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THE DISTRIBUTION OF BIDDER'S ORGAN  
IN THE BUFONIDAE

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Few structures in the Amphibia have been subjected to more continuous investigation than has the small body lying between the gonads and the fat body in certain salientians. The name "Bidder's organ" was suggested for this structure by Spengel, and as such it has been known since. Apparently discovered by Roesel von Rosenhof more than 175 years ago, it has long been the subject of speculation and debate, which was occasionally acrimonious and unscientific to an extraordinary degree. The mystery of the significance of this curious structure has defied repeated attacks by a number of the most able morphologists and physiologists, and today definite knowledge concerning it is still remarkably meager. Indeed, little is certain beyond the fact that it is present in both sexes of many bufonids, that in males as well as females it is composed of immature egg cells, and that in both sexes, following removal of the gonads, it is capable of developing into a functional ovary, normal in every respect except that genetically the original sex of the animal is retained. This highly interesting fact was shown several years ago by Mlle. Ponse, who succeeded in raising tadpoles from male toads thus feminized. The abrupt deviation from the normal 50-50 sex ratio in this offspring showed that the "mother" was still a male as far as its chromosomes were concerned. Witschi (1933) has recently given a good, though brief, review of the history of several phases of research on this structure.

Since the literature contains a number of excellent figures and descriptions of the gross morphology, histology, and cytology of Bidder's organ, only the barest outline need be presented here. The testes in toads are more or less elongate and cylindrical. Bidder's organ lies directly at the anterior end of these organs (fig. 9, B), usually distinctly separated from them, but occasionally fitting over

the anterior end like a cap. In the larger species of toads Bidder's organ is readily distinguished from the testis by its nodular surface. Its characteristic pinkish color in freshly killed animals serves further to differentiate it from the testis, although it fades rapidly in preserved specimens. Histological examination shows that the organ is composed of ovocytes in an immature, unpigmented stage. Witschi (1933) has recently demonstrated that only the cortical layer of the primary gonad supplies the germ cells of Bidder's organ, exactly as in the developing ovary. On the basis of this discovery, he advances the interesting hypothesis that the withdrawal of the medullary (testis-forming) part of the gonad from the anterior region of the larval gonad results in the formation of a typically female region in an otherwise male gonad. The reasons for this strange condition and its restriction to a small, phylogenetically related group of animals are, of course, unknown.

Curiously enough, although a long and varied series of investigations has grown up around this structure during the past seventy-five years, only twice has a comprehensive survey of its distribution been undertaken. Neither of these met with any great degree of success. Thus, Rau and Gatenby (1923) worked on material in the collections of the British Museum, but failed to examine the critical genera that would have given significance to their results. The more recent attempt of Stohler (1931), based on the collections of the Basel Museum, is obviously inaccurate, and his results have not been considered here. The present study, however, results in agreement with Rau and Gatenby. My primary purpose was therefore to extend the survey to genera not examined by these authors, thus giving a complete picture of the situation with respect to Bidder's organ in the genera of the families Bufonidae and Leptodactylidae, which had been combined as the Bufonidae by Noble (1922, 1931). A distinction between these two salientian families is re-established, with some rearrangement of the genera. In addition, a number of genera already examined by Rau and Gatenby have been dissected, including all but two of the Bufoninae and most of the Leptodactylinae (as defined by Noble), together with enough genera of other subfamilies to confirm definitely the absence of Bidder's organ in them. Thanks are due to Dr. Doris M. Cochran and the authorities of the United States National Museum for the privilege of examining a specimen of *Pseudobufo*, and to Mr. Arthur Loveridge and the Museum of Comparative Zoology for the loan of a series of oriental bufonids. In addition, I am under continued obligation to Mr.

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BIDDER'S ORGAN—DAVIS

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Karl P. Schmidt of Field Museum for advice and criticism throughout the course of the study.

