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A Review of New World Fossil Bufonids

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ABSTRACT: The form originally described as *Neoprocoela edentata*† from the Patagonian Oligocene is thought to be actually a *Bufo* related to the extant CALAMITA group, now confined to the Old World. *B. alienus*† n. sp. from the Middle Pliocene of Kansas is referred with reservations to this same group. Members of the South American section of the VALLICEPS group known as fossils are: *B. arenarum* from the Pleistocene of Argentina, *B. m. horribilis* from the late Pleistocene or sub-Recent of Yucatan, and an unnamed form related to *marinus* from the Upper Miocene of Colombia. Members of the Mexican section of this group are: *B. alvarius* from the Blancan of Arizona, *B. campi*† from the Middle Pliocene of Chihuahua, and *B. valliceps* from the late Pleistocene or sub-Recent of Yucatan. Members of the Caribbean section are: *B. praeivius*† from the Miocene of Florida, *B. punctatus* from the Pleistocene of Nevada, *B. quercicus* from the Pleistocene of Florida, and *B. suspectus*† n. sp. from the Blancan (Rexroad) of Kansas and possibly from the Lower Pliocene of Nebraska. Members of the AMERICANUS group known as fossils are: *B. a. americanus* from the Pleistocene of Pennsylvania and Virginia, *B. cognatus* from the Middle Pliocene and Pleistocene of Kansas, probably also from the Middle Pliocene of Nebraska, *B. compactilis*(?) from the Blancan (Rexroad) of Kansas, *B. hemiophrys*(?) from the Pleistocene of Kansas, *B. hibbardi*† from the Middle Pliocene of Kansas (*B. arenarius* Taylor is considered a synonym of *hibbardi*), *B. repentinus*† n. sp. from the Pleistocene of Kansas, *B. rexroadensis*† n. sp. from the Blancan of Kansas, *B. spongifrons*† n. sp. from the Middle Pliocene of Kansas, *B. terrestris* from the Pleistocene of Florida, *B. tiheni*† from the Middle Pliocene of Florida; *B. w. woodhousei* from the Pleistocene of Kansas and the Blancan of Arizona, *B. w. hexarensis*† from the Pleistocene of Texas, *B. w. fowleri* from the Pleistocene of Arkansas, Florida, Pennsylvania and Virginia, and an unnamed form from the Miocene of Nebraska. The BOREAS group is represented as fossils only by *B. boreas* cf. *halophilus* in the Pleistocene of California (*B. nestor* Camp is considered a synonym of *halophilus*).

Three entries of the genus *Bufo* into the New World are postulated. One, no later than the beginning of the Oligocene, represented the CALAMITA group, not now occurring in this hemisphere. The second, perhaps equally early but certainly by the earliest Miocene, was the stock that presumably gave rise to all other New World toads except the BOREAS group. The ancestors of the BOREAS group were probably related to the ancestors of the Old World *B. bufo*, and may have arrived in this hemisphere at a relatively late date.

Several limitations on the accuracy of identifications and the determination of relationships are discussed. Certain peculiarities in the osteology of all Floridian toads, fossil and Recent, are noted, and the possibility that intergroup hybridization or introgression may have been a factor in the evolution of the toads of that region discussed briefly.

INTRODUCTION

Our knowledge of the paleontological history of the genus *Bufo*, as for nearly all living amphibian genera, is extremely limited. The

first nominal fossil species from the New World was proposed by Camp in 1917; only six other specific or subspecific names have been based on fossil specimens from this hemisphere, and the fossil occurrence of a slightly greater number of extant forms has been recorded.

Recently, I have been permitted to examine several collections of fossils containing representatives of this genus. These collections contain both undescribed species and representatives of previously known, mostly Recent, species that constitute additional records of those forms. This paper presents descriptions and records based on these specimens, and a brief review of other fossil specimens of *Bufo* from the Americas.

Acknowledgments.—During the course of this study I have become indebted to a large number of institutions and individuals. Their assistance has taken many forms — permission to borrow and examine specimens, aid in procuring Recent material for comparative purposes, the use of facilities, the generous sharing of unpublished information, and the proffering of many stimulating suggestions and comments. The aid of many of these persons was acknowledged in a recent paper (Tihen, 1962) dealing with the comparative osteology of Recent species. In addition to the persons mentioned there, others to whom I owe a special debt of gratitude are: Dr. Bayard Brattstrom of Orange County (California) State College, Mr. D. Dwight Davis of the Chicago Natural History Museum, Dr. Theodore Downs of the Los Angeles County Museum, Drs. David Dunkle and C. Lewis Gazin of the United States National Museum, Dr. Richard Estes of Boston University (formerly of the University of California), Dr. Joseph T. Gregory of the University of California (formerly of the Yale Peabody Museum), Dr. Claude W. Hibbard of the University of Michigan, Dr. Neil Richmond of the Carnegie Museum, Dr. Bobb Schaeffer and Mrs. Rachel Nichols of the American Museum of Natural History, and Dr. Robert Wilson of the South Dakota School of Mines and Technology (formerly of the University of Kansas). Miss Alice Boatright of the University of Illinois prepared most of the line drawings, and the Photographic Department of the American Museum of Natural History provided photographs of the type specimen of *Neoprocoela edentata*.

In our present state of knowledge, the value and validity of a review such as here attempted are limited by several factors in addition to the competence of the reviewer. Important among these are the nature of the specimens recovered and our incomplete knowledge of the variational aspects of the comparative osteology of Recent forms. The following remarks apply specifically to the genus *Bufo*, but would be equally true of many other genera or groups.

In identifying preserved or living specimens of Recent toads, one must use combinations of characteristics. There is no single structure or condition on which an accurate identification of every species of the genus can be based. The same thing is understandably true of skeletal characteristics. This would present no unique problem if the fossil remains recovered were, for the most part, more or less complete skeletons, exhibiting the combinations of characteristics that occur in individual animals. Unfortunately, such specimens are extremely rare. The vast majority of fossil material consists of single, completely dissociated, individual skeletal elements, and even these are commonly incomplete. This presents obvious problems in the proper associa-

tion of characteristics. If the collections from a given deposit contain a large number of each of many separate elements, and if there is no indication from any of these elements that more than a single species is represented, it is then reasonable to assume that all of the specimens are derived from a single species, and that the combination of characters presented by the various individual elements is the combination truly characterizing that species. Even though more than one form may be present in the collection, if the numbers are highly disproportionate, or if strong similarity to living forms exists, reasonable assumptions concerning the proper associations can still be made. The certainty of proper association steadily lessens with decrease in the size of the collection, with increase in the number of forms represented, with approach to equality in the number of specimens of each form and with an increasing degree of similarity in structure of the forms present.

Under such conditions it is clearly desirable to base identifications on the same skeletal element for all forms, insofar as this is practicable. Ideally, the element used would exhibit universal interspecific variation and a minimum of intraspecific variation. As stated above, no such single element exists. The next choice is an element in which the ratio of interspecific variation to intraspecific variation is as high as possible. No comprehensive variational studies have been conducted in any *Bufo*; accurate comparisons of the two levels of variation are therefore, not available. However, as judged from the Recent skeletons that I have examined, it is my opinion that the frontoparietal is the most reliable single element for identification of the greatest number of New World *Bufo*.

There is, though, one more factor that must be considered — the likelihood, or frequency, of recovery of the element in fossil collections. In this respect the frontoparietal is a very unsatisfactory key element. Often one must resort to some other less accurately identifiable element or elements to determine what forms may be represented in a given fossil collection. Iliæ are among the more frequently recovered elements and in the *AMERICANUS* group, as well as for some members of other groups, will often allow a fairly accurate specific determination. Considerable intraspecific variation does occur, with a great deal of overlap between some species, but this element will at least serve to limit greatly the number of possible forms represented. If a series is available, so that the general pattern and mode of variation is recognizable, many species can be identified with a reasonably high level of confidence.

Much of the ilial variation involves the size and shape of the ilial prominence. Identifications are based primarily on direct comparisons with ilia from Recent skeletons, but I have attempted to describe some of the major features objectively. These descriptions make use of a coined terminology that is explained here, with reference to Figure 1. The "base of the prominence" is the line between the point (A) at which the anterior border of the prominence disappears medial to the

shaft and the lowest point (B) of the "supra-acetabular depression." The height is simply the perpendicular distance from the base to the peak, or highest point. The "anterior angle" is that angle formed by the base (AB) and a line (AC) drawn from the anterior end of the base tangent to the anterior slope. The "posterior angle" is the corresponding angle formed by the base and a tangent (BC) to the posterior slope; the "peak angle" is the angle formed by the intersection of these two tangents. The dorsal border of the ilium posterior to the prominence can be approximated by a straight line; the angle formed by this line (BD) and the tangent to the posterior slope is termed the "supra-acetabular angle."

Linear and angular measurements are made with the plane of the acetabular portion of the ilium oriented as nearly as possible perpendicular to the line of vision. Minor differences in orientation produce appreciable differences in measurement of the angles and, to a lesser extent, in linear measurements. These measurements are reproducible only as close approximations, and should not be used as a substitute for direct comparisons when such comparisons are feasible.

With a few special exceptions, the limb bones, the girdle elements other than the ilia, the vertebrae other than the sacrum, and even many of the cranial elements are useful at best only in determining the general group represented, and are seldom identifiable to the specific level on the basis of any characteristics that I have able to recognize.

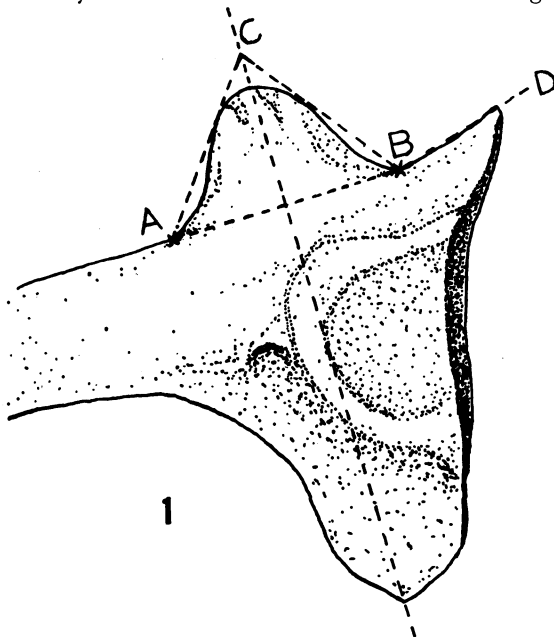


Fig. 1.—A generalized ilium, to illustrate the terminology employed. See text for explanation.

Given the presence of the proper elements, and especially if there are a good many specimens of some of these elements, it is frequently possible to be reasonably certain that some given form *is* represented in a particular collection. But because many elements are not specifically identifiable, and because others such as the ilia exhibit considerable overlapping variation, it is much more difficult to state with any certainty that some second related form is *not* also present. The general unreliability of negative paleontological evidence is thus compounded by the likelihood that positive evidence of the presence of some forms may not always be recognized even when specimens are recovered. My general procedure in instances of this sort has been tentatively to refer all specimens in a collection to the identifiable form unless there is some strong indication that more than one form is actually present.

The difficulties of accurate identification resulting from the nature of the fossil specimens are augmented by our limited knowledge of the comparative osteology of Recent forms. Several papers in the last ten years have greatly increased our understanding of interspecific osteological variation within the genus, but the systematic significance of much of this variation is still not completely clear. And there are no thorough studies of the intraspecific variation — geographic, ontogenetic and individual — within even one species. The need for such study as a guide in the interpretation of fossil remains should be obvious.

Despite these limitations, indeed in part because of them, it is felt that a summary and review of the present status of our knowledge will be of some value. The fossil record, incomplete as it may be, and as uncertain as some of the specific identifications may be, does provide some information of use in understanding the distribution and relationships of the present members of the genus. At the very least, the existence of various species groups at certain times and places in the past is clearly demonstrated, and these occurrences must be taken into account in any attempt to reconstruct the evolutionary history of *Bufo* in the New World. It is hoped that this review may serve to make manifest the many problems and unanswered questions that exist, and help to stimulate investigation of these problems.

SYSTEMATIC ARRANGEMENT

All of the New World fossil specimens are referable to the genus *Bufo*. The osteological characteristics of the genus have been described previously (Tihen 1960, 1962). Its geological age is uncertain. The frequently encountered statement that it is first known from the Oligocene of Europe is apparently based solely on the description by Filhol (1877) of "*Bufo servatus*" from the phosphorites of Quercy (France). These deposits range in age from Upper Eocene to Lower or Middle Oligocene, and dating of particular specimens within this range is uncertain. Actually, the generic identification, and even the family reference, of the specimen described as *Bufo servatus* is on very

unstable ground. There is no information concerning the skeleton; like many specimens from the phosphorites, it is a mummy-like specimen in which the tissues of the entire organism have been replaced by calcium phosphate. Details of structure in the resulting fossil are greatly obscured. Filhol's text references to the figures, figure captions, and figures are not in complete agreement, but none of the figures that might be intended to represent this specimen show any definite evidence of the parotid glands that Filhol purported to observe. I have not seen any of these phosphorite specimens, and prefer to quote a passage from Piveteau (1927) respecting their adequacy: "Les caractères du tégument sont alors les seuls observables, mais, altérés par les transformations qu'ils ont subies, leur étude ne permet pas d'atteindre, dans les déterminations, la précision que nous fournissent en général les caractères ostéologiques. Je ne ferai donc que donner ici, sous toutes réserves, les noms de fossiles signalés par Filhol."

I believe that *B. servatus* should be only questionably referred to *Bufo* or the bufonids until confirmatory evidence is available, even though I consider the presence of *Bufo* in Europe by the Oligocene very likely on other grounds. If we do not accept this record as confirmed, the earliest definite recorded occurrence of *Bufo* is in the Lower Miocene of Florida (Tihen, 1951; Auffenberg, 1956); the earliest undoubted occurrence in the Old World is in the Upper Miocene of Oeningen, whence Tschudi (1838) described *Palaeophrynos gessneri*. This form is considered by European authors to belong to the genus *Bufo*; the descriptions and figures I have seen offer no evidence to the contrary.

Though there are no definite records prior to the Miocene that can be unequivocally referred to *Bufo*, the genus almost certainly antedates that epoch. Miocene forms from Florida, Nebraska, Colombia, and probably the European *B. gessneri*, are all referable to extant species groups, indicating a very considerable spread and diversification of the genus before that time. The Argentinian *Neoprocoela edentata* from the Lower Oligocene, if it is truly a *Bufo*, as will be suggested, is probably referable to another of the extant species groups. One must postulate, then, that the genus dates at least from the very beginning of the Oligocene.

The arrangement into species groups and sections follows that proposed previously (Tihen, 1962) for New World forms, with the addition of one group, not adequately delimited or defined here, that is now confined to the Old World. All of the forms considered are tentatively referred to a particular group, although in some cases the propriety of the reference is not clearly established. Fossil representatives of four species groups are known.

The CALAMITA Group

This is strictly an Old World group insofar as Recent forms are concerned. The affiliation of certain New World fossils with this

group is perhaps not conclusively demonstrated, but is so strongly suggested as to require discussion.

The group is characterized by the fusion of the frontoparietals with the pro-otics, the absence of cranial ornamentation, the presence of an occipital groove as opposed to an enclosed canal, and the extreme reduction or absence of any otic plate of the squamosal. As thus defined, the group would include a number of African species, but on the basis of other considerations not germane to the present study it seems likely that it should be limited to include only *B. calamita*, *carens*, *raddei* and *viridis* among the Recent species I have seen. When so limited, it can be further characterized as having relatively long vertebral centra, rather short and broadly expanded sacral diapophyses, a short medial arm of the pterygoid (in contact with the pro-otic, but not with the parasphenoid), and a somewhat reduced quadratojugal, in only limited contact with the maxilla.

