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Two Pelobatid Frogs from the Tertiary of North America and Their Relations to Fossil and Recent Forms

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Knowledge of the phylogenetic relationships and past distributions of anurans has been in large part derived by inference from studies of the morphology and distribution of recent forms. Frogs are seldom common fossils, and many available specimens have gone unsorted and unstudied. In this setting, the study of any fossil material is likely to contribute significantly to our knowledge of anuran distribution and evolution.

The purpose of the present study is to report upon two pelobatid fossils from South Dakota and Nevada, and to attempt to discern their places in the pattern of pelobatid evolution. The first fossil to be discussed was found by Dr. John Clark in 1953 and made available to me through the courtesy of Dr. Glenn L. Jepsen. The remaining specimen was found by Miss Annie M. Alexander and Miss Louise Kellogg in 1925 and brought to my attention by Dr. Charles L. Camp, who kindly turned it over to me for study. Dr. Bobb Schaeffer and Mr. Charles M. Bogert read the paper in manuscript and made valuable suggestions. Dr. Charles Walker, University of Michigan, and Dr. Robert C. Stebbins, Museum of Vertebrate Zoölogy, University of California, lent skeletal material. Dr. Frederick Shannon, Mr. Wilfred T. Neill, and Mr. Ernest Liner furnished information on the distribution of spadefoot toads in Arizona, Georgia, and Louisiana, respectively. To all these gentlemen I am grateful for their generosity with both time and specimens.

The illustrations of the fossil *Scaphiopus* and companion comparative figures of recent species (figs. 10-18) were done by Mr. Chester Tarka. Other illustrations are by the author.



FIG.1. Type specimen of *Eopelobates grandis*, Princeton University No. 16441, in dorsal aspect, $\times 1.5$.

FAMILY PELOBATIDAE
GENUS *EOPELOBATES* PARKER, 1929

Eopelobates PARKER, 1929, Ann. Mag. Nat. Hist., ser. 10, vol. 4, p. 277.

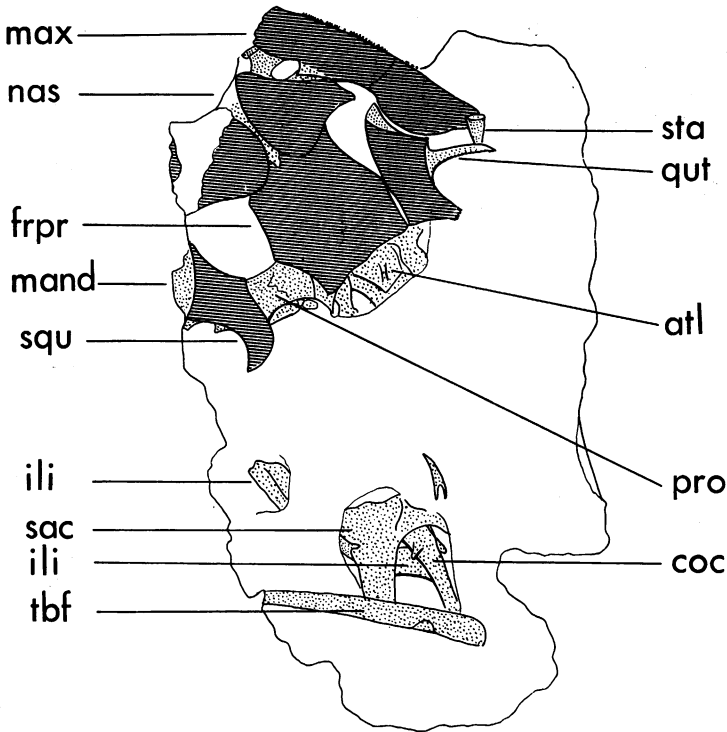


FIG. 2. Dorsal aspect of *Eopelobates grandis*. Cross-hatched bones are dermal bones encrusting the skull; other bones are stippled, matrix left unshaded. *Abbreviations*: atl., atlas; coc., coccyx; frpr., frontoparietal; ili., ilium; mand., mandible; max., maxilla; nas., nasal; pro., prootic; qut., quadrate; sac., sacral vertebra; squ., squamosal; sta., stapes; tbf., tibio-fibula.

Eopelobates grandis, new species

TYPE: Princeton University No. 16441; nearly complete skeleton lacking only some skull and distal limb bones.

HORIZON AND LOCALITY: Early Oligocene; middle part of Ahern member of Chadron formation, 25 feet above base. Divide between West Fork and Main Fork of Indian Creek, one-half mile south of forks; southeast corner of the SE. $\frac{1}{4}$ of sect. 34, T. 3 S., R. 12 E., Pennington County, South Dakota. Collected by Dr. John Clark in 1953 on a Scott Fund grant.

DIAGNOSIS: Most similar to *Eopelobates anthracinus* Parker of the Miocene of Europe, from which species it differs in its much larger size, having an estimated length of 110 mm. as contrasted to 32 mm. for *anthracinus*. The frontoparietal region of *E. grandis* is relatively much

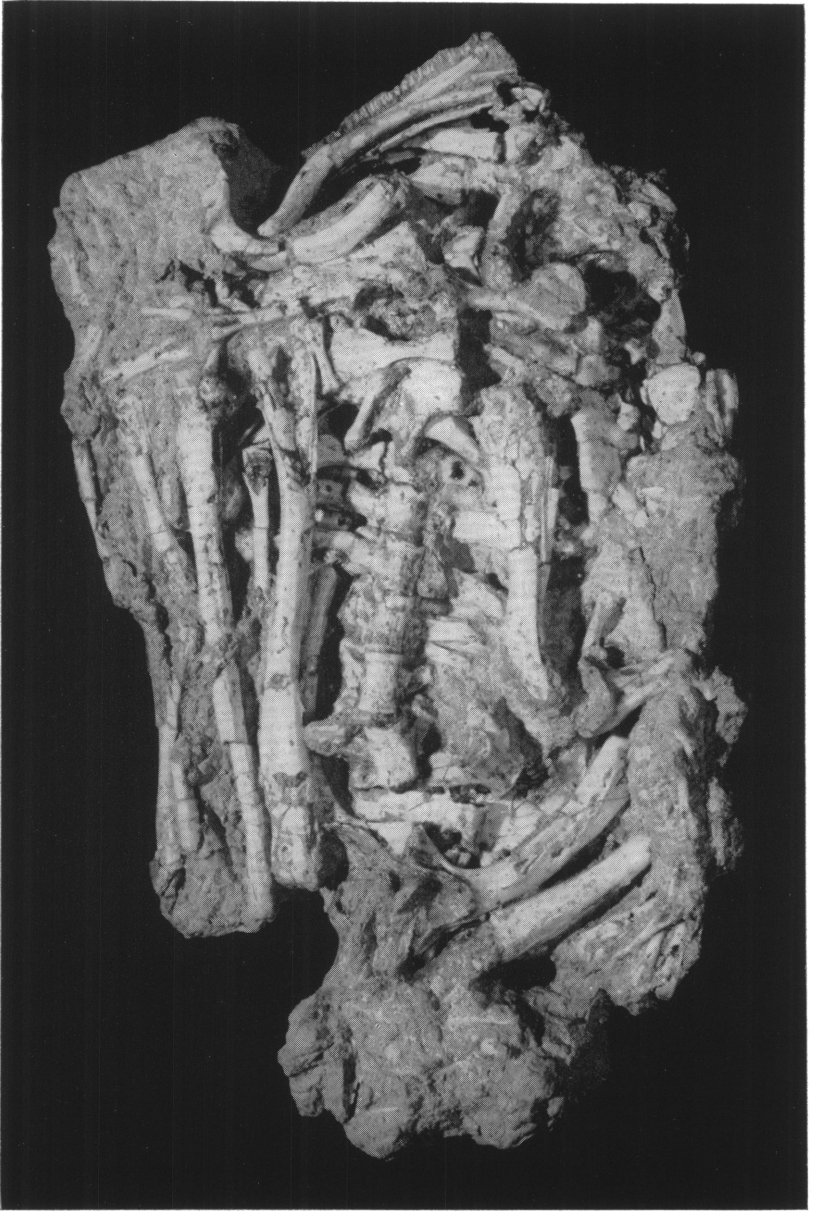


FIG. 3. Type specimen of *Eopelobates grandis*, in ventral aspect, $\times 1.5$.
broader than that of the other species assigned to this genus, *E. bayeri*
Spinar from the Miocene-Oligocene boundary region of Czechoslovakia.

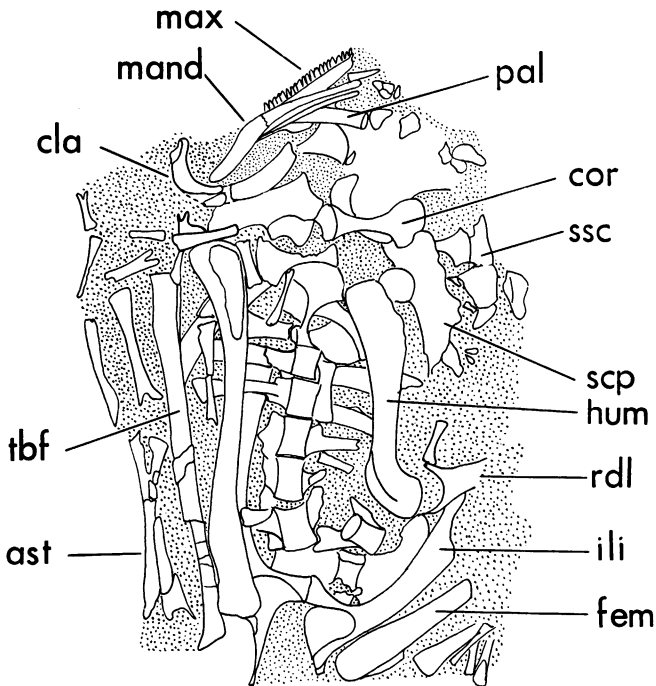


FIG. 4. Ventral aspect of *Eopelobates grandis*. Matrix stippled, bone left unshaded. Abbreviations: ast., astragalus-calcaneum; cla., clavicle; cor., coracoid; fem., femur; hum., humerus; ili., ilium; mand., mandible; max., maxilla; pal., palatine; rdl., radio-ulna; scp., scapula; ssc., suprascapula; tbf., tibio-fibula.

DESCRIPTION: The shapes of the bones can be seen in the accompanying photographs and drawings (figs. 1-7). The skull is broad, with a heavy dermal encrustation of bone on the nasals, maxillaries, frontoparietal, and squamosals. There is a complete roof over the temporal region, the squamosal making broad contact with both frontoparietal and maxilla. Premaxillaries are not present in the fossil. It is not possible to determine whether or not a quadratojugal was present. The maxillaries are toothed; the presence or absence of vomerine teeth cannot be demonstrated. The mandible is edentulous. A strong palatine bone is present on the right side, but whether it is sutured or fused to the maxillary cannot be seen.

There are eight presacral vertebrae, the seventh and eighth procoelous and the others probably so. Vertebrae two, three, and four possess long diapophyses that are inclined very slightly to the rear. The diapophyses of vertebrae five through eight are much shorter; those of vertebra five stand at a right angle to the column, while the more posterior ones are angled progressively more and more anteriorly (fig. 5A). The sacral

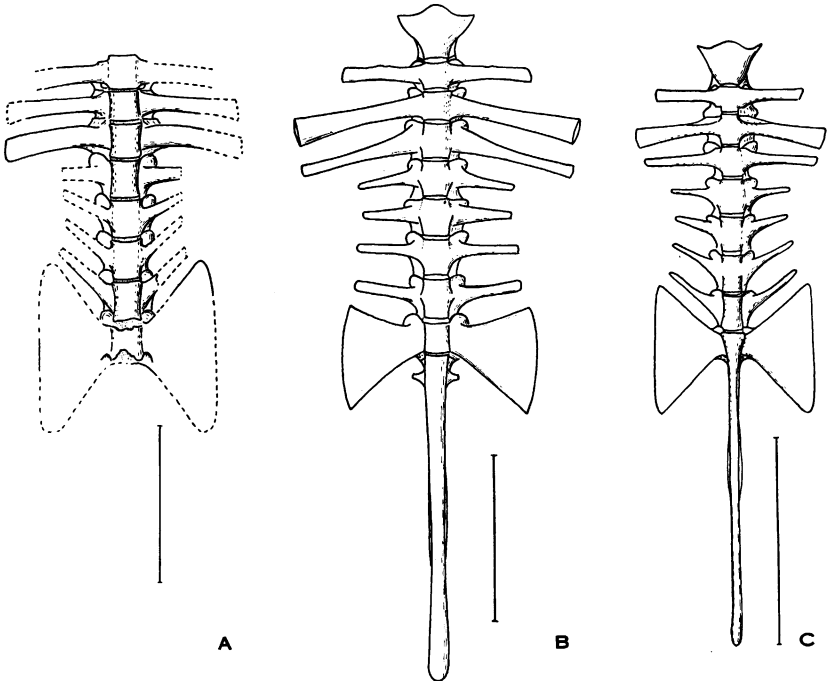


FIG. 5. Ventral aspects of vertebral columns. A. *Eopelobates grandis*. B. *Megophrys carinensis*. C. *Megophrys* (cf.) *monticola*. Scale line beside each indicates a length of 2 cm.

vertebra possesses greatly widened diapophyses (fig. 6). Probably a single condyle for the coccyx was present, though this cannot certainly be determined. However, the absence of any evident posterior expansion of the centrum may be taken as evidence favoring the single condyle interpretation. The coccyx is free from the sacrum. It possesses a low dorsal keel that bifurcates anteriorly. One pair of short diapophyses, angled sharply posteriad, is present, but there is no distinct post-sacral vertebra (fig. 6).

