A STUDY OF THE URINOCENTAL SYSTEM
OF SALIENTIA

By

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that the urinogenital organisation was essentially of the Ranid type with the exception of the male Chiromantis xerampelina. The modification of the Wolffian duct was compared with that of Cryptobranchus and considered to be a primitive character. Further observations on the modification of the Wolffian duct in the male of Ch. xerampelina are presented in a recent monograph (Hoffman, 1942.) He is in full agreement with my findings, and supports my view that the modification of the Wolffian duct can be correlated with the breeding habits. He has added also some comparative notes on other species. In a further contribution (Hoffman, 1943) he has dealt with the question of the site of production of the mass of secreted material that is found in the modified male Wolffian duct of these tree-frogs.

Eggert (1926), Witschi (1933), Koch (1933-34) and Horie (1938) all studied the urinogenital organs of several species of Bufo, but their main interests were focussed on Bidder's organ. Among them, however, Koch appears to have studied this system fairly fully. The other three authors have given quite an exhaustive review of the history of several phases of researches on Bidder's organ. Eggert (1926) gave also an exhaustive review of the rudimentary Müllerian ducts in males of Bufo, and noted their seasonal variation in B. bufo. According to him the ducts, like the oviducts in the
female, are provided with a secretion during the breeding season, which is afterwards resorbed. He is, however, vague about their opening into the cloaca.

Rau and Gatenby (1923), Stohler (1931-32) and Davis (1936) studied the distribution of Bidder's organ in Salientia. Davis writes: "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." Davis has, however, extended Rau and Gatenby's survey of Bidder's organ in the genera of the Bufonidae (sensu Noble 1931). The examination of the critical genera has led him to raise Noble's sub-family Bufoninae to a full family rank, and the family Leptodactylidae (which, according to him, includes also Rhinophrynus) is reinstated with some rearrangement of genera. Further, he notes: "It is suggestive that certain leptodactylids show an elongation of the testes similar to 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 Villiers (1934) has made a valuable contribution to the 'pelvic complex' of a male *Ascaphus truei*. The so-called 'tail' is, according to him, a true phallic organ. In this connection he makes some interesting observations on the urino-
genital ducts of the male. For the first time he observed a urinogenital sinus in the Salientia.

Bhaduri and Banerjee (1939) studied the morphological relation of the Wolffian and Müllerian ducts in Bufo melanostictus and after reviewing the observations of Eggert (1926) and Koch (1933-34) and others claimed that the Wolffian ducts coalesce just before opening into the cloaca, and the persistent Müllerian ducts of males end blindly in a cloacal papilla.

Al-Hussaini (1939) studied the Egyptian toads which do not show anything of interest, and made no mention of the vestigial Müllerian ducts of males.

Rugh (1941), describing the reproductive physiology of the male spring peeper Hyla crucifer, considers its urinogenital organisation to be more like that of the frog (Rana) than the toad (Bufo). According to him the seminal vesicle is a slight enlargement and thickening of the walls of the most posterior section of the Wolffian duct just before it enters the cloaca. It acts not only as a storage place for spermatozoa but also as a copulatory accessory.

Bhaduri and Rudra (1944) described the urinogenital organs of a narrow-mouthed frog Microhyla ornata and observed a 'Wolffian sinus' in this species.

It is clear from this brief review that very few authors have studied in detail the openings of the Wolffian and Müllerian ducts into the cloaca.
Studies on the distribution of the persistent Müllerian ducts in males of several species of Salientia have been made in fair detail, but their actual relation to the cloaca has not in general been described. Moreover, it may be pointed out that inadequate attention has been paid to the uterine union, nor has the nature of its opening into the cloaca been properly studied. It is only very recently that the question of the occlusion of the uterine opening into the cloaca after spawning has been raised by me (Bhaduri, 1946.) Previous workers have not examined the urinogenital organs in the light of the breeding habits except Bhaduri (1932) followed by Hoffman (1942.) For these reasons the present investigation has been undertaken.
MATERIAL AND METHODS

Members of every family of the Salientia have been examined with the exception of the Discoglossidae, Pipidae and Atelopodidae. These three families were omitted from the study, since descriptions of the urinogenital organs were already available (Spengel, 1876; Grönberg, 1894; Boulenger, 1896; Gadow, 1901; Gilchrist and von Bonde, 1922; Boonacker, 1927) or no material was obtainable.

The material of this study consists of thirty-four species belonging to twenty genera and eleven families. The sources from which the species were obtained and other relevant information are acknowledged in each case. Eleven species are represented by both sexes, ten species by females only and thirteen species by males only.

Both sexes of:

- *Ascalaphus truei* Stejneger
- *Scaphiopus couchii* Baird
- *Scaphiopus holbrookii* (Harlan)
- *Eleutherodactylus nubicola* Dunn
- *E. alticola* Lynn
- *Leptodactylus podicipinus* (Cope)
- *Pleurodema cinerea* Cope
- *Dendrobates tinctorius* (Schneider)
- *Phyllobates nubicola flotator* Dunn
- *Phyllomedusa dacnicolor* Cope
- *Gastrotheca boliviana griswoldi* Shreve

Females only of:

- *Megophrys parva* (Boulenger)
- *Eleutherodactylus orcutti* Dunn
- *Leptodactylus melanophrys* (Hallowell)
- *L. pentadactylus* (Laurenti)
- *Heleophryne purcelli* Sclater
In order to obtain a proper knowledge of the urinogenital organs I have tried to secure sexually mature or adult specimens of each species. It is well known that the reproductive organs are fully developed only during the breeding season, but in spite of this a few only turned out to be sexually immature. Most of my material was preserved in spirit or formalin. In several cases the cloacal parts were not well preserved, but suitable for the study of the topographical anatomy. I have to express my special debt of gratitude to Prof. James R. Slater, who, at my request, collected the rare Ascaphus material.

The urinogenital organs were examined after careful dissection and removal of other visceral organs. The topographical anatomy of several parts were examined under the binocular microscope.
Special attention was paid to the course and fate of the urinogenital ducts in the cloaca. The method of examining the opening of ducts into the cloaca by means of a probe or coloured injection was rejected for obvious reasons. An erroneous conclusion will inevitably result from such a method, especially in the case of smaller species. Instead, serial sections were cut of the urinogenital ducts of all species. To do this the hind gut with the accompanying urinogenital ducts was carefully dissected out from the pelvic complex under the binocular microscope. Following dehydration and embedding in paraffin by standard technique, transverse sections were cut at 10 \mu and stained with haematoxylin and eosin. Permanent preparations were mounted in Canada balsam. A few kidneys with the associated ducts were also sectioned for investigation of special points.
I am indebted to the following persons for the material used during the present investigations.

The late Dr. T. Barbour and Dr. A. Loveridge (for specimens from the Museum of Comparative Zoology, at Harvard College, Cambridge, Massachusetts (M.C.Z.)); Dr. Charles M. Bogert (for specimens from the American Museum of Natural History, New York, (A.M.N.H.)); Dr. K. P. Schmidt and Dr. C. H. Pope (for specimens from Chicago Natural History Museum, Chicago, (C.N.H.M.)); Prof. C. H. de Villiers and Dr. C. A. du Toit (for specimens from the Zoological Institute, Stellenbosch, South Africa, (S.I.)); Dr. W. G. Lynn (for specimens of Eleutherodactylus from his own collection, the Catholic University of America, Washington, D.C.); the Director (for a specimen of Megophrys parva, Zoological Survey of India, Indian Museum, Benares Cantt., (Z.S.I.)); Prof. James R. Slater (for the rare Ascaphus material, College of Puget Sound, Tacoma, Washington); Mr. D. Mukerji, my colleague in the University of Calcutta, for the specimen of male Uperodon globulosum; and Mr. Subrata Bhattacharya, my pupil in the University of Calcutta, for a specimen of Rhacophorus bimaculatus. The source of origin of each specimen is acknowledged at the beginning of the description. To all of them I tender my sincerest thanks.

I am grateful to Dr. H. W. Parker of the British Museum (Natural History) for much help in the
systematic treatment of the species dealt with in this paper. I wish to thank Dr. R. A. R. Gresson, and Dr. D. M. Steven, Department of Zoology, University of Edinburgh, for rendering me help in various ways in my studies, and also Mr. R. J. Fant, Chief Technician, Department of Zoology, University of Edinburgh, for the photomicrographs illustrating this paper.

The work was carried out entirely in the Department of Zoology, University of Edinburgh. It is a great pleasure to express my indebtedness to Professor James Ritchie for granting me facilities to work in his laboratory, for securing some material for my studies, for taking a keen interest in my work and for making helpful suggestions.

Lastly, I wish to thank the authorities of the University of Calcutta, for granting me a Ghosh Travelling Fellowship which enabled me to carry out this work in the Department of Zoology, Edinburgh University.
TERMINOLOGY

It is necessary to give a brief explanation of the terminology used in this paper. I have in general adopted the terminology currently used in standard text-books. The terms are used either in their original form, or their English equivalents. Since a certain amount of confusion exists in some cases, it is advisable to define more clearly the following:

1. The Wolffian duct:- The duct which proceeds from the kidney to the cloaca carrying urinary or urinogenital products has been called the Wolffian duct. In the literature the most currently used designation for the duct from the kidney of the female is the 'ureter' (Harnleiter) and that of the male is the 'urinogenital duct' (Harnsamenleiter). Some authors have used the former term for the duct of the male (Haslam, 1889; Boulenger, 1896; O'Donoghue, 1920; Gilchrist and von Bonde, 1922; Holmes, 1927; Lloyd, 1928; and others), whereas some have called it the 'vas deferens' (= Harnsamenleiter) as an alternative to the ureter (Marshall, 1912; O'Donoghue, 1920; Koch, 1933-34). Gaupp (1904, pp.235-36) in advocating the term 'ductus deferens' makes the following comments: "Der hintere Theil des ursprünglichen Vornierenganges bleibt als Ausführungsgang der bleibenden Urniere
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Gaupp's terminology is used only by some German authors (Werner, 1930; van den Broek, 1933). Bhaduri and Banerjee (1939) prefer to call it the 'urinogenital (Wolffian) duct.' Borradaile (1938) uses the 'Wolffian duct' for both sexes, and points out in a footnote on p. 76 that it is "often called ureter, although it does not correspond to the ureter of man." The Wolffian duct is the name adopted from the embryology, and owing to certain modifications in function in the two
sexes, the different terminologies, stated above, probably came into vogue. While not contending Gaupp's terminology 'ductus deferens', I prefer to call it by the embryological term Wolffian duct. In males it may be called the Wolffian (urinogenital) duct in order to distinguish it from the female duct, but this is too long for everyday convenience.

2. The seminal vesicle or vesicula seminalis:-

The part of the male Wolffian duct which is dilated or provided with a glandular chamber for storing sperms is designed the vesicula seminalis. This term is widespread in the literature, although in strict sense it ought not to be used, if we accept the view of Gaupp (1904, p.261) who states: 'Mit dem Vesiculae seminales der Säuger sind die Samenblasen des Frosches weder functionell noch morphologisch zu vergleichen.'

3. The Müllerian duct:- This is undoubtedly the oviduct of the female, but it is well known that remnants or vestiges of this duct persist in some degree of development in males of many Salientia. The earlier authors considered that this duct opens into the Wolffian duct and functions as a reservoir for sperms. They described it under a confusing variety of names, such as, "Samenblase" (von Rosenhof 1758; Bidder, 1846), "Samenleiter" (Rathke, 1825; Muller, 1830; Burrow, 1834), "Canal déférent
accesoire, sorte de diverticulum" (Lereboullet, 1851), "Ueberrest des Ausführungsganges der Müllер-Wolfschen Drüse (von Wittich, 1853a) etc. Spengel (1876) called this "männliche Tube", and described this structure correctly for the first time in Bufo bufo as not opening into the Wolffian duct. Disselhorst (1904) gave a diagram of the urino-genital apparatus of B. bufo in which he named the duct "Ductus deferens"; he described its caudal part (which is, in fact, the slightly dilated portion of the Wolffian duct) as "zur Samenblase entwickelte Ampulle desselben." Gaupp (1904) calls it rightly 'Die Müllerschen Gänge.' Eggert (1926) followed the mammalian terminology and called it 'uterus masculinus.' Some authors called it by the English equivalent 'oviduct' (Witschi, 1933; Horie, 1938). Koch (1933-34) adopted Spengel's terminology 'männliche Tube.' However, a few authors have stated correctly that it does not open into the Wolffian duct and named it (remnants of or vestigial) Müllerian duct (Gaupp, 1904; Noble, 1931; Bhaduri and Banerjee, 1939). Since this duct corresponds to the Müllerian duct in development, I prefer to retain this name.

4. The uterus:- It is well known that the Müllerian duct or oviduct is divided into four sections, viz., ostium abdominale, pars recta, pars convoluta, and uterus (Gaupp, 1904). No objection
seems to have been taken to the first three terms. The use of the term 'uterus' has, however, given rise to considerable confusion. Some early authors who described this structure often wrote 'uterus' within inverted commas, while others have objected to the use of this term (Spengel, 1876; Hoffman, 1873-78; Boulenger, 1896). Nevertheless, the term has survived. There appears to be, however, a tendency to abandon it in recent years. A few writers have totally discarded the term 'uterus' and substituted it by 'ovisac' (Marshall, 1912; O'Donoghue, 1920; Gilchrist and von Bonde, 1922; Al-Hussaini, 1939; Ritchie, 1944). It may be true that according to the strict definition of the term, 'uterus' is inadequate, but, we must remember that anatomical terms should be used from the point of view of anatomical relationships or homology, and not in relation to their functional importance. The development of the Müllerian duct of vertebrates is not completely known (Goodrich, 1930). It is, therefore, difficult to homologize the dilated posterior section of the Salientian oviduct with the mammalian uterus. It is curious that nobody seems to have urged any objection to using the term 'uterus' in viviparous lower vertebrates, viz., some fishes and reptiles. It will also be seen that in a general way it is customary to use this term for the dilated posterior part of the oviduct in the
vertebrate series irrespective of the function it subserves. In Amphibia, especially Salientia, it is no doubt mainly concerned with holding the eggs prior to spawning, but attention may be directed to the case of the African viviparous toads, Nectophrynoides, in which development and metamorphosis take place within this dilated chamber (Noble, 1927, 1931; Angel and Lamotte, 1944). While I do not advocate the use of this term, if it is not homologous with the true uterus, I do not see any advantage in replacing it by 'ovisac', which may also be used in the sense of a "closed ovary" as in some fishes (vide Goodrich, 1930, p.704). Unsatisfactory as it may be, it is expedient in the present state of our knowledge, to retain the name 'uterus' as has been done by so many authors, both early and recent.
Below is a list of species of frogs and toads investigated by previous authors (Spengel, 1876; Beddard, 1907-11; Rau and Gatenby, 1923; and others) the names of which have undergone considerable changes. For example, the common toad called Bufo cinereus by Spengel was more usually known as Bufo vulgaris, but is now established as Bufo bufo (Linn.) Unfortunately these authors did not pay adequate attention to the names of species, nor did they record the locality of the specimens they dealt with by which proper allocation could be made subsequently. Even if material is identified by expert systematists, citation of the locality, or, if the specimen is preserved, details of its whereabouts, should be needed in order that the original identification may be amended, if need be, in the light of later taxonomic findings. For instance, Rau and Gatenby (1923) examined the British Museum material, and among other species they reported on "Helioporus pictus", but it has since been discovered that this "species", as understood in 1923, was a composite of two distinct forms, Heleioporus pictus and H. centralis, but it is now impossible to determine which of these two the authors examined. Similarly it is difficult to place Spengel's Bufo americana and B. scaber (vide infra, List.) These uncertain identifications are a hindrance not only to
systematists in evaluating the anatomical work, but also to anatomists who cannot with certainty compare their own findings with those of previous authors. Moreover, the allocation of species to their proper families is often difficult, since the classification of families of Salientia is still in turmoil, and there are some species which are still tossing from family to family. To the students of anatomy this is very disturbing, but must be accepted as inevitable, since taxonomic certainty is not to be expected. For this reason and also to place the works of previous authors in the perspective of up-to-date nomenclature, an attempt has been made to provide the following species with the accepted nomenclature in current literature. In the preparation of the following list I have been largely helped by Dr. H. W. Parker, of the British Museum (Natural History.)
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<td>Pipa pipa (Linn.).</td>
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<td>P. americana</td>
<td>P. pipa (Linn.).</td>
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<td>Dactylethra capensis</td>
<td>Xenopus laevis (Daudin).</td>
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<td>Megophrys montana (Gravenhorst).</td>
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<td>M. hasselti (Tschudi).</td>
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<td>Xenophrys monticola</td>
<td>M. monticola (Günther).</td>
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<td>Megalophrys</td>
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<td><strong>BUFONIDAE</strong></td>
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<td>B. americanus Holbrook, and/or, B. terrestris (Bonnaterre).</td>
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<td>B. cinereus</td>
<td>B. bufo (Linn.).</td>
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<td>B. intermedia</td>
<td>B. intermedius Günther.</td>
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<tr>
<td>B. maculiventris</td>
<td>B. marinus Linn.</td>
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<td>B. ornatus</td>
<td>B. crucifer Wied.</td>
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<tr>
<td>B. musculus</td>
<td>B. terrestrius (Bonnaterre).</td>
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<tr>
<td>B. scaber</td>
<td>B. crucifer Wied., or B. granulosus Spix possibly.</td>
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<td>B. viridis Laur.</td>
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<td>B. vulgaris</td>
<td>B. bufo (Linn.).</td>
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<td>Crinia georgiana Tschudi.</td>
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<td>Limnodynastes dorsalis grayi (Steindachner.)</td>
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<td>Pseudophryne bibronii Günther</td>
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<td>? Telmatobius acmaricus (Cope.)</td>
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<td>Cacopus systoma</td>
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<td>Hypopachus variolosus (Cope).</td>
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<td>Uperodon systoma (Schneider).</td>
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Text-fig. 1. - Diagrammatic ventral view of the urinogenital organs of a male *Ascaphus truei* (right testis with fat-bodies not shown). X 6.

(For Key to letterings in this and subsequent figures in the plates see p. 198)
Since Spengel's (1876) publication on the comparative anatomy of the urinogenital system of Salientia, no attempt has been made to survey the group in the light of recent knowledge of this system. Such, for instance, are the terminal union of the Wolffian ducts before they open into the cloaca of Xenopus (Gilchrist and von Bonde, 1922) and Bufo melanostictus (Bhaduri and Banerjee, 1939); the occurrence of a urinogenital sinus in Ascappus truei (de Villiers, 1934) and in Microhyla ornata (Bhaduri and Rudra, 1944); the course and fate of the vestigial Müllerian ducts in males of some species of Bufo (Koch, 1933-34; Bhaduri and Banerjee, 1939), the correlation between the modified Wolffian ducts and the breeding habits of Rhacophorus and Chiromantis (Bhaduri, 1932; Hoffman, 1942) etc. The present investigations were designed to obtain further knowledge of the urinogenital system of the Salientia in the light of the work cited above, and to ascertain whether there exists any correlation between these organs and the breeding habits of the animals. Thirty-four species, belonging to twenty genera have been investigated; in most of these species and eleven of the genera the urinogenital system is now described for the first time.

Roesel von Rosenhof (1758) was probably the first to describe the urinogenital system of Salientia.
OBSERVATIONS

Liopelmidae

*Ascaphus truei* Stejneger.

**MALE:** 41.5mm. from snout to vent.

Loc. Outlet stream of Lake George, Rainier National Park (Pierce County, Washington, U.S.A.)

Date. August 22, 1929.

Coll. and source. Prof. James R. Slater.

(Text-fig. 1; Pl. I, figs. 1-7.)

The kidneys (K.) are greatly elongated bodies, dull whitish in colour. The right kidney measures 15.3 X 2.8mm. and the left kidney 15.0 X 2.7mm. They are much flattened dorso-ventrally; the ventral surface is flat except at the anterior end, while the dorsal surfaces are slightly convex. The anterior and posterior ends are narrow and more or less pointed. The posterior half is much broader transversely and its outer edge broadly convex. The kidneys are broadly diverging anteriorly.

The testes (T.) are large white oval bodies, much broader than the kidneys. They are unpigmented and loosely held to the middle of the kidneys by the mesorhia through which pass six or eight vasa efferentia. The right testis measures 7.8 X 4.6mm., and the left 8.3 X 4.4mm. The fat-bodies are attached to the testis and possess three long finger-like processes.

Careful examination shows that both the Wolffian
and Müllerian ducts are present. The Wolffian duct (W.d.) arises from the anterior end of the kidney and runs along its outer edge. The Müllerian duct (M.d.), however, begins more anteriorly. It is a white flattened tube extending forward as far as the roots of the lungs. It adheres to the outer edge of the kidney and runs close to, and parallel with, the Wolffian duct. It gradually diminishes in diameter posteriorly, whereas the Wolffian duct increases in diameter. The relation of the two ducts are best seen in sections (figs. 1 and 2, W.d. and M.d.). The Müllerian duct gradually disappears posteriorly and could not be traced beyond the posterior part of the kidney. Towards the posterior end of the kidney, the Wolffian duct assumes a definite shape. It becomes stouter and its wall is composed of two or three layers of cells. After leaving the kidneys the two ducts approach each other (fig. 3, W.d.) and towards their posterior ends are encapsuled in a common sheath of connective tissue (fig. 4, W.d.). In this capsule, which may be described as a urinogenital capsule, the remnants of the Müllerian ducts appear again (fig. 4, M.d.). They lie ventrolaterally to the Wolffian ducts. But the Müllerian tissue cannot be discerned in the free portions of the Wolffian ducts, and, in fact, appears to be absent. In the urinogenital capsule the tip of the diverticulum which is given off from the cloaca
appears to be situated between the Wolffian ducts above and the cloaca below (fig. 4, U.S.). About 30 sections posterior to fig. 4, this diverticulum surrounds the Wolffian ducts in an inverted horseshoe-shaped canal (fig. 5, U.S.). The remnants of the Müllerian ducts (fig. 5, M.d.) are still seen in these sections, but disappear further posteriorly. The urinogenital capsule gradually comes to lie upon the outer wall of the cloaca. The Wolffian ducts in the meantime coalesce with each other and form a common Wolffian duct (fig. 6, W.d.). The diverticulum opens into the cloaca at this level. The dorsal wall of the diverticulum enclosing the common Wolffian duct forms a urinogenital papilla in the cloaca; about 6 sections posteriorly, the common Wolffian duct opens at its top (fig. 7, W.d.). The common Wolffian duct is very short, 0.40mm. (40 sections) long. The diverticulum is incorporated within the cloaca and persists for some distance as a dorsal ridge within the latter.

The diverticulum represents the urinogenital sinus described by de Villiers (1934). It is given off from the mid-dorsal wall of the cloaca and only half a millimetre in length, running anteriorly above the cloacal wall in the form of a U-shaped structure within the urinogenital capsule.

There is a lumen in the Müllerian duct at the anterior end (figs. 1 and 2, M.d.); it is lined by a
single layer of cells surrounded by a thin sheet of connective tissue. In the urinogenital capsule area (figs. 3 and 4, M.d.) the duct appears between the Wolffian ducts and the sinus, a minute lumen is seen in some sections.

In its anterior portion the Wolffian duct consists of one or two layers of endothelial cells. Towards the posterior region of the kidney there are three or four layers of cells surrounded by a few muscle fibres. After leaving the kidney the Wolffian duct is provided with a connective tissue layer which thickens posteriorly to form the urinogenital capsule. In this region the Wolffian duct consists of two or three layers of cells, but the endothelial lining of the sinus is three or four layers deep.

As mentioned above the urinogenital papilla runs for a considerable distance within the laterally compressed cloaca. The latter extends into the 'tail' which has been described as a phallic organ (de Villiers, 1934.) In this region of the cloaca there are a number of tubular glands on its ventral wall. The structure of the 'tail' has been elaborately described by de Villiers and need not be repeated here.

The urinary bladder (Text-fig. 1, U.B.) is thickish and moderately extensive. It opens ventrally opposite the opening of the urinogenital sinus.
Text-fig. 2. - Diagrammatic ventral view of the urinogenital organs of a female Ascaphus truei (right ovary with fat-bodies not represented.) X 5.
**FEMALE**: 40.0mm. from snout to vent.

