with the lower jaw in contact with the stream bottom (Oliver, 1955). The manner by which *Cryptobranchus* "hears" is intimately associated with this practice. Vibrations from the substrate are received by the lower jaw or, a bone supporting it, and transmitted to the inner ear. The primitive condition; i.e., the presence and connection of the columella to the inner ear, is maintained by *Cryptobranchus* (Kingsbury and Reed, 1909).

The background noises in riffles of many hellbender streams are relatively great and might jam certain wavelengths. However, acoustics would seem useful in territoriality and other biological phenomena.

Larvae and adults of some aquatic amphibians, including *Cryptobranchus* have lateral-line sense organs (Oliver, 1955). The general pattern of the sensory lines of amphibians resembles that of choanate fishes (Jollie, 1962). Hellbender lateral-line structure has received considerable attention and has been described in detail (Malbranc, 1876; Cope, 1889; Kingsbury, 1896; Chezar, 1930; and Jollie, 1962). These organs are sensitive to vibrations in the water and may be used in orientation, locating food, or determining a predator's approach, etc. (Oliver, 1955).

Thigmotaxis and Rheotaxis

Hellbenders are well adapted for a lotic habitat, both morphologically and physiologically. Their dorsoventrally flattened bodies would seem to offer a minimum of resistance to flowing water. Additionally, they exhibit positive rheotaxis and positive thigmotaxis. When released in a strong current they may be swept downstream headfirst, but they almost invariably orient themselves upstream or seek an area of reduced current. Their positive thigmotaxis may be more or less dependent upon the amount of light present.

Shock-like States

There are scattered accounts of hellbenders being exposed to extreme physical injury and critical conditions for considerable time before dying (Frear, 1882; Netting, 1929; Green, 1933 and

Riss et al. 1963). We have observed Ozark hellbenders go into shock-like states during transportation. In all instances the salamanders were crowded and there was considerable regurgitant contaminating the water. Many of the animals were considered dead. However, many of these *Cryptobranchus* were revived when they were removed from the fouled water and placed in flowing freshwater. Time for revival varied from a few minutes to several hours.

One amazing incident occurred during the summer of 1969. In late July, 1969 we provided the Missouri Conservation Commission with a large *C. a. bishopi* (total length 53 cm) for their exhibit at the West Plains Regional Fair. The following day it was believed dead and buried late that morning. Later the same day, at about 6:30 P.M., as we visited the exhibit, an excited lady appeared. She told us of a large, ugly lizard crossing the fair grounds. The "dead" Ozark hellbender was discovered crawling across the grass. Air temperatures had surpassed 100° F that day. The salamander was fortunate to have been buried in a shady location.

Activity

Activity Patterns

Hellbenders are basically nocturnal and remain concealed under rocks, logs, etc. in the daytime (Bishop, 1941; Smith, 1961). Townsend (1882) stated that they are often observed during the early summer in considerable numbers. Typically, the smaller hellbenders are more active than larger ones (Reese, 1903). According to Smith (1907), they also become diurnal before and during the fall breeding season, when they may roam restlessly poking under rocks and into crevices or they may lie quietly in the open or congregate in groups (Bishop, 1941). However, Hillis and Bellis (1971) observed no diurnal activity.

During our studies of the Ozark hellbender; October, 1968 — September, 1972; we made at least 48 observations of diurnal activity. Listed by month these were: June — 12, July — 3, August — 3, September — 16 and October — 14. The number of man hours of observation during these months varied greatly. Over two-thirds of our total number of man hours was in June and July with the amount each month being nearly equal. The combined September and October samples represent about five per cent of the total. These data show that the Ozark hellbender's diurnal activity pattern varied throughout the year. Furthermore, our data indicate a positive correlation between Ozark hellbender activity and cloudy days; i.e., light and diurnal activity.

The greatest diurnal activity was observed by Nickerson on 25 September 1972 during a moderate rain. The morning was heavily overcast with some mist. While working a 280 meter section of the North Fork of the White River, between 11:00 A.M. and 12:30 P.M., no diurnal activity was observed. At about 12:15 P.M. a moderate rain began. Between 12:30 and 1:45 P.M., 12 Ozark hellbenders were observed actively moving about. Most of the active hellbenders were adult males; however, adult females were also active. Rain, perhaps coupled with overcast skies, may have served as a stimulus for activity. Another factor might be food accessibility. However, since crayfish represent the bulk of hellbenders' diets, this seems unlikely unless crayfish behavior was also affected. Additionally, such "intense diurnal activity" was not documented during summer rains and thus hormone levels may be suspect as an additional factor. Riss et al. (1963) has suggested that *Cryptobranchus* endocrine activity may be affected by day length.

Swimming

In addition to adaptive coloration and repulsive skin secretions, hellbenders use swimming to escape predation. With one exception, all of our "in nature observations" of *Cryptobranchus* swimming have been associated with capture, attempted capture or release. Some consider *Cryptobranchus* a weak swimmer. Alexander (1927) noted that when alarmed, hellbenders could swim with "amazing rapidity". Both viewpoints have merit. Certainly hellbenders are unable to swim against a rapid current. However, utilizing this current, they can travel many meters quickly. They appear to tire rapidly during rigorous swimming. Usually they attempt escape with a burst of sidewise undulating movements, the primary propelling forces being the laterally flattened tail and lower body movements. Both water clarity and velocity are factors which mediate the effectiveness of swimming as an escape mechanism. When Ozark hellbenders are sufficiently startled to swim, they typically travel only a few meters. Then they actively seek shelter under a rock or in a crevice or remain motionless briefly before hunting for cover.

Non-aquatic Activity

According to Barton (1812) hellbenders will forsake water for a minute or two and are "seen sitting upon stones . . . in the water". Holder (1885) has depicted them doing this and Fitch (1947) made a similar observation. Beck (1965) occasionally trapped hellbenders away from the water, presumably on nocturnal sojourns. Dr. Paul Burch found that in the spring and less often during the summer, hellbenders left the water crawling over rocks beneath a dam (Bogart, 1961). Certainly *Cryptobranchus* is capable of aerial respiration (Robin and Murdaugh, 1967 and Guimond, 1970) and Hughes (1967) cites its ability to secrete mucus "as a habit which is common in animals which can live on land in most conditions". We have observed no non-aquatic activity in either the hellbender or Ozark hellbender in their native habitat. However, they will readily leave the aquatic environs of aquaria, styrofoam coolers, etc., especially at night.

Intraspecific and Interspecific Relationships

We know that hellbenders are cannibalistic and will consume other hellbenders and hellbender eggs. Another intraspecific relationship is territoriality. Evidence for hellbender territoriality is along two lines; i.e., defending nesting sites and distribution (spacing).

Alexander (1927) noted fierce strife among male hellbenders during competition for good nesting sites. Smith (1907) seldom found more than one hellbender per rock and Hillis and Bellis (1971) only once found more than one hellbender under the same rock. The latter noted that "frequently, when one was released or chased . . . it would crawl under a nearby rock, then clouds of silt would emerge from under the rock, followed by . . . the salamander that had crawled under". Turning the rock would always produce another hellbender.

Of perhaps 2,000 *C. a. bishopi* uncovered from beneath rocks, the most observed under one rock was three (two occasions) and two were encountered only 14 times. These observations led us to forward the "one rock = one hellbender hypothesis" very early in our studies. It was not always possible to determine if large rocks created compartments so that the animals under them were not in contact. Additionally, we were unable to sex *C. a. bishopi* in the spring and early summer. During the late summer and fall, when two or more hellbenders were found under a rock in a single compartment, only once were they two adult males. Thus, this hypothesis has merit.

The only "field" observation of strife between Ozark hellbenders was made by Bradford Ott. He observed one *C. a. bishopi* with a larger one's head in its mouth at about 2:30 P.M. on 22 June 1972. Both salamanders were 35 to 40 cm in length. The incident occurred in the open, and considerable blood was in evidence. Unfortunately, they were not sexed.

We have discussed some interspecific relationships; i.e., prey parasites and predators of *Cryptobranchus*. Our knowledge of other interactions are poorly understood. Barbour (1971) believed that the hellbender competes with fish, particularly catfish for food. He doubted if their populations were ever sufficiently high to offer serious competition. However, we know of amazingly dense populations of *C. a. alleganiensis* and *C. a. bishopi* in many river systems and have reported on one of these (Nickerson and Mays, 1973).

The only sizeable vertebrates we observed sharing the same rock with an Ozark hellbender were a channel catfish, *Ictalurus punctatus* and a rock bass, *Ambloplites rupestris.* Additionally, we found fish eggs sharing the same rock with a 24.5 cm long *C. a. bishopi.* Alexander (1927) found *Necturus maculosus* in hellbender nest cavities. He believed *Cryptobranchus* might eat *Necturus.* Throughout our studies of Ozark hellbender habitat we have only found two *Necturus maculatus.* Both were in the North Fork of White River research section. Green (1971) believed that *Necturus* replaces *Cryptobranchus* in many larger streams. The larger streams he considered were muddier, more polluted with mine waste and subject to more frequent flooding than the smaller streams.