The pectoral girdle was evidently arciferal; the clavicles are very heavy and are strongly arched. The scapula shows no particularly distinctive features. Fragments of the left suprascapula are present, but its form cannot be made out. The coracoid has a relatively long and slim shaft. An ossified sternal style is present.

An important feature of the pectoral girdle is the relatively great extent of the ischium to the rear. The pubis was probably ossified. The ilial blade is relatively deep (fig. 7A).

The humerus and partial radio-ulna visible in the fossil show no fea-

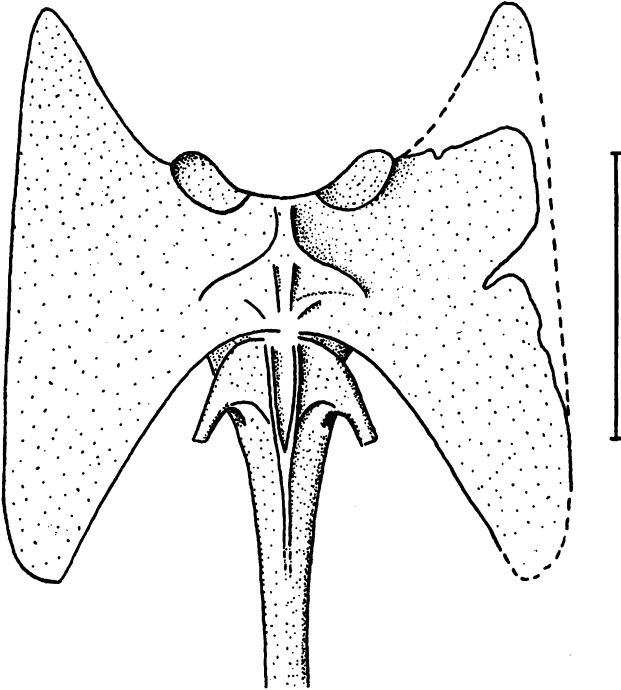


FIG. 6. Sacral vertebra and proximal part of coccyx of *Eopelobates grandis* in dorsal aspect, partly restored. Scale line is 1 cm.

tures worthy of special notice. The femur and tibia-fibula are slender and about equal in length. Presumably the epiphyses were cartilaginous, for they were not preserved. The femur shows a slight sigmoid curvature. The astragalus and calcaneum are slender and about half of the length of the tibia-fibula. There is no evidence that a bony pre-hallux (spade) was present, but the foot region of the animal was not well preserved. However, it is probably a safe assumption that a spade was not present, because in digging forms, the astragalus and calcaneum are relatively much shorter and stockier than in this fossil. What appears to be a claw-shaped terminal phalanx is present in the matrix, but its identity as such cannot be confirmed as it is not associated with other foot bones.

The following are measurements, in millimeters, of such bones as are complete or nearly so: width of frontoparietal, 18.9; length of frontoparietal, 19.7; length of squamosal, 19.0; length of coracoid, 13.2; width at mesial end of coracoid, 6.7; width at lateral (scapular) end of coracoid, 4.6; narrowest part of coracoid shaft, 1.9; length of humerus, 27.7; length of femur, 47.2; length of tibia-fibula, 47.2; length of astragalus,

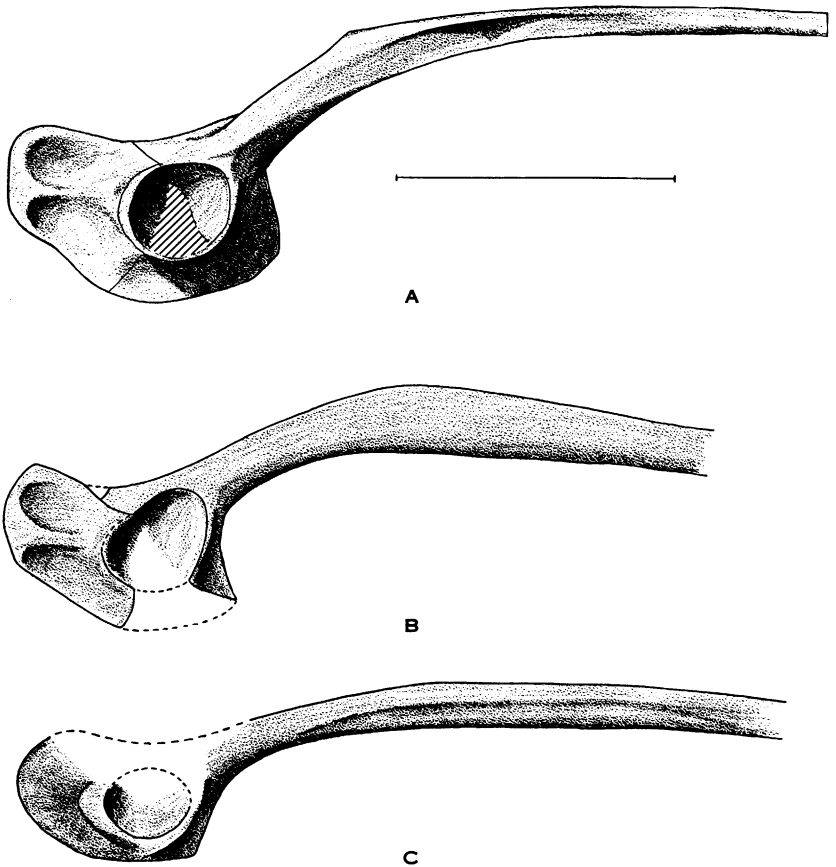


FIG. 7. Lateral view of pelvis. A. *Megophrys carinensis*. B. *Eopelobates grandis*. C. *Macropelobates osborni*. Scale line is 2 cm. Cartilaginous part of acetabulum of *Megophrys* is cross-hatched.

24.9; distance between tips of diapophyses of vertebra three, 28.4; width at sacral diapophyses, 20.0; length of expanded sacral diapophyses, 19.1. The estimated total length (head and body) of the animal is 110 mm.

DISCUSSION

FAMILY ASSIGNMENT: The distinctly arciferal pectoral girdle of this specimen allows the elimination of several families from consideration—the Ranidae, Rhacophoridae, and Microhylidae. The primitive Ascaphidae differ in several ways, most notably in the amphicoelous vertebral column with more vertebrae and free ribs. The Discoglossidae, Rhinophrynidae, and Pipidae are opisthocoelous. The palaeobatrachids, bufonids, lept-

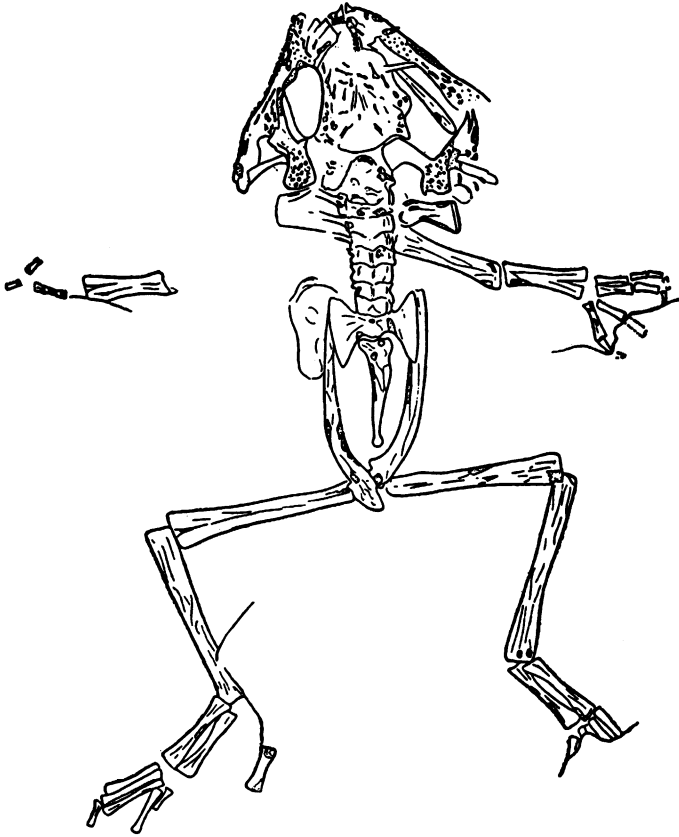


FIG. 8. *Eopelobates anthracinus*, from Parker, 1929.

dactylids, hylids, pelodytids,¹ centrolenids, and brachycephalids all possess a double sacral condyle articulating with the coccyx.

¹ I am in agreement with Taylor as to the desirability of recognizing this family as distinct from the Pelobatidae. Taylor (1941a) refers to the coccygeal condyle as double, while Noble (1926, pp. 7-8) argued that Boulenger's interpretation of a double condyle was in error, that it actually is single as in the pelobatids. In the single skeleton that I prepared, the condyle is quite plainly double. The double nature is evident both on the sacral vertebra and on the coccyx and not due to an artifact of preparation as Noble suggested. It is possible that this character may show intraspecific variation. In addition to the characters of double coccygeal condyle, fused astragalus and calcaneum, and fused first and second vertebrae considered by Taylor as diagnostic of the family, *Pelodytes* is distinguished from pelobatids by the shape of the parasphenoid wings, which are very thin and splint-like, while in all pelobatids that I have seen they are as wide as the anterior median process.

The characters mentioned in the preceding paragraph are not, of course, the only ones that distinguish the fossil from the members of the families mentioned. As the presence of a single sacral condyle articulating with the coccyx cannot be definitely established in the fossil, though it is strongly indicated, it is necessary to discuss other features excluding *Eopelobates* from the families characterized by a double condyle.

In the Paleobatrachidae, the sacrum is formed of two or three slightly dilated precoccygeal vertebrae, thus quite different from the fossil at hand. Bufonids are characteristically toothless, and in addition do not show such great expansion of the sacral diapophyses. The fusion of astragalus and calcaneum into a single bone amply distinguishes both the Pelodytidae and the Centrolenidae from the fossil. The brachycephalids (considered as two separate families, Atelopodidae and Dendrobatidae, by some authors) are small, neotropical frogs that frequently show reduction in vertebral number and tend towards the development of a firmisternal pectoral girdle.

The Hylidae and Leptodactylidae are of special interest, because in some New World members of each of these families dermal ossification on the skull is similar to that seen in the fossil. The very widely dilated sacral diapophyses of the fossil distinguish it from the vast majority of hylids and leptodactylids. In the few hylid skeletons examined, I have not noted the striking differences in lengths of anterior and posterior vertebral diapophyses seen in the fossil. Also the bony sternal style should serve as an additional character to separate it from hylids, which usually have one or two cartilaginous plates. Several genera of leptodactylids show a bony sternum, however, and some resemble the fossil in the character of the vertebral diapophyses. The leptodactylid genera *Ceratophrys* and *Calyptocephalus* resemble the fossil in having the skull heavily encrusted with dermal bone, but the resemblance goes little further. With respect to the expansion of sacral diapophyses, posterior extent of the ischium, proportions of the coracoid, and shape of the skull bones, these leptodactylids have nothing in common with the fossil. The presence of short diapophyses on the urostyle may serve further to distinguish the fossil from leptodactylids and hylids, though I am not certain that coccygeal diapophyses are consistently absent in these families.

The only family not discussed so far is the Pelobatidae, and it seems highly probable that the relationships of the fossil lie within this group. There is nothing in the fossil to exclude it from the Pelobatidae, and many features it possesses are to be found in one or more modern pelobatids. Thus the sacral vertebra with widely expanded diapophyses and (presumably) a single condyle articulating with the coccyx can be dupli-

cated in the genus *Megophrys*. Varying degrees of development of dermal ossification in the region of the skull are seen among the recent pelobatids, ranging from the complete temporal roof of *Pelobates cultripes* to no dermal ossification at all, with intermediate steps present in some species of *Megophrys*, *Pelobates*, and *Scaphiopus*. Relatively greater length of the anterior vertebral diapophyses is common to *Megophrys*, *Pelobates*, and *Scaphiopus*, and coccygeal diapophyses occur as a common variant in *Megophrys*. The relatively great posterior extent of the ischium can be duplicated in *Megophrys*. An ossified sternal style is present in *Megophrys* and *Pelobates*. In short, characteristics of the vertebral column and pelvic and pectoral girdles are consistent with the assignment of this fossil to the family Pelobatidae, and there are no features of other parts of the skeleton to contradict this disposition.

