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A NEW PLIOCENE SPECIES OF *AMBYSTOMA*, WITH REMARKS ON OTHER FOSSIL AMBYSTOMIDS

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CONTENTS

INTRODUCTION

URODELE remains have been recovered from various deposits of Middle Pliocene to late Wisconsin age in many localities in western Kansas and northwestern Oklahoma. The majority of specimens are dissociated, commonly incomplete, individual bones. Although all are referable to the family Ambystomidae, the collection from any given deposit, in most instances, is inadequate for positive specific identification. The species represented, however, are related to the *tigrinum* (tiger salamander) group of *Ambystoma.*

Nearly all of the specimens are deposited and catalogued in the University of Michigan Museum of Paleontology and the University of Kansas Museum of Vertebrate Paleontology.[1] Dr. C. W. Hibbard, Curator of Vertebrates at Michigan and Dr. Robert W. Wilson, Associate Curator of Vertebrate Paleontology at Kansas, have generously permitted me to examine their collections. I wish to acknowledge my indebtedness to them for this courtesy and also their assistance and suggestions in the preparation of this report. I am obligated to Dr. E. H. Taylor, of the University of Kansas Museum of Natural History; Dr. Karl P. Schmidt, of the Chicago Natural History Museum; Dr. Hobart M. Smith, of the University of Illinois; and Dr. Coleman J. Goin and Dr. Arnold B. Grobman, of the University of Florida, for assistance in procuring comparative skeletal material of Recent forms.

[1] The abbreviations U.M.M.P. (University of Michigan Museum of Paleontology) and K.U.M.V.P. (University of Kansas Museum of Vertebrate Paleontology) are used to identify the specimens in the two institutions.

Two deposits that yielded extensive collections of Ambystomidae have already been studied. They are the Middle Pliocene Edson beds of Sherman County, Kansas, from which Adams and Martin (1929) described *Plioambystoma kansense,* and the late Wisconsin Jones Ranch beds of Meade County, Kansas, from which Tihen (1942) recorded a neotenic population of *Ambystoma tigrinum.*

My study deals with a third large collection, which was accumulated during the summers of 1947 to 1952, particularly that of 1950, by field parties from the University of Michigan Museum of Paleontology. It contains approximately 1750 isolated bones or parts of bones, and is from the Upper Pliocene Fox Canyon section (see Hibbard, 1950, pp. 120–21) of the Rexroad formation of Meade County, Kansas. Nearly 1100 are trunk and caudal vertebrae, but there are 76 centra of cervical vertebrae, which indicates a minimum of 76 animals. At least two types of individuals occur. The differences between them are such that they are considered larval and adult stages of a single species. A count of skeletal structures, such as dentaries, premaxillae, and others, having distinct ontogenetic characteristics, gives a ratio of about 70 per cent from larval to 30 per cent from adult animals. Other features less accurately determinable, as the extent of variation of ossification of the epiphyseal parts of the limb bones, give the same proportion of larvae to adults. As far as one can determine all larvae are normal larvae. There is no evidence of neoteny.

I take great pleasure in naming the species, which is new, in honor of Dr. Claude W. Hibbard, whose efforts have contributed greatly to the knowledge of the late Cenozoic vertebrate faunas of Kansas.

SYSTEMATIC DESCRIPTION

Ambystoma hibbardi, sp. nov.

(Pl. I; Fig. 1A, C and E–F)

Holotype.—U.M.M.P. No. 31440, the posterolateral part of a left prevomer (see Fig. 1A; cf. Fig. 1B).

Paratypes.—U.M.M.P. No. 31616, a complete right premaxilla (Fig. 1C); U.M.M.P. No. 31617, a left otic capsule (Fig. 1E).

Horizon and type locality.—Upper Pliocene, Rexroad formation, Rexroad fauna. Locality UM-K1-47, Fox Canyon, XI Ranch, sec. 35, T. 34 S., R. 30 W., Meade County, Kansas.

Diagnosis.—A species of *Ambystoma* that closely resembles the extant *A. tigrinum* in size (the estimated snout to vent length approximates 100 mm.), proportions, and general features. *A. hibbardi* agrees with *A. tigrinum*

in the absence of a diastema in the prevomerine tooth series at the level of the choana, in the possession of a nearly straight-sided parasphenoid, and in similarity of form and proportions of the vertebrae. It differs from it in having a narrower premaxillary spine, in the apparently usual failure of the columellar footplate to fuse with the otic capsule, and in the probable faulty ossification of certain cartilage bones, particularly the orbitosphenoids, quadrates, and ischia.

Description of holotype.—The original anterior-posterior length cannot be determined because part of the prevomer is missing. The portion of the tooth row preserved is 5.7 mm. long, but the medial section (probably about 1.6 mm.) is lacking; about 2.3 mm. of the tooth row lies laterad of the medial border of the choana. The teeth are absent; approximately 35 tooth bases, somewhat eroded, are present. The full number of teeth on a complete prevomer would probably be about 45. The extent of the choanal border comprises slightly less than a semicircle.