Reproduction

Sexual Differences

Cryptobranchus normally exhibits little or no sexual dimorphism, although males are sometimes heavier and broader than females of the same length (Bishop, 1941). During the breeding season, an adult male may be recognized b; the presence of a swollen ring surrounding the cloaca. The swelling is due to an enlarged cloacal gland. Often a marginal row of enlarged tubercles encircle the vent. Males also show more expansive folds of skin on the toes and a larger fold on the outside of the leg and upper tarsal regions than do females (King, 1939). Females in the breeding season can sometimes be distinguished by a swollen abdomen as a result of egg storage. Grote (1877) referred to the general changes in external appearance during the breeding season as the "marriage dress".

Sex Ratios

Previous work indicates that males are generally captured more often than females. Whether this is due to a difference in numbers or merely to the fact that females are more inaccessible is unknown. Smith (1912) reported a male to female ratio of 2:1 to 3:1 based on several years of data. However, he did find a higher proportion of females than males in non-breeding areas during the summer, and at the height of the breeding season, both sexes were found on the breeding grounds in about equal numbers. In several instances during the breeding season, we have collected a higher proportion of females than males. Mid-summer samples of 30 or more *Cryptobranchus* revealed the following male to female ratios of *C. a. bishopi:* North Fork of White River, Ozark County, Missouri, 1:1; Eleven Point River, Oregon County, Missouri, 1.00:2.45; and of *C. a. alleganiensis* from the Niangua River, Dallas County, Missouri, 1.3:1.0.

Breeding Habits

The mating season of *C. a. alleganiensis* in northwestern Pennsylvania and southwestern New York begins about the last of August and lasts for about two weeks (Smith, 1907; Bishop, 1941). Green (1933) reported a similar spawning season in the vicinity of Elkins, West Virginia as did King (1939), Fitch (1947) and Huheey and Stupka (1967) for streams in Tennessee.

Missouri populations of *Cryptobranchus* appear to breed over a more extended period than do the eastern forms. In additional, seasonal variation in reproduction has been observed among Missouri populations. Dundee and Dundee (1965) noted a *C. a. alleganiensis* nest on 3 September 1954 in the Niangua River that contained 138 eggs; whereas, all large females taken from the Gasconade River on the same date were far from ready for deposition. Furthermore, "ripe" females were taken as late as 14 November in the Niangua River. Our earliest observations of egg laying in the North Fork of White River were 13 September 1970 and 6 October 1972. On 3 November 1971 males were dispelling great quantities of milt but most females appeared spent. However, a decomposing female, apparently killed by gigging was "ripe".

Dissections of females collected in mid-September 1970 revealed that the ovarian eggs of *C. a. alleganiensis* from the Niangua River were much less developed than those of *C. a. bishopi* from the North Fork of White River. Populations of *C. a. bishopi* from the Spring River, in northern Arkansas, apparently spawn at about the same time as those in Missouri (Baker, 1963; Dundee and Dundee, 1965; Ratcliff, 1965). Seasonal differences in hellbender reproduction appear to be related to environmental factors (Dundee and Dundee, 1965).

With the onset of the breeding season, a marked change in the behavior of *Cryptobranchus* takes place (Smith, 1907). They no longer remain secluded, but come out into the open, often in congregations of six to twelve. Since good nesting sites are scarce, bickering often occurs between two or more males for "right of ownership" (Alexander, 1927). Minton (1972) observed increased irritability in a captive male as the mating season approached.

Nest

The nests of *Cryptobranchus* are excavations beneath large flat rocks, planks or submerged logs, and are partially embedded in the stream bottom with an entrance out of the direct current and often on the downstream side (Alexander, 1927; Bishop, 1941). The nests are prepared, for the most part, at night by the males. Upon their completion, females move into the area and are driven into the chambers prepared and guarded by the males to deposit their eggs (Alexander, 1927). If the female is obstinant, the male keeps her prisoner in the next until she finally lays her eggs (Beck, 1965). Several females often share a common nest, and it may contain as many as a thousand eggs. Bishop (1941) reported a total of 1,946 eggs, in an 18 x 15 inch nest, in water only 15 inches deep.

Egg laying under natural conditions is difficult to observe. However, Smith (1912) describes such an event as follows:

> "Egg laying begins slowly, a short string of eggs sometimes protruding from the cloaca for several hours before spawning begins in earnest. In the natural habitat, such short strings are often found in the open. Later, two long strings of eggs proceed slowly from the cloaca, one from each uterus; the majority of the eggs are then deposited more rapidly in multiple strands, the process requiring less than five minutes. When egg laying is completed, the strings are usually twisted together in a single tangled mass."

Once the eggs are deposited, they are often eaten by males and females alike (Smith, 1907; Alexander, 1927; Bishop, 1941). The number of eggs found in the stomach of a single adult usually ranges from fifteen to twenty-five, a number sometimes greatly exceeded in the stomachs of spent females (Smith, 1912). However, both Smith (1907) and Green (1933) observed that the eaten fertilized eggs are sometimes soon regurgitated and develop successfully.

Egg laying in the laboratory has been reported by various authors (Townsend, 1882; Reese, 1904a; Smith, 1907), and it appears to closely parallel the process under natural conditions. In captivity, egg laying usually takes from two to three days to complete, and, as under natural conditions, the eggs are often eaten by the female while they are being deposited (Mays and Nickerson, 1972).

Laboratory observations of *C. a. bishopi* are in accordance with those reported by Smith (1912) for *C. a. alleganiensis* in that the larger and presumably older females tend to lay more mature eggs than the smaller ones. Smith found that an adult female of average size deposits about 450 mature eggs each season, 225 from each ovary. This is somewhat higher than the number of eggs deposited by an average sized female *C. a. bishopi.* The average number of eggs layed by three female *C. a. bishopi* in our laboratory was 270. The fact that adult *C. a. bishopi* from the North Fork of the White River are generally smaller than adult *C. a. alleganiensis* could be a factor in explaining this difference.

Eggs

Each egg is a spherical yellow body 5 mm to 7 mm in diameter and is surrounded by a transparent gelatinous envelope arranged in two distinct layers. The egg is surrounded by a small amount of watery material, which in turn, is enclosed in a capsule of more dense jelly. This inner envelope continues as a tough, solid cord of jelly from egg to egg, and results in the formation of egg strings (Fig. 25a). The total diameter of the egg with its envelope is approximately three times the diameter of the egg alone. The distance between two adjacent eggs is usually about four or five times the diameter of the egg. Within several hours after the eggs are laid, the envelope swells as a result of water absorption. The eggs and envelopes may expand to a total diameter of 18 mm (Smith, 1912).

Sperm

The sperm of *Cryptobranchus* develop in the seminiferous tubules of paired testes. The size of the testes varies considerably with the season of the year and the size of the animal. During the spawning season, the testes enlarge in all planes and acquire a "puffed" appearance. The sperm mature as they move centrally toward the lumen of the seminiferous tubules where they are transported through the intratesticular network to the vasa efferentia. The entire testis is active in sperm production (Ratcliff, 1965).

The sperm of *C. a. alleganiensis* are about 225μ long with the nucleus comprising about one third of that length (Smith, 1912). The nucleus is capped by a gradually tapering acrosome and is separated from the tail by a very short middle-piece. The tail-piece consists of an undulating membrane surrounded by a convoluted transparent envelope (Fig. 25b).

The sperm of *C. a. bishopi* have a much reduced neck piece; the ring does not elongate down the axial filament; there is no evidence of the cytoplasm and cell membrane passing down the axial filament of the tail; no mitochondria are evident on the tail; and the middle-piece cannot be distinguished from the principal piece. The axial filament reaches a maximum length of 185μ in early development, with the paralleling flagellum extending for twice this length (Baker, 1963).

Makino (1935), using adult *C. alleganiensis*, reported chromosome numbers of 62 (2N) for spermatogonia and 31 (N) for spermatozoa.

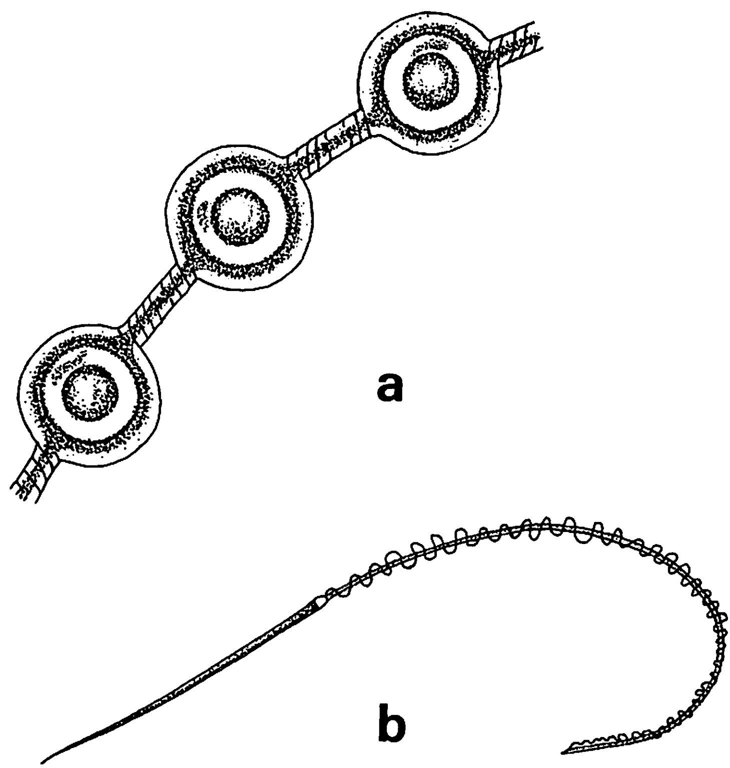

Figure 25. (a) Part of *Cryptobranchus* egg-string showing eggs and their envelopes. (b) Sperm of *C. a. alleganiensis* (after Smith, 1912).