**Loc.** Olympic Hot Springs, Olympic National Park, Clallam County, Washington, U.S.A.

**Date.** September 3, 1939.

**Coll. and source.** Prof. James R. Slater.

(Text-fig. 2, Pl. II, figs. 8-13.)

The kidneys (K.), as in the male, are elongate and extend as far forward as the oesophagus. The measurements are: the **right** kidney 13.6 X 2.0mm., and the **left** kidney 13.1 X 2.2 mm. The anterior ends are rounded and the posterior ends are somewhat narrow. The outer edge is more or less straight and the posterior half is no broader transversely than in the male.

The ovaries (O.) which do not appear to be fully mature are comparatively small in size and held to the middle of the kidneys by the mesovaria. Each is a compact mass consisting of a single sac, not thrown into lappets. It contains ova of different sizes; larger ones are cream-coloured and the smaller ones whitish. A large ovum measures 1.3mm. in diameter. The fat-bodies (F.B.) are long flattened finger-like processes, three or four in number, given off from the anterior end of the ovary.

The Wolffian duct arises from the anterior end as a white cord which increases slightly in diameter at the level of the posterior part of the kidney. As it leaves the kidney it passes dorsally over the uterus (U.). The oviduct (M.d.) does not appear to be
well developed, since it is not greatly convoluted. A long pars recta follows from the ostium abdominale which, as is usual, opens at the roots of the lungs. It is slightly convoluted at the level of the middle of the kidney. The uterine segment (U.) begins at the posterior level of the kidney and is not dilated into a thin sac as in other frogs and toads. It is narrow and passes ventrally over the Wolffian duct. It is provided with longitudinal folds having a glandular epithelial wall (fig. 8, M.d.). The uteri with the Wolffian ducts approach one another mesially, and, as they meet, the connective tissue surrounding the ducts forms a continuous sheet which constitutes a urinogenital capsule, as in the male, and in which appears the tip of the urinogenital sinus (fig. 9, U.S.). The Wolffian ducts approach each other in the capsule, and the urinogenital sinus extends laterally; the uteri which are at first situated laterally, (fig. 9, M.d.) come to lie between the sinus below and the Wolffian ducts above (fig. 10, M.d.). In this region the Wolffian ducts unite forming a broad transverse canal (fig. 10, W.d.). Figure 10 shows that the sinus has expanded laterally and vertically, and the uteri are reduced to mere narrow tubes with no longitudinal folds. The urinogenital capsule is applied to the cloaca, and from this region the sinus assumes a characteristic form quite unlike that of the male in having ventro-lateral pouches. In this region it establishes a
connection with the cloacal lumen (fig. 11, U.S.). As the uterine tubes approach each other and fuse together, they are enclosed by the common Wolffian duct (fig. 11, M.d.). A secretory mass was found in the fused lumina of the uteri. Immediately afterwards the common Wolffian duct opens into the sinus, while the common uterus remains occluded (fig. 12, W.d. and M.d.). No opening from the uterus into the sinus was found in the series of sections. The whole of the urinogenital sinus is incorporated into the cloaca forming a dorsal papilla within it as in the male. The cloaca in this region is laterally compressed and provided with a few special glands (fig. 13, Gl.).

The urinogenital sinus is a minute structure measuring about a millimetre in length. It is slightly larger than that of the male. The common Wolffian duct runs for about 0.75mm. before opening into the sinus. The united portion of the uteri is still shorter than the common Wolffian duct.

The urinary bladder is similar to that of the male, and opens ventrally into the cloaca when the urinogenital sinus is fully incorporated within the cloaca (fig. 13, U.B.).
EXPLANATION OF PLATE I.

Ascaphus truei Stejneger.

(Male.)

Photomicrographs from a series of transverse sections passing through the kidney region (figs. 1 and 2) and of the gut with the urinogenital ducts behind the kidneys (figs 3-7.)

Fig. 1.- Showing the Müllerian and Wolffian ducts (M.d. and W.d.) in the anterior region of the kidney (K.) X 45.

Fig. 2.- Same as above, in the posterior region of the kidney. The Müllerian duct (M.d.) before disappearing. X 45.

Fig. 3.- Showing the Wolffian ducts (W.d.) after leaving the kidneys. X 45.

Fig. 4.- (0.66mm. after fig. 3.) Showing the Wolffian ducts (W.d.) and the appearance of the urinogenital sinus (U.S.) in the urinogenital capsule. The vestigial Müllerian duct (M.d.) is also evident. X 45.

Fig. 5.- (0.29mm. after fig. 4.) Showing the horse-shoe-shaped urinogenital sinus (U.S.) enclosing the Wolffian ducts (W.d.); the Müllerian duct (M.d.) persisting still as vestige. X 45.

Fig. 6.- (0.34mm. after fig. 5.) Showing the common Wolffian duct (W.d.) and the opening of the urinogenital sinus (U.S.) into the cloaca (C1.); the Müllerian duct completely disappeared. X 45.

Fig. 7.- (0.09mm. after fig. 6.) Showing the opening of the common Wolffian duct (W.d.) into the urinogenital sinus (U.S.). X 45.

(For key to letterings in this and subsequent plates see p.198).
He gave a diagram of *Bufo calamita* in his *Historia naturalis ranarum nostratium.*

Prior to Spengel (1876) several authors had attempted comparative studies of the urinogenital system (Rathke, 1825; Müller, 1830; Burrow, 1834; Bidder, 1846; Lereboullet, 1851; Leydig, 1853; von Wittich, 1855), but their main attention was directed to Bidder’s organ of *Bufo.* Most of these authors noticed also the remnants of the Müllerian duct in males of *Rana* and *Bufo,* and showed the duct to be united with the anterior free portion of the Wolffian duct, but interpreted it incorrectly as the "seminal vesicle" (Samenleiter, Samenblase.)

Spengel was probably the first to give a fairly complete account of the comparative anatomy of the urinogenital organs of Salientia. He investigated some thirty-two species of frogs and toads including members of practically all the families of Salientia. He examined ten species of living animals of both sexes, the remainder one sex only, preserved in spirit. His list includes most of the species investigated by previous workers. Concerning the Wolffian duct he noted: "Eine Vereinigung der Lumina aber habe ich in keinem Falle beobachtet." He observed also separate openings of the Müllerian ducts (uteri) into the cloaca in all the species, excepting *Bufo* and *Alytes obstetricans* and possibly *Hyla.* According to him the rudimentary Müllerian ducts (= männliche Tube) are present in males of some species, but, in spite
EXPLANATION OF PLATE II.

Ascaohus truei Stejneger.

(Female.)

Photomicrographs from a series of transverse sections through the urinogenital ducts behind the kidneys. Figs. 9-13 represent terminal parts of the ducts in their relation to the cloaca.

Fig. 8. - Showing the Müllerian (uterine portion) and Wolffian ducts (M.d. and W.d.) behind the kidneys. X 33.

Fig. 9. - (1.13mm. after fig. 8.). Showing the Müllerian (uterus) and Wolffian ducts (M.d. and W.d.) in the urinogenital capsule in which the urinogenital sinus (U.S.) appears. X 33.

Fig. 10. - (0.44mm. after fig. 9.). Showing the confluence of the Wolffian ducts (W.d.); the Müllerian (uteri) ducts (M.d.) reduced to narrow tubes and the extension of the urinogenital sinus (U.S.). X 33.

Fig. 11. - (0.26mm. after fig. 10.). Showing the confluence of the uteri (M.d.) and the opening of the urinogenital sinus (U.S.) into the cloaca (Cl.). X 33.

Fig. 12. - (0.13mm. after fig. 11.). Showing the opening of the common Wolffian duct (W.d.) into the urinogenital sinus (U.S.) and the common uterus (M.d.) ending blindly. X 33.

Fig. 13. - (0.36mm. after 12). Showing the opening of the urinary bladder (U.B.), glands (G.i.) on the cloacal wall and the urinogenital ridge lying dorsally. X 33.
Text-figs. 3 & 4. - Diagrammatic ventral views of the urinogenital organs of Scaphiothus couchii. (3) - Male (specimen A) X 4; (4) - Female (Left ovary with fat-bodies and right oviduct not shown.) X 3
Scaphiopus couchii Baird.

MALE: Specimen A, 54.0 mm. and Specimen B, 59.0 mm., from snout to vent.

Loc. ? America.
Date. Not known.
Source. Turtox (purchased, 1937.)

(Text-fig.3; Pl.III, fig.14.)

The kidneys (K.) are narrow, elongate and somewhat dorso-ventrally flattened. They are thicker on the mesial sides, becoming thinner gradually towards the outer side. The outer side is almost straight and the anterior and posterior ends are broadly rounded. The kidney measurements are:
Specimen A, right kidney 13.7 X 2.8 mm., left kidney 13.8 X 3.0 mm.; Specimen B, right kidney 16.0 X 3.5 mm., left kidney 15.6 X 3.2 mm. They are more or less symmetrical in shape, size and position. The testes (T.) are small ovoid bodies, lying on the middle region of the kidneys. The mesorchium holding each testis contains patches of black pigment and ten or eleven vasa efferentia in Specimen A and five or six in Specimen B. The testis measurements are: Specimen A, right testis 5.3 X 1.9 mm., left testis 5.1 X 2.0 mm.; Specimen B, right testis 4.7 X 2.1 mm., left testis 7.2 X 2.0 mm. The fat-bodies (F.B.) are divided into two main lobes at the attachment to the testis, and each lobe splits into four or five finger-like processes.
Each Wolffian duct (W.d.) arises from the anterior end of the kidney about the level of the anterior head of the testes. On reaching the posterior portion of the kidney it dilates into the vesicula seminalis (S.V.). After leaving the kidneys the two ducts approach each other in the middle line and gradually diminish in diameter as they proceed towards the cloaca. The two ducts open separately into the cloaca on either side of a mid-dorsal papilla (fig.14, W.d.). No villi are found in the endothelial lining of the Wolffian duct, although it is somewhat irregular in outline. There is no pigment on the outer walls of the ducts.

In specimen B a whitish thread-like cord was observed running for a short distance on either side of the pigmented peritoneum holding the kidneys. This is presumably the vestigial Müllerian duct, but no trace of it was found in the Specimen A.

The urinary bladder is thin and extensive and opens opposite the openings of the Wolffian ducts.

FEMALE: 66.0 mm from snout to vent.

(Text-fig.4; Pl.III, figs.15-16a).

The kidneys (K.) are similar to those of the male. The right kidney measures 17.0 X 4.5 mm, and the left 17.3 X 4.0 mm.

The ovary (O.) is extensive with ova in various stages of development. A large ovarian ovum
measures about a millimetre in diameter and its
dorsal hemisphere is pigmented. The immature ova
are without pigment. Small round pigmented bodies
are scattered in patches within the inner walls of
the ovary. The right ovary has a dozen lappets,
while the left has one less. The posterior three or
four lappets are held tightly to the uterine wall of
their respective sides. The fat-bodies (F.B.) are
very small, and consist mainly of two lobes at the
base, as in the male, with a few short digitations.

The oviducts (M.d.) are well developed, and
highly convoluted like those of *Bufo*. The ostium
abdominale is a funnel-shaped opening situated at
the root of the lungs. There is no pars recta.
From the posterior level of the kidney the pars
convoluta expands dorsally into a thin-walled uterine
sac (U.) which extends anteriorly at the outer side
of the kidney. The two uteri approach each other
mesially till they meet and coalesce into a common
chamber which runs towards the cloaca gradually
diminishing in diameter. Longitudinal folds are
present throughout the course of the uterus (figs.
15-16, M.d.). The common uterus is gradually
incorporated into the cloacal wall, where it forms a
urinogenital papilla in its lumen and finally opens
into the cloaca (figs.16, 16a, M.d.).

The Wolffian ducts arise from the outer dorso-
lateral sides of the kidneys, and after leaving the
latter, they do not dilate, but run in uniform
diameter towards the cloaca lying upon the uterine
sac; and in so doing they gradually approach each
other till their outer walls meet mesially.
Towards the posterior end, the two juxtaposed ducts
diverge and move downwards encircling the uterine
tube and enter the cloacal wall. Figure 15 shows
the Wolffian ducts lying below the common uterus in
the urinogenital papilla just anterior to their
separate openings into the cloaca. It is of interest
that these openings, unlike those of any other known
Salientia, are situated anterior to the opening of
the common uterus. The urinary bladder is similar
to that of the male.

*Scaphiopus holbrookii* (Harlan)

**MALE:** 60.0 mm. from snout to vent.

Loc.  ? America.
Date.  Not known.
Source. Turtox (purchased, 1937.)

(Pl.III, fig.17.)

The kidneys are similar to those of *S. couchii*.
The right kidney measures 13.6 X 3.9 mm, and the
left 14.2 X 4.1 mm.

The testes are oval bodies lying, as in *S.
couchii*, on the middle region of the kidneys.
Sparse patches of pigment are scattered on their
surface, and there are seven or eight vasa efferentia.
The right testis measures 5.0 X 1.8 mm, and the left
4.0 X 1.8 mm. The creamy white fat-bodies are massive with seven or eight long digitations.

The Wolffian ducts follow the same course and fate as in the male *S. couchii*. Figure 17 shows the separate openings of the Wolffian ducts into the cloaca. There is no trace of the Müllerian ducts. The urinary bladder is similar to that of *S. couchii*.

**FEMALE:** 57.0 mm. from snout to vent.

*(Pl.IV, figs.18-21.)*

The relations of the kidneys are in general the same as those of *S. couchii*, and they measure:

- Right kidney, 13.7 X 4.5 mm.
- Left kidney, 14.0 X 4.5 mm.

The ovaries appear to be mature and each consists of nine lobes. One of the lobes of the left ovary contains a fairly large number of ripe ova, the largest being about 1.4 mm. in diameter. The immature ova are unpigmented. The ovary and the fat-bodies look like those of *S. couchii*.

The oviducts are well developed. Figures 18-20 show the uteri and Wolffian ducts following the same course as described above for *S. couchii*. The further course of the Wolffian ducts is, however, quite different from what one would expect. The two ducts join within the cloacal wall, and the united portion runs for about only 0.10 mm. (10 sections) before opening into the cloaca (fig.21, W.d.).
Here also the uterine opening is situated behind the opening of the Wolffian duct as in S. couchii. The urinary bladder is the same as that in the preceding species.

**Megophrys parva** (Boulenger).

**FEMALE**: 49.0 mm. from snout to vent (Regd. No. 9693, Z.S.I.)

**Loc.**: Cherrapunji, Assam, India.

**Date**: October, 1872.

**Source**: The Director (Z.S.I.)

(Pl. IV, fig. 22.)

This is a fully mature female specimen of **Megophrys parva**. The internal organs, probably owing to long preservation in spirit, were very hard. The eggs being discharged from the ovary are all lodged within the extensive uteri, and being hard and brittle prevented a proper examination of the structures.

The kidneys are comparatively small. They are much dorso-ventrally flattened, leaf-like in appearance, and not lobed as in *Bufo*. The outer lateral edge is almost straight, and the anterior and posterior ends are elegantly rounded. The right kidney measures 9.0 X 4.0 mm., and the left 8.7 X 4.0 mm.

The ovary is spent owing to the discharge of eggs which are all lodged within the uteri. There are only four or five ovarial lobes, and the fat-
bodies are minute.

The oviducts are well developed and look much like those of a typical *Rana*. The pars recta is, however, very short. The uterine portion is extensive, and occupies the greater part of the posterior portion of the body cavity, so that other structures were hidden from view. The Wolffian ducts could not be examined properly. However, examinations of the sections prepared of the cloacal region with the urinogenital ducts showed that the two uteri are confluent posteriorly, but the extent of confluence could not be determined owing to the brittle nature of the tissue. Figure 22 shows the aperture of the common uterus through the uterine papilla into the cloaca. No longitudinal folds were observed. The Wolffian ducts (fig.22, W.d.) lying upon the uterine portion are displaced a little to the left side and unite terminally just prior to opening into the cloaca a few sections posterior to the single opening of the common uterus.

The urinary bladder is thin-walled and extensive and opens into the cloaca opposite the uterine opening.
of a thorough search, are absent in others. He showed that in male *Bufo bufo* at least these ducts followed the same course and fate as the oviducts of the female.

Spengel's major observations have been accepted by several subsequent authors, (Hoffmann, 1873-78; Gadow, 1901; Felix and Bühler, 1906; Wiedersheim, 1907; Noble, 1931; van den Broek, 1933.)

Cope (1889) dealt in a general way with the reproductive organs of Salientia. He noted nothing of special importance except that the vestigial Müllerian ducts persisted in all Salientia, except *Rana* and allies in which they were aborted.

Grönberg (1894) stated that *Pipa pipa* is similar to other Salientia in the general organisation of the urinogenital system. The only interesting feature that can be gleaned from his observations is the union of the two oviducts (uteri) for ten millimetres before they open into the cloaca. Beddard (1895) in his paper on the 'Anatomy of *Pipa*' made no mention of the urinogenital organs, although portions of oviducts and ovaries were shown in a diagram; he did not even note the union of uteri.

Boulenger (1896) studied the urinogenital organs of the European Salientia in some detail, and observed that the male reproductive organs differed considerably in different species. He figured the male urinogenital apparatus of *Discoglossus pictus*, *Bombina pachypus*, *Alytes obstetricans*, *Bufo viridis*
EXPLANATION OF PLATE III.

Photomicrographs from series of transverse sections passing through the cloacal region with the urinogenital ducts.

Scaphiopus couchii Baird.

(Male.)

Fig. 14. - Showing the Wolffian ducts (W.d.) opening separately into the cloaca (Cl.), the left having opened already. The urinary bladder (U.B.) has already opened. X 33.

(Female.)

Fig. 15. - Showing the common uterus (M.d.) and the Wolffian ducts (W.d.) in the cloacal wall forming a urinogenital papilla, just before the latter open separately into the cloaca (Cl.) X 45.

Fig. 16. - (0.45 mm. after fig. 15.) Showing the common uterus (M.d.) opening through the uterine papilla into the cloaca (Cl.) X 21.

Fig. 16a. - Magnified view of the same as above. X 45.

Scaphiopus holbrooki Harlan.

(Male.)

Fig. 17. - Showing the separate openings of the Wolffian ducts (W.d.) and the opening of the urinary bladder (U.B.) into the cloaca (Cl.) X 33.
EXPLANATION OF PLATE IV.

Photomicrographs from series of transverse sections through the gut with the urinogenital ducts behind the kidneys.

Scaphiopus holbrookii (Harlan).

(Female.)

Fig. 18. Showing the two uteri (M.d.) in juxtaposition just before becoming confluent, the Wolffian ducts (W.d.) lying over them. X 17.

Fig. 19. (0.38 mm. after fig. 18.) Showing the confluence of the uteri (M.d.) with the overlying Wolffian ducts (W.d.) X 17.

Fig. 20. (0.73 mm. after fig. 19.) Showing the Wolffian ducts (W.d.) moving downwards towards the cloaca (Cl.), separated by the common uterus (M.d.) X 45.

Fig. 21. (0.97 mm. after fig. 20.) Showing the united Wolffian ducts (W.d.) opening into the cloaca (Cl.), the common uterus (M.d.) lying above them in the cloacal wall. X 45.

Megophrys parva Boulenger.

(Female.)

Fig. 22. Showing the single opening of the common uterus (M.d.) into the cloaca (Cl.). The Wolffian ducts (W.d.) are separated by a partition wall which disappears just before opening into the cloaca. The urinary bladder (U.B.) opens ventrally. X 33.
Text-fig. 5. - Diagrammatic ventral view of the urinogenital organs of a male Rhinophrynus dorsalis. X 5
RHINOPHYNIDAE

Rhinophrynus dorsalis (Dum. et Bibr.).

MALE: 45.0 mm. from snout to vent.
Date. March-July, 1927.
Coll. Mr. W. W. Brown.
Source. Mr. A. Loveridge (M.C.Z., Donor: Prof. T. Barbour.)

(Text-fig.5; Pl. V, figs. 23-26).

This is a fully mature specimen of the Mexican burrowing toad, Rhinophrynus dorsalis. The kidneys (K.) are light brown in colour and flattened dorso-ventrally. The left kidney is divided transversely by a groove into an anterior and a posterior lobe. The former is broad, the latter narrow, and the outer edge of the kidneys is broadly convex. The right kidney is situated a little anterior to the left. The kidney measurements are: right kidney 12.0 X 2.8 mm., left kidney 12.5 X 2.6 mm.

The testes (T.) are broadly oval, creamy white bodies. The left testis, like the kidney, is two-lobed, the transverse demarcation line lying just above that of the kidney. The testes are loosely held to the kidneys by the mesorchia through which pass 8 or 10 vasa efferentia. The testis measurements are: right testis 7.2 X 3.0 mm., left testis 8.5 X 3.2 mm. The fat-bodies (P.B.) are attached to the anterior end of each testis, of yellowish colour, with about a dozen digitations originating from the
basal portion.

The vestigial Müllerian duct (M.d.) appears as a thin whitish cord extending forward as far as the roots of the lungs, but the ostium abdominale is not visible. It does not reach the free portion of the Wolffian duct (W.d.) posteriorly.

The Wolffian duct (W.d.) originates from the anterior end of the kidney, and there is no sign of a seminal vesicle. Posteriorly the ducts run together with a partition between them, which breaks down and the cavities of the tubes become confluent (fig. 23, W.d.). The connective tissue sheath surrounding the ducts is slightly thickened on the ventral side, and here the tip of the urinogenital sinus appears as a hollow diverticulum (fig. 23, U.S.). As it runs posteriorly the urinogenital sinus extends laterally and encircles the cloacal region lying below it (fig. 24, U.S.). It should be noted that the Wolffian ducts become confluent approximately at the level of the anterior tip of the urinogenital sinus, and the united portion of the duct runs for about 0.30 mm. (30 sections) before opening into the sinus (fig. 24, W.d.). Immediately posterior to this opening, the urinogenital sinus connects with the cloaca by four apertures without forming a papilla (figs. 25 and 26, U.S.). Posteriorly the urinogenital sinus covers the entire dorsal portion of the cloaca with which it is intimately connected.
The urinogenital sinus is a minute conical diverticulum about 0.80 mm. (80 sections) in length, arising from the mid-dorsal wall of the cloaca. The inner walls of the sinus consist of one or two layers of cells; a few low longitudinal folds are present on the ventral side (fig. 24, U.S.). The endothelial lining of the Wolffian duct consists of a single layer of cells throughout its course without villi-like processes. The Wolffian ducts and the cavity of the sinus are filled with masses of spermatozoa (figs. 23-26), suggesting that the urinogenital sinus serves as a reservoir for storing sperms, and thus acts as a seminal vesicle.

The urinary bladder is bilobed, thick and attached to the lateral peritoneum. It opens ventrally into the cloaca slightly behind the opening of the urinogenital sinus on the opposite side.
EXPLANATION OF PLATE V.

Rhinophrynus dorsalis (Dum. et Bibr.).
(Male).

Photomicrographs from a series of transverse sections passing through the posterior region of the gut with the urinogenital ducts.

Fig. 23. - Showing the Wolffian ducts (W.d.) confluencing through the disappearance of the partition wall, and the appearance of the tip of the urinogenital sinus (U.S.). X 33.

Fig. 24. - (0.31 mm. after fig. 23). Showing the opening of the common Wolffian duct (W.d.) into the urinogenital sinus (U.S.). The mass in the duct and the sinus consists of spermatozoa. X 33.

Fig. 25. - (0.10 mm. after fig. 24). Showing the opening of the urinogenital sinus (U.S.) into the cloaca (Clo.). The Wolffian duct and the spermatic masses are also evident. X 33.

Fig. 26. - (0.16 mm. after fig. 25). Showing the nature of opening of the urinogenital sinus (U.S.) and the extent it covers the dorsal wall of the cloaca (Clo.). X 33.
and *Rana temporaria*. He also noted the variable nature of the vesicula seminalis in different species. According to him the rudimentary Müllerian ducts are most developed in males of *Alytes* and *Bufo*; in the former they are functional acting as seminal ducts. He claimed, however, that they are absent in males of Pelobatidae and Hylidae. With regard to the openings of the Wolffian and Müllerian ducts his statement ("the oviducts open, together with the ureters, into the cloaca") is somewhat vague. He did not mention the union of uteri in *Alytes* and *Bufo*, although it was known at this time and he himself referred to Spengel's work.