Description of paratypes.—U.M.M.P. No. 31616, a premaxilla (Fig. 1C), has a chord width of the dentigerous portion of 4.9 mm. and a depth of 1.1 mm. The chord length of the spine, including the dentigerous portion, is 7.7 mm.; the width, 1.6 mm. Corresponding measurements for a specimen of *A. tigrinum mavortium* (Fig. 1D) are: width of dentigerous part 6.0 mm., depth 1.2 mm.; length of spine 7.4 mm., width 1.8 mm. No. 31616 lacks teeth but has 23 tooth bases. The spine arises from the extreme medial edge of the dentigerous part, so that a premaxillary fontanelle, if not absent, was very small.

U.M.M.P. No. 31617, an otic capsule (Fig. 1E), has a total length of 7.7 mm. and a maximum depth 3.7 mm. The foramen ovale has a vertical diameter of about 2.2 mm. and a longitudinal diameter of about 2.8 mm. In general form and in arrangement of the foramina the specimen is practically identical with the corresponding skeletal part in advanced or neotenic larvae of *A. tigrinum.* It primarily differs from the otic capsule in adult *tigrinum* in the absence of a fused columellar footplate. There is reason to believe (see below) that the failure of the columella to fuse with the otic capsule is a normal condition in adult *hibbardi,* despite the similarity to the larval condition in the Recent species.

Referred material.—Topotypes: U.M.M.P. Nos. 27187, 27189, 27190, 27195, 31234, 31235, 31261, 31618, and 31619. These specimens were the source of the following descriptions of individual skeletal structures.

Premaxillae: Six, in addition to the paratype. Only one exhibits the adult condition, the remainder are larval, with the spine arising from the dentigerous portion lateral to its medial border. One larval specimen, with an apparently complete tooth row, has bases for 18 teeth.

Maxillae: Eight, all incomplete. Two have nearly complete tooth rows, with bases for 29 to 30 teeth. The full number of maxillary-premaxillary teeth in adults was 55 to 60 on each side.

Dermal roofing bones: (1) Nasals and prefrontals were not found. These fragile bones are very rare in the large collections of *Plioambystoma* from Sherman County, Kansas, and of *Ambystoma* from the Jones Ranch beds of Meade County, Kansas; hence, their absence from the Rexroad fossils in Meade County is to be expected, even though presumably they occurred in *A. hibbardi.* (2) A single frontal, fifteen parietals or parietal parts, and six squamosals were found. The parietals vary in proportions and in the extent and details of arrangement of the parietal crests; these variations are believed to primarily represent ontogenetic differences. The squamosals and frontal are essentially identical with those of *A. tigrinum.*

Pterygoids: Pterygoids were not found. Compared with the number in the Sherman County and Jones Ranch collections, only one or two pterygoids were expected for a collection of this size. Absence of any is probably a matter of chance. They are presumed to have been present in *A. hibbardi* and resemble the pterygoids of *A. tigrinum.*

Prevomers: Two: the holotype, the only adult specimen, and one other, a larval prevomer.

Parasphenoids: Four occur, a slightly smaller number than expected. In three the sides are nearly parallel, in the fourth there is a slight expansion of the part underlying the otic region. The shape and extent of variation in shape agree closely with conditions in Recent members of the *tigrinum* group.

Dentaries: One hundred and one, all incomplete but some very small parts. Sixty-nine are believed to be larval, 32 adult. Although the interpretation of a few of the smaller fragments is doubtful, this number is too

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Figure 1 ⇛➤

(All figures approximately 8 times natural size)

A.—*Ambystoma hibbardi,* holotype (U.M.M.P. No. 31440); posterolateral part of left prevomer.