GENERIC ASSIGNMENT: The genus *Eopelobates* was established by Parker (1929) for a fossil from the lower Miocene beds of Rott, near Bonn, Germany. He suggested its affinities were with the Pelobatidae, but as important features of the pectoral girdle and the type of vertebral articulation could not be determined, he could not place its relationships more precisely. His specimen, *Eopelobates anthracinus*, exists as an impression on a lignite slab with a few fragments of bone present (fig. 8). The skull was heavily encrusted with dermal bone, a complete bony arch being present over the temporal region. There is particularly close similarity to the fossil herein described in the shape of the squamosal bone, while the other skull bones, insofar as they can be seen, also agree with those of *E. grandis*. In the shape of the sacral diapophyses the two fossils are very much alike. Parker mentions (1929, p. 279) that the coccyx is without transverse processes, but as processes are not visible on several of the presacral vertebrae, which almost certainly had them, it cannot be said for certain that they were absent from the coccyx prior to fossilization. This is a minor point, in view of the variability of recent pelobatids where these structures are concerned. Other bones are either too poorly indicated in the fossil or too variable in recent species to be trustworthy in a comparison of the fossil species. The aspect of the two specimens is in general quite similar. They differ in size, for *E. anthracinus* had a head-body length of only 32 mm., while *E. grandis* is much larger, with an estimated length of 110 mm. A similar interspecific adult range of size is seen among species of the recent genus *Megophrys*.

Another species of fossil frog has been described and referred to this genus. This is *Eopelobates bayeri* from the late Oligocene or early Miocene of Czechoslovakia (Špinar, 1952). Two of the fossils, *E. anthracinus* and *E. grandis*, share a combination of characters not seen

in other pelobatids, namely, the presence of a complete temporal arch and the absence of a bony pre-hallux. In addition, their skull bones, the squamosals in particular, are of similar shape, and the two forms agree in habitus. It seems reasonable to refer these two species to the same genus, *Eopelobates*. The genus may be defined as follows: pelobatid frogs with an encrustation of dermal bone on the skull; squamosals making broad contact with both maxillae and frontoparietals to form a complete roof over the temporal region; no bony pre-hallux; coccyx free from sacrum¹; maxillary teeth present; tibia and femur of about equal length, the two together somewhat shorter than the head-body length; sacrum with widely expanded diapophyses. I omit from this statement of generic characters features visible on only one or the other fossil which may prove to be of value in generic diagnosis if more specimens become available.

While *Eopelobates bayeri* Špinar is possibly correctly assigned to this genus, the skeletal features that would best indicate its relationships are not to be seen in the fossil. The posterior limbs and pelvic girdle are missing, so that it cannot definitely be stated that the animal was not a spadefoot. The temporal region is incomplete, so it is not known whether or not there was a complete temporal roof. One feature that favors assigning *bayeri* to *Eopelobates* rather than to the spadefoot line of evolution is the length of the urostyle. In the recent species of *Pelobates* as well as in the Oligocene *Macropelobates osborni* (Noble, 1924) the urostyle is relatively short, being shorter or only slightly longer than the length of a sacral diapophysis, while in *E. anthracinus*, *grandis*, and *bayeri* the urostyle is much longer. *Eopelobates bayeri* has dermal bony encrustation on the skull roof, and the squamosal is in contact with the maxillary. The frontoparietal region is somewhat narrower than in *anthracinus* or *grandis*.

SPECIFIC DISTINCTION: *Eopelobates grandis* differs most strikingly from *E. anthracinus* in size, the former being over three times the length of the European species. The possibility that *anthracinus* was a juvenile cannot be ruled out, but such development of dermal bone as is seen in that fossil is usually indicative of adulthood. This size difference, together with their differences in age and geographic location, I feel justifies their assignment to different species. A case might be made for some differences in bone shapes and proportions, but without knowing some-

¹ This character shows much intraspecific variability in at least one genus of recent pelobatids (*Megophrys*) and thus may prove to be of little value in diagnosis of fossils.

thing of the variation that existed in the species, the argument would be relatively meaningless. *Eopelobates bayeri* has a narrower frontoparietal region than *anthracinus* or *grandis*, and almost certainly represents a distinct species.

RELATIONSHIPS OF *EOPELOBATES* TO RECENT PELOBATIDS

Parker (1929, pp. 280–281) noted the resemblance of *E. anthracinus* to *Pelobates*, particularly with respect to the skull. He also noted that none of the non-fossorial pelobatids possessed a complete postorbital arch. *Eopelobates* seemed to fill the roll of a non-fossorial ancestor to the spadefoots, except that it appeared too late in the geologic record, as the spadefoot line was evidently established by the Oligocene, as shown by the Mongolian fossil *Macropelobates osborni*.

Working with the more complete specimen of *Eopelobates* described above, I have been struck by its similarities to members of the recent Asian genus *Megophrys*. In fact, only the complete postorbital arch will distinguish the fossil from that genus. The characteristically long transverse processes of the second, third, and fourth vertebrae, the greatly expanded sacral diapophyses, the free coccyx with transverse processes, the shape of the bony sternal style, the great posterior extent of the ischium—these features can be duplicated in many, and in some cases perhaps all, of the species of *Megophrys*. It might be reasonably argued that *Eopelobates* should be regarded merely as a subgenus of *Megophrys*, but such action would properly require an investigation of other units within *Megophrys* probably worthy of subgeneric rank, an effort beyond the scope of the present work. Špinar also suggested the relationship of *Eopelobates* to the forms today restricted to Asia: "The genus *Eopelobates* Parker, 1929, seems in certain respects to be more primitive, and its many relations and osteological characters, in which it resembles its Asian thermophile relatives, indicate the route by which the genus penetrated into Europe" (Špinar, 1952, p. 487).

ZOOGEOGRAPHIC AND EVOLUTIONARY CONSIDERATIONS WITH RESPECT TO *EOPELOBATES*

The presence in the Tertiary of North America and Europe of genera now Asiatic forms a pattern familiar to biogeographers. Among the Amphibia, Noble (1928) records the salamander genus *Tylostrotion* (now living in southeast Asia) and a species of *Hyla* (which genus shows its greatest development in the New Guinea-Australia region and in tropical and subtropical regions of the New World) from the European Miocene.



FIG. 9. Present distribution of family Pelobatidae and fossil localities. Hatching in North America, Europe, and North Africa indicates range of subfamily Pelobatinae; hatching in southeast Asia, that of Megophryinae. Arrow points to Seychelles Islands, to which subfamily Sooglossinae is restricted. Fossil localities are: 1, *Eopelobates grandis*; 2, *Eopelobates anthracinus*; 3, *Macropelobates osborni*; 4, *Eopelobates bayeri*.

Also the giant salamander *Megalobatrachus*, now Asiatic, is known from the European Miocene. The genus *Cryptobranchus*, the only other recent genus in the family, is restricted to eastern North America, while the related fossil *Plicognathus* is recorded from the lower Pliocene of Nebraska.

Regional biotic similarities suggested by the past and present distribution of these amphibians are considerably reënfforced when the floras and higher vertebrate faunas, both fossil and recent, are examined. The presence in the Oligocene of North America of a frog genus with its closest relationships to a Miocene European form and to recent Asiatic species is, then, not at all anomalous.

The question of where *Eopelobates* stands with respect to the evolution of the recent pelobatids must be considered. Its similarity to *Megophrys* is emphasized in the account above; *Eopelobates* very likely lies in the megophryne line of descent. As the only major difference that can be discerned between *Eopelobates* and *Megophrys* is in the greater skull roofing of the former, it is tempting to suggest that the primitive condition is that where considerable dermal bone is present on the skull. As far as I know, no *Megophrys* ever attains the degree of development of bony encrustation on the skull bones seen in *Eopelobates*, but among the species I have seen, *M. monticola nasuta* and *M. carinensis* have at least some development along this line. Gislén (1936) agreed with Müller (1932) that the occurrence of a postorbital bone bridge such as is seen in *Pelobates cultripes* (and in *Eopelobates*) was more primitive than the ligamentous condition seen in *P. fuscus*. Their opinion contradicted that of Mertens (1923).

Very probably the genus *Eopelobates* had a holarctic distribution in early and middle Tertiary time. Climatic change through the Tertiary eliminated *Eopelobates* from the American and European faunas and restricted its descendant *Megophrys* to the Asian region where, with the greatly increased mountain-building activity of late Tertiary and Quaternary time, the montane genera *Scutigera*, *Aelurophryne*, *Vibrissophora*, and *Ophryophryne* evolved. While it has been customary to assume that the Pelobatidae arose in southeast Asia (Noble, 1924; Špinar, 1952, p. 487), the only evidence for this assumption is the present restriction of primitive pelobatids to that region. The demonstration of a holarctic distribution of primitive pelobatids does not necessarily invalidate the assumption of Asian origin, but serves to emphasize the caution necessary when undertaking to infer past distribution and dispersal routes from present distributions.

It is possible that *Eopelobates* also stands close to the base of the

pelobatine (spadefoot) line of descent, but as this line had been established by the Oligocene, as shown by *Macropelobates*, the separation of the two types may have been somewhat earlier. The subject of spadefoot evolution is dealt with in a subsequent section of this paper.

FAMILY PELOBATIDAE

GENUS *SCAPHIOPUS* HOLBROOK, 1836

Scaphiopus HOLBROOK, 1836, North American herpetology, ed. 1, vol. 1, p. 85.

Scaphiopus alexanderi, new species

TYPE: University of California Museum of Paleontology No. 45030;

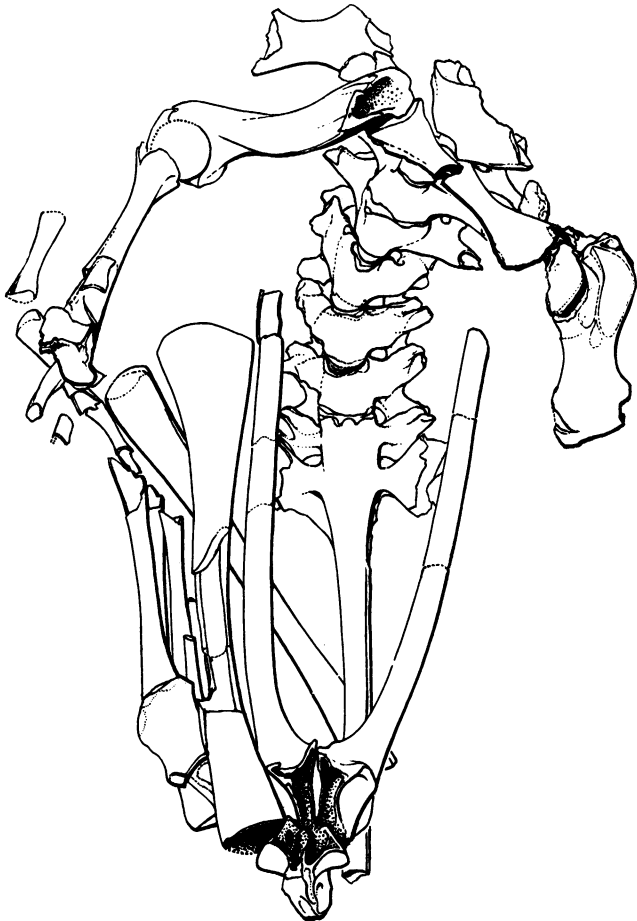


FIG. 10. Type specimen of *Scaphiopus alexanderi*, University of California Museum of Paleontology No. 45030, *in situ* (ventral aspect).

posterior part of skull, vertebral column, parts of pectoral and pelvic girdles, some limb bones.

HORIZON AND LOCALITY: Lower Pliocene, Esmeralda formation, Fish Lake Valley, Nevada, T. 1 N., R. 35 E., elevation 5500 feet, on the west side of a 6000-foot ridge, University of California locality number V 2804. Collected by Annie M. Alexander and Louise Kellogg in 1925. The lower Pliocene age of this formation is attested to by the mammalian fauna (Stirton, 1936) and the flora (Axelrod, 1940).

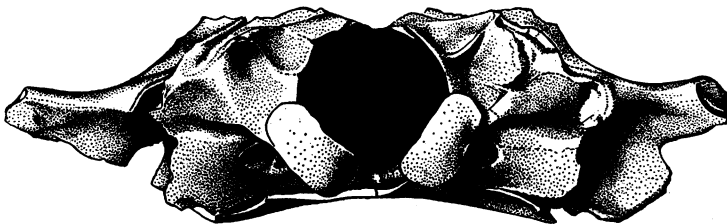
DIAGNOSIS: Differs from all fossil and recent species of *Scaphiopus* except *S. (Neoscaphiopus) noblei* Taylor in having the ninth (sacral) vertebra fused to the eighth (presacral) vertebra. The decision to refer *alexanderi* to a new species distinct from *noblei* is based on their differences in geologic age and geographic position, as the fossil *noblei* is not believed to present features worthy of specific diagnosis.

DESCRIPTION: Only the posterior part of the skull was recovered. This portion shows close agreement in size and form with recent species of the genus *Scaphiopus* (fig. 11).

There are seven free presacral vertebrae, the eighth being fused with



A



B

FIG. 11. Rear of skull. A. *Scaphiopus hammondi*. B. *Scaphiopus alexanderi*. Both $\times 6.75$.