Gadow (1901) attempted to show the male urino-genital organs of Salientia, comprising the genera *Rana*, *Bufo*, *Alytes*, *Bombina* and *Discoglossus*, more or less as an evolutionary series. The ducts of Discoglossids are said to show the most advanced and specialised condition. He noted also the confluence of oviducts (uteri) before opening into the cloaca in *Alytes* and *Bufo*, and added further that *Hyla* has a single unpaired opening of the uteri into the cloaca.

Gaupp's (1904) monograph on the European species of *Rana* may be taken as the standard work on the anatomy of this genus, and in a general way for the Salientia.

Sweet (1907) in her studies on the openings of nephrostomes and the connection of the vasa efferentia
Text-figs. 6, 7 & 8. - Diagrammatic ventral views of the urinogenital organs of males of Bufo.
(6) - B. fowleri, X 3; (7) - B. woodhousii (right fat-bodies not fully shown.) X 2;
(8) - B. compactalis. X 3
BUFONIDAE

Bufo fowleri Hinckley.

MALE: 66.0 mm. from snout to vent.

Loc.  ? America.
Date.  Not known.
Source. Turtox (purchased, 1937.)

(Text-fig.6; Pl.VI, figs.27-29.)

The kidneys (K.) are about the same size and situated at about the same level in the body. They are much lobed on the mesial sides. The kidney measurements are: right kidney 17.5 X 4.5 mm., left kidney 16.8 X 4.6 mm.

The testes (T.) are highly irregular in shape, especially the right one which is divided into three portions. The left testis is an elongate body which extends slightly beyond the posterior level of the kidney. There are twelve vasa efferentia on the right and ten on the left. The testis measurements are: right testis (3 portions) 15.4 X 2.4 mm., left testis 13.4 X 2.4 mm. Bidder's organ was not identified, although looked for carefully, even in sections of the testes. The fat-bodies (F.B.) are quite small consisting of small digitations at the caput of each testis.

The Wolffian duct (W.d.) arises from the posterior half of the kidney and gradually dilates into a spindle-shaped seminal vesicle (S.V.) The vestigial
Müllerian ducts (M.d.) are well developed, especially the posterior portion. Anteriorly they run as a thin whitish cord as far forward as the anterior level of the kidney. They increase slightly in diameter at the posterior level of the kidney; the right duct forms a single loop before it passes over the Wolffian duct. The Müllerian and Wolffian ducts are intimately apposed to one another (fig. 27, M.d. and W.d.) towards the cloaca. Sections (fig. 27, M.d. and W.d.) reveal longitudinal glandular folds in the Müllerian duct, and low villi-like processes are apparent within the Wolffian duct. Figure 27 shows the Müllerian ducts just anterior to the point where they coalesce. The Müllerian ducts unite through the disappearance of the partition wall, and the common duct thus formed runs for about 2.5 mm. (248 sections) ending blindly within a cloacal papilla (figs. 28 and 29, M.d.). The Wolffian ducts unite posteriorly within the cloacal wall (fig. 28, W.d.), and the common duct runs for about 0.3 mm. (i.e., 31 sections) before opening into the cloaca on the right side of the papilla containing the Müllerian duct (fig. 29, W.d.).

The urinary bladder is large and of the typical Bufonid type. It opens into the cloaca opposite the opening of the common Wolffian duct.
Bufo woodhousii Girard.

MALE: 80.0 mm. from snout to vent.

Loc. Montana, America.
Date. April, 1935.
Source. Turtox (purchased.)

(Text-fig. 7.)

The kidneys (K.) are similar to those of
B. fowleri, and the measurements are: right kidney
23.8 X 6.0 mm., left kidney 22.5 X 8.2 mm.

The testes (T.) are irregular in shape and size,
and lie ventral to the middle portion of the kidney.
The testis measurements are: right testis 13.1 X
5.0 mm., left testis 14.4 X 4.7 mm. There are ten
vesa efferentia on the right and twelve on the left.
Bidder's organ (B.O.) is moderately developed. The
fat-bodies (F.B.) are massively developed with short
digitations at the free end.

The Müllerian ducts (M.d.) persist for their
full length as thin tubes which run anteriorly as far
as the roots of the lungs, where each appears to
form a funnel. At about the posterior level of the
kidneys each duct forms a number of closely adjacent
coils (M.d.) and then runs ventrally over the
Wolffian duct, to unite finally and end blindly on
a cloacal papilla as in B. fowleri. The course and
fate of the Müllerian and Wolffian ducts are exactly
similar to those of B. fowleri. The only difference
is that the common Wolffian duct which is formed
terminally in the cloacal wall runs for about 0.3 mm.
(80 sections) before opening into the cloaca. The urinary bladder is typical of Bufonids.

**Bufo compactalis** Wiegman.

**MALE**: 62.0 mm. from snout to vent.

Loc.  Texas, America.
Date.  May, 1935.
Source.  Turtox (purchased.)

(Text-fig. 8; Pl. VI, fig. 30.)

The kidneys (K.) are asymmetrical in shape, size and position. They measure as follows: right kidney 18.0 X 5.0 mm., left kidney 16.5 X 5.0 mm.

The testes (T.) are more or less cylindrical in shape but not so elongate as in *B. fowleri*. They lie ventral to the middle of the kidneys. There are only ten or eleven vasa efferentia. The right testis measures 7.5 X 2.5 mm. and the left 7.8 X 2.5 mm.

Bidder's organ is not well differentiated; it covers the anterior caput of each testis. The fat-bodies (F.B.) are massive with a large number of blunt digitations.

The Müllerian ducts (M.d.) are poorly developed, and persist as thin whitish cords on the pigmented peritoneum attached to the kidney. Each duct extends anteriorly a little beyond the kidneys, while posteriorly they approach the Wolffian ducts of the same side but do not touch them. Examination of sections did not reveal any trace of the Müllerian tubes ventral to the part of the Wolffian ducts.
Text-figs. 9, 10 & 11. - Diagrammatic ventral views of the urinogenital organs of males of Bufo. (9) - B. stomaticus. X 3; (10) - B. quercicus. X 9; (11) - B. boreas. X 2
situated posterior to the kidney. The Wolffian ducts (W.d.) dilate into seminal vesicles (S.V.) and their inner walls do not have villi. The two ducts unite before they are incorporated into the cloacal wall, and the common duct (fig.30, W.d.) runs for about 1 mm. (96 sections) before opening into the cloaca. The urinary bladder is typical of Bufonids.

**Bufo stomaticus** Lütken.

**MALE:** 64.5 mm. from snout to vent.

Loc. Calcutta, Bengal, India.

Date. September, 1945.

(Text-fig.9; Pl.VI, fig.31.)

The kidneys (K.) are slightly asymmetrical in position, the right being situated at a slightly higher level than the left. The kidney measurements are: right kidney 16.7 X 4.5 mm., left kidney 16.6 X 4.5 mm.

The testes (T.) are more or less elliptical bodies with a few pigment granules on their surface. They lie ventral to the anterior half of the kidneys. Five *vasa efferentia* originate from each testis. The testis measurements are: right testis, 5.7 X 2.7 mm., left testis 5.1 X 3.0 mm. Bidder's organ is small and devoid of pigment. The fat-bodies (F.B.) appear to be small and possess a number of digitations.

Traces of Müllerian ducts (M.d.) were found in the anterior region of each kidney, but no ostium abdominale was observed. Faint traces of the
Müllerian ducts were also seen lateral to the kidneys; they did not, however, reach the posterior level of the kidneys. The duct appears to have no lumen. The Wolffian ducts (W.d.) are similar to those of the species already described, but the outer walls of the ducts are moderately pigmented. The two ducts unite as they enter the cloacal wall (fig. 31, W.d.), and the common duct runs for about a half millimetre (51 sections) before opening into the cloaca.

The urinary bladder is not extensive but shows the typical condition found in other species of Bufo.

Bufo quercicus Holbrook.

MALE: Specimen A, 21.0 mm. and Specimen B, 23.0 mm. from snout to vent.

Date. April, 1935.
Source. Turtox (purchased.)

(Text-fig. 10; Pl. VII, fig. 32.)

As in B. stomaticus, the kidneys (K.) are slightly asymmetrical in position and much lobed posteriorly on the mesial sides. The measurements are: Specimen A, right kidney 6.2 X 2.2 mm, left kidney 5.9 X 2.2 mm; and Specimen B, right kidney 6.8 X 2.5 mm, left kidney 6.6 X 2.5 mm.

The testes (T.) are globular bodies lying ventral to the anterior portion of the kidneys. The seminiferous tubules are apparent through the thin walls of the testes. Four or five vasa efferentia only connect from the testis to the kidney.
The testis measurements are: Specimen A, right testis 2.6 X 1.4 mm., left testis 2.3 X 1.5 mm; and Specimen B, right testis 3.0 X 1.3 mm., left testis 4.0 X 1.2 mm. Bidder's organ (B.O.) is of whitish colour and irregular in shape. The fat-bodies (F.B.) are elongate with a few irregular digitations.

The Wolffian duct (W.d.) arises from the posterior end of the kidney, and does not expand into a seminal vesicle as in other species, but runs posteriorly as a more or less uniform tube. The two ducts which are slightly pigmented unite before entering the cloacal wall (fig. 32, W.d.). The common duct diminishes gradually in diameter where it becomes incorporated within the cloacal wall, and finally opens into the cloaca between two adjoining cloacal villi. The common duct runs for about 0.26 mm. (26 sections.) There are no villi and the endothelial lining consists of a single layer of cells. It is of interest to note that there is no trace of the Müllerian ducts in this species.

The urinary bladder appears to be thick-walled but this may be due to its shrunken condition. It opens into the cloaca about 0.40 mm. (40 sections) behind the opening of the common Wolffian duct on the opposite side.
Bufo boreas Baird and Girard.

MALE: 90.0 mm. from snout to vent.

Date.  May, 1937.
Source.  Turtox (purchased.)

(Text-fig.11; Pl.VII, figs.33 and 34.)

The right kidney (K.) is situated at a much higher level than the left. Both kidneys are slightly lobed on the mesial sides. The right kidney measures 27.2 X 5.0 mm., and the left kidney 26.7 X 5.0 mm.

The testes (T.) are rather small bodies lying ventral to the posterior half of the kidneys. There are seven or eight vasa efferentia. The testis measurements are: right testis 9.2 X 5.0 mm., left testis 7.8 X 4.4 mm. Bidder's organs (B.O.) are elongate bodies of irregular shape which contain scattered pigments here and there. The fat-bodies (F.B.) are small, attached to Bidder's organ and the kidney, and possess a number of short digitations.

The persistent Müllerian ducts (M.d.) are prominent, though by no means well developed. They are whitish tubes gradually thinning anteriorly; each appears to have a funnel-shaped opening at the roots of the lungs. Each duct is slightly coiled at the posterior level of the kidney; it then dilates slightly and proceeds towards the cloaca. The Wolffian ducts (W.d.) originate from the anterior third of the kidney, and there appears to be no
with the kidney of eight species (Hylidae and Leptodactylidae) of Salientia, paid some attention to the general structure of the kidney and testis.

Beddard (1907-'11) made some observations of several species of frogs and toads, dealing mainly with the general musculature, hyoid etc. His observations, though scanty and by no means complete, are of interest, since he noted a coalescence of the uteri in Megophrys nasuta and Rhinoderma darwini. He (1911, pp. 404-05) later withdrew his earlier statements on Breviceps verrucosus (1908a), since they do not agree with those of Br. gibbosus. His (1908c) observations on Hemisus are very inadequate. For reasons best known to himself he did not embody in the resumé any of the interesting peculiarities of the urinogenital organs which he had observed. Unfortunately these data remained unnoticed by later workers.

Devanesen (1918) in an obscure publication on the anatomy of Oberodon systoma dealt in some detail with the urinogenital system. He did not give a diagram, and there is nothing very striking in this frog except that the urinary bladder is stated to contain a hard stone-like structure. This he found in eight specimens, six females and two males.

Gilchrist and von Bonde (1922) gave a comparative account of the urinogenital organs of Rana and Xenopus. According to them the Wolffian
vesicula seminalis. The free portion of the ducts is heavily pigmented. The Müllerian ducts behave in the same manner as those of *B. fowleri* in that a common duct is formed which runs for about 1.2 mm. (120 sections) and ends blindly within a cloacal papilla (figs. 33 and 34, M.d.). The Wolffian ducts, however, remain quite separate throughout their course, and unlike all the examples of *Bufo* described above, they open separately into the cloaca through the right side of the cloacal villus which bears the aborted Müllerian duct (fig. 34, W.d.). The urinary bladder is typical of Bufonids.
EXPLANATION OF PLATE VI.

Photomicrographs from series of transverse sections through the urinogenital ducts behind the kidneys.

**Bufo Fowleri** Hinckley.
*(Male)*.

Fig. 27.- Showing the Müllerian ducts (M.d.) just before coalescing, and the relation of the Wolffian ducts (W.d.) to one another. X 17.

Fig. 28.- (1.57 mm. after fig. 27). Showing the coalescence of the Wolffian ducts (W.d.), and the persistence of the common Müllerian duct (M.d.) in the cloacal papilla. X 45.

Fig. 29.- (0.25 mm. after fig. 28). Showing the opening of the Wolffian ducts (W.d.) into the cloaca on the right side of the papilla containing the Müllerian duct (M.d.) in which it ends blindly. X 45.

**Bufo compactalis** Wiegman.
*(Male)*.

Fig. 30.- Showing the common Wolffian duct (W.d.) just before opening into the cloaca (Cl.). The urinary bladder (U.B.) has already opened on the ventral side. X 33.
EXPLANATION OF PLATE VII.

Photomicrographs from series of transverse sections passing through the cloacal region with the urinogenital ducts.

**Bufo stomaticus** Lütken.

*(Male)*

Fig. 31. - Showing the coalescence of the Wolffian ducts (W.d.) in the cloacal wall before the common duct opens into the cloaca (C1.), and the opening of the urinary bladder (U.B.). X 33.

**Bufo quercicus** Holbrook.

*(Male: Specimen B.)*

Fig. 32. - Showing the union of the Wolffian ducts (W.d.) before entering the cloacal wall. X 45.

**Bufo boreas** Baird and Girard.

*(Male)*

Fig. 33. - Showing the separate Wolffian ducts (W.d.), and the common Müllerian duct (M.d.) ending blindly in the cloacal papilla. X 17.

Fig. 34. - (0.17 mm. after fig. 33.) Showing the Wolffian ducts (W.d.) opening separately, the right duct having opened already into the cloaca. The tissues of the blind Müllerian duct (M.d.) still persisting in the cloacal papilla. X 17.
Text-figs 12 & 13. - Diagrammatic ventral views of the urinogenital organs of *Eleutherodactylus nubicola*. (12) - Male X 6; (13) - Female (right ovary with fat-bodies not shown and left oviduct not fully represented.) X 9
LEPTODACTYLIDAE

Eleutherodactylus rubicola Dunn.

MALE: 30.0 mm, from snout to vent.

Loc. Near Morce's Gape, Parish of St. Andrew, Alt. 5,000 ft., Jamaica.
Date. July 3, 1941.
Coll. and source. Dr. W.G. Lynn.

(Text-fig.12; Pl.VIII, figs.35-37).

The kidneys (K.) are long fleshy white bodies hidden by large testes; the right one lies at a little higher level than the left. The ventral surface is flat, the dorsal slightly convex. The kidney measurements are: right kidney 6.7 X 2.0 mm, left kidney 6.6 X 2.4 mm.

The testes (T.) are enormous compared with the kidneys or the specimen. The right testis measures 4.7 X 3.1 mm and the left 5.0 X 3.4 mm. They are more or less oval in shape and unpigmented. They are placed asymmetrically, but cover the kidneys completely from the ventral aspect; the left testis is at a lower level than the right. Both are so tightly held to the kidneys by the narrow mesorchia that the vasa efferentia cannot be discerned. The fat-bodies (F.B.) are yellowish consisting mainly of two moderately long finger-like processes.

Each Wolffian duct (W.d.) arises from the posterior end of the kidney and swells out at once into a thick-walled vesicula seminalis (S.V.). Transverse sections through this region show that the
inner walls are thrown into a large number of glandular villi-like processes (fig. 35, W.d.) which are remarkably high. The two ducts unite and form a common duct (fig. 36, W.d.) which runs for about one and a half millimetre (154 sections) before opening into the cloaca. It is interesting to note that it opens into the cloaca without being fully incorporated within the wall of the latter (fig. 37, W.d.). Villose processes occur throughout the course of the duct. Villi are seen also in the portion of the Wolffian duct at the posterior end of the kidney, but only on the outer side. The wall on the inner side, adjacent to the kidney, which shows no villi, consists of a single layer of cells, while the wall on the outer side has two or three layers of cells. There is no trace of the Müllerian ducts.

The urinary bladder is thin-walled and extensive, and opens ventrally opposite the opening of the common Wolffian duct. (fig. 37, U.B.).

**FEMALE:** 35.0 mm. from snout to vent (No. F. 775).


Date. July 31, 1941.

Coll. and source. Dr. W. G. Lynn.

(Text-fig. 13; Pl. IX, figs. 38 and 39).

The kidneys (K.) are similar to those of the male and measure as follows: right kidney 6.1 X 2.0 mm., left kidney 6.2 X 1.8 mm.

Each ovary (O.) consists of a single sac and
appears to be spent. Dr. Lynn writes (in litteris) that this specimen was taken with a nest of eggs and had presumably discharged its ova. The largest ovarian ovum measures about 0.3 mm in diameter. The fat-bodies (F.B.) consist mainly of two or three fairly long finger-like processes.

The oviduct (O.) is well developed. The diameter of the tube gradually increases posteriorly where it measures about 1.3 mm at maximum breadth. The pars recta is rather short. The uterus (U.) starts at the posterior level of the kidney. The two uteri extend mesially over the kidneys and coalesce into a common uterus at their point of contact. No partition wall appears to divide them. The uterus is thin-walled and slight villosity is apparent (fig. 38, M.d.), but in the posterior region where it enters the cloaca, longitudinal folds and a secretory mass were observed within the tube. The folds and mass extend to the point where the uterine tube terminates in the cloaca. The longitudinal folds on the ventral side become less apparent where the uterus penetrates the cloacal wall. The ventral uterine wall is fused with the epithelium of the cloacal wall (fig. 39, M.d.). No opening from the uterus into the cloaca was found by examination of sections. A membrane consisting of a single layer of cells was present throughout the length of the bulging uterine papilla. It is concluded, therefore,
Text-figs. 14 & 15. - Diagrammatic ventral views of the urinogenital organs of *Eleutherodactylus alticola*. (14) - Male (Specimen B) $\times 12$; (15) - Female (left ovary with fat-bodies not shown, and right oviduct not fully represented.) $\times 9$
ducts run united for a considerable length in males only of the latter. In the female Xenopus the condition is similar to that of Rana, in that the Wolffian ducts remain separate throughout the length.

Boonacker (1927) studied the development of the urinogenital system of the male Alytes obstetricans, and concluded that the duct which conveys the sperms is not the Müllerian duct, as Spengel (1876) thought it, but is homologous with the Wolffian duct. The Müllerian duct is quite separate from the Wolffian duct, although they may be united anteriorly.

Noble (1925) in his studies on Ascaphus truei has pointed out that the cloacal appendage or the 'tail' of the male is used as an intromittent organ for effecting internal fertilisation, since he found great masses of spermatozoa from sections of the oviduct of a breeding female. He also stated that the oviducts act as a spermatheca. He made no mention of any other peculiarity in the structure of the urinogenital organs of either male or female Ascaphus. Noble (1927) noted that in the African viviparous toad Nectophrynoides, the caudal union of the oviducts form a large, highly vasculated 'bicorneate' uterus. Angel and Lamotte (1944) published a diagram of the female urinogenital organs of a recently discovered toad N. occidentalis, showing this 'bicorneate' type of uterus in which tadpoles were developing. The diagram on p.71 of their paper
that the opening had recently become closed after spawning.

The Wolffian duct arises from the kidney, but does not dilate after leaving the kidney. The two ducts join, as in the male, and the common duct (fig.38, W.d.) runs for about 3.0 mm. (288 sections) before opening into the cloaca posterior and dorsal to the occluded uterine papilla. The urinary bladder is similar to that of the male.

Eleutherodactylus alticola Lynn.

**MALE:** Specimen A, 20.8 mm. and Specimen B, 21.5 mm. from snout to vent.

Loc. Blue Mountain Peak between 6,000 ft. and 7,500 ft., Jamaica.

Date. July 30, 1941.

Coll. and source. Dr. W. G. Lynn.

(Text-fig.14; Pl.IX, figs.40-42).

The kidneys (K.) are similar to those of *E. nubicola*, and measure as follows: Specimen A, right kidney 5.5 X 1.2 mm., left kidney 4.9 X 1.3 mm., and Specimen B, right kidney 5.0 X 1.3 mm., left kidney 4.6 X 1.2 mm.

The testes (T.), as in *E. nubicola*, are extremely large and placed asymmetrically on the kidneys. In Specimen B they are very unequal in size. The testis measurements are: Specimen A, right testis 2.0 X 0.8 mm., left testis 1.7 X 0.9 mm., and Specimen B, right testis 2.6 X 1.7 mm., left testis 4.0 X 2.8 mm. As in *E. nubicola*, the testes are held so tightly to the kidneys that the vasa efferentia are not visible.
The fat-bodies (F.B.) are moderate in size and dull in colour compared with the testis. A single finger-like process is given off from the basal mass attached to each testis.

As in *E. nubicola*, the Wolffian duct (W.d.) dilates immediately into a seminal vesicle (S.V.) after leaving the kidney. Sections of this region show that glandular villi are not so pronounced as in *E. nubicola*. In Specimen B the villi are moderately developed, although not so highly as in *E. nubicola* (fig. 40, W.d.). The villi disappear at the point where the two ducts coalesce. In Specimen A villi are hardly discernible (fig. 41, W.d.) possibly due to some stage in the breeding cycle. The common Wolffian duct runs for about 1.3 mm. (132 sections) before opening into the cloaca. Figure 42 shows the common Wolffian duct opening into the cloaca. There is no trace of the Müllerian ducts. The urinary bladder is similar to that of *E. nubicola*.

**FEMALE:** 22.3 mm. from snout to vent.

(Text-fig. 15; Pl.X, figs. 43-45).

The kidneys (K.) are similar to, though slightly smaller than, those of the male. The dorsal surface, however, is pigmented. The kidney measurements are:

- right kidney 4.7 X 1.2 mm.,
- left kidney 4.6 X 1.3 mm.

As in *E. nubicola*, each ovary (O.) consists of a single simple sac. The ovarian ova measure about 0.6 mm. in diameter. The fat-bodies (F.B.) consist
Textfigs. 16, 17 & 18. - Diagrammatic ventral views of the urinogenital organs of (16) - an immature female Eleutherodactylus orcutti, X 6; (17) - a male E. portoricensis, X 12; (18) - a male Leptodactylus podicipinus (right testis with fat-bodies not shown.) X 8
of two moderately long finger-like processes.

The oviduct is well developed, and the pars recta small. The course of the uteri and the Wolffian ducts are similar to that of *E. nubicola* (figs. 43 and 44, M.d., W.d.). The common uterus forms a papilla which bulges in the cloacal lumen so as to occupy the entire space of the cloaca (fig. 45, M.d.). The uterus opens by a small slit at the summit of the papilla; and the appearance of this opening suggests that it had just opened for the breeding period. The common Wolffian duct runs for about 1.3 mm. (134 sections) before opening into the cloaca. The urinary bladder is typical of Eleutherodactylids.

**Eleutherodactylus orcetti** Dunn.

**FEMALE:** 33.0 mm. from snout to vent.


(Text-fig. 16; Pl. X, fig. 46).

The kidneys are similar to those of the preceding species of the genus, and the measurements are as follows: right kidney 7.0 X 1.7 mm., left kidney 6.8 X 1.8 mm.

The ovaries (0.) consist of single sacs with immature ova, and the yellowish fat-bodies possess two digitations similar to those of *E. alticola*.