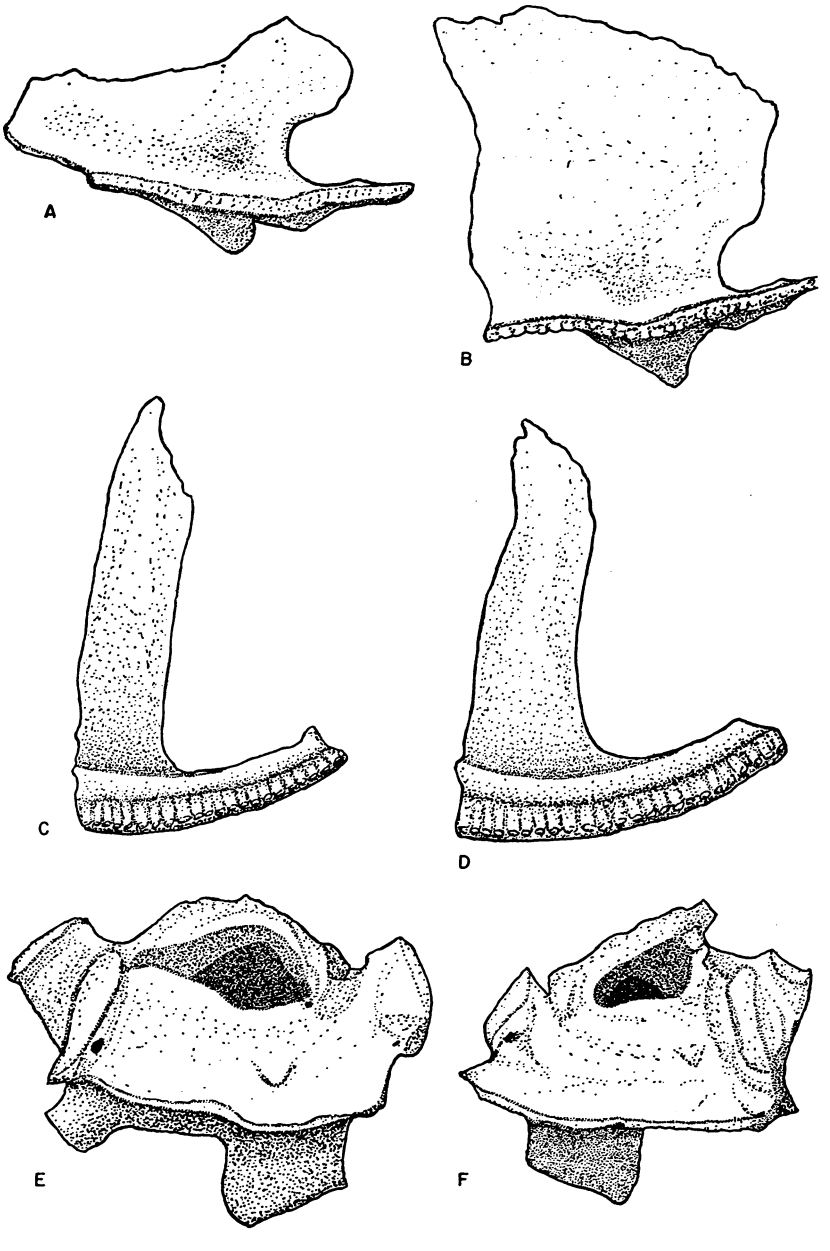
B.—Left prevomer of *A. tigrinum mavortium,* for comparison. Note the similarity in shape of the choanal border and general form.

C.—*A. hibbardi,* paratype (U.M.M.P. No. 31616); right premaxilla, lingual aspect.

D.—Right premaxilla of *A. tigrinum mavortium,* for comparison. Note the relatively shorter, broader proportions.

E.—*A. hibbardi,* paratype (U.M.M.P. No. 31617); left otic capsule.

F.—*A. hibbardi* (*?*), an atypical otic capsule (U.M.M.P. No. 32000) from Fox Canyon, differing from others collected in possessing a fused stapedial footplate (see page 235).


A
B
C
D
E
F

small to make any appreciable difference in the ratio. The two adult specimens with the most nearly complete tooth rows have bases for about 55 teeth. A complete specimen would probably bear between 60 and 65.

Prearticulares: Forty-two. As in all Ambystomidae the so-called prearticulare is a compound element; it is made up of the true prearticulare and the angulare. Thirty specimens are long and low and lack a strong distinct coronoid portion; these resemble the prearticulares of larval *A. tigrinum*. Twelve are shorter and higher and have a rather distinct coronoid portion like that in the adult of *A. tigrinum*. In nine of these twelve the articulare is fused with the prearticulare, a condition which is usual in adults of most species of *Ambystoma*.

Orbitosphenoids, Quadrates, and Ischia: These three skeletal elements are discussed under one head, because there are so few of each in comparison with the number expected. In the Sherman County collection of *Plioambystoma,* the Jones Ranch collection of *A. tigrinum,* and this, the Fox Canyon collection of *A. hibbardi,* the percentage of most bones (the number of cervical vertebrae used as reference) corresponds closely. In the first two collections, the orbitosphenoids about equal the cervical vertebrae; the quadrates are about 80 per cent of the vertebrae; and the ischia approximately 50 to 60 per cent. On this basis, the Fox Canyon collection of *hibbardi* would be expected to include about 75 orbitosphenoids, 60 quadrates, and 40 ischia. Instead, there are only three orbitosphenoids, two quadrates, and a single ischium. So great a discrepancy can scarcely be due to chance. Techniques of collection were very similar for all three localities. Dr. Hibbard was in charge of the parties that made the Jones Ranch and the Fox Canyon collections and he assisted in collecting the *Plioambystoma* in Sherman County. Hence, it is very unlikely that the discrepancy results from any differential in the method or percentage of recovery. The Fox Canyon collection does contain a rather high percentage of non-neotenic larvae, in which the orbitosphenoids, quadrates, and ischia may not have been fully ossified. This lack of ossification might contribute to a reduction in the number of these bones preserved and recovered, but it cannot be the sole factor involved, for the collections from Sherman County and Jones Ranch also contain an appreciable number of normal (non-neotenic) larvae. In Recent species these three bones are fairly well ossified in all except very young larvae. Even if one assumed that these skeletal structures were ossified only in adults of *A. hibbardi,* one would expect to obtain approximately 22 orbitosphenoids, 18 quadrates, and 12 ischia, over 50 of these three bones as compared with the six actually recovered. Negative evidence must be regarded with extreme caution, but I believe there is strong support for the view that these three types of bone