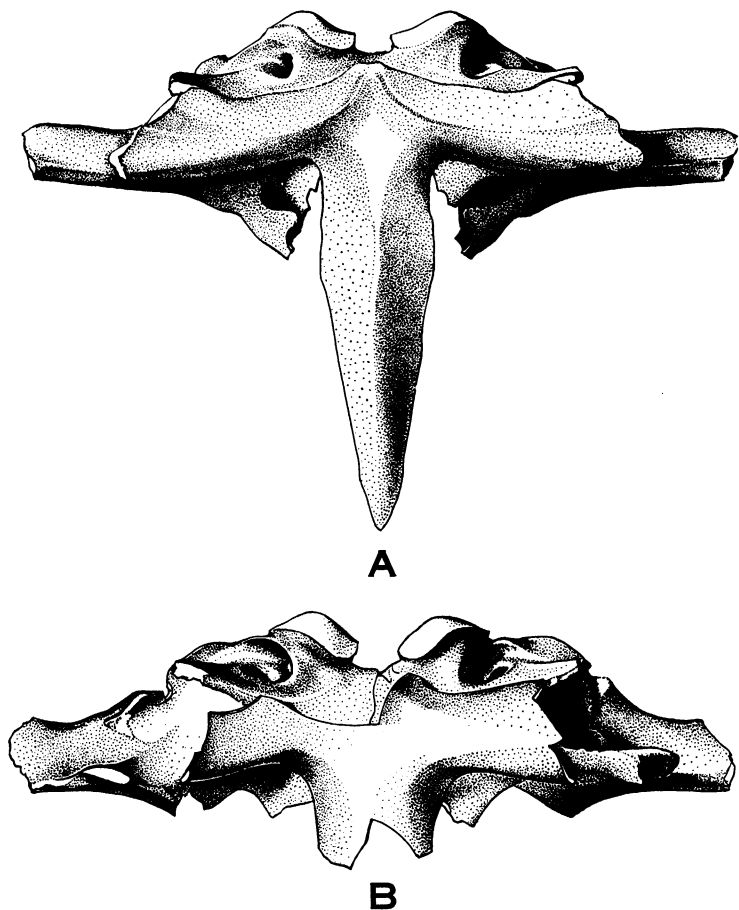


FIG. 12. Parasphenoid and occipital regions from beneath. A. *Scaphiopus hammondi*. B. *Scaphiopus alexanderi*. Both $\times 6.75$.

the sacral (ninth) vertebra which is in turn fused to the urostyle. A faint wavy line on the ventral surface marks the point of fusion of the eighth and ninth vertebrae; no such point of contact is evident between the sacrum and urostyle (fig. 13). The diapophyses of vertebrae two, three, and four are longer than those of the remaining presacral vertebrae, as is typical of pelobatids. The forward inclination of the diapophyses of vertebrae five through eight is relatively slight, and virtually identical with that seen in *Scaphiopus* (fig. 14), though the angle the diapophyses make with the vertebral column shows intraspecific variation in *Scaphiopus*.

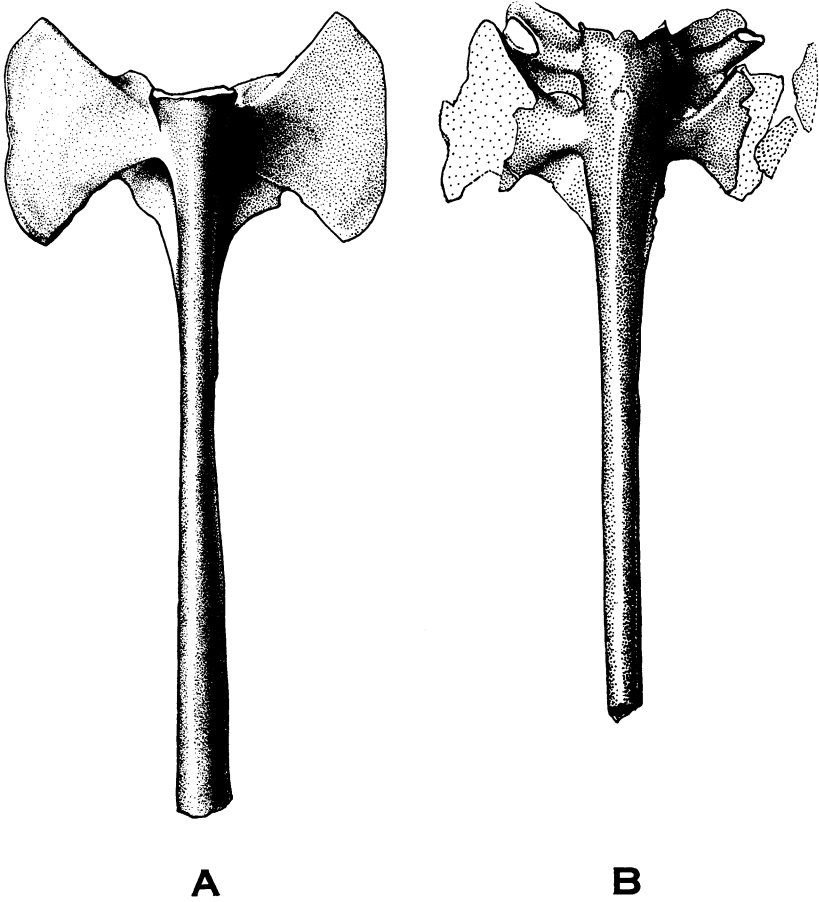


FIG. 13. Sacral vertebrae in ventral aspect. A. *Scaphiopus hammondi*. B. *Scaphiopus alexanderi*. Both $\times 6.75$.

The left scapula is nearly complete and closely resembles that of recent *Scaphiopus*. The left coracoid is present but lacks the medial end. It too may be closely approximated in recent *Scaphiopus*.

The pubis was not preserved and was probably cartilaginous. The proportions of the ilial blades and the ischium are as in *Scaphiopus* (fig. 15).

A humerus (fig. 16), radio-ulna, femur, tibia-fibula (fig. 17), and astragalus-calcaneum (fig. 18) are present. These bones also closely resemble the corresponding elements in recent *Scaphiopus*. Significantly for the identification of this form as a spadefoot toad, a well-developed pre-hallux is present.

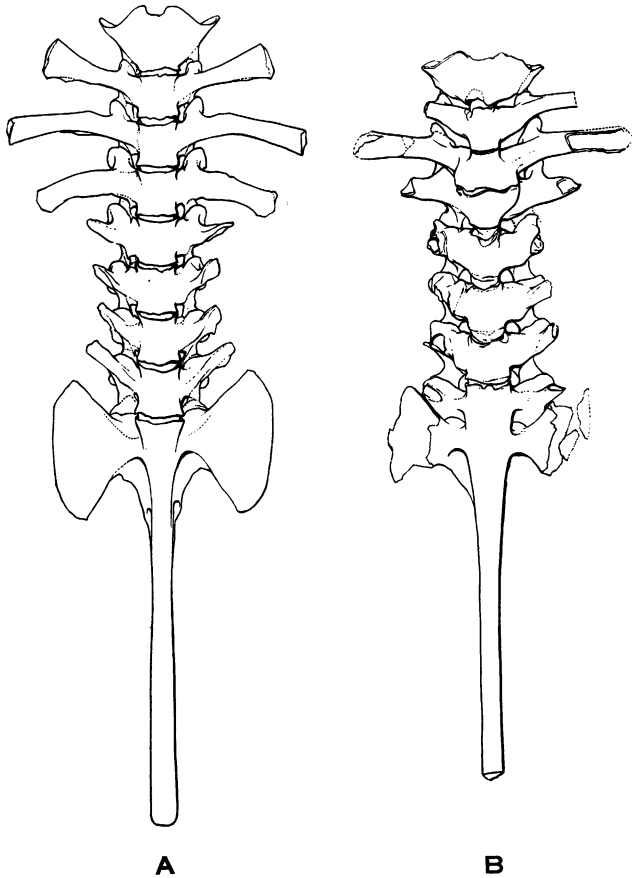


FIG. 14. Vertebral columns in ventral aspect. A. *Scaphiopus hammondi*. B. *Scaphiopus alexanderi*. Both $\times 4$.

MEASUREMENTS (IN MILLIMETERS) : Length of scapula, 7.2; width of atlas, 3.8; height of atlas, 3.7; width to tips of diapophyses of vertebra three, 9.0; width at sacral diapophyses, 5.5; length of sacral diapophyses, 3.1; length of urostyle plus centrum of sacral vertebra, 12.1; length of ilial blade, 14.3; length of femur, 15.7; length of tibia-fibula, 13.7; length of humerus, 10.0; length of radio-ulna, 8.2.

ASSIGNMENT TO FAMILY : The very close similarity of this fossil to living members of the genus *Scaphiopus* makes it rather certain that it is correctly placed in the Pelobatidae, and more specifically in the subfamily Pelobatinae. The short posterior extent of the ischium and the presence of a spade are important features confirming the subfamily assignment.

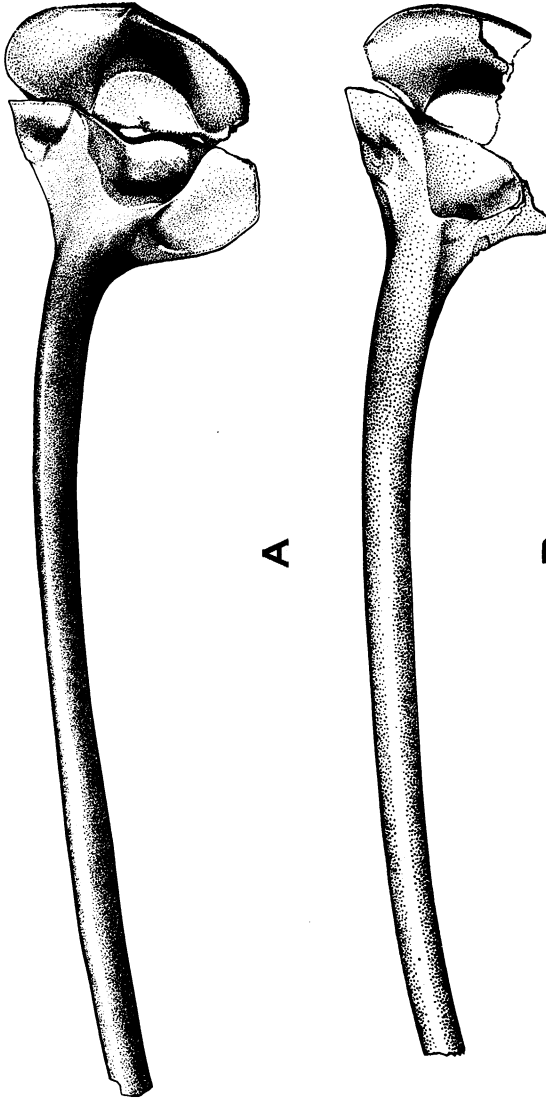


FIG. 15. Lateral aspect of pelvis. A. *Scaphiopus hammondi*. B. *Scaphiopus alexanderi*. Both $\times 6.75$.

GENERIC ASSIGNMENT: The only feature in which *Scaphiopus alexanderi* differs conspicuously from recent forms of the genus is in the fusion of the eighth and ninth (sacral) vertebrae. Such a fusion is recorded in the fossil record for the unique specimen of *Neoscaphiopus noblei* Taylor, from the upper Pliocene of Kansas, and occurs as a rare variant in recent *Scaphiopus*. The question of whether the species described in the present paper should be referred to *Scaphiopus* or *Neoscaphiopus* necessitates a short review of the generic units within the Pelobatinae.

The generic distinctness of the North American and European spadefoot toads has not been questioned. But within the North American forms, the existence of two rather distinct groups of species has led some workers to refer the groups to two genera, *Scaphiopus* Holbrook, 1836, and *Spea* Cope, 1866. Among recent workers, Stebbins (1951), Bragg (1944, 1945), and Blair (1955) have treated the two groups as subgenera, while Smith (1950) and Brown (1950) have recognized *Spea* as a distinct genus.

The pertinent skeletal characters of the five groups within the subfamily (*Pelobates*, *Scaphiopus*, *Spea*, and the extinct forms *Macropelobates* and *Neoscaphiopus*) are contrasted in table 1. Skeletons of *Scaphiopus* and *Spea* are closely similar in all respects except for the presence of an encrustation of dermal bone on the skull of *Scaphiopus*. This encrustation is involved in the maxillary-squamosal contact and the absence of a frontoparietal fontanelle. *Scaphiopus* resembles *Pelobates* in the more extensive skull roof; in all other respects it is much closer to *Spea*.

Among other structural features that have been used to separate *Scaphiopus* and *Spea* are the shape of the metatarsal tubercle (sickle-shaped in *Scaphiopus*, cuneiform in *Spea*) and the absence of a parotid gland in *Spea* (present or indistinct in *Scaphiopus*). The eggs of *Spea* are large and dark, those of *Scaphiopus* small and light colored. Larvae of *Spea* attain a relatively large size, while those of *Scaphiopus* are smaller (Bragg, 1945, p. 65). Size relationships in the adults are reversed, *Scaphiopus* reaching a larger size. Blair (1955) has shown by means of sonograms the characteristic differences between the calls of *Scaphiopus* and *Spea*.