Fertilization

Unlike most salamanders, fertilization is external in *Cryptobranchus*. Smith (1907) observed that while a female deposits eggs in the nest, a male moves to a position alongside or sometimes slightly above the female, so that it may be next to or above the eggs. In this position, he makes swaying lateral and vertical movements of the posterior end of the body, raising and lowering it with his hind legs. Through these movements, the male sprays the eggs with large quantities of milt, a snowy-white cloudy mass, which consists of seminal fluid mixed with the secretion of the cloacal glands. These masses may reach a diameter of 4 mm and attain a length of 10 mm to 30 mm. Large quantities of sperm released in the confined space of the nest become scattered rapidly, especially with the movements of the animals so that the eggs can be quickly reached and fertilized. Sometimes more than one male may occupy the nest area, perhaps to insure fertilization (Smith, 1907).

Polyspermy, another means which helps to insure fertilization, is the rule in *Cryptobranchus.* Smith (1912) found cases of egg penetration by more than one sperm within fifteen minutes after fertilization. He also noted that after one hour, the majority of eggs had been penetrated by from one to ten sperm. Apparently fertilization in *Cryptobranchus* is quite efficient, because few unfertilized eggs are found (Smith, 1912).

Brooding Habits

Usually the male remains in the nest following fertilization, and offers fairly efficient protection to the newly fertilized eggs. Smith (1907) observed a male that fought and drove several other males away from an egg-containing nest he was occupying. Bishop (1941) also reported similar defensive gestures on the part of the guardian male. The duration of the brooding period is not known, but is thought to vary a great deal. Smith (1912) found males guarding nests with embryos up to about three weeks old, but his observations were incomplete.

Embryonic Development

Since McGregor (1897) first described a *Cryptobranchus* embryo, several excellent accounts of hellbender embryology have been reported. Among these are the descriptions of Smith (1912) and Grenell (1939). The following is a brief summary of Smith's findings.

The follicular layer proper of the ovarian egg of *Cryptobranchus* is formed from some of the deeper non-germinal cells of the ovarian wall, which resemble the epithelial cells of the outer and inner limiting membranes. The follicular membrane proper completely surrounds the egg and is suspended in a two-layered flask-shaped sac, which projects from the inner surface of the wall of the ovary into the central cavity. In a broad sense, the entire three-layered structure may be called the follicle. The zone radiata is formed from the peripheral substance of the egg proper. It becomes transformed into a simple cell wall in organic connection with the egg at the time of the rupture of the germinal vesicle. The zona pellucida is formed as a secretory product of the follicular layer proper. It persists unchanged as the vitelline membrane of the embryo.

The earliest observed phenomenon, which may indicate polarity, occurs in the ovarian eggs of young females 26 to 30 cm in body length. There is a shifting of the region of most abundant vitelline bodies from the future vegetal to the future animal hemisphere. In the ovarian eggs of young females with a body length of 35 cm, there is a concentration of nucleoli on the side of the germinal vesicle toward the future animal pole.

Yolk formation begins in the most advanced oocytes of young females 35 cm in body length. The yolk is first laid down in concentric zones. With respect to the position of the germinal vesicle, the distribution of cytoplasm, and the size of the yolk particles in the different zones, the egg exhibits radial symmetry until after it is nearly filled with yolk. About the time when the egg becomes completely filled with yolk, the germinal vesicle migrates from its central position toward a point on the surface, which is thus defined as the animal pole. Coincident with the migration of the germinal vesicle, axial differentiation of the cytoplasmic and yolk contents of the egg lead to the formation of a germinal disc in the region of the animal pole. In general, the animal pole lies within the stalk of the follicle and toward the periphery of the ovary. In the late ovarian egg, a structure called the yolk cup is interpreted as the physiological equivalent of the concentric layers of dense fine yolk found in the eggs of birds and various other vertebrates.

Shortly before maturation, the germinal disc is temporarily differentiated into two layers; a thin layer of yolk-free cytoplasm, and underlying this, a thicker layer of very fine yolk particles rich in cytoplasm. Both layers are continuous with much thinner layers of the same character surrounding the remainder of the egg.

In the oocyte ready for maturation, the germinal vesicle lies close to the surface at the animal pole and is surrounded by the germinal disc. A mass of cytoplasm has accumulated beneath the germinal vesicle during the later stages of its migration. The arrangement of materials is now quite strongly telolecithal.

Shortly before the rupture of its wall, the germinal vesicle appears at the very surface of the animal pole. The rupture of the germinal vesicle takes place just before the egg leaves the ovary. At this time, the cytoplasmic and yolk layers of the blastodisc mingle, and the materials of the germinal vesicle, together with the cytoplasm brought with it from the interior of the egg, are incorporated into the blastodisc. Absorption of degenerating oocytes is accomplished by means of the follicle cells, which reverse their usual role as nurse cells of the egg and function as phagocytes.

The polar spindle is formed about the time the egg leaves the ovary and disappears about the time the egg enters the uterus. There are marked size differences in the chromosomes. The second polar spindle is formed shortly after the egg enters the uterus. It lies beneath a deep pit readily visible from the surface.

The late stages of the second maturation division, culminating in the formation of the second polar body and the egg-nucleus, are passed through only after the sperm has entered the egg. Thus, the processes of maturation and fertilization overlap. A structure resembling a micropyle is formed in the cell wall of the egg around the perforation made by the entering sperm. The influence of the entering sperm upon the egg is shown by characteristic changes in the distribution of the yolk and cytoplasm. Physiological polyspermy is a normal occurrence. The supernumerary sperm lead only a transient existence.

The period prior to hatching has been divided by Smith (1912) into twenty-three stages defined on a morphological basis. For these early stages, this method is more accurate than one based on age or length of body (Grenell, 1939). Stages 21 through 23 are summarized below:

Stage 21

This stage is attained about two weeks before hatching. The embryos are 12 to 14 mm in length, and the yolk mass is still large and greatly distended. The external gill rudiments are present as simple ridges. Small front limb buds are present, but there is no external indication of hind limb rudiments. Pigmentation is beginning, but is almost entirely confined to the dorsal surface. The pharyngeal plate is not yet perforated.

Stage 22

This is one week prior to hatching. The embryos are 15 to 22 mm long. At this time the rudiments of the external gills are no longer simple ridges, but are branched. The front limb rudiments are conspicuous structures. Toward the end of this stage, small hind limb rudiments appear. The pharyngeal plate is not yet perforated.

Stage 23

This is the time of hatching, when the larvae are 23 to 26 mm in length. The moderate pigmentation of the two earlier stages becomes more evident. The dorsal surface of the body and the sides of the tail are well pigmented. The yolk mass is now only moderately distended. The external gills are bushy. Each front limb rudiment has two digits. The pharyngeal plate has ruptured.

Larval Development

Smith (1912), Grenell (1939), and Bishop (1941) are responsible for most of the known information concerning larval development of *Cryptobranchus* and should be consulted for further details.

Incubation Period

Bishop (1941) reported the period of incubation for New York and Pennsylvania populations of *C. a. alleganiensis* ranges from 68 to 84 days.

New Larvae

Although embryonic stages of development can be satisfactorily defined on a morphological basis, the body length in millimeters affords a better index of the stage of larval development (Grenell, 1939). From six weeks to more than two months after fertilization, the larvae, approximately 25 mm to 30 mm in length are ready to escape from the egg capsule (Fig. 26). Newly hatched larvae are well pigmented dorsally. The eyes are more conspicuous than in the adults, and the mouth is quite well developed. They possess gills with comparatively short, flattened filaments (Bishop, 1941). Outlines of two toes can be seen on the front limbs, but the hind limbs are mere paddle-shaped lobes directed backwards (Bogert, 1961). The tail is broad and flat, and the dorsal keel extends forward to a point