In *B. calamita* and *raddei* there is a large frontoparietal fontanelle (Fig. 8); the other two species lack a fontanelle, although in *B. viridis* the two frontoparietals are distinctly separated from each other for much of their length. The ilium of *B. calamita* (Fig. 2) is unique, characterized particularly by a marked ventral expansion of the posterior part of the shaft. The ilia of *B. viridis* and *raddei* have a slight, but far less obvious, expansion of this sort, but none is recognizable in *B. carens*.

Two New World fossil forms are referred tentatively to this group.

Bufo alienus, sp. nov.

Definition.—A *Bufo* of moderate size, tentatively referred to the *calamita* group, with a very low ilial prominence; the posterior slope of the prominence is decidedly steeper than the anterior, and the prominence projects somewhat medially from the axis of the shaft.

Description of the holotype.—The specimen is illustrated as Figure 3. The chord length from the dorsal tip of the acetabular expansion to the anterior end of the shaft is 17.7 mm; it is estimated that one or two millimeters of the anterior end are missing. The shaft is rather strongly curved, with a low dorsal crest along the central two-thirds of its length; the posterior portion is slightly compressed. The prominence is small; the height is slightly under 25% of the length of the base, but the base itself seems of limited longitudinal extent. The posterior slope of the prominence is sharply sigmoid, the anterior slope more even. The anterior angle (as defined in the introduction) is about 23°, the posterior angle about 32°, and the supra-acetabular angle about 135°.

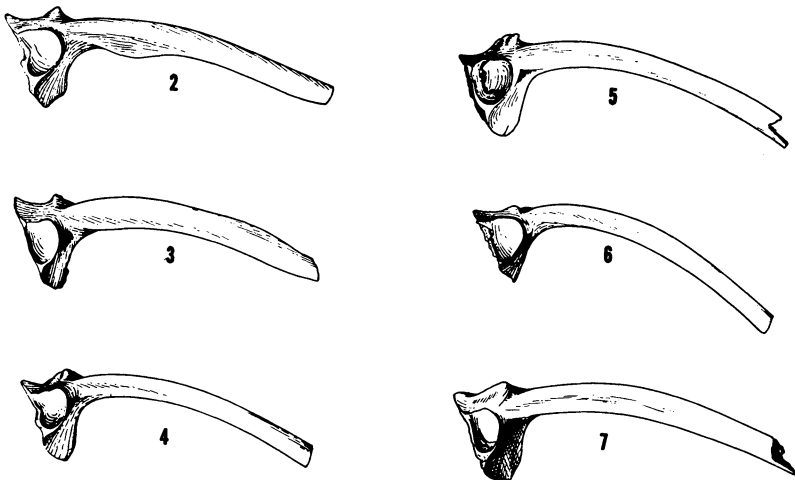
Type and type horizon.—The holotype specimen is a virtually complete right ilium, USNM No. 22233, from the Middle Pliocene (Hemphillian) Ogallala formation, "Quarry E," Sec. 1, Twp. 2 S, Range 20 W, near Long Island, Phillips County, Kansas. Collected by J. B. Hatcher in 1884.

Referred material.—The holotype is the only known specimen.

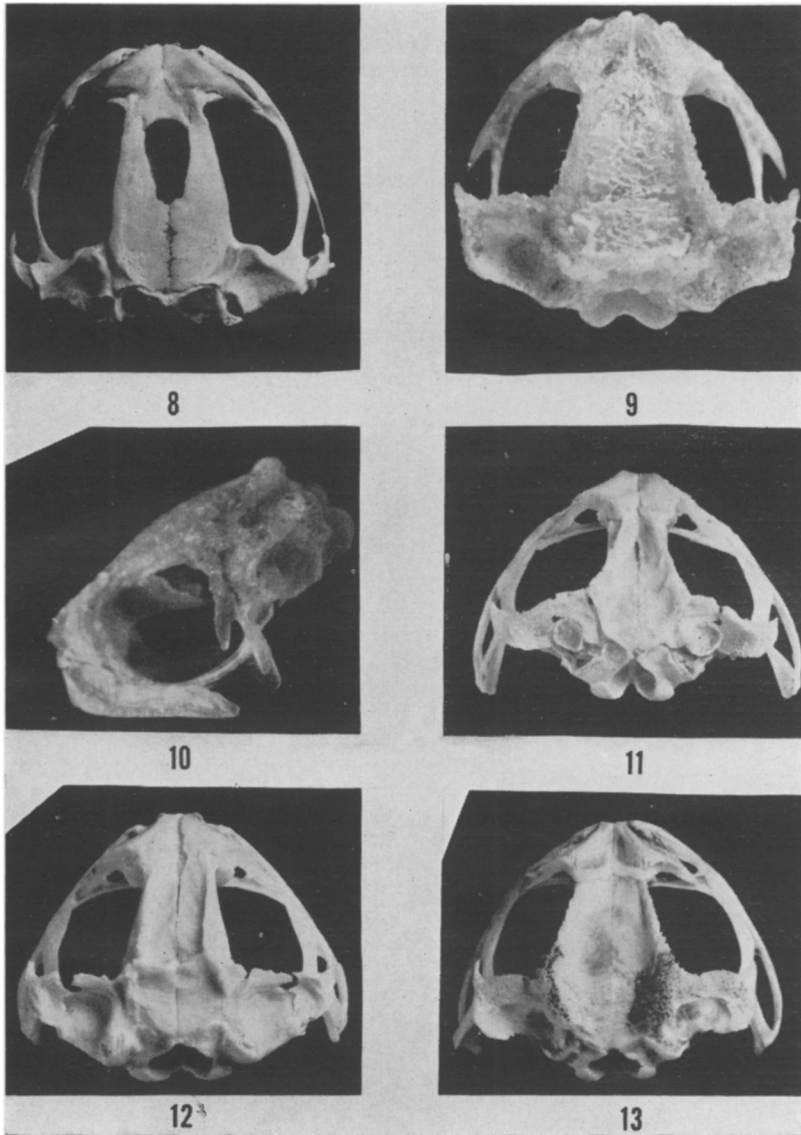
Discussion.—The collection containing this specimen also includes a number of specimens referred to *B. cognatus* and a smaller number thought to represent a previously undescribed member of the AMERICANUS group. The probable association of the various specimens will be discussed more fully in connection with *B. cognatus*, but it can be stated here that all other specimens identifiable to group are clearly referable to the AMERICANUS group, and that none except for the holotype of *B. alienus* are inconsistent with such a reference.

I think there is no possibility that this specimen can represent a member of the AMERICANUS group, but the propriety of reference to the CALAMITA group is by no means fully established. The ilia of several other groups differ from that of *B. alienus* only in details. On direct comparison with Recent forms this specimen resembles, in general appearance, the ilia of members of the CALAMITA group more closely than it does those of members of any other group (see Figs. 2-7); it is on this basis only that tentative reference to the CALAMITA group is made. There is, in fact, no conclusive evidence that the group has ever existed in North America, but if the next form to be discussed is properly interpreted, representatives must have at least passed through North America in the early Tertiary. Perhaps *B. alienus* is a relict of this postulated early migration.

The deposit from which this collection came was formerly considered Lower Pliocene. Gilmore (1938) described a snake, *Palaeoelaphe kansensis*, from the same collection, stating the horizon to be "Republican River formation, Lower Pliocene." Most of the deposits of this



Figs. 2-7.—Ilia of various *Bufo*. 2. *B. calamita* (actual length 23 mm); 3. *B. alienus*, holotype (actual length 18 mm); 4. *B. boreas* (actual length 30 mm); 5. *B. viridis* (actual length 27 mm); 6. *B. bufo* (actual length 25 mm); 7. A Rancho La Brea specimen referred to *B. boreas halophilus* (actual length 28 mm).



Figs. 8-13.—Skulls of various living *Bufo*. 8. *B. raddei* (actual length 15 mm); 9. *B. quercicus* (actual length 8 mm; quadratojugals missing); 10. same, lateral aspect; 11. *B. cognatus* (actual length 16 mm); 12. *B. hemiophrys* (actual length 14 mm); 13. *B. terrestris* (actual length 16 mm).

general area formerly placed in the Republican River formation are actually in the Ogallala, and of Hemphillian age. Dr. Joseph T. Gregory has kindly furnished (in litt.) the following information: "The fossils came from silty sandstones of the Ogallala formation a short distance below the top of the plain's surface, essentially in or just below the caprock material in that area. The quarries are in a draw which lies near the center of section 1, township 2 south, range 20 west, about two and one-half miles south and one-half mile east of the town of Long Island. The Ogallala is quite thin in this region, and presumably has only the one fossiliferous level." Frye, Leonard and Swineford (1956) state that ". . . on the bases of its topographic position and of the occurrence of fossil plants in nearby localities it is judged that this quarry is situated in the lower to middle part of the Ash Hollow member."

Bufo(?) *edentatus* (Schaeffer)

Definition.—An Oligocene *Bufo* of moderate size, presumably referable to the CALAMITA group, with a large frontoparietal fontanelle; sacral diapophyses perhaps less broadly expanded than in others of the group.

Description.—This specimen has been rather fully described by Schaeffer (op. cit.); it was figured by him, and additional photographs kindly provided by the Photographic Department of the American Museum are shown here as Figures 14 and 15. Since most of the important features bear not only on the specific identification but, more importantly, also on the generic and family allocation, they are incorporated into the discussion which follows rather than being presented separately.

Type and type horizon.—AMNH No. 3248, a partial skeleton consisting of skull, vertebral column, and proximal portion of left forearm. Sarmientan Group, Deseadan Stage, Lower Oligocene of the Scarritt Pocket, southwest portion of Rinconada de los Lopez, west side of Sierra Canquel, central Chubut, Argentina (Schaeffer, 1949).

Referred material.—Known only from the holotype.

Discussion.—This specimen was originally described as *Neoprocoela edentata* and referred to the Leptodactylidae. Schaeffer noted a strong resemblance to *Bufo* in several features, but he was influenced by the fact that, at the time this specimen was found, there was no fossil evidence of *Bufo* in the New World earlier than the Middle Pliocene. He states: "To consider this Oligocene form as a specialized *Bufo*, however, would require the presence of the Bufonidae (*sensu stricto*) in South America by no later than the early Oligocene, an occurrence which is not supported by the known paleontological facts." He concluded that it ". . . is a true leptodactylid retaining several primitive features. The toothless condition was probably an independent development. . . ."

This may indeed be the case, since several bufonid-like features have apparently developed independently in different groups of leptodactylids. However, the evidence that *Bufo* was widespread and

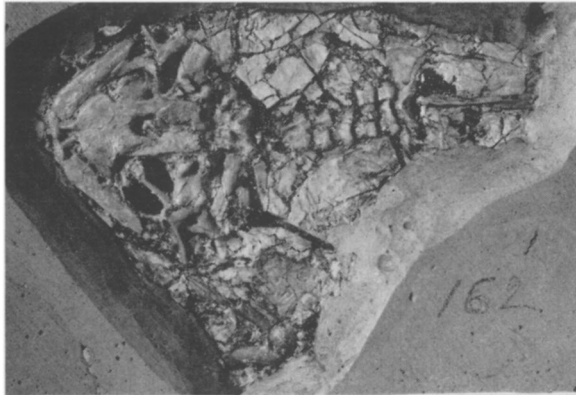
considerably diversified in this hemisphere by the Lower Miocene has removed much of the objection to recognizing an Oligocene form in South America. And this form presents so many *Bufo*-like features as to merit very careful consideration.

It is a completely edentulous species; the vomers are, however, fairly extensive. In most edentulous leptodactylids the vomers themselves are noticeably reduced in extent. The ascending processes of the premaxillae are angled towards the midline; this is true of some leptodactylids, but in many these processes are directed directly dorsally or are angled away from the midline. The sphenethmoid is entire; this is also true in many leptodactylids, but in others this element is divided, and this is always the case in the Australian forms among which we find a close resemblance to *Bufo* in other respects. The large frontoparietal fontanelle is certainly not typical of *Bufo*, but is duplicated in *B. calamita* and *raddei*. The absence of an extensive otic plate on the squamosal is similarly not typical, but is again duplicated in these same species and their relatives. The crushing and displacement of the skull prevent an accurate determination of the squamosal angle as defined by Griffiths (1954, 1959), but the shape of the squamosal and its relatively long shaft suggest that this angle had a fairly high value, as in *Bufo*, thus differing from the apparently universal condition in leptodactylids. The broad nasals in contact with each other medially, the long pterygo-maxillary contact, and the wide maxilla are all features that are duplicated in some leptodactylids, but are more characteristic of *Bufo* than of leptodactylids, and particularly New World leptodactylids, as noted by Schaeffer.

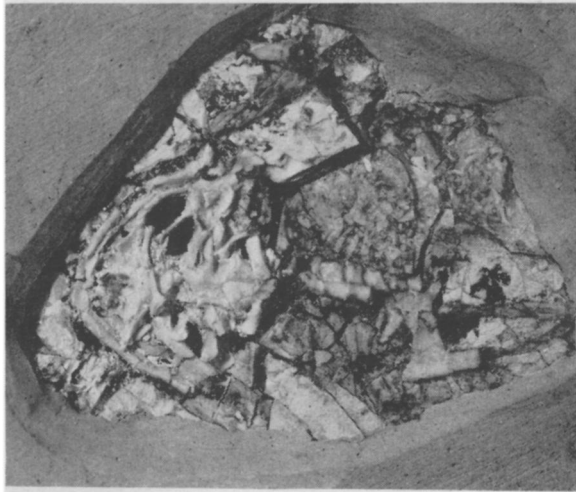
The atlantal cotyles are closely approximated ventrally; the first transverse processes are expanded and directed anterolaterally; the sacral diapophyses are distinctly expanded. All of these features are common in *Bufo* but appear only occasionally among leptodactylids. The third transverse processes appear to be longer than the second; this is perhaps a questionable interpretation, since these processes are represented in part only by faint impressions, but independent observations kindly made by colleagues support this interpretation. This is true of most *Bufo*, but is only rarely the case in leptodactylids. The structure of the ilium cannot be determined; other girdle and limb elements present are not diagnostic, but are not inconsistent, so far as their characteristics can be determined, with reference of the specimen to *Bufo*. All vertebral centra are subcylindrical in form and the intervertebral bodies are fully fused with the centra.

This specimen thus agrees with *Bufo* in many features that are found only occasionally among leptodactylids; it presents no features that do not occur in at least one group of *Bufo*. While it is admitted that any one, or even several, of the features listed may be duplicated in some particular species of leptodactylid, it is unlikely that the entire assemblage would be present in any single form. This combination of features, along with the general toad-like appearance of the skeleton, lead me to believe this is actually a *Bufo*. If the generic reference is

correct, affinity with the CALAMITA group is clearly indicated. All observable characters show a strong resemblance to *B. calamita* and *raddei*; the problem is not one of recognizing similarities to this group, but of finding and recognizing characteristics that will distinguish this form from those two species. Many details, and even presumably important features such as whether or not the frontoparietals and pro-otics are fused, are not clear on this specimen; one perhaps diagnostic character is the apparently somewhat lesser expansion of the sacral diapophyses in this form than in the extant members of the CALAMITA group.



14



15

Figs. 14-15.—Type specimen of *Neoprocoela* (= *Bufo* ?) *edentata*. 14. Dorsal view; 15. Ventral view. Photographs by courtesy of the Photographic Department of the American Museum of Natural History.

The VALLICEPS Group

Members of this group have broad, ornamented frontoparietals, usually bearing distinct crests, and always fused with the pro-otics. The occipital groove is enclosed to form a canal. The skull is of normal or depressed proportions. In most forms the ilial prominence is low, never reaching the height attained in many members of the AMERICANUS group. The pelvic plate is elongate (Baldauf, 1959), but this feature is not always recognizable from the dissociated ilium or ischium.

Three sections within the group have been recognized, all of which are represented by fossil specimens.

THE SOUTH AMERICAN SECTION

In members of this section the dermal ornamentation and the crests are of moderate extent, the ornamentation usually being of a striate (as opposed to cancellous or granular) texture. The suprapterygoid fenestra is often slightly, but never markedly, occluded by a flange of the medial arm of the pterygoid and/or the shaft of the squamosal; the shaft of the squamosal is of normal extent. A virtually unique feature is the fact that the medial arm of the pterygoid broadly overlaps the ala of the parasphenoid. The ilial prominence is consistently low, about 25% of the length of the base, or slightly less (Fig. 20). The skull, vertebrae and limb bones are all of normal proportions, though they may be quite large.

