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EDITED BY FRANK E. LUTZ

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DATES OF PUBLICATION OF SEPARATES

The edition of separates is 300 copies, of which about 100 are mailed on the date of issue, and the others placed on sale in the Library.

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ERRATA

Page   6, line 20 from bottom, for *Kallula* read *Kaloula*.
"   38, line 12 from bottom, for *Kallula* read *Kaloula*.
"   100, line 6 from bottom, for Argyradite read Argyrodite.
"   106, line 18 from bottom, for Sommerville read Somerville.
"   120, line 18 from top, for Breithopite read Breithaupite.
"   120, line 8 from bottom, for Brochanthite read Brochantite.
"   138, line 3 from top, for Gereas read Geraes.
"   163, line 6 from bottom, for Freidlerite read Fiedlerite.
"   193, line 18 from bottom, for 1.39.1 read 13.9.1.
"   195, line 6 from bottom, for Mauzellite read Mauzeliite.
"   230, line 16 from bottom, for Realger read Realgar.
"   230, line 14 from bottom, for Alchar read Allchar.
"   232, line 4 from top, for Reibeckite read Riebeckite.
'   238, line 1 from top, for Seligmanite read Seligmannite.
"   241, line 11 from bottom, for Sousmansite read Soumansite.
"   249, line 15 from bottom, for Sulphoborate read Sulphoborite.
"   265, line 14 from top, for $\frac{1}{3}^7$ read $\frac{1}{2}^7$ and for 3 read 2.
"   265, line 19 from top, for 17 read 27 throughout line.
"   265, line 15 from bottom, for $\overline{91}$ read $\overline{19}$.
"   439, line 18 from bottom, delete the second with.
"   448, line 14 from top, for disk on read disk than on.
"   449, line 7 from bottom, for *Macrolapmis* read *Macrolampis*.
"   456, line 10 from bottom, for *Claucus* read *Glaucus*.
"   467, line 1 from top, for *sauvis* read *suavis*.
"   470, line 20 from bottom, for in *nefarius* read is *nefarius*.
"   542, line 14 from top, for *Bratrachiderpeton* read *Batrachiderpeton*.
"   630, line 17 from top, for *Phyolldactylus* read *Phyllodactylus*.

Article I.—THE PHYLOGENY OF THE SALIENTIA

I. THE OSTEOLOGY AND THE THIGH MUSCULATURE; THEIR BEAR-
ING ON CLASSIFICATION AND PHYLOGENY

By G. K. NOBLE

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INTRODUCTION

Although the frog is perhaps as well known anatomically as any vertebrate except man and is one of the most familiar animals of both anatomical and physiological laboratories, nevertheless, our knowledge of the structure of frogs other than the genus *Rana* is extremely limited and based upon the study of very few types. This lack of information concerning the structure of any but the most familiar forms is chiefly responsible for the artificial and largely arbitrary classification at present in use. In recent years a few of the specialized forms have been studied, chiefly by Beddard, but these accounts are neither sufficiently detailed nor include enough forms to be of value to us in a phylogenetic study. The great need has been a detailed study of any structure carried through a large series of genera, in order that it may be definitely stated whether or not the various modifications of that structure may be utilized in bolstering up our present weak classification, or perhaps can form the basis of a more solid one. In the present paper, I have first tried to place our present classification on a firmer basis, and then have examined in detail the modifications of a single complex, the thigh musculatures through a great many genera with a view to determining how far this evidence supports the revised classification. Much more work remaine to be done in studying other structures throughout a sufficiently large number of genera. It is only then that this revised classification can be fully accepted. In the meantime, I believe it will remain a suggestive scheme, and it is the only one that seems to be supported by all the known facts.

In studying the specialization which the thigh musculature of the frogs has undergone, it was found advisable to attempt to homologize the thigh muscles with those of the salamander. Attempts by former workers could not be accepted for various reasons. I have had the advantage of examining numerous genera of both frogs and salamanders. Of equal importance is the fact that I have been able by means of the acetic-osmic method to study the innervation of the thigh musculature in more detail than have these former writers. The thigh musculature of the most primitive frogs was found to be not very different from that of the more generalized salamanders. Starting with this primitive type, it was possible to trace out several distinct but often parallel lines of specialization.

Lastly, the different point of view expressed in this paper regarding the classification of the Salientia has called for a reconsideration of

the migrations and adaptations of the frogs and toads.   Amphibians, because of their dependence on many factors in the environment, have been recognized as excellent material for zoögeographic studies.   It is obvious that no zoögeographical discussion can have much importance unless based on a consideration of natural groups.   The present paper is primarily an attempt to determine what are the natural groups and, while it is realized that these conclusions may be modified as more structures are fully examined, nevertheless, it is believed that we have now sufficient data assembled to warrant the establishing of a sounder concept of the phylogeny of the Salientia.

In the course of the work I have supplemented my study of the extensive material in The American Museum of Natural History by an examination of many unique or rare forms in the Museum of Comparative Zoölogy, Cambridge, Mass. My thanks are due to Dr. T. Barbour for this privilege.   I am also indebted to Dr. A. G. Ruthven of the University of Michigan for the loan or exchange of several interesting species. I am especially obliged to him for the opportunity of dissecting a unique specimen of the remarkable frog *Amphignathodon*.   Dr. L. Stejneger of the U. S. National Museum has loaned me several interesting neotropical forms.   Mr. H. A. Fowler of the Philadelphia Academy of Natural Sciences has placed the collections of the Academy at my disposal.   I am indebted to Dr. E. D. Merril of the Bureau of Science, Manila, and to Mr. E. H. Taylor for a paratype of *Hazelia spinosa*.   Throughout the work I have had the kindly aid and advice of Dr. W. K. Gregory.

INADEQUACY OF TAXONOMIC CHARACTERS AT PRESENT IN USE

PRESENT STATUS OF CLASSIFICATION

Our present classification of the Salientia dates from the appearance of Boulenger's 'Catalogue' in 1882, although this system was but a modification of that proposed by Cope in 1864 and 1865. The history of the classification has been outlined by Hoffmann (1878) and Gadow (1901) and need not be entered into here. Since the appearance of Boulenger's 'Catalogue' much evidence has been brought forward from time to time tending to show that our present classification of the frogs and toads is largely artificial. This evidence has not been brought forward in any one paper, although Gadow (1901) and Boulenger (1910) in their recent general books have made certain constructive changes in the system.

It is very regrettable that so few characters are utilized in our system of classification. Not only are these characters few in number but some of them are certainly not of primary importance. It is, perhaps, not surprising that so much destructive evidence has been brought forth in recent years against our present classification. Of constructive contributions, there have been but few. The chief objection to all of these is that the investigators have considered far too few forms. Even such an extensive work as that of Beddard (1907a) on the Pelobatidæ must be carried further through other genera before it can be accepted.

But a small proportion of the few characters given by Beddard (1907a, p. 904) as defining the Pelobatidæ are actually distinctive of the family. I find that the œsophageal muscle is wanting in both *Scaphiopus holbrookii* and *Pelodytes punctatus*. Beddard was apparently not aware of either the earlier work of Perrin (1892) or that of Nussbaum (1898); otherwise he would not have stated that the absence of a deep-seated semitendinosus was peculiar to the Pelobatidæ. Many leptodactylids (for example *Leptodactylus pentadactylus*) possess a special slip of the rectus abdominis attached to the posterior border of the coracoid. In *Rhinophrynus dorsalis*, this slip is enormously developed. I find a pectoralis, portio epicoracoidea, in *Megalophrys montana* as well as in all other pelobatids which I have examined. On further investigation some of the structures described by Beddard may be found to be characteristic of the family. This is especially true of the hyoid apparatus and of the urinogenital system.

From what will appear below under the discussion of the pectoral girdle and that of the thigh muscles, it will not seem so remarkable as

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Beddard (1908a, p. 684) would have us believe "that *Rhinoderma* not only shows no likeness to its ally *Breviceps*, but is even more simple than *Rana*."

The anatomy of at least one of the primitive brevicipitids should be described in detail before one can judge how many, if any, of the specialized features of *Breviceps* and *Hemisus* as described by Beddard are really of value in tracing out a phylogenetic scheme. Unfortunately, the work of Beddard cannot be accepted without verification. For instance, the coraco-radialis is not absent in *Breviceps* as stated by Beddard (1908, p. 40) but is present as a very well-developed muscle.

The recent work of Anthony and Vallois (1914) on the myology and osteology of the shoulder region includes too few forms and is not sufficiently detailed for us to draw conclusions of value to us in determining the inter-relations of the Salientia. Characters which they find diagnostic of genera cannot be utilized as distinctive of families. Thus, I find the two muscles which they call the scapulohumeralis profundus anterior and the subscapularis present not only in *Alytes* but in *Bufo marinus, Hyla maxima, Atelopus ignescens, Pternohyla fodiens*, and in all leptodactylids examined, including the specialized *Batrachophrynus microphthalmus* and *Ceratophrys americana*. These authors indicate both muscles as present in such a specialized brevicipitid as *Kallula pulchra*. The presence or absence of these muscles cannot be used in defining families.

Further, the muscle called supracoracoideus profundus by Anthony and Vallois (*loc. cit.*) seems to be altogether too variable to be utilized in distinguishing the primary groups of Salientia. Still, it is obvious from the work of Anthony and Vallois that the discoglossids have the most primitive pectoral musculature and that the pipids and pelobatids possess a complex but little advanced over the conditions found in the discoglossids, while the representatives of all the other families show more specialized conditions. These conclusions support the conclusions reached below. Still, it must be emphasized that all the work which has been done until now on the pectoral musculature of the Salientia is too incomplete for utilization at this time in a classification.

It is unfortunate that none of this myological work can be utilized at the present moment. We are thus forced to return to the osteological characters which are both few and often untrustworthy. But, as they have been the primary structures about which our ideas of salientian phylogeny have until this time been woven, it is essential that we examine them carefully before rejecting them or continuing to accept them.

DENTITION

The presence or absence of teeth have, since the appearance of Duméril and Bibron's 'Erpétologie Générale' in 1841, been considered of primary importance in defining the larger groups of Salientia. In all classifications proposed since that time the families of frogs and toads have been in part distinguished by this presence or absence character. That such a character may not always be of primary importance was noticed long ago by Cope (1867a, p. 189). Although Boulenger considered it such in his catalogue (1882), he soon after (1888) called attention to its secondary importance. Gadow (1901) considered the character as worthy of subfamily distinction. This, however, does not seem to me to be any advance. A number of toothless genera have been known since the early investigations of Cope to be more closely related to toothed than to any other toothless genera. The mere relegating of the toothless genera to separate categories, whether these be called families or subfamilies, does not express the genetic relationship. The discovery of *Ophryophryne* (Boulenger, 1903, p. 187) further confirmed the growing opinion that at least some of the toothless families were heterogeneous assemblages composed of genera derived from totally different stocks simply by the loss of teeth.

It had long been noticed that the so-called teeth in the lower jaw of some forms were not true teeth. Brocchi (1877) had made it clear that in *Hemiphractus* these mandibular teeth were nothing but sawtooth-like prolongations of the bones composing the lower jaw. Still, these mandibular protuberances were commonly considered the equivalent of teeth in the classifications and, further, were often called teeth. As late as 1917, Arldt speaks (p. 126) of them as teeth and theorizes that the forms possessing them must be more primitive than their relatives having teeth only in the upper jaw, presumably because the ancestral Salientia were supposed to have teeth in both jaws. It was not until Boulenger pointed out the close affinity of *Dimorphognathus* to *Arthroleptis*, the former being merely an *Arthroleptis* which develops "teeth" on the lower jaw in the case of the male, that it became well recognized that families or subfamilies founded on the presence of "teeth" in both jaws were just as artificial groupings as those founded on the total absence of teeth.

The old system of classification, although obviously not expressive of genetic relationship, was apparently without a better substitute when Boulenger (1910) wrote his general work, 'Les Batraciens.' Boulenger

did, however, make a distinct improvement in the system by eliminating the families (or subfamilies) Dendrobatidæ, Ceratobatrachidæ, and Genyophrynidæ, and by referring the genera of which they were composed to the families from which these genera were directly derived either by a loss of teeth or by the development of protuberances on the lower jaw. This system apparently was not accepted by all. Ruthven (1915) described *Geobatrachus*, a new genus, which he referred to the Dendrobatidæ. This genus is a very interesting one, and I shall have occasion to discuss it in more detail below. It is sufficient to say now that Ruthven was mistaken in regard to its lacking the maxillary teeth. They are present in three specimens which I have examined.

I have recently found good reason to reject the Dendrobatidæ. In a study of the osteology, chiefly the pectoral girdle of a great many African ranids, it has been possible to trace out various lines of specialization. I found that *Cardioglossa leucomystax* agrees in regard to its pectoral girdle with *Arthroleptis wahlbergii*, while *Dimorphognathus africanus* is practically identical in a great many characters with *A. batesii*. There is much evidence that *Cardioglossa* has been derived directly from the *A. wahlbergii = A. variabilis* stock by a loss of teeth and *Dimorphognathus* from the *A. batesii* stock by the development of protuberances on the mandible. Further, I find that *Mantella ebenaui* agrees with *Arthroleptis* in possessing a widely forked omosternum, in striking contrast to *Dendrobates*. The absence of paired disks on the digital expansions, as well as certain other features, would lead one to infer at once that *Mantella* is in no way related to *Dendrobates*, but has been derived from *Arthroleptis* simply by the loss of teeth.

Arthroleptis is apparently an unstable genus in regard to its dentition. That is, a loss of teeth has taken place more than once within the group. This opinion is confirmed by the very recent discovery of *Schoutedenella*, which seems to have developed from some other species of *Artholeptis* than did *Cardioglossa*. The characters which Witte (1921, p. 18) employs to distinguish *Schoutedenella* from *Cardioglossa* are hardly generic but are sufficient to show that *Schoutedenella* has arisen neither from *Cardioglossa* nor from exactly the same stock as that genus, since *Cardioglossa* has arisen from one species of *Arthroleptis*, and *Schoutedenella* from another. In other words, we can hardly attribute generic importance to the loss of teeth for, when the data are complete as in the case of *Arthroleptis* and its derivatives, we see various species of a single genus losing the maxillary teeth independently of one another, just as various species of a group might independently lose a green coloration or a sharp snout.