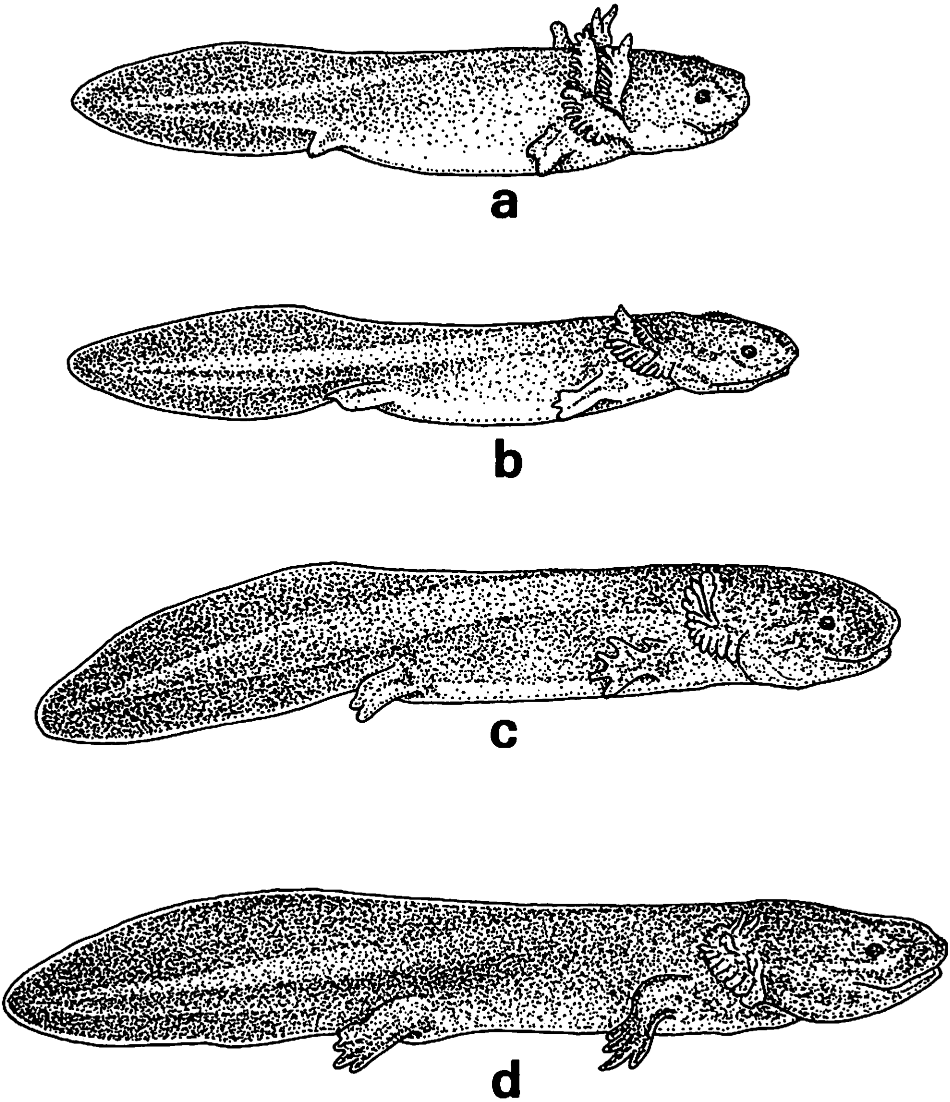

Figure 26. Hellbender larvae: (a) at hatching, actual length 29 mm; (b) 12-13 days old, actual length 31 mm; (c) 30-31 days old, actual length 35 mm; (d) 55-57 days old, actual length 41 mm (after Bishop, 1941).

just posterior to the insertion of the hind legs. Grenell (1939) designated larvae between 35 mm and 60 mm as being three to nine months old. Bishop (1941) reported an average length of 57.08 mm for specimens collected approximately nine months after egg laying; i.e., about six and one-half months after hatching.

First Year Larvae

Smith (1907) collected four larvae in August that had presumably hatched the previous fall or early winter. They measured 64, 68, 70 and 83 mm respectively. Since these specimens were captured approximately one year from the time of egg laying, 68 to 70 mm may represent a rough estimate of the length attained by the hellbender during its first year.

Second Year Larvae

Larvae do not lose their gills until about a year and a half or two years after hatching (Grenell, 1939; Bogert, 1961). Reports of larval length at this stage vary from slightly over 100 mm to more than 130 mm. Bishop (1941) collected 16 specimens, presumed to be in their second year, that averaged 114.5 mm in length. The largest of the 16 had a total length of 137 mm and showed no evidence of gills. The largest hellbender with gill rudiments was 133 mm in length, and the smallest one without gills measured 107 mm in length. Seven of the 16 specimens without gills or rudiments averaged 120.8 mm as compared to 109.5 mm for the other nine specimens with gills or rudiments.

Two *C. a. bishopi* larvae taken on 11 March 1972 measured 95 and 130 mm. The smaller one was thought to be about one year and three months old (post-hatching). Six larvae taken during the summer months ranged from 110-130 mm, with a mean of 121.7 mm. The largest Ozark hellbender with gills measured 130 mm. The 95 mm larvae had far more poorly developed gills than the 130 mm larvae taken on the same date.

Three Year Larvae

Smith (1907) collected a series of six specimens during a single week in August that ranged from 140 mm to 267 mm in length with an average length of 196 mm. Since all of these hellbenders had lost their external gills, but had not yet reached sexual maturity, they may represent third year larvae.

Sexual Maturity

The exact period necessary for *Cryptobranchus* to attain sexual maturity is unknown. The smallest hellbender, a *C. a. bishopi*, to lay eggs in our laboratory measured 385 mm in length. Smith (1907, 1912) found that sexual maturity was attained in eastern forms of *C. a. alleganiensis* at a length of about 340 mm with smallest sexually mature male measuring 300 mm and the smallest sexually mature female measuring 350 mm. Smith estimated that three or four years were required from the time of fertilization until sexual maturity was reached. Bishop (1941) believed that sexual maturity may not be attained until about the fifth or sixth year. We believe Bishop's estimate to be a more realistic estimate of maturity for *C. a. bishopi* in the North Fork of White River.

Longevity, Growth and Size

Cryptobranchids may live 55 years in captivity (Nigrelli, 1954). One *C. alleganiensis*, in the Amsterdam Zoological Gardens, survived from 1902 until 1931 (Bogert, 1961). Almost nothing is known about their longevity under "non-captive conditions". Our recapture data indicate that *C. a. bishopi* are long lived (Table 8).

Additionally, upon attaining adult size the growth rate of *C. a. bishopi* is relatively slow (Table 8). The most rapid growth rates we observed were about a 2 cm/year length increase and a 109 g/year weight increase. Since weight was determined at the capture site, fluctuation in the amount of food in the digestive tract was a variable. However, only two of those *Cryptobranchus* recaptured at annual or biannual intervals weighed less than initial capture weight.

The longest hellbender recorded was a 74 cm *C. a. alleganiensis* taken in the Little Pigeon River in Gatlinburg, Sevier County, Tennessee (Fitch, 1947), while the longest *C. a. bishopi* recorded was 62.0 cm (Dundee, 1971). We have discovered Ozark hellbenders measuring about 57.0 cm in the Spring River, Fulton County, Arkansas. However, the longest of perhaps 2,000 *C. a. bishopi* collected in the North Fork of White River, Ozark County, Missouri measured 53.5 cm. There are certainly differences in the mean individual weight of *Cryptobranchus* between populations.

The largest Ozark hellbenders observed were taken from the Spring River, Fulton County, Arkansas. Their mean weight was 671 g (n=33). The smallest were from the Eleven Point River, Oregon County, Missouri, (mean weight = 193 g; n = 31), and the North Fork of White River, Ozark County, Missouri population was intermediate (mean weight 365 g; n = 435). A sample of *C. a. alleganiensis* from the Niangua River, Dallas County, Missouri had a mean weight of 777 g (n = 30). These data are more accentuated, since only the North Fork of White River sample was made in the field. The others were determined in the laboratory after most of animals had regurgitated their food during transport.

Several series of *Cryptobranchus*, used for blood research, were sexed by dissection after weighing. Weight data from these revealed that female *C. a. bishopi* from the Eleven Point River and the North Fork of White River, taken during early to mid-summer, had mean weights considerably greater than males while the opposite was true of *C. a. alleganiensis* from the Niangua River. The number of weight samples from all streams, excluding the North Fork of the White River, was small (n = 94). However, we have examined hundreds of other *Cryptobranchus* from these streams and believe that considerable differences in individual mean sizes exist between these populations. A comparison of total length data revealed no trend.

Anatomical Studies

Hellbender anatomy has received considerable attention. Branch (1959) published a hellbender laboratory manual and Jollie (1962) treats *Cryptobranchus* extensively in his comparative anatomy text. It is beyond the scope of this publication to condense all of this anatomical information. However, for the convenient reference of those involved in structural studies this material is summarized in Table 9.

IV. MAN AND HELLBENDERS

Perhaps no species of organism has escaped the effects of man's presence. Certainly hellbenders have not! Man has dammed, channeled and polluted much of the aquatic habitat in which they live or formerly lived.

Gentry (1955) recorded numbers of them dead in a reservoir following the impoundment of a stream in Tennessee. However, Brodie (1972) does not believe the impoundment of the Cumberland River (Old Hickory Dam) has caused "ill effects" to hellbender populations. Smith and Minton (1957) noted that man was actively shrinking their habitat. Silt and chemical pollutants are suspected of destroying the eggs and young (Minton, 1971). In some areas acid mine drainage is probably responsible for their demise (McCoy, 1971).

In our studies of Missouri hellbenders we have noted several other factors which we suspect affect local populations. The gigging season spans the reproductive season of the Ozark hellbender in the North Fork of White River and overlaps that of the hellbender elsewhere. We have found dead gigged specimens and Metter (1972) has data showing how susceptible they are to this method of destruction. The large numbers of Ozark hellbenders encountered with gashes cut in their heads, etc. suggest that heavy canoe traffic probably takes its toll of these animals. The force delivered by a canoe hitting a rock might easily damage or kill these animals.

The practice of dynamiting large boulders and rocks out of stretches of certain rivers; e.g., Current River, saves canoe renters money by reducing canoe damage. It may also reduce hellbender nesting sites. In 1971-72 a new canoe ranch operator "cleared to the bank" a section along our research stretch. The character of the bottom has been changed for several hundred meters downstream; i.e., sand and silt covered. The effects this may have on the river and its populations remain to be seen. Riverside cattle and hog pens also post a potential threat.

Not all of man's activities have adversely affected hellbenders. Alexander (1927) believed saw mill debris, along the Allegheny River, was a very important source for hellbender nesting sites. We observed an Ozark hellbender utilizing a one pound coffee can for shelter.