Several forms within the group are very similar osteologically; on the basis of the limited number of specimens I have seen of some of the forms involved, I am unable to recognize with any certainty characteristics that will differentiate the various members of the *marinus-paracnemis-arenarum* complex. The fossil specimens listed below are certainly members of this complex, and readily identifiable as such. The tentative specific identifications are, however, based primarily on geographic and temporal probability rather than on specifically identifiable morphological features.

Bufo cf. arenarum Hensel

This is an extant species. One group of fossil specimens, AMNH No. 243, is referred to this species. This collection includes, among other less diagnostic elements, six incomplete frontoparietals and/or otoccipitals and two parasphenoids. All specimens in the collection are large, indicating that they have originated from toads comparable to *B. marinus* in size. The frontoparietals are fully characteristic of this group and the parasphenoids clearly exhibit a large area that was overlapped by the pterygoid (Fig. 24).

The only information available concerning the origin is that included on the label in the box — "Collected by F. Ameghino, from the Pampean of Argentina." They thus presumably date from the Pleistocene, and a tentative reference to the species *B. arenarum* seems geographically most plausible.

Bufo cf. marinus horribilis Wiegmann

This also is an extant form, and again the fossil specimens are referred to this particular form primarily on the basis of geographic probability. No other member of the section is known to have, at any time, inhabited the area in which the fossils were found. The only recorded occurrences are perhaps better considered sub-Recent than fossil, and are certainly no older than the very late Pleistocene. Langebartel (1953) reported specimens from three caves of the Yucatan peninsula — Actun Has, Loltun and Actun Spukil.

Bufo sp.

Through the courtesy of Dr. Richard Estes, now of Boston University, I have been permitted to examine University of California No. 41159, a part of a toad skull included in the collection reported by Savage (1951) from the La Venta fauna, a late Miocene assemblage from the Upper Magdalena Valley, Department of Huila, Colombia. Dr. Estes is preparing a fuller report on the specimen, but has given me permission to mention at this time that the form represented is without question a member of the South American section of the *VAL-LICEPS* group, agreeing very closely with *B. marinus* and related forms in a number of features, including the diagnostic broad overlapping of the parasphenoid ala by the pterygoid.

The South American section has obviously been in existence as such since at least the late Miocene, and was in South America at that time. This relatively early origin and present diversification and widespread distribution in South America, along with the apparent ability of some members of the section to live in many areas when introduced, suggest that the sole North American representative, *B. m. horribilis*, represents a relatively late entry into North America. Presumably this entry did not occur until the re-establishment of land connections in the Pliocene, the section previously having been confined to South America.

THE MEXICAN SECTION

The extent of dermal ornamentation and of crests is variable within the section; most commonly both are fairly extensive, and the ornamentation is of a granular texture. The suprapterygoid fenestra is not occluded; the shaft of the squamosal is of normal extent; the medial arm of the pterygoid may come in contact with, but does not appreciably overlap, the parasphenoid. The ilial prominence is usually low, moderately high in a few forms (Figs. 16, 17). The skull, vertebrae and limb bones are of normal proportions.

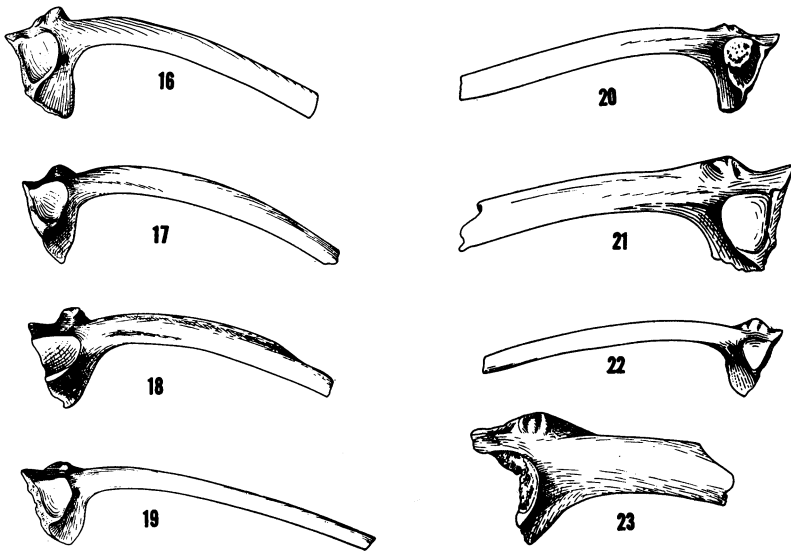
Bufo cf. alvarius Girard

This is an extant form. A single fossil specimen, part of AMNH No. 3256, from the Blancan Benson Locality of Cochise County, Arizona, is tentatively referred to this species. The specimen is the anterior end of a coccyx; as judged from comparison with Recent skeletons, it must represent an individual of 140 mm to 150 mm snout-

vent length. Other large forms of the VALLICEPS group, such as *B. marinus* and its relatives and *B. peltocephalus* seem to be eliminated on geographic bases. The articular portion of the fossil coccyx has a width of 6.9 mm and a height of only 2.8 mm, or about 41% of the width. These proportions are fairly typical of the VALLICEPS group, in which the height usually varies between 35% and nearly 55% of the width; in the AMERICANUS group the height is 45% to 60% of the width (see Fig. 27). The spine is also usually relatively high in the AMERICANUS group, but is broken and cannot be measured on the fossil specimen. It seems unlikely, on the basis of the proportions given, that this specimen represents a large extinct member of the AMERICANUS group, comparable to *B. w. bexarensis*. The present occurrence of *B. alvarius* in the same general geographic area, and the absence of any other toads of comparable size, make tentative reference of the fossil to *B. alvarius* seem reasonable.

Bufo campi Brattstrom

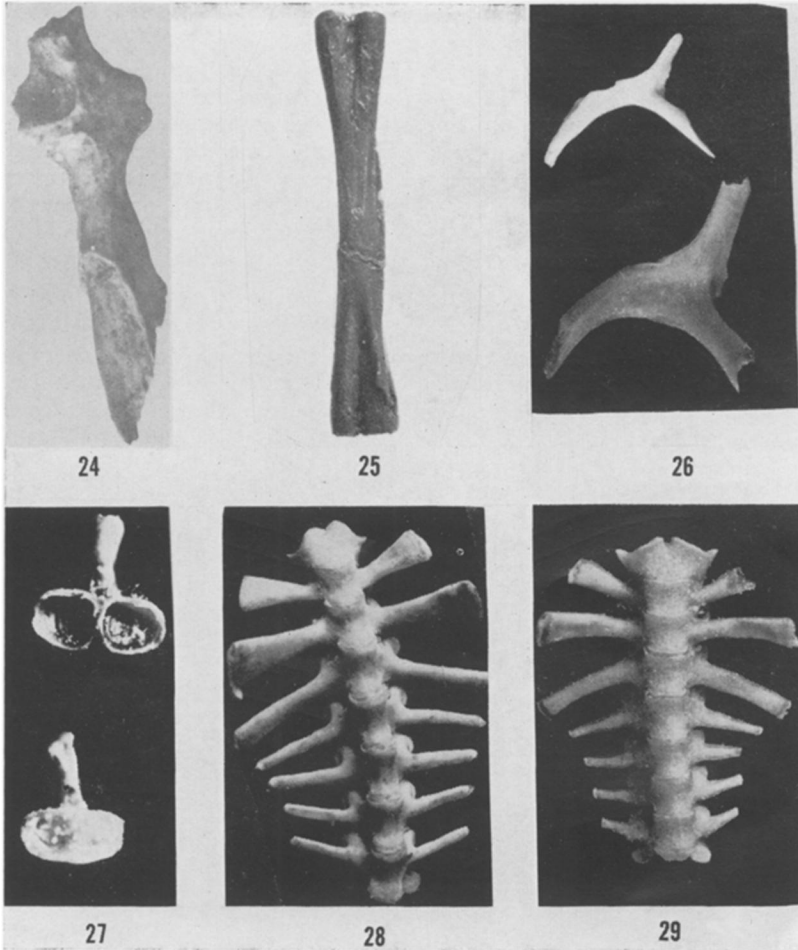
Definition.—A moderately large *Bufo*, tentatively considered to be a member of the Mexican section of the VALLICEPS group, with a thin, wide longitudinal ridge along the central portion of the postaxial surface of the tibiofibula.



Figs. 16-23.—Ili of various members of the *valliceps* group. 16. *B. alvarius* (actual length 51 mm); 17. *B. valliceps* (actual length 26 mm); 18. *B. quercicus* (actual length 9 mm); 19. *B. punctatus* (actual length 14 mm); 20. *B. m. horribilis* (actual length 45 mm); 21. *B. praeivius* from Thomas Farm Miocene (actual length 31 mm); 22. *B. debilis* (actual length 13 mm); 23. *B. suspectus*, holotype specimen (actual length 8.3 mm).

Type and type horizon.—The holotype specimen is a left tibiofibula, Calif. Inst. Technol. No. 275/5120, from C. I. T. Locality 276, Pliocene, Yepomara formation (Hemphillian), Petterson Field locality, Arroyo de los Burros, Rincon, Chihuahua, Mexico (Brattstrom, 1955).

Referred material.—Known only from the type specimen.



Figs. 24-29. Miscellaneous skeletal elements. 24. Posterior tip and right ala of Pleistocene parasphenoid referred to *B. arenarum* (actual width 17 mm); 25. Cast of holotype specimen of *B. campi*, courtesy of the Los Angeles County Museum (actual length 35 mm); 26. Pterygoids of *B. valliceps* (upper) and *B. woodhousei* (lower) showing differences in proportions between the two groups; 27. Anterior view of coccyges of *B. alvarius* (upper) and *B. cognatus* (lower), showing average differences in proportions; 28. Vertebral column, except sacrum, of *B. americanus*, ventral view, showing proportions of the centra; 29. Same, *B. cognatus*.

Discussion.—Figure 25 is a photograph of a cast of the type specimen, procured through the courtesy of the Los Angeles County Museum. The presence of a prominent ridge, or flange, is a highly distinctive characteristic, without a true counterpart in any other known Recent or fossil member of the genus. Even though the form is known only from the tibiofibula, and as a general rule limb bones are of little diagnostic value, there is in this instance, as Brattstrom pointed out, little probability of confusion of this species with other known forms.

This same distinctiveness, in the absence of other parts of the skeleton, leads to considerable uncertainty concerning the affinities of *B. campi*. Brattstrom states that “the only North or Central American species of *Bufo* having a lateral spine or ridge on the tibiofibula are *B. simus* (where the ridge is just barely discernible) and *B. valliceps* (where there is a small ridge even less evident than in *simus*).” The *B. simus* here referred to is presumably the form now known as *B. occidentalis* (Firschein, 1950). The inference is that *B. campi* is more closely related to *B. valliceps* and *occidentalis* than to any other extant forms, though differing markedly even from these.

My own observations differ slightly from the above in certain details. Among the specimens of *B. valliceps* seen, there is complete gradation from a rounded posterior surface of the tibiofibula, through moderately and to sharply angular surfaces, the latter perhaps slightly produced as a slight ridge. In general the more sharply angular surfaces occur most frequently in larger, presumably older specimens. Much this same pattern of variation seems to occur throughout the section, but for most species the number of specimens available is too small to demonstrate it clearly. In the two specimens of *B. occidentalis* seen, one small and the other of average size, there is no appreciable ridge.

In the BOREAS and AMERICANUS groups the posterior surface of the tibiofibula is usually at most only slightly angular, even in large specimens. An exception occurs in *B. microscaphus*; six specimens, all of moderate size, have an indistinct ridge comparable to those observed in the VALLICEPS group. In proportions, the tibiofibula of *B. campi* is more typical of the VALLICEPS group than of the AMERICANUS group, most of which have relatively short and heavy limb bones. There is some variation within each group, and *B. microscaphus* has more slender limb bones than most AMERICANUS group members, resembling closely those of many members of the VALLICEPS group.

The affinities of *B. campi* are thus not completely clear. Brattstrom implied possible relationship to the Mexican section of the VALLICEPS group. The specimen indicates a toad approaching *B. alvarius* in size, and affinity with that species is at least possible. However, the possibility that it is actually a member of the AMERICANUS group cannot be completely dismissed.

Bufo valliceps Wiegmann

This is an extant species. As for *B. m. horribilis*, the fossil records are perhaps best considered sub-Recent, and are certainly no older than

the very late Pleistocene. It has been reported (Langebartel, 1953) from two caves of the Yucatan peninsula — Actun Coyok and Actun Spukil.

THE CARIBBEAN SECTION

Members of this group have a skull of normal or depressed proportions with extensive ornamentation; the extent of the crests is variable. Most forms have the suprapterygoid fenestra partially or largely occluded by flanges of the pterygoid or squamosal, or both. In some the squamosal shaft is very short, failing to reach the quadratojugal; it may be markedly expanded horizontally. There is usually no overlapping of the parasphenoid alae by the pterygoid. The ilial prominence is usually very low, but one or two marked exceptions exist. The vertebrae are of normal proportions or depressed.

Bufo praeivius Tihen

Definition.—A moderate-sized *Bufo* of the VALLICEPS group, probably of the Caribbean section, with high, granular supraorbital crests oriented almost vertically and forming a sharp angle with the post-orbital crests; height of the ilial prominence about 20% of the length of its base.

Type and type horizon.—MCZ No. 1991, the distal 13 mm of a right ilium. From the Thomas Farm deposits, Lower Miocene terrestrial deposits of Hawthorne age, Gilchrist County, Florida.

Referred material.—A number of specimens have now been recovered, most of which are in the collections of the University of Florida and of the Museum of Comparative Zoology. All consist of dissociated individual skeletal elements, and all are from the Thomas Farm locality.

Description.—Auffenberg (1956) has discussed the cranial crests in considerable detail. As he pointed out, and as may be judged from the brief description given in the definition, the disposition of the crests on the frontoparietal is typical of conditions found in the AMERICANUS group. It thus differs markedly from the usual arrangement in the VALLICEPS group. In texture the crests are distinctly granular, as in most of the VALLICEPS group and few of the AMERICANUS group; the dorsal surface of the frontoparietals between the crests is heavily ornamented (Fig. 30), as is typical for the Caribbean section of the VALLICEPS group and some members of other sections. Several specimens are sufficiently complete to demonstrate conclusively that the frontoparietals and pro-otics were fused. These, and other minor details, show that this form, despite the disposition of the cranial crests, is a member of the VALLICEPS group, and probably of the Caribbean section of that group.

In a few specimens the exoccipital is also fused with the frontoparietal-pro-otic complex. In some species the fusion of the occipital with the pro-otic is clearly a matter of ontogenetic variation, fusion occurring only in large, presumably old, individuals. Whether or not this is the usual situation throughout the genus, or in *B. praeivius* itself, cannot be determined on the basis of available material.