### METHOD

Bidder's organ is a relatively small, and remarkably soft, structure lying far forward in the body cavity. It is more or less completely covered (viewing the animal from the ventral side) by the liver, stomach, and several intestinal loops. Consequently, the frequently employed practice of attempting to discover it through a small slit in the abdominal wall is dangerous and untrustworthy, particularly with small species. It is even more uncertain to try to work with females, unless they had recently ovulated or are sexually immature. This is true both because of the large size and fragile condition of the ovaries, and because Bidder's organ seems to be absent, at least occasionally, in sexually mature females of some species. Naturally, except when series are available, specimens of rare forms must be handled with care. Fortunately, most of the species examined in this study are represented in the collections of Field Museum by series, and in these instances an adult male was selected and the animal completely eviscerated, thus exposing the entire urogenital system. Otherwise a long slit was made in the abdominal wall and the digestive tract pulled out and fastened to one side. Ordinarily this permitted restoring the animal practically to its original condition, while still permitting an unobstructed view of the gonads. By pinning the animal in an extended position on a piece of balsa wood, examination could be made with ease, both hands being free for manipulation of instruments. A hand lens was used in examining the larger species, while the binocular microscope was used on the smaller forms.

### DISTRIBUTION OF BIDDER'S ORGAN

One or more specimens of each of the currently recognized genera of the Bufoninae have been examined, with the exception of the doubtful *Werneria*, which apparently is known only from the type. Unfortunately, the South African *Heleophryne*, which Noble (1931) recognizes as a distinct monogeneric subfamily, equivalent in rank to the Bufoninae, was also unavailable. Hoffman (1931) has described the anatomy of this form, but says of the testes only that they are "very small" and that they "more or less resemble those of *Crinia* in shape and size." The testes of *Crinia* are not elongated in the characteristic bufonid fashion. In addition, since Hoffman does

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not mention Bidder's organ in connection with the urogenital system of *Heleophryne*, it seems reasonable to assume that none is present in this genus. At least one genus of each of the other subfamilies has been checked, either in this study or by Rau and Gatenby.

I have dissected one or more specimens of each of the following genera and species:

Bidder's organ present: *Bufo americanus*, *B. bufo*, *B. carens*, *B. fowleri*, *B. leptopus*, *B. muelleri*, *Nectophrynoides vivipara*, *Pedostibes guentheri*, *P. hosii*, *P. signata*, *Pseudobufo subasper*.

Bidder's organ absent: *Cacophryne borbonica*, *Calyptocephalus gayi*, *Eleutherodactylus rugulosa*, *Engystomops pustulosus*, *Leptodactylus ocellatus*, *L. pentadactylus*, *Limnomedusa macroglossa* (from Misiones Territory), *Nectophryne afra*, *Physalaemus fuscomaculatus*, *Pleurodema bibronii*, *Pseudophryne guentheri*.

Rau and Gatenby (1923) examined the following genera:<sup>1</sup> *Borborocoetes*, *Bufo*, *Ceratophrys*, *Chiroleptis*, *Cryptotis*, *Eleutherodactylus*, *Helioporus*, *Hylodes*, *Hyperolia*, *Leptodactylus*, *Limnodynastes*, *Limnomedusa*, *Nectophryne*, *Pseudis*, *Pseudophryne*, *Rhinophrynus*, *Telmatobius*.

Among these genera they observed a Bidder's organ only in the several species of *Bufo* examined. It will be observed, however, that their results are in complete agreement with those presented here. In other words, they simply failed to examine those genera (*Nectophrynoides*, *Pedostibes*, *Pseudobufo*) that would have made their results taxonomically significant.

#### RELATIONSHIPS AS INDICATED BY BIDDER'S ORGAN

Noble (1922), after a critical examination of the characters that had been used in defining salientian groups, concluded that all would have to be discarded either wholly or in part if the families and genera were to represent natural groups, and not convenient but artificial assemblages. This view is, of course, needlessly pessimistic, since the exceptions cited indicate a need for caution and discrimination in evaluating these characters rather than wholesale rejection of all that fail to hold in every species involved. Few indeed of the characters so discarded have been found to be wholly without value. Nevertheless his highly critical analysis undoubtedly represented a distinct advance in the correct interpretation of the genetic affinities of these animals, although it left the group in a state of chaos

<sup>1</sup> As far as possible their nomenclature has been revised and brought up to date.

from which it has not yet been completely freed. Noble's attempt to reconstruct the classification on the basis of the vertebral column and thigh musculature resulted in a redefinition of the higher groups, but many of the family and generic relationships and allocations are still problematical. Parker's discovery that no less than sixteen microhylids have a procoelous, instead of a diplasiocoelous, vertebral column is disquieting, to be sure, particularly since Noble's analysis of the thigh musculature has not yet been confirmed and extended.