The question, then, is not whether two groups can be recognized, but rather whether or not it is desirable to emphasize their similarities by referring them to the same genus. In the present work, *Scaphiopus* and *Spea* are treated as subgenera. The reference of *Scaphiopus* and *Spea* to a single genus is in agreement with the ecological-morphological concept of the genus recently emphasized by Inger (1954) in his treatment of

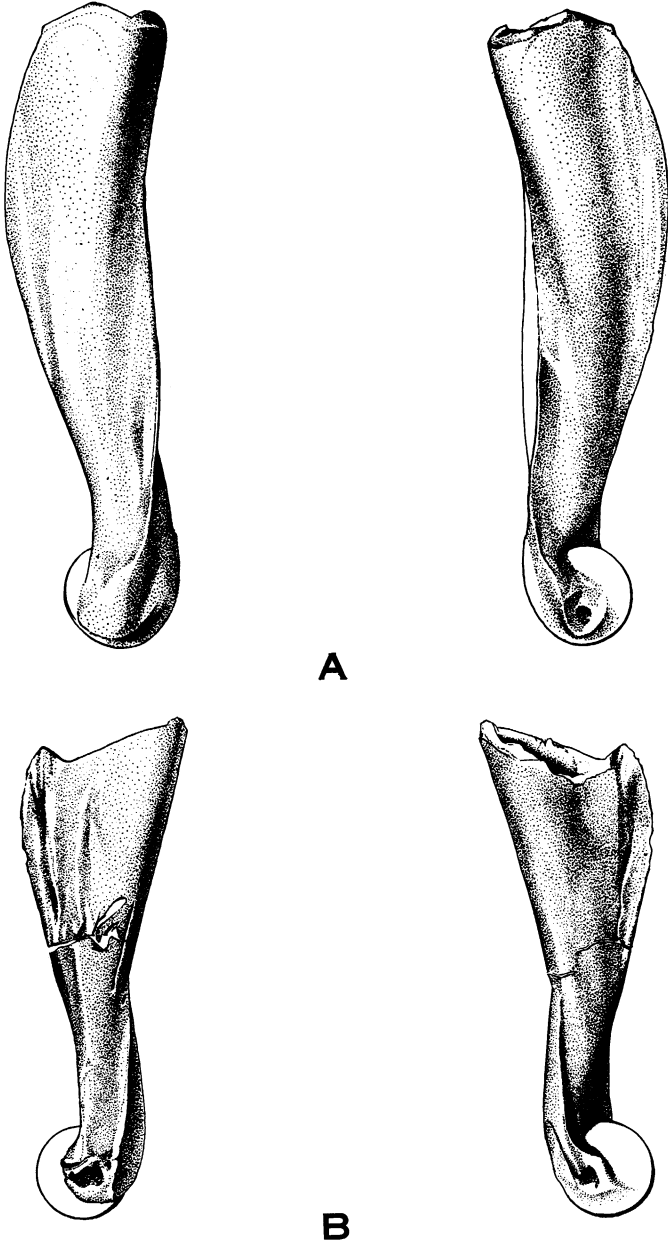


FIG. 16. Humerus. A. *Scaphiopus hammondi*. B. *Scaphiopus alexanderi*. Both $\times 6.75$.

TABLE 1
COMPARISON OF THE SKELETAL CHARACTERISTICS OF THE GENERA AND SUBGENERA OF THE PELOBATINAE.

<i>Pelobates</i>	<i>Macropelobates</i>	<i>Scaphiopus</i> (<i>Scaphiopus</i>)	<i>Scaphiopus</i> (<i>Spaa</i>)	<i>Scaphiopus</i> (<i>Neoscaphiopus</i>)
Maxilla and squamosal in contact	Probably in contact	Maxilla and squamosal in contact	Maxilla and squamosal not in contact	Cannot be determined
Skull with roof of dermal encrusting bone	Skull with roof of dermal encrusting bone	Skull with roof of dermal encrusting bone	Skull without roof of dermal encrusting bone	Cannot be determined
Frontoparietal fontanelle absent	Frontoparietal fontanelle absent	Frontoparietal fontanelle absent	Frontoparietal fontanelle present	Cannot be determined
Quadratojugal present	Cannot be determined	Quadratojugal absent	Quadratojugal absent	Cannot be determined
A strong palatine present	Cannot be determined	Palatine greatly reduced	Palatine greatly reduced	Cannot be determined
A bony sternal style	Cannot be determined	Sternum cartilaginous	Sternum cartilaginous	Cannot be determined

TABLE 1—Continued

<i>Pelobates</i>	<i>Macropelobates</i>	<i>Scaphiopus</i> (<i>Scaphiopus</i>)	<i>Scaphiopus</i> (<i>Spea</i>)	<i>Scaphiopus</i> (<i>Neoscaphiopus</i>)
Transverse processes of vertebrae 5 through 8 slanted very strongly forward	Transverse processes of vertebrae 5 through 8 less strongly slanted forward than in <i>Pelobates</i> , more than in <i>Scaphiopus</i>	Transverse processes of vertebrae 5 through 8 less strongly slanted forward	Transverse processes of vertebrae 5 through 8 less strongly slanted forward	Transverse processes of vertebrae 5 through 8 less strongly slanted forward
Sacral diapophyses greatly expanded, the expansion equal to the length of 4 presacral vertebrae	Sacral diapophyses greatly expanded, the expansion equal to the length of 4 presacral vertebrae	Sacral diapophyses less greatly expanded, expansion equal to the length of 2 presacral vertebrae	Sacral diapophyses less greatly expanded, expansion equal to the length of 2 presacral vertebrae	Sacral diapophyses less greatly expanded, expansion equal to the length of 2 presacral vertebrae
Coccyx short; length of coccyx plus sacral vertebra less than 6 presacral vertebrae	Coccyx incomplete, but length of coccyx plus sacral vertebra equal to at least 5½ presacral vertebrae	Coccyx long; length of coccyx plus sacral vertebra greater than 7 presacral vertebrae	Coccyx long; length of coccyx plus sacral vertebra greater than 7 presacral vertebrae	Coccyx long; length of coccyx plus sacral vertebra greater than 7 presacral vertebrae
Coccyx fused to sacrum	Coccyx free from sacrum	Coccyx fused to sacrum	Coccyx fused to sacrum	Coccyx and first presacral vertebra fused to sacrum

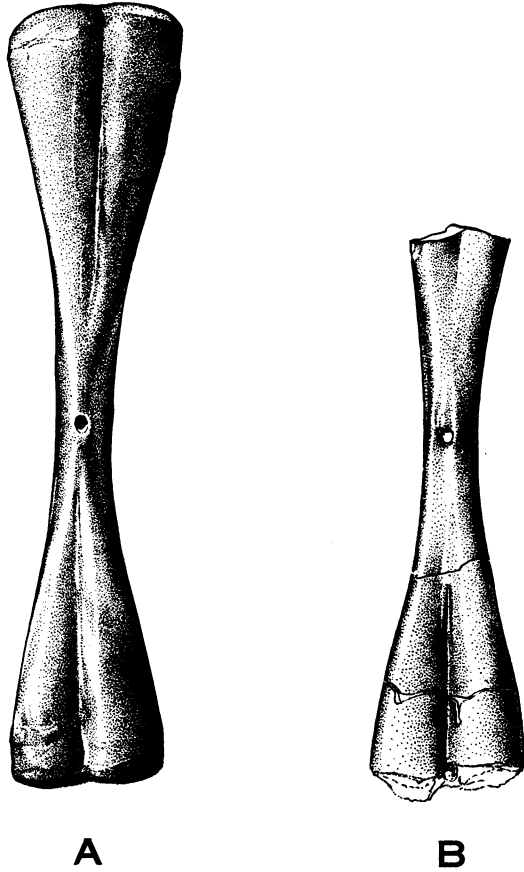


FIG. 17. Tibia. A. *Scaphiopus hammondi*. B. *Scaphiopus alexanderi*. Both $\times 6.75$.

Philippine Amphibia. Though *Scaphiopus* and *Spea* show morphological differences, these are relatively slight and not clearly correlated with any major ecological differences between the species involved. It is not meant to deny that ecological differences between the subgenera exist but merely to emphasize the great similarities over the slight differences.

The genus *Neoscaphiopus* Taylor, 1942, was proposed for a fossil from the upper Pliocene Rexroad fauna of Kansas. The remains consist of parts of the fused coccyx, sacral vertebra, and first presacral vertebra of a presumed pelobatid toad. The chief feature that distinguishes this fossil from *Scaphiopus* is the fusion of the sacral and presacral vertebrae. Because this situation is a sort that suggests an abnormal condition, I have examined the skeletons of a number of *Scaphiopus* to see if this

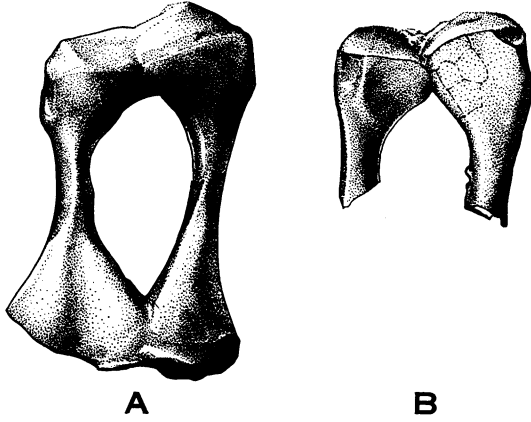


FIG. 18. Astragalus-calcaneum. A. *Scaphiopus hammondi*. B. *Scaphiopus alexanderi*. Both $\times 6.75$.

fusion could be found in recent specimens. Among 53 specimens (35 *Scaphiopus* and 18 *Spea*), the condition occurs only once. I am indebted to Mr. William Duellman for calling this specimen (U.M.M.Z. No. S-964, *S. hammondi multiplicatus* from Distrito Federal, Mexico) to my attention.

It may be that *Neoscaphiopus noblei* Taylor is nothing more than an abnormal *Spea*, the chances being that one out of 18 might show the fused condition. (Actually the odds are probably somewhat greater. Other workers such as Taylor and Tihen have examined numbers of skeletons and have not reported this condition.) But the appearance of the fused condition in *Scaphiopus alexanderi* adds weight to the argument that *Neoscaphiopus* is a natural unit. Out of seven specimens of fossil spadefoot toads reported in the literature (including the form described in this paper) and ranging in time from lower Pliocene to Pleistocene, two show the fusion of sacral and presacral vertebrae. Thus individuals with this fusion would appear to be at least five times as numerous among fossil individuals as among living *Spea*. However, the number of specimens available is far too small for a meaningful statistical analysis. I feel that the best course for the present is to recognize *Neoscaphiopus* as a subgenus of *Scaphiopus* probably most closely related to *Spea*, while keeping in mind the distinct possibility that *Neoscaphiopus* may represent nothing more than slightly abnormal individuals of *Spea*. Elucidation of the true affinity of *Neoscaphiopus* awaits discovery of a fossil with the skull roof preserved.

SPECIFIC DISTINCTION: The fusion of the sacral and first presacral vertebra will serve to distinguish *alexanderi* from all known recent and

fossil *Scaphiopus* except *S. (Neoscaphiopus) noblei*. The only known specimen of *noblei* is a sacral vertebra fused to the first presacral and the urostyle. Only the base of the urostyle is present, and the sacral diapophyses are missing. It might be possible to diagnose differences between *alexanderi* and *noblei* in terms of positions of nerve foramina and amounts of webbing, but these features show considerable intraspecific variation in recent forms. Perhaps when and if more complete material of *noblei* becomes available it will be possible to demonstrate just what, if any, the significant differences between the forms are. In consideration of the span in time (lower to upper Pliocene) and distance (Nevada to Kansas) involved, it seems the best course to refer the two specimens to different species.

THE HABITAT OF *Scaphiopus alexanderi*

The Esmeralda formation is largely a fresh-water deposit. Remains of fossil plants from these beds have been studied most recently by Axelrod (1940). His conclusions with respect to the floristic and climatic relationships were that "the arid basin was surrounded by an oak-juniper community whose associates included species of barberry, manzanita, mountain mahogany, and desert peach. Growing along the streams that flowed into the lake, and about its margins, were species of hackberry, California laurel, aspen, cottonwood, and willow. Rushes and ferns formed dense communities along the borders of the lake, which also supported colonies of water-lily . . . the predominance of grazing vertebrates in the formation indicates grassland was dominant. Rainfall was in the neighborhood of 12 to 15 inches annually and was distributed as summer thundershowers and winter rains. . . . Temperature conditions in the Esmeralda area were more like those now found on the western slopes of the southern Sierra Nevada and in southern Arizona. . . ." (Axelrod, 1940, p. 167). *Scaphiopus hammondi* inhabits today both the California and Arizona regions that resemble in climate and floristics the conditions indicated by the Esmeralda plant fossils.

FOSSIL FORMS OF *SCAPHIOPUS*

The oldest known fossil *Scaphiopus* is the lower Pliocene form, *S. alexanderi*, described in this paper. From middle Pliocene beds in Kansas, Taylor has described *S. pliobatrachus* (1936), *S. studeri* (1938), and *S. antiquus* (1941b) and from the upper Pliocene of Kansas, *S. diversus*, and *S. (Neoscaphiopus) noblei* (1942). *Scaphiopus bombifrons* is recorded from the Pleistocene of Kansas by Tihen (1954).