did not ossify normally even in adults of *A. hibbardi*. All three are cartilage bones. The failure of the columellar footplate to fuse with the otic capsule may well be another example of incomplete ossification of cartilage bone. Both the otic capsules and the scapulocoracoids appear more weakly ossified than those of Recent forms at comparable stages of development (see discussion of those structures). Despite the uncertainties, therefore, the evidence at least warrants a tentative conclusion that *A. hibbardi* is characterized by an incomplete ossification of certain cartilage bones.

Otic capsules: Twenty three. One of them, which is not quite complete, is practically identical with the corresponding structure in the adult of *A. tigrinum* (see Figure 1F); it differs from all the rest in having the foramen ovale partly occluded by the fused stapedial footplate. The remaining 22 specimens exhibit varying degrees of ossification (presumably corresponding to ontogenetic stages), but none of them has the footplate fused with the capsule. The six to eight that are the largest are also the most completely ossified and agree closely among themselves in size and completeness of ossification. Paratype No. 31617 was chosen as most typical of this particular group. It is believed that these larger specimens, including the paratype, represent the normal adult condition in *A. hibbardi* and that the single specimen having the fused footplate is atypical. With adults comprising approximately 30 per cent of the total, about seven of the otic capsules could be expected to represent adults. The probability of finding only one that is adult is very slight. A count of specimens of nearly identical size and osteological development, that I interpreted to be mature, agrees closely with the expected number of adults.

Os triangulare: Three, all of which resemble the corresponding bone in *A. tigrinum*.

Vertebrae: Approximately 1150, including 76 cervical and 13 sacral vertebrae; the balance consists of trunk and caudal vertebrae. None are distinguishable from those of *A. tigrinum*. In most of the trunk and caudal vertebrae a canal that passes through the centrum indicates the former presence of a continuous notochord; these are assumed to be larval. Others, presumed to be adult, had the notochord interrupted. There were two instances of the fusion of two successive trunk vertebrae.

Scapulocoracoids: Forty-three. In many of them only the scapular and glenoid portion remains. Nearly all have the coracoid region either poorly developed or partly broken off or eroded. It is not always possible to tell whether this part was incompletely developed or had been fully developed and subsequently broken. In only four or five specimens is the extent of the coracoid region comparable to that in adult *A. tigrinum*. If the relative number of scapulocoracoids representing the different onto-

genetic stages is the same as the relative number of other elements for these stages, then the scapulocoracoid is definitely less fully ossified in *A. hibbardi* than in corresponding stages of *A. tigrinum*. But this may only be an apparent difference due to the chance presence of a somewhat greater than expected proportion of scapulocoracoids representing the earlier stages of development.

Ilia: Thirty-seven, all indistinguishable from that of *A. tigrinum*.

Limb bones: Very few complete but parts of 125 humeri, 36 radii, 24 ulnae, 50 femora, 37 tibiae, and 6 fibulae. These bones are not distinguishable from the corresponding bones of *A. tigrinum*. There is no evidence of incomplete ossification such as postulated for some of the other cartilage bones.

In addition to the skeletal structures discussed, the Fox Canyon collection contains a few ribs, metacarpals, metatarsals, and phalanges.

Relationship.—A. hibbardi is a member of the *tigrinum* group of *Ambystoma*. The average size and proportions of the animals and the vertebral dimensions correspond, as does the shape of the parasphenoids. There is the same lack of a diastema in the prevomerine tooth row and the same relatively incomplete bony choanal border, and there is a general resemblance of all skeletal parts in *A. hibbardi* to those in *A. tigrinum*.

If the conclusion that *A. hibbardi* is characterized by an incomplete ossification of certain cartilage bones is correct, it is very unlikely that *hibbardi* was ancestral to any Recent members of the genus. More probably, it represents a specialized branch of the *tigrinum* group, a branch that subsequently became extinct. In any event, presence of *hibbardi* in the Upper Pliocene provides strong evidence not only that the genus *Ambystoma* was established by that time, but that differentiation into the various species groups was well under way, possibly even completed, during or before the Upper Pliocene.