Myths, Misinformation, Folklore and Problems

The hellbender's appearance has been considered forbidding by many people, including early naturalists. Barnes (1826) notes the "terrible aversion that prevails" against an animal with such an "uncouth and revolting figure".

They have certainly been a problem to anglers. They are considered troublesome, often stealing bait or being caught (Townsend, 1882; Hibbard, 1936; Welter & Carr, 1939). Many fishermen cut their lines to keep from touching them and consider them exceedingly poisonous (Townsend, 1882; Barbour, 1971). Some claim that when hellbenders move in, fish leave or will avoid a line smeared with their slime (Beck, 1965). In actuality a hellbender may inflict a painful, but nonvenomous, wound with its teeth. The skin secretions may be toxic only when injected (Oliver, 1955; Brodie, 1971).

Dr. N. Bayard Green (1971) related how a former editor of the Pocahontas Times (Pocahontas, West Virginia) in 1926 continually tried to vilify the hellbender as a destroyer of game fish and their eggs. Throughout West Virginia many sportsmen's groups attempted to eradicate many of the so-called enemies of fish and game. Green (1933, 1935) found no evidence of their consumption of trout eggs and did not believe they were menaces to game fish.

Vernacular Names

North American Indian names for *Cryptobranchus* include Tokomeg (Chippeway Indians), Twechk (Minsi or Monsees Indians) and Tweeg or Tweche (Delaware Indians) (Barton, 1812; Harlan, 1827; Harper, 1940). It was described by Sonnini, as "la salamandre des monts Alleganis" or salamander of the Allegheny Mountains (Sonnini and Latreille, 1801; Harper, 1940). Since that time it has picked up an amazing variety of names including mud-devil, ground-puppy, vulgo, water-dog, leverian water newt, alligator, little alligator, Allegheny alligator, young alligator, alligator of the mountains, big water lizard, devil dog and hellbender (Barnes, 1826; van der Hoeven, 1866; Townsend, 1882; Holder, 1885; Morse, 1904; Alexander, 1927; Harper, 1940 and Cagle, 1942). The only name we can add to this list is "walking catfish".

The name hellbender was supposedly applied to this salamander by Negroes in Virginia, who so named it because "of its slow oscillatory motions in its natural habitation . . . " which slaves thought suggestive of the horrible tortures of the infernal regions" (Barton, 1812; van der Hoeven, 1866). However, Bogert (1961) stated that we didn't know the origin of the name hellbender and suggested that it was probably invented by an early fisherman . . . who concluded that "it was a creature from hell where it's bent on returning".

Utilization of Cryptobranchus

"What are they good for?" Verbatim, this was inevitably the first question we were asked by curious onlookers, when we answered their query, "What are you guys doing?"

From the anthropocentric viewpoint their utility for display within zoo's aquaria or possible as "exotic office conversation pieces" is obvious. Their live value on various animal lists during 1972 ranged from $15 to $35 each. Preserved non-latex injected specimens (10-12 in.) were bringing $4 in 1969-70 (Anonymous, 1969). They are reportedly excellent bait for muskellunge *(Esox masquinongy)* and northern pike *(Esox lucius)*, when used where there are no rocky bottoms (Beck, 1965).

Can you eat them? This was, of course, another question we received. Yes! Although we never tried them, Surface (1913) thought they would be at least as good as catfish. Brimley (1939), Swanson (1948), Beck (1965) and Minton (1972) mention human consumption, although Brimley stated they were "quite tough". Hellbender bones are common in many archeological sites in Pennsylvania (Guilday, 1961; Lang, 1968; and Buker, 1970). Lang (1968) treats them as a food item of Woodland Indians. However, Barton (1812) stated that the Indians in the vicinity of Lake Erie did not eat hellbenders but dried them for "purposes of witchcraft".

Probably the most innovative and bizarre use was thought up by a Pennsylvania resident who placed them in his "booze cache" (a lily pond) to scare away his mother-in-law (Beck, 1965). It worked!

Past and Present Populations

The following is an attempt to gage the status of *Cryptobranchus* populations. For utility this is presented on a state by state basis. It is based upon published accounts and communications from "representative state authorities". Unfortunately, a survey of all current museum collections is not included.

Alabama

Specimens are known from 1.5 mi W of Zip City in Little Cypress Creek (AUM 8738, 8739), 18.2 mi N of St. Florian in Butler Creek (AUM 16347) and 5.0 mi N of Florence (UMMZ 66760); all in Lauderdale County. Other specimens are from 10.0 mi NE of Huntsville in the Flint River at Three Forks, Madison County (AUM 8740); the Tennessee River, Morgan County (five specimens, UMMZ 115704); I-65 at Flint River (Flint Creek), Morgan County (JSU-A). They have also been taken in Flint River at Sulphur Springs and Walker Creek at Fisk, both sites in Madison County (Mount, 1971).

Current Status: Unknown, but undoubtedly, the channelizing and impounding of many of the Tennessee River tributaries by the Corps of Engineers and Soil Conservation Service has reduced the hellbender habitat.

Arkansas

Hellbenders are known from the upper Spring River near Mammoth Springs, Fulton County, Arkansas (Black and Dellinger, 1938; Dowling, 1957; Ratcliff, 1965). Downstream, Ozark hellbenders are occasionally caught on banklines near Hardy, Sharp County, Arkansas (Bruce Dietsche, 1972). We have specimens (MPM 4,402-4,415) from near Mammoth Springs, Fulton County.

Current Status: A large population of Ozark hellbenders exists along the upper Spring River. Presumably, populations of the North Fork of the White River were destroyed following the construction of the dam which formed Norfolk Lake. Populations possibly exist in the Current, Eleven Point and Black Rivers near the Missouri border.

Georgia

There are old records from Anderson and Abbeville (South Carolina side) on the Savannah River and from "Georgia" (USNM 5037) (Yarrow, 1882); Bishop, 1941). Neill (1957) collected a specimen (ERA and WTN 15653) in a tributary of the Savannah River near Wylie, Raburn County. Firschein (1951) reported hellbenders from coastal streams and upper headwater regions. Martof (1955) noted a specimen from a tributary of the Oconee River, Barrow County, in the Altamaha River drainage system. As other Georgia specimens were from the Tennessee River drainage, Martof considered introduction possible.

Current Status: Unknown.

Illinois

Hellbenders were probably first listed as part of the herpetofauna by Gerhard (1857). They are reported from tributaries of the Mississippi River (Davis and Rice, 1883); the Wabash River near Ridgway, Gallatin County (Garman, 1892); and near Maunie, White County (Stein and Smith, 1959); Cache River near Ullin, Pulaski County; and the Ohio River (in INHC) near Metropolis, Massac County; and Cave in Rock, Hardin County (Stein and Smith, 1959). They are also known from the Big Muddy and Mississippi Rivers (Cagle, 1942).

Current Status: Endangered or extinct. We know of no specimens collected since June 1956.

Indiana

Specimens are known from Evansville, Vanderburgh County (ENMC and USNM 9204); the Ohio River at Madison, Jefferson County (MCZ 14846) and New Harmony, Posey County (MCZ 247) (Wied, 1834; Yarrow, 1882; Hay, 1891; Meszoely, 1966). They are recorded from Whitewater River at Brookville, Franklin County; the Ohio River at Vevay, Switzerland County; near Vincennes, Knox County; and Madison, Jefferson County (Hay, 1891; Minton, 1972). The "Necturus", referred to by Blatchley (1891) in Vigo County were probably *Cryptobranchus*, since they were described as "two feet long or over". There are old records of hellbenders scattered along the length of the Ohio River, the Whitewater River to Brookville, the Blue River to Milltown and the Wabash River to near Terre Haute (Minton, 1971; 1972).

Current Status: Endangered. Only in the Blue River is it found in fairly good numbers (Minton, 1972).

In the early 1930's they were regularly caught in Silver Creek near New Albany, Floyd County (Minton, 1971). However, Dr. Minton has not seen a specimen from any stream other than the Blue River in about 20 years. By the 1950's what was left of the hellbender's habitat in Indiana was rapidly undergoing shrinkage as a result of human modification of stream habitat (Smith and Minton, 1957). In 1966 fisherman were still taking them regularly in the Blue River near Milltown, Crawford County (Minton, 1971). Dr. Minton suspects that a few hellbenders may be left in rocky tributaries, but believes silt and chemical pollutants have destroyed the eggs and young.

Iowa

The hellbender's presence in Iowa is mentioned by Cope (1889), Hay (1891), Pratt (1923), McMullen and Roudabush (1936), Bishop (1941), Firschein (1951) and Bogert (1961). Specific localities recorded are Ames, Boone County, Iowa and the Skunk River in the southeastern part of the state.

Current Status: Probably extinct, if ever present.

Kansas

Specimens (KSTC 586, 4562) are known from the Neosho River 8 miles west of McCune and one mile north of Riverton, Cherokee County (Hall and Smith, 1947; Smith, 1950).

Current Status: Dundee (1971) doesn't believe that the Neosho River is a suitable habitat for hellbenders.

Kentucky

Early naturalists recorded hellbenders from the Cumberland and Kentucky Rivers (Barton, 1812; Rafinesque, 1822). They are known from the Green River near Mammoth Cave, Edmonson County (including UKMNH 19472), the Triplett and Licking River drainage, Rowan and Carter (?) Counties (Hibbard, 1936; Welter and Carr, 1939; Hall and Smith, 1947; and Maldonado-Koerdell and Firschein, 1947). Its general distribution is statewide excluding that part of the state west of the Cumberland River (Barbour, 1971).