Of the species described by Taylor, only *S. studeri* is known from a

reasonably complete skeleton. The others are based on sacral vertebrae, as is Tihen's *bombifrons*, though some disassociated bones are also referred to *S. pliobatrachus*. I have not examined any of Taylor's types; hence I am in no position to pass on the validity of the species. However, I wish to draw attention to the rather considerable intraspecific variation to be found in the sacral vertebrae of recent species, variation that seems to include much of the range of variation seen in Taylor's several species.

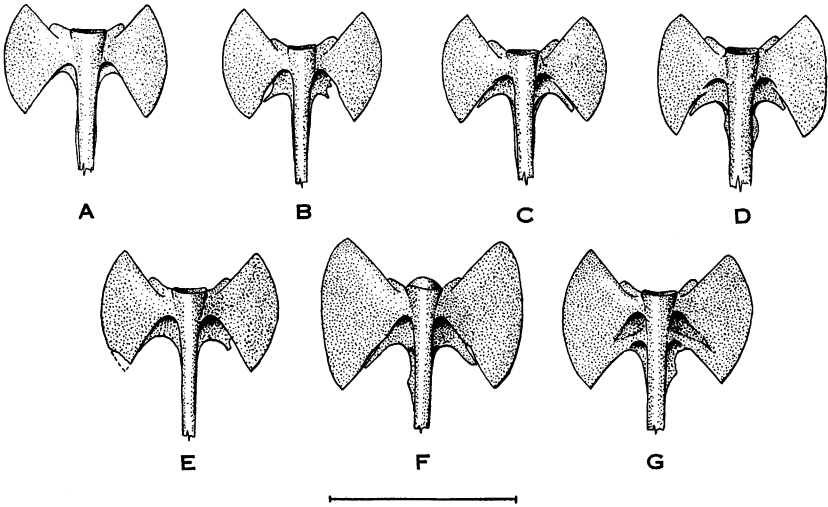


FIG. 19. Sacral vertebrae in ventral aspect. A-D. *Scaphiopus hammondi*, Mariposa County, California. E-G. *Scaphiopus bombifrons*, Wyoming. Scale line is 1 cm. Note particularly variation in amount of webbing between diapophyses and shaft, and variation in location of tenth nerve foramina.

In figure 19 are shown the sacral vertebrae of several specimens of *S. hammondi* and *S. bombifrons*. The *hammondi* came from the same local population in California, while the *bombifrons* are from two different places in Wyoming. Particularly evident is the extent of variation in webbing between the diapophyses and the coccyx.

Tihen has informed me (*in litt.*) that the variation in my specimens of *bombifrons* is somewhat greater than in his recent material, although he examined more specimens than I. I do not find it possible to identify species of *Scaphiopus* with any degree of consistency from isolated sacral vertebrae. Even the separation of the subgenera *Scaphiopus* and *Spea* is difficult. There are average differences in the angles the sacral diapophyses make with the axis of the vertebral column, but overlap in the ranges of variation prevents 100 per cent separation.

Taylor (1938) felt that *Scaphiopus studeri* was closest to *S. bombi-*

frons among the living forms. In the fossil, the frontoparietal bones appear relatively deep, and there is a large frontoparietal fontanelle. This fossil is clearly referable to the subgenus *Spea*. Taylor (*ibid.*, p. 409) mentions the presence of a quadratojugal bone in this fossil, but there is no evidence in his illustrations that such a bone was present. I prefer not to attempt a subgeneric assignment for *S. antiquus*, *S. pliobatrachus*, and *S. diversus*.

THE RECENT FORMS OF *SCAPHIOPUS*

Although it is not the purpose of this paper to present a revision of the taxonomy of *Scaphiopus*, it is necessary to express my tentative conclusions as to the systematics of the species involved in order that the reasons for the use of the various specific names will be clear. The taxonomic conclusions are based largely on the morphology of the skull and on evidence of sympatric existence.

The distribution maps (figs. 20–21) are based largely on literature records and on maps published by previous authors (Tanner, 1939; Wright and Wright, 1949; Stebbins, 1951, 1954), with modifications dictated by my views on distributional correlations with features of vegetation and physiography.

SUBGENUS *SCAPHIOPUS*

Scaphiopus holbrooki HARLAN: As appears to be the case with all species of *Scaphiopus*, the configuration of the frontoparietal region of the skull is quite distinctive. In *S. holbrooki*, this region is broad and reaches its greatest width about two-thirds of the length of the frontoparietal from the anteriormost point of suture with the nasals where the lateral borders flare out somewhat and then converge towards the rear of the skull (fig. 22A).

The distribution map for this species is essentially the same as that of Wright and Wright (1949, p. 124), with main differences falling in the southwestern part of the range. As Brown has noted (1950, p. 39), there are as yet no authentic records for this species in Texas. As *S. hurteri* is now known farther to the east than shown on the Wrights' map, it may be that the two species meet and replace each other east of the Texas-Louisiana border.

Scaphiopus holbrooki is found largely within the region of the Deciduous Forest formation (Braun, 1950). However, this should not be taken to mean that this species is restricted to the forest as such. In fact, it probably occurs infrequently or not at all where the forest, in the form of the Mixed Mesophytic Association, reaches its maximum of

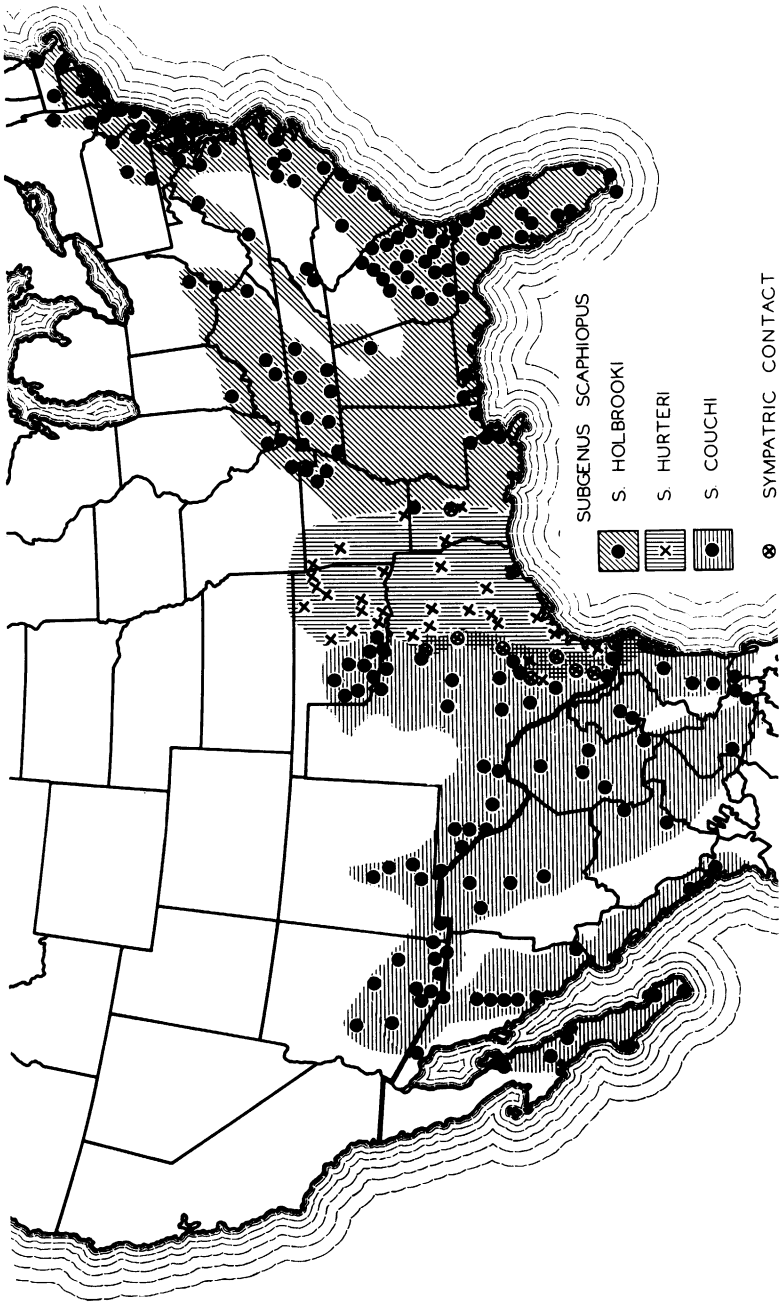


FIG. 20. Distribution of species of the genus *Scaphiopus*, subgenus *Scaphiopus*.

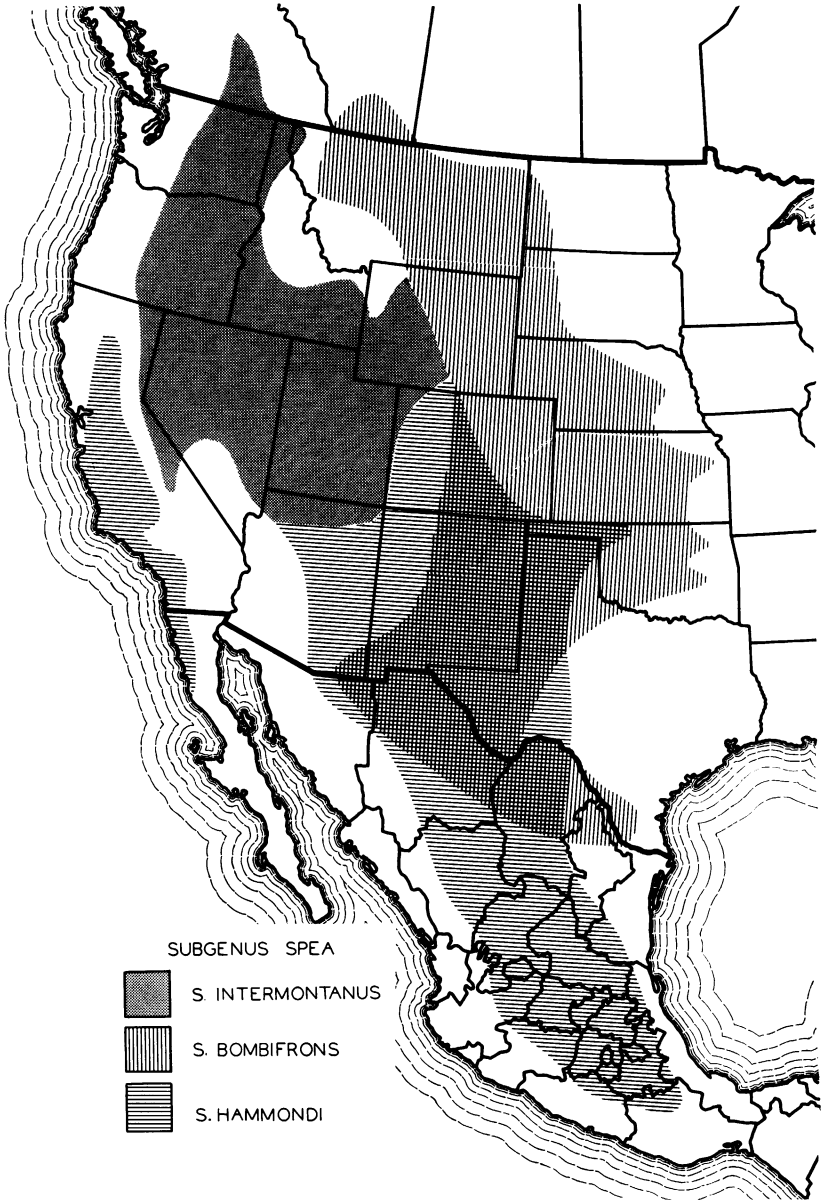


FIG. 21. Distribution of species of the genus *Scaphiopus*, subgenus *Spea*.
 expression. Much of the area inhabited by *holbrooki* is within the South-eastern Evergreen Forest region, much of which is held in subclimax states by the nature of the soil (Braun, 1950, p. 532) and by fire. Very

probably sandy or at least light soils are a necessary part of optimum spadefoot habitat; thus these animals may be (and may have been in the past) more regularly associated with seral and stable subclimax stages of forest vegetational development than with the higher stages of succession.

Past authors have recognized a race of *holbrooki*, *S. h. albus*, with type locality at Key West, Florida. Duellman (1955) has shown that this population is not worthy of taxonomic distinction.

Scaphiopus hurteri STRECKER: Despite Smith's (1937) demonstration of the distinctiveness of the skull of *hurteri*, some recent authors have persisted in referring to it as a subspecies of *holbrooki* (Wright and Wright, 1949; Schmidt, 1953). Bragg, who has had considerable field experience with *hurteri*, has treated it as a distinct species. The skull is relatively deeper than that of *holbrooki*, and has a narrower frontoparietal region without the well-developed lateral expansions of that species (fig. 22B). Ernest Liner (*in litt.*) informs me that there are specimens of both species from Pollock, Grant Parish, Louisiana, in the collection of Tulane University. I have not seen these specimens, but the region is one where the two might be expected to come in contact.