The bufonids had long been divided on the basis of presence and absence of teeth. After demonstrating the untenability of this character in defining natural groups, Noble was left without a basis for distinguishing the Bufonidae from the Leptodactylidae, and so merged both families into one, for which he retained the name Bufonidae. A consideration of Noble's conclusions in the light of the distribution of Bidder's organ is extremely interesting. Reference to the list on page 118 shows that, among the genera of Noble's subfamily Bufoninae, Bidder's organ is lacking only in the genus *Nectophryne*. Furthermore, it is not known to occur in a single member of any other group. The only apparent exception to this rule, besides *Nectophryne*, was in the case of the small East Indian toad that had long been known as *Bufo borbonica*. It has been shown, however (Davis, 1935), that *borbonica* actually has no relationship with the Bufoninae, but is, in spite of its toad-like external appearance, an atelopodid.

The case of *Nectophryne*, on the other hand, is not so easily disposed of. Partly because of lack of material for examination and comparison, I have been unable to find any character other than the absence of Bidder's organ to differentiate it from other genera of the Bufoninae. It is significant, however, that Parker (1931, p. 1247; 1934, p. 5) has also arrived at the conclusion that *Nectophryne* is not a bufonid. Apparently he is inclined to regard both *Nectophryne* and *Didynamipus* as atelopodids. Should this opinion be borne out, it would give a curiously extended distribution for this supposedly exclusively neotropical family, placing two genera (*Nectophryne* and *Didynamipus*) in Africa and a third (*Cacophryne*) in the East Indies. But even in the absence of other characters to bear out the supposition, I believe that the presence of Bidder's organ characterizes a group of such homogeneity that its absence in *Nectophryne* indicates that *Nectophryne* has heretofore been improperly allocated rather than that Bidder's organ is erratic in its distribution. Whether this is true or not, and what the proper

allocation of *Nectophryne* may actually be, must be left for further investigation.

If, then, *Nectophryne* is excluded from the Bufoninae, a group of forms remains in which the possession of a Bidder's organ seems to be a constant and exclusive feature. It is suggestive that certain leptodactylids show an elongation of the testes (fig. 9, A) similar to

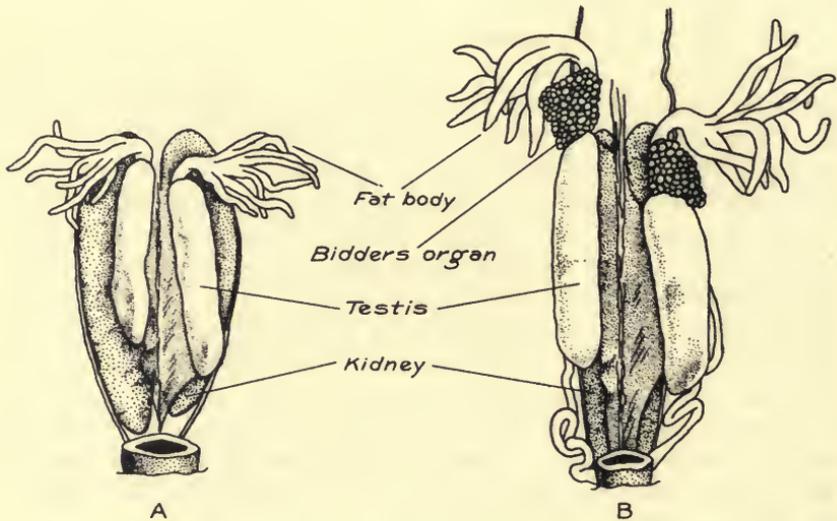


FIG. 9. Urogenital system of male toads. A. *Leptodactylus ocellatus*, showing elongation of the testes and absence of Bidder's organ. B. *Bufo americanus*, showing the typical bufonid urogenital system.

that of the genus *Bufo*. In other leptodactylids (*Physalaemus*) the testes are ovate, as in *Rana*. There is a possibility that further examination of the urogenital system in this group might yield interesting results. De Vos (1935) has recently examined the South African species of *Bufo* with reference to Bidder's organ. According to her description Bidder's organ presents an interesting condition in *Bufo carens*. The structure is highly aberrant, seemingly almost vestigial, although present in each of sixteen males examined. Field Museum has no adult specimens of this species, but I have examined a young male and found a well-developed Bidder's organ at the anterior end of the testis. The organ is usually better developed in juvenile animals than in adults. The situation described by de Vos is particularly interesting in view of Liu's (1935) statement that this is the only species of *Bufo* examined by him that had

a linea masculina. I have examined the pectoral girdle and found it typically bufonid.