The oviduct (M.d.) is a simple straight tube,
which suggests that the specimen is immature. The uterine tube is thin-walled and slightly broader than the anterior region. As in the preceding species, the two uteri join to form an unpaired uterus (U.) at their point of contact. There are no villi in any part of the uterus (fig. 46, M.d.). The latter ends blindly in a cloacal papilla which does not bulge within the cloacal lumen. The Wolffian ducts follow the same course as those in the preceding congeneric species, and the common duct (fig. 46, W.d.) runs for about 2 mm. (206 sections) before opening into the cloaca. The urinary bladder is typical of Eleutherodactylids.

**Eleutherodactylus portoricensis** Schmidt.

**MALE:** 29.0 mm. from snout to vent.

Loc. S. Carovanaa, Porto Rico.

Date. July 24, 1932.

Source. Mr. A. Loveridge (M.C.Z.).

(Text-fig. 17; Pl. X, fig. 47).

The kidneys (K.) are situated asymmetrically as in *E. nubicola*. The outer lateral edge is broadly semi-lunar and somewhat pointed at both the anterior and posterior ends. The measurements of the kidneys show that they are much smaller than those of the male *E. nubicola* of about the same length. The right kidney measures 4.7 X 1.6 mm., and the left 4.5 X 1.8 mm.

The testes (T.) are small and situated at the anterior ends of the kidneys. They are more or less
oval-shaped bodies, held tightly to the kidneys so that the vasa efferentia are not visible. The testis measurements are: right testis 1.7 X 0.9 mm, left testis 2.2 X 0.8 mm. The fat-bodies are moderately well developed with two main lobes.

The Wolffian duct (W.d.) arises from the anterior end of the kidney. It is more or less similar to that of *E. alticola* in that the villi are not very prominent in the vesicula seminalis. The common Wolffian duct (fig. 47, W.d.) measures about 1.3 mm. (130 sections) from its point of union with the separate ducts to its opening into the cloaca. There is no trace of the Müllerian ducts. The urinary bladder is typical of Eleutherodactylids.

**Leptodactylus podicipinus** Cope.

**MALE:** 33.0 mm. from snout to vent.


(Text-fig.18; Pl.XI, figs.48, 49).

The kidneys (K.) are slightly asymmetrical in position. The inner edge of both kidneys is relatively thick, thinning gradually towards the outer edge. The kidney measurements are: right kidney 8.3 X 2.2 mm, left kidney 8.2 X 2.2 mm.

The testes (T.) are enormous, pigmented bodies, and much broader than the kidneys; the right testis is 6.9 X 3.3 mm, and the left 6.9 X 3.2 mm. They
are loosely held by mesorchia through which pass twelve or thirteen vasa efferentia. The fat-bodies are fairly large with a number of digitations.

The Wolffian ducts (W.d.) originate from the anterior end of the kidneys. There is no vesicula seminalis, and after leaving the kidneys the ducts appear to be of uniform diameter until they approach each other mesially when they slightly decrease in size. They do not fuse but towards their posterior ends a muscle is found between them (fig. 48). The ducts open separately into the cloaca forming no papilla (fig. 49, W.d.). The endothelial lining of the Wolffian ducts consist of a single layer of cells without villi. There is no trace of the Müllerian ducts.

The urinary bladder is rather small, thickish and compact; it opens into the cloaca in the usual manner (fig. 49, U.B.).

**FEMALE:** 36.0 mm. from snout to vent.  
(Pl. XI, figs. 50, 51).

The kidneys are similar to those of the male and measure as follows: right kidney 10.8 X 2.5 mm, left kidney 9.7 X 2.7 mm.

The ovaries are full of eggs which appear to be ripe. A superficial examination showed that each consists of four or five lobes. They occupy a considerable part of the body cavity, obscuring other organs. The fat-bodies could hardly be distinguished
being small and hidden by the hard ovarian mass. The ovarian ova measure about a millimetre in diameter on the average.

The oviducts are well developed and the ostium abdominale is followed by a short pars recta. Each is thrown into a large number of convolutions in the region between the level of the heart and lungs and the kidney. From the posterior level of the kidney they suddenly increase in diameter, and in this region a few convolutions are especially broad being distended with secretion that they obliterate all other structures. The uterus, therefore, cannot be seen without breaking this highly dilated hard portion of the oviduct. The uteri are thin-walled with a number of longitudinal folds, and remain quite separate throughout their course (figs. 50, 51, M.d.). Towards their posterior end a muscle intervenes between them (fig. 50). They are in contact with each other within the cloacal wall and form a uterine papilla which projects into the cloacal lumen. The left uterus opens into the cloaca, but the right remains closed (fig. 51, M.d.). This suggests that the uteri were probably just beginning to open in preparation for spawning. The Wolffian ducts follow the usual course and open separately on the mesial side of the two uteri (fig. 51, W.d.). The urinary bladder is similar to that of the male.
*Leptodactylus melanoptus* (Hallowell).

**FEMALE:** 37.0 mm. from snout to vent. (No. 38268 C.N.H.M.).

Loc. Michoacan, Apatzinagan, Alt. 1,000 ft., Mexico.

Date. August 12-15, 1941.

Coll. Mr. Frederick Shannon.

Source. Dr. C. H. Pope (C.N.H.M.).

The urinogenital system of this species is similar to that of the female of *L. podicipinus.*

The kidney measurements are: right kidney 11.1 X 2.7 mm., left kidney 9.8 X 3.2 mm. The right is, therefore, distinctly longer than the left.

The ovaries are well developed, filling the entire body cavity. The visceral organs were much hardened by the fixative, and an examination of the structures was not possible without breaking the various organs. Each ovary consists of four or five lobes. The oviduct, anterior to the uterus, is greatly dilated as in *L. podicipinus.* The two uteri remain separate throughout, and although they form a bipartite papilla, there is no opening into the cloaca. The condition of the ovary, oviduct and uterine papilla, however, suggests that the openings would soon be developed. The Wolffian ducts and the urinary bladder are similar to those of *L. podicipinus.*
Leptodactylus pentadactylus (Laurenti).

**FEMALE:** 130.0 mm. from snout to vent (A.M.N.H. No. 40785).

Loc. Camp Creek, Camp Townsend, Panama Marsh-Darien Exp.
Date. March 17-21, 1924.
Source. Dr. C. M. Bogert.

(Pl. XII, figs. 52, 53).

The urinogenital system of this toad is in general similar to that of the female of *L. podicipinus*. The kidneys differ greatly in length; the right kidney is 22.0 X 3.2 mm., and the left kidney 18.0 X 3.6 mm.

The ovaries appear to be spent and are displaced to the anterior side of the body cavity. They are so much distorted that the ovarial lobes cannot be easily counted. However, each appears to have about half-a-dozen lobes. The largest ovarien ova measure 2.2 mm. in diameter on the average. The fat-bodies are very small with a few (3 or 4) short digitations.

The oviducts are well developed. The most striking feature is the enormous development of the pars convoluta anterior to the uterus which occupies much of the space of the abdominal cavity. It measures roughly about 50.0 X 3.0 mm. This dilated part of the oviduct is comparable with that of the preceding two species, although it is greatly exaggerated here. It contains a cream-coloured mass. The entire mass looks like a large convoluted
shows that the lower parts of the uteri are united into a common chamber which runs into the cloaca. In his book (1931) Noble treated the urinogenital system in a general way. He gave, however, a diagram of the urinogenital organs of a male *Ascaphus truei*, in which he showed the Müllerian duct lying closely by the side of the Wolffian duct in the kidney region.

Lloyd (1928) in a little note pointed out that in the common frog *Rana temporaria* the sperms instead of passing through longitudinal and transverse ducts in the kidney (as stated in some text-books) reach the Wolffian duct by passing through the ordinary kidney tubules.

Hoffman (1931) in his paper on the general anatomy of the genus *Heleophryne*, published some comparative notes on the urinogenital organs of *Heleophryne, Crinia, Bufo* and *Rana*. According to him the two uteri unite before entering the cloaca in *Heleophryne*. He did not mention anything about the opening of the Wolffian ducts.

The urinogenital organs of *Rhacoporus* studied by me (Bhaduri, 1932) showed that the Wolffian duct of the males of *Rh. maximus* is modified in a manner that can be correlated directly with the breeding habits of these tree-frogs. About the same time Hoffman (1932) made a contribution to the anatomy of the African Rhacophorids in which he treated the urinogenital system in a general way. He stated
mass of coagulum. The uteri, as in L. podicipinus, take the usual course (fig. 52, M.d.). A close examination of the series of sections failed to show the uterine tubes opening into the cloaca, although a bipartite uterine papilla was apparent (fig. 53, M.d.). Scattered masses of secretion are present within the uteri right up to their end. It appears, therefore, that the uterine openings are completely occluded after spawning. The Wolffian ducts are similar to those of the preceding two species of Leptodactylus. It should be noted that they lie very close together just before opening into the cloaca behind the occluded uterine papilla. The urinary bladder is typical of Leptodactylus.

**Pleurodema cinerea** Cope.

**MALE:** 41.0 mm from snout to vent.

Loc. Incachaca, Dept. of Cochabamba, Bolivia.

Date. March, 1921.

Coll. Mr. Jose Steinbach.

Source. Dr. C. M. Bogert (A.M.N.H.).

(Text-fig. 19; Pl.XII, fig. 54).

The kidneys (K.) are deep brown in colour, flattened dorso-ventrally and situated in the posterior part of the body cavity. The inner edge of each kidney is thick, thinning gradually towards the outer side as in Leptodactylus. The anterior region of the kidneys diverge when viewed ventrally; both together give the appearance of a shield (Text-fig. 19). The kidney measurements are: right kidney
Text-figs. 19, 20 & 21. - Diagrammatic ventral views of the urinogenital organs of (19) - a male Pleurodema cinerea (left fat-bodies not shown) X 6; (20) - a female P. cinerea (left ovary with fat-bodies not shown and right oviduct not fully represented) X 6; (21) - a male Euphemphix pustulosus (left testis with fat-bodies not shown) X 10
11.3 X 3.2 mm., left kidney 11.2 X 3.4 mm.

The testes are small, elongate oval bodies lying ventral to the middle of the kidneys. There are eight or ten vasa efferentia. The testis measurements are: right testis 4.9 X 1.6 mm., left testis 4.8 X 1.8 mm. The fat-bodies are very large; they are light brownish in colour and possess many long digitations.

Posterior to the kidneys the Wolffian ducts (W.d.) increase slightly in diameter. As in Leptodactylus, a muscle intervenes between the two ducts before they enter the cloacal wall. The ducts, slightly decrease in diameter and come to lie very close together before opening separately into the cloaca without forming a papilla (fig.54, W.d.). There is no trace of the Müllerian ducts. The urinary bladder is similar to that of Leptodactylus.

**FEMALE:** 33.0 mm. from snout to vent.

(Text-fig.20; Pl.XII, fig.55).

The small size of this specimen suggests that it is not fully adult.

The kidneys (K.) are similar to those of the male and lie in contact with each other mesially for almost two-thirds of their length posteriorly.

The kidney measurements are: right kidney 9.5 X 2.8 mm., left kidney 9.0 X 3.0 mm.

The ovaries (O.) are poorly developed consisting
of eight or ten lobes with unpigmented ova. The largest ovum measures about 0.5 mm. in diameter. The fat-bodies are moderately developed with several digitations.

The oviducts (M.d.) are also poorly developed with small narrow convolutions. The pars recta is short. The oviduct (pars convoluta) increases in diameter at the posterior level of the kidney, and takes a few irregular turns before finally dilating to form the uterine sac. This dilated part is comparable with that of Leptodactylus, although not so pronounced as in that genus. The two uteri approach each other mesially ventral to the kidneys and diminish gradually in diameter towards the posterior end. As in Leptodactylus, a muscle intervenes between the posterior end of the two uteri. The uteri form two separate papillae in which the ducts end without opening into the cloaca (fig.55, M.d.). The Wolffian ducts take the same course as in the male and open separately into the cloaca behind the occluded uteri. The urinary bladder is similar to that of the male.
**Bupemphix pustulosus** (Cope).

**MALE**: 30.0 mm. from snout to vent.

Loc. Barro Colorado Island, Canal Zone.

Date. ? 1929.

Coll. Dr. E. R. Dunn.

Source. M. A. Loveridge (M.C.Z.).

(Text-fig. 21; Pl.XII, fig.56).

The kidneys (K.) are flattened dorso-ventrally but somewhat thickened at the extreme periphery. They measure as follows: the right kidney 6.6 X 2.2 mm., left kidney 6.1 X 2.2 mm.

The testes (T.) are very large, elongate oval bodies covering the entire ventral surface of the kidneys except for a small part at the posterior end. Small rounded seminiferous tubules are apparent through the pigmented epithelium which covers each testis. The testes are attached tightly to the anterior end of the kidney, but the posterior end is held freely by the mesorchium through which pass six or eight vasa efferentia. The testis measurements are: right testis 5.0 X 2.1 mm., left testis 5.4 X 2.3 mm. The fat-bodies are massive, creamy white in colour with a number of blunt digitations.

The Wolffian ducts (W.d.) run with uniform diameter after leaving the kidneys. The vesicula seminalis appears to be absent. There are no villi and the endothelium consists of a single layer of cells. Towards the posterior end a muscle intervenes, as in *L. nodicininus*, between the ducts. The two
Text-fig. 22. - Diagrammatic ventral view of the urinogenital organs of a female *Heleophryne purcelli* (ovaries removed and right oviduct not fully shown), X 5
EXPLANATION OF PLATE XI.

Photomicrographs from series of transverse sections passing through the posterior region of the gut with the urinogenital ducts.

**Leptodactylus podicipinus** Cope.

(Male).

Fig. 48. Showing the Wolffian ducts (W.d.) separated by the muscle before reaching the cloacal wall. X 45.

Fig. 49. (0.80 mm. after fig. 48). Showing the Wolffian ducts just anterior to their separate openings into the cloaca (Cl.). The urinary bladder (U.B.) has already opened ventrally. X 45.

(Female).

Fig. 50. Showing the separate uteri (M.d.) with the overlying Wolffian ducts (W.d.) adjacent to the cloaca. X 21.

Fig. 51. (0.91 mm. after fig. 50). Showing the left uterus (M.d.) opening into the cloaca, but the right remains unopened. Note the mass of secretion filling the lumina of uteri. The Wolffian ducts (W.d.) before opening separately into the cloaca (Cl.). The urinary bladder (U.B.) has already opened ventrally. X 33.
general category which may be named the *uterus septatus* group.

These three groups have been arranged with typical examples, in a linear series in the accompanying text-figure 37.

In the *uterus separatus* group (Text-fig. 37, I) which is typical of all *Rana*, are included all those genera and species which exhibit separate uteri, namely, *Pelobates, Discoglossus, Rhacophorus, Philautus* (Spengel, 1876), *Uperodon systoma* (Devanesen, 1912), *Xenopus* (Gilchrist and von Bonde, 1922), *Rhacophorus maximus* (Bhaduri, 1932), *Megalixalus, Hyperolius, Hylambates, Pyxicephalus, Natalobatrachus* (Hoffman 1942), and *Microhyla ornata* (Bhaduri and Rudra, 1944); and *Leptodactylus* (3 species) *Pleurodema* and *Phrynobatrachus* (present studies).

Spengel and later Gadow (1901) stated that in *Hyla* the partition wall between the uteri vanishes just before opening into the cloaca. Evidently *H. arborea* was the species referred to by them. Since it differs from *H. gratiosa* as described in the present studies, and in view of the fact that this point has not been considered by subsequent authors (Noble, 1931; van den Broek, 1933), it is best to leave the decision on this genus open for the present.

It is difficult to put any *Salientia* studied by
previous authors in the uterus communis group
(Text-fig.37, VI), although one would be inclined to
include Alytes (Spengel, 1876) and Pipsa (Grönberg,
1894). The following are placed in this group:
Scaphiopus (2 species), Eleutherodactylus (3 species),
Dendrobates (2 species), and Phyllobates. Hemisus
may possibly be brought under this category, although
the uteri differ somewhat from those of the other
genera.

The remaining genera and species may be considered
in the uterus septatus group (Text-fig.37, II - V).
From previous accounts, especially Spengel's, the
condition of the uteri of Bufo (III) appears to stand
intermediate between the uterus separatus and uterus
communis groups. Nectophrynoides (Noble, 1927;
Angel and Lamotte, 1944) and Haeleophryne (present
studies) may well fall within the Bufo group (III) or
very near to it. Gastrotheca (II) is placed between
the Bufo and uterus separatus groups, but very near
to the latter on account of the very small common
uterus. Phyllomedusa (IV) and Rhinoderma(V) are
placed between the Bufo and uterus communis groups in
view of the greater proportion of common uterus.

I have omitted Ascaphus from any of these
categories, although the uteri unite terminally,
because in the first place they are not dilated as in
others, and secondly the common uterus tends to
communicate with the urinogenital sinus and not directly with the cloaca. It is necessary to exclude Megophrys, Bombina and Kassina from any of the above groups as no adequate information is available concerning the extent of the union of the uteri in any of the species.

It is remarkable that the extremes of modifications in the uterine condition are found within the limits of some families, as for instance, Pelobatidae (cf. Scaphiopus and Pelobates), Leptodactylidae (cf. Leptodactylus and Eleutherodactylus) etc., but within the same genus and species it appears to be fairly constant. It is indeed difficult to evaluate the significance of the degree of union of the uteri in the present state of our knowledge, since very few genera have been investigated from this point of view. Nevertheless, the broad groupings, indicated in the text-figure 37, suggest that the derivation of the uterus communis group from the uterus separatus group, or vice versa, has occurred frequently in a family, especially in view of the fact that intermediate forms (uterus sertatus) occur in some genera (e.g., Heleophryne). All these considerations emphasize that a restudy of the Salientian uteri is necessary, especially of those representative genera of a family which exhibit extremes of modifications, in order that its real value may properly be assessed.

Witschi (1933) states that the terminal fusion
of the uteri in *Bufo* accounts for the well-known arrangement in two rows of eggs in the spawn strings. While it may be true for *Bufo* it remains unexplained for other cases where double strings of spawn are not laid, although the uteri are united. It is not easy to offer an explanation, but it may well be that owing to the large size of eggs in some genera and species a union of the uteri occurs. The reverse is not necessarily true however (cf. *Bufo*, *Phyllomedusa* and *Scaphiopus*). Noble (1927) has pointed out that time and again the egg size varies considerably within allied genera and even within species of the same genus. Data on this point are scanty, but my studies show that the egg size is comparatively large in such species of the genera with fused uteri as *Rhinoderma*, *Eleutherodactylus*, *Heleophryne*, *Dendrobates*, *Phyllobates* and *Gastrotheca*.

The uterine opening into the cloaca.—In connexion with the later development of the Müllerian duct in vertebrates in general Kerr (1919, p.245) observed: "it should be noted that its completion and opening into the cloaca, is commonly delayed till a comparatively late stage - often till a period shortly before sexual maturity." In dealing with Salientia Felix and Bühler (1906 p.754) expressed the same opinion. Gallien (1944) has provided support for this view by his experimental work on *R. temporaria*. 
No author seems to have questioned what happens to the opening of the Müllerian duct into the cloaca after sexual maturity. It was perhaps generally believed that the uterine aperture of the cloaca remains open. Recently I (Bhaduri, 1946) have pointed out an occlusion of the uterine opening after spawning in some Salientia (*vide infra*). I am not aware of any such record in Salientia before. None of the authors who have previously studied the urinogenital organs of frogs and toads have recorded a closure of the uterine opening, but they have always noted the uterine opening into the cloaca.

In the present investigation I have observed openings of the uteri in the following species, *Scaphiopus* (2 species), *Megophrys parva*, *Phyllobates nubicola flotator*, *Hyla gratiosa*, *Phyllomedusa dacnicolor* and *Hemisus m. marmoratum*. The uterine openings indicate that the specimens are mature sexually. In the following, however, the uterus appears to be on the point of opening, namely, *Eleutherodactylus alticola*, *Leptodactylus podicipinus*, *Dendrobates tinctorius*, *Rhinoderma darwini*, and *Phrynobatrachus keniensis*. In fact, the case of *L. podicipinus* is interesting in that its one of the uteri had opened into the cloaca while the other remained occluded, though its appearance indicates that it was about to open.
On the other hand, no opening of the uteri was observed in the following species, *Ascarhus truei*, *Eleutherodactylus orcutti*, *Dendrobates auratus*, *Pleurodema cinerea*, *Leptodactylus melanomotus* and *Heleophryne purcelli*. It is difficult to question the adolescence of these specimens from the body size alone. Nor have I any evidence to prove that they had spawned once before. It is, therefore, necessary to assume that they are still sexually immature. It seems, however, from the appearance of ovaries and oviducts in *A. truei*, *E. orcutti* and *P. cinerea* that these specimens had not attained sexual maturity. The appearance of the remaining three species suggests near-maturity, since their ovaries and oviducts were well developed.

There is a complete occlusion of the uterine opening into the cloaca in *Eleutherodactylus nubicola*, *Leptodactylus pentadactylus* and *Gastrotheca boliviana griswoldii* of which I made a previous report (Bhaduri 1946). It is obvious that the occlusion had occurred after spawning, especially in the last species, which was carrying developing eggs in the integumentary pouch on its back. In *E. nubicola* the condition of the ovary and oviduct indicates that it is a female which had recently spawned. Moreover, Dr. Lynn who collected and sent me the material writes (in literis) that this specimen was
captured with nests of eggs, reinforcing the view that it is a female which had recently spawned. No such information, however, accompanies the specimen of *L. pentadactylus*. I have relied instead upon the size of the specimen and the condition of the ovary and the oviduct. A spent ovary with a well-developed oviduct in a toad, 130.0 mm. long, is scarcely likely to be an immature specimen. Mention is necessary of cases in which the uterine opening is patent, but the ovary looks spent, and the oviduct well developed as in *Phyllomedusa* and *Hemisus*. Probably in these specimens the uterine opening had not yet closed.

If a closure of the uterine opening is the general rule after spawning, then we shall have to withhold judgment regarding those which have been considered immature, especially *D. auratus*, *L. melanonotus* and *H. purcelli* in which the reproductive organs do not show any sign of immaturity. It may be that they are non-gravid adults.

The general conclusion is that the Müllerian ducts open into the cloaca at the onset of the breeding phase, remain patent till spawning is over, and then close again. The exact time and method of opening and closure cannot be predicted from these studies. But from the cases of *Gastrotheca* and *Eleutherodactylus* it would appear that the opening closes soon after oviposition.
In order to support my observations on the occlusion of the uterine opening I have pointed out an analogous case in a fish (vide Bhaduri, 1946). This raises the fundamental question whether the uterine aperture in the cloaca of all lower vertebrates may not, in fact, close after spawning. It would be interesting to know the condition of the uterine aperture in Discoglossus and Alytes which are said to breed "as often as three or four times at distant intervals during warmer months." (Boulenger, 1896, p. 66).

In the male.

A critical review of the earlier accounts of the Müllerian ducts in the male is given by Spengel (1876) and Eggert (1926). Prior to Spengel's studies the ducts were recorded in Bufo, Bombina, Discoglossus, Ceratophrys, Uperodon and Rana (Leydig 1853, von Wittich 1853 and other earlier authors). Spengel showed that the Müllerian duct occurs in Bufo (6 species), Rana (only R. temporaria), Bombina, Leptodactylus, Pyxicephalus, Discoglossus and Alytes; but absent from Pelobates, Hyla (2 species), Philautus, Phyllomedusa, Limnodynastes, Adelotus, Pseudophryne, Corunafer, Hyporachus, Pipa and Xenopus. It appears to be absent in the majority of the genera he studied. Despite this Cope (1889) stated that the Müllerian duct is of reduced size in all Salientia except the "Ranae" and allies where it is aborted, although he
mentioned it to be present in *R. virens*. Gadow (1901) believed that remnants of the Müllerian ducts persist or are common in Salientia, best developed in the genus *Bufo*, while much reduced and absent from some individuals of *Rana*. He stated, moreover, that in *Discoglossus* and *Alytes* all traces of them seemed to have vanished at least in adult males. Subsequent authors, not excluding those (Rau and Gatenby, 1922; Stohler, 1931; Davis, 1936) who have made searches for Bidder's organ, do not seem to have paid any attention to the distribution of this structure in different genera and species of Salientia. Noble (1931) also states that it develops in both sexes of most Amphibia. He figured the urinogenital organs of a male *Ascanthus* in which he depicted the Müllerian ducts running alongside the Wolffian ducts. He did not show what happens to this duct in the region beyond the kidney. De Villiers (1934) on the other hand, denied the occurrence of this duct in *Ascanthus*. He does not make it clear, however, whether the anterior part of the kidneys was examined for this structure.