Current Status: Most common in the upper reaches of the Cumberland, Kentucky, Licking and Triplett River systems (Welter and Carr, 1939; Barbour, 1971).

Louisiana

Yarrow (1882) records a specimen (USNM 3879) from Prairie Mer Rouge. This and other references to the presence of hellbenders in Louisiana by Hay (1891), Pratt (1923), Rankin (1937), and Stejneger and Barbour (1917) are surely mistakes. It is believed that the early records; e.g., Cope (1889), were larval *Ambystoma talpoideum* (Grobman, 1943).

Maryland

Hellbenders are typically found only on the Piedmont Plateau and in the mountains (Hardy, 1972). These salamanders have been reported from the Susquehanna River drainage near Conowingo, Octoraro and Bald Friar in Cecil County (Fowler, 1915). McCauley and East (1940) reported them from the Youghiogheny River, Garret County. A specimen (MCZ 129) is known from the Chesapeake Bay Region, Havre du Grace, Harford County (Meszoely, 1966).

Current Status: Unknown. However, the Youghiogheny River Reservoir and development along the Susquehanna River must have greatly reduced the available habitat. They are now protected under Maryland's rare and endangered species law.

Michigan

Garman (1892) noted specimens from Ecorse, Wayne County, Michigan, a city located on the Detroit River. This record is presumably based on a misidentification. It is doubtful if a Michigan population ever existed. Records attributed to the Great Lakes by Barton (1812); Yarrow (1882); e.g., USNM 9205 are discredited by other authors (Smith, 1882; Bishop, 1941).

Mississippi

Ferguson (1961) obtained nine hellbenders from Bear Creek, Tishomingo County. This is on the Tennessee River drainage. They have not been found on the adjacent Tombigbee River watershed.

Current Status: Although apparently restricted to a small area, this population appears to be holding its own. Presumably the damming of the Tennessee River to form Pickwick Lake, has destroyed much of the original hellbender habitat.

Missouri

Hellbenders have been recorded from Phelps, Jefferson and Dallas Counties (Hurter, 1897; Boyer and Heinze, 1934; Firschein, 1951; and Wortham, 1970). There are specimens from Camden, Franklin (UKNHM), Dent (USNM 99751) and Dallas (MPM 4417-4418) Counties (Grobman, 1943; Duellman, 1972). They are known from tributaries of the Meramec, Osage, the Big Piney, Gasconade, Niangua Rivers and other streams of the Missouri-Mississippi River drainage (Grobman, 1943; Firschein, 1951; Dundee and Dundee, 1965; Woolley, 1973).

Ozark hellbenders are reported from Dent, Douglas, Carter, Ozark and Oregon Counties (Grobman, 1943; Firschein, 1951; Myers, 1959; Meszoely, 1966; Wortham, 1970). Fishermen claim their presence in the upper Black River, and they may occur in the St. Francis River, which flows directly into the Mississippi River (Firschein, 1951). The Vernon County record (UKNHM 16143) is discredited by Firschein (1951).

There are specimens from Carter (MCZ 27792, UMMZ 68930), Douglas (UKNHM 27814), Oregon (UMMZ 68415, 68897, 68916, 68929-68932; USNM 57042, 94356; AMNH 23053, 23054) and Ozark (MPM 4200, 4202, 4282, 6118) Counties (Grobman, 1943; Firschein, 1951; Meszoely, 1966).

Current status: Although the hellbender's range has undoubtedly been affected by damming and pollution, large populations exist in the Bourbeuse, Meramec, Niangua and Gasconade Rivers (Metter, 1972; Wilkinson, 1972; Woolley, 1973). Large populations of Ozark hellbenders exist in sections of the Current and Eleven Point Rivers (Black River system) and the North Fork of the White River.

New Jersey

Alexander (1927) mentions a successful "stocking" of the Delaware River with hellbenders. Mr. Henry W. Fowler suggested that New Jersey specimens were probably introduced about 1860. Philadelphia citizens, who became uninterested in maintaining them in aquaria, presumably released them in the Delaware Valley (Surface, 1913). This might imply a New Jersey population. However, no specimens have been recorded from there recently.

Current Status: It would appear that no hellbender populations are extant from this "supposed stocking".

North Carolina

Hellbenders were recorded as early as 1812 and a specimen, USNM 9202, is known from Hillsboro (Hillsborough), Orange County (Barton, 1812; Yarrow, 1882; Cope, 1889). They occur in streams on the North Carolina slopes of the Great Smoky Mountain Park (Huheey and Stupka, 1967). Brimley (1939) reported them from Ashe, Buncombe, Cherokee, Madison, Transylvania and Yancey Counties.

Current Status: Unknown, but presumably those populations within the Great Smoky Mountain Park are not in danger.

New York

Within New York, hellbenders are restricted to the Allegheny and Susquehanna River systems (Bishop, 1941).

There are specimens from Allegheny (USNM 7068, NYSM 3084), Broome (UR 3879), Cattaraugus (NYSM 3080-3083, 3065, 3079, 3281; UR 1236, 1278-85; CM 4054), Chenango (NYSM 4796), and Delaware (MCZ 1281) Counties (Yarrow, 1883; Cope, 1889; Bishop, 1927; Bishop, 1941). Those recorded from the Great Lakes (Yarrow, 1883; Cope, 1889) and Cayuga Lake (Dunn, 1918; Meszoely, 1966) are doubtlessly mislabeled (Bishop, 1941).

Additionally, hellbenders are recorded from New York by Barton (1812), Harlan (1825), DeKay (1842), Allen (1869), Grote (1877), Eckel and Paulmier (1902), Dunn (1918), Pratt (1923), Stejneger and Barbour (1923), Alexander (1927), and Chezar (1930).

Grote (1877) mentions collecting 100 during July and August. Alexander (1927) and Bishop (1927) indicated they were common, during breeding season, along parts of the Allegheny drainage. They specifically sited Oswaya and Wolf Run Creeks in Cattaraugus County.

Current Status: Unknown.

Ohio

Barton (1812) reported these salamanders in many Ohio streams. Early general state references include Smith (1882) and Morse (1904). Specimens are known from near Poland, Mahoning County (USNM 7055); near Henley, Scioto County (OSM 220); Athens County (OU Zool. Dept.); and Washington County (MC) (Yarrow, 1882; Seibert and Brandon, 1960). They have been recorded from the Ohio river near Marietta, Washington County (Krecker, 1916) and are reported from numerous other sites along this drainage.

Current Status: Industrialization and changes in agricultural practices have greatly modified and reduced the hellbender's habitat in Ohio.

Pennsylvania

In Pennsylvania *Cryptobranchus* has a complicated distribution pattern. It occurs in the Allegheny River from the headwaters (Potter and McKean Counties) to the mouth (Allegheny County). Most of the localities in the western tier of counties are from major tributaries of the Allegheny (French Creek, Oil Creek, Shenango River and the Conemaugh-Kiskiminitas System). They are also found in Beaver River, which enters the Ohio from the north downstream. Hellbenders occur in the headwaters of the Monongahela River, and in the Youghiogheny drainage. The Indiana County localities are all in the Allegheny drainage, in the Conemaugh and Mahoning drainages. The Clearfield site, however, is in the West Branch of the Susquehanna River drainage. *Cryptobranchus* is widespread in the West Branch tributaries, and extends downriver some distance (Bainbridge, Lancaster County) and upriver in the main branch (Tunkhannock, Wyoming County). There are numerous records in the southcentral part of the state from the Juniata River drainage, a main tributary of the Susquehanna (McCoy, 1971).

John Bartram logged information about a small "alligator" near Ft. Pitt, Allegheny County, in 1762 (Barton, 1812). Early references attributing the hellbender's presence within the state include Hay (1891), Smith (1912) and Alexander (1927). They are recorded from Beaver, Crawford, Cumberland, Dauphin, Erie, Indiana, Lancaster, McKean, Somerset, Venango, Westmoreland and York Counties (Townsend, 1882; Surface, 1913; LaRue, 1914; Keim, 1915; Bishop, 1925; Raney and Lachner, 1939; Swanson, 1948; Smith, 1950; Beck, 1965 and Hillis and Bellis, 1971).

Additionally, there are specimens from Allegheny (CM, AMNH, ANSP); Beaver (ANSP); Butler (CM); Clearfield (CM); Crawford (CM, FM, AMNH, USNM); Erie (UMMZ); Greene (CM); Indiana (ANSP, CM); McKean (CM); Mercer (CM); Mifflin (ANSP); Perry (CM); Potter (ANSP); Somerset (CM); Venango (FM, CM, USNM, AMNH); Warren (UMMZ, AMNH, USNM); Westmoreland (CM, FM, ANSP, USNM) and Wyoming (CM) Counties (Yarrow, 1882; Netting, 1929; McCoy, 1971).

Current Status: Many of the streams in western Pennsylvania have been sterilized by acid mine drainage. The "big river" populations are probably all gone. However, Pennsylvania still has large populations of hellbenders in scattered localities (McCoy, 1971).

South Carolina

Yarrow (1882), Hay (1891), Bishop (1941) and Neill (1957) list old records; e.g., USNM 7005, from Abbeville, Abbeville County and Anderson, Anderson County on the Savannah River drainage. Dunn (1918) and Meszoely (1966) cite a Charleston, Charleston County, record (MVZ 256). Pickens (1927) questions the Abbeville records.