The presence of *S. hurteri* in southern Arkansas (Burger, Smith, and Smith, 1949) and in central Louisiana (Ernest Liner, *in litt.*) fills in the rather considerable gap between *hurteri* and *holbrooki* shown on the Wrights' map. The literature record of *hurteri* in the panhandle region of Oklahoma (see Bragg, 1944, p. 529, for discussion) awaits verification by specimens. The presence of this species at the southernmost tip of Texas makes it seem probable that it occurs in Mexico, though yet unrecorded from there.

Scaphiopus hurteri inhabits woodland and savanna areas in Oklahoma (Bragg, *ibid.*, p. 528). To judge from the distribution of locality records in Texas, in that area more xeric vegetation types such as mesquite-chaparral are also entered.

Scaphiopus couchi BAIRD: This species has had a relatively stable taxonomic history, and cannot readily be confused with any other spadefoot. The skull is quite distinctive, with the frontoparietal region narrow in front and much wider to the rear, the greatest width being reached about three-quarters of the way back, contrasted to two-thirds in *holbrooki* (fig. 22C).

There appear to be no records of this species in the Llano Estacado region of eastern New Mexico and Texas; hence I exclude that area (which was included within the species range by Stebbins) from the range shown on my map (fig. 20). Also, the presence of *couchi* at the head of the

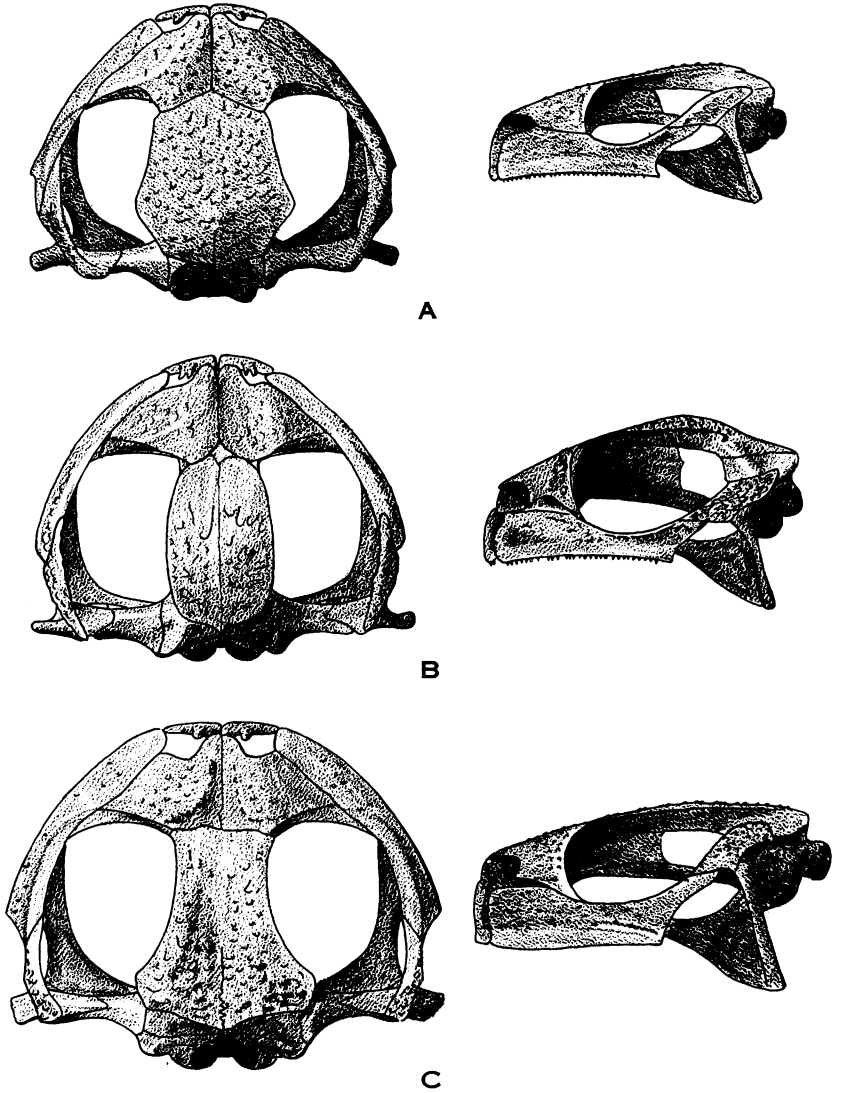


FIG. 22. Dorsal and lateral aspects of skulls of species of *Scaphiopus*, subgenus *Scaphiopus*. A. *S. holbrooki*. B. *S. hurteri*. C. *S. couchi*. All approximately $\times 2.5$.

Gulf of California remains to be verified by specimens. Attention should be drawn to the highly inaccurate range given for this species in the recent "Check list" (Schmidt, 1953, p. 58) and the inappropriate common name ("Great Plains spadefoot") referring to that range.

According to Bragg (1944, p. 524), *S. couchi* is "confined to quite xeric habitats in short-grass plains and deserts." But along the west coast of Mexico this species occurs abundantly in the more mesic Thorn Forest and Tropical Deciduous Forest.

Smith and Sanders (1952, p. 209) resurrect the name *Scaphiopus rectifrenis* Cope, type locality Rio Nazas, Coahuila, for western populations of this species. Geographic variation in *couchi* is worthy of study, and the recognition of geographic races should properly await a detailed, analytic study, rather than the few lines devoted to the subject by Smith and Sanders.

SUBGENUS *SPEA*

Scaphiopus hammondi BAIRD: The skull of *hammondi* is characterized by an extensive frontoparietal fontanelle and relatively smooth, flat frontoparietal bones (fig. 23C). I can detect no significant differences between Mexican (*multiplicatus*) and Californian (*hammondi*) specimens with respect to the skulls and have no hesitancy in referring them to the same species. The problem of proper subspecific assignment of various populations awaits study (Firschein, 1950).

For the range of this species within the United States, I have followed Stebbins (1954, p. 142). There are no records of *hammondi* in central or southern Sonora, despite the considerable collecting that has been done there. Evidently *hammondi* does not penetrate south in the Sonoran Desert, as shown on Stebbins' map, but is confined to the northeastern part of the state.

Scaphiopus hammondi has a wider ecological distribution than accorded by Bragg (1944, p. 524). Far from being limited to short-grass plains and deserts, *hammondi* penetrates the pine forests bordering the Mexican Plateau and in California is found in Chaparral and in Blue Oak-Digger Pine Woodland, as well as in grassland. In California *S. hammondi* is absent from the deserts, probably because of insufficient rainfall there. This species breeds in California with the rains of late winter and early spring. Probably the ability to breed in relatively cool waters is of great importance for the survival of this species on the Pacific coast.

Scaphiopus bombifrons COPE: In *bombifrons* the frontoparietal fontanelle is generally somewhat smaller than in *hammondi*. The anterior ends of the frontoparietals are elevated and enlarged into a usually somewhat rugose, bony boss. These bones do not always meet on the midline as in the individual illustrated (fig. 23B).

The recent record of this species in southern Texas (Axtell and

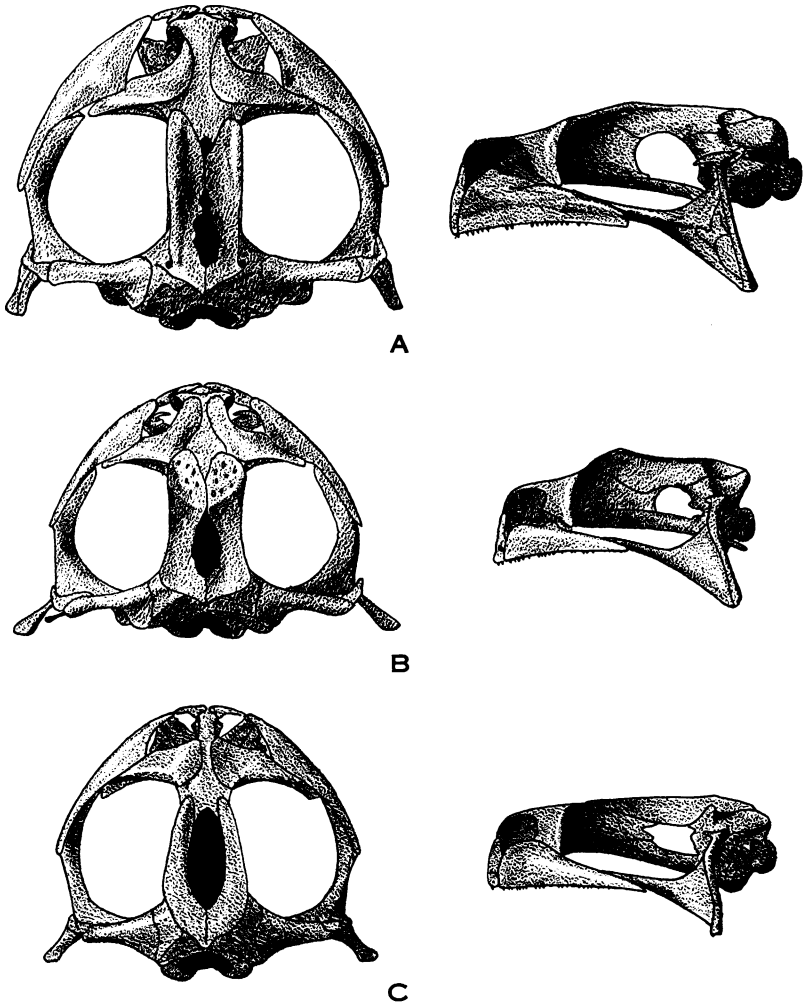


FIG. 23. Dorsal and lateral aspect of skulls of species of *Scaphiopus*, subgenus *Spea*. A. *S. intermontanus*. B. *S. bombifrons*. C. *S. hammondi*. All $\times 2.5$.

Wasserman, 1953) was shown on Stebbins' map as a disjunct population. Axtell and Wasserman state that "numerous other vertebrates which are widely distributed in the plains region of west Texas range eastward into the brushlands of south Texas, avoiding the Edwards Plateau." As *S. bombifrons* has only recently been recognized as a member of the Mexican fauna (Firschein, 1950), it seems reasonable to suppose that the range is continuous across northern Coahuila and Nuevo Leon to southern Texas, though records are still lacking for Mexican

states other than Chihuahua. The occurrence of this species in north-eastern Sonora is virtually certain.

Scaphiopus intermontanus COPE: The tendency in recent years has been to treat this form as a subspecies of *hammondi* (Stebbins, 1951; Schmidt, 1953). The skull shows greater closure of the frontoparietal fontanelle than is seen in *hammondi* (some specimens of *intermontanus* show more or less closure than the individual illustrated) and possesses elevated rather than smooth and flat frontoparietals. The statement of some authors that a fontanelle is absent is incorrect. In contrast to *bombifrons*, where the elevation of the frontoparietal bones is restricted to the anterior part, in *intermontanus* the highest point is reached nearer the mid-point of the length of these bones (fig. 23A).

I have recently been privileged to hear a recording of the mating call of *intermontanus* made in eastern Washington by Robert C. Stebbins, and another recorded in southern Utah by Charles M. Bogert. The call is totally unlike that of *hammondi* and more reminiscent of that of *bombifrons* and of members of the subgenus *Scaphiopus*. The weight of evidence favors the interpretation of *hammondi* and *intermontanus* as distinct species, as they were treated by Tanner (1939). It is possible that *intermontanus* may prove to be a subspecies of *bombifrons*, but there is as yet no conclusive evidence for this.

The exact distributional relations of this species to *bombifrons* and *hammondi* remain to be worked out. I have followed Stebbins' mapping (1954, p. 142).

Scaphiopus intermontanus is found in the high desert region of the Great Basin. Although most records are in regions of sagebrush or juniper-piñon vegetation, *intermontanus* may be found at high elevations in the spruce-fir belt (Cedar Breaks, Utah, C. M. Bogert, personal communication).

The rough correlations that exist between spadefoot distribution and vegetational regions are not considered to represent direct adaptation of the animals to particular vegetation types, as evidently occurs in some higher organisms, but rather reflect similarity of adaptation to climate and soil in the animals and plants.

EVOLUTION OF THE NORTH AMERICAN SPADEFoot TOADS

The subject of spadefoot evolution has received brief attention from Tanner (1939) and a more extended treatment by Bragg (1945). Both authors were in agreement that the genus *Scaphiopus*, used in the wide

sense employed in this paper, had arisen in the region that is now southwestern North America and radiated from there. Also, both referred the genus to the family Scaphiopodidae, Tanner without comment and Bragg stating that the species of *Scaphiopus* were "now more commonly considered as members of a separate [from the Pelobatidae] group, the Scaphiopodidae" (Bragg, 1944, p. 517).¹ Thus both authors seem to have eliminated from consideration the possibility that the American and European spadefoots had common spadefoot ancestry, ignoring the highly significant Mongolian Oligocene fossil *Macropelobates*.