Furthermore, Leydig (1853) von Wittich (1853a) Spengel (1876) and others have pointed out the variable degree of development of the Müllerian ducts in different species and individuals of the same species (as in *B. bufo*). It may be fully represented in some specimens in the form of a rudimentary
oviduct, but in others reduced to a mere string with or without a lumen, and not extending much behind the posterior level of the kidney.

In the present investigations I have observed the Müllerian ducts in ten out of twentythree species studied, namely, *Ascanthus truei*, *Scaphiopus couchii* (in one specimen only), *Rhinophrynus dorsalis*, *Gastrotheca boliviana griswoldi*, *Bufo compactalis*, *B. stomaticus*, *B. fowleri*, *B. woodhousii*, *B. boreas* and *Phyllomedusa dacnicolor*. It should be noted that in the last four species the ducts extend fully as far as the cloaca. It will be seen that they occur in many families of Salientia, though certain genera (as *Eleutherodactylus*, *Dendrobates*), are characteristically without any trace of them. Attention may be directed also to Lynn's (1942) studies on the embryology of *E. nubicola* in which the ducts do not seem to be present even in the tadpole stage. The Müllerian ducts have so far not been recorded from members of Dendrobatidae, Atelopodidae, Rhinodermatidae, Rhacophoridae and probably also of Microhylidae. Therefore, their sporadic occurrences and total absence in some allied genera and species are indeed enigmatical.

There is, however, no doubt that the Müllerian ducts are present in some form of development in all the species of *Bufo* so far studied, but it is curious that they are absent in *B. quercicus*, even though
Bidder's organ is present in this species (present studies and Witschi, 1933). Witschi holds that there is some relationship between Bidder's organ and the Müllerian ducts. According to him toads with large Bidder's organ possess well-developed Müllerian ducts, and toads with marked ovarian character of Bidder's organ possess more well-developed ducts, as for example, in *B. canorus*, *B. americanus* and most markedly so in *B. bufo*. Horie (1938) working on *B. bufo* and *B. sachalinensis* confirmed the latter conclusion only. Now, while it may be true for certain species of *Bufo*, it is not true for other genera, since the ducts have been reported from widely different genera without Bidder's organ. Probably *B. quercicus* may be cited as an example which breaks this seemingly apparent relationship totally.

Spengel stated that whatever the condition of the Müllerian duct, an ostium abdominale was evident in all the species he studied. I have, however, failed to observe this feature in several cases, especially in those where the Müllerian duct is much reduced. Further, it has been shown that the ducts terminate at varying distances from the free portion of the Wolffian ducts in several species examined, as is perhaps to be expected, seeing that they are rudimentary structures. In *Ascaphus* the anterior end of the duct is fairly well developed
(Pl. I, figs. 1 and 2), but only faint traces of it have been shown to persist in the urinogenital capsule (Pl. I, figs. 4 and 5). This is an example which shows the manner in which the posterior section of the duct tends to disappear first.

There is some divergence of opinion concerning the terminal relation of the Müllerian duct to the cloaca. Spengel pointed out that earlier accounts were inadequate as to its posterior course and fate. Mention has been made that prior to Spengel the general view was that the Müllerian duct opened into the Wolffian duct. But, according to him, in B. bufo the duct opens into the cloaca anterior to the openings of the Wolffian ducts, behaving in the manner of female oviducts. From his observations on other species, it appears that he was somewhat uncertain about the final fate of the ducts. Later authors did not pay much attention to this question, though some believed that the ducts do open into the cloaca (Starks and Howard, 1929; Witschi, 1933). Bhaduri and Banerjee (1939), in their studies on the fate of this duct in B. melanostictus, claimed that it ends blindly in the cloacal papilla, and commented upon the findings of Eggert (1926) and Koch (1933–34) who confirmed Spengel's observation on B. bufo.

Spengel stated that in B. marinus, of which he examined four examples, the ducts were constituted differently in that on their course from the ostium
abdominale towards the anterior third of the kidney they adhered to, but did not communicate with, the Wolffian ducts. Koch, however, working on the same species disagreed, and claimed that the ducts do open into the Wolffian ducts in the region of the kidney. She confirmed this observation by sectioning and injection methods, but did not figure her findings.

The present studies have shown clearly and conclusively that wherever the Müllerian ducts persist throughout their whole length, as in B. fowleri, B. woodhousii, B. boreas and Phyllomedusa dacnicolor they appeared similar to the female oviducts, but ended blindly in the cloaca. These observations, taken in conjunction with those of Bhaduri and Banerjee (1939), lead to the conclusion that the Müllerian ducts do not open into the cloaca. To support this view it may be mentioned that in immature females the Müllerian ducts do not normally open into the cloaca, and it is well known that in males these ducts when present are not only rudimentary but somewhat more ill-developed than those of the females. Indeed, I am inclined to believe that the blind ending of the Müllerian ducts in the cloaca will ultimately be found to hold good for all those species in which they are persistent throughout their whole length.
The urinogenital organs and breeding habits.

In 1932 I described a curiously modified Wolffian duct in the male *Rhacophorus* and offered an interpretation of this condition. Hoffman (1942) adduces substantial corroborative evidence from his special studies on *Chiromantis xerempelina*. He states (p. 119): "The urinogenital duct of *Chiromantis* exhibits peculiarities almost similar to those of *Rhacophorus* as described by Bhaduri (12)," and further: "Bhaduri suggests that the modifications of the urinogenital organs of *Rhacophorus* resulted as an adaptation to the terrestrial breeding habits, and gives a lengthy explanation and a very plausible theory as regards the functions of the modified urinogenital duct. Similar conditions are found in *Chiromantis*, which also possesses terrestrial breeding habits. These modifications do not, however, necessarily indicate a very close relationship between *Chiromantis* and *Rhacophorus*, because Spengel (29), who made a comparative study of the urinogenital systems of Amphibians, found no modifications in the male of *Philautus*, a close ally of *Rhacophorus* and stated to possess breeding habits similar to those of the latter." It may be pointed out, in passing, that, the latter part of his statement carries the implication of a parallel evolution of the same modification in the two genera due to
similar modes of breeding habits. On the other hand, Noble (1927) believed that the African Chiromantis is directly derived from Rhacophorus, and later in his book (Noble, 1931), he emphasized the close relationship between the two genera on both anatomical and ethological grounds. I am inclined to agree with Noble's view.

The present studies on Rh. bimaculatus show more or less the same type of modification in the Wolffian duct as in Rh. maximus and Ch. xerampelina, and thus lend further support to the view postulated above.

This work has brought to light some further interesting modifications of the urinogenital ducts of both sexes in several species which suggest a correlation with the peculiar breeding habits of the animals. An attempt, therefore, has been made to discuss these modifications in the light of breeding habits. The term 'modification' is used in this discussion to express deviations from the pattern found in the typical Ranids and Bufonids.

Under the expression breeding habits I include copulation, nursery sites, laying of eggs and their fertilization, nest building, parental care and later development. It is generally held that as eggs are extruded by the female, the embracing male milts immediately over them, thus fertilizing the eggs. This may indeed be true of those Salientia which breed in the water, and is probably the usual
practice of a large number of Salientia. No adequate information is available, however, as to how fertilization is effected in eggs which are laid out of water (i.e., on land, on leaves of trees overhanging water, etc.). We have reason to believe that in these cases the eggs are provided with an extra amount of liquid material enabling the sperms to live and move and so to fertilize the eggs. Evidence had been obtained that some female frogs produce an extra gelatinous material (Noble, 1927; 1931) which may serve this purpose (vide infra), though the material is said to be used for constructing a 'nest'. In the case of frogs and toads which lay their eggs out of water the quantity of seminal fluid required for adequate fertilization is unknown. Another fact that needs consideration in this connexion is the number of eggs laid. It is well known that some species (both aquatic and terrestrial breeders) lay a large number of eggs (e.g., Rana, Bufo, Leptodactylus, Rhacophorus, Phyllomedusa, etc.), and some (mainly out-of-water breeders) very few (e.g., Gastrotheca, Rhinoderma, etc.). Noble (1927) states that small species lay a small number of eggs. Data on this point, however, are scanty. It should also be mentioned that of Salientia which lay eggs that are fertilized out of water, some are said to complete their final development in the water (e.g., Rhacophorus, Phyllomedusa, etc.), while others have
an entirely non-aquatic development (e.g., Eleutherodactylus). Noble (1927, p.116) states: "No Salientia which undergo direct development are known to lay their eggs in the water." The frogs and toads that breed in water do not show any marked deviation in the pattern of the urinogenital ducts from the ordinary types such as those of Rana or Bufo.

(1) Leptodactylus and Eupemphix build 'foam nests' which float on the surface of water (not far from the edge of the pond). It is nowhere clearly stated exactly where the eggs are laid, whether on the surface of water or at the edges of ponds or pools. Further, no information is available concerning the manner in which the 'foam nests' are built. Assuming that they are built in the same manner as those of the Rhacophorids, it can be said that the eggs are laid on some solid substratum (with or without water) on which they are whipped into a foamy mass by the action of the hind legs of either, or both, of the copulating partners. The foam nest builders are said to produce an extra gelatinous (nest) material before the eggs are laid (Noble, 1931, p.282). No work seems to have been done on the site of the production of this material. I have shown above that in all the species of Leptodactylus the terminal portion of the pars convoluta (i.e., the portion which lies just anterior to the uterus) is enormously
expanded and much distended with secretion. This modification was also noted by Cope (1889) in \textit{L. ocellatus} (\textit{vide} p.162). Now, this modified portion of the oviduct seems to be responsible for the production of the extra gelatinous material to which Noble refers. While the extra secretion may serve the purpose of kneading a froth for the eggs, it is also quite probable that it may allow the sperms to live and move, and, during the beating of the egg mass effect adequate fertilization. Whatever may be the rôle of this mass, it may safely be assumed that the oviduct is modified in consequence of this particular mode of breeding, and thus a correlation between structure and function is a reasonable deduction from the facts.

Noble (1927, p.38) states: "\textit{Leptodactylus} is closely related to \textit{Paludicola}, but perhaps more closely to \textit{Pleurodema}" but, unfortunately, the life history of the species of the last-named genus is unknown. I have observed a modification of the oviduct in \textit{Pleurodema cinerea} similar to, though not so pronounced as, that of \textit{Leptodactylus}. It is not unlikely, therefore, that \textit{Pleurodema} may have similar breeding habits.

I have been unable to obtain females of \textit{Eupemphix} for comparison. Nevertheless, since \textit{Eupemphix} is related to \textit{Leptodactylus} and has similar
breeding habits (*vide supra*), it is not unlikely that the oviduct of this toad may show a similar modification.

Some Australian Leptodactylids, e.g., *Limnodynastes*, build 'foam nests' (*Parker, 1940*) resembling those of *Leptodactylus*. Further, Klingelhöffer reports that the female of *Limnodynastes tasmaniensis* produces a gelatinous material with which it can build a 'foam nest' without eggs (*vide* Noble, 1931, p.282). It would be of interest to examine this genus to find out whether its oviduct is modified in a similar fashion.

I have studied the males of *Eupemphix*, *Pleurodema* and *L. podicipinus* which do not show any modification in the Wolffian ducts that warrants a correlation with their breeding habits.

(2) The other Leptodactylids, *viz.*, the West Indian piping toads, *Eleutherodactylus* undergo direct development, i.e., lay their eggs on land where they develop into toads (*Noble, 1927; Lynn, 1942*). I have studied four species of this genus. It is stated that the number of eggs in a batch varies considerably, the average is 43 for *E. nubicola* (*Lynn, 1942*) and 23 for *E. alticola* (*Lynn, 1943*); the number is not known for the other two species. In these cases no observations seem to have been made on the method of fertilization. One would expect
that the eggs laid on (dry) land should require some fluid material to enable the sperms to effect fertilization. There is no evidence that the female discharges extra gelatinous material, nor is there any modification in the oviduct which can be associated with this function. There is, moreover, no evidence to show that the egg mass is stirred to mix the milt. On the other hand, the Wolffian ducts of the males are modified to form a greatly dilated vesiculae seminales possessing a circlet of very prominent glandular villi. This is especially evident in *E. mubicola* (vide Pl. VIII, figs. 35, 36). Such a remarkable modification has not been encountered either in the literature or among the Salientians which I have studied. It is highly probable that the glandular villose walls provide a secretion in which the sperms are discharged over the eggs. It may well be that the whole egg mass is bathed in this spermatic fluid. It seems, therefore, that in this instance there is a definite correlation between the modified Wolffian duct and the terrestrial mode of breeding of these toads.

(3) All species of *Phyllomedusa* lay their eggs on leaves overhanging the water, and some specialized species apparently curl leaves around the egg mass, probably for the purpose of building nests (Noble, 1927). Noble (1931) further points out that
EXPLANATION OF PLATE XII.

Photomicrographs from series of transverse sections passing through the posterior region of the gut with the urinogenital ducts.

*Leptodactylus pentadactylus* (Laurenti).

(Female).

**Fig. 52.** Showing the uteri (M.d.) with overlying Wolffian ducts (W.d.) separated by the muscle in the posterior region. X 12.

**Fig. 53.** (ca 5.0 mm. after fig. 52). Showing the two uteri (M.d.) occluded, and the Wolffian ducts (W.d.) just anterior to the opening into the cloaca. X 12.

*Pleurodema cinerea* Cope.

(Male).

**Fig. 54.** Showing the separate openings of the Wolffian ducts (W.d.) into the cloaca (Cl.); the left has opened and the right just anterior to the opening. The urinary bladder (U.B.) just before opening. X 33.

(Female).

**Fig. 55.** Showing the uteri (M.d.) remaining unopened into the cloaca and the Wolffian ducts (W.d.) lying below them. X 45.

*Eupemphix punctulosus* (Cope).

(Male).

**Fig. 56.** Showing the separate Wolffian ducts (W.d.) before opening into the cloaca. X 45.
Phyllomedusa normally deposits empty egg capsules which may be used in the construction of its 'nest'. No evidence has been brought forward to show which part of the oviduct is responsible for the formation of these empty egg capsules. I have observed, in my studies on Phyllomedusa dacnicolor, some striking modifications of both the oviduct and the male Wolffian duct. The portion of the oviduct lying just anterior to the uterus is greatly dilated and filled with secretion (Text-fig. 31, M.d.) which appears to be responsible for providing material for building the 'nest' to which Noble refers. From the appearance of the ovary and the size of the egg it seems that a fairly large number of eggs are laid. The male is provided with a large thick-walled glandular seminal vesicle (Text-fig. 30, S.V.) which probably secretes and discharges a copious flow of seminal fluid. This may well be all the more necessary for effecting fertilization of eggs which are not stirred or beaten into a foam.

(4) I have also studied some other species which have peculiar breeding habits, namely, Dendrobates, Phyllobates and Gastrotheca. The first two genera have similar breeding habits, and "all species of both genera, so far as known, have aquatic larvae which their paternal parents carry to the pools on their backs." (Noble, 1927, p. 103).
It is well known also that all species of *Gastrotheca* carry their eggs in a single mass on their backs, but no observations have been made as to how the eggs reach the dorsal pouch (Noble, 1927). In every case the eggs are relatively large and few in number. No account has been published, however, of the mode of oviposition. I have not observed in these Salientians any modification in the urinogenital ducts that would suggest a correlation with the breeding habits. The enlarged transverse dilatation of the oviducts of *Dendrobates* and *Phyllobates* may well be due to large egg size. It is conceivable, however, that, owing to large size and reduced numbers, the eggs are laid one by one, and do not require a large amount of seminal fluid for fertilization. It, therefore, seems likely that species which breed out of water but lay only a few eggs, do not require any modification of the urinogenital ducts.

It may be mentioned, in passing, that for various anatomical reasons, Noble (1925, 1927, 1931) holds that *Dendrobates* and *Phyllobates* are closely related genera. The structural similarities of the urinogenital organs which I have observed in these two genera lend further support to Noble’s view.

Although *Rhinoderma* and *Hemisus* possess peculiar breeding habits, according to Noble (1927) and Wager (1929) respectively, I have not included them in this discussion, since males have not been
investigated by me.

(5) The ovoviviparous toads of Africa, *Nectophrynoides* and the "tailed" frog of America, *Ascaphus* are the only salientians which are alleged to practise internal fertilization. Although the former species has no external organs for transferring the sperms, the male of the latter possesses a 'tail' - an extension of the cloaca - which is believed to serve as an intromittent organ (Noble, 1925, 1931). Noble reported that males of *A. truei* possess a ring of enlarged cloacal glands inside the orifice of the 'tail', and just posterior to these glands lie a cluster of spines inside the cloaca. In his book (Noble, 1931, p.485, Fig.154c) these spines are shown in a figure of a fully distended cloacal appendage. In view of the presence of spines within the orifice of the cloacal 'tail', Noble and Putnam (1931) later raised the question whether the cloacal appendage could actually serve as an intromittent organ. De Villiers (1934) described and discussed the anatomy and physiology of the 'tail' as a true phallic organ in greater detail than Noble. He noted also that there is a system of dermal glands in the terminal part of the cloaca (tail), but did not observe the spines noted by Noble. He interpreted Noble's spines as actual bulges on the cloacal wall caused by the large
dermal glands. He is clearly right in saying that "it is quite impossible to miss spinose cuticular structures in sections." I fully agree with him, since I also did not find any such structures in my sections of this region. The female urinogenital organs have not previously been adequately described; sperms have, however, been found in the oviducts (Noble, 1925) (vide discussion on the urinogenital sinus, pp.159 - 160). I have shown that the cloaca of the female possesses a few glands in its walls (Pl.II, fig.13, Gl.) which have not been described for any other species of the Salientia. These glands are believed to play a part in the process of copulation. Thus both sexes show modifications which can be correlated with their breeding habits.

All the above remarks are in the nature of tentative suggestions. Nevertheless, it is apparent that the various modifications of the urinogenital organs can be better understood when examined in the light of breeding habits. Likewise the peculiarities in the breeding habits may be intelligently interpreted from a knowledge of the structure of the reproductive organs. It is concluded, therefore, that the structure of the urinogenital organs and the breeding habits, especially of those species which breed out of water, are interdependent. The ideal method is to combine
studies in the laboratory and the field, but where this is not possible, studies of one subject in the light of knowledge of the other, will lead to a better understanding of the correlation between structure and habit than investigations of either alone.
SUMMARY

1. The urinogenital organs of thirty-four species belonging to twenty-three genera of eleven families are described, in most of these species and eleven of the genera for the first time.

2. Some terminologies used in this paper and nomenclature of species investigated by previous authors are discussed.

3. The kidney pattern is more or less constant in all species, though variable in shape, length-breadth relation and position. The peculiarities in the kidneys of Uperodon and Dendrobates are emphasized.

4. Testes vary in shape and size, and also in position relative to the kidneys. They are attached tightly to the kidneys in Eleutherodactylus only. Testis size as indicative of relationship between Bufo and Leptodactylids is discussed.

5. Bidder's organ is present in all the species of Bufo only, except in my single specimen of B. fowleri.

6. The variation in the number of lobes of ovaries is discussed; and a number of genera and species
are shown, for the first time, to possess a simple sac-like ovary in which the ovum size is generally relatively large. It is indicated that the larger the ova the fewer are the number of eggs laid.

7. The relations of the urinogenital ducts of all the species were investigated by serial sections.

8. Various modifications of the Wolffian ducts are discussed. Evidence is presented to show that they are united terminally in some genera and species. The relative positions of the openings of the Wolffian and Müllerian ducts in the cloaca are reversed in Scaphiopus only.

9. Morphological variation of the vesicula seminalis is discussed; and Rana temporaria type of seminal vesicle is recorded for Phrynobatrachus.

10. The site of the production of the secretory mass that fills the Wolffian ducts of male Rhacophorus (and Chiromantis) is discussed.

11. A urinogenital sinus is recorded for the first time in a female Ascanthus and a male Rhinophrynus and its function discussed.

12. The uteri remain separate in most Salientia, but united uteri have been recorded in seventeen
genera, of which eight are here recorded for the first time. The function of the united uteri is discussed. Uteri of Salientia are divided into three groups - (i) uterus separatus, (ii) uterus communis, (iii) uterus septatus, - which are arranged in a linear series. The significance of these variations is discussed. Evidence is presented to show the occlusion of the uterine aperture into the cloaca after spawning. It is concluded that the uterus opens into the cloaca with the onset of the breeding phase and becomes occluded after spawning.

13. Rudimentary Müllerian ducts in males are recorded in ten out of twenty-three species examined; and it is suggested that the degeneration of the ducts takes place postero-anteriorly. Evidence is presented that they do not open into the cloaca as generally believed.

14. Modifications in the urinogenital organs of several species are discussed in relation to their breeding habits, and their interdependence is emphasized.
ABBREVIATIONS USED IN TEXT AND PLATE FIGURES.

B.O. — Bidder's organ.
Cl. — Cloaca.
F.B. — Fat-bodies.
Gl. — Gland.
K. — Kidney.
M.d. — Müllerian duct (oviduct).
O. — Ovary.
P.C.S. — Posterior cardinal sinus.
P.C.V. — Posterior vena cava.
R. — Rectum.
S.V. — Seminal vesicle.
T. — Testis.
U. — Uterus.
U.B. — Urinary bladder.
U.S. — Urinogenital sinus.
W.d. — Wolffian duct.
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EXPLANATION OF PLACE XIII.

Heleophryne purcelli Sclater.

(Female).

Photomicrographs from a series of transverse sections passing through the posterior region of the gut with the urinogenital ducts.

Fig. 57. Showing the two uteri (M.d.) separated by the partition wall; the Wolffian ducts (W.d.) lying juxtaposed over them. X 21.

Fig. 58. (0.50 mm. after fig. 57). Showing the confluence of the uteri (M.d.) and the Wolffian ducts (W.d.) X 21.

Fig. 59. (1.5 mm. after fig. 58). Showing the common uterus (M.d.) remaining unopened through the uterine papilla in the cloaca (Cl.). The common Wolffian duct (W.d.) lies in the cloacal wall before opening into the cloaca. X 33.

Fig. 60. (0.62 mm. after fig. 59). Showing the opening of the common Wolffian duct (W.d.) through the right side of the unopened common uterus (M.d.). The urinary bladder (U.B.) opens ventrally into the cloaca. X 33.
Text-figs. 23 & 24. - Diagrammatic ventral views of the urinogenital organs of *Dendrobates tinctorius*. 

$\times 4$ (23) - Male; (24) - Female (left ovary with fat-bodies not shown, and right oviduct not fully represented.)
DENDROBATIDAE

Dendrobates tinctorius (Schneider).

**MALE:** 40.0 mm. from snout to vent (A.M.N.H. No. 49298).

Loc. Shudikarwan, British Guiana.

Date. Not known.

Source. Dr. C. M. Bogert (A.M.N.H.).

(Text-fig. 23; Pl.XIV, fig. 61).

The kidneys (K.) are very long and narrow, extending to the posterior end of the body cavity. The right kidney extends beyond the anterior and posterior limits of the left. The ventral surface of both kidneys is flat at the anterior but distinctly concave at the posterior end, and the dorsal convex. The inner sides are thrown into incipient lobes, especially where the renal veins originate. The mesial edges are much thicker than the outer, and both ends are somewhat pointed. The kidney measurements are: right kidney 15.0 X 2.2 mm., left kidney 13.5 X 2.1 mm.

The testes (T.) are very small and lie ventral to the anterior end of the kidneys. They are more or less cylindrical bodies, though the posterior ends are much narrower than the anterior. There are only four or five vasa efferentia. Irregular patches of pigment are scattered over the testes. The testis measurements are: right testis 3.7 X 1.0 mm., left testis 3.7 X 1.0 mm. The fat-bodies (F.B.) are not extensive and of yellowish colour,
with only a few short digitations.