If it can be demonstrated that Bidder's organ is paleogenic, non-erratic in its distribution and not duplicated in any other member of the Salientia, it is obvious that the Bufoninae embrace an unusually sharply defined group of species—a situation which is all too rare among the tailless Amphibia. In other words, Noble's reason for reducing them to subfamily rank (non-existence of a defining character) no longer remains. The reasons for believing that

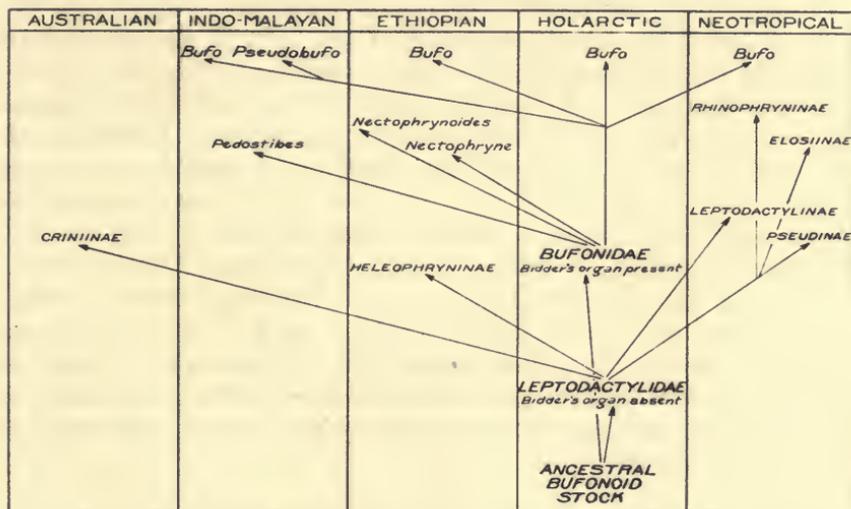


FIG. 10. Phylogenetic relations of the Bufonoidea, as indicated by the available anatomical and zoogeographic evidence.

Bidder's organ evolved but once, and once formed has persisted through all the vicissitudes of the group in which it originally appeared, will be outlined below. It will be shown also that Bidder's organ has existed since the middle of the Tertiary—i.e., that the Bufoninae arose from the bufonid stock at least as early as this. The lumping of all toads together in a single family certainly seems natural no longer, and the re-elevation of the Bufoninae to family rank is strongly indicated. The relations of the remaining forms are doubtful, pending further anatomical investigation. At present it seems best to refer them all to the family Leptodactylidae. The kinship of the Bufonidae and Leptodactylidae could then very easily

be expressed by including both families in a superfamily, the Bufonoidea. My understanding of the interrelationships of the bufonoid stock is shown in fig. 10.

It may be mentioned that the distribution of Bidder's organ justifies several rather arbitrary re-allocations of species that have recently been proposed. Thus, Noble (1926) removed the curious African species *vivipara* from the genus *Pseudophryne* and placed it in his newly erected genus *Nectophrynoides*, although he admits being unable to find any anatomical character to support this action. The correctness of his assumption is amply proved by the presence of a well-developed Bidder's organ in *vivipara* and its absence in the Australian species of *Pseudophryne*. Later (1931), the same author removed *Pseudophryne* (now strictly Australian) from close association with the genus *Bufo*, and placed it in the subfamily Criniinae of his extended family Bufonidae, again without justifying his action. While the presence in Australia of a single genus more closely related to *Bufo* than to the other Australian leptodactylid frogs would have been a startling zoogeographic enigma to any disciple of the Matthewsian school, the first actual proof that this was not a bufonine genus was forthcoming when it was demonstrated that it lacked a Bidder's organ. H. W. Parker's language indicates that he is somewhat diffident in removing *Nectophryne* from the Bufonidae of authors (Bufoninae of Noble). The absence of a Bidder's organ in this genus provides concrete evidence that his action was correct.