There may be more than one species of *Ambystoma* in the Fox Canyon collection. The orbitosphenoids, quadrates, and ischium and the atypical otic capsule with a fused columellar footplate may represent a species distinct from *A. hibbardi*. If this were the case, some interspecific variation in other bones would also be expected. But if a second species is present, it has to be a member of the *tigrinum* group, for no specimens that are referable to any other group occur. Interspecific differences within a species group are not, as a rule, very striking or obvious. The number of specimens representing a second species, if there is one, is relatively small and any interspecific variation that may exist is obscured by the extensive intraspecific, primarily ontogenetic, variation in the far more numerous specimens of *A. hibbardi*.

FOSSIL AMBYSTOMIDS

Other ambystomid specimens in the collections of the Kansas University Museum of Vertebrate Paleontology and the University of Michigan Museum of Paleontology are treated below. The faunas containing the specimens are arranged according to geological occurrence; the dating of the various deposits is based largely on that proposed by Hibbard (1954*a* and prior publications).

Middle Pliocene—Ogallala Formation

Edson Quarry fauna (Sherman County, Kansas).—The large collection of *Plioambystoma* derived from the Edson Quarry by Adams and Martin (1929, 1930) is part of this fauna. They pointed out the similarity of *Plioambystoma* to larval *Ambystoma* and suggested this to be evidence that *Plioambystoma* is a primitive ambystomid. Resemblance between the two is indeed marked. I find no characteristics, other than minor proportional differences, by which *P. kansense* can be distinguished from neotenic larvae of *A. tigrinum*. The likeness is so striking that *Plioambystoma* must be, not a primitive ambystomid but a neotenic species, or at least a neotenic population of a species that is very close to, if not actually a member of, the genus *Ambystoma*. Some of the specimens of *Plioambystoma* unquestionably represent normal immature larvae, but the majority are neotenic. This can be seen particularly in the interruption of the notochord. Furthermore, most specimens are nearly identical in size and in a stage of development only comparable to neotenic or very advanced larvae of Recent forms, yet none show evidence of metamorphic change having commenced. This itself demonstrates that these are neotenous as opposed to normal larvae.

Taylor (1941) in part redescribed briefly the specimens available to Adams and Martin and described, as well, specimens obtained subsequently. All of these specimens were isolated individual bones. Others now in the University of Kansas Museum (K.U.M.V.P. No. 9919), though not derived from the Edson beds, should be mentioned. They include several more or less complete, somewhat distorted and greatly fragmented, skeletons imbedded in slabs of diatomaceous earth. The earth came from deposits adjoining the Rhino Hill Quarry of Wallace County, Kansas, which are essentially contemporaneous with the Edson beds. The slabs containing the specimens were derived from a different outcrop but from the same deposit that yielded the type specimen of *Scaphiopus studeri* Taylor (1939). As Taylor (1941) pointed out, there are no prevomers in any of the dissociated *Plioambystoma* material, but in some of these diatomaceous slabs this bone is present.

No structural basis for distinguishing *Plioambystoma* generically from *Ambystoma* is apparent. In the absence of any adult specimens a proposal to refer *P. kansense* to the genus *Ambystoma* is perhaps premature. Therefore, I tentatively retain the genus *Plioambystoma.*

Besides *Plioambystoma kansense,* Taylor (1941) recognized another form from the Edson Quarry, for which he proposed the name *Lanebatrachus martini.* This was based on an aberrant lower jaw (K.U.M.V.P. No. 1468), but it is very possible that the jaw is simply an anomalous specimen of *P. kansense.* Clarification of its status will have to await the recovery of additional material.

Rhino Hill fauna (Wallace County, Kansas).—Although at a slightly higher level topographically, the beds yielding this fauna are nearly contemporaneous with those of the Edson Quarry. Specimens of *Plioambystoma kansense* from diatomaceous earth adjoining the Rhino Hill Quarry have just been discussed. A few vertebrae in the University of Kansas collection, which are from the quarry itself, have been referred to *Plioambystoma.* The genus *Ogallalabatrachus* Taylor (1941) was proposed on the basis of a large trunk vertebra (K.U.M.V.P. No. 1470) of peculiar proportions and a sacral rib definitely larger than typical for *Plioambystoma.* Again, it is possible that these represent aberrant specimens of *P. kansense* rather than a separate genus, particularly since the type specimen of the only species, *O. horarium,* is a vertebra that is slightly distorted and asymmetrical.

Buis Ranch fauna (Beaver County, Oklahoma).—This fauna lived at a somewhat later period than either the Edson Quarry or the Rhino Hill, and the deposit from which it is derived occurs in the uppermost part of the Ogallala formation (Hibbard, oral communication), rather than in the lowermost Rexroad formation as first reported (Hibbard, 1954*b*). The only ambystomid specimens (U.M.M.P. No. 31258) from it are seven vertebrae and two humeri and the material is inadequate for specific identification.