Other toothed families besides the Ranidæ must be made to include toothless forms. Boulenger (1888, p. 188) has regarded *Pseudophryne* as a toothless *Crinia*. *Eupemphix* has been definitely called a lepto-dactylid without teeth (Méhely, 1904, p. 217). Boulenger (1919, p. 470) regards *Scutiger*, *Ophryophryne*, and *Aelurophryne* as toothless pelo-batids. The recently discovered *Pseudhymenochirus* gives us further evidence of the loss of teeth within the Pipidæ. I have shown elsewhere (Barbour and Noble, 1920, p. 408) that the family Dendrophryniscidæ should be eliminated from the system for the reason that it is composed of two toothless genera which have been derived from totally different stocks simply by the loss of teeth. In the case of one toothless genus, it has been possible to determine not only the toothed genus from which it was derived but also the exact species.

If the families of Salientia are to embrace only natural assemblages, it is obvious that both the Hemiphractidæ and Amphignathodontidæ should be eliminated. The obvious close relationship of *Dimorphognathus* to *Arthroleptis* and of *Ceratobatrachus* to the Ranidæ forced Boulenger to delete the Ceratobatrachidæ. He recognized, too, that *Genyophryne* was but a brevicipitid which had developed pseudo-teeth on the lower jaw, just as many genera of frogs develop bony growths on other parts of the body, chiefly on the top of the skull and along the back. It is im-portant to emphasize this comparison for, in all cases except two, these pseudo-teeth are essentially the same and may be considered excess bony growths. They are formed by the extended and serrated edges of the angular and dentary. The part played by each of these two elements in the formation of the edge varies with the species. This is readily seen in figures (Plate I) of *Dimorphognathus*, *Ceratobatrachus*, and *Cerathyla*.

No vertebrate, fossil or recent, bears true teeth on the angular. The lower jaw of all frogs is formed chiefly by the angular. I, therefore, doubted very much if true teeth were found on the lower jaw of any frog. Thanks to the kindness of Dr. A. G. Ruthven, I have been permitted to dissect out the jaw of the only specimen of *Amphignathodon* in this coun-try. The conditions found in this remarkable frog are shown in Plate I, figs. 5, 6. As Boulenger stated in 1882, true teeth are present in this genus. I find that they agree with the maxillary teeth even to the minute detail of pulp cavity, ring-furrow, dentine and enamel cap. Further, in this genus, the dentary is extensive and these true teeth lie on its medial face (Plate I, fig. 5). The angular overlaps the dentary and covers the bases of all the posterior teeth, which are inserted only upon the dentary. The presence of these true teeth is even more re-

markable because there can be no doubt that *Amphignathodon* is simply a specialized *Gastrotheca*. These marsupial frogs stand among the most specialized hylids, while hylids, as will be pointed out below, are but specialized leptodactylids. Our knowledge of the internal structure of *Amphignathodon* is small, but sufficient, I believe, to place it among the outermost twigs of leptodactylid specialization. How then did *Amphignathodon* come by its mandibular teeth? Is this a case of reversion? We know that not only the immediate ancestors of *Amphignathodon* but even the most primitive frogs, recent and fossil, lacked mandibular teeth. So far as our classification is concerned, *Amphignathodon*, although unique, may be definitely assigned to a position and therefore need not be considered the sole member of a monotypic family.

The only other frog besides *Amphignathodon* having on the lower jaw tooth-like protuberances which are not of the serrate-edge category is *Grypiscus*. Boulenger (1882) referred this genus to the Amphignathodontidæ. I have recently examined the type and unique specimen (Mus. Comp. Zool., 1497) and find that it has no relation to *Amphignathodon*. Cope (1867) described the specimen as having caducous pleurodont teeth. At the present time the specimen possesses no mandibular teeth at all, and it cannot be stated whether or not there were true teeth such as those of *Amphignathodon*. Still, in the specimen, the dentary of each side is very extensive and extends well above the angular, forming a blade. The pars mentalis of each side is bony, pointed, and inflected backward, forming two spines as in certain species of *Ceratophrys*. *Grypiscus* seems to be closely related to *Cycloramphus*. It possesses straight, not claw-shaped, phalanges. The sacral diapophyses are scarcely dilated (the distal part about a fifth wider than the proximal part). A well-developed omosternum is present. It has vomerine teeth behind the choanæ. In brief, there can be no doubt that *Grypiscus* has evolved from a leptodactylid stock, if not directly from *Cycloramphus*, and has nothing to do with *Amphignathodon*.

The exact structure of the maxillary teeth of *Amphodus* is not known. From Boulenger's (1917) recent description, it seems to be a specialized *Hyla* or *Eleutherodactylus*. The fact that its sacral diapophyses are cylindrical would seem to show its relation to the latter genus. But many small Hylas have practically cylindrical diapophyses. *Hemiphractus* is certainly neither a *Hyla* nor an *Eleutherodactylus*. I (1917, p. 802) have given some reason to believe that *Cerathyla* is closely allied to the leptodactylids, although to just which genus it is difficult to state. In brief, there is at present no evidence that any of the genera having

teeth or pseudo-teeth on the mandible may be grouped into natural categories. They all have arisen independently of one another from less specialized stocks. In the case of many of the genera, we may place our finger on the exact genus, and in one case species, from which the specialized forms have evolved. A system to be natural should recognize the diverse origin of these specialized genera and should not group them together. For this reason, I would not only follow Boulenger in eliminating from our classification the Ceratobatrachidæ and Genyophrynidæ, but I would also delete the Hemiphractidæ and Amphignathodontidæ.

SACRAL VERTEBRA

The form of the sacral diapophyses has been generally conceded to be of considerable importance in defining the primary groups, but I have convinced myself that the exact form of this structure is not diagnostic of the real affinities of many forms. Thus, *Hemisus*, although a brevicipitid, has its sacral diapophyses as nearly cylindrical as the majority of leptodactylids. There is one leptodactylid, *Centrolene*, that has its sacral diapophyses more dilated than many hylids. It is well known that several of the Australian leptodactylids have the sacral diapophyses somewhat dilated, certainly more dilated than the hylids *Gastrotheca* and *Pseudacris*.

The problem of the value of the form of these structures in classification has recently been the subject of considerable discussion. Fry (1915, p. 75) has shown that the pelobatid *Lechriodus* is so nearly identical to the leptodactylid *Phanerotis* "that it is difficult to find even specific characters with which to distinguish them." *Lechriodus* is retained in the Pelobatidæ because it possesses sacral diapophyses which are a trifle more dilated than in *Phanerotis* or the closely related leptodactylids *Limnodynastes* and *Ranaster*. If Fry's sketch (*loc. cit.*, fig. 2c) is a correct representation of the sacral vertebra of *Lechriodus*, that genus is very probably not a pelobatid at all but a leptodactylid. Two articular surfaces for the coccyx are indicated, a condition characteristic of the leptodactylids but not the pelobatids (see below). An examination of the muscular anatomy of *Lechriodus* would do much to confirm the opinion that *Lechriodus* is a leptodactylid with sacral diapophyse as much expanded as the typical pelobatids.

Hewitt (1919), in describing his *Anhydrophryne*, experienced considerable difficulty in assigning it to a place in the system where it would be near its closest relatives and at the same time not stand as a glaring exception to the characteristics defining its family. He based his

conclusions on its affinities chiefly from a study of its pectoral girdle, but its distribution also showed that it was probably related to *Phryno-mantis* and *Cacosternum*. Hewitt concluded with a good deal of justification that *Anhydrophryne* was a brevicipitid with teeth in the upper jaw as in the "dyscophids" and with sacral diapophyses as nearly cylindrical as in the ranids. If Hewitt's conclusions as to the affinities of *Anhydrophryne* are correct, it is apparent that the dilated sacral diapophyses are not invariably characteristic of the Brevicipitidæ.

I (1917, p. 806) have recently shown that *Hyla fuhrmanni* should be referred to *Hyloscirtus*, a leptodactylid genus, chiefly because of its cylindrical sacral diapophyses. It may still be argued by some that *Hyloscirtus* is a *Hyla* with cylindrical diapophyses. Very small species of *Hyla* often possess nearly cylindrical diapophyses but such conditions are not known in any large species of that genus. It seemed, therefore, justifiable when characters of the vomerine teeth, etc. were also considered to refer *Hyla fuhrmanni* to the leptodactylids. In brief, each case must be considered on its own merits; we cannot arbitrarily state that the form of the sacral diapophyses is diagnostic in all families.

VERTEBRAL COLUMN

By far the most important contribution toward a natural grouping of the frogs and toads made in recent years has resulted from the careful studies of Nicholls (1916) on the vertebral column. But in the five years since the appearance of this paper little comment or criticism has been aroused. Nicholls, with the osteological wealth of the British Museum at his disposal, has been able to demonstrate clearly that the classical researches of Gadow were not wholly correct. He has shown that four types of vertebral columns are found in the Salientia and has attempted to divide the Phaneroglossa into four "tribes" on the basis of this structure. He (p. 86) defines these four tribes as follows.

I. Opisthocœla. Sacral vertebra biconvex, free from coccyx; pre-sacral vertebræ eight, opisthocœlous; with ribs.

Includes but one family, the Discoglossidæ.

II. Anomocœla. Sacral vertebra ankylosed to coccyx or articulating herewith by a single condyle; vertebræ procœlous (rarely opisthocœlous); without ribs.

Includes a single family, the Pelobatidæ.

III. Procœla. Sacral vertebra free, articulating with the coccyx by a double condyle; vertebræ uniformly procœlous.

Includes the Bufonidæ, Hylidæ, and Cystignathidæ.

IV. Diplasiocœla (=Firmisternia). Sacral vertebra biconvex, eighth vertebra biconcave; the first seven vertebræ procœlous.

Includes the Ranidæ and Engystomatidæ.

It is interesting to note that these four divisions group the frogs and toads into natural categories. It has been shown that certain bufonids and leptodactylids have been derived directly from leptodactylid genera by that often repeated phenomenon—a loss of the maxillary teeth. It has been further demonstrated that the form of the sacral vertebra does not invariably distinguish a brevicipitid from a ranid or a hylid from a leptodactylid. It might, therefore, be desirable to use these four "tribes" as our primary units—our first natural units larger than genera. Within these units we might be able to arrange a number of parallel series illustrating the loss of teeth or the dilation of the sacral diapophyses. This, I believe, would give us for the first time a natural grouping of the frogs and toads.

Unfortunately, the solution of our problem is not so simple. The units defined by Nicholls are not nearly so circumscribed as he was led to believe by an examination of the largest collection of batrachian skeletons in existence. The collection of frog and toad skeletons in The American Museum of Natural History numbers only one hundred and thirteen specimens but, as the greater part of this collection was prepared by myself with special reference to forms which would yield exceptions to the principles laid down by Nicholls, it clearly demonstrates that the principles of Nicholls cannot be accepted in an unmodified form. In the preparation of these skeletons, I have used a modification of the Schultze corrosive technique which, when combined with a staining process, gives the best results. Since the resulting specimens were preserved in glycerin, the vertebral columns could be readily handled under the binocular and, with the aid of the dissecting needles, the vertebræ manipulated until the exact form of each centrum was determined. Nicholls was not so fortunate in the determination of all of his material and was forced to leave an element of doubt in a small percentage of his results.

The following sixty-five skeletons in The American Museum of Natural History agree entirely with the conclusions reached by Nicholls. The number of specimens and the locality, when important, are included in brackets.

OPISTHOCŒLOUS

  Pipa pipa (2); *Xenopus tropicalis*, *X. mulleri*; *Bombina maxima*; and *Ascaphus truei.*

PROCŒLOUS

  Bufo marinus (3), *B. fowleri*, *B. superciliaris* (14); *Cerathyla johnsoni*; *Eleutherodactylus martinicensis* (3), *E. montanus* (2); *Gastrotheca bolivianum*; *Hyla andersonii*, *H. dominicensis*, *H. rubra*, *H. septentrionalis*, *H. versicolor*; *Leptodactylus lineatus*; *Pseudacris septentrionalis*; *Telmatobius culeus.*

DIPLASIOCŒLOUS

    Arthroleptis feæ; Cacosternum boettgeri; Chiromantis rufescens; Dimor-phognathus africanus; Gastrophryne carolinensis (3); *Hemisus mar-moratum; Hyperolius concolor, H. nasutus; Kassina senegalensis; Hypo-pachus variolosus* (2); *Leptopelis aubryi; Megalixalus fornasinii, M. lep-tosomus; Otophryne robusta; Phrynobatrachus natalensis; Rana aesopus, R. albolabris, R. catesbeiana, R. occipitalis, R. septentrionalis, R. sylvatica, R. temporaria, R. virgatipes.*

The following fifty specimens are at variance with the conclusions reached by Nicholls. Nicholls mentioned that *Rhombophryne testudo, Atelopus ignescens, A. oxyrhynchus,* and four species of *Polypedates* did not agree with his conclusions but he chose (p. 91) to consider these as "persisting forms which appear to connect the several groups," and not as serious obstacles to the acceptance of his system. A few of the speci-mens indicated below are undoubtedly instances of abnormality, but the majority are "persisting forms"—much too numerous for us to dis-regard in our classification. All of these specimens are firmisternal and should therefore be diplasiocœlous if they were to agree with Nicholls' conclusions.

    Arthroleptis pœcilonotus and *A. variabilis* (4), uniformly procœlous. Nicholls (p. 82) states that the specimen of *A. variabilis* examined by him was diplasiocœlous.

    Atelopus elegans, A. ignescens, and *A. varius* (2), all procœlous and with vertebræ I+II fused (as in *Pipa*). Three additional skeletons of *A. varius* show the following conditions: A. M. N. H. No. 11278, vertebræ I+II fused and the potential VIII+IX (sacral) fused (Plate III, fig. 2); A. M. N. H. No. 11279, only seven precoccygeal vertebræ; I+II fused, potential VIII forming the left sacral diapophyses, and IX the right, but vertebræ IX part of coccyx (Plate III, fig. 3); A. M. N. H. No. 11280, vertebræ I+II fused; potential VIII+IX fused to form a sacral vertebra of prac-tically the same form as the normal sacral vertebra (Plate III, fig. 1).