#### PHYLOGENY OF BIDDER'S ORGAN

The foregoing data on the distribution of Bidder's organ, when considered in connection with certain well-known factors of animal distribution, make possible several interesting deductions as to the phylogenetic history of this structure. The presence of a Bidder's organ has already been accepted as evidence of kinship among a group of salientian species which, in the aggregate, covers a good share of the earth's surface. This thesis cannot, of course, be summarily reversed and used as a basis for sweeping deductions as to the phylogeny of the structure in question. Fortunately, the case for the monophyletic origin of the Bufonidae by no means rests solely on the possession of a Bidder's organ. In this connection it need only be mentioned that the Bufonidae have long been recognized as a taxonomic unit on the basis of other (chiefly osteological) characters. Most differences of opinion have arisen from the

fact that each of these characters has been weakened by the discovery of exceptions among the outlying members of the group, thus making difficult or impossible a concise and accurate diagnosis of the family. The naked skin and undifferentiated dentition characteristic of all salientians having deprived taxonomists of two of the most widely used taxonomic characters, a host of parallels to this situation is found throughout the Class Salientia. If, then, Bidder's organ *confirms*, rather than establishes, the phylogenetic unity of the Bufonidae, we may attempt with some degree of confidence a synthesis of the anatomical and zoogeographical evidence that bears on the history of Bidder's organ. A consideration of these combined data is extremely interesting and suggestive.

The probability of a holarctic origin of the primary bufonoid stock (=Bufonidae+Leptodactylidae) has never been contested. The Bufonidae probably originated from this bufonoid stock in Asia, whence they have spread southward into the Indo-Malayan and Ethiopian regions. The more recent *Bufo* has subsequently invaded all zoogeographic regions except the Australian. Two features characterized this group. The first was the loss of maxillary teeth, in which it was paralleled on several occasions in other more or less distantly related groups, while the second was the peculiar modification of the urogenital system that resulted in the production of Bidder's organ. This modification does not seem to have taken place in any other group. There is abundant evidence to show that the Bufonidae and Leptodactylidae are offshoots of a common stem. While it is highly improbable that the Leptodactylidae themselves represent a natural group, this fact does not materially affect the picture. With respect to Bidder's organ, we are faced with alternative possibilities. Either it was present in the postulated bufonoid stem stock and has persisted in the Bufonidae, in which case the urogenital system of the Leptodactylidae would have been modified from the ancestral type, or Bidder's organ was one of the anatomical modifications which marked the divergence of the Bufonidae from the ancestral stock. Again, the significance of the elongation of the testes in certain leptodactylids cannot be lost sight of. The distribution of Bidder's organ in modern forms shows conclusively that there are no other possibilities that fit the known facts. Its presence in all members of the Bufonidae shows that it must have characterized this family from the beginning. On the whole, the evidence strongly favors the view that Bidder's organ originated with the Bufonidae, and this view will be adopted here.

An arciferal condition of the shoulder girdle is usually regarded as a "primitive" character, but it seems likely that the Bufonidae represent a comparatively recent development. This is certainly true of the genus *Bufo*. In the New World, where the evidence is most clear, the situation is quite simple. The Leptodactylidae, or the ancestral stem stock from which they have been derived, probably occupied North America in the late Mesozoic and were swept into Central and South America along with the rest of the typically Neotropical fauna at the beginning of the Tertiary. The Bufonidae (represented in this region only by the genus *Bufo*) subsequently invaded North America from the west and pushed southward into South America during the invasion of that continent by the Holarctic fauna that recurred in the Pliocene. If these faunal movements took place at the same time as those of mammals (and there is no reason to suppose otherwise), we may justifiably assume that Bidder's organ was already well differentiated by the middle of the Tertiary.

The reasons for the origin and persistence of this structure are unknown. It may have arisen, perhaps genetically associated with some structure having definite survival value, as a wholly negative physiological element, and have persisted for the same reason. It is not a vestigial or "atavistic" organ, as has been suggested.

The distribution of the Bufonoidea, as already pointed out by Noble (1926), affords no evidence whatever in favor of the existence of trans-oceanic land bridges. The distribution of this group coincides perfectly with the principles laid down by Matthew in his "Climate and Evolution."

#### SUMMARY

A number of bufonid genera were examined for the presence or absence of Bidder's organ. It was found in all genera of Noble's subfamily Bufoninae, with the single exception of the African genus *Nectophryne*. It was lacking in all other genera examined. The Bufoninae are therefore raised again to family rank, and the family Leptodactylidae reinstated. *Nectophryne* is provisionally referred to the Leptodactylidae.

All available evidence indicates that Bidder's organ evolved along with the family Bufonidae. The zoogeographic evidence shows that this took place during the Tertiary. The *Bufo*-like elongation of the testes in certain leptodactylids, and its possible significance, is pointed out.

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