Upper Pliocene—Rexroad Formation

Saw Rock Canyon fauna (Seward County, Kansas).—The Saw Rock Canyon fauna is of lower Upper Pliocene age (Hibbard, 1953). Ambystomidae are represented by a single vertebra and one femur (U.M.M.P. No. 31255). The material is inadequate for specific identification.

Rexroad fauna (Keefe Canyon and Rexroad Locality No. 3, Meade County, Kansas).—The Rexroad fauna was first described from Rexroad Locality No. 3. The fossiliferous deposits of Keefe Canyon and Fox Canyon are contemporaneous with those of Locality No. 3 and the vertebrates

collected from them are, therefore, a part of the Rexroad fauna (Hibbard and Riggs, 1949; Hibbard, 1950). At Locality No. 3 salamanders are represented by a number of vertebrae and a humerus (U.M.M.P. No. 31226). All of the vertebrae have a canal for a continuous notochord and are probably larval. From Keefe Canyon there is only the distal part of one femur (K.U.M.V.P. No. 6985). Material from both localities is inadequate for specific identification. In view of its contemporaneity and since there is no recognizable difference, the specimens can probably be safely referred to *A. hibbardi.*

Pleistocene

Dixon fauna (Kingman County, Kansas).—The Dixon fauna is tentatively considered from the earliest interglacial stage, the Aftonian. It occurs in the Meade formation[2] as defined by Hibbard, but was collected at a locality and from beds that Frye and Leonard (1952, pp. 64–65) assigned to the Blanco formation. Salamander and other vertebrate elements were found in the fauna, in association with the invertebrates they reported. The Ambystomidae, however, are represented only by a single, incomplete trunk vertebra (U.M.M.P. No. 31221, in part). As far as can be determined, the vertebra is exactly like those in the Sanders fauna (below) and it is tentatively referred to *Ambystoma tigrinum.*

Sanders fauna (Meade County, Kansas).—The specimens discussed here were collected from a deposit in the Meade formation (as recognized by Hibbard and Taylor), in the SE.¼ sec. 23, T. 32 S., R. 29 W., on the Big Springs ranch, in Meade County, Kansas (Locality UM-K2-53). The fauna is not yet described, but it indicates an equable, mild, humid climate, and is, therefore, assigned to the Aftonian interglacial stage (Hibbard, *in litt.*). The Sanders is slightly younger than the Dixon fauna. Ambystomid remains (U.M.M.P. No. 31723) include ten vertebrae, two femora, one radius, and a rib. The vertebrae show that the notochord was interrupted. All specimens have about the same size and proportions as the corresponding structures in normal adult *A. tigrinum.* The material is inadequate for accurate specific identification. Owing to the similarity and because specimens clearly referable to *Ambystoma tigrinum* occur in deposits of the immediately succeeding Kansan glacial stage, it is provisionally referred to that species.

Cudahy fauna (Meade County, Kansas).—This is a fauna that occurs in deposits which immediately underlie the Pearlette Ash of the Crooked Creek formation and probably represents the late Kansan glacial stage.

[2] A detailed discussion of the stratigraphic and faunal relationships of this formation is being prepared by Hibbard.

Ambystoma is represented by 90 to 100 isolated bones from the Wood Pasture, Meade County, Kansas (K.U.M.V.P. No. 6711) and by a few bones from the Sunbrite Ash Pit, Meade County, Kansas (K.U.M.V.P., uncatalogued). The vertebrates in these deposits are part of the Cudahy fauna according to Hibbard (1944). Most parts of the skeleton, except a few of the thin cranial dermal bones, occur, which allows specific identification to be made with reasonable certainty. The specimens represent a giant neotenic population of *Ambystoma tigrinum* of the same sort as that described from the Jones Ranch beds (Tihen, 1942).

Borchers fauna (Meade County, Kansas).—The Borchers fauna comes from a deposit overlying the Pearlette Ash of the Crooked Creek formation, which represents the Yarmouthian interglacial stage. Ambystomid remains (U.M.M.P. No. 31217; K.U.M.V.P. Nos. 5753 and 9920) include approximately 75 vertebrae and a smaller number of fragmentary limb bones. No cranial bones were found. Septa are present in the centra of the vertebrae, which shows that the notochord was interrupted. None of the specimens can be distinguished from corresponding bones of adult *Ambystoma tigrinum,* though possibly they average slightly smaller than those in *A. t. mavortium.* I am tentatively referring all of the Borchers specimens to *A. tigrinum,* pending recovery of additional material, particularly cranial elements, to confirm or disprove the reference. They certainly represent a member of the *tigrinum* group.