  Brachycephalus ephippium, procœlous, IV+V fused.

  Cardioglossa elegans, procœlous, VIII+IX (sacral) fused.

  Dendrobates parvulus, D. trivittatus and *D. tinctorius* (1 Costa Rica and 1 British Guiana), uniformly procœlous. *D. typographus* (4 Nicaragua, 2 Costa Rica, and 2 probably from Costa Rica) and "*D. tinctorius*" (1 Colombia and 2 Ecuador), vertebræ II+III and ' 'III+IX fused. One *D. typographus* (?) from Costa Rica has I+II+III and VIII+IX fused ·(and thus as in *Hymenochirus,* has only five pre-sacral vertebræ). One immature *D. typographus* (A. M. N. H. No. 8217), only 14 mm. in length, has vertebræ VIII+IX fused and II+III approximated (Plate II, fig. 3). Another immature specimen (A. M. N. H. No. 3814) doubtfully referred to *D. typographus* does not show these fusions. From the above series of *Dendrobates,* it may be concluded that the normal adult condition of *D. typographus* and the Colom-bia-Ecuador races of that assemblage known as *D. tinctorius* is the fusion of the vertebræ II+III and VIII+IX.

  Geobatrachus walkeri, uniformly procœlous.

  Hyloxalus collaris, uniformly procœlous.

Phyllobates boulengeri, P. infraguttatus (7), and *P. trinitatus*, uniformly pro-
cœlous.

Phrynobatrachus dendrobates, VIII opisthocœlous, VII biconcave.

Rana cæruleopunctata, R. christyi, and *R. pipiens* (?), VIII+IX (sacral) fused.

Rhinoderma darwinii, uniformly procœlous.

Sminthillus limbatus, S. peruvianus, uniformly procœlous.

If the above list is added to that of Nicholls, the following funda-
mental conclusions may be reached.

(1) The uniformly procœlous condition is typical, not only of the
Bufonidæ, Hylidæ and Leptodactylidæ, but also of all the firmisternal
neotropical genera examined except *Hypopachus* and its close allies,
Gastrophryne, Otophryne, etc. These typically procœlous genera include
*Sminthillus, Geobatrachus, Brachycephalus, Phyllobates, Hyloxalus, Den-
drobates, Atelopus*, and *Rhinoderma*.

(2) *Atelopus* is characterized not only by a procœlous condition but
also by a fusion of I+II vertebræ.

(3) *Dendrobates typographus* and a race of frogs at present referred
to *D. tinctorius* have normally the II+III and the VIII+IX vertebræ
fused.

Only the first of these three conclusions is of interest to us from a
taxonomic standpoint. The second and third is of interest from a more
general phylogenetic point of view. As we shall point out below, it is
very probable that the typically procœlous firmisternal forms are not at
all related to the diplasiocœlous firmisternal genera. In other words,
the neotropical firmisternal genera, except *Hypopachus, Gastrophryne*,
and their close allies, are not at all related to the palæotropical or, in
fact, to any other firmisternal forms.

The third statement calls for further explanation in regard to my
uncertainty in referring a name to the race mentioned. No name can at
the present time be given to the Ecuadorian-Colombian specimens of
D. tinctorius because of the great confusion in the synonymy of that
species. I have shown elsewhere (Noble, 1918, p. 320) that the Colom-
bian specimens are apparently most like the typical *D. tinctorius* as
regards certain characters. Nevertheless, it seems extremely probable
that they are closely allied to *D. typographus* and only distantly related
to the *D. tinctorius* of Guiana. This opinion is supported by the fact
that the omosternum of the adult *D. typographus* and the *D. tinctorius*
of northwestern South America remains cartilaginous and often rudi-
mentary, while in one specimen of *D. tinctorius* from Guiana and an-
other from Costa Rica it is bony, similar to that of *D. trivittatus* and *D.
parvulus*. In brief, it seems that *D. typographus* might well be considered

the type of a new genus characterized by a vertebral column of only six presacral segments and a rudimentary omosternum. Until the internal structure of many more specimens of *D. tinctorius* can be examined, especially specimens from Guiana, the status of such a genus would be on a very weak footing.

SKULL

It is well known that Cope was misled in laying considerable stress on small differences in skull form in his early classical studies on the Salientia. It is now generally conceded that the degree of ossification of the skull and the exact extent of the derm bones is not even of generic importance, although recent attempts have been made to erect subgenera on a basis of skull differences. Future detailed work may show that some of the differences are sufficiently constant to be used in defining the families. But at the present time far too few skulls have been examined to determine what these differences are.

The boldest attempt in recent times to depart from the view that the skull of the Salientia is a plastic structure of little importance in classification was made by Méhely (1901) after a study of the Brevicipitidæ of New Guinea. Méhely proposed two new subfamilies, Symphygnathinæ and Eleutherognathinæ, because of differences which he found in the symphysis of the maxillæ of the various genera he studied. This contribution to the classification has not been considered seriously by later workers. Van Kampen (1919, p. 53) has very recently referred Méhely's genera *Gnathophryne* and *Metopostira*, representatives of Symphygnathinæ and Eleutherognathinæ respectively, to a single genus *Hylophorbus*. In other words, Van Kampen would lay primary importance upon the girdle, not skull form, in defining genera.

PECTORAL GIRDLE

Cope (1864 and 1865) was the first to seize upon the importance of the structure of the shoulder girdle in defining the primary groups of Salientia. His system was not accepted at first and later various other systems were proposed. Although Cope (1867a and 1875) later modified his system somewhat, laying undue emphasis on the peculiar form of the shoulder girdle of *Hemisus*, it is now generally recognized that he did not improve his original scheme. An outline of the history of the classification has been given by Hoffmann (1878) and Gadow (1901). The more recent account is by no means complete. It omits, for instance, the interesting schemes proposed by Lataste (1879) and by Blanchard

(1885). Boulenger's (1886) and Lataste's (1888) criticisms of Blanchard's scheme are also of importance. Lataste's classification based on the position of the spiracle is now known to be of little value. Rao (1919) has shown that certain brevicipitid tadpoles possess a median spiracle similar to that of the discoglossids. Boulenger (1882) accepted Cope's scheme in a modified form. He divided the Phaneroglossa into two series, the first possessing a shoulder girdle with two halves fused in the midline, and the second with the two halves free and broadly overlapping. Since that time, no conclusive evidence has been brought forward to disprove that the first of these two groups, the Firmisternia, did not embrace a natural group of genera much more related to each other than to any genus of the second series, the Arcifera. It has been pointed out several times that the shoulder girdle of the Firmisternia in its ontogeny passes through an arciferous stage, and it was assumed that Firmisternia were, therefore, higher, more advanced forms than the Arcifera. It would seem *a priori* that this difference between the Firmisternia and Arcifera was structurally a very slight one, and the change from one type to the other might have taken place more than once phylogenetically. Mivart (1869a) would not accept Cope's system for he did not believe so much emphasis should be placed on the condition of the pectoral girdle. He adds (*loc. cit.*, p. 281, footnote): "I am fortified in this, I rejoice to say, by the valuable opinion of one of the very first of existing osteologists, I mean my esteemed friend, Mr. W. K. Parker, F. R. S."

Nevertheless, Cope's scheme as modified by Boulenger was universally accepted and since that time no one has pointed out a firmisternous genus that was more certainly allied to an arciferous genus than to any of its firmisternous allies. We have found reason to doubt the trustworthiness of characters of dentition, sacral vertebræ, skull, vertebral column and terminal phalanges; in fact, practically all the major characters at present in use, save only those of the pectoral girdle, have been found to be unreliable in at least one instance.

It will now appear that not even the condition of the pectoral girdle is always diagnostic. There is one genus, *Sminthillus*, recently described by Barbour and myself, in which the pectoral girdle, viewed from the ventral surface, seems to be firmisternous as recently figured (Barbour and Noble, 1920, fig. 2; unfortunately this figure was reversed in printing). This is due in part to its fragile nature and in part to the fact that it is covered with an adherent membrane. But when the girdle is viewed dorsally, and the coracoids pressed gently downward, the two coracoid

cartilages readily separate for about half their length. As this separation occurs only in the region of the coracoids, the girdle must be functionally firmisternous. Morphologically, it is exactly intermediate between the arciferous and firmisternous condition.

I (1921) have very recently described a second species of the genus *Sminthillus*. *S. limbatus* is confined to Cuba, while this second species was secured from southern Peru. Both species agree very well externally and internally, except for the pectoral girdle, with some of the smaller species of *Syrrhophus*. The latter genus is a polyphyletic group of species of *Eleutherodactylus* which have independently lost the vomerine teeth. (A parallel occurs in *Hylella*, etc.) The difference between the pectoral girdle of *Syrrhophus* or *Eleutherodactylus* and *Sminthillus* (Plate IV) is not great. It is certainly simpler, when all things are considered, to assume that *S. limbatus* in Cuba and *S. peruvianus* in southern Peru have arisen independently from a *Syrrhophus* or *Eleutherodactylus* stock rather than to try to account for the distribution by assuming a former greater range and at present restricted distribution. If we carry the argument further, we might ask whether other species of *Eleutherodactylus* or, better, arciferous genera have not repeated this process of fusing the two halves of the pectoral girdle in the midline and have carried the process a step further than *Sminthillus*. It is very suggestive to compare the pectoral girdles of *Eleutherodactylus*, *Sminthillus*, and *Rhinoderma* (Plate IV). The latter has not only its coracoid cartilages completely fused but the metasternum is not distinct from the sternum, suggesting that the process of fusion did not stop with the coracoid cartilages.

But what right have we to assume that any genus except *Sminthillus* has recently made this change from an arciferal to a firmisternal type? All the neotropical firmisternous genera, except *Gastrophryne, Hypopachus*, and their close allies, have typically a procœlous vertebral column. We have seen that certain species of African ranids may occasionally possess a procœlous type of vertebral column and also, according to Nicholls, four species of *Polypedates* having very diverse ranges in the east. But these cases are certainly abnormalities. Sufficient material has been examined to state definitely that the Old World ranids are typically diplasiocœlous. We may state from our own observations that the neotropical ranids, except one group, are procœlous. The Leptodactylidæ, Hylidæ, and Bufonidæ, a very natural group of families, are also procœlous. The two former families of frogs are the dominant Salientia of the neotropics. Only a scattering of firmisternal genera occur. Did not these procœlous firmisternous genera arise as *Sminthillus*

from the leptodactylids? *Hypopachus* and its allies may well, as we shall discuss below, have arisen from ranid stock and have reached South America at some early time. It does not seem likely that they have come in recently with *Rana*. Hence, from the evidence of-the vertebral column and the pectoral girdle, the majority of South American firmisternous genera may not have arisen in very ancient times. Further, they have evolved from a stock very different from that of the Old World ranids. That this is probably the correct interpretation of the above facts will appear from the evidence derived from a study of the muscles of the posterior limb.

DISCUSSION AND SUMMARY

It is obvious from the above brief criticism that the few pegs on which our classification has hung for so many years are giving way, if not already worthless. We can no longer be sure that the toothless forms are related or that those frogs with tooth-like protuberances on the lower jaw are anything but highly specialized forms which have developed these growths quite independently of any other form. It also appears that the shape of the sacral vertebræ is by no means always diagnostic of a family or even a group of related genera (*Cacosternum*, etc.)   We have shown that certain neotropical genera possess a shoulder girdle exactly intermediate between the arciferous and firmisternous condition. There never has been sufficient evidence for us to place much faith in any of the numerous skull differences as defining larger groups.   Lastly, we have just shown that there are a number of suggestive exceptions to the recent conclusions derived from a study of the vertebral column. At first glance, it would seem useless for us to attempt to reconstruct a classification on the basis of any of the above characters. Still, some of them are certainly indicators of natural relationships, even if not always reliable indicators.   Until more structures have been studied in detail and throughout a sufficient series of forms, we must depend on the characters at hand.

Of the characters discussed, only those of dentition seem absolutely worthless and of little use for us to consider further. Boulenger realized this and eliminated the three families Ceratobatrachidæ, Genyophrynidæ, and Dendrobatidæ, based primarily on such structures. We have shown equally good reason to delete the Dendrophryniscidæ, Hemiphractidæ, and Amphignathodontidæ. The relationships of *Phrynomantis* to *Anhydrophryne* and *Cacosternum* suggest that the Brevicipitidæ are but toothless dyscophids. The many extraordinary similarities we find in

both internal and external structure, especially as regards the greatly reduced pectoral girdle in certain genera of both groups, brings one to the conclusions that all Old World brevicipitids, those with diplasiocœlous vertebral columns, have been derived either directly or more often indirectly from the Dyscophidæ, that is, from a stock similar to themselves but possessing maxillary teeth. For that reason, I do not hesitate to merge the brevicipitid and dyscophid genera into a single family and, as the genus *Breviceps* has priority over *Dyscophus*, the name Brevicipitidæ may be used for that family.

There remains to be considered only one family based primarily on the absence of teeth. This is the Bufonidæ. It has been shown that certain bufonids (*Eupemphix* and *Pseudophryne*) are nothing but toothless leptodactylids. Are all bufonids toothless leptodactylids? The distribution of the two families would seem at first to deny this. But, if we admit with Boulenger that *Pseudophryne* is simply a toothless leptodactylid, the problem becomes less difficult. I have shown (in manuscript) that *Pseudophryne* is hardly separable from *Nectophryne*. The latter genus has a wide distribution in the oriental region. May not some of the oriental bufonids have been derived from *Nectophryne* or at least in some such indirect way from true leptodactylids, that is, from bufonid-like creatures still retaining the maxillary teeth? It may, of course, be argued that we cannot place our finger on the leptodactylid genus from which *Bufo* was derived and thus, even if we should relegate a number of bufonids to the leptodactylids and admit that they cannot be distinguished by any family character from *Bufo*; nevertheless, we should not part with the time-honored family Bufonidæ, but should retain it if only for the genus *Bufo*. Conservatism in classification is much to be desired but I cannot see the point of retaining a family when there is not a single character to define it. Moreover, Oeder (1906, p. 538) has shown that the tadpole of *Bufo* possesses a tooth ridge and tooth furrow in the upper jaw. He regards these as rudimentary organs, definite evidence that the immediate ancestors of *Bufo* possessed teeth in the upper jaw. The bufonid and leptodactylid genera exhibit no constant features by which to distinguish them. I am therefore forced to merge them into a single family and, as the name *Bufo* is older than *Leptodactylus*, the name Bufonidæ may be retained for this family.