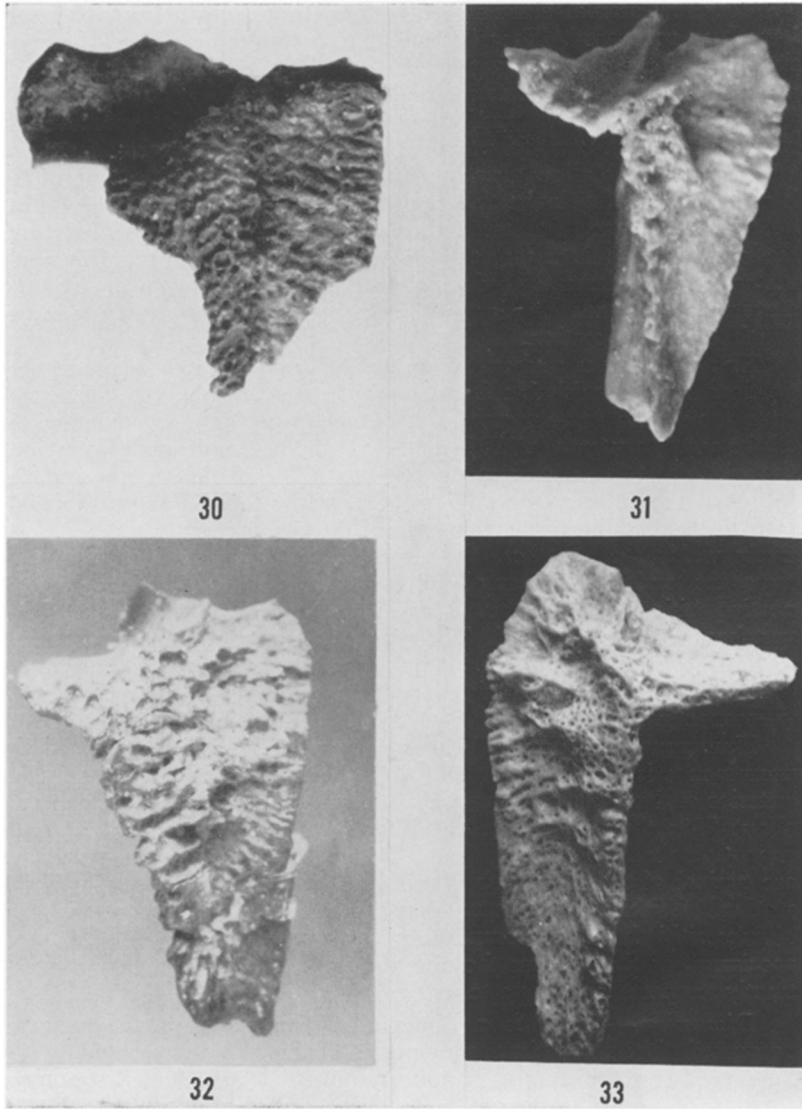
Very few cranial elements other than fragmentary frontoparietals have been recovered. There is no way of determining, as yet, the relationships of the quadratojugal, the disposition of the nasals, the full extent and shape of the squamosal shaft, nor the exact form of the pterygoid. Some small portions of squamosals have been recovered, mostly the otic plates and part of the tympanic portion, but these are too incomplete to allow accurate reconstruction of that element; there is a suggestion of a flange that may have partially occluded the supra-terygoid fenestra, further indicating affinity with the Caribbean section, but this interpretation is questionable. The parasphenoids recovered are adequate to demonstrate that there was no area of the alate portion broadly overlapped by the pterygoid such as occurs in the South American section.

The limb bones and vertebrae are of approximately average proportions, indistinguishable from those of many members of the VALLICEPS group and some members of other groups. The condylar width of the sacral centrum is 120% to 145% of the length of the centrum; the width at the anterior end is 78% to 100% of the length, and the height at the anterior end is 53% to 67% of the length (six specimens). It is likely that the proportions given indicate a slightly shorter, relatively wider sacrum than the form actually possessed in life; this apparent tendency in many fossil specimens will be discussed in connection with *Bufo cognatus*. There is one case of fusion of the sacral vertebra with the presacral. The crest of the coccyx is low, in contrast to the most usual condition in the AMERICANUS group, as Auffenberg pointed out. It is fully consistent with assignment of *B. praeivius* to the VALLICEPS group.

Numerous ilia (Fig. 21) are now available. The height of the prominence is consistently about 20% of the length of its base. The anterior and posterior slopes are subequal, their angles each averaging about 28°; the peak angle varies between 115° and 130°, and the supra-acetabular angle between 135° and 145°. These measurements are typical of the VALLICEPS group, and particularly of the Caribbean section. Within the AMERICANUS group, only *B. terrestris* and *charlesmithi* have a comparably low prominence, and in most specimens of these forms the anterior slope of the prominence is distinctly steeper than the posterior.

Discussion.—There is no indication from any of the material recovered that more than one species of *Bufo* is represented in the Thomas Farm collections. It appears quite safe to refer all specimens to *B. praeivius*. The over-all characters, and particularly the frontoparietal-pro-otic fusion, demonstrate that this species is a member of the VALLICEPS group; reference to the Caribbean section of that group is not so conclusively demonstrated, but is suggested.

The disposition of the cranial crests is not at all typical of the group, but is strongly reminiscent of the AMERICANUS group. It will be shown subsequently that most of the forms known from the Florida peninsula, both fossil and Recent, exhibit some comparable discrepancy involving



Figs. 30-33.—Fossil frontoparietals. 30. *B. praeivus*, Miocene, Florida (actual width, including pro-otic, 6.5 mm); 31. *B. cognatus*, Middle Pliocene, Kansas (actual length 9 mm); 32. *B. rexroadensis*, Blancan, Kansas, holotype specimen (actual length 12.4 mm); 33. *B. spongifrons*, Middle Pliocene, Kansas, holotype specimen (actual length 8.5 mm).

group characteristics. Discussion of the possible significance of this is postponed until these other forms have been described, but will be reconsidered in the discussion of *Bufo tiheni*.

Bufo punctatus Baird and Girard

This is an extant species. Only one fossil occurrence has been recorded, that by Brattstrom (1958) from the late Pleistocene Gypsum Cave of Nevada. He states that "As with many of the snakes and lizards from this Late Pleistocene cave, this toad still has dried skin on its back . . . with small brick-red tubercles. . . ."

Discussion.—In general I have not attempted in this paper to describe Recent forms known as fossils in any detail, mentioning only those features involved in the identification of actual fossil specimens. But since the present species is not in all respects a typical member of the Caribbean section, if a typical member can be said to exist, and since its distribution (along with that of *B. debilis* and its allies) does not seem to form an integral part of the general distribution of the group, it is desirable to point out the features that indicate its affinities with that section.

The skull is very low and broad, its height scarcely if at all exceeding 40% of its length. The crests are obsolete, but there is extensive sculpturing of the roofing bones and maxillae, with co-ossification of the dermis. There is a limited flange on the pterygoid and a slightly more extensive one on the squamosal, slightly occluding the supra-terygoid fenestra. The squamosal shaft is short, failing to reach the quadratojugal. The latter element is also short; it is in only limited contact with the maxilla, despite the fact that the jaw articulation is set far forward. The vertebral centra are slightly depressed, the ilial prominence very low (Fig. 19), the limb bones rather long and slender, but the scapula quite short and relatively broad.

The obsolete crests and limited occlusion of the supra-terygoid fenestra are not typical of the Caribbean section, but all of the other features listed are. The species certainly cannot be referred to any other recognized section, and does exhibit the majority of characters used to define the Caribbean section. There are some similarities to *B. debilis* and its allies; these two forms may represent a stock that was derived from early members of the section that presumably inhabited northern South America; this stock may have reached the North American mainland across a Central American water barrier. The distribution of other members suggest that, as a group, this section is somehow better equipped for island-hopping than are most toads.

Bufo quercicus Holbrook

This also is an extant form. The only fossil specimen clearly referable to *quercicus* that I have seen is an ilium (UF 6573) from Reddick Locality I-B, Marion County, Florida. This deposit has been tentatively dated as late Illinoian (Auffenberg, 1958).

Like *B. punctatus*, this species exhibits several features that require description and discussion in any attempted analysis of its relationships. That it is properly referable to the Caribbean section is clearly indicated by a pronounced occlusion of the suprapterygoid fenestra, involving both the squamosal and the pterygoid. The squamosal shaft is very short, not reaching the quadratojugal; the latter element is also short, in limited contact with the maxilla. The jaw articulation is set well forward; the vertebral centra are distinctly depressed. These features leave little doubt of its affinities with the Caribbean section.

Nevertheless, *B. quercicus* is distinctive in several respects. The skull (Figs. 9-10) is not at all depressed, even approaching the lower limits of the range of variation in the AMERICANUS group in height. The crests, though distinct, are low, and sculpturing of the cranium is not particularly prominent nor extensive. The otoparietal is always fused with the pro-otic, but in the orbit the perpendicular lamina of the frontoparietal often remains distinct from the pro-otic, giving a first impression that these two elements are not fused. The supraorbital and postorbital crests meet at a rounded angle, rather than the broad curve of most members of the group. The scapula is of normal proportions. The ilium (Fig. 18) has an exceptionally high prominence for this group, particularly for this section of the group. The height of the prominence is 27% to 35% of the length of its base.

These exceptional features are, in large part, not due simply to the absence of specializations found in other members of the section, but, in appearance at least, they suggest an approach to conditions typical of the AMERICANUS group. It was pointed out in the discussion of *B. praeivius* that many Floridian toads, fossil and Recent, exhibit an apparent intermingling of features of the AMERICANUS and the VALLICEPS groups. This topic will be mentioned again in connection with *B. terrestris*, and discussed more fully in connection with *B. tihenii*.

***Bufo suspectus*, sp. nov.**

Definition.—A moderately small *Bufo*, tentatively referred to the Caribbean section of the VALLICEPS group, with an ilial prominence whose height is less than 20% of the length of its base, the posterior slope slightly steeper than the anterior, the peak broadly rounded, and the shaft of the ilium slightly compressed.

Description.—The type specimen is illustrated as Figure 23. The height of the prominence is about 17% or 18% of the length of its base. The anterior angle is approximately 22°, the posterior angle 28°, and the peak angle 130°. Part of the extreme tip is missing, so that the supra-acetabular angle cannot be determined accurately, but it appears to be nearly 150°. The peak of the prominence is broadly rounded. Most of the acetabulum and the subacetabular expansion are missing. The shaft, as judged from the portion present, is moderately curved and slightly compressed; there is no evidence of any dorsal crest.

Type and type horizon.—UMMVP No. 40155, a portion 8.3 mm long from

very near the distal end of a right ilium. From the Fox Canyon Locality, Sec. 35, Twp. 34 S, Range 7 W, in the Blancan Rexroad Formation of Meade County, Kansas.

Referred material.—Subsequent to the time this description was originally prepared, I have seen a small collection from the Lower Pliocene Valentine Formation of Brown County, Nebraska. In this collection, as part of UMMVP No. 42192 is a fragmentary ilium indistinguishable from the type specimen of *suspectus*, along with a few fragmentary limb bones that exhibit no distinctive features. Neither this material nor the type specimen are fully adequate for accurate specific identification, but pending further information I think it appropriate to refer the Nebraska Valentinian specimens tentatively to *B. suspectus*.

Discussion.—Reference of these specimens to an undescribed species, and reference of that species to the Caribbean section of the VALLICEPS group are both admittedly somewhat speculative procedures, without adequate purely morphological evidence to support the conclusions. Reference to the AMERICANUS group is virtually eliminated by the low ilial prominence; even *B. terrestris* and *charlesmithi*, the two species with the lowest ilial prominence in that group, rarely are as low as 20%. Occurrence of either of these forms in the Rexroad is very unlikely on ecological grounds. In addition, in both those forms, the anterior slope of the prominence is usually steeper than the posterior; occasionally they may be subequal, but the posterior slope is never distinctly steeper than the anterior, as it is in the specimens referred to *B. suspectus*.

Exactly these same considerations and, for some species, geographical ones, tend to eliminate the known species of the Mexican section of the VALLICEPS group from consideration. It is possible that minor and unrecognized erosion and wear could alter the shape and proportions of the prominence somewhat, but in the absence of evidence that this has happened, it seems unwarranted to assume its occurrence simply for the sake of being able to refer the specimen to some extant species.

A very low ilial prominence is characteristic of the Caribbean section of the VALLICEPS group, and it is primarily on this basis that *B. suspectus* is tentatively referred to that section. In *B. debilis* and *punctatus*, the species now inhabiting the same general geographic area as *B. suspectus*, the anterior and posterior slopes of the prominence are customarily subequal, but with the anterior slope being slightly the steeper more frequently than is the posterior. The shaft of the ilium appears somewhat more nearly cylindrical in both of those species than in *B. suspectus*. And the two ilia referred to *B. suspectus* suggest that this was a somewhat larger form than *B. punctatus*, certainly larger than *B. debilis*. While they probably do not represent specimens completely outside the size range of *B. punctatus*, they are appreciably larger than the largest *B. punctatus* ilium that I have seen, and must have come from individuals very near the maximum known size for *B. punctatus*.

The use of the term Blancan, with particular reference to the

depositional and faunal sequences of southwestern Kansas and adjacent areas, has been discussed at length by Taylor (1960). The toads of the Rexroad Formation, of themselves, offer little information bearing on the problem of location of the Pliocene-Pleistocene boundary within or below the Blancan as thus used, and it is not appropriate in this report to attempt any over-all analysis of the herpetological, or even complete amphibian, fauna of the Rexroad.

The AMERICANUS Group

This group is characterized particularly by the possession of a distinctly elevated skull. The frontoparietals are relatively narrow, not diverging strongly posteriorly nor forming an extensive supraorbital shelf; they are not fused with the pro-otics. Crests are usually present, variable in degree of development and in disposition. The roofing bones are less extensively ornamented than is typical for the VALLICEPS group; in most forms, the occipital groove is open dorsally in at least its posterior part. Many, but not all, species have shorter vertebral centra and shorter, heavier limb bones than do most members of other groups. In the majority of species the ilial prominence is very high, sometimes almost spike-like. The maxillary arm of the pterygoid is relatively short and strongly curved (see Fig. 26).

Although osteological similarities among certain species are recognizable, there is no clear division of the group into two or more distinct sections on any osteological basis. One may, for convenience, speak of an eastern section comprised of *B. americanus*, *houstonensis* and *terrestris*, and a western section including *B. cognatus*, *compactilis* and *woodhousei*. But these two sections are not clearly defined nor accurately delimited; the species not mentioned are not fully typical of either section, and even if those other species were ignored it would be difficult to frame a valid osteological definition that would clearly differentiate the sections.

Bufo americanus americanus Holbrook

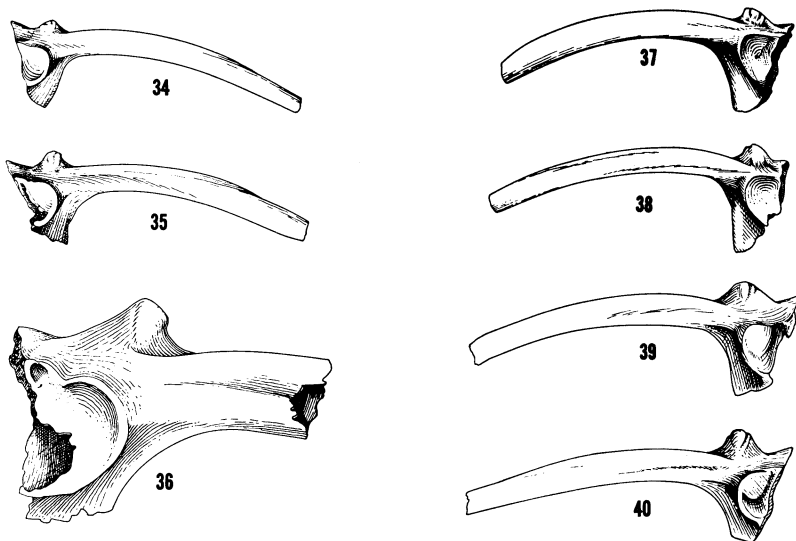
This is an extant form. The cranial crests are heavy and cancellous in texture; the occipital groove is open dorsally in immature specimens, the anterior part roofed over by the juncture of supraorbital and postorbital crests in mature ones. The vertebral centra are relatively long for this group (Fig. 28); the width of the sacral centrum at the condyles is 110% to 135% of its length, the width at the anterior end about 90% of the length, and the height of the anterior end about 60% of the length. The ilial prominence is of moderate height (Figs. 35, 37, 38), i.e., the height usually about 30% to 35% of the length of its base. In young individuals the anterior and posterior slopes are subequal, but with maturity the anterior slope becomes very steep, so that the peak of the prominence is located very distinctly anterior to the midpoint of its base.