Kentuck assemblage (McPherson County, Kansas).—The deposit containing the Kentuck fossils fills a channel in volcanic ash, presumably Pearlette Ash, in the McPherson formation. Two separate faunas may be involved in this assemblage (Hibbard, 1952), but the two vertebrae of *Ambystoma* (U.M.M.P. No. 24503), at least tentatively, represent the Yarmouthian interglacial stage and are thus approximately contemporaneous with the Borchers fauna. Since they appear identical with specimens from the Borchers fauna, they may also be tentatively referred to *Ambystoma tigrinum.*

Undescribed fauna (Meade County, Kansas).—The deposit from which this fauna is derived is known as Locality No. 7, in the SE.¼ of sec. 32, T. 34 S., R. 29 W., XI Ranch, in Meade county, Kansas. From this same locality but a different horizon Hibbard (1943) reported a specimen of *Microtus pennsylvanicus.* The present specimens were collected from the "High Terrace" sands (Hibbard, 1943). The fauna of this horizon is undescribed, but a cold climate is clearly indicated and Hibbard (*in litt.*) has stated "I consider it Illinoian in age." The salamander remains are one otic capsule, one prearticulare, and four vertebrae, one of which is a cervical. All of them are fully as large as the corresponding bones in the

Ambystoma of the Cudahy and Jones Ranch faunas. The prearticulare is larval in form, for it lacks a strong coronoid process; the vertebrae possess a septum, which shows that the notochord was interrupted. Despite the few specimens, there is no doubt that they are of the same giant neotenic type of *A. tigrinum* that occurs in the preceding (Kansan) and following (Wisconsin) glacial stages in this area (See Cudahy Fauna, above, and Jones Fauna, below.)

Jinglebob fauna (Meade County, Kansas).—A single vertebra from this fauna can be tentatively referred to *A. tigrinum*. It appears to represent a normal adult and has been previously reported (Tihen, 1954). The deposit yielding it is a part of the Kingsdown formation and has been tentatively assigned to the Sangamon interglacial stage (Tihen, 1954; van der Schalie, 1953).

Jones fauna (Meade County, Kansas).—Approximately 20,000 individual bones have been recovered from the Jones Ranch beds and a much smaller number from the nearby Horse Quarry, which is probably a slightly earlier phase of the same sink-hole deposition that produced the Jones Ranch beds. The deposits are a part of the Vanhem formation and represent the late Wisconsin glacial stage. The collections of *Ambystoma* from these deposits have been discussed in considerable detail previously (Tihen, 1942). It is clear that they constitute a population of giant neotenic larvae of *Ambystoma tigrinum* that is like those occurring in certain mountain lakes at the present time.

COMMENTS

Even though specific identification of much of the fossil material cannot be made, all of the species of *Ambystoma* in deposits younger than Middle Pliocene can be referred with certainty to the *tigrinum* group. In many respects *Plioambystoma kansense* Adams and Martin (1929) also appears referable to this group, but a lack of adult specimens leaves such an assignment open to question. Although there is good reason to believe that *P. kansense* is actually a neotenic form or population of *Ambystoma,* it seems better to retain *Plioambystoma* as a genus, until some information concerning its adult form is available.

Probably the species *Ambystoma tigrinum* has been in existence from the beginning of the Pleistocene. The *tigrinum* group had definitely been established by Upper Pliocene time; a form that may properly be referable to the genus *Ambystoma,* possibly even to the *tigrinum* group, occurs in the Middle Pliocene. It is not unlikely, therefore, that the genus *Ambystoma* had become established by the early Pliocene, perhaps even earlier. The absence of specimens from deposits of pre-Hemphillian age has little sig-

nificance. The techniques for, and interest in, collecting microvertebrates are relatively recent (see Hibbard, 1949). The areas from which the specimens here reported were collected have been worked far more intensively for microvertebrate faunas than have any others in the United States. As these techniques and intensive collecting methods are more widely applied to geologically earlier deposits, there is every reason to believe that urodelan remains will be discovered elsewhere.

Peabody (1954) reported trackways which he referred to the Ambystomidae from the Paleocene of Montana. Work in Europe (Herre and Lunau, 1950, and others) indicates that a number of the extant families of salamanders occurred during or before that same period. The present study establishes that at least one extant species existed throughout most of the Pleistocene and that closely related species lived in the Pliocene. All of these items provide additional evidence that the major amphibian groups were established in the earliest Tertiary, or possibly even in the late Mesozoic, and that the evolution of most amphibians throughout Cenozoic time has been very slow, as compared with that in many other vertebrate groups.

Of considerable interest, but of unclear significance, is the fact that, in all Pleistocene deposits of this Kansas–Oklahoma area the populations represented in the interglacial stages are of the normally metamorphosing types, whereas those from the glacial stages are of the giant neotenic type. Despite the very considerable work that has already been done on the phenomena of neoteny and metamorphosis in the laboratory, the interrelationship between genetic constitution, environmental factors, and neoteny in natural populations remains obscure.