Current Status: Unknown.

Tennessee

Barton (1812) and Troost (1844) noted the presence of the hellbender in the state. Cope (1889) and Rhoads (1895) mentioned its presence in the Tennessee River near Knoxville. Specimens are known from Tyree Springs (Tyree's Springs), Davidson County (USNM 7069); the Nolichucky River (Nolachucky or Nol'lichuck River), Greene and Washington Counties (USNM 7004); Little Pigeon River, Gatlinburg, Sevier County, Tennessee (SMNPNHC); and the Tennessee River at Pickwick Dam, Hardin County (F-HCC) (Yarrow, 1882; Peale, 1886; Fitch, 1947; Endsley, 1954). They are reportedly widespread in the Cumberland and Tennessee River systems (Gentry, 1955; Johnson, 1958). They probably occur in most of the larger streams within the Great Smoky Mountains National Park below 2,200-2,500 ft. (King, 1939). Hellbenders have been taken in every major drainage system of the park save those east of the Balsam Mountains (Huheey and Stupka, 1967).

Current Status: Damming along the Tennessee River has decreased " liveable hellbender habitat" and apparently killed off some populations. They are common in sections of the Cumberland and Tennessee River systems, except for the western tributaries of the Tennessee River (Gentry, 1955).

Virginia

By 1802 this species was known from the state (Barton, 1812). Hutchison (1956) noted that hellbenders were common in the New River and its tributaries in Giles County. Specimens were collected at Ripplemead in Wolf Creek and in Spruce Run. Bogert (1961) found them near Radford, Montgomery County.

Current Status: Unknown.

West Virginia

There are specimens (WVSC-MU) from Cabell, Clay, Greenbrier, Kanawha, Marshall, Monroe, Nicholas, Pocahontas, Randolph, Ritchie, Summers, Tucker, Tyler, Wayne, Webster and Wyoming Counties, and published records exist for Marion and Monongalia Counties (N. Bayard Green, 1961, 1969, 1971).

In 1933 hellbenders were rather common in the Ohio River (except tributaries near Huntington), and plentiful in the Cheat River and its tributaries, the Monongahela and Greenbrier Rivers (Bond, 1931; Green, 1933, 1937). They are often caught by fishermen from the Little Kanawha River on the Ohio River drainage (Green and Dowler, 1966). There are apparently no records from the Atlantic or Potomac drainage of West Virginia (N. Bayard Green, 1971).

Current Status: Green (1933) believed that hellbenders were more abundant in West Virginia than any other area of the Ohio River drainage. Although its habitat has been reduced by damming, mining and other developments, large populations of hellbenders are extant in West Virginia.

TABLE 1

Mean Discharge (cu. ft./sec.) of the North Fork of the White River

Day	Discharge
28 January 1969	1,310
29 January 1969	4,210
30 January 1969	18,500
31 January 1969	4,890
1 February 1969	3,480
2 February 1969	2,810
3 February 1969	2,330
4 February 1969	1,980

From U. S. Geological Survey, 1969-1971

TABLE 2

Water Analysis Ozark County, Missouri Research Site

	North Fork of the White River (Blair's Ford)						Spring Creek (Brockman's Ford)					
Date	Temperature °C		Dissolved O_2 ppm	CO_2 ppm	Alkalinity Methyl Orange ppm	pH	Temperature °C		Dissolved O_2 ppm	CO_2 ppm	Alkalinity Methyl Orange ppm	pH
	Air	Water					Air	Water				
21 February 1970	16.5	9.8	12.8	** 0	191	8.10						
7 March	14.4	11.1	10.4	9.8	192	8.00						
2 April	15.1	13.1	11.6	4.5	153	7.80						
18 April	19.7	15.4	10.6	2.0–3.0	170	8.90						
22 April	24.9	14.4	10.6	2.5	130	9.00						
4 June	16.0	17.9	9.0	6.5	152	— —	25.0	17.0	9.4	6.0	168	— —
10 June	28.0	17.0	9.8	3.0	156	— —	28.0	17.0	9.0	2.0	166	— —
12 June	25.0	18.6	8.4	2.0	164	— —						
17 June	28.0	18.0	9.6	3.5	188	7.80						
18 June							25.0	17.0	9.6	4.5	174	7.50
25 June	27.0	19.0	9.4	2.5	170	— —	26.5	17.5	10.4	5.0	188	— —
1 July	27.0	19.5	9.2	3.5	170	7.60	27.0	19.0	9.2	4.5	154	7.60
8 July	28.5	22.5	12.4	1.0	126	8.00	28.5	20.2	10.6	1.5	148	7.60
16 July	26.0	19.5	10.0	1.5	136	— —	23.5	18.0	10.4	4.6	156	— —
22 July	25.5	21.5	12.2	0	130	— —	23.5	20.0	10.4	0	158	— —
5 August	29.8	20.0	8.8	2.0	142	7.60	27.8	17.3	8.2	3.5	162	7.60
13 August	26.0	19.0	9.6	1.0	158	7.90	25.0	17.0	6.0	1.0	200	7.80
19 August	27.0	22.0	11.2	0	140	7.70	31.0	20.5	10.0	0	164	7.60
12 September	29.5	21.0	11.6	0	158	7.70	28.5	20.0	11.8	0	168	7.60
26 September	16.0	17.0	9.6	3.0–4.0	144	8.29	14.5	16.5	9.6	0–1.0	166	— —

(continued)

TABLE 2 (Cont.)

Date	North Fork of the White River (Blair's Ford) Temperature °C Air	Water	Dissolved O_2 ppm	CO_2 ppm	Alkalinity Methyl Orange ppm	pH	Spring Creek (Brockman's Ford) Temperature °C Air	Water	Dissolved O_2 ppm	CO_2 ppm	Alkalinity Methyl Orange ppm	pH
10 October	11.5	14.0	10.8	2.0	126	8.00	15.0	– –	10.0	1.0–2.0	170	8.08
24 October	21.0	16.0	11.4	0–1.0	134	8.25	20.0	16.0	11.2	0–1.0	158	8.21
21 November*	15.0	11.0	11.6	5.0	122	8.17	16.0	14.0	11.6	4.0–5.0	122	8.08
6 December	8.0	12.0	9.6	3.0	– –	– –	9.0	12.0	10.4	3.5	300+	– –
30 January 1971*	7.0	10.0	11.2	1.5	– –	7.95						
30 January	8.0	11.0	12.8	0	– –	8.04						
12 March*	21.0	13.0	10.4	3.0	173	8.32						
12 March	21.5	13.0	12.0	2.0	171	8.35						
3 April	17.0	12.0	12.0	3.0	179	8.07						
3 April*	18.5	12.0	11.2	1.5	201	8.11						
24 April*	19.0	14.5	13.6	5.0	228	7.75						
24 April	22.0	14.5	10.4	4.0	223	7.80						
15 May*	20.0	15.0	9.6	2.5	231	7.95						
15 May	24.4	15.0	10.0	2.0	289	7.85						
29 May*	– –	– –	11.8	3.5	240	– –						
29 May	– –	– –	10.4	3.0	232	– –						
30 June*	23.3	20.0	10.4	0	– –	– –						
30 June	23.3	19.4	10.8	0	– –	– –						

* North Fork of White River at Althea Springs campground, immediately downstream from Patrick Bridge.

**Indicates that levels were insufficient to be measured (Cooper & Nickerson, 1971)

TABLE 3

Lengthy Movements of Ozark Hellbenders
in the North Fork of White River, Ozark County, Missouri

Number	Date Tagged or Released	Station of Tagging or Release	Date of Recapture	Station of Recapture	Direction of Movement	Distance Moved (m)
110	6-19-69	28	7-17-69	17	upstream	990
	7-17-69	17	7-28-69	16	upstream	60
383	7-23-69	7	8-10-69	0 (200 m above)	upstream	900
54	6-18-70	2	6-26-70	8	downstream	525
	6-26-70	8	8-4-70	2	upstream	525

TABLE 4

Stomach and Intestinal Contents of 40 *Cryptobranchus a. bishopi* From North Fork of the White River, Ozark County, Missouri

(Nickerson & Selby, 1969).

Item	Frequency Encountered
Crayfish — *Orconectes* sp.	87.5%
Snails — *Goniobasis livescens, Pleurocera acutum, Somatogyrus subglobosus*	52.5%
Mayfly nymphs including *Tricorthodes* sp.	12.5%
Unidentified animal material	10.0%
Leaves	2.5%
Small rocks	77.5%
Sand	10.0%

Stomach Contents of 34 *Cryptobranchus a. alleganiensis* From the Headwaters of Shavers Fork of Cheat River, West Virginia (Green, 1935)

Crayfish	59.0%
Insects, worms and tadpoles	21.0%
Fish	35.0%
Extraneous material (leaves, mud, pebbles, and sticks)	53.0%
Empty	3.0%

TABLE 5

Hematology of Hellbender Salamanders, *Cryptobranchus alleganiensis*
(from Wintrobe, 1933 and Jerrett & Mays, 1972)

	Lymphocytes %	Monocytes %	Leukocytes Eosinophiles %	Neutrophiles %	Basophiles %
C. a. alleganiensis	40.0	0.0	5.0	50.0	5.0
	66.6	9.3	4.0	20.7	0.0
C. a. bishopi	60.7	8.3	4.9	25.9	0.0

	Blood pH 25°C	Hematocrit % Cells	Hemoglobin g/100 ml	Coagulation Time Seconds	Erythrocyte Fragility % NaCl for Lysis
C. a. alleganiensis	7.43	43.33	10.07	61.94	0.096
C. a. bishopi	7.39	40.08	8.32	80.40	0.090

	Erythrocytes No. per mm^3	Erythrocytes Diameter	Leukocytes No. per mm^3	Thrombocytes No. per mm^3
C. a. alleganiensis	70,000	40.5 x 21.0	1,900	
	72,544	49.8 x 26.8	179	5,827
C. a. bishopi	92,713	43.5 x 24.6	198	4,863

TABLE 6

Mean Values of Various Serum Constituents of Freshly Collected *Cryptobranchus a. alleganiensis.*

S.D. $\bar{x}$ are in parenthesis. N=6. (From Stone, 1971).