All known fossil records are late Pleistocene. Several specimens of various elements, including ilia, are included under Carnegie Museum No. 18786 from a sink hole near New Paris, Bedford County, Penn-

sylvania. A definitely boreal fauna exists at the level from which these specimens were derived (Guilday and Bender, 1960), suggesting that they may represent a time near the Wisconsin maximum, and radiocarbon dating (*idem*) indicates an age of approximately 11,000 years. Other late Pleistocene to sub-Recent specimens in the Carnegie Museum are from Rattlesnake Cave in Westmoreland County and Franks-town Cave in Blair County, Pennsylvania. Some specimens from these collections are decidedly larger than the average *B. a. americanus* of today, but are not, I believe, outside of the known size range, and are otherwise quite typical. Specimens probably of Recent origin, that is, not more than a few hundred years old, were obtained associated with mammalian remains in Sullivan's Cave, Lawrence County, Indiana (vide Bader & Hall, 1960). Other Carnegie Museum specimens, and University of Florida Nos. 2678 and 2781 also include ilia, frontoparietals and other elements referable to *B. americanus*. These specimens originate from the Pleistocene of Natural Chimneys, Augusta County, Virginia; exact dating is uncertain, but probably Wisconsin or slightly later than the Wisconsin maximum.

Bufo arenarius Taylor

This name was proposed by Taylor (1936) on the basis of a sacrum (KUMVP No. 1452) from the Middle Pliocene Edson Quarry beds



Figs. 34-40.—Ilii of various members of the *americanus* group. 34. *B. terrestris* (actual length 24 mm); 35. *B. americanus*, immature (actual length 18 mm); 36. *B. hibbaridi*, Middle Pliocene, Kansas (actual length 11 mm); 37-38. *B. americanus*, mature (actual length 28 and 24 mm respectively); 39. *B. hemiophrys*, Recent (actual length 21 mm); 40. *B. cf. hemiophrys*, Cudahy fauna (actual length 19 mm).

of Sherman County, Kansas. This sacrum differed in some details from another sacrum from the same beds designated in the same paper as the type specimen of *Bufo hibbardi*. I have examined the two types, and all other material available from the Edson Beds, and am of the opinion that the variation found, both in the sacra and in other elements present in the collections, is no greater than that which would be expected to occur if only a single species were represented. I am therefore considering all of the specimens to represent *B. hibbardi*, and considering *B. arenarius* synonymous with that species, which has page priority. The specimens and characteristics will be discussed under the name of *B. hibbardi*.

Bufo cognatus Say

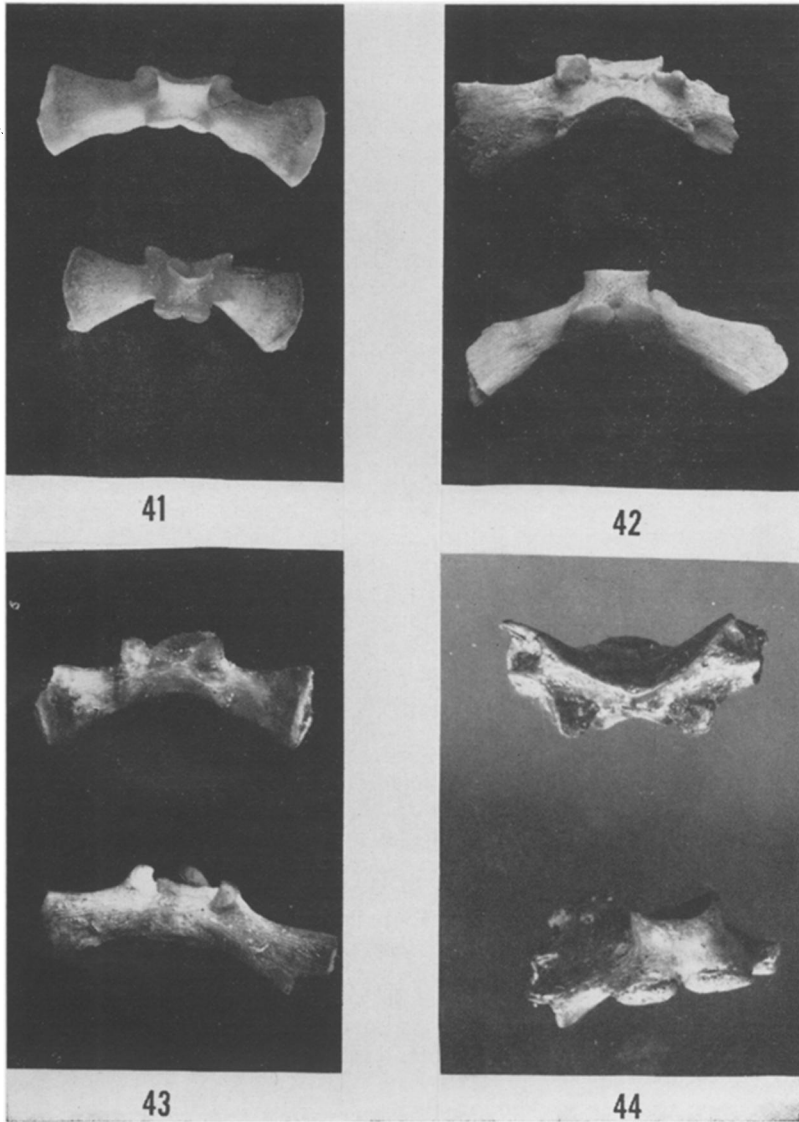
This is an extant form. The frontoparietals are distinctive in that the supraorbital crests converge sharply anteriorly, obliquely traversing the dorsal surface of the frontoparietals (Fig. 11). There is a nasal boss, a rather prominent feature on the intact skull but less readily recognizable on dissociated nasal bones, where it can be recognized primarily as a thickening of the bone near its medial border. The anterior part of the occipital groove is roofed in mature specimens, the posterior part open dorsally. The ventral part of the sphenethmoid is extended forward in the midline between the vomers, often very nearly reaching the palatal processes of the premaxillae.

The proportions of the vertebral centra are variable, and the variation can to at least some extent be correlated with geographic distribution, the centra of Recent specimens from Kansas are distinctly shorter and wider than those of Recent specimens from Arizona (Fig. 41). Using the sacrum as an example, comparative measurements, expressed as a percentage of the length of the centrum, are as follows:

	Kansas	Arizona	Fossil specimens
Width at the condyles	120-140	95-110	120-150
Width at the anterior end	100-120	78-97	95-117
Height at the anterior end	63-75	50-58	66-73

The range of variation shown is that occurring in twelve specimens from Kansas (Harper and Meade counties) and six from Arizona (Maricopa County). The fossil specimens are from various deposits, mostly Pleistocene, in Kansas or nearby Oklahoma. Measurements of the Recent specimens were rechecked after the discrepancy was noted, to assure that no differences in technique were involved. In this group of specimens, there was no overlap of proportions between the two localities, but it is to be expected that some overlap would occur in a larger series. All of the fossils referred to *B. cognatus* resemble the Kansas specimens, or in some cases have even higher values for the proportions given.

Even though the total range of variation in the fossil specimens is not markedly greater than in the Recent ones, there is a definite ten-



Figs. 41-44.—Sacra of various members of the *americanus* group. 41. *B. cognatus*, Recent, from Kansas (above) and Arizona (below); 42. *B. cognatus* or *B. spongifrons* from Middle Pliocene Long Island Quarry, dorsal and ventral views; 43. Recent *B. cognatus* (above) and *B. woodhousei* (below), dorsal views to show most frequent arrangement of crests on the neural arch; 44. *B. rexroadensis*, Blancan, dorsal and ventral views.

dency for the distribution to be concentrated around the higher values for these proportions, indicating a relatively shorter and wider vertebra. An indication of this same phenomenon has been noted in all extant forms of which a sufficient number of fossil specimens have been recovered to allow meaningful, or at least suggestive, comparison, i.e., *B. terrestris*, *B. woodhousei* and *Rana pipiens* (Tihen, 1954) as well as *B. cognatus*. The relatively soft articular portions of the condyles (and the anterior end of the centrum in ranids) are apparently more subject to slight erosion than are the other portions of the vertebrae, composed of more compact bone. This would act to decrease the apparent length of the centrum, correspondingly increasing all measurements expressed as a proportion of the length.

The crests on the dorsal surface of the sacral neural arch are variable. Typically they meet medially in an arc of short radius (Fig. 43), but they may occasionally meet in a rounded angle or, on the other hand, may occasionally form a broad arch of long radius such as usually is found in *B. woodhousei*.

The shaft of the ilium is weakly curved, much of the posterior part somewhat compressed, and there is a low, inturned dorsal crest along approximately the central half of its length (Figs. 45-47). The prominence varies in height from about 40% of the length of its base in young specimens to about 50%, occasionally slightly more, in large individuals. The anterior and posterior slopes are commonly subequal, but the anterior is occasionally distinctly the steeper. The anterior angle is usually between 45° and 55°, the posterior approximately 45°, the peak angle 80° to 95°, and the supra-acetabular angle 115° to 130°.

There are numerous fossil specimens at least tentatively referable to *B. cognatus*; they range in age from Middle Pliocene to late Pleistocene.

Middle Pliocene (Hemphillian).—In the same collection (most of which is under USNM No. 8033) as that containing the holotype of *B. alienus* there are several specimens that can be referred confidently to *B. cognatus*. The collection includes ten fairly complete ilia; one is the holotype of *B. alienus*, six are fully within the usual range of variation of *B. cognatus*, and the other three are referred to another species of the AMERICANUS group to be described subsequently. There are eight more or less complete frontoparietals; five of these exhibit the characteristic convergence of the supraorbital crests found otherwise only in *B. cognatus* (Fig. 31); one nasal bone is thickened along the medial border, suggesting a boss as in *B. cognatus*. The numerous other elements, mostly postcranial, could all be referred to *B. cognatus*, but could equally well be referred to any of several related forms. The frontoparietals and nasal indicate clearly that *B. cognatus* is represented in the collection as the most common form, and the ilia resembling those of *B. cognatus* are, then, presumably referable to this species. The three ilia not fully typical of *B. cognatus*, and the three frontoparietals not referable to *B. cognatus* can reasonably be assigned to a second form, as suggested. The unidentifiable elements presumably represent

both *B. cognatus* and this second form, but lack diagnostic characters that I was able to observe which would allow specific differentiation.

In addition to the above series, there are several *Bufo* elements, including two fragmentary ilia, in AMNH Nos. 1634-1636 that are tentatively referred to *B. cognatus*. These specimens could almost equally well represent a related form, particularly *B. woodhousei*, but that species is not known from the Middle Pliocene, and they do not seem to belong to any of the other known Middle Pliocene forms. The collection is stated to be from the "Lower (?) Pliocene, Driftwood Creek, Hitchcock County, Nebraska," but the exact point of origin is not given. In view of our present knowledge of the deposits of that area, it seems probable that these are Hemphillian, rather than Lower Pliocene, in age.

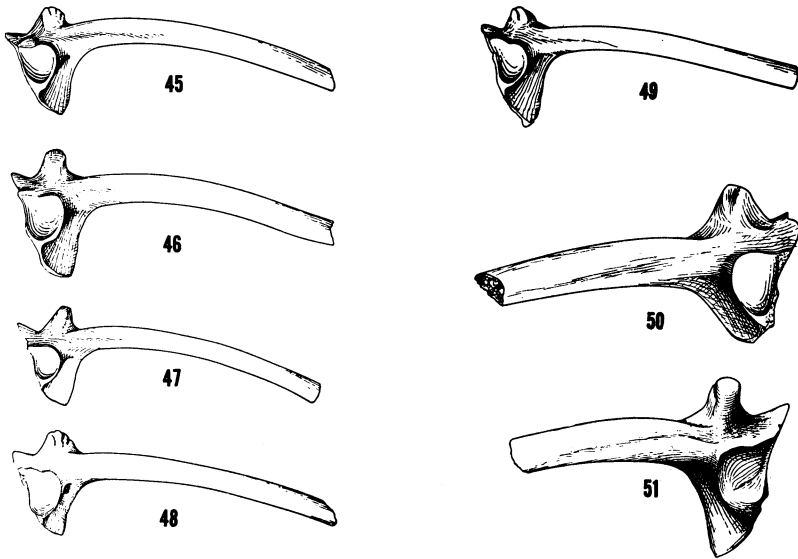
Blancan (Rexroad).—The presence of this species in the Rexroad is not clearly demonstrated. Only one frontoparietal has been recovered from this formation, and this is definitely not referable to *B. cognatus*. Over thirty ilia are available; these exhibit a wide range of variation, suggesting the presence of at least two forms, possibly three, belonging to the AMERICANUS group. The two recognized forms do not include *B. cognatus*, but some of the ilia are definitely within the range of variation of that species. It is not at all clear whether these actually represent specimens of *B. cognatus*, or simply demonstrate that the range of variation in one or both of the recognized forms overlaps broadly with that of *B. cognatus*. Since the species lived in Kansas both prior and subsequent to the Rexroad, it might well be expected, but cannot be conclusively demonstrated.

Pleistocene.—No frontoparietals have been recovered from the Pleistocene, but some other elements from various deposits, particularly ilia and sacra, are so thoroughly typical of the usual condition in *B. cognatus* that they can be referred to this species with considerable confidence. Such specimens are found in the late Illinoian Butler Springs fauna of Beaver County, Oklahoma (Herrington and Taylor, 1958), the Sangamonian Cragin Quarry fauna of Meade County, Kansas, a "late Pleistocene" deposit in section 21-30-23 of Clark County, Kansas, and the late Wisconsin Jones fauna of Meade County, Kansas. Vertebrae and limb bones clearly representing some member of the "western section" of the AMERICANUS group, but not even tentatively identifiable as to species, are found in the Illinoian Doby Springs fauna (Smith, 1958) of Harper County, Oklahoma, and the Kentuck assemblage (Hibbard, 1952), containing reworked specimens of various ages, probably mostly Yarmouthian, of McPherson County, Kansas. Specimens from the Sangamonian Jinglebob fauna and Yarmouthian Borchers fauna, both of Meade County, Kansas, when identifiable at all, seem to resemble *B. woodhousei* more closely than they do *B. cognatus*, and have been so tentatively referred, though some may actually represent the latter species. All of these specimens are in the collections of the University of Kansas and the University of Michigan.

Bufo cf. *compactilis speciosus* Girard

This is an extant form. The species *B. compactilis* is characterized by the combination of obsolete cranial crests but an occipital canal that is rather fully covered dorsally. No fossil frontoparietals have been recovered, and most postcranial elements are virtually indistinguishable from those of *B. cognatus*; the only element of significance in the tentative identification of any known fossil specimens as *B. compactilis* is the ilium (Figs. 49-50). In this species the height of the prominence varies between 45% and 55% of the length of its base. The posterior slope is usually distinctly steeper than the anterior. The anterior angle approximates 45° , the posterior angle 55° , and the peak angle 80° ; the supra-acetabular angle is between 105° and 115° , decidedly more acute than in most other species.

Several ilia from the Rexroad formation agree very closely with those of *B. compactilis* and are tentatively referred to this species, although on the basis of ilia alone I am unable to distinguish it from the Middle Pliocene *B. spongifrons*, to be described subsequently. The average height of the prominence in the Rexroad ilia referred to *B. compactilis* is perhaps somewhat less than in Recent specimens, but the majority of the fossils are relatively small and this feature is subject to some ontogenetic influence; the larger Rexroad specimens here



Figs. 45-51.—Ilia of various members of the *americanus* group. 45-47. Recent *B. cognatus*, showing variation in form; 48. Middle Pliocene ilium from Long Island Quarry referred to *B. cognatus*; 49. Recent *B. c. speciosus*; 50. Blancan ilium from Rexroad tentatively referred to *B. compactilis*; 51. Middle Pliocene ilium from Long Island quarry referred to *B. spongifrons*.

referred agree closely with Recent specimens. Several sacra are also tentatively referred to this form.