If, then, we have rid the classification of dentition characters, which of the other characters are the most stable and at the same time divide the Salientia up into what we realize are natural groups? I say "realize" because there is much evidence to be derived from zoögeography and

from a handling of many species. The first kind of evidence is indirect while the second cannot be expressed in definite terms for it comes from an appreciation of many small indefinable characters. A few other characters besides those discussed above have been suggested as a basis of classification. As the value of certain of these has not been disproved, they remain available to us. Perhaps the most important of these characters is the presence or absence of ribs. Féjérvary (1918) has attempted to throw doubt on the importance of this character by claiming that the anterior diapophyses of all frogs are potentially ribs. The fact remains that these diapophyses in most frogs are morphologically not ribs, since at no stage of their ontogeny are they isolated from the vertebræ. In the Pipidæ, the ribs are distinct only in the larva. Upon metamorphosis they ankylose to the vertebræ. This, I (in manuscript) have shown by photographs. Still, these larval ribs are not found in any other family save the Discoglossidæ, in which group they are retained throughout life.

The Pipidæ have been placed in a suborder by themselves by practically all recent workers. The suborder, the Aglossa, has been characterized by the absence of a tongue, vertebræ opisthocœlous, sacral diapophyses dilated, ribs present. The last three characters are shared equally by the Discoglossidæ, while the first does not seem to me to be very fundamental. It is almost certainly an adaptation to aquatic life. *Batrachophrynus* is one of the most aquatic of the Bufonidæ (employing our new terminology), and this genus possesses but the slightest indication of a tongue. Further, it has lost the eustachian tubes, which structures seem to be highly modifiable in the Salientia.

Of all the characters which have been fully investigated, those of the vertebral column seem to me the most important. Then follows a choice of several characters, none free from exceptions. As these characters will be discussed more fully at the end of the paper, we shall simply state them briefly here in order that we may have before us, as we consider the musculature of the thigh, a scheme which, if not entirely satisfactory, is nevertheless the best working basis to be derived from the data available. It will be noted that this scheme is an elaboration of that proposed by Nicholls (1916), together with certain important changes, additions and omissions.

Order.—SALIENTIA

Sub-Order I.—OPISTHOCŒLA

      Presacral vertebræ opisthocœlous; ribs present at some stage in development.

1.—PIPIDÆ. Sacral vertebra fused with coccyx; presacral vertebræ seven to five; opisthocœlous with ribs in early stage of development; eyes without movable eyelids (except in *Pseudhymenochirus*); no tongue; pectoral girdle arcifero-firmisternal; coracoid cartilages not overlapping but attached to each other along the medial edge.

2.—DISCOGLOSSIDÆ. Sacral vertebra free, with biconvex centrum; presacral vertebræ not less than eight; opisthocœlous; with ribs in adult; tongue and eyelids present; pectoral girdle arciferal.

Sub-Order II.—ANOMOCŒLA

Sacral vertebra procœlous, ankylosed to coccyx or if free with only a single articular condyle for coccyx (except in *Pelodytes*); presacral vertebræ eight, uniformly procœlous (rarely opisthocœlous); without ribs at any stage in development.

3.—PELOBATIDÆ. Sacral diapophyses dilated; pectoral girdle arciferal.

Sub-Order III.—PROCŒLA.

Sacral vertebra free, procœlous, with double condyle for coccyx; presacral vertebræ eight to five, procœlous; without ribs.

4.—BUFONIDÆ. Pectoral girdle arciferal; sacral diapophyses cylindrical or dilated; presacral vertebræ eight; terminal phalanges T-shaped or simple (very rarely claw-shaped).

5.—HYLIDÆ. Characters of Bufonidæ but terminal phalanges claw-shaped, supported by an intercalary cartilage or bone; the sacral diapophyses dilated.

6.—BRACHYCEPHALIDÆ. Pectoral girdle arcifero-firmisternal (Pl. IV, figs. 2, 3) or firmisternal; sacral diapophyses cylindrical or dilated; presacral vertebræ eight to five, but generally less than eight; terminal phalanges never claw-shaped.

Sub-Order IV.—DIPLASIOCŒLA

Sacral vertebra biconvex with double condyle for coccyx; eighth vertebra biconcave, preceded by seven procœlous vertebræ; without ribs.

7.—RANIDÆ. Sacral diapophyses cylindrical or slightly dilated; pectoral girdle firmisternal.

8.—BREVICIPITIDÆ. Characters of Ranidæ but sacral diapophyses more dilated.

THE THIGH MUSCULATURE AS A BASIS OF CLASSIFICATION

HISTORICAL

There are many accounts, most of them not at all complete, of the myology of the more familiar genera. The earlier accounts are meagre, but in some points more accurate than some of the most recent. *Rana* has been the most exhaustively studied. The work of Gaupp (1896–1899) has been considered a standard for the present paper. Although it will be obvious from the following that there is little basis for the mammalian names which Gaupp has retained, since in the great majority of cases the frog muscles are not at all homologous with the mammalian muscles of the same name, nevertheless, these inappropriate names have been used throughout this paper in order to save confusion. Once the homologies suggested in this paper have been generally accepted, it will be time enough either to abolish the mammalian names, utilizing the urodele names instead, or, perhaps better, to apply the mammalian names to truly homologous muscles.

Gaupp's work (1896–1899) is generally considered the classical treatise on *Rana*. It is based chiefly on *R. esculenta*. Gaupp includes references to most of the earlier works but, as these accounts add nothing to Gaupp's descriptions, we shall not consider them here. Only one later paper may be mentioned as an important contribution to the study of the thigh muscles of *Rana*. Nussbaum (1898) has considered the minute differences between the thigh muscles of *R. esculenta* and *R. fusca*, as well as several other forms. His description of the nerves of this region is more detailed than that of Gaupp. Some mention of other species of *Rana* has been made in more recent contributions. The thigh muscles of *R. guppyi* have been figured by Beddard (1907*a*, fig. 234). The differences in musculature between the various species of *Rana* are not sufficiently great to concern us in the present paper.

Various species of the toad *Bufo* have been studied. The first good account considering the myology of the posterior limb available to me is that of Zenker (1825). Altena (1829) considers the muscles of the toad in a more comparative way. The most complete of these earlier papers is that of Dugès (1834). It has been considered the basis of much of the later work. I have not been able to examine the paper by Collan (1847). Unfortunately, the important paper of Klein (1850) is without figures. Stannius (1856) reviews a part of this earlier literature, and Hoffmann (1878) considers the more important papers. The more recent papers have been more broadly comparative and therefore of greater value to

us. De Man (1873, 1874) and Perrin (1892) have furnished the most detailed of these contributions. Gaupp (1896a) has recently added some notes on the skin muscles of *Bufo*.

Hyla has been considered together with *Bufo* in most of the accounts. Zenker, Altena, Dugès, Klein, Stannius, and Hoffmann have considered *Hyla* in more or less detail. The comparisons of De Man (1873, 1874) and Perrin (1892) have been the most useful in our present study.

The aberrant *Pipa* has been the subject of considerable study. The thigh muscles have been investigated by Breyer (1811), Mayer (1825), and Klein (1850), and critically reviewed by Hoffmann (1878). It is unfortunate that Beddard (1895) did not consider all of these reports. He has confused badly some of the most essential features in the thigh of *Pipa*. For instance, he claims that the pectineus is absent while the pyriformis is lacking. As a matter of fact, the pectineus is present as a well-developed muscle while the pyriformis is absent. This was recognized long ago by Klein (1850).

Other genera of frogs and toads have not been considered in as much detail as any of the above. Zenker (1820), Altena (1829), Dugès (1834), Hoffmann (1878), Perrin (1892), and Nussbaum (1898) have studied one or more of the discoglossids. If this group had been studied in greater detail, the homologies of the saliential thigh muscles would have been better understood.

A few of the toothed bufonids ("leptodactylids") have been investigated in regard to their thigh muscles. One of the earliest papers is that of Kloetzke (1816) on *Ceratophrys cornuta*. Steffen (1815) considers the skin muscles of a species of *Leptodactylus*. Klein (1850) has studied *L. ocellatus*. Hoffmann (1878) has reviewed the literature and made some comparative notes.

Only the most incidental reference to the thigh muscles of the pelobatids appears in the earlier literature. These references, such as those of Dugès (1834), are of little value in a detailed study. The first good account of the pelobatid thigh musculature is that of Nussbaum (1898). Unfortunately, Beddard (1907, 1907a, and 1911) was not familiar with this work when he wrote his papers on the pelobatids.

Other families of frogs and toads have been very superficially studied. The specialized brevicipitids, *Breviceps* and *Hemisus*, have been investigated by Beddard (1908, 1908b, and 1911). The brachycephalid *Rhinoderma* has been briefly treated by the same author (1908a). The myology of the pipid *Xenopus* has been compared by Beddard (1895a) with that of *Pipa*. Unfortunately, some of this later work leaves much to be desired.

The above work may for the most part be classed under one of two categories. The authors have either attempted to homologize the muscles directly with those of mammals, or they have described the muscles as they found them, assigning them mammalian names and making brief comparative note of the conditions found in other genera of Salientia. None of the authors have examined a sufficiently large series of genera to discuss at all fully the specializations found within the Salientia. The specialization of certain muscles, such as the sartorius and the semitendinosus, have been considered chiefly by De Man (1873, 1874), Perrin (1892), and Nussbaum (1898). The first and last of these authors have pointed out some differences in the distal tendons of the thigh in *Rana* and *Bufo*. De Man (1873, 1874) and Perrin (1892) have attempted to homologize the muscles of the frog with that of the salamander, but these authors have not understood the several types of modification which occur again and again in the Salientia. They have not compared the most primitive type of musculature found in the Salientia with the most generalized in the urodeles. The present paper attempts to fulfill both these needs: first, to give an account of the specialization of musculature found within the various families of frogs and toads, and, second, to compare primitive conditions in the frog with those in the salamander.

MUSCULATURE SPECIALIZATION

A detailed description of the slight variations in proportion, origin, and insertion found in the thigh muscles of the various genera of Salientia would be voluminous and quite beyond the scope of the present paper. It has been observed that certain of these differences have a phylogenetic bearing, and they alone are discussed below. Detailed descriptions of the thigh muscles, together with their innervation, have been given by Gaupp (1896–1899) for *Rana* and by Nussbaum (1898) for several other genera. It is only the deviations from these accepted conditions that are emphasized below.

Adductor longus

The homologies of no muscle in the thigh of the frog is more certain than that of the adductor longus and yet none of the many investigators who have considered salientian myology have brought out these relations. The adductor longus is merely a separate slip of the pectineus. In primitive Salientia it remains undifferentiated. The adductor longus is not present as a definitive muscle in the pipids (Plates VIII, IX, and X)

in spite of Beddard's (1895) statement to the contrary. The primitive discoglossids and pelobatids have similarly not developed an adductor longus, while the specialized genera and species have one. *Ascaphus* and *Bombina* are in many ways the most generalized of the discoglossids. *Ascaphus* lacks any indication of an adductor longus. *Bombina* possesses a wide pectineus which, on being tweezed, splits up into two or three masses. Still, I cannot agree with Nussbaum (1898) that the anterior of these masses should be called an adductor longus, for it is bound in the same sheet of connective tissue as is the rest of the pectineus and can be distinguished from it only by careful dissection. *Discoglossus* and *Alytes*, on the other hand, have a very distinct adductor longus. In the pelobatids, it is not present in *Scaphiopus* (Plate XI) but it is well developed in *Pelobates fuscus* (Plate XII, fig. 3) and *Pelodytes punctatus* (Plate XII, fig. 4). The actual morphogenesis of the adductor longus may be seen within the genus *Megalophrys*. In *M. hasseltii* (Plate XII, fig. 1) it is not distinct, while in *M. montana* it has barely split off from the pectineus. *M. major*, *M. nasuta*, and *M. feæ* possess a well-developed adductor longus. The innervation of the adductor longus shows its very close genetic relationship to the pectineus.

Beddard (1895a, p. 847) claims that in *Xenopus* the adductor longus is present, while the obturator externus and pectineus form an inseparable mass. The innervation and relative positions of the muscles show that what Beddard described as the adductor longus is the pectineus, while his pectineus-obturator externus is actually the obturator externus alone (Plate X). Beddard (1895, p. 840) describes an adductor longus in *Pipa*. Here, too, he has badly confused the muscles.

All of the higher types of frogs possess an adductor longus. It is universally present in the ranids, brevicipitids, and hylids. Two brachycephalids (*Atelopus* and *Oreophrynella*) and two bufonids (*Nectophryne* and *Mixophyes*) lack the adductor longus. It is impossible to say whether the muscle has secondarily fused with the pectineus, or dropped out entirely. All the other brachycephalids and bufonids which I have examined for this structure possess it as a well-developed muscle.

Pectineus

The pectineus is one of the fundamental muscles of the Salientian thigh. It is present in all the numerous species which I have examined. Beddard (1895, p. 840) claims it is absent in *Pipa*. I have found it present in this genus as a very distinct muscle, although covered by the abdominal muscles attaching to the femur. It has exactly the same relations in *Hymenochirus* (Plate IX, fig. 2).

In *Pipa*, the pectineus attaches to the pubo-ischium on the antero-ventral process, which in this genus is pronounced. In *Bombina maxima*, the pubic cartilage is not calcified and the pectineus attaches to its anterior margin. In *Ascaphus* (Plates VI and VII), the pectineus attaches not only to the anterior face of the calcified pubic cartilage, but also to the prepubis along its median line (Plate VII, fig. 2). It is probable that this prepubis, like the two post-pubic cartilages, is an adaptive structure of recent acquisition. The former occurs also in *Xenopus* and a portion of the pectineus originates from it. The greater part of the pectineus attaches to the pubic cartilage and it would seem that this was the primitive position from which a few muscular fibers have shifted their attachment onto the prepubis. One is tempted to homologize the prepubis with the ypsiloid apparatus of the salamander. This homology is supported by the fact that the prepubis is found in only the more primitive Salientia. Still, it occurs in very few species of Salientia and, further, the puboischiofemoralis internus of the salamander, which, as we shall point out below, is homologous to the pectineus, does not insert on the ypsiloid apparatus. It seems most probable that the prepubis is a recently acquired structure of no phylogenetic significance.