The Wolffian ducts (W.d.) arise about the middle of the outer edge of the kidneys. There appears to be no vesicula seminalis. Posteriorly the inner sides of both ducts come into close apposition to each other but remain quite separate throughout their entire course. They form terminally a bipartite papilla which does not bulge into the cloacal lumen (fig. 61, W.d.). It was noted, however, that the ducts decrease considerably in diameter within the papilla, and open separately into the cloaca by minute apertures. Another point of interest is that, due to the posterior extension of the kidney, the free portion of the Wolffian duct is much shorter than is usual. The outer walls of the ducts are unpigmented. There is no trace of the Müllerian ducts.

The urinary bladder is compact and the wall is somewhat thick; it opens ventrally into the cloaca opposite the openings of the Wolffian ducts.

**FEMALE:** 42.0 mm. from snout to vent.

(Text-fig. 24; Pl. XIV, figs. 62-64).

The kidneys (K.) are much the same as in the male, but not so asymmetrical. The kidney measurements are: right kidney 16.0 X 1.8 mm., left kidney 15.0 X 2.0 mm.

The ovaries (O.) are simple single thin-walled sacs (i.e., the ovary is not lobed), as in
Eleutherodactylus. Each ovary is held by mesovarium to the anterior end of the kidney, and contains ova in various stages of development. The immature ova are white, while the large ova, which seem to be quite ripe, are much darker in colour on one pole than on the other. There are nine or ten large ripe ova in each ovary with a maximum diameter of about 2.5 mm. The fat-bodies (F.B.) are very small with about half a dozen short digitations.

The oviducts (M.d.) are well developed, and flattened transversely throughout. The ostium abdominale is situated as usual at the roots of the lungs and is followed by a fairly long pars recta. The pars convoluta shows some convolutions at both the anterior and posterior level of the kidneys. Its diameter (about 2.7 mm.) is greatest at about the middle level of the kidney. The duct is of creamy white colour, but examination by binocular microscope revealed a scanty deposit of pigment on the inner side of the oviduct. The uterus is thin-walled and possesses low longitudinal folds. The two uteri are fused to form an unpaired chamber at their immediate point of contact. The common uterus (fig. 62, M.d.) extends for about 3.5 mm. before opening into the cloaca. It forms a bulging uterine papilla in the cloacal lumen (fig. 63, M.d.). Terminally the Wolffian ducts lie very close together. They
ducts lie close together within the cloacal wall before opening separately into the cloaca (fig. 56, W.d.). There is no trace of the Müllerian ducts. The urinary bladder is thick and compact and opens into the cloaca in the usual manner.

**Heleophryne purcelli** Sclater.

**FEMALE:** 49.0 mm. from snout to vent (S.I. No. 134).

**Loc.** Bainskloof, Wellington, S. Africa.

**Date.** November 11, 1930.

**Source.** Dr. C. A. du Toit (S.I.).

(Text-fig. 22; Pl. XIII, figs. 57-60).

The kidneys (K.) are elongate and flattened dorso-ventrally. The anterior and posterior ends are bluntly rounded and the outer edge broadly convex. The kidney measurements are: right kidney 14.9 X 2.6 mm., left kidney 14.6 X 2.3 mm.

The ovaries which are full of apparently ripe eggs are very hard due to the action of the preservative. Each ovary consists of four or five lobes. The ova are unpigmented and measure, on an average, 3.4 mm. in diameter. There is no pigment in the ovary. The fat-bodies (F.B.) are very small with five or six slender digitations and are attached to the ovary and the kidney.

The oviducts (M.d.) are well developed. The pars recta is short and broad. Some portion of the pars convoluta is thickened and gorged with a cream-coloured secretion. The uteri (U.) meet mesially and cover a small part of the ventral region of the
decrease in diameter in the cloacal wall and open separately, as in the male, by minute apertures into the cloaca (fig. 64, W.d.). Sections show that the walls of the urinogenital ducts are heavily pigmented.

The urinary bladder is similar to that of the male and opens into the cloaca opposite the opening of the common uterus (figs. 63, 64, U.B.).

**Dendrobates auratus** Girard.

**FEMALE**: 31.5 mm. from snout to vent.

Loc. Taboga Island, Panama.
Date. December 28, 1939.
Coll. Mr. G. C. Wood.
Source. Mr. A. Loveridge (M.C.Z.).

(Pl. XV, fig. 65.)

The urinogenital organisation is more or less similar to that of *D. tinctorius*. The kidney measurements are: right kidney 8.2 X 1.5 mm., left kidney 8.0 X 1.5 mm.

The ovary contains only immature ova which measure scarcely a millimetre in diameter. The fat-bodies are yellowish and so extensive that they occupy much of the space of the body cavity. No parts of the urinogenital organs were evident till they were carefully removed.

The oviducts have but few convolutions. The pars recta is long, and the largest transverse diameter of the oviduct is about 1.3 mm. As in *D. tinctorius*, the two uteri unite to form a common uterus (fig. 65, M.d.) which extends for about 2.34 mm. It does not
Text-figs. 25 & 26. - Diagrammatic ventral views of the urinogenital organs of Phylllobates nubicola flotator. X 12. (25) - Male; (26) - Female (left ovary and fat-bodies not shown, and right oviduct not fully represented.)
open into the cloaca, although a uterine papilla is formed; this is probably due to the immature condition of the specimen. The Wolffian ducts open separately into the cloaca on the right side of the uterine papilla. The urinary bladder is similar to that of D. tinctorius.

**Phyllobates nubicola flotator** Dunn.

**MALE:** 14.5 mm. from snout to vent (F.M.N.H. 13400).

Loc. Canal Zone, Barro Colorado Island, Panama.

Date. December 18, 1928.

Coll. Dr. K. P. Schmidt.

Source. Dr. C. H. Pope (C.M.N.H.).

(Text-fig. 25).

The kidneys (K.) are flattened dorso-ventrally, and slightly asymmetrical in size and position. The posterior end of each kidney is thick, especially its inner side. The anterior which are much narrower than the posterior ends, are slightly folded against each other dorsally. They are pigmented on the dorsal but fleshy white on the ventral surface. The kidney measurements are: right kidney 4.0 X 1.2 mm., left kidney 4.2 X 1.2 mm.

The testes (T.) are more or less globular bodies lying on the anterior half of the kidneys. The mesorchia holding the testes to the kidneys are very narrow and the vasa efferentia not visible. The round seminiferous tubules are quite apparent through the thin wall of the testes. The testis measurements are: right testis 1.1 X 0.8 mm., left testis
1.0 X 0.7 mm. The fat-bodies (F.B.) are simple, long finger-like processes attached to the testes with two digitations on the right and one only on the left.

The Wolffian ducts (W.d.) arise from the posterior outer end of the kidneys. There is no sign of a seminal vesicle. The endothelial linings of the Wolffian ducts are without any villi and consist of a single layer of cells. Posteriorly the ducts are juxtaposed and run through the cloacal wall forming a low papilla through which they open separately into the cloaca. There is no trace of the Müllerian ducts.

The urinary bladder is not extensive and is somewhat thickish and compact. It opens into the cloaca almost opposite the openings of the Wolffian ducts.

FEMALE: 15.5 mm. from snout to vent (F.M.N.H. 13399).

(Text-fig.26; Pl.XV, figs.66-68).

The kidneys (K.) are much like those of the male. The right kidney is situated distinctly at a higher level than the left. The kidney measurements are: right kidney 3.9 X 1.0 mm., left kidney 4.0 X 0.9 mm.

The ovaries (O.) consist of thin-walled simple sacs, as in Dendrobates, and appear to be fully mature. The ripe ova are pigmented and about 4 mm. in diameter. The small ova which are whitish and of
various sizes measure 1.3 mm. in diameter on the average. The fat-bodies are insignificantly small.

The oviducts (M.d.) are white, unpigmented and well developed. They are somewhat flattened transversely, as in Dendrobates, and measure about 1.1 mm. in diameter about the middle level of the kidney. The ducts have few convolutions, but are folded upon themselves into loops throughout their length. The pars recta is not evident between the ostium abdominale and the pars convoluta. The two uteri are confluent with each other at their point of contact as in Dendrobates. Anteriorly there are no longitudinal folds within the common uterus, but as it tapers towards the posterior end, a circle of prominent longitudinal folds gradually become evident (fig. 66, M.d.). A bulging uterine papilla is formed through which the common uterus opens into the cloaca (fig. 67, M.d.). The common uterus is about 2 mm. in length. The Wolffian ducts are similar to those of the male. Lying on a low papilla they open separately into the cloaca behind the uterine opening (fig. 68, W.d.). The urinary bladder is similar to that of the male.
EXPLANATION OF PLATE XIV.

Photomicrographs from series of transverse sections passing through the posterior region of the gut with the urinogenital ducts.

**Dendrobates tinctorius** (Schneider).

(Male).

Fig. 61. Showing the Wolffian ducts (W.d.) just before opening into the cloaca (Cl.) X 45.

(Female).

Fig. 62. Showing the common uterus (M.d.) and the separate Wolffian ducts (W.d.) behind the kidneys. X 33.

Fig. 63. (2.19 mm. after fig. 62). Showing the opening of the common uterus (M.d.) into the cloaca (Cl.), and the Wolffian ducts (W.d.) prior to opening. The urinary bladder (U.B.) is opening on the ventral side. X 45.

Fig. 64. (0.73 mm. after fig. 63). Showing the Wolffian ducts (W.d.) just before opening into the cloaca (Cl.). The openings of the uteri (M.d.) and the urinary bladder (U.B.) are still seen. X 45.
EXPLANATION OF PLATE XV.

Photomicrographs from series of transverse sections passing through the posterior region of the gut with the urinogenital ducts.

**Dendrobates auratus** Girard.
(Female).

Fig. 65. Showing the common uterus (M.d.) and the overlying separate Wolffian ducts (W.d.) prior to entering the cloacal wall. X 45.

**Phyllobates rubicola flotator** Dunn.
(Female).

Fig. 66. Showing the common uterus (M.d.) with the overlying Wolffian ducts (W.d.) prior to entering the cloacal wall. X 60.

Fig. 67. (0.17 mm. after fig. 66). Showing the opening of the common uterus (M.d.) into the cloaca (Cl.); the Wolffian ducts (W.d.) prior to opening separately. X 66.

Fig. 68. (0.19 mm. after fig. 67). Showing the Wolffian ducts (W.d.) just before opening separately into the cloaca (Cl.). X 66.
Text-fig. 27. - Diagrammatic ventral view of the urinogenital organs of a female *Rhinoderma darwinii* (right ovary with fat-bodies not shown.) X 9.
kidneys. They run separately towards the cloaca divided by a partition wall (fig. 57, M.d.). The Wolffian ducts arise from the anterior portion of the kidney, and run close together lying dorsally apposed to the uteri (fig. 57, W.d.). The uteri and the Wolffian ducts unite at almost the same level (fig. 58, M.d. and W.d.). The common uterus tapers gradually towards the cloaca, and a large number of longitudinal folds appear within it. A large uterine papilla which almost occupies the entire lumen of the cloaca is apparent, and the folds persist even within this structure (fig. 59, M.d.). The common uterus extends for about 2.5 mm. without opening into the cloaca, although its ventral wall, which hangs into it, is greatly attenuated (figs. 59, 60, M.d.). This indicates that it was about to establish an opening into the cloaca. The duct common Wolffian runs for about 2.2 mm. (220 sections) and narrows a little before opening into the right side of the cloaca above the occluded uterine papilla (fig. 60, W.d.).

The urinary bladder is thin-walled and moderately extensive and opens ventrally into the cloaca in the usual manner (fig. 60, U.B.).
RHINODERMATIDAE

Rhinoderma darwini Dum. et Bibr.

FEMALE: 26.0 mm. from snout to vent.

Loc. Banos de Toihuaca, Dept. of Cantin, Chile.  
Date. February, 1924.  
Coll. Mr. Carlos Reed.  
Source. Mr. A. Loveridge (M.C.Z.).  

(Text-fig.27; Pl.XVI, figs.69-72.)

The kidneys (K.) are cream-coloured and slightly asymmetrical in position, the left slightly anterior to the right. The ventral surface is flat, the dorsal slightly convex. The outer edge is distinctly semi-lunar. The kidney measurements are: right kidney 7.0 X 2.0 mm., left kidney 7.3 X 2.0 mm.

The ovaries (O.), which consist of single sacs, are held by mesovaria to the posterior two-thirds of the kidneys. Each one contains about a dozen ripe ova, the largest about 3 mm. in diameter. These ova are of deep brownish colour with one black pole. The small immature ova are of whitish colour. The fat-bodies (F.B.) attached to the ovary, are moderately developed and of a deep yellowish brown colour. They are compact masses with but few digitations.

The oviducts (M.d.) seem to be well developed and are greatly convoluted only at the posterior level of the kidneys. The pars recta is, however, fairly long and extends posteriorly as far as the middle level of the kidney. The uterus is thin-walled with longitudinal folds which are somewhat
low at the anterior, but much more prominent at the posterior end. The two uteri are in contact mesially and divided by a partition wall between them (fig. 69, M.d.) which soon disappears posteriorly, and an unpaired common uterus is formed (fig. 70, M.d.). The latter runs for about 2 mm. before opening through a low papilla into the cloaca (fig. 71, M.d.).

The appearance of the uterine papilla suggests that the uterus was opening in preparation for spawning. The thin-walled Wolffian ducts arise from the posterior part of the kidney. As they approach the cloaca they lie so close together that a partition wall intervenes between them (fig. 71, W.d.), but open separately into the cloaca (fig. 72, W.d.).

The urinary bladder is thick and compact and opens ventrally into the cloaca.
EXPLANATION OF PLATE XVI.

Rhinoderma darwini Dum. et Bibr.
(Female).

Photomicrographs from a series of transverse sections passing through the urinogenital ducts with the gut.

Fig. 69. Showing the uteri (M.d.) with the partition wall between them; the Wolffian ducts (W.d.) lying apposed to them. X 21.

Fig. 70. (1.07 mm. after fig. 69). Showing the confluence of the uteri (M.d.) through the disappearance of the partition wall. The Wolffian ducts (W.d.) lying slightly close to each other. X 21.

Fig. 71. (1.60 mm. after fig. 70). Showing the opening of the common uterus (M.d.) into the cloaca (Ct.); the Wolffian ducts (W.d.) lying in the cloacal wall separated by a thin partition prior to opening into the cloaca. X 33.

Fig. 72. (0.43 mm. after fig. 71). Showing the Wolffian ducts (W.d.) opening separately into the cloaca (Ct.). X 33.
Text-fig. 28. - Diagrammatic ventral view of the urinogenital organs of a male *Hyla regilla*. X 9.
HYLIDAE

_Hyla regilla_ Baird and Girard.

**MALE:** 29.0 mm. from snout to vent.

**Loc.** ? America.
**Date.** Not known.
**Source.** Turtox (purchased).

(Text-fig.28; Pl.XVII, figs.73,74).

The kidneys (K.) are similar to those of _Rana_ and asymmetrical in position, the right being situated at a slightly higher level than the left. Their posterior ends are narrower than the anterior ends. The ventral surface of the posterior portion of the kidneys bear some lobes. The measurements of both kidneys are: 5.5 X 1.7 mm.

The testes (T.) are highly pigmented ov oid bodies lying ventral to the anterior end of the kidneys. Three or four vasa efferentia enter the kidney from each testis. The testis measurements are: right testis 2.3 X 1.3 mm., left testis 2.4 X 1.2 mm. The fat-bodies (F.B.) are massive with a number (about 10) of digitations.

The Wolffian ducts (W.d.) arise from the posterior end of the kidneys and each dilates slightly to form a seminal vesicle (S.V.). The two ducts run close together towards the cloaca, but remain separate and distinct throughout. They form a bipartite papilla through which they open separately into the cloaca (fig.74, W.d.). Sections reveal
Text-fig. 29. - Diagrammatic ventral view of the urinogenital organs of a female *Hyla gratiosa* (left ovary with fat-bodies not shown, right oviduct not fully represented.) X 5.
that the inner wall of the seminal vesicle is raised into a number of low villi-like processes (fig. 73, W.d.) which however, disappear towards the posterior end.

There is no trace of the Müllerian ducts.

The urinary bladder is thickish, and opens into the cloaca as is usual in frogs and toads.

*Hyla gratiosa* Le Conte.

**FEMALE:** 60.0 mm. from snout to vent.

Loc. S. Carolina, America.

Date. March 8, 1935.

Source. Turtox (purchased).

(Text-fig. 29; Pl.XVII, figs. 75-77).

The kidneys (K.) are elongate and much lobed mesially; they are unpigmented except at the outer edges. The anterior ends are pointed and the posterior more or less rounded. The left kidney is situated at a slightly higher level than the right. The right kidney measures 15.0 X 3.1 mm., and the left 14.7 X 3.4 mm.

The ovaries (O.) appear to be quite well developed and mature. There are nine or eleven lobes. The ova are in various stages of development, the larger ones are pigmented on one pole and about a millimetre in diameter. The fat-bodies (F.B.) are very small with a number of short digitations.

The oviducts (M.d.) are well developed and greatly convoluted at the posterior level of the kidneys. The pars recta is fairly long. The two uteri (U.) are in contact with each other mesially
over the posterior ends of the kidneys and run separately towards the cloaca. Just before entering the cloaca a muscle intervenes between the uteri with their overlying Wolffian ducts as in *Leptodactylus*. Longitudinal folds are seen in this region, but anteriorly they are not much in evidence (fig. 75, M.d.). The uteri form a bulging uterine parilla through which they open separately into the cloaca (fig. 76, M.d.). The Wolffian ducts are uniform in diameter and open separately into the cloaca behind the uterine openings (fig. 75-77, W.d.). The urinary bladder is similar to that of *H. regilla*.

**Phyllomedusa dacnicolor** Cope.

**MALE:** 85.0 mm. from snout to vent.

Loc. Chilpancingo, Guerrero, Alt. 4,000 ft. Mexico.

Date. July-August, 1932.

Coll. Mr. W. W. Brewer.

Source. Mr. A. Loveridge (M.C.Z.).

(Text-fig. 30; Pl.XVIII, figs. 78-80).

The kidneys (K.) are cream-coloured and flattened dorso-ventrally; the dorsal surface is slightly convex. The right kidney is situated at a slightly higher level than the left. The edges are slightly thickened uniformly, and the outer edges almost straight. The kidney measurements are: right kidney 24.3 X 6.0 mm., left kidney 25.0 X 6.0 mm.

The testes (T.) are non-pigmented whitish ovaloid bodies and placed asymmetrically, the left being at a much lower level than the right, which lies
Text-fig. 30. - Diagrammatic ventral view of the urinogenital organs of a male *Phyllomedusa dacnicolor.* X \( \frac{2}{3} \).
EXPLANATION OF PLATE VIII.

Photomicrographs from a series of transverse sections passing through the Wolffian ducts after leaving the kidneys.

Eleutherodactylus rubicola Dunn.

(Male).

Fig. 35. Showing the Wolffian ducts (W.d.) in the region of the seminal vesicle after leaving the kidneys. Note the glandular villi on the inner walls of the ducts. X 45.

Fig. 36. (0.57 mm. after fig. 35). Showing the confluence of the Wolffian ducts (W.d.) with villi. X 45.

Fig. 37. (1.46 mm. after 36). Showing the opening of the common Wolffian duct (W.d.) into the cloaca without being fully incorporated within the cloacal wall. The urinary bladder (U.B.) opening on the ventral side. X 45.
adjacent to the anterior half of the kidney. The posterior ends of the testes are somewhat narrow. Seven vasa efferentia are given off from each testis to the kidney. The testis measurements are: right testis 12.8 X 5.0 mm., left testis 11.8 X 5.3 mm. The fat-bodies (F.B.) are moderately developed with a number of digitations.

The Wolffian duct (W.d.) on each side arises from the anterior end of the kidney as a distinct whitish tube which gradually increases in diameter along the outer edge of the kidney. It dilates into a thick-walled sac at the posterior level of the kidney, becoming folded upon itself with further increase in diameter. This is presumably the vesicula seminalis (S.V.) which receives also a few additional ducts from the posterior end of the kidney. The Müllerian ducts (M.d.) persist very prominently as in some species of Bufo. They appear as white unpigmented tubes a few millimetres from the kidney. There are a few transverse loops just anterior to the seminal vesicle. Anteriorly the Müllerian duct is slightly dilated and extends forward as far as the roots of the lungs, but no ostium abdominale was visible. Posteriorly the Müllerian duct passes ventrally over the Wolffian duct towards the cloaca. The wall of the seminal vesicle is greatly thickened (fig.78, W.d.) consisting of four or five layers of cells. There are also low glandular villi in the
region, which, however, disappear posteriorly. The Müllerian ducts unite posteriorly (fig. 79, M.d.) into a large transverse common chamber (common uterus) which gradually tapers towards the posterior end. The common Müllerian duct, with its overlying Wolffian ducts, forms a low urinogenital papilla within the cloaca. The common Müllerian duct, as in *Bufo*, ends blindly within this papilla, while the Wolffian ducts which at first run separately unite just prior to opening into the cloaca (fig. 80, M.d., W.d.). The opening is on the left side of the papilla containing the blind ending of the Müllerian duct.

The urinary bladder is thin-walled and fairly large. It opens ventrally into the cloaca just anterior to the opening of the Wolffian ducts on the opposite side.

**FEMALE:** 95.0 mm. from snout to vent.

(Text-fig. 31; Pl. XIX, figs. 81-83).

The kidneys (K.) are elongate and narrow and not easily visible ventrally. The anterior two-thirds are thickened and slightly convex on both surfaces, but the posterior portion is much flattened dorso-ventrally. The kidneys are slightly lobed mesially which are visible from the dorsal side only. The kidney measurements are: right kidney 28.3 X 6.0 mm., left kidney 27.7 X 5.2 mm.

The ovaries (O.) appear to be spent and contain non-pigmented ova in various stages of development.
Text-fig. 31. - Diagrammatic ventral view of the urinogenital organs of a female *Phyllomedusa dacnicolor* (left ovary with fat-bodies not shown and right oviduct not fully represented.) X 3.
There are eight or nine lobes in each ovary. The largest ovarian ovum measures 1.8 mm. in diameter. The fat-bodies (P.B.) are minute with a bunch of very small digitations.

The oviducts (M.d.) are very well developed and the pars recta moderately long. There are many convolutions which extend from the anterior to the middle level of the kidneys. The tube then suddenly increases in diameter (about 5.0 mm.) and the convolutions appear as transverse folds at the posterior level of the kidney. This portion seems to be comparable with the wide dilated part of the oviduct of *Leptodactylus*. The uterus arises dorsal to this dilated part and extends mesially over the posterior portion of the kidney to meet its fellow of the opposite side. Here a partition wall is formed between them which, however, soon disappears and an unpaired common uterus results (fig. 81, M.d.). The common uterus runs for about 7 mm. before opening into the cloaca. The uterus is thin-walled and devoid of longitudinal folds except in the posterior part adjacent to the cloaca. A bulging uterine papilla is formed which occupies the entire cloacal lumen; the opening of the common uterus is situated on its summit (fig. 82, M.d.).

The Wolffian ducts arise, as in the male, from the anterior end of the kidneys. After leaving the kidneys they increase slightly in diameter but
Text-fig. 32. - Diagrammatic ventral view of the urinogenital organs of a male Gastrotheca boliviana griswoldi (right fat-bodies not shown) X 7.
gradually narrow towards the posterior end. In the cloacal wall the two ducts lie close together (fig. 82, W.d.), and the wall between them breaks down just as they open into the cloaca (fig. 83, W.d.).

The urinary bladder is similar to that of the male. It occupies a considerable portion of the posterior body cavity, and opens into the cloaca opposite the opening of the uterus.

Gastrotheca boliviana griswoldi Shreve.

MALE: 37.0 mm. from snout to vent.

Loc. Maraynide, 45 miles N.E. of Tarma, 12,000 ft., Dept. Jumin, Peru.
Date. March 6 - May 13, 1939.
Coll. Mr. J. A. Griswold, Jr.
Source. Mr. A. Loveridge (M.C.Z.).