In a consideration of the evolution of *Scaphiopus*, its relationships to *Pelobates* and *Macropelobates* must be discussed. The placing of *Scaphiopus* and *Pelobates* in separate families is quite untenable. Indeed, it is most difficult to see what features of their anatomy could be used as diagnostically different on the family level. The problem is not so much whether or not they belong in the same family, as whether *Pelobates* and *Scaphiopus* evolved from the same fossorial stock or were independently derived from primitive, non-fossorial types, as Gislén (1936) suggested and as is implicit in Bragg's scheme. With regard to the recent spadefoot genera, *Macropelobates* is primitive in several respects. The coccyx is free from the sacrum, the ischium has a greater posterior extent (as in *Megophrys*), and the astragalus and calcaneum are relatively longer. On the basis of skeletal morphology, *Macropelobates* could very well represent the fossorial ancestor of both *Pelobates* and *Scaphiopus*.

One of the peculiarities of *Scaphiopus* is the great reduction of the palatine bone and its replacement by a process of the vomer (fig. 24). *Spea* shows the greatest reduction, and the subgenus *Scaphiopus* slightly less. If the condition wherein a form has a strong palatine bone can be taken as primitive, then *Scaphiopus* represents the more advanced (specialized) type and *Pelobates* and *Macropelobates* the more primitive. Within *Scaphiopus*, the subgenus *Spea* is more specialized. The chief difference between the two subgenera of *Scaphiopus* lies in the absence of a roof of secondary bone on the skull of *Spea*. As the earliest known pelobatids (*Macropelobates* and the three species of *Eopelobates*) all possessed

¹ Myers (1952) criticized Stebbins (1951, pp. 194-195) for mentioning that the American spadefoots were sometimes placed in a separate family from the Old World forms, stating that Stejneger's proposal to replace the name Pelobatidae with Scaphiopodidae was on nomenclatural grounds, not meant to indicate the presence of two families of spadefoots. Whatever Stejneger had in mind, it is quite evident that many subsequent authors did consider the New World and Old World forms to belong to separate families. Stebbins' remarks on relationships of Old and New World forms were quite in order.

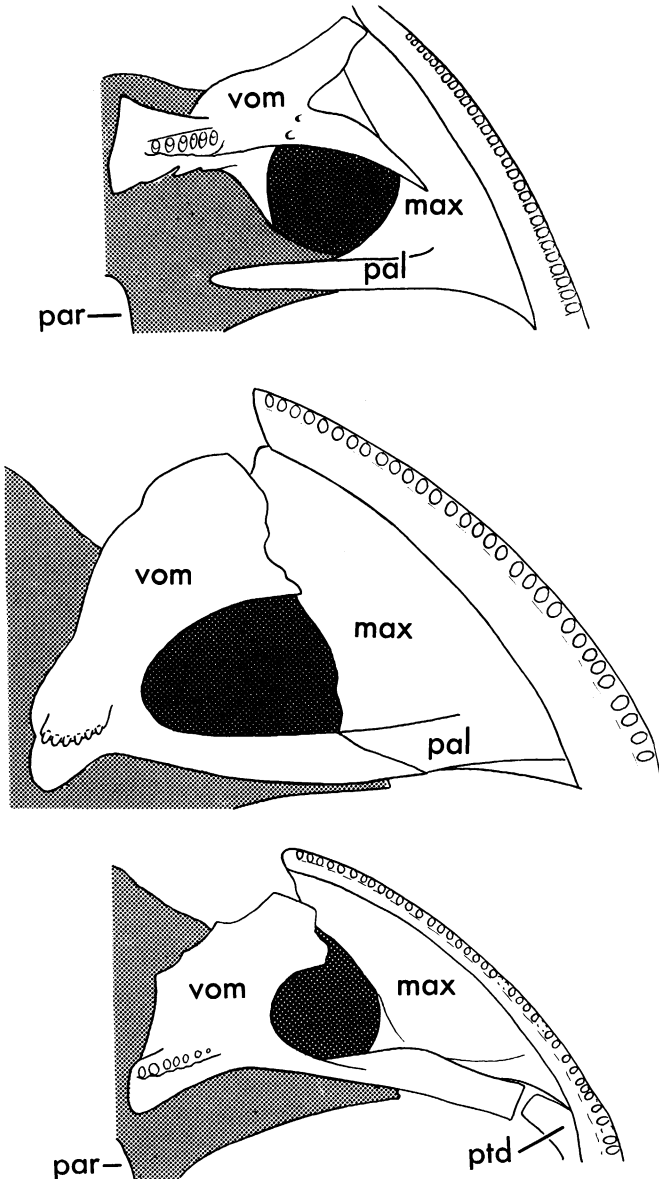


FIG. 24. Anterior part of roof of mouth, left side (premaxilla omitted). A. *Pelobates cultripes*. B. *Scaphiopus couchi*. C. *Scaphiopus hammondi*. Internal narial opening cross-hatched, ethmoid bone stippled. Abbreviations: max., maxilla; pal., palatine process of maxilla; par., parasphenoid; ptd., pterygoid; vom., vomer.

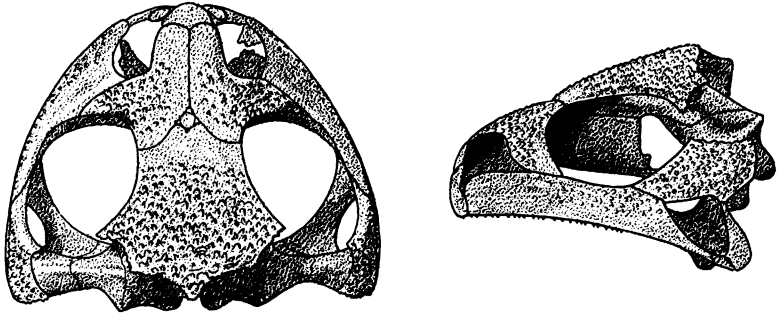


FIG. 25. Dorsal and lateral aspects of skull of *Pelobates fuscus* (Germany), $\times 2.5$.

extensive dermal bony roofing of the skull, it is perhaps reasonable to assume that such a condition is primitive within this family. *Pelobates cultripes* has a more complete skull roof than any *Scaphiopus*, while *Pelobates fuscus* more closely resembles members of the subgenus *Scaphiopus* in this respect. The extensive skull roofing, together with the presence of quadratojugal (fig. 25) and strong palatine bones (fig. 24A), marks *Pelobates* as less advanced than *Scaphiopus*. The cartilaginous sternum of *Scaphiopus* was thought to be more primitive than the bony condition seen in *Pelobates* (Noble, 1931, p. 494), but could as reasonably be regarded as a specialized condition.

Bragg's assumption that *Scaphiopus* arose in the southwest and spread out from there was based on the breeding patterns of the members of the genus. In contrast to most anurans living in mesic regions, the spadefoots have no fixed breeding season but are likely to breed whenever sufficient rain falls to form temporary pools. Temperature, amount, and rate of rainfall evidently are important factors in determining whether there is breeding, and all species do not react alike. Nevertheless, the habit of breeding in temporary pools whenever (within limits) these are available and the very rapid rate of larval growth mark these animals as well-adapted to existence in arid regions. Bragg regarded the logical place for such xeric adaptation to have arisen to be the arid southwest.

Is it possible to reconcile the breeding patterns seen in *Scaphiopus* with derivation from a northern ancestor such as *Macropelobates*? *Pelobates* is similar to *Scaphiopus* in its breeding habits (see, for example, the *Pelobates* breeding pond illustrated by Gislén, 1936, p. 129, fig. 13) and may have inherited its breeding habits from the same source. As I see it, the breeding pattern that Bragg considers basically adapted to an arid environment may be of adaptive value in a variety of circumstances and might be considered as preadapted to the arid environment. Where-

ever there are temporary pools formed, there will be ecological pressure to fill that habitat. There are many anurans that breed for the most part in temporary waters and have rapid larval growth, but are not necessarily or even at all creatures of arid regions. The wood frog, *Rana sylvatica*, is an example of such a species.

If we assume that the North American spadefoot toads are of northern origin and did not arise in southwestern North America independently of the European and extinct Asiatic forms, then the evolutionary sequence in *Scaphiopus* may have been something like this: An ancestral fossorial type, perhaps close to *Macropelobates*, was associated with high-latitude deciduous forests and in the early Tertiary moved southward on the North American continent. This primitive *Scaphiopus* was adapted to breeding in temporary pools and hence preadapted to existence in the more arid environments that were later to develop. *Scaphiopus holbrooki*, the species that bears the closest similarity to *Pelobates*, may represent the most primitive member of its genus existing today. The distribution of *holbrooki* is largely within the Deciduous Forest region of eastern North America, leaving that region only in Florida. The Deciduous Forest of eastern North America has been derived in large part from an early Tertiary holarctic forest which has been recognized in a number of deposits, some of quite high latitude. It is entirely appropriate that the most primitive *Scaphiopus* should be associated with an ancient environment.

Scaphiopus couchi possibly evolved in association with the thorn scrub and mesquite-grass formations that were being established in the southwestern interior region by mid-Oligocene (MacGinitie, 1953, p. 59). *Scaphiopus hurteri* inhabits the broad ecotone between the Deciduous Forest to the east and the plains to the west. Both in its ecology and morphology (skull roofing much less than in *couchi* or *holbrooki*) it trends towards *Spea*. The evolution of *S. hurteri* may be correlated with the early development of grasslands and the establishment of the forest-grasslands ecotone.

The evolution of *Spea* may be correlated with the establishment of grassland as a distinct and wide-ranging formation at least as early as the lower Pliocene and perhaps as far back as mid-Miocene. The existence of the relatively specialized *Scaphiopus* (*Neoscaphiopus*) *alexanderi* in the lower Pliocene of Nevada and its probable derivation from *Spea* points to a Miocene (or earlier) origin for *Spea*, though the oldest known *Spea* (*Scaphiopus studei*) is from middle Pliocene deposits.

While most spadefoot toads breed in temporary waters following rains, it is worthy of note that *S. intermontanus* has been recorded as breeding

without the stimulus of rain. Linsdale (1938, pp. 20–23) gives an account of breeding activity independent of rainfall in Nevada, and C. M. Bogert (personal communication) has recently found this species breeding in southern Utah where there had been no recent rainfall. Similarly, Stebbins (1951, p. 209) mentions individuals calling in Utah where it had not rained for three weeks. It may be that this species is undergoing an adaptive shift to breeding habits more suited to a region where summer rains are most uncertain.

Tanner (1939, p. 15) expressed the following opinion on the evolutionary relationships within *Spea*: "The evolution of the subgenus *Spea* seems to be from *hammondii* through *bombifrons* to *intermontanus*. In these species there is a progressive development of the osseous parts of the cranium with a closure of the frontoparietal fontanelle in practically all specimens of *intermontanus*." My interpretation of the relationships of these species is opposed to that of Tanner in that I regard the larger species with the greater amount of bone in the frontoparietal region, *intermontanus*, as the more primitive and *hammondi* as the more advanced. This is in accord with my suggestion that the members of the subgenus *Scaphiopus*, of larger size and with more skull ossification, are more primitive than *Spea*.

Bragg (1945, pp. 64–65) notes that on the basis of larval specialization *hammondi* might be placed at the end of its phylogenetic line rather than at the base, but states that the large jaw muscles and peculiar mandible of the *hammondi* larva may be specific larval adaptations of no use in the placing of this species in its proper relationship to *bombifrons* and *intermontanus*.

SKELETAL MATERIAL EXAMINED

Complete skeletons, skulls, and partial skeletons or skulls alone from the following localities were examined in the course of this study. Where more than one specimen was available from a single locality, the number of specimens is indicated in parentheses following the locality. In addition to the specimens listed as examined here, pertinent skeletal features were checked by dissection in many other specimens.

Megophrys, sp., 1: Mt. Carin, Burma.

Megophrys carinensis, 1: Burma.

Megophrys parva, 1: Burma.

Megophrys kuantunensis, 1: Fukien, China.

Megophrys lateralis, 1: Kuangtung, China.

Megophrys boettgeri, 2: Fukien, China.

Megophrys monticola, 1: Tjibodas, Java.

Sooglossus schellensis, 1: Seychelles Islands.

- Pelobates fuscus*, 1: Germany.
Pelobates cultripes, 1: Portugal.
Scaphiopus holbrooki, 21: South Carolina: Charleston Co. (12). Georgia: Glynn Co. (2). Florida: Dade Co.; Putnam Co. (2); Alachua Co.; Flagler Co. (2). Long Island, New York.
Scaphiopus hurteri, 3: No data. Texas: McLennan Co., Denton Co.
Scaphiopus couchi, 12: Arizona: Cochise Co. (7); Pinal Co. Texas: Cameron Co.; Duval Co. Mexico: Sinaloa; Baja California Sur.
Scaphiopus intermontanus, 4: Utah: Kane Co.; Washington Co. (3).
Scaphiopus bombifrons, 7: Wyoming: No data; Fremont Co. (2). Arizona: Cochise Co. (2). Kansas: Douglas Co. Mexico: Chihuahua.
Scaphiopus hammondi, 12: California: Mariposa Co. (4). Arizona: Cochise Co. (3); Pima Co. Mexico: Distrito Federal (2); Michoacán; San Luis Potosí.

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