Iliacus internus and externus

These two muscles are undoubtedly closely related and must have formed in the Pro-Salientia a single mass. They are both innervated by branches from a single trunk. It is probable that the twisting of the ilium in the morphogenesis of the salientian pelvis split the mother mass into the two muscles.

The most primitive condition of the iliacus internus and externus is that found in *Ascaphus*. The two muscles are fairly distinct but the iliacus externus is broad, and strap-shaped, inserting on the head of the femur by a wide, non-tendinous head. A comparison of these muscles in *Ascaphus* with the same in *Bombina* will show that the accessory head, so well described by Nussbaum (1898) in the latter genus, has arisen by a splitting of the iliacus externus and has no genetic relation to the iliacus internus, as Nussbaum would have us believe. All the discoglossids except *Ascaphus* exhibit a well-developed accessory head. In *Bombina* and *Alytes* the accessory head, although much longer than the iliacus externus, is not much wider; in *Discoglossus*, the relations are about the same but both muscles are better developed.

All pipids have both iliacus externus and the accessory head well developed. In *Xenopus*, the latter is enormous and broadly overlaps the

former.   All pelobatids except *Pelodytes* possess an accessory head, although in most cases it is greatly reduced. In *Scaphiopus*, the accessory head is short, extending not more than one-third the length of the ilium; still, it is a very distinct muscle (Plate XI, fig. 1). The loss of the accessory head in *Pelodytes* may not be very significant in view of its reduction in other genera of the family.

All families of frogs and toads above the discoglossids, pipids, and pelobatids lack the accessory head of the iliacus externus. It is probable that this lack is due to a loss. The series, *Ascaphus,* the other discoglossids, and the pelobatids, illustrates how the iliacus externus, when originally formed, was early associated with an accessory head which in higher forms dwindled and finally disappeared.

Great variation is found in the extent of both iliacus externus and iliacus internus in the numerous species before me. These differences do not seem to be correlated with any natural grouping of the genera and need not be considered here.

Tensor fasciæ latæ

In most Salientia, this muscle appears like a mere slip of the cruralis-glutæus mass attached to the ilium. The reduced condition found in most ranids and bufonids is not the primitive one. The tensor fasciæ latæ is well developed in *Ascaphus* and *Hymenochirus*, less so in other primitive genera. It is most reduced in the ranids, hylids, and bufonids having the longest legs. Its insertion relative to the cruralis and glutæus is variable (Plate VI, fig. 1; Pl. IX, fig. 1). This variation seems to have no phylogenetic significance.

An extraordinary development of the tensor fasciæ latæ occurs in *Atelopus*. Here the muscle is very powerful and attached to the ilium very far forward. The exact position is variable with the species, but in general this attachment is not far from the extreme anterior end of the ilium. The insertion of the tensor fasciæ latæ onto the cruralis-glutæus mass is more distal than in most brachycephalids. The enlargement of the tensor fasciæ latæ in *Atelopus* must be looked upon as a secondary specialization, very probably correlated with the peculiar locomotion characteristic of this group.

Adductor magnus, caput dorsale

' The adductor magnus consists primitively of two very distinct muscles which have undoubtedly arisen from two different muscle masses of the Pro-Salientia. The accessory head of the adductor magnus is

nothing but a small slip of the dorsal head which has become secondarily attached to the ventral head of the semitendinosus. The accessory head of the adductor magnus is present in only the most advanced groups of Salientia. That the adductor magnus is actually composed of two distinct muscles is shown by the fact that all the discoglossids, pipids, and pelobatids have these two muscles quite separate, although in some of the discoglossids the distal ends of the two muscles are more or less fused. In all higher families, this distal fusion is more pronounced.

No taxonomic value may be placed on the presence of the accessory head. It is altogether too variable a structure. Bufonids exhibit all stages in the development of the accessory head.

The caput ventrale of the adductor magnus, being in no way genetically related to the caput dorsale, will not be considered until further in the discussion. This will facilitate comparison with the table of homology given below.

Obturator externus

Primitively, this is a very well-developed muscle as shown in *Pipa* (Plate VIII) or *Hymenochirus* (Plate IX). Not all generalized Salientia have such a large obturator externus as occurs in these two genera but in all it is a very distinct muscle lying immediately dorsal to the proximal part of the adductor magnus, caput ventrale. In *Pipa* and *Hymenochirus*, the abdominal muscles attach to the femur between the obturator externus and pectineus; in all other genera these two muscles lie closely adpressed.

Quadratus femoris

This small muscle is so closely associated with the obturator externus that it is often difficult to distinguish it from the latter. Its innervation seems to indicate that it arose genetically from the latter. Still, it is present in even the most primitive genera as a small but definite element which exhibits little variation in extent or proportions throughout the order. Beddard (1895, p. 840) has badly confused this muscle, together with several of the other short muscles of the thigh.

Semitendinosus

No muscle in the thigh of the Salientia undergoes more radical change than the one I have designated in the more primitive genera as sartorio-semitendinosus (Plate VI, fig. 2). In the less specialized discoglossids, pipids, and pelobatids, this muscle retains its primitive super-

ficial position and has not split off its anterior part as the definitive sartorius. The posterior part of the sartorio-semitendinosus is divided in all forms, even in such primitive genera as *Ascaphus*. The most posterior portion lies deeper (more dorsal) than the anterior portion, whether or not this anterior portion has split off a sartorius. In the discoglossids, pipids, and pelobatids the sartorio-semitendinosus lies much more superficial than in any of the higher families. Moreover, its proximal end is very much broader and flatter than that found in the higher groups.

In both discoglossids and pelobatids, the proximal end of the sartorio-semitendinosus may be tendinous, especially the proximal end of the anterior portion. This occurs in the specialized genera of each family, as, for example, in *Pelodytes* (Plate XII, fig. 4). But even such generalized forms as *Ascaphus* (Plate VI, fig. 2) show some indication of the tendinous origin of this muscle. *Bombina*, *Alytes*, and *Discoglossus* have a very broad sheet of tendinous tissue attaching the anterior portion of the semitendinosus to the pelvis. The conditions in *Discoglossus* have been figured by Perrin (1892, fig. 34) and Nussbaum (1898, fig. 27). The tendinous portion is about as wide in *Alytes* and exactly as superficial. In *Bombina maxima* the anterior head is equally tendinous but in *B. igneus* it is more muscular.

The sinking of the two heads of the definitive semitendinosus deep within the thigh to the position they occupy in *Rana* must have taken place phylogenetically very gradually. Some bufonids and a few brachycephalids (*Atelopus*) represent intermediate stages between the conditions found in the pelobatids and that in the ranids. The relative position of the proximal heads of the semitendinosus is difficult to determine as well as somewhat variable. It cannot be used as a basis of classification. But the distal attachment, the insertion on the lower leg may be easily examined, and its position relative to the surrounding tendons and muscles is fairly constant in each natural group of genera. This will be discussed in more detail below.

Sartorius

As we have pointed out above, the sartorius arises by a division of the anterior part of the sartorio-semitendinosus of the more primitive genera. The actual morphogenesis is suggested by the conditions found in *Xenopus* (Plate X, fig. 2), but more particularly by that in *Bombina maxima* and *Discoglossus pictus*. The innervation also shows the close genetic relationship of sartorius and semitendinosus (compare Plate XVIII, figs. 1 and 2 with fig. 3).

No discoglossid possesses a sartorius distinct from the semitendinosus, nor does any pelobatid. The pipids, *Hymenochirus* and *Pipa*, likewise lack the sartorius, but *Xenopus*, more primitive than either genus in dentition, is more specialized in possessing a partly formed sartorius. The proximal end of this sartorius (Plate X, fig. 2) is not distinct from the semitendinosus, but the distal end is a very distinct tendon, as will be pointed out below.

All higher families of frogs and toads possess a sartorius. A detailed study of the distal tendons has revealed certain differences which will be discussed under a separate heading. The sartorius varies considerably in width and thickness in the various species. These differences in proportion are of no taxonomic importance.

Adductor magnus, caput ventrale

It has been pointed out above that the adductor magnus is composed primitively of two distinct muscles, which in the higher types tend to fuse distally. As these two muscles have very probably had a different origin, we have discussed each under separate headings. The more ventral and anterior of the two elements is present throughout the order. It exhibits considerable variation in proportion but very little in relative position. Primitively, as is well shown in *Pipa* (Plate VIII, fig. 2), *Hymenochirus* (Plate IX, fig. 2), and *Ascaphus* (Plate VI, fig. 2), the ventral head is a long muscle arising from the pubo-ischium immediately ventral to the obturator externus, and inserting on the distal end of the femur. In higher forms, the muscle becomes thickened; the proximal end looses its tendinous character; and the distal end secures a very broad attachment to the distal part of the femur. Although there is considerable variation, pipids and discoglossids agree in the main as regards the form and attachments of the ventral head. Pelobatids possess a more muscular element, while all the higher families possess the broad non-tendinous attachments characteristic of *Rana* (see Gaupp, 1896, fig. 101).

Semimembranosus

This muscle is subject to little change throughout the series. It varies somewhat in proportion but very little in relative position. In *Hymenochirus* and *Scaphiopus*, it is constricted longitudinally as if beginning to divide. But in neither *Pipa* or *Xenopus* is this constriction present, and in no salientian is the semimembranosus split into two definitive heads.

Gracilis major and minor

The gracilis major varies little in proportion or relations throughout the order but the gracilis minor is subject to extreme diversity. These differences seem to have little taxonomic value. The origin, insertion, and innervation (Plate XVIII, fig. 2) show that the gracilis minor is merely a slip of the gracilis major. In *Ascaphus*, only the proximal half is distinct from that muscle, while in *Hymenochirus* there is no gracilis minor present. Whether these two cases represent a retention of the primitive condition or whether they are due to secondary fusion cannot be stated. All other discoglossids and pipids, as well as all the higher families, possess a complete gracilis minor.

Beddard (1908a) has considered the attachment of the gracilis minor to the skin a feature of taxonomic importance. He would not have had to search very far to see the fallacy of this assumption. Not only do the brevicipitids, which Beddard has examined, but also most bufonids and all discoglossids show this attachment to various extents. In *Alytes obstetricans* and *Bombina maxima* among the discoglossids, and *Bufo* among the bufonids, the attachment is exceptionally broad. The greatest expansion of the gracilis minor occurs in *Rhinophrynus*, where it forms a panniculus carnosus wrapping around three sides of the femur (Plate XVI, fig. 6) and attaching along much of its proximal end to the skin. Altogether too much variation is shown in the degree of attachment among the members of even a single family such as the Bufonidæ to make the degree of this attachment a taxonomic character of any great importance.

The gracilis minor varies greatly in thickness. It is largest in *Pipa* and *Xenopus* and thinnest in some of the long-limbed ranids, hylids, and bufonids. Its development is not directly correlated with function. At least, the purely aquatic genera, *Batrachophrynus*, *Pseudis*, and *Xenopus*, vary greatly in the extent of its development. Still, it may be said that fossorial forms tend to have a greater expansion and attachment of the gracilis minor to the skin than do the terrestrial or aquatic genera.

Gemellus and Obturator internus

These two muscles may be considered together for they show very little diversity throughout the order. The conditions described and figured so well by Gaupp (1896) may be considered typical of the order. In *Pipa*, the pelvis is more triangular than in any of the other genera; the origin of the gemellus lies immediately dorsal to the obturator in-

ternus, directly beneath the semimembranosus. A slight shift of position such as this has no phylogenetic significance.

Pyriformis

There is no reason why the pyriformis should be so badly confused with other muscles as Beddard (1895, 1895a) has done. It originates in all genera where it is present from the tip of the coccyx (this may be bony or cartilaginous) and inserts on more or less of the posterior surface of the femur at a point about a fourth to a half its length, according to the species. Nussbaum (1898) showed that it was absent in *Pelobates fuscus*. It is also absent in *Pipa* and *Hymenochirus* (Plates VIII and IX), and represented by a very slender muscle in *Xenopus* (Plate X). In all other genera which I have examined for this feature (this does not include all the species listed under the discussion of the distal tendons), the pyriformis is present. I have examined numerous forms in every family, and it may be safely said that the presence or absence of the pyriformis has no taxonomic value.

Caudalipuboischiotibialis

The most surprising discovery made during my study of the thigh muscles of the Salientia was the finding of a tail muscle in addition to the pyriformis attaching to the thigh of *Ascaphus*. We have seen some reason above to consider this genus (possibly with *Bombina*) the most primitive of existing Salientia. It has been assumed for many years that the Salientia arose from tailed ancestors; that pelvic musculature of the Pro-Salientia was probably not unlike that of the urodele; and that the pyriformis of existing Salientia is a compound muscle having resulted from a fusion of the two urodelian tail muscles, caudalifemoralis and caudalipuboischiotibialis. It now appears that *Ascaphus*, alone of all the Salientia, possesses both these urodelian tail muscles in practically their original position. This is a startling fact, for it demonstrates that the Pro-Salientia very probably retained their tail until fairly recently in the history of the order and, further, it gives us a fairly definite landmark in homologizing the thigh muscles of the frog with those of the salamander.

Ascaphus has long been known as possessing a "tail" in the adult male. Arldt (1917, p. 118) has recently fallen into the error of considering this structure a larval tail retained in the adult, direct evidence of the lowly position of *Ascaphus* among discoglossids. The most superficial examination of a specimen of *Ascaphus* (Plate V) will demonstrate that this structure cannot be a true tail, since it is in no way associated

with the vertebral column and the cloaca opens near its tip. In fact, none of the investigators who have studied *Ascaphus* have considered it a true tail. But, specimens of *Ascaphus* have been very rare and no one until this time has studied its structure or discussed its function.