Specimens referred to *B. compactilis* (UMMVP Nos. 40151-40154) have been recovered from the Fox Canyon Locality, from Rexroad Locality No. 3 and from the Wendell Fox Pasture Locality, all in the Rexroad formation of Meade County, Kansas. In addition, Nos. 27673 and 40156-40160 from these same localities comprise a number of elements for which no specific identification is feasible, but some of which would presumably represent this species.

Tentative reference to the subspecies *B. c. speciosus* is made purely on geographic grounds.

Bufo cf. hemiophrys Cope

This is another extant form. As in the preceding, the frontoparietals are distinctive, but have not been recovered in the fossil collections tentatively referred to the species. The frontoparietals bear high but thin crests, with a unique transverse crest extending medially from, and at right angles to, the supraorbital crest at about the level of the junction of the latter with the postorbital crest (Fig. 20). The tentative reference of certain fossils to this species is again based primarily on ilia. The ilial prominence varies in height from 30% of the length of the base in young individuals to nearly 45% in some mature specimens. The anterior slope is distinctly steeper than the posterior, much as in *B. americanus* (Fig. 39), and, also as in *B. americanus*, the steepness is more pronounced in mature individuals than in young. The anterior angle of the prominence approximates 55° in mature specimens, the posterior angle 40°, and the peak angle 80° to 100°; the supra-acetabular angle is between 125° and 135°.

A few toad limb bones, vertebrae and ilia are known from the Pleistocene Cudahy fauna of Meade County, Kansas, probably of Kansan glacial age (Hibbard, 1958). Specimens (KUMVP uncatalogued and UMMVP 39338) have been recovered from both the Sunbrite and the Cudahy pits. All of the *Bufo* remains from both localities are relatively small; the largest represents an individual that could scarcely have exceeded 60 mm in snout-vent length. There are five ilia complete enough to allow measurements; in these, the height of the prominence varies from 30% to 43% of the length of the base (Fig. 40). In the smallest of the five the anterior and posterior slopes are subequal; in the others the anterior slope is distinctly steeper than the posterior. The anterior angle in these four is between 50° and 55°, the posterior between 40° and 45°; in three with the posterior part of the dorsal border of the ilium present the supra-acetabular angle is between 125° and 132°. None of these values is completely outside the range of variation in some other species, but all are more typical of *B. hemiophrys* than of any other species. The fact that all specimens from both localities are small, and that the slopes of the ilial prominence are distinctly asymmetrical despite the small size of the specimens, suggests that these were mature individuals of a rather small

form instead of the young of some undetermined larger form. I am, therefore, tentatively referring the *Bufo* of the Cudahy fauna to *B. hemiophrys* pending recovery of material that is more accurately identifiable.

Bufo hibbaridi Taylor

Definition.—A fairly large *Bufo* of the AMERICANUS group with very heavy, porous to granular supraorbital and postorbital crests; nearly the entire posterior portion of the frontoparietal, including the otic plate, is covered by the material of the crests; ilial prominence high, with the anterior slope much steeper than the posterior; sacral centrum relatively long and narrow; crests on the neural arch of the sacrum variable.

Type and type horizon.—KUMVP No. 1437, a sacral vertebra, complete excepting for the terminal portions of the diapophyses, from the Middle Pliocene (Hemphillian) Edson Beds, Ogallala formation, Sherman County, Kansas.

Description.—As has been mentioned previously, I think it likely that the entire collection of *Bufo* from the Edson Beds represents a single species. The following comments are made on this basis, and apply to specimens previously referred to *B. arenarius* as well as to those originally referred to *B. hibbaridi*.

Two frontoparietals have been recovered. Both exhibit the very heavy crests apparently typical of this form. Their entire dorsal surface is roughened, and almost the entire surface of the bone at the level of and posterior to the postorbital crests is covered by the material of the crests. The supraorbital and postorbital crests meet at a slightly obtuse angle. There is no occipital crest as such, but the thickened supra- and postorbital crests themselves occupy the area adjacent to and including that normally occupied by the occipital crest. The anterior part of the supraorbital crests are, as in most forms, thinner than the posterior part, but are still heavier than the corresponding parts in *B. woodhousei* or *americanus*. No other dermal cranial elements are known. Two otoccipitals (exoccipital and pro-otic fused) are in the collection, but exhibit no special features distinguishing them from the same elements in most other members of the group.

The width of the sacral vertebrae (Fig. 62) at the condyles varies from 116% to 127% of the length of the sacral centrum, with the type specimens of both *B. hibbaridi* and *arenarius* falling near the lower end of this range. The total variation in width of the anterior end of the centrum, expressed as a percentage of length of the centrum, is only from 88% to 91%, and the height of the anterior end of the centrum varies from 61% to 68% of its length. The crests in the neural arch meet at a definite, but obtuse angle in one specimen, though they are somewhat thickened medially, and their posterior border forms a broadly curved angle; in other specimens they meet in a broad, slightly angular arch. There is a low median longitudinal crest anterior to the transverse crests, no longitudinal crest or a very faint one posterior to the transverse ones. The extremes of variation in the crests occur among the specimens assigned by Taylor to *B.*

arenarius on the basis of certain features of the centrum, such as the extent of the median depression on the ventral surface and a difference in the degree of separation of the condyles medially. I have not found these features to be constant intraspecifically in Recent forms, and question that they indicate the presence of more than a single form in this fossil collection.

The shaft of the ilium is moderately curved, and bears a low, in-turned dorsal crest along the central to anterior three-fourths of its length. In all specimens with a complete prominence, the height of the prominence varies only from 43% to 48% of the length of the base. All have a characteristic shape, very reminiscent of that in *B. americanus* (Fig. 36). The posterior slope is not particularly steep, and is a very even slope; the anterior slope is very steep dorsally, with a sharp inflection about halfway between the peak of the prominence and the dorsal edge of the shaft, becoming much less steep at this point, and forming a sort of web between the ventral half of the prominence and the shaft. The posterior angle approximates 40°, the anterior angle 50° to 55°, and the peak angle 90°. The posterodorsal tip is missing in most of the specimens, but the supra-acetabular angle appears to approximate 125°.

Other appendicular and vertebral elements are present in the collection, but offer no diagnostic features (see Taylor, 1936 & 1941).

Known fossil occurrences.—The form is known only from the Middle Pliocene (Hemphillian) Edson Beds of Sherman County, Kansas. I know of no specimens other than those reported by Taylor, and a few additional vertebral and appendicular elements also in the collection of the Kansas University Museum of Vertebrate Paleontology (Nos. 6395-6417, 7704).

Discussion.—The close uniformity of the ilia present in the collection, the close resemblance of the sacral vertebrae in proportions, and the lack of intraspecific constancy in Recent forms in respect to the features in which these elements, particularly the sacra, do differ among themselves in the fossil collection, all indicate the probability that only a single form is present. Since the name of *B. hibbardi* has page priority over *B. arenarius*, the latter name is considered as a synonym of *B. hibbardi*.

The form is clearly a member of the AMERICANUS group, but its relationships within the group are not clear. The shape of the ilial prominence is similar to that of *B. americanus*, but a relatively steep anterior slope is also found in some members of the *woodhousei-cognatus* section; the height of the prominence is more typical of the latter section. The proportions of the sacral vertebra are similar to those of *B. americanus*, *terrestris*, and related forms; the cranial crests perhaps more nearly comparable to those of *B. terrestris* or *americanus* than to those of any other extant form.

There is no indication of close relationship to any of the forms known from the Long Island Quarries, also of Hemphillian age, and in rather close geographical proximity. There is, however, a possibility

that this form is closely related to the Upper Pliocene *B. rexroadensis* (to be described subsequently) from Meade County, Kansas. Frye, Leonard and Swineford (1956) consider the Edson local fauna to be "clearly in the upper part of the Ash Hollow member."

***Bufo repentinus*, sp. nov.**

Definition.—A *Bufo* of the AMERICANUS group with a high ilial prominence; the ilium characterized particularly by a rather extensive palmation between the ventral surface of the posterior part of the shaft and the subacetabular expansion; anterior slope of the ilial prominence decidedly steeper than the posterior.

Description of the holotype.—The type specimen is shown in Figure 54. The posterior portion is broken off beyond the level of the supraacetabular depression dorsally. The exact location and the extent of the base of the prominence cannot, therefore, be determined exactly, but they can be estimated reasonably accurately. The height of the prominence must be nearly 60% of the length of its base, the anterior angle nearly 70°, and the posterior angle approximately 50°. The peak of the prominence is thus situated decidedly anterior to the midpoint of the base. The most distinctive feature of the specimen is the relatively extensive palmation anterior to the subacetabular expansion. This is clearly evident on comparison of the figure of the type with those of the ilia of other forms.

No specimens other than the holotype have been referred to *B. repentinus*, but it is possible that some of the nondiagnostic elements in the Cragin Quarry collections represent this form.

Type and type horizon.—UMMVP No. 34491, the distal portion of a right ilium, but lacking the extreme posterior end and much of the subacetabular expansion. Collected by C. W. Hibbard and party in the summer of 1955 from the Cragin Quarry, SW ¼ sec. 17, t. 32 S, R. 28 W, 4 miles southwest of Meade, Meade County, Kansas. This is a Pleistocene deposit, probably of Sangamon age (cf. Etheridge, 1958; Hibbard, 1958 et al.).

Discussion.—The height and shape of the ilial prominence show this form to be a member of the AMERICANUS group, probably related to the western section.

The opinion has sometimes been expressed, by the present writer among others, that any new species of amphibian from the Pleistocene is automatically subject to suspicion. When any form is based on a single specimen, it is impossible to be certain that this specimen is not simply an abnormal variant of some previously known form. If this is true in the present case, *B. woodhousei*, *cognatus* and the next species discussed, *B. rexroadensis*, are the possibilities to be considered. The ilial prominence is definitely higher than customary in the first two species, but probably not outside of the range of variation in either; it is more nearly comparable to *B. rexroadensis* in this respect. The extensive ventral palmation is a feature I have not seen in any specimen of any other form, fossil or Recent.

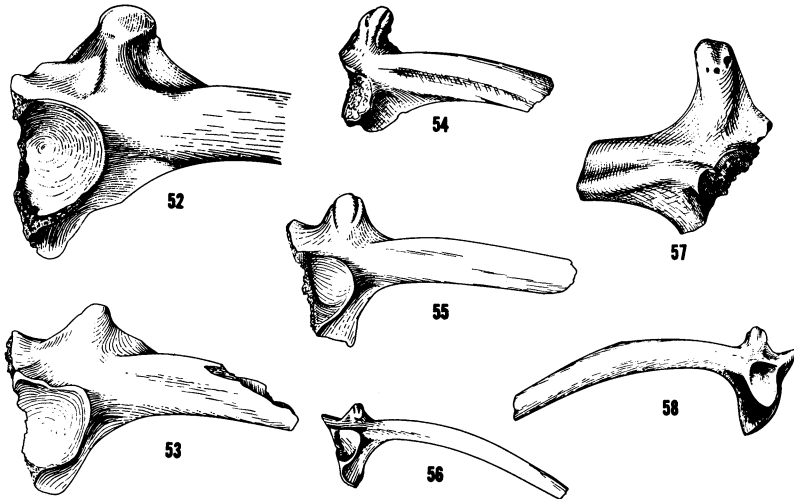
***Bufo rexroadensis*, sp. nov.**

Definition.—A moderately large *Bufo* of the AMERICANUS group with heavy supraorbital and postorbital crests meeting each other at an obtuse angle; crests greatly thickened at this point of juncture, but not covering the entire posterior portion of the bone; ilium (if associations have been made correctly) with a very high prominence having subequal anterior and posterior slopes, or with the anterior slope slightly steeper; sacral centrum short; crests of the sacral neural arch usually meet in a broad, subangular arc.

Description of the holotype.—The specimen lacks only the extreme anterior tip, and possibly the extreme lateral tip of the otic plate. The length is 12.4 mm, the greatest width, including the otic portion 8.0 mm. The crests are quite extensive (Fig.32), but slightly less so than in *B. hibbardi*. An articular surface is recognizable on the ventral face of the otoparietal, and the perpendicular lamina is mostly intact, with no broken edge, indicating clearly that this element was independent from the pro-otic.

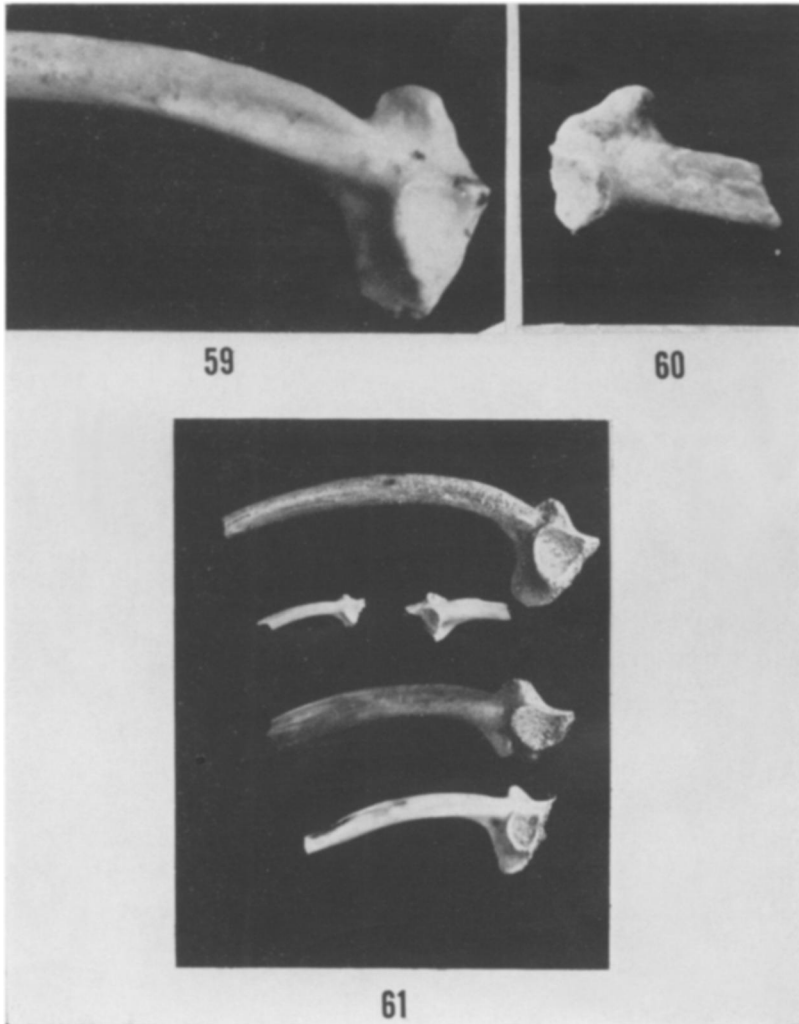
Type and type horizon.—UMMVP No. 40139, a virtually complete right frontoparietal. Fox Canyon Locality (Sec. 35, Twp. 34 S, R. 30 W), Rexroad Formation, of Blancan age, Meade County, Kansas. Collected by C. W. Hibbard and party, 1952.

Referred material.—This is the only frontoparietal as yet recovered. Other skeletal elements suggest that at least three forms are present. One of these is



Figs. 52-58.—Ilium of other members of the *americanus* group. 52. *B. tihenii*, Middle Pliocene, Florida; 53. Ilium from Cragin Quarry (Sangamon) referred to *B. cognatus*; 54. *B. repentinus*, holotype specimen; Cragin Quarry, Sangamon; 55. Blancan (Rexroad) specimen from immature individual referred to *B. rexroadensis*; 56. Recent *B. fowleri*; 57. Large Blancan (Rexroad) specimen referred to *B. rexroadensis*; 58. Recent, *B. w. woodhousei*.

very rare, and has been previously referred to the VALLICEPS group under the name of *B. suspectus*. The other two, or more, are referable to the AMERICANUS group and are each apparently represented by a number of specimens. Proper association of these elements has not been firmly established, but a tentative reference has been made for some, as suggested in the discussion of *Bufo compactilis*.