(Text-fig. 32; Pl.XX, fig. 84).

The kidneys (K.) are moderately large, compact and thick. The ventral surface is slightly convex, anterior end broadly rounded and the posterior bluntly pointed; the outer edge is almost straight. The kidneys are slightly lobed mesially. The dorsal surface only is pigmented. The posterior ends of the kidneys diverge, and the left kidney is situated at a slightly higher level than the right. The kidney measurements are: right kidney 8.7 X 2.1 mm., left kidney 8.0 X 2.3 mm.

The testes (T.) are whitish oval bodies situated anteriorly on the kidneys. The mesorchia holding the testes to the kidney are narrow and contain three or four vasa efferentia. The right testis measures
4.2 X 1.6 mm., and the left 3.5 X 1.7 mm. The fat-bodies (F.B.) are massive and extensive, of yellowish colour, and a large number of long finger-like processes arise from a thick broad basal mass.

The Wolffian ducts (W.d.) arise from the middle of the kidneys. They are more or less uniform in diameter and do not dilate into a vesicula seminalis. Posteriorly the two ducts curve round a muscle, as in *Leptodactylus*, and come to lie in apposition to each other as they enter the cloacal wall. A bipartite papilla is formed through which the ducts open separately into the cloaca (fig. 84, W.d.). No villi were observed on the inner walls of the Wolffian ducts.

The Müllerian ducts (Text-fig. 32, M.d.) are greatly aborted and present as black pigmented fine cords lying lateral to the kidneys. They run anteriorly as far as the roots of the lungs where pigment is absent, and no ostium abdominale was observed. Posteriorly they extend almost to the anterior free portion of the Wolffian ducts, but do not actually touch them.

The urinary bladder is thick and compact, and opens ventrally almost opposite the openings of the Wolffian ducts.
Text-fig. 33. - Diagrammatic ventral view of the urinogenital organs of a female Gastrotheca boliviana griswoldi (left ovary with fat-bodies not shown and right oviduct not fully represented.) X 3.
FEMALE: 38.0 mm. from snout to vent.

(Text-fig.33; Pl.XX, figs.85-87).

This is a female carrying eight developing eggs in the dorsal integumentary pouch, four on each side.

The kidneys (K.) are narrow and elongate, but almost of equal shape and size. They are dorso-ventrally convex. The right kidney is situated at a slightly higher level than the left. The outer edge is almost straight and the anterior and posterior ends are somewhat rounded. As in the male, the dorsal surface only is pigmented. The posterior halves of the kidneys are slightly lobed. The measurements of both the kidneys are: 9.3 X 1.7 mm.

Each ovary (O.) is a simple sac without lobes, and held tightly by the mesovarium to the kidney. The ovaries are spent, although the right one contained one large ripe ovum, 3.7 mm. in diameter. The fat-bodies attached to the ovary, and also lightly to the kidney, are extensive and yellowish in appearance with a large number of digitations.

The oviducts (M.d.) are well developed, and greatly convoluted throughout their length. The pars recta appears to be absent. The uteri approach each other mesially and cover the posterior ends of the kidneys. They run together posteriorly in apposition to each other so closely that a partition wall only separates them (fig.85, M.d.). Anteriorly
this uterine wall is somewhat thick, but without any prominent longitudinal folds. Longitudinal folds however, appear in the posterior narrow region where they are very prominent (fig. 86, M.d.). Towards the cloaca, the partition wall disappears and a common uterus is formed with a circle of longitudinal folds (fig. 86, M.d.). The common uterus extends for about a millimetre (90 sections) before terminating in the cloaca. It pushes into the cloacal lumen forming a bulging uterine papilla. No opening was visible in sections passing through this uterine papilla. The uterus, therefore, appears to be completely occluded (fig. 87, M.d.). As this is a breeding female the condition suggests that the uterine aperture may have closed after the eggs were discharged.

The Wolffian ducts (figs. 85-87, W.d.) are similar to those of the male, and open separately into the cloaca.

The urinary bladder is similar to that of the male. Figure 87 shows the opening of the urinary bladder (U.B.) into the cloaca.
EXPLANATION OF PLATE XVII.

Photomicrographs from series of transverse sections passing through the posterior region of the gut with the urinogenital ducts.

_Hyla regilla_ Baird and Girard.

**(Male).**

Fig. 73. Showing the Wolffian ducts (W.d.) in the posterior region of the seminal vesicle. Note the villi. X 45.

Fig. 74. (1.84 mm. after fig. 73). Showing the Wolffian ducts (W.d.) opening separately into the cloaca (C1.); the urinary bladder (U.B.) also opening ventrally. X 45.

_Hyla gratiosa_ Le Conte.

**(Female).**

Fig. 75. Showing the separate uteri (M.d.) and Wolffian ducts (W.d.) in relation to one another behind the kidneys. X 21.

Fig. 76. (3.90 mm. after fig. 75). Showing the two uteri opening separately through the uterine papilla into the cloaca (C1.). The Wolffian ducts (W.d.) lying above them in the cloacal wall. X 33.

Fig. 77. (0.19 mm. after fig. 76). Showing the Wolffian ducts (W.d.) just before opening separately into the cloaca behind the uteri (M.d.); the urinary bladder (U.B.) opening ventrally. X 33.
EXPLANATION OF PLATE XVIII.

Phyllomedusa dacnicolor Cope.

(Male).

Photomicrographs from a series of transverse sections passing through the posterior region of the gut with the urinogenital ducts.

Fig.78. Showing the thick-walled Wolffian ducts (W.d.) in the region of the seminal vesicle with the vestigial Müllerian ducts (M.d.) behind the kidneys. X 12.

Fig.79. (3.36 mm. after fig.78). Showing the confluence of the Müllerian ducts (M.d.) through the disappearance of the partition wall, and the Wolffian ducts (W.d.) lying above them. X 21.

Fig.80. (2.42 mm. after fig.79). Showing the Wolffian ducts (W.d.) becoming confluent through the disappearance of the partition wall just before opening into the cloaca (Cl.); and the vestigial Müllerian duct (M.d.) ending blindly in the cloacal papilla. X 33.
EXPLANATION OF PLATE XIX.

*Phyllomedusa dacnicolor* Cope, (Female).

Photomicrographs from a series of transverse sections passing through the posterior region of the gut with the urinogenital ducts.

Fig. 81. Showing the united uteri (M.d.) and the separate Wolffian ducts (W.d.). X 21.

Fig. 82. (5.50 mm. after fig. 81). Showing the opening of the common uterus (M.d.) into the cloaca (Cl.); the Wolffian ducts (W.d.) lying separately in the cloacal wall, and urinary bladder (U.B.) opening ventrally. X 21.

Fig. 83. (0.70 mm. after fig. 82). Showing the Wolffian ducts (W.d.) becoming confluent just before opening into the cloaca (Cl.). The uterine opening (M.d.) still persists; and the urinary bladder (U.B.) opening ventrally. X 21.
EXPLANATION OF PLATE XX.

Gastrotheca boliviana griswoldi Shreve.

Photomicrographs from series of transverse sections passing through the posterior region of the gut with the urinogenital ducts.

(Male).

Fig. 84. Showing the Wolffian ducts (W.d.) just before opening into the cloaca (Cl.). X 60.

(Female).

Fig. 85. Showing the two uteri (M.d.) with the partition between them; the Wolffian ducts (W.d.) lying above the uteri. X 21.

Fig. 86. (2.01 mm. after fig. 85). Showing the uteri (M.d.) becoming confluent through the disappearance of the partition wall; the Wolffian ducts (W.d.) lying separately. X 33.

Fig. 87. (0.88 mm. after fig. 86). Showing the occlusion of the uterine opening (M.d.) in the cloaca (Cl.); the Wolffian ducts (W.d.) lying in the cloacal wall prior to opening separately. The urinary bladder (U.B.) has opened ventrally. X 33.
Text-fig. 34.—Diagrammatic ventral view of the urinogenital organs of a male Phrynobatrachus kinangopensis. X 10.
RANIDAE

Phrynobatrachus kinangopensis Angel.

MALE: 20.0 mm. from snout to vent.


Date. February 3, 1934.

Source. Dr. C. A. du Toit (S.I.).

(Text-fig.34; Pl.XXI, figs.88 and 89).

The kidneys (K.) are distinctly of the ranid type, and almost of the same size and shape, though the left kidney is situated at a very slightly higher level than the right. The right kidney measures 4.0 X 1.7 mm., and the left 4.1 X 1.9 mm.

The testes (T.) are white oval bodies lying ventral to the middle region of the kidneys. There are three or four vasa efferentia. The right testis measures 1.7 X 1.3 mm., and the left 2.2 X 1.2 mm. The fat-bodies (F.B.) are enormously developed and more white in colour than the testis. Two finger-like processes are given off from a basal mass attached to the testis.

The Wolffian ducts (W.d.) after leaving the kidneys, expand laterally into vesiculae seminales (S.V.) more or less similar to those of R. temporaria. The seminal vesicles are composed of a number of minute chambers (fig.88, W.d.). The two ducts run in the usual manner towards the cloaca, and form a bipartite papilla which does not bulge into the cloaca (fig.89, W.d.), and open separately.
EXPLANATION OF PLATE IX.

Photomicrographs from series of transverse sections passing through the posterior region of the gut with the urinogenital ducts.

**Eleutherodactylus nubicola** Dunn.

*(Female)*

Fig. 38. Showing the common uterus (M.d.) and the united Wolffian ducts (W.d.) behind the posterior level of the kidneys. X 21.

Fig. 39. *(2.66 mm. after fig. 38)*. Showing the occlusion of the common uterus (M.d.) in the bulging uterine papilla. Note the secretory mass filling the entire lumen. The common Wolffian duct (W.d.) lying in the outer wall of the cloaca before opening into the cloaca. X 33.

**Eleutherodactylus alticola** Lynn.

*(Male)*

Fig. 40. Showing the Wolffian ducts (W.d.) posterior to the kidneys. Note the glandular villi (Specimen B). X 45.

Fig. 41. Same as above, but villi are absent in the Wolffian ducts (W.d.) (Specimen A). X 45.

Fig. 42. *(2.10 mm. after fig. 40)*. Showing the opening of the common Wolffian duct (W.d.) into the cloaca (Cl.). X 45.
is no trace of the Müllerian ducts.

The urinary bladder is compact, small and thickish; it opens into the cloaca opposite the openings of the Wolffian ducts.

Phrynobatrachus keniensis Barbour and Loveridge.

**FEMALE:** 21.5 mm. from snout to vent.

Loc. Lari Forest Station, Kenya Colony, Africa.

Date. February 3, 1934.

Source. Dr. C. A. du Toit (S.I.).

(Fl.XXI, fig.90).

The kidneys are essentially of the ranid type, but slightly folded on the dorsal side. Pigment is scattered on both surfaces. As in Ph. kinangopensis, they are slightly asymmetrical in position. The right kidney measures 5.0 X 1.3 mm., and the left 4.6 X 1.5 mm.

The ovaries are extensive and pushed back into the posterior part of the body cavity. Each consists of three or four lobes, containing ova of different sizes, the largest being about a millimetre in diameter. The ovarial wall possesses black pigmented bodies. One pole of the ripe ovum is brownish black; and immature ova are without pigment. The fat-bodies are small with one or two moderately long digitations.

The oviducts are well developed, but the pars recta is almost absent. The coilings begin close to the base of the lungs and the convolutions are similar to those of frogs (Rana). The oviducts
dilate dorsally into the thin-walled uteri which extend mesially to cover a small portion of the posterior end of the kidneys. They are of the usual ranid type forming a bulging uterine papilla through which they open separately into the cloaca (fig. 90, M.d.). The appearance of the openings suggests that they had recently ruptured. The Wolffian ducts are of uniform diameter after leaving the kidneys, and open separately into the cloaca behind the uterine papilla as is usual in Ranids.

The urinary bladder is similar to that of the male Ph. kinangopensis and opens into the cloaca almost opposite the openings of the Wolffian ducts.

**Hemisus marmoratum marmoratum** Peters.

**FEMALE.** 29.0 mm. from snout to vent.

Loc. Sokoki Forest, Kenya Colony, Africa.  
Date. June, 1932.  
Source. Dr. C. A. du Toit (S.I.).

(Pl.XXI, figs.91-93).

This specimen was unfortunately very poorly preserved. All the organs, viz., the ovaries, fat-bodies etc., were distorted, and their topography could not be determined without difficulty.

The kidneys are elongate and very narrow. They are smooth and flattened dorso-ventrally, but slightly thicker on the mesial inner margins than elsewhere. The outer edge is almost straight. The kidneys are not lobed. The right kidney measures 9.1 X 1.4 mm. and the left kidney 8.7 X
The ovaries are squeezed into two small pieces, situated anteriorly to the kidneys. The left ovary covers the anterior portion of the kidney of the same side. It was not possible to determine easily, but from a careful topographical examination it appears that the ovaries consist of single sacs. The ovarian ova are about 0.7 to 0.8 mm. in diameter. The ovaries appear to be spent. The fat-bodies are white and moderately developed with only three or four small digitations.

The oviducts are well developed, though less convoluted than those of other Ranid frogs. The pars recta is very small. There is no uterine dilatation as in other Salientians, but from the posterior level of the kidneys the two oviducts are slightly dilated and approach each other mesially. This portion is somewhat thinner than the anterior part of the oviduct. This, no doubt, represents the uterus. A little posterior to the dilatation, the two uteri fuse into an unpaired common chamber (figs. 91, 92, M.d.) which runs for about 5.2 mm. (521 sections) before opening into the cloaca. It forms a bulging uterine papilla within the cloaca through which it opens opposite the opening of the urinary bladder (fig. 93, M.d. and U.B.). The cavity of the uterus adjacent to the opening is completely filled with a secretory mass. The Wolffian ducts run as usual from the posterior end of the kidneys
(fig 91, W.d.). They fuse about 3.0 mm. (235 sections) from the point of union of the uteri (fig. 92, W.d.). The common Wolffian duct (fig. 93, W.d.) extends for about 2.5 mm. (240 sections) before opening into the cloaca behind and left of the uterine papilla.

The topography of the urinary bladder cannot be followed. Sections show that it is thin-walled and opens opposite the opening of the common uterus.
EXPLANATION OF PLATE XXI.

Photomicrographs from series of transverse sections passing through the posterior region of the gut with the urinogenital ducts.

Phrynobatrachus kinangopensis Angel.

(Male).

Fig. 88. Showing the Wolffian ducts with the seminal vesicles (W.d.) just behind the kidneys. X 60.

Fig. 89. (1.35 mm. after fig. 88). Showing the Wolffian ducts (W.d.) before opening separately into the cloaca (Cl.). The urinary bladder (U.B.) situated ventrally over the cloaca before opening. X 60.

Phrynobatrachus keniensis Barbour and Loveridge.

(Female).

Fig. 90. Showing the uteri (M.d.) opening separately into the cloaca. The Wolffian ducts (W.d.) remain separate. X 60.

Hemisus marmoratum marmoratum Peters.

(Female).

Fig. 91. Showing the coalescence of the uteri (M.d.). The Wolffian ducts (W.d.) remain separate. X 45.

Fig. 92. (2.96 mm. after fig. 91). Showing the common uterus (M.d.), and the confluence of the Wolffian ducts (W.d.). X 60.

Fig. 93. (2.27 mm. after fig. 92). Showing the opening of the common uterus (M.d.) into the cloaca (Cl.); the common Wolffian duct (W.d.) lying above it in the cloacal wall. The urinary bladder (U.B.) has opened already. X 45.
Text-fig. 35. — Diagrammatic ventral view of the urinogenital organs of a male *Rhacophorus bimaculatus*, X 6.
RHAACOPHORIDAE

Rhaconhorus bimaculatus  Boulenger.

MALE: 36.8 mm. from snout to vent.
Loc. Cherrapunji, Assam, India.
Date. July 28, 1943.
Coll. and Source. Mr. S. Bhattacharya.

(Text-fig. 35; Pl. XXII, figs. 94-97).

The kidneys (K.) are symmetrically placed and essentially of the Ranid type. The ventral surface is flat and the dorsal slightly convex. The right kidney measures 10.6 X 2.5 mm., and the left 10.0 X 2.5 mm.

The testes (T.) are rather small ovaloid whitish bodies, held loosely by mesorchia to the anterior end of the kidneys. Five vasa efferentia pass from each testis to the kidney. The right testis measures 3.6 X 1.7 mm., and the left 3.2 X 1.7 mm. The fat-bodies (F.B.) are rather small with a few short irregular digitations.

The Wolffian ducts (W.d.) are very striking. Unlike any of the preceding species, each arises from the anterior end of the kidney as a separate tube joined by a number of small ducts arising from the outer side of the kidney. Anteriorly the ducts are narrow but gradually increase in diameter towards the posterior end. They are not much dilated behind the kidneys, run side by side in apposition, but remain quite separate throughout their course till they open finally by two apertures into the cloaca.
The sections (figs.94,95, W.d.) show that the Wolffian duct consists of a glandular endothelial lining in the region situated lateral to the kidney, i.e. up to the posterior level of the kidney. The duct appears to have a few villi-like processes, which, however, disappear towards the posterior end. No villi were observed in the free portion of the Wolffian duct (fig.96, W.d.). Although there is a very slight dilatation of the duct behind the kidney, it can scarcely be described as a vesicula seminalis comparable with that of some frogs and toads. On the contrary, it appears that the anterior portion of the Wolffian duct lying lateral to the kidney may from the vesicula seminalis.

The urinary bladder is somewhat thickish and of the usual Ranid type.
Text-fig. 36. - Diagrammatic ventral view of the urinogenital organs of a male *Uperodon globulosum*, X 5.
MICROHYLIDAE.

Uperodon globulosum ( Günther).

MALE: 54.0 mm. from snout to vent.

Loc. Belghurria, Bengal, India.
Date. August 27, 1945.
Coll. and Source. Mr. D. Mukerji (C.U.).

(Text-fig. 36; Pl. XXII, fig. 98).

This species, the only male of which was first recorded by me (Bhaduri, 1945), is a rare burrowing Microhylid frog. The kidneys (K.) are somewhat flattened dorso-ventrally, and the outer borders broadly convex. The most peculiar feature is a cylindrical lobe which is folded upon the inner mesial side of the posterior region of each kidney extending forwards as far as the middle. The kidney is a little thicker in the anterior region than in the posterior. They are asymmetrical both in size and position, the right kidney extending the anterior and posterior ends of the left one. The kidney measurements are:

right kidney 12.0 X 4.0 mm., left kidney 10.0 X 3.5 mm.

The testes are rather small, highly pigmented, bean-shaped bodies, measuring 3.0 X 1.6 mm. Each is held loosely to the anterior portion of the kidney by the mesorchium through which pass seven vasa efferentia. The fat-bodies (F.B.) are not massive and are irregular in shape with a few short blunt digitations at the free end.

The Wolffian ducts (W.d.) arise from the
posterior third of the kidneys. The portion of the duct attached to the posterior end of the kidney is dilated slightly, and does not increase further in diameter on leaving the kidney. There appears to be no vesicula seminalis. The two ducts run as usual in apposition to each other and open separately into the cloaca (fig. 98, W.d.). There is no trace of the Müllerian ducts.

The urinary bladder is thin-walled and of the usual Ranid type.
Photomicrographs from series of transverse sections passing through the kidney and the posterior region of the gut with the urinogenital ducts.

**Rhacophorus bimaculatus** Boulenger.

(Male).

Fig. 94. Showing the Wolffian ducts (W.d.) in the anterior region of the kidney (K.). Note the glandular walls in the ducts. X 60.

Fig. 95. Showing the Wolffian ducts (W.d.) in the posterior region of the kidney (K.). Note also the glandular walls of the ducts. X 60.

Fig. 96. Showing the Wolffian ducts (W.d.) behind the kidney region. X 45.

Fig. 97. (1.57 mm. after fig. 96). Showing the Wolffian ducts (W.d.) opening separately into the cloaca (Cl.), the left duct having opened already. The urinary bladder (U.B.) has opened ventrally. X 45.

**Uperodon globulesum** Günther.

(Male).

Fig. 98. Showing the Wolffian ducts (W.d.) opening separately into the cloaca (Cl.), the right duct having opened already. The urinary bladder (U.B.) has already opened ventrally. X 33.
DISCUSSION

The kidney.

The kidneys are of much the same pattern in different species, and their size does not appear to bear any close relation to the total length of the animal. The length of the kidney varies considerably in different species and genera. That of Ascaphus truei is probably the longest. The length-breadth ratio also varies considerably. Spengel (1876) states that in Rana and Bufo the kidneys are 3 - 4 times as long as they are broad; in Xenopus 6 times, while in Cornufer vitianus, Adelotus brevis, Philautus and others the breadth is nearly half the length of the kidney. Koch (1933-34) does not seem to agree with Spengel in regard to Bufo, since she observed that in B. marinus the length of the kidney is more than 4 times its breadth. The present investigations show that in the majority of species the kidneys are 3 - 4 times as long as they are broad, while in Ascaphus, Heleophryne and Hemisus the length is about 5 - 6 times the breadth. In Dendrobates, however, the length is 5 - 8 times the breadth. The length-breadth ratio does not seem to be a useful generic feature, though it may be specific.

The kidneys are not in general lobed except
those of Bufo which are well known to be so. In Rhinophrynus, Dendrobates and Hylids they are slightly lobed. In Uperodon globulosum the folded lobe on the postero-mesial side of the kidney is very characteristic. This agrees with Devanesen's (1912) observations on U. systoma, and is probably a unique feature of the genus.

The shape of the kidney also varies in different species. In some species the outer lateral edge is almost straight, as in Scaphiornus, Gastrotheca, the female of Ascaphus etc.; in the majority, however, it is semilunar or broadly convex.

In Gastrotheca the kidneys appear to be folded upon each other. A somewhat similar condition is also apparent in Pleurodema. Sweet (1907) mentions that there is a tendency to folding in Cyclorana alboguttatus.

The asymmetry of the kidneys is neither specific nor generic, but is of frequent occurrence in Salientia as the present studies show. It is noted by Koch (1933-34) in Bufo and by Hoffman (1942) in a number of species of African Rhacophorids and Ranids.

The posterior extension of the kidneys in Dendrobates is very characteristic. In this feature Dendrobates differs from Phyllobates - a member of the same family, but resembles Atelopus varius of the allied family Atelopodidae described by Spengel (1876).
The testes.

The testes are in most species held loosely by the mesorchia to the mesial edges of the kidneys, but in *Eleutherodactylus* they are held very tightly to the kidneys so that the vasa efferentia are extremely difficult to discern.

It is well known that the testes vary considerably in shape and size in different species. This is related no doubt to the phase of the breeding cycle.

The position of the testes relative to the kidneys varies considerably. The testes are usually situated at the anterior end of the kidneys, but in some species they are placed in the middle, as in *Ascalaphus*, *Scaphiopus* and *Pleurodepa*. In *Eleutherodactylus nubicola* and *E. alticola* they are asymmetrically situated, but not in *E. portoricensis*. The greatest variability with regard to shape, size and position is exhibited by *Bufo*. Davis (1936) holds that the testes of *Bufo* are elongate. In the majority of species this is probably true, but in some they are characteristically small and of the usual *Ranid* type, for example, *E. stomaticus* and *B. quercicus* (*vide* Witschi, 1933, for the latter species). In view of the presumed elongate nature of the testes, Davis further suggested that *Leptodactylids* and *Bufonids* are very similar, but
this may not be important, since in both groups there are many species in which the testes are not elongate. Davis cites Physalaemus as having an ovate testis similar to that of Rana. The testes of Leptodactylids (excluding Eleutherodactylus), studied by me vary in shape. In Leptodactylus podicipinus and Eunemphix pustulosus they are broad and elongate, but narrow and small in Pleurodeina. Rau and Gatenby (1923) have pointed out that the testes are very small in L. pentadactylus, especially in comparison with L. bolivianus. Hoffman (1931) states that in Crinia georgiana the testes are very small as compared with those of Bufo. The Australian Leptodactylids also vary greatly in this respect (Sweet, 1907).

Hoffman (1942) holds that in the adult African Rhacophorids and Ranids the testes cover more than half the length of the kidneys, and that the left testis is invariably longer than the right. My studies do not, however, support such generalisations.