I have had the opportunity of examining several live specimens of male *Ascaphus* sent to me by mail across the continent from the Olympic Mountains, Washington. Their "tails" were slightly variable in proportion, as is well shown in the several figures (Pl. V). The tail is a very soft structure, examined to the best advantage when floating in water. It is obviously highly vascular and turgid with blood, for the unpigmented ventral surface is of a pinkish hue. When floating in water, it is roughly pyramidal in shape, with a very definite terminal point.

Removal of the skin confirmed the opinion that the "tail" is purely a cloacal organ. It consists chiefly of an outer and an inner layer of muscular tissue. The outer layer is free both dorsally and laterally from the inner layer. The vascularity is greatest distally and ventrally. The inner wall of the deep layer, in other words, the surface of the cloaca, exhibits numerous longitudinal furrows. The ventral surface of the "tail" after removal of the skin shows an hour-glass-shaped structure (Plate VI, fig. 2). The rectus abdominis seems to form the anterior part of this structure. Further dissection demonstrated that the structure owed its form to two cartilages which, like a pair of scissor-forceps, reached out to grasp the end of the "tail" (Plate VII).

A comparison of the "tail" with the cloacal region in the other Salientia has convinced me that the inner layer represents the sphincter ani cloacalis of other genera. The outer layer seems to be a muscle which I have found very pronounced in *Scaphiopus* (Plate XI, fig. 1) and *Rhinophrynus* (Plate XIII). I have called it the ischio-cutaneus for want of a better name. The ischio-cutaneus is present as a very incipient structure in *Bombina*. It is apparently a portion of the sphincter ani cloacalis which has become attached ventrally to the ischium and dorsally to the skin. The ventral surface of the "tail" is firmly attached to the cartilaginous prongs (Plate VII, fig. 3) which very probably represent a specialized portion of the rectus abdominis. The female *Ascaphus* does not help us in determining these homologies for the "tail" is already differentiated, although very rudimentary.

I have given this cursory sketch of the structure of the "tail" of *Ascaphus* to demonstrate that it is a very specialized cloacal structure and bears no relation to the coccygeal muscles of that genus. One would

imagine, of course, that the "tail" must be an intromitant organ. Field observation alone will prove this point. I may emphasize, however, that the organ is so large that even in the freshly killed specimen not more than the point can be inserted into the cloaca of the female. It is conceivable that the lips of the male cloaca might be so adpressed that the spermatozoa could be squirted directly into the cloaca of the female when the pair is in copulation. Still, it is extremely probable that internal fertilization does not take place and that the "tail" acts merely as a directing organ. In such a capacity it might be very useful. I have often watched the oviposition of *Hyla crucifer*. The female sticks each egg (sometimes more than one is emitted at a time) as it leaves the cloaca to a bit of waterweed or other object. To do this her cloaca must in general be bent well up under the body. The cloaca of the male at this moment is in practically all cases more than an inch from the cloaca of the female. But, just as the egg is laid, he brings the rear part of the body forward with a sudden jerk and emits a jet of spermatozoa. It should be noted that the only strong muscle in the "tail" of *Ascaphus* is the ventral one. It is probable that the "tail" is moved in only one direction, i.e., directly beneath the body. It seems to me that, if *Hyla crucifer* were provided with a "tail" such as *Ascaphus*, fertilization would be greatly facilitated.

To return from the speculative to the descriptive, it may be added that the caudalipuboischiotibialis of *Ascaphus* attaches to the inscriptio-tendinea of the semimembranosus exactly as the caudalipuboischio-tibialis of the salamander attaches in part to a small inscriptio of the ischio-flexorius (Plate XVII). We shall show reason below for homologizing the semimembranosus with the ischio-flexorius. It may be noted at this point that there is good reason for applying to this additional coccygeal muscle the name of a salamander tail muscle. No mammalian name can be applied to it, for there is good reason to believe that the caudalipuboischiotibialis drops out in the Reptilia just as it has done in all frogs except *Ascaphus*. The pyriformis is a well-developed muscle in *Ascaphus*. There is no longer need of considering it a duplex muscle in the Salientia. All the evidence seems to indicate that the caudalipuboischiotibialis has dropped out in all genera higher than *Ascaphus* and has not fused with the pyriformis, as has been hitherto assumed.

Cruralis and Glutæus

Gaupp (1896, p. 177) groups these two muscles, together with the tensor fasciæ latæ, under the name triceps femoris. As we shall see

below, the tensor fasciæ latæ has no genetic relation to the cruralis and glutæus. These two muscles are undoubtedly the two heads of a single muscle. There is a tendency, especially in the pelobatids, for the splitting off of a third posterior head. Nussbaum (1898, p. 381) has described in some detail this muscle in *Pelobates fuscus*. In *Scaphiopus* it has much the same relations. This third, or accessory head, is not peculiar to the pelobatids. An incipient condition is found in several bufonids. It is interesting that even in its incipient stages, as in *Acris* (Plate XIX, fig. 1), the accessory head is supplied chiefly by a separate nerve from the trunk innervating the cruralis and glutæus.

The small differences in proportion exhibited by the cruralis, glutæus, and accessory head (when present) throughout the series of forms examined have no taxonomic value. The conditions found in *Rana* may be considered characteristic of the order.

Iliofemoralis and Iliofibularis

These two muscles may be considered together, not because of any genetic relationship but because neither shows any great variation throughout the order. The exact point of origin is somewhat variable. In *Rana*, both muscles arise from a single tendon. In other genera, such as the primitive *Bombina* and *Ascaphus*, the iliofemoralis seems to wrap partly around the head of the iliofibularis and attach to the ilium dorsal to the latter muscle. In *Pipa*, the iliofemoralis arises partly from the tendon of the iliofibularis and partly posterior to it. In most Salientia, the two muscles originate from practically the same point, and if their proximal tendons are not fused, that of the iliofemoralis is dorsal to that of the iliofibularis. Slight shiftings in the relative position of these proximal tendons seem to have no phylogenetic importance.

DISTAL TENDONS OF THE THIGH

It was noticed long ago by DeMan (1873, 1874) that there is a considerable difference in the relative arrangements of the distal heads of the sartorius, semitendinosus and gracilis major in *Rana* as contrasted to those in *Hyla* and *Bufo*. Nussbaum (1898) has considered these differences in more detail and has brought out other differences found in *Pelobates* and in *Discoglossus*. Beddard (1907, 1907a) has discussed certain of these features in the pelobatids which he examined. But no investigator has examined more than a few genera, and none of these authors with their limited series were in a position to discuss these features from either a phylogenetic or a morphogenetic point of view. I

have brought together a huge series of species and have succeeded in determining certain constant differences which alone might serve to define natural groups. I may anticipate my conclusions by stating that the differences exhibited by the insertions of these thigh muscles lend considerable support to the classification which I have proposed on totally different grounds in the first part of this paper. This agreement of two such diverse lines of evidence has led me to the conclusion that we have now before us for the first time a natural classification of the Salientia.

Rana, which has been considered the typical salientian in most morphological work, is the most specialized in regard to the insertions of the posterior thigh muscles, just as it is the most specialized in many other ways. I have represented the conditions as found in *Rana clamitans* in Plate XIV, fig. 3. It will be noticed that the gracilis major and minor dip under the tendon of the sartorius to insert on the head of the distal end of the femur. Further, the head of the semitendinosus lies entirely dorsal (deep) to the gracilis major and minor. This complex we may call the ranid type. By way of contrast, we may examine the conditions of *Leptodactylus pentadactylus* (Plate XIV, fig. 2). Here the sartorius attaches to the distal tendon of the semitendinosus, which is ventral (superficial) to the common tendon of the gracilis major and minor. We may speak of this complex as the bufonid type. The fundamental difference, then, between the ranid and bufonid types is that in the latter the head of the semitendinosus crosses outside (superficial) to that of the gracilis major and minor while in the ranid type it has in some way secured a position on the inside (deep) to this tendon; while the sartorius, which in the bufonid type attached to the head of the semitendinosus, in the ranid type attaches to the knee. This might not seem a great difference if the distal tendons were subject to a shifting of their insertions. But within a family these insertions are remarkably constant, regardless of the diverse habits of the species in the group. All of the ranids which I have examined have these distal tendons in precisely the arrangement which I have described for *Rana clamitans*. There are some differences in the degree of development of certain binding and connecting ligaments. We shall discuss these in more detail below. These secondary ligaments neither alter nor confuse the arrangement of the distal tendons, which remains constant throughout the family. I have examined one or more specimens of each of the following species of ranids and find no deviation from the ranid type: *Rana æsopus, R. albolabris, R. clamitans, R. cyanophlyctis, R. fasciata, R. fus-*

cigula, R. goliath, R. limnocharis, R. mascareniensis, R. pileata, R. pipiens, R. signata, R. virgatipes; Babina holsti; Ceratobatrachus guentheri; Scotobleps gabonicus; Leptopelis[1] aubryi, L. anchietæ, L. calcaratus, L. rufus; Cornufer corrugatus, C. guppyi; Leptodactylodon ovatus; Petropedetes newtonii; Chiromantis rufescens, C. xerampelina; Astylosternus robustus; Gampsosteonyx batesii; Phyrnobatrachus bonebergi,[2] P. boulengeri, P. dendrobates, P. natalensis, P. perpalmatus, P. plicatus; Arthroleptis batesii, A. pœcilonotus, A. variabilis, A. wahlbergii; Sooglossus seychellensis; Megalixalus fornasinii, M. immaculatus, M. spinosus; Kassina senegalensis; Cardioglossa leucomystax; Dimorphognathus africanus; Hyperolius concolor, H. picturatus, H. steindachneri; Polypedates dennysii, P. goudoti, P. japonicus, P. leucomystax, P. maculatus maculatus, P. m. quadrilineatus, P. mocquardi, P. reinwardtii, P. viridis; Hazelia spinosa; Oxyglossus lævis martensii, O. lima; Mantella ebenaui; Staurois natator; Platymantis solomonensis; Philautus leucorhinus, P. pictus; Nyctibatrachus pygmæus; Nannophrys ceylonensis, and Nannobatrachus beddomii.

The opinion has been expressed in the first part of this paper that the Brevicipitidæ (as defined above) are closely allied to the Ranidæ, being distinguished from them only by the dilation of the sacral diapophyses. It was to be expected, then, that, if the numerous genera of ranids considered above exhibited no variation in the insertions of the muscle heads under consideration, the Brevicipitidæ would also show no variation but would agree with the ranid type. This is exactly what I have found to hold true. All brevicipitids which I have examined exhibit the ranid type of distal tendon complex. I have dissected at least one specimen of the following species of Brevicipitidæ: *Breviceps gibbosus, B. mossambicus; Kallula mediolineata, K. pulchra, K. verrucosa; Kalophrynus pleurostigma; Glyphoglossus molossus; Phrynomantis bifasciata; Microhyla berdmorii, M. butleri, M. inornata, M. leucostigma, M. pulchra; Cacosternum boettgeri; Anhydrophryne rattrayi; Cacopoides borealis; Rhombophryne testudo; Pomatops valvifera; Hemisus guttatum, H. marmoratum; Mantophryne lateralis; Phrynella pulchra; Sphenophryne anthonyi, S. celebensis, S. loriæ, S. monticola, S. verrucosa; Calliglutus smithi; Plethodontohyla notosticta; Caluella guttulata; Hypopachus cuneus, H. pearsei, H. variolosus; Otophryne robusta; Stereocyclops incrassatus; Gastrophryne carolinensis, G. texensis, G. ovalis, G. usta.*

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[1]For use of this name see Noble (in manuscript).
[2]I have discussed the status of this species in the paper referred to above (Noble, in manuscript).

The bufonid type of complex is not restricted to the Bufonidæ but occurs also in the Brachycephalidæ and the Hylidæ. In other words, the suborder Procœla is characterized by the bufonid type of complex. We have seen above that the suborder Diplasiocœla (Ranidæ and Brevicipitidæ) is characterized by the ranid type. Further, all Diplasiocœla possessed a typical ranid type of complex in spite of the diverse habits of the species. All the Procœla do not exhibit the typical bufonid type. The vast majority possess the typical condition but a few exceptions occur. These are not damaging to our scheme of classification, for the variations are but modifications of the bufonid plan. The following Procœla possess the typical bufonid tendon complex (Plate XIV, fig. 2):
Leptodactylus caliginosus, L. gracilis, L. lineatus, L. melanonotus, L. mystacinus, L. ocellatus, L. olfersi, L, pentadactylus, L. prognathus, L. typhonius; Pseudis mantidactyla, P. paradoxa; Eleutherodactylus briceni, E. conspicillatus, E. longirostris, E. polyptychus, E. ranoides, E. richmondi, E. unistrigatus, E. wightmanæ; Syrrhophus campi, S. ridens; Ceratophrys americana, C. ornata; Borborocœtes bibronii, B. miliaris, B. nodosus, B. quixensis, B. rosius; Paludicola bufonia, P. fuscomaculata, P. pusilla; Pleurodema bibronii, P. nitida; Batrachophrynus microphthalmus; Hyloscirtus boulengeri, H. fuhrmanni; Centrolene geckoideum; Centrolenella antioquiensis; Zachænus parvulus; Elosia vomerina; Eupemphix pustulosus, E. trinitatus; Heleioporus albopunctatus, H. pictus; Philocryphus flavoguttatus; Mixophyes fasciolatus; Phractops alboguttatus, P. australis, P. platycephalus; Limnodynastes dorsalis, L. olivaceus, L. peronii; L. salminii, L. tasmaniensis; Hyla andersonii, H. arenicolor, H. aurea, H. baudinii, H. bipunctata, H. boans, H. boulengeri, H. caerulea, H. dolichopsis, H. elegans, H. evittata, H. eximia, H. gracilenta, H. infrafrenata, H. maxima, H. minuta, H. punctata, H. raddiana, H. rosenbergi, H. variabilis, H. wilsoniana, Pternohyla fodiens; Agalychnis helenæ; Phyllomedusa bicolor, P. burmeisteri, P. dacnicolor, P. hypochondrialis, P. tarsius; Gastrotheca marsupiatum; Cerathyla johnsoni, Bufo macrotus, B. marinus, B. melanostictus, B. penangensis, B. polycercus, B. punctatus, B. raddei, B. rostratus, B. simus, B. stelzneri,[1] *B. tuberosus, B. typhonius; Notaden bennetti; Pseudobufo obscurus; Nectophryne afra, N. batesii, N. guentheri, N. signata; Brachycephalus ephippium; Sminthillus lim-*

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[1] *Bufo stelzneri* is well known in the literature under the name of *Phryniscus nigricans* Duméril and Bibron (nec Wiegmann). *Phryniscus* of Wiegmann was shown by Boulenger (1894, p. 374) to be a *Bufo*. The name *Phryniscus* was shown to be untenable and Boulenger referred the species to *Atelopus* Duméril and Bibron. Boulenger (*loc. cit.*) found it necessary to change the specific name to *stelzneri*. It has appeared to me on dissection that *A. stelzneri* is a true *Bufo*, possessing all the generic structures of that group. The genus *Atelopus* was based on *A. flavescens*, a firmisternal form, and should be retained for all other species, save *stelzneri*, which have recently been referred to that group.

batus, S. peruvianus; Geobatrachus walkeri; Rhinoderma darwinii; Oreo-phrynella quelchii; Atelopus carrikeri, A. elegans, A. flavescens, A. gracilis, A. ignescens, A. oxyrhynchus, A. varius.