Serum Constituent	Mean ($\bar{x}$) Value
Calcium	9.4 (1.4) meq/1
Inorganic Phosphorus	5.3 (0.8) mg/100 mlP
Glucose	56 (25) mg/100 ml
Blood Urea Nitrogen	1.4 (0.7) mg/100 mlN
Uric Acid	0.4 (0.1) mg/100 ml
Cholesterol	86 (49) mg/100 ml
Total Protein	3.0 (0.6) g/100 ml
Albumin	0.4 (0.1) g/100 ml
Alkaline Phosphatase	224 (70) micro-units/ml
Lactic Dehydrogenase	265 (219) micro-units/ml
Serum Glutamic Oxaloacetic Transaminase	145 (34) micro-units/ml
Total Bilirubin	0.1 (0) mg/100 ml

TABLE 7

Temperature Tolerance of *Cryptobranchus a. alleganiensis* from Reese (1906b).

Temperature of Initial Tank	Temperature of Transfer Tank	Reactions
18° C	33° C	None
5° C	26° C	None
14° C	26° C	"signs of slight discomfort"
18° C	42° C	violent struggles within two or three seconds
26° C	5° C	None
18° C	0° C	None

TABLE 8

Growth Data From Tag-Recapture Studies of Ozark Hellbenders in the North Fork of White River, Ozark County, Missouri. Lengths Are Expressed as Total Lengths and Weight in Grams.

Tag No.	1970 Captures	1971 Recaptures	1972 Recaptures
79	24 June/27.5cm/130g		24 Sept./30.5cm
80	24 June/37.0cm/336g	17 June/37.5cm/445g	12 June/38.5cm
82	24 June/34.5cm/253g	17 June/34.5cm/300g	
106	26 June/34.8cm/317g	1 July/37.0cm/382g	
125	1 July/32.5cm/285g	1 July/33.3cm/294g	
185	7 July/39.0cm/405g	17 June/40.0cm/434g	
187	7 July/37.0cm/344g	17 June/37.0cm/402g	
201	15 July/37.0cm/447g	17 June/39.0cm/494g	
207	15 July/39.7cm/383g		7 June/40.0cm
208	15 July/47.5cm/841g	17 June/47.5cm/767g	
210	15 July/42.5cm/593g		20 June/43.5cm/630g
212	15 July/41.0cm/509g		12 June/41.5cm
232	22 July/40.0cm/444g	1 July/41.0cm/427g	
242	24 July/50.5cm/955g		20 June/50.5cm/1044g
243	24 July/45.0cm/619g		1 July/45.5cm/685g
286	11 Aug./33.0cm/250g	17 June/34.5cm/309g	

TABLE 9

"Anatomical Studies" concerning *Cryptobranchus*. Listing is by "Anatomical System" and Reference. (See Bibliography).

SYSTEMS AUTHOR	General	Integumentary	Skeletal	Muscular	Nervous	Circulatory	Endocrine	Respiratory	Digestive	Excretory	Reproductive
Alexander, 1927	X										
Baker, 1949							X				
Barnes, 1826	X										
Barton, 1812	X	X						X			
Baur, 1888			X								
Bernstein, 1953		X									
Bishop, 1941	X							X			
Bishop, 1947	X										
Branch, 1959	X	X	X	X	X	X	X	X	X	X	X
Browman, 1937							X		X		
Bruner, 1914				X				X			
Chezar, 1930					X						
Cope, 1866			X								
Cope, 1888			X								
Cope, 1889	X		X								
Craigie, 1938					X	X					
Daudin, 1802	X										
Despax, 1922	X										
Dundee, 1971	X										
Dunn, 1941			X	X	X						

(continued)

TABLE 9 (Cont.)

AUTHOR \ SYSTEMS	General	Integumentary	Skeletal	Muscular	Nervous	Circulatory	Endocrine	Respiratory	Digestive	Excretory	Reproductive
Edgeworth, 1922			X	X				X			
Edgeworth, 1935			X	X	X						
Estes, 1965	X										
Fisher, 1864	X		X	X	X						
Fox, 1957			X		X						
Fox, 1962					X					X	
Furbringer, 1922			X	X							
Gage, 1885a		X							X		
Gage, 1885b		X							X		
Gage, 1891		X							X		
Garman, 1896	X										
Grenell, 1939					X		X				
Griffin, 1961			X								
Grobman, 1943	X										
Guimond, 1970	X							X			
Harlan, 1825	X		X			X		X	X	X	X
Harlan, 1827	X								X		
Hay, 1892	X	X									
Hillis, 1969	X										
Hilton, 1948			X		X						
Hilton, 1950			X								
Hilton, 1951			X						X		

(continued)

TABLE 9 (Cont.)

AUTHOR (SYSTEMS)	General	Integumentary	Skeletal	Muscular	Nervous	Circulatory	Endocrine	Respiratory	Digestive	Excretory	Reproductive
Hilton, 1952a					X	X					
Hilton, 1952b			X	X		X		X			
Hilton, 1959				X							
Hilton, 1962			X	X	X						
Hoffman, 1930			X								
Holbrook, 1842	X										
Hughes, 1967								X			
Johnson, 1958	X										
Johnson, 1971	X										
Jollie, 1962	X		X	X		X			X		
Kerr, 1960		X							X		
Kingsbury, 1896					X						
Kingsbury & Reed, 1909			X	X	X						
Kuhn, 1965	X										
LeConte, 1824	X										
Leuckart, 1821	X										
Lucas, 1886			X								
Low, 1926			X	X							
Luckhardt & Carlson, 1921					X			X			
Mason, 1965		X			X						

(continued)

TABLE 9 (Cont.)

AUTHOR	SYSTEMS: General	Integumentary	Skeletal	Muscular	Nervous	Circulatory	Endocrine	Respiratory	Digestive	Excretory	Reproductive
McGregor, 1896					X						
McGregor, 1897	X										
Meszoely, 1966			X								
Minton, 1972	X										
Mivart, 1869				X	X						
Mivart, 1870			X								
Noble, 1925		X		X		X		X			
Oliver, 1955	X										
Osborn, 1884					X		X				
Osborn, 1888					X						
Parker, 1885			X		X						
Piatt, 1939				X	X	X		X			
Piatt, 1940				X							
Pratt, 1923	X										
Ratcliff, 1965	X									X	X
Reeder, 1964									X		
Reese, 1903	X										
Reese, 1905a		X							X		
Reese, 1905b		X		X	X						
Reese, 1906			X			X		X		X	
Richmond, 1964			X								
Riss et al, 1963					X		X				

(continued)

TABLE 9 (Cont.)

AUTHOR	SYSTEMS General	Integumentary	Skeletal	Muscular	Nervous	Circulatory	Endocrine	Respiratory	Digestive	Excretory	Reproductive
Saunders, 1935	X						X				
Shmal'gauzen, 1964			X	X	X						
Smith, 1907					X	X					
Smith, 1911		X									
Smith, 1912	X										
Smith, 1961	X										
Steven, 1963		X			X		X				
Surface, 1913	X										
Thenius, 1954			X								
Walls, 1942	X				X						
Wellborn, 1936	X										
Wiedersheim, 1887	X		X								
Wilder, 1892			X		X						
Wonderly, 1963						X			X		
Wortham, 1970	X										
Young, 1965	X		X								

TABLE 10

Explanation of Abbreviations for Institutions

Throughout the text these abbreviations are used for the following museums or private collections.

AMNH = American Museum of Natural History

ANSP = Academy of Natural Sciences of Philadelphia

AUM = Auburn University Museum

CM = Carnegie Museum

ERA = E. Ross Allen

F-HCC = Freed-Hardeman College, Henderson, Tennessee

FM = Field Museum of Natural History

INHC = Illinois Natural History Collection

JSU = Jacksonville State University (Alabama)

KSTC-Pittsburg = Kansas State Teachers College

MC = Marietta College, Marietta, Ohio

MCZ = Museum of Comparative Zoology, Harvard

MPM = Milwaukee Public Museum

MVZ = Museum of Vertebrate Zoology, Berkeley

OSM = Ohio State Museum

OU Zool. Dept. = Ohio University Zoology Department

SMNPNHC = Smoky Mountain's National Park Natural History Collection

UKMNH = University of Kansas Museum of Natural History

UMMZ = University of Michigan Museum of Zoology

UR = University of Rochester

USNM = United States National Museum

WTN = Wilfred T. Neill

WVBS-MU = West Virginia Biological Survey — Marshall University

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