The number of vasa efferentia is also extremely variable both in individuals of the same species and on the two sides of the same individual (vide Sweet, 1907; Hoffman, 1942).

It is possible that the testis is characteristic for each species, but this is not borne out by the present studies. It appears, that their position may be constant in some species and even in some
genera, such as, Scaphiopus.

Bidder's organ.

Bidder's organ is the most characteristic structure of Bufo. It disappears generally from adult females (Witschi, 1933; Davis, 1936) and is very irregular in shape and size. It is now held to be a universal feature of the genus Bufo and of some other genera (Nectophrynoides, Pedostibes and Pseudobufo) which constitute the Bufonidae (sensu Davis, 1936). Owing to the absence of this structure, among other anatomical features, Bufo borbonica has been placed in a new genus of Atelopodidae (Davis, 1935). In Rhinophrynus dorsalis Bidder's organ is also stated to be absent (Rau and Gatenby, 1923; Stohler, 1932). Walker (1938) mentioned the absence of this structure as one of the characters for defining this monotypic family Rhinophrynidae. Further, it is not clear whether Bidder's organ is a permanent structure, but it is believed to be present in all juvenile specimens. I did not observe Bidder's organ in my examination of a single male specimen of B. fowleri, although it has been stated to be present in this species (Witschi, 1933; Davis, 1936). Bidder's organ may well be vestigial in some species, as in B. carens (Davis, 1936), or it may occasionally be missing (vide Witschi, 1933, p.432). However, its presence or absence is quite
enigmatical. Davis (1936, p.115) aptly remarks: "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 meagre."

The ovary.

According to Spengel (1876) the number of ovarian lobes differs in different species, but is almost constant within one and the same species. He notes that a simple undivided ovary is found in *Pelodytes punctatus*, 3 - 4 lobes in *Alytes*, 5 in *Discoglossus*, 6 - 8 in *Philautus* and *Rhacophorus*, 9 in *Hyla*, 9 - 12 in *Pelobates*, 15 in *Rana*, and there may be as many as 30 in *Bufo*. Only a few authors other than Spengel, have recorded data on the number of ovarian lobes possessed by frogs and toads (vide van den Broek 1933). Van den Broek comments that the number varies in different races of the same species and that in old specimens several lobes may unite into one. He concludes that both these facts probably explain the discrepancies in the accounts of other authors. He does not, however, cite the case
EXPLANATION OF PLACE X.

Photomicrographs from series of transverse sections passing through posterior region of the gut with the urinogenital ducts.

**Eleutherodactylus alticola** Lynn.  
(Female).

Fig. 43. Showing the common uterus (M.d.) and the separate Wolffian ducts (W.d.) behind the kidneys. X 45.

Fig. 44. (1.0 mm. after fig. 43). Showing the common uterus (M.d.) and the united Wolffian ducts (W.d.). X 45.

Fig. 45. (1.16 mm. after fig. 44). Showing the opening of the common uterus (M.d.) through the bulging uterine papilla into the cloaca (Cl.). The common Wolffian duct (W.d.) is within the cloacal wall. X 45.

**Eleutherodactylus orcuttii** Dunn.  
(Female).

Fig. 46. Showing the common uterus (M.d.) and the common Wolffian duct (W.d.) entering the cloaca (Cl.). X 45.

**Eleutherodactylus portoricensis** Schmidt.  
(Male).

Fig. 47. Showing the common Wolffian duct (W.d.) before entering the cloaca (Cl.). X 45.
of Pelodytes, nor show any species in which there is a single sac-like ovary without lobes on each side. The present investigations show that a number of genera and species possess on each side a simple sac-like ovary without apparent lobes, namely, *Ascaphus truei* (though immature), all the species of *Eleutherodactylus*, *Rhinoderma darwini*, the two species of *Dendrobates*, *Phyllobates nubicola flotator* and *Gastrotheca boliviana griswoldii*. *Hemisus m. marmoratum* may also have this simple type. The remaining species I have studied, have lobed ovaries, and I cannot make any comments on the numbers, since my observations are confined to examination of single specimens.

The size of the ripe ovum is subject to great fluctuations in *Salientia*; even within the limits of a single genus it may vary considerably (Noble, 1927). It may be noted in a general way that ovum size is proportionately larger in the simple sac-like type of ovary, so far as the species of *Salientia* studied in this paper are concerned. In some species it is rather small irrespective of body size, and the ovary in such species is generally lobed (*cf. Scaphiornus* and *Phrynobatrachus*). In some species the ova are relatively large, even in lobed ovaries, as in *Alytes* (Noble, 1927) and in *Heleophryne*. Noble holds that small species lay a small number of eggs. Data on the number of eggs laid by different species are
scanty, especially in the case of those which breed out of water. In some species the number is definitely small, as in Rhinoderma and Gastrotheca, probably also in Dendrobates and Phyllobates. It is reasonable to conclude that the larger the ova the fewer are the number of eggs laid.
The Wolffian duct.

The Wolffian ducts show some remarkable modifications in Salientia, especially in their terminal endings in the cloaca and in providing a seminal vesicle in males of some species.

As mentioned in the introduction, Spengel (1876) did not observe a union of the Wolffian ducts in any of the species he examined. According to him the ducts are always separate throughout their course. He gave the following list of species in which he observed separate openings of the ducts: both sexes of Rana temporaria, R. esculenta, Bufo bufo, B. calamita, Pelobates fuscus, Alytes obstetricians, Hyla arborea and Discoglossus pictus; females of Bufo melanostictus and Rhaconhorus leucomystax; and males of Bufo americanus (or B. terrestris), Bombina bombina, Limnodynastes dorsalis grayi, L. peronii, Adelotus brevis and Pyxicephalus sp. Subsequent authors paid but little attention to the actual openings of the Wolffian ducts, rather accepting the view that separate openings of the ducts are the rule.

According to Gilchrist and von Bonde (1922) the Wolffian ducts of Xenopus are united into a common duct, but in the male only and not in the female. This appears to be the only account on the ducts of this toad.

In describing separate openings of the Wolffian
ducts for *Bufo bufo*, *B. marinus* and *B. melanostictus* Koch (1933-34) credited a single male specimen of the last species with a terminal union of the ducts. Bhaduri and Banerjee (1939) showed that union is a normal feature in both sexes of *B. melanostictus*.

The present investigations show that the Wolffian ducts unite at their caudal ends in both sexes of *Ascaphus* and that the common duct does not open into the cloaca directly but into a urinogenital sinus. This has previously been observed by de Villiers (1934) in a male *Ascaphus* only. A similar terminal union of the ducts is recorded in the case of a male *Rhinophrynus* in which also the urinogenital sinus receives the common duct.

A terminal union of the ducts is found in the females of *Scaphiopus holbrookii* and *Megophrys parva*, while in both sexes of *S. couchii* and in the male of *S. holbrookii* they open separately. Probably separate openings are normally present in *Scaphiopus*, and the fusion, stated above, in the female *S. holbrookii* may, for the present, be viewed as an isolated case.

Most interesting observations are recorded in the genus *Bufo*. In all the male species of *Bufo* I have studied, the Wolffian ducts unite terminally with the exception of *B. boreas*. Incidentally it may be mentioned here that Witschi (1933, p.496, fig.39)
gave a diagram of a hermaphrodite specimen of *B. bufo*; he added some sections through the cloacal parts showing the relation of the Wolffian and Müllerian ducts, and stated in the legend, "with common opening of the Wolffian ducts." This, however, is not mentioned in the text. It should especially be noted that the united portion of the ducts in all species of *Bufo* where it is recorded, is of very short length, viz., less than one millimetre. It would appear that united Wolffian ducts may be a usual feature in many species. There may, however, be some species with separate ducts, as in *B. boreas*. In this light the condition of the posterior end of the Wolffian ducts in the genus *Bufo* may well be in a state of evolutionary flux.

Among the Leptodactylids I have studied, all the species of *Eleutherodactylus* as well as *Heleophryne purcelli* show a well-marked union of the Wolffian ducts adjacent to the cloaca. Hoffman (1931) has, however, missed this in *Heleophryne*.

Union of the ducts may not be clearly defined in *Phylomedusa dacnicolor*, although the partition wall disappears just before opening into the cloaca. (Pl. XVIII, fig. 80 and Pl. XIX, fig. 83, W.d.).

Union of the Wolffian ducts has not previously been recorded from the Ranids. It is, therefore, of great interest to find a pronounced union of the
ducts in a female *Hemius marmoratum*. In the remaining species I have studied, the openings of the Wolffian ducts remain separate.

Concerning the position of the openings of the Wolffian and Müllerian ducts into the cloaca, Spengel (1876) pointed out that the former is always situated behind the latter, and this holds good in all the species I have studied except *Scaphiopus*. It is interesting, therefore, to find the order reversed in *Scaphiopus*, i.e., the uteri open behind the Wolffian ducts, a unique feature among Salientian genera.

It is clearly seen then that in a number of genera and species a terminal union of the Wolffian ducts is a characteristic feature, which, therefore, clearly disproves Spengel's general conclusion (op. cit.) that the Wolffian ducts of Salientia remain separate throughout their length.

**The vesicula seminalis.**—Spengel (1876) gave a list of Salientia possessing a simple bottle-like dilatation at the free end of the Wolffian duct, namely, *Rana esculenta*, *R. pipiens*, *Hyla arborea*, *H. crepitans*, *Phyllomedusa*, *Philautus* and *Hypopachus*; in *R. temporaria* he stated that the lateral wall of the free portion of the Wolffian duct provides a chamber with extremely branched glandular tubes. Both these structures are generally described as
seminal vesicles, since sperms are said to be stored in them before discharge. He also pointed out that the seminal vesicles become much reduced in the non-breeding period. The spindle-shaped vesicula seminalis has since been recorded in many species, especially in *Bufo* and some *Rana* (Holmes, 1927; Koch, 1933-34; Witschi, 1933; Bhaduri and Bannerjee, 1939), and probably in some African Ranids and Rhacophorids (Hoffman, 1942), but very few have been recorded of the *R. temporaria* type. Boulenger (1896) gave a list of species of *Rana* which possess the latter type, but of slightly reduced size. Noble (1931) mentions a vesicula seminalis for *R. sylvatica*, and from his statement it appears to be of the *temporaria* type. I am not aware of any other genus of Salientia in which this type is recorded. So it is of interest to note a vesicula seminalis of this type in another Ranid genus *Phrynobatrachus kinangopensis*.

The present investigations show that the vesicula seminalis is very variable in different groups. The bottle-like dilatation of the seminal vesicle is present in *Scaphiopus* (2 species), *Hyla regilla* and all species of *Bufo* excepting *B. quercicus* (vide also Witschi, 1933, fig.18) and perhaps *B. boreas*. Rugh (1941) has shown that in *Hyla crucifer* it is of a different type and situated terminally.
The seminal vesicle which is recorded for *Eleutherodactylus* in the present investigation is very remarkable, especially as it is present in *E. rubicola* (Pl. VIII, figs. 35 and 36). In a similar way the vesicula seminalis of *Phyllomedusa dacnicolor* is also characteristic. In both these genera the vesicula seminalis seems to play a special part in the discharge of sperms.

In *Rhacophorus bimaculatus* the Wolffian duct lying lateral to the kidney is a remarkable feature. It is not exactly comparable with that of *Rh. maximus* (Bhaduri 1932) or *Chiromantis xerampelina* (Hoffman, 1932, 1942), though it appears to be more or less of the same type. The slightly dilated part of the Wolffian duct which lies behind the kidney has been interpreted as a vesicula seminalis by Hoffman (1942). I believe, however, that it would be better to confine the term to the anterior part which lies lateral to the kidney, since it is dilated and its walls are glandular. It has been pointed out previously that a secretory mass fills the Wolffian duct of *Rhacophorus* (Bhaduri, 1932). Hoffman (1943) investigated the site of production of this secretory mass in *Chiromantis*, and his findings show that the vasa efferentia and the anterior portion of the Wolffian ducts are responsible for its production. Although there is no secretory mass in the Wolffian ducts of *Rh. bimaculatus*, I do not find any
modification in the vasa efferentia likely to produce a secretion that will fill the Wolffian duct. Whereas the whole of the Wolffian duct situated laterally to the kidney possesses a glandular wall, while the portion of the duct lying behind the kidney does not (cf. figs. 94, 95 and 96, Pl. XXII). I believe, therefore, that only the anterior portion of the Wolffian duct is responsible for the production of the secretory mass.

In the remaining species I have studied, the vesicula seminalis is absent or not apparent owing probably to the stage of the breeding cycle.

The urinogenital sinus.— The urinogenital sinus, described first by de Villiers (1934) in a male Ascaphus truem, is the most remarkable feature of the urinogenital system of Salientia. Bhaduri and Rudra (1944) reported a slightly different urinogenital sinus in Microhyla ornata. The present investigations show that a urinogenital sinus is present also in the female Ascaphus, although very slightly different in shape and size from that of the male. The author adds now another example possessing a urinogenital sinus, in a male Mexican burrowing toad Rhinophrynus dorsalis. The urinogenital sinus into which the Wolffian ducts open, is situated dorsally to the cloaca in all these three species. It has already been pointed out that in Ascaphus
and Rhinophrynus the Wolffian ducts unite before opening into the sinus (vide supra), but in M. ornata they open separately. In the last-named species, moreover, the uteri do not open into the sinus, while in Ascaphus the relation between the uteri and the sinus indicates that a connection between them exists, though not observed. The apparent similarity between Ascaphus and Rhinophrynus, so far as this feature is concerned, seems to be interesting. It may be mentioned, in passing, that Walker (1938), in studying the relationships of the latter, directed attention to its resemblance to the former in the structure of the individual vertebrae.

Bhaduri and Rudra (1944) believed that the urinogenital sinus in the male of M. ornata probably acts as a vesicula seminalis, since the sperms descend into it before reaching the cloaca, while in the female it is a relic structure. In Rhinophrynus a mass of sperms has been identified descending from the Wolffian ducts into the sinus. It is quite likely, therefore, that the sinus acts as a sperm storing device similar to the vesicula seminalis. Noble (1925) encountered sperms in sections of oviducts of breeding females of Ascaphus without noticing the urinogenital sinus, and held that the spermatheca of Ascaphus lies in the oviduct. Unaccompanied by figures this statement is vague,
especially since it is difficult to miss the sinus if oviducts are cut serially adjacent to the cloaca. From the anatomical relationships that I have observed in the female *A. truei*, it seems that sperms reaching the oviducts (uteri) must pass through the sinus, and if this is the case, the urinogenital sinus may well act as a spermatheca instead of the oviduct. Whatever may be its function, the urinogenital sinus of Salientia is a highly interesting structure occurring as it does in the three genera of unrelated families.
The Müllerian duct.

The Müllerian duct has long been a puzzling problem in the vertebrate anatomy and embryology (Goodrich, 1930). The following discussion is an attempt to define its relations in Salientia.

In the female.

The müllerian duct in the female Salientia is the oviduct of which Spengel (1876) gave a general account. It is a straight tube in the young and extraordinarily coiled in the adult, most markedly so during the breeding season. He did not, however, find any differences worthy of mention between the anterior (pars recta) and middle (pars convoluta) sections of the oviduct in the species he studied.

The pars recta which is characteristic of some species of Rana and Bufo is not evident in all, especially in those which are of small size. It is very long and extended in Rhinoderma, though reported to be short by Beddard (1908b). In Ascaphus it is probably also long. It is almost absent in Scaphiopus, Phyllobates, Gastrotheca and Phrynobatrachus, while in the remaining genera and species it is rather short or very slightly extended.

The pars convoluta appears to be characteristic in some forms, such as, Dendrobates and Phyllobates in which it is dilated transversely and little
convoluted. In *Rhinoderma* it is slightly dilated transversely, but coilings are restricted to the posterior level of the *kidney* or anterior to the uterus. The pars convoluta is differently modified in *Leptodactylus* (3 species) and *Pleurodema* among the *Leptodactylids* and in *Phyllomedusa* among the *Hylids*. The posterior portion of the pars convoluta, i.e., the portion lying just anterior to the uterus, increases enormously in diameter and is markedly evident in *L. pentadactylus* and *Ph. dacnicolor*. No author except Cope (1889) has observed such a modification in any Salientia. He casually mentioned this feature in *L. ocellatus* by saying that "the 'uterine' sacs at the exit of the oviducts are of great size, and at certain seasons distended with an albuminous gelatine, when they present several convolutions. In spirits they occasion the presence of a large convoluted mass of coagulum." He is, however, wrong in considering this portion as the anterior end of the uterus. It thus appears that this modification has something to do with an extra gelatinous secretion during laying of eggs (*vide* pp. 186-187).

The uterus.— The uterus is the most interesting section of the oviduct from the anatomical point of view. It is thin-walled and provided with longitudinal folds which may be glandular. These
longitudinal folds may be absent in some species, especially in the anterior section of the uterus. It is capable of enormous expansion which becomes quite apparent when eggs are lodged within it. Spengel made an important contribution to our knowledge of uteri in different species. The species of Bufo which he studied, all possess a terminal union of the uteri, and the common uterus extends for about 5 mm. before opening into the cloaca. With regard to Alytes and Hyla, however, he states (Spengel, 1876, p.92): "Zu wirklicher Vereinigung und gemeinsamer Ausmündung der Eileiter kommt es ferner bei Alytes obstetricans; nur scheinbar ist dieselbe indessen bei Hyla, wo die Eileitermündungen zwar auf einer gemeinsamen Papille liegen, aber die Lumina durch eine mittlere Scheidewand vollständig getrennt sind." It is not clear what Spengel meant by 'wirklicher Vereinigung' in Alytes. Subsequent authors appear to have accepted Spengel's observations, though interpreting them differently. I like to quote here these authors to show the vagueness of the statement of the 'real union' in Alytes. Gadow (1901, p.52) states: "As a rule each oviduct opens separately into the cloaca, but in Hyla they have one unpaired opening, while in Bufo and Alytes the lower parts of both oviducts are themselves confluent." Felix and Bühler (1906, p.754) write:
"Die vereinigung beschränkt sich meist nicht nur auf die Mündung, sondern betrifft auch die Endabschnitte der Müller'schen Gänge, so dass sich ein kleiner unpaaren Uterus ausbilden kann."

Besides citing Alytes and Bufo (from Spengel's account) they included the example Pipa pipa from Grönberg's (1894) account. Noble (1931, p.273) says: "The Müllerian ducts usually open separately into the cloaca in most Amphibia, but in Bufo and Alytes they may (italics mine) unite just anteriorly to the cloaca, while in Nectophrynoides the chamber resulting from the fusion produces a bicornuate uterus in which the young develop."

Lastly, van den Broek (1933, pp.80-81) writes: "Die kaudalen Enden der Eileiter der Anuren können getrennt bleiben (Rana) oder über eine kürzere (Alytes obstetricans) oder längere (Bufo vulgaris) Strecke median verbunden sein." It is indeed difficult from such statements to appraise the uterine condition in Alytes.

Spengel's unequivocal statement of a 'real union', read in context with the condition seen in Bufo, it appears to me, must mean that there is no partition wall, and that the two uteri become confluent into an unpaired uterus at the point where they touch each other.

Further, in reference to Bombina, Spengel showed great variability both in the uterine condition as well as in the Wolffian ducts. Of the
eight individuals he examined, seven possessed simple oviducal openings, i.e., the uteri united, and possessed a common opening; in the eighth individual the uteri remained quite separate throughout. With regard to the course and openings of the Wolffian ducts, the first seven cases were divided into three groups. He figured these relations of the urinogenital ducts in three diagrams (vide Taf. IV, figs. 10a, 10b, 10c). No subsequent authors have treated Bombina in their writings probably on account of these variations.

Spengel gave a list of Salientia with separate openings of the uteri, namely, *Rana* (all species) *Rhacophorus leucomystax*, *Philautus* sp, *Discoglossus* and *Pelobates*. He did not mention the condition of uterus and its opening in *Pelodytes*, *Megophrys*, *Pseudophryne* and *Atelopus*.

From the point of view of a united uterus there are a few more records which have either escaped notice of, or have been ignored by authors (Noble, 1931; van den Broek 1933). Beddard's (1907a; 1908) studies showed that the uteri unite terminally in *Megophrys nasuta* and *Rhinoderma darwini* at least. A common uterus has been noted also in *Heleophryne purcelli* (Hoffman, 1932) and in *Kassina s. senegalensis* (Hoffman, 1942), though Hoffman's statement regarding this point is somewhat vague. He
(Hoffman, 1932, p. 405) writes for H. purcelli:
"The two oviducts unite before entering the cloaca (Cf. Rana, Bufo and Crinia)." In the case of the last genus he studied only a male of C. georgiana, nor did he point out which genus Rana or Bufo, H. purcelli resembles more closely. Again, in the case of an immature female specimen of K. senegalensis he (Hoffman, 1942, p. 118) states: "Posteriorly the oviducts run along the outer borders of the kidneys, expand considerably, and unite before entering the cloaca as in Rana and in Bufo." The comparison with Rana is not only vague but misleading. Angel and Lamotte (1944) have figured a common uterus for Nectophrynoides occidentalis. Other recent authors (Starks and Howard, 1929; Witschi, 1933; Koch, 1933-34; Bhaduri and Banerjee, 1939; Al-Hussaini, 1939) who have studied species of Bufo, have merely confirmed Spengel's observation.

From this review it is apparent that nine genera (Alytes, Bombina, Pipa, Megophrys, Bufo, Nectophrynoides, Heleophryne, Rhinoderma and Kassina) have been credited with a common uterus, although the cases of Bombina and Kassina appear to be doubtful. The present studies alone have added this feature in a number of genera and species, namely, Ascaphus, Scaphiopus (2 species), Megophrys, Eleutherodactylus (3 species), Heleophryne, Dendrobates (2 species), Phyllobates, Rhinoderma, Phylomedusa, Gastrotheca
and Hemisus. Excluding Megophrys, Helaophryne and Rhinoderma, since these confirm previous observations, I have added eight more genera. Seventeen genera, including representatives of almost every family of Salientia, are now known to possess a common uterus. Separate uteri have been recorded previously in thirteen genera, namely, Rana, Rhacophorus, Philautus, Uperodon, Microhyla, Discoglossus, Pelobates, Xenopus, Megalixalus, Hyperolius, Hylambates, Pyxicephalus, Natalobatrachus. To these the present studies add the following, Leptodactylus (3 species), Pleurodema, Hyla and Phrynobatrachus.

It is seen from the above that in a large number of genera a common uterus is as often a characteristic feature as the separate uteri, and it, therefore, disproves clearly the view of earlier authors (Gadow, 1901; Noble, 1931; van den Broek 1933, vide quotations above) that the uteri open separately in most Salientia.

So far I have discussed the condition of the uteri only as united or separate. The union, however, may be far from complete, and I shall now discuss variations in the degree of union observed in different species. Little attention has been paid by previous authors to this aspect, though it possibly may be of functional or evolutionary significance.
The present investigations have shown clearly that the extent of the union of uteri differs from genus to genus. In *Eleutherodactylus*, *Dendrobates* etc., the two uteri coalesce into a common uterus at their point of contact mesially. In *Rhinoderma* a partition runs between the uteri, but disappears soon, while it persists over a considerable length in *Heleophryne* and *Gastrotheca*, particularly marked in the latter. Viewed in this light the uterine condition (separate and united) of different genera and species may conveniently be divided into three following broad groups.

(1) The *uteros separatus* group. The Ranid condition of the uteri is very well known. Since they remain quite separate throughout their whole length, the condition may be called the *uteros separatus*.

(2) The *uteros communis* group. In cases where the two uteri become confluent into an unpaired common uterus, i.e., the partition does not run between them, the condition of the uteri may be called the *uteros communis*.

(3) The *uteros septatus* group. In between the above two extreme types are cases in which a partition runs antero-posteriorly between the uteri in varying degree forming posteriorly a common uterus, the extent of which differs in different genera. These cases are grouped, for the present, under a
Text-fig. 3. — Schematic figures of the uteri of Salientia.
I. Uterus separatus group (Rana and others);
II-V. Uterus septatus groups (II. Gastrotheca; III. Bufo; IV. Phyllomedusa; V. Rhinoderma; and others);
VI. Uterus communis group (Eleutherodactylus and others).