The simplest type of deviation from the bufonid plan of tendon complex is that found in *Rhinophrynus* (Plate XVI, fig. 6). It has already been mentioned that in this genus the gracilis minor is enormous and wraps around the greater part of the knee. This expansion of the gracilis minor has apparently caused a slight shifting of the insertion of the gracilis major, which attaches to the outer (ventral) side of the tendinous head of the semitendinosus instead of passing under it (dorsal). This slight modification of the bufonid plan of complex is found in no other Salientia. It cannot be considered of any great importance.

A remarkable change in the insertions of the thigh muscles lying on the posterior side of the thigh occurs within certain genera of bufonids. For example, *Pleurodema bibronii* (Plate XV, fig. 1) exhibits these distal heads in their typical bufonid arrangement (compare with *Leptodactylus pentadactylus*, Plate XIV, fig. 2). But in *Pleurodema cinerea* (Plate XV, fig. 2) the tendon of the semitendinosus has cut its way into the center of both gracilis major and minor and its distal end pierces both these muscles to attach to the lower limb. In *P. brachyops* the head of the semitendinosus had proceeded a step further in its migration into the deeper part of the leg. In this species it does not pierce the gracilis major but lies entirely dorsal (deep) to it (Plate XV, fig. 3). Its relationship to the gracilis minor is about the same as that in *P. cinerea*.

Another case of the inward migration of the tendon of the semitendinosus occurs in the Australian genus *Limnodynastes*. *L. dorsalis* possesses the typical bufonid arrangement. In *L. ornatus* (Plate XV, fig. 4) the tendon pierces both the gracilis major and minor very much as in *Pleurodema cinerea* (Plate XV, fig. 2). We may consider the arrangement seen here in *L. ornatus* and *P. cinerea* as the first stage in the inward migration of the tendon of the semitendinosus. The insertion of the semitendinosus is changed very little by this migration. The tendon has apparently become pulled within the gracilis muscle mass and, in doing so, it has left the sartorius attached to the knee. Just what factors have forced the inward migration of the tendon it is impossible to say. It is remarkable that the phenomenon has occurred in so few forms.

The extreme stage of this tendon migration as found in the Procœla is exhibited by *Pseudophryne australis* (Plate XV, fig. 5). In this form, the tendon of the semitendinosus does not pierce the muscular part of the gracilis mass but only the ligamentous head. Conditions are very

similar in *Hyloxalus* (Plate XV, fig. 6). Here it is more apparent that the tendon has migrated through the muscular gracilis major and minor and has become bound by their secondary ligaments. *Dendrobates* and *Phyllobates* exhibit an identical arrangement of these elements.

It will be noticed that this extreme stage of tendon specialization found in the Procœla is not very different from the ranid type of complex, which I have already indicated as peculiar to the Diplasiocœla. The difference, although small, seems to be constant. I have found none of the Procœla with the tendon of the semitendinosus free from the gracilis mass, or, in other words, in the typical ranid position. I have mentioned above that the Ranidæ exhibit a great variation in the development of binding and secondary ligaments. I use the term "binding" for ligaments which hold the tendon of the semitendinosus to the gracilis mass (Plate XV, fig. 5), while I designate those ligaments as "secondary" which run between the main heads of the thigh muscles and do not function in the insertion of those heads. I have found a binding ligament well developed in very few Diplasiocœla, perhaps best in *Astylosternus robustus*. But even here the tendon is not tightly bound to the gracilis mass as in the specialized Procœla; further, it lies more posterior to the head of the gracilis major. Typically, there is no binding ligament present in the Diplasiocœla, or at best a very weak, nontendinous one (Plate XVI, fig. 1). The variations in form and attachment of the secondary ligaments do not concern us here for these variations have no taxonomic value.

There can be little doubt that the Diplasiocœla developed their peculiar type of tendon complex by carrying conditions similar to those found in the most specialized types of Procœla a step further. The step is not a great one, and it may be asked if the specialized types of Procœla could not have developed their tendon complex by a modification of the ranid type. Leaving aside all other evidence, osteological, distributional, etc., it still seems extremely unlikely, for the Diplasiocœla, as we have seen above, are extraordinarily stable in regard to their distal tendons. In no case do we find any muscle fibers from the gracilis binding the tendon of the semitendinosus, and in very few cases do we find a ligament in this position. It does not seem likely that a "reversion" of evolution could have taken place in the morphogenesis of the distal tendons of any of the Procœla.

I have examined the following species of Procœla showing conditions intermediate between the bufonid and ranid types of tendon complexes. These species may be roughly grouped into less specialized, Grade A

(Plate XV, fig. 4), and more specialized, Grade B (Plate XV, fig. 5), types.

GRADE A.—*Limnodynastes ornatus; Pleurodema brachyops, P. cinerea, P. marmorata; Crinia georgiana, C. signifera; Uperolia marmorata.*

GRADE B.—*Pseudophryne australis, P. bibronii, P. coriacea; Adelotus brevis; Dendrobates braccatus, D. parvulus, D. tinctorius, D. trivittatus, D. typographus; Phyllobates alboguttatus, P. infraguttatus, P. inguinalis, P. subpunctatus; Hyloxalus collaris, H. fuliginosus, H. granuliventris.*

The Opisthocœla and Anomocœla exhibit the most primitive type of tendon complex. In this, the head of the sartorio-semitendinosus crosses outside (ventral) of the head of the combined gracilis tendon to insert on the lower leg (Plate XIV, fig. 1). From this, the bufonid complex was evolved by the mere splitting off of the sartorius head without a shifting of its insertion.

The Anomocœla show little deviation from the discoglossid type of tendon complex. In *Scaphiopus* the gracilis minor attaches in part to the tendon of the semitendinosus. This gives a peculiar appearance (Plate XI, fig. 2).

The pipids exhibit a remarkable specialization in their distal thigh tendons. In *Xenopus* only the distal half of the sartorius has separated from the expanded sartorio-semitendinosus and yet *X. tropicalis* (Plate XVI, fig. 4) exhibits an arrangement of the tendons practically as specialized as in *Pleurodema cinerea* (Plate XV, fig. 2), while *X. mülleri* (Plate XVI, fig. 5) has carried the specialization a step further to the typical ranid type. An early stage in the migration of the tendon of the semitendinosus through the gracilis mass is well shown in *Pipa.* In brief, the Pipidæ do not retain the primitive complex of the Discoglossidæ, but have specialized along exactly the same stages found in the other Salientia. This is a striking case of orthogenetic variation.

It may be argued that if the pipids with at best half a sartorius can undergo all the modifications found in the distal tendons throughout the Salientia as a whole, little faith can be placed in these modification in determining our groups of higher Salientia. An examination of these higher genera has shown an extraordinary stability of these tendons. In some way we must account for the fact that the Bufonidæ, Hylidæ, and Brachycephalidæ possess one type of complex, while the Ranidæ and Brevicipitidæ possess another. I have accounted for this discrepancy by assuming that the first three families embrace a natural group

of genera unrelated to those of the last two families. In this assumption I have the support of comparative osteology.

I have examined the distal tendons of the thigh on the following species of Anomocœla: *Scaphiopus hammondii, S. holbrookii; Pelobates cultripes, P. fuscus; Pelodytes punctatus; Megalophrys feæ, M. hasseltii, M. major, M. montana, M. nasuta, M. parva, M. longipes, M. pelodytoides, M. böttgeri; Xenophrys monticola.*

The following species of Opisthocœla have been studied in regard to their tendons: *Ascaphus truei; Bombina igneus, B. maxima; Discoglossus pictus; Alytes cisternasii, A. obstetricans; Xenopus mülleri, X. tropicalis; Pipa pipa; Hymenochirus boettgeri.*

DISCUSSION AND SUMMARY

From the above, it is apparent that the thigh musculature supports our conclusions, derived from a study of the osteology, that the Opisthocœla and Anomocœla are more primitive than the Procœla and Diplasiocœla. The structural features in the thigh of the two former suborders which are indicative of the stem position of these groups may be listed as follows.

(1). Absence of a sartorius (partly present in *Xenopus*).
(2). Semitendinosus broad and superficial to other muscles.
(3). Adductor longus typically undifferentiated, but present in the more specialized genera.
(4). Accessory head of iliacus externus retained.
(5). Adductor magnus composed of two muscles distinct for practically their entire length (except some discoglossids); no accessory head present.
(6). Obturator externus well developed.

There are many structural features which distinguish the two more primitive suborders from the more advanced groups or from one another, but there are few characters distinguishing the Procœla from the Diplasiocœla. It is, therefore, very interesting that the Diplasiocœla should be found to be characterized by a distinctive type of tendon complex in the distal part of the thigh, while most Procœla should be distinguished by a much more primitive type. A few Procœla have this complex modified to approach that characteristic of the Diplasiocœla. But even here, there is a gap between them which is not bridged over. Thus the arrangement of the distal tendons of the thigh groups all the higher Salientia into two categories, two great natural groupings. It is highly significant that these two categories should agree exactly with the two which we have already distinguished on the basis of the vertebral column.

From a morphological standpoint, perhaps the most interesting

discovery made during the study was the finding of two pairs of coccygeal muscles in *Ascaphus*, the anterior homologous to the caudalifemoralis of the salamander and pyriformis of the other Salientia, while the posterior is represented in no other salientian although undoubtedly homologous to the caudalipuboischiotibialis of the urodeles. This extra pair of tail muscles has been shown above to have no relation to the "tail" of the male *Ascaphus*, which is purely a copulatory apparatus. The extra muscles may well be considered vestigial structures, even if not entirely functionless ones.

Lastly, a word may be said in regard to the generalized salientians. If one is dealing with doubtful structures, the common frog, *Rana*, would be apt to prove the most confusing member of the order for, in many ways, it is the most specialized. This holds especially true for the thigh muscles. It would appear only from examining representatives of the more primitive families that the adductor longus was merely a specialized slip of the pectineus; the sartorius, the anterior portion of a formerly superficial and broad semitendinosus; the adductor magnus, a composite of two distinct muscles which have fused and finally separated off an accessory head. The less specialized discoglossids, *Ascaphus* and *Bombina*, or even some of the pelobatids possess a thigh musculature which may be considered sufficiently generalized to form a prototype or pattern from which all the more advanced types of thigh musculature may have arisen.

HOMOLOGIES OF THE THIGH MUSCLES

GENERAL CONSIDERATIONS

It is obvious that, if the thigh muscles of the Salientia are to be homologized at all with those of other vertebrates, they should be compared first with those of the salamander, since the salamander is the nearest living relative of the Salientia possessing appendages. It has been possible to homologize the muscles of man with those of the marsupials and to trace their apparent homologies through to the urodeles. The frog is obviously very specialized in its locomotory apparatus. Direct comparison with man or even reptiles present serious difficulty unless we are sure of the homology in the urodeles.

Until now we have been by no means sure of these homologies. Various attempts have been made to homologize the thigh muscles of the frog with those of the urodele. Perhaps the most extensive of these attempts have been made by DeMan (1873) and Perrin (1892). These attempts have not been successful for one or more of the following reasons.

(1). Primitive frogs have not been compared with primitive salamanders. The conditions found in the genus *Rana* have been accepted as typical of the order.

(2). Mistakes have been made in determining the innervations of the muscles, or the nerves have not been considered at all.

(3). Certain muscles in the thigh of the salamanders have not been recognized as distinct from others. The range of variation within the urodeles has not been understood.

(4). The absence of an obturator foramen and obturator nerve in the frog has removed one landmark of considerable importance in determining homologies.

From what has been said above, it is obvious that there is a great range of differences among the various groups of Salientia. In making our comparisons, we should necessarily select a little specialized form such as *Ascaphus* and not a ranid. It will appear from the figures that the primitive type of musculature in the thigh of the Salientia is not very different from that of the urodele. This is not surprising in that the Salientia have apparently evolved from the rhachitomous labyrinthodonts and the pelvis of such a form as *Eryops*, although somewhat compressed, is essentially like that of the urodele type. A study of a beautifully preserved pelvis of *Eryops* in the American Museum has led me to place the muscle origins in the positions indicated in Plate XXII, fig. 2. By comparison with Plate XXII, fig. 1, it will appear that this musculature

is not very different from that of the urodele. It seems probable from a study of this pelvis that the immediate ancestors of the Salientia possessed a thigh musculature similar to that of the urodele. The musculature of the less specialized discoglossids approaches this urodele type. The homologies of the muscles are best understood by comparing these primitive frogs with the urodele.