CONCLUSIONS

The Middle Pliocene *Plioambystoma kansense* Adams and Martin (1929) is not a primitive ambystomid but a neotenic species or population believed properly referable to the genus *Ambystoma*. In the absence of information concerning the adult form, however, the generic name *Plioambystoma* is tentatively retained.

The two genera, *Lanebatrachus* and *Ogallalabatrachus,* established by Taylor (1941), may be based on anomalous specimens of *Plioambystoma kansense.*

The new species, *Ambystoma hibbardi,* of the Upper Pliocene, is closely related to *A. tigrinum,* but is presumed to be distinguished from it by an incomplete ossification of certain cartilage bones.

The genus *Ambystoma* was certainly established by Upper Pliocene time, probably much earlier, and differentiation into species groups was

well under way, possibly completed, during or before Upper Pliocene time.

An extant species, *A. tigrinum,* has been in existence throughout most, perhaps all, of Pleistocene time.

In the Kansas–Oklahoma area considered, populations of *A. tigrinum* that lived in the interglacial stages were of the normally metamorphosing type; those that lived in the glacial stages were of the giant neotenic type.

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EXPLANATION OF PLATE I

(All figures approximately 8 times natural size)

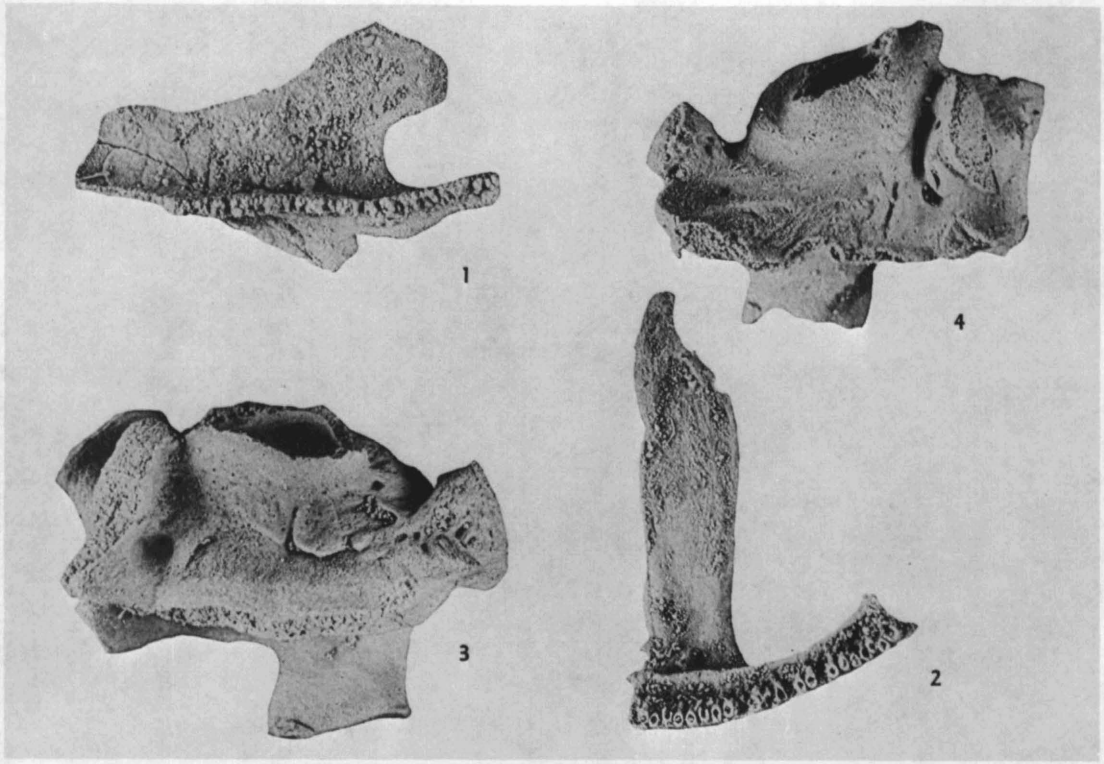
FIG. 1. *Ambystoma hibbardi,* holotype (U.M.M.P. No. 31440); posterolateral part of left prevomer.

FIG. 2. *A. hibbardi,* paratype (U.M.M.P. No. 31616); right premaxillary, lingual aspect.

FIG. 3. *A. hibbardi,* paratype (U.M.M.P. No. 31617); left otic capsule.

FIG. 4. *A. hibbardi (?)* (U.M.M.P. No. 32000); an atypical otic capsule from Fox Canyon, differing from others collected in possessing a fused stapedial footplate.

PLATE I



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