Figs. 59-61.—Ilium and sacrum of members of the *americanus* group. 59-60. *B. tihenii*, Middle Pliocene, Florida; 61. Unnamed species referred to *americanus* group from Miocene of Nebraska; the top four specimens represent the largest and smallest fossil specimens; the bottom one is a large Recent *B. americanus* for comparison.

Other than the holotype frontoparietal, cranial elements from the Rexroad include only one portion of a parasphenoid, one fragmentary sphenethmoid, two otoccipitals, one pro-otic not fused with an occipital, and the posterior portions of two lower jaws. None of these specimens, none of the numerous limb bones and girdle elements other than ilia, and none of the numerous vertebrae other than the sacra, exhibit any features allowing identification to species, though all are consistent with reference to the western section of the AMERICANUS group.

Approximately fifty portions of ilia have been recovered; of these only thirty-odd are sufficiently complete to allow even tentative identification. All but the type of *B. suspectus* are referred to the AMERICANUS group. The total variation is decidedly greater than would be expected if only a single species were present, but it is virtually impossible to determine the number of modes around which this variation is distributed. All ilia in which the posterior slope of the prominence is distinctly steeper than the anterior have been referred to *B. compactilis*, all others tentatively to *B. rexroadensis*. In general, the group referred to *B. rexroadensis* are larger, or at least reach a greater maximum size, have a higher ilial prominence (though with considerable overlap) and, as would be expected, have a more obtuse supra-acetabular angle. Even within this group the variation is somewhat greater than might be expected if only a single species were present, but I have been unable to arrive at any satisfactory method of subdividing the group. Some may represent variants of the form tentatively identified as *B. compactilis*; the possibility that some may represent specimens of *B. cognatus* has already been mentioned.

The ilia referred to *B. rexroadensis* are characterized particularly by the height of the prominence (Figs. 55, 57) — 55% to 60% of the length of the base in mature individuals, usually over 50% even in smaller ones. The anterior and posterior slopes are subequal; the palmation between the lower part of the prominence and the shaft seems more limited than in most forms, but this impression may be due as much to the greater height of the prominence itself as to any actual reduction in the extent of palmation. In large individuals the anterior and posterior angles each vary between 50° and 55°; the peak angle is 70° to 80° and the supra-acetabular angle approximately 110° to 115°.

The sacrum is subject, among Recent forms, to even greater intraspecific

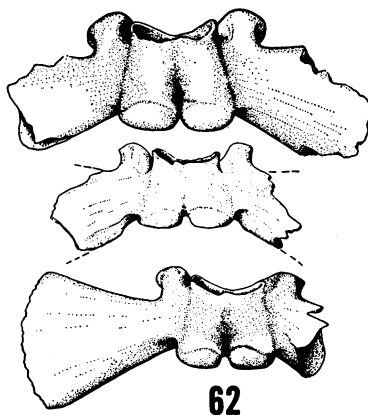


Fig. 62.—Sacra of *B. hibbardi*, Middle Pliocene, Kansas; from Taylor, 1941.

variation than is the ilium. Reference of particular sacra from the Rexroad to *B. rexroadensis* is correspondingly on an even less substantial basis than exists for the ilia. Larger specimens are assumed to be referable to this species, and the smaller ones that look most similar to these are also so referred. This group comprises somewhat over half of the total number of sacra in the collection. There is great variation in the proportions of the sacral centrum. Its width at the condyles is usually 125% to 150% of its length, but may be as high as 175% in presumably partially eroded specimens. Similarly, the width at the anterior end is usually 90% to 100% of the length, but may be as much as 125%, and the height at the anterior end 63% to 75% of the length in most cases, but may be as high as 80%. The wide range of variation is thus produced primarily by the presence of some exceptionally short, wide, centra — beyond the extreme observed in any living form. I feel this is probably a reflection of erosion of the ends rather than original difference in proportions. The crests on the neural arch (Fig. 44) meet medially in a broad, but often slightly angular, arc.

The majority of the known specimens are from the Fox Canyon locality of the Rexroad formation, Meade County, Kansas. The sacra and ilia from this locality tentatively referred to *B. rexroadensis* include UMMVP Nos. 40140-40146; similarly referred specimens from Rexroad Locality No. 3, also of Meade County, are UMMVP Nos. 40147-40149. In addition to these, unidentifiable elements undoubtedly including representatives of this form are catalogued under UMMVP No. 27673 and Nos. 40156-40160.

Discussion.—This form shows certain resemblances to the modern *B. w. woodhousei* on the one hand and to the Middle Pliocene *B. hibbardi* on the other, and the two fossil forms together form an incomplete and far from perfect morphological bridge between a more *americanus*-like hypothetical ancestor and modern *B. woodhousei*.

It seems likely that heavy cranial crests, tending to be granular in texture and involving much of the dorsal surface of the frontoparietals, were present in early members of the *AMERICANUS* group. The frontoparietals of *B. hibbardi* bore crests of much this same nature; some reduction in extent is shown in *B. rexroadensis*, which is more or less intermediate in this respect between *B. hibbardi* and those extant *B. woodhousei* with the most prominent crests.

The ilial prominence of *B. americanus*, and presumably of early members of the group, is low, with a distinctively steep anterior slope. In *B. hibbardi* the distinctive shape is retained, but the prominence has developed the height characteristic of *B. woodhousei* and other forms. The height is retained, even developed excessively, in *B. rexroadensis*, but the shape is more typical of *B. woodhousei*-like forms. The sacral centrum is comparable to *B. americanus* in proportions in *B. hibbardi*, comparable to *B. woodhousei* in *B. rexroadensis*. The crests of the neural arch usually meet at a distinct, rather sharp angle in *B. americanus*, in a broadly rounded angle or a broad but slightly angular arc in *B. hibbardi*, in a broad arc in *B. rexroadensis* and *woodhousei*.

Whether this apparent morphological series would still exist if the skeletal anatomy of *B. hibbardi* and *rexroadensis* were better known is, of course, a question. And even if it did, whether it could be assumed to represent in any way a phylogenetic series is yet another

question. Nevertheless, it is tempting to postulate that these two fossil forms do represent the population line, in their respective ages, that has led to *B. woodhousei*. I think it very likely that this is the case for *B. rexroadensis*, but the position of *B. hibbarði* is less clear.

Bufo spongifrons, sp. nov.

Definition.—A moderate-sized *Bufo* of the AMERICANUS group with high, but not especially heavy, cranial crests; supraorbital and postorbital crests and, to a lesser extent the entire dorsal surface of the frontoparietals of a light, porous, spongy texture; if associations have been correctly made, the ilial prominence is high, its posterior slope steeper than the anterior; sacral centrum presumably short and broad.

Description of the holotype.—The specimen (Fig. 33) is 8.5 mm long and 5.2 mm wide at the widest part, including the otic plate. It was unquestionably an independent element, not fused with the prootic, in life. The entire dorsal surface presents a light, spongy, porous appearance, least marked anteriorly and medially, more so laterally and posteriorly. The crests are of this same texture and, though high, do not appear particularly heavy; they are thickest at the point of junction of the supraorbital and postorbital crests. The supraorbital and postorbital crests meet at a sharp angle of just slightly more than 90°; there is a short occipital crest, decreasing rapidly in height posteriorly.

Type and type horizon.—USNM No. 22234, a virtually complete left frontoparietal. Collected by J. B. Hatcher in 1884 from "Quarry E," sec. 1, Twp. 2 S, R. 20 W, near Long Island, Phillips County, Kansas. The deposit is presumably part of the Ogallala formation of Middle Pliocene (Hemphillian) age. Further details concerning the locality have been mentioned in connection with the description of *Bufo alienus*.

Referred material.—A right frontoparietal of about the same size agrees fully with the holotype, as does also a third, very incomplete, such element. A discussion of the vertebral and limb elements, which are not identifiable to species, can be found in connection with the discussion of *B. cognatus*.

Three ilia have been referred to *B. spongifrons*, one of which (USNM 22236) is illustrated as Figure 51. These differ from the ilia referred to *B. cognatus* in having a steeper posterior slope to the prominence and, correlatively, a more acute supra-acetabular angle. The height of the prominence is between 45% and 50% of the length of its base in all three specimens, the anterior angle approximately 45° in all, the posterior between 55° and 65°, the peak angle thus varying from 70° to 80°; the supra-acetabular angle varies between 95° and 105°.

The ilia thus agree closely with those of *B. compactilis*, including those from the Rexroad tentatively referred to that species.

Discussion.—The affinities of *B. spongifrons* are certainly with the western section of the AMERICANUS group, but it is not obviously closely related to any other particular known species within the section. The ilia resemble those of *B. compactilis*, as has been stated. But the association of these ilia with the frontoparietals seems entirely reasonable, as

set forth in the discussion of *B. cognatus*, and the frontoparietals bear no resemblance to those of *B. compactilis*.

Whatever the relationships of *B. spongifrons* may be, and whether or not the association of ilia with frontoparietals is correct, there can be no doubt that three species of *Bufo* were present in the Long Island fauna, and that none of the three are identical with the species found in the Hemphillian Edson Quarry fauna. Nor, except for the fact that the Edson Quarry form (*B. hibbardi*) and two of the Long Island forms may all be referable to the western section of the AMERICANUS group, does there appear to be any close relationship between any of the three.

Bufo terrestris Bonnaterre

This extant form is characterized by the possession of high, rather heavy, granular cranial crests, with the occipital crest developed into a very conspicuous and characteristic bony knob (Fig. 13). The occipital canal is completely roofed in mature specimens. The vertebral centra are long and narrow in comparison with other members of the AMERICANUS group, the width of the sacral centrum at the condyles being 105% to 125% of its length, the width at the anterior end 80% to 90% of the length, and the height at the anterior end 45% to 60% of the length. The ilial prominence is low for the group, its height usually about 25%, never more than 30%, of the length of its base. The anterior and posterior slopes of the prominence may be subequal, but the anterior slope is usually steeper than the posterior, sometimes decidedly so.

The form is known from a number of localities in the Florida Pleistocene, probably ranging in age from late Illinoian to sub-Recent (see Auffenberg, 1958). Specimens tentatively or conclusively identified as *B. terrestris* have been recovered from the following such localities: Arredondo IA (UF 5583-5586, 5588, 6172, 6551); Arredondo IC (UF 6559); Arredondo ID (UF 5590); Arredondo II (UF 1720, 2147); Bradenton, Canal locality (UF 6605); Bradenton, 51st St. (UF 2313, 2666); Haile IB (UF 2152, 6168-6170); Haile IIA (UF 6562, 6564); Haile IIB (UF 2268, 2277, 6584); Haile VIIA (UF 6280); Hornsby Springs (UF 1736); Itchatucknee (UF 5264, 6504); Knapaha IA (UF 5560-5561); Reddick I (UF 5650); Reddick IB (UF 2453, 5580, 6449, 6577, 9685, 9888); Vero Beach, Stratum 3 (vide Brattstrom, 1953 and Auffenberg, 1957); Winter Beach (UF 1684); Orange Lake and Williston (vide Holman, 1959, 1959a).

Bufo tiheni Auffenberg

Definition.—A small *Bufo*, presumably of the AMERICANUS group, with an ilial prominence of moderate height, its anterior slope decidedly steeper than the posterior; a relatively long sacral centrum that is also somewhat depressed. (Frontoparietals not known.)

Description.—Other than the type, only six elements representing the genus *Bufo* are known from the deposit. All are tentatively referred to *B. tiheni*, although they are rather variable among themselves.

The condylar width of the type sacrum is scarcely greater than the width at the anterior end of the centrum; both are 85% to 90% of the

central length. The crests of the neural arch meet at an obtuse angle. A second sacrum, UF 5095, is of markedly different proportions. The width at the anterior end is slightly greater than the length, the height at the anterior end about 80% of the length, and the width at the condyles a full one-third greater than the length. This is, however, a very small specimen, the centrum being only about 0.9 mm long; in all forms very young specimens have relatively short and broad sacral centra. It is easily possible, therefore, that this is simply an immature specimen of *B. tiheni*.

Five ilia have been recovered. One of these, UF 6363 (Fig. 52) was described and figured by Auffenberg (1957). Four others are essentially similar. The height of the ilial prominence varies between 33% and 42% of the length of its base. In most specimens the anterior slope is somewhat steeper than in the one figured by Auffenberg, quite markedly so in one (Fig. 59). The anterior angle of the prominence is 45° to 60°, except that it is nearly 75° in the one just mentioned; the posterior angle is between 40° and 50° in all; the supra-acetabular angle is about 120° or 130°, insofar as it can be determined. The ilia with the lowest prominences, and with the least steep anterior slopes, are the smaller specimens, suggesting that the variation is at least partially ontogenetic.

Type and type horizon.—UF 5203, a fragmentary sacral vertebra from the Middle Pliocene (Hemphillian) Alachua Formation, Locality Haile VI A (SW ¼ Sec. 24, Twp. 9 S, R. 18 E), near Haile, Alachua County, Florida.

Discussion.—If these specimens are all properly referable to *B. tiheni*, that species exhibits a distinctive combination of characteristics. The form is referred to the AMERICANUS group on the basis of height and shape of the ilial prominence. Among extant forms, the ilium seems to resemble most closely that of *B. m. californicus*; this does not imply any close relationship.

The dorsoventral depression of the sacral centrum has a close parallel only in the Caribbean section of the VALLICEPS group. The modern *B. quercicus* in that section has a similarly depressed sacral centrum and, as has been mentioned, a fairly high ilial prominence, though not so high as in *B. tiheni*. This must have been a small toad (though larger than *quercicus*); the smaller specimens probably represented individuals of 25-30 mm snout-vent length, the larger ones individuals that could hardly have exceeded 45 or 50 mm.

The affinities of *B. tiheni*, even as to group, are thus not clear. It is yet another Floridian form having some characteristics usually considered typical of the AMERICANUS group, others usually considered typical of the VALLICEPS group. It will be recalled that the Miocene *B. prae-vius* appears to have been a typical VALLICEPS group form except for the disposition of the cranial crests, in which respect it approached the AMERICANUS group. The Pliocene *B. tiheni* is poorly known, but the few characters observable are in part characteristic of one group, in part of the other. The two extant forms are similarly peculiar. Several features in which *B. quercicus* approaches the AMERICANUS group

were described; of all members of the AMERICANUS group, *B. terrestris* approaches the VALLICEPS group most closely in the height and form of the ilial prominence, in the texture and disposition of the cranial crests, in the closure of the occipital canal, and other minor respects.

In brief, excepting the temporary intrusion of *B. w. fowleri* during the Pleistocene, all toads known from peninsular Florida, from the Miocene to the present, exhibit some peculiar combination of characteristics. A full explanation is not immediately apparent, but some speculation may be permitted.

Sanders has recently (1961) suggested that *B. terrestris* is of hybrid origin, with "Mexican" (i.e., VALLICEPS group) and "American" progenitors involved. He has provided considerable evidence compatible with this opinion, and has further postulated that the VALLICEPS group ancestor reached Florida via a Caribbean route at a time when the Floridian region was itself insular. I am in close general agreement with this suggestion, at least as a possibility, but with certain qualifications or extensions. It is not necessary that the species of *B. terrestris* arose as such directly from VALLICEPS group and AMERICANUS group ancestors; it is possible that hybridization — at least limited introgression — has played a part in the evolutionary development not only of *B. terrestris*, but of all Floridian toads from the Miocene to the present. This does not require that hybridization or introgression be either extensive at any one time, nor continuous throughout that entire time, but simply that it may have occurred at one or several times in the past.

During much of the Tertiary the region now comprising Florida was largely inundated, with scattered, and shifting, portions exposed as islands. That the VALLICEPS group, specifically the Caribbean section, had reached insular Florida by or in the early Miocene is evidenced by *B. praeivius*. That it arrived there by way of Cuba, as Sanders suggests, is highly probable. The AMERICANUS group, whatever may have been the time of its entry into the area, must have come from the mainland. It is possible that representatives of this group had arrived by the Miocene also. Whether they would have been forced to actually cross an ocean barrier to do so before the late Tertiary is neither certain nor necessarily pertinent. Shifting land levels may have provided land routes over a period of time, despite the fact that there was probably no continuous connection at any one time, thus no continuous influx of AMERICANUS group representatives.

If we assume that AMERICANUS group members did reach insular Florida by the early Miocene, whether or not they managed to become permanently established at that time, and if we admit the possibility of at least limited introgression in this area, then a possible basis for all of the peculiarities observed would be established.

It should be noted that no really extensive interspecific (actually intergroup) hybridization is either required or postulated. I do not envision that any of the species involved are derived from something of the nature of a hybrid swarm. To be effective over the period of

time involved, only an extremely low average rate of introgression is required. Anderson (1949) pointed out that

As raw material for evolution, the bizarre hybrid swarms . . . are not so important as . . . introgression . . . barely noticeable in any one locality and extended as a trend through a long intermediate zone. . . . By the time of the third backcross there would be little or no external indication of hybridity. . . . Yet in terms of gene frequencies, the effects . . . would far outweigh the immediate effects of gene mutation.

One may simply substitute the word "time" in place of "locality" and "intermediate zone" in this quotation, and the same conclusions will apply.

Even today, after several million more years of separate evolution than had occurred in the Miocene, occasional natural hybrids between members of the *VALLICEPS* and *AMERICANUS* groups can be found (Blair, 1956; Volpe, 1957), with no obvious selective disadvantage insofar as viability is concerned. These particular hybrids are sterile (Thornton, 1955; Volpe, 1959), but it does not necessarily follow that all possible intergroup hybrids, now or in the past, would be completely sterile. If sterility is due largely to meiotic disturbances during gametogenesis in the hybrid, one might expect to get, rarely, a few gametes by pure chance that would possess so nearly the same chromosomal constitution as one of the parental species that fertilization would be possible. Such an occurrence might introduce into that parental species only a very limited portion of one chromosome, for example, from the other species; in such a case introgression would probably be completely unrecognizable phenotypically even in the first backcross generation, but occasional repetition over many generations could still produce a marked genotypic and phenotypic effect over a long period of time.

It is not claimed here that the peculiarities exhibited by these Florida toads provide conclusive evidence that introgressive hybridization has been a major factor in their development, nor that they are inexplicable on any other basis. I do feel, however, that it is a distinct possibility, and one which should not be arbitrarily dismissed as unworthy of serious consideration.

Bufo woodhousei woodhousei Girard

This extant form possesses prominent, fairly heavy, striated or cancellous cranial crests, especially thick at the point of juncture of the supraorbital and postorbital crests. The occipital groove is open in young specimens, its anterior part roofed by the cranial crests in mature ones. The vertebral centra are short and broad. The width of the sacral centrum at the condyles is 120% (usually at least 130%) to 150% of its length, the width at the anterior end 95% to 115% of the length, and the height at the anterior end approximately 70% of the length. The crests of the sacral neural arch usually form a very broad arc, but are occasionally slightly angular or form a sharper arc.

The height of the ilial prominence is about 45% of the length of its base, slightly less in young specimens. The anterior angle varies from 45° in young individuals up to nearly 60° in large, fully mature specimens; the posterior angle is approximately 45° in all, and the supra-acetabular angle between 115° and 130°.

The earliest verifiable appearance of this form is in the Jinglebob fauna of Sangamon age (Tihen, 1954). Collections from the Wisconsin Jones Fauna in the Kansas University collections contain several sacra, some of which are fully typical of *B. woodhousei* with respect to the disposition of the crests on the neural arch. Others are fully typical of *B. cognatus*, and while this is not an absolutely constant feature in either species, the occurrence of several specimens typical of each makes it likely that both forms are indeed represented. A few fragmentary sacra from the Yarmouthian Borchers fauna also appear more typical of *B. woodhousei* than of any other form, and are tentatively so referred. All of the above originate from Meade County, Kansas.

AMNH No. 3257 from the Blancan Benson Locality of Cochise County, Arizona, also appears very similar to *B. woodhousei*, and can be referred to this species with confidence, though not so confidently to the typical subspecies. Both the ilia are consistent with such an identification, as is also a small portion of one frontoparietal, but it is doubtful whether indications of subspecific differences could be recognized in this material.

Bufo woodhousei bexarensis Mecham

Definition.—A very large *Bufo* of the AMERICANUS group, similar to *B. w. woodhousei* in most respects, but differing primarily in being much larger, with an adult size of over 100 mm, up to 160 mm.

Description.—I have not seen this recently described form; the following is quoted directly from the information given by Mecham (1959):

The femur is moderately slender, with a low crest on the back face which bifurcates to form a narrow V-shaped elevation, the apex of which is directed distally. The wings of this expansion become subparallel proximally, and attain a maximum width of approximately one half the diameter of the shaft at the proximal end of the crest. The lower wing of the elevation formed by the crest slopes toward the shaft at a steeper angle than the upper one, with the result that the surface of the elevation is tilted slightly toward the ventral side of the bone. . . . Aside from size the fossil ilia are indistinguishable from those of modern *Bufo w. woodhousei*. . . . One right tibio-fibula [and] . . . two bufonid humeri have also been assigned to the fossil subspecies. . . . There is no evidence of a ridge just proximal to the median epicondyle and only slight development of one just proximal to the lateral epicondyle. These ridges are well developed in many modern forms, including large *Bufo w. woodhousei*.

Type and type horizon.—Texas Memorial Museum No. 933-3708a. A left femur lacking the distal epiphysis and a portion of the proximal end. From the late Pleistocene, zone 3, Friesenhahn Cave, Bexar County, Texas.

Known fossil occurrences.—Known only from the type locality — the Late Pleistocene Friesenhahn Cave of Bexar County, Texas.

Discussion.—Again I quote extensively from Mecham:

All of the skeletal elements assigned to the fossil form indicate a toad of large to very large size. Conservatively estimated, this form must have had an average adult size which fell above 100 mm snout-vent length, and ranged up to 160 mm. On the basis of size alone this Pleistocene toad can be distinguished from all recent North American forms of the genus with the exception of *Bufo marinus* and *Bufo alvarius*. It is readily distinguished from these two forms, however, on the basis of a number of characters. . . . Apparently the fossil form falls closest to . . . *Bufo w. woodhousei*. . . . Relationship is strongly indicated by the ilium, which agrees closely in the two forms in the height of the dorsal prominence and general shape of the wing. The femur is also quite similar. In *Bufo w. woodhousei* the femoral crest is low, and in most specimens (as in *bexarensis*) shows a distinct bifurcation or flattening, giving rise to a secondary ridge which slopes gradually toward the shaft, forming, with the primary ridge or crest, a narrow V-shaped elevation or plateau which is tilted slightly toward the lower side of the bone. . . . The fossil tibio-fibula . . . agrees well with *woodhousei*. . . .

The most obvious difference exhibited by the fossil form as compared with recent *Bufo w. woodhousei* is that of size. . . . Differences also distinguish the limb elements. These differences seem most marked as compared with the largest *Bufo w. woodhousei*. . . . In all femora of *bexarensis* the V-shaped elevation formed by the femoral crest is narrow, and reaches a greatest width of approximately one half or slightly more of the width of the shaft at the proximal end of the crest. In large specimens of *Bufo w. woodhousei* there is a tendency for the crest to become expanded, and in the largest specimens examined the crest attained a width equal to the diameter of the shaft. The tibio-fibula of *bexarensis* also appears to be somewhat more slender than the same element in the larger *woodhousei*. . . . As already mentioned, the two fossil humeri show no development of a median epicondylar ridge or crest and only slight development of a lateral one. . . . They are present in *Bufo w. woodhousei*. . . .

Mecham considers this form most likely to be subspecifically related to *B. woodhousei*; this seems a logical assumption. He further suggests the possibility that the *B. woodhousei* reported from the Jinglebob fauna of Meade County, Kansas (Tihen, 1954) might be properly referable to this subspecies. Such reference appears to me very doubtful. Although some of the Jinglebob specimens represent fairly large animals, none would represent individuals greatly, if at all, exceeding 100 mm in snout-vent length, and the average size of the individuals represented would be well under this figure. The extant subspecies of *B. woodhousei* exhibit differences in the cranial crests that would be identifiable, or at least indicated, in the frontoparietals; the single frontoparietal recovered from the Jinglebob seems identical with those of *B. w. woodhousei*.

The possible existence of geographic variation in extant *B. w. woodhousei* with respect to the V-shaped expansion of the femoral

crest is suggested by Mecham's remarks. Although the provenance of his Recent specimens is not stated, it can be assumed to be Texas. In his larger individuals the crest was stated to attain a width equal to the diameter of the shaft at the proximal end. In none of my Recent specimens from Kansas, including three between 95 and 98 mm in snout-vent length, nor in any fossil specimens referred to *B. woodhousei*, does the width of the crest exceed half of the diameter of the shaft. A noticeable expansion of this crest is, on the other hand, quite evident even in rather small specimens of *B. w. velatus* that I have seen. It seems possible that a geographic gradient exists in this feature that is perhaps not fully correlated with the geographic gradient in other characters used to distinguish these two living subspecies.

Bufo woodhousei fowleri Hinckley

This is an extant form. As might be expected, it is very similar to *B. w. woodhousei* osteologically, the major recognizable distinctions being the lower and thinner cranial crests, and a lower ilial prominence. The height of the ilial prominence varies from 30% to 45% of the length of its base. There is a suggestion that some geographic variation occurs within the range of the subspecies with respect to the size and shape of the ilial prominence, but I have seen too few specimens from any given locality, and specimens from too few localities, to be sure that this is actually true.

A number of collections from the Pleistocene of Florida contain specimens of *Bufo terrestris*, and have been listed in connection with that form. Several of these collections also contain one or a few ilia that are certainly not typical of *B. terrestris*, and seem best referred to *B. w. fowleri* both on morphological and geographical bases, though they tend to be slightly larger than average Recent *B. w. fowleri* from neighboring states. Such specimens were included in collections from the following localities: Reddick IB, Kanapaha I, Bradenton, Kendrick I, Haile IIA, and Itchatucknee.

In addition to these Florida occurrences, a few specimens referable to *B. w. fowleri* also occur in UF 2681 from the late Pleistocene of Natural Chimneys, Augusta County, Virginia, and a frontoparietal, sacrum and ilium possibly referable to this form in the Carnegie Museum collection from the sub-Recent Rattlesnake Cave of Westmoreland County, Pennsylvania.

The specimens (AMNH No. 6400) reported by Brown (1908) from the Conard fissure near Harrison, Arkansas, also seem referable to *B. w. fowleri*. While this can safely be considered Pleistocene in age, dating within the Pleistocene is not feasible at the present time (see Dowling, 1958).

Bufo sp.

University of California No. 31985 includes several ilia, fragmentary limb bones, and a few vertebrae from the Upper Miocene of Nebraska. Dr. Richard Estes is preparing a description of these speci-

mens, but has permitted me to mention and figure them in this report. The larger ilia in the collection bear a marked resemblance to those of *B. americanus* (Fig. 61). Other elements are fully consistent with reference to the AMERICANUS group, and I think it very likely that this species can be safely referred to that group.

The *boreas* Group

Members of this group have a skull of normal proportions. The frontoparietals and pro-otics are independent, the former relatively narrow, not projecting as a supraorbital shelf, and without, or with only very limited, ornamentation or crests. The occipital groove is open. Vertebral centra are of normal proportions and the ilial prominence low. A fairly close relationship between this group and the Old World *B. bufo* has been postulated previously (Tihen, 1962).

Bufo boreas cf. *halophilus* Baird and Girard

This is an extant form. Its appearance in the late Pleistocene to sub-Recent tar pits of Rancho La Brea, Los Angeles County, California, has been recorded a number of times (see Brattstrom, 1953). Except for the Rancho La Brea records, the only reported fossil occurrence of which I am aware is from the Pleistocene of Potter Creek Cave, Shasta County, California (Brattstrom, 1958).

I have been unable to demonstrate that the specimens referred by Camp (1917) to *Bufo nestor* lie outside of the usual range of variation of *B. halophilus*. An appreciable sculpturing of the dorsal cranial elements is not infrequent in modern *B. b. boreas* and *halophilus*, particularly in large specimens. The extent of ossification of cartilaginous elements is somewhat variable, particularly ontogenetically. The proportions of the parasphenoids referred to *B. nestor* appear to fall within the observed range in *B. b. halophilus*; my specimens of *B. b. halophilus* tend to center between those given by Camp for *B. nestor* and those given for *B. b. halophilus*, with overlap in both directions. Brattstrom's (1953) measurements for *B. b. halophilus* are, if I have interpreted correctly, in closer agreement with Camp's measurements for *B. nestor* than with his measurements for *B. b. halophilus*. I am, therefore, proposing that *Bufo nestor* Camp be placed in the synonymy of *Bufo halophilus* Baird and Girard.

SUMMARY

The data presented here support an already established belief — that the genus *Bufo* was probably in existence in the early Tertiary, and had attained a considerable degree of dispersal and diversification by the middle of that period. The major features of a postulated history of the genus in the New World have been presented previously (Tihen, 1962), based primarily on the distributions and apparent relationships of living forms. The fossil record shows that the major distributional patterns must have been formed, and the major species groups established, before or, at the latest, during the Miocene. It also

suggests that another species group, now confined to the Old World, was formerly present in this hemisphere.

It may be useful to summarize the known fossil occurrences by geologic age, instead of by systematic arrangement as in the body of the paper.

Oligocene.—The form described originally as *Neoprocoela edentata* is thought to be a *Bufo*. If so, it is probably related to the extant CALAMITA group, now confined to the eastern hemisphere. Though it is the earliest known *Bufo* in the Americas, there seems no possibility that this form, nor the group it represents, could be ancestral to the other American members of the genus. The form is known only from the lower Oligocene of Argentina.

Miocene.—Three Miocene forms are known. *B. praeivius* occurs in the lower Miocene of Florida. An undescribed species closely related to *B. marinus* is found in the Upper Miocene of Colombia, and another undescribed species, apparently a member of the AMERICANUS group is found in the Upper Miocene of Nebraska. These occurrences suggest that the species groups, and sections within the VALLICEPS group were already established at that time, and probably occupied much the same major geographic areas as at present.

Lower Pliocene (Valentinian).—No species can be identified with certainty. An ilium from Brown County, Nebraska, has been tentatively referred to *B. suspectus*.

Middle Pliocene (Hemphillian).—Five fossil and one extant species are recognized from the Hemphillian. The extant *B. cognatus* is found in the Middle Pliocene of Kansas, possibly also of Nebraska. Two fossil members of the AMERICANUS group also occur in Kansas, *B. spongifrons* and *B. hibbardi*. Another presumed member of the group, *B. tiheni*, is found in Florida. The VALLICEPS group is represented by *B. campi* of Chihuahua. Another species of uncertain affinities, but possibly referable to the CALAMITA group, is found in Kansas associated with *B. cognatus* and *B. spongifrons*.

Blancan.—Two different time periods within the Blancan are represented. Three forms are tentatively recognized in the Rexroad of Kansas; these are the fossil *B. rexroadensis* and extant *B. compactilis* of the AMERICANUS group, and the fossil *B. suspectus* of the VALLICEPS group. It is suggested that *B. rexroadensis* represents the *B. woodhousei* population line of that particular time and area. Specimens from the Benson Locality of Arizona are referred to *B. alvarius* and *B. woodhousei*.

Pleistocene.—The extant *B. hemiophrys* is tentatively identified in the Cudahy fauna of Kansas, presumably of Kansan glacial age. A number of forms occur in the Yarmouthian and later deposits of various areas. All are extant forms excepting *B. w. bexarensis* from Texas and *B. repentinus* from Kansas. Extant forms include: *B. arenarum* in Argentina, *B. m. horribilis* and *B. valliceps* in Yucatan, *B. punctatus* in Nevada, *B. quercicus* in Florida, *B. a. americanus* in Pennsylvania and Virginia, *B. cognatus* in Kansas and Oklahoma, *B. terrestris* in Florida,

B. w. woodhousei in Kansas, *B. w. fowleri* in Arkansas, Florida, Pennsylvania and Virginia, and *B. b. halophilus* in California.

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