THE THIGH MUSCULATURE OF THE URODELES

A detailed description of the thigh musculature of a salamander for comparison with that of a frog might seem superfluous with the numerous accounts of urodelan myology available. There are, to be sure, a few discrepancies in some of these accounts. It would not appear from these accounts that the thigh muscles of all salamanders, save those of the Proteidæ, are essentially alike, differing only in development and extent of the same set of elements. Nor is this misconception of the uniformity of the urodele thigh muscles due entirely to the diverse nomenclatures used by the various authors. One element, the adductor femoris (Perrin), has been overlooked by all but one of the investigators, while two elements, the iliotibialis and the ilio-extensorius, have been generally taken for a single one by authors considering the advanced types. Thus, these two elements are considered one in several forms recently investigated by Sieglbauer (1904). Not only do they have a different innervation but, without exception, they have a different origin. In some urodeles, the distal ends insert into a common tendinous sheath. But, as this sheath is generally two-headed, I consider it formed in part by a coalescense of the distal tendons of the two muscles which throughout their length are nearly always distinct. It is surprising that the distinctness of these two muscles has not been universally accepted. In all probability this is due to the fact that none of the investigators have examined a wide range of species. In selecting my series I have tried to secure as many diverse types as possible. The following species have been examined: *Salamandra salamandra; Triturus cristatus, T. alpestris, T. viridescens; Notophthalmus torosus; Tylototriton verrucosus; Pachytriton sinensis; Rhyacotriton olympicus; Dicamptodon tenebrosus; Ambystoma tigrinum; Aneides lugubris; Pseudotriton ruber, Desmognathus quadra-maculatus; Megalobatrachus maximus; Cryptobranchus alleganiensis; Amphiuma means; Necturus maculosus; Proteus anguinus;* and *Typhlomolge rathbuni.*

With this series before me it can be definitely stated that there is very probably a constant number of elements in all urodeles except the

Cryptobranchidæ, which exhibit a nearly complete fusion of the pubo-ischiotibialis and pubotibialis, and the Proteidæ, which do not have the adductor femoris distinct from the pubotibialis. It is not my purpose to discuss here the variations in proportions of the thigh muscles as exhibited in the various species. The description of the thigh musculature given by DeMan (1873) for *Triturus cristatus* or by Wilder (1912) for *Necturus* might serve our purposes if these and the various other authors had laid sufficient emphasis on the distinctness of two muscles important for us in a study of homology.

In all of the salamanders which I have examined, the iliotibialis[1] arises on the anterior edge of the ilium and never on the outer face where it might be confused with the ilio-extensorius. Its proximal head may be attached either well up on this anterior edge of the ilium (most salamanders) or, in aquatic forms, may shift to a very low point on this anterior edge, as in *Megalobatrachus*, where a few fibres may trespass on to the pubis.

The insertion of the iliotibialis is much more variable than its origin. It is due to the fact that the distal end of the iliotibialis is often closely associated with the ilio-extensorius that these two muscles have been confused. Thus, in *Typhlomolge rathbuni*, where the appendages are greatly elongated and the muscles consequently narrowed, the iliotibialis and ilio-extensorius are not readily separable distally. They are also closely adherent in *Triturus alpestris* but in *Triturus cristatus* they are quite distinct. In the majority of salamanders, these two muscles are associated as indicated in the figure of *Rhyacotriton* (Plate XVII, fig. 2). But in *Cryptobranchus* (Plate XVII, fig. 1) and *Megalobatrachus*, the iliotibialis and ilio-extensorius are not at all in contact. In *Proteus anguinus*, the iliotibialis is associated distally with the head of the puboischiofemoralis internus, from which, as we shall discuss below, the muscle has very probably arisen. It is interesting that the Cryptobranchidæ should have the iliotibialis and ilio-extensorius so widely separated. The two genera included in this family are closely related to primitive Hynobiidæ. The wide separation of the iliotibialis and ilio-extensorius seems to me to be a primitive feature. This does not seem to have been recognized by the various writers (Humphry, Mivart, and Osawa) who have considered the myology of *Cryptobranchus* or *Megalobatrachus*.

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[1] I follow Wilder in the use of this name; the iliotibialis of DeMan includes both this element and the ilio-extensorius.

The second muscle which has been generally overlooked is one designated by Perrin (1892) as the "Adducteur du fémur" (Plate xvii, figs. 12, 13, and 14, muscle No. 117). Dugès (1834) did not distinguish this muscle from the puboischiofemoralis externus; Humphry, DeMan, and Hoffmann considered it part of the puboischiofemoralis internus. Neither Mivart (1869) nor Osawa (1904) recognized that the great sheet on the ventral surface of the thigh of the cryptobranchids is formed by the nearly complete fusion of the puboischiotibialis and the pubotibialis. That there is actually a fusion is shown by the innervation, but especially by the fact that certain ambystomids and salamandrids have the puboischiotibialis and pubotibialis closely adpressed and bound together by connective tissue. Directly dorsal to the anterior portion, which must be recognized as the pubotibialis, lies a well-developed muscle, distinct distally from both the puboischiofemoralis externus and internus. This is the adductor femoris. Mivart, Humphry, and Osawa confused the muscle with one of those lying adjacent to it. In all the genera of salamanders which I have examined except *Proteus* and *Necturus*, I have found the adductor femoris present, lying immediately dorsal to the pubotibialis and between the puboischiofemoralis externus and internus. In these two genera it is apparently fused with the pubotibialis. It cannot be stated offhand that this undifferentiation of the adductor femoris is a larval condition, just as many of the other structural peculiarities of this family. *Typhlomolge rathbuni*, which is certainly a neotenous plethodontid, has a well-developed adductor femoris.

The adductor femoris is not always as distinct as it is in the forms studied by Perrin. In *Megalobatrachus*, which has the greater part of the pubotibialis fused with the puboischiotibialis, as in *Cryptobranchus*, the adductor femoris is a very large muscle, distinct from the puboischiofemoralis externus distally, but more or less fused with it proximally. This apparent fusion is not surprising in a salamander where the muscle bundles are so loosely grouped into definitive muscles. In *Dicamptodon tenebrosus*, the puboischiotibialis is massive, the puboischiofemoralis externus is narrow and broadly overlaps the adductor femoris. In *Triturus cristatus* and *T. alpestris*, the adductor femoris is long and narrow. Its proximal head, as usual, arises from the pubis directly beneath (as viewed ventrally) the pubotibialis. Its distal head inserts on the femur considerably proximal to that of the pubotibialis. In *Pachytriton sinensis*, the adductor femoris is very distinct distally from the pubotibialis but proximally some of its fibres may run into it. It would seem that this fusion of the two elements, carried to an extreme in the

Necturidæ, may represent a primitive condition and that the adductor femoris arose phylogenetically from the pubotibialis. The innervation of the two muscles is so distinct that this separation could not have taken place very recently. Perhaps the extreme specialization of the thigh musculature is found in *Typhlomolge*, where the legs are greatly elongated and have been stated to function as feelers or balancers as much as limbs. In *T. rathbuni*, the pubotibialis is narrow and tendinous. It lies directly over (as seen from below) the adductor femoris, which is well developed and stands out in striking contrast to the very much shortened puboischiofemoralis externus.

In brief, the thigh muscles of all salamanders are essentially the same. In the Cryptobranchidæ, the puboischiotibialis is nearly completely fused to, or at least bound together with, the pubotibialis; in the Necturidæ, the adductor femoris is completely fused with the pubotibialis. In all other salamanders, variations include only differences of proportion and relative position. In the Cryptobranchidæ, the iliotibialis has succeeded in shifting its origin downward along the anterior edge of the ilium. Primitively, the iliotibialis was perfectly distinct from the ilio-extensorius with which it has become associated distally in some forms.

NERVE SUPPLY

Here again it is not our intention to discuss in detail any nerves except those which have been overlooked or incorrectly identified. With the acetic-osmic method it has been possible to pick out both inter- and intra-muscular nerves. This method not only assures accuracy and speed in the identification of the nerves trunks, but it also gives us for the first time a simple means of picking out a nerve fibre for practically its entire length, that is, for the length ot its myelin sheath.

The acetic-osmic method was first used extensively by Nussbaum. But he (1898) succeeded in staining very few of the intra-muscular nerves. In 1909, Müller, working with elasmobranch material, claimed he was able to stain every nerve "von Anfang zu Ende" by means of this method. Müller implied that the acetic-osmic method was original with him but, as his method differs but little from that of Nussbaum, it is surprising that he was able to secure so much better results. Braus (1910), using the same material as Müller, denied many of Müller's conclusions and contended that the acetic-osmic method was useless for determining intra-muscular innervations. The probability is that both Braus and Müller are right in part. I find that results vary enormously

on slight variations in the technique. With amphibian material intra-muscular nerves may be well stained if the specimens are sufficiently macerated before treating with acetic. I have secured my best results by using the following solutions: (*1*) 15 per cent alcohol—48 hours; (*2*) 1 per cent glacial acetic—24 hours; (*3*) 1 per cent osmic—12 minutes; (*4*) 12 per cent ammonia (stock considered 100 per cent)—10 minutes. It is very necessary to dissect away any connective tissue binding the muscles together. The osmic solution should be squirted between the muscles with a fine pipette. After washing overnight in running water the preparations are cleared in glycerine. Cleared specimens show at a glance the complete innervation (exclusive of endings). The fine intra-muscular nerves are generally so numerous that it has been found confusing to attempt tracing out the nerves without first dissecting free some of the more superficial muscles. All observations stated below have been checked up from several preparations. It cannot be claimed that every preparation will show a complete innervation. The main branches are uniformly stained but, unless the material is sufficiently macerated, all of the terminal twigs will not be stained.

In both urodeles and Salientia, we have found a great uniformity in the musculature, especially as regards the number and relative position of the elements. Such is not the case as regards the innervation. The nerves do not always have a constant relation to the other nerves. The number of branches to a muscle is variable. This was recognized long ago. Gadow (1882) recognized that homologous muscles, even in closely related species, may occasionally have a different innervation. Adolphi (1893, 1895, 1898) showed that there is great variation in the pelvic plexus of certain Salientia. I have found considerable variation in the relative position of the nerves. For example, in a specimen of *Acris gryllus*, the nerves on the left side which supply the gemellus arise as shown in Plate XIX, fig. 2, while on the right side of the same specimen they arise from practically the same point on the ischiadic stem as the nerve to the obturator internus. Another case: the branch to the tensor fasciæ latæ in one of four specimens of *Acris gryllus*, collected at the same locality, arises from the nerve to the iliacus internus; in the other three specimens, this branch comes off the branch common to the iliacus externus and internus. Although a muscle in a series of genera may have a constant relation to the surrounding muscles, the nerve which inner-vates it may have a variable relation to the surrounding nerves. In both *Pipa pipa* and *Xenopus mülleri*, the branch to the iliofibularis and the one to the iliofemoralis do not arise from the main peroneal nerve, as

in *Acris, Hyla, Rana*, etc., but arise from the ramus profundus anterior. Although *Pipa* and *Xenopus* are unquestionably closely related, there is a great difference in the number and position of the branches innervating their semimembranosus and the semitendinosus respectively. It has been sometimes assumed that if two muscles are innervated by two nerves arising from the same point on a main branch, the two muscles must have arisen from a single mass. Obviously, this cannot always be true in cases where the innervation is so variable as we find it in both urodeles and Salientia. Still, throughout the series of frogs and toads examined, certain nerves were found to be more or less constantly associated. These associations are interesting in that they afford us a basis of homologizing not always the nerve branches themselves, for they are sometimes too variable, but the muscles which they in general supply. The following groups may be distinguished in all Salientia.

Group I. *Iliacus externus and internus.*

The nerves supplying these two muscles arise from nearly the same point on the cruralis trunk.

Group II. *Pectineus and Adductor longus.*

The branch innervating the adductor longus (if present) is always more closely associated with the nerves to the pectineus than with any other.

Group III. *Tensor fasciæ latæ.*

The nerve supplying the tensor fasciæ latæ may arise from the cruralis or from one of its branches. It is generally more closely associated with one of the branches supplying the iliacus externus than with any other crural nerve.

Group IV. *Obturator internus and Gemellus.*

The nerves to these muscles may arise from a single stem or they may arise from different portions of the ischiadic. The extreme separation is shown in *Acris.*

Group V. *Quadratus femoris, Obturator externus and Adductor magnus.*

In all Salientia examined, the nerves supplying these muscles arise from a single stem. The nerves to the quadratus femoris and obturator externus are closely associated but the nerves to the dorsal and ventral head of the adductor magnus vary greatly in relative position according to the genus.

Group VI. *Semimembranosus, Semitendinosus, Gracilis major and minor.*

The main nerves to these muscles arise from a common stem. The semimembranosus in *Acris* and *Hyla* receives a branch from the ramus

profundus posterior of the ischiadic. The number and relative position of the branches supplying the muscles of this group are extremely variable.

Group VIII.   *Cruralis and Glutæus.*

The ramus profundus anterior alone supplies the glutæus and cruralis.

Group VIII.   *Iliofibularis.*

The nerve to this muscle has a variable position as regards the other peroneal nerves.

Group IX.   *Iliofemoralis.*

The nerve to the iliofemoralis cannot be grouped with any of the other nerves because of its variable position in relation to other peroneal and ischiadic nerves.

Group X.   *Pyriformis.*

The nerve to the pyriformis (if present) is always distinctly separated from the other nerves. In *Ascaphus*, the nerve to the caudalipuboischiotibialis arises as a branch from this nerve.

It would be less difficult to homologize the thigh muscles of the Salientia with those of the urodele if we could recognize in the salamander nerve groups homologous to the above. It is quite useless to attempt to homologize any but these larger categories of nerves. Although we have found great uniformity in the thigh musculature of the urodeles, the nerves show no such regularity. This will at once be obvious by a comparison of DeMan's (1873, Plate II, fig. 4) figure of the main nerve trunks in the thigh of *Triturus cristatus* with my figure (Plate XX, fig. 1) of the same in *Desmognathus*. Further, I find considerable differences in the thigh nerves of two such closely related forms as *Eurycea bislineata* and *Desmognathus fuscus*, especially as regards the innervation of the puboischiofemoralis externus. These differences lie chiefly in the number and relations of the branches. In *Rhyacotriton*, the obturator nerve supplies the puboischiotibialis. I have not been able to find any twigs of the obturator extending into the puboischiotibialis of either *Desmognathus* or *Eurycea*. It seems that the more primitive condition is that found in *Rhyacotriton* and the loss in the plethodontids is very suggestive of how the Pro-Salientia may have commenced a reduction of the obturator innervation.

The iliotibialis of *Rhyacotriton* is supplied not only by the femoral innervation of the plethodontids but also by a small twig from the peroneal nerve to the iliofemoralis. The question immediately arises

whether this double innervation is a primitive condition, or whether it is a specialized one. The fact that the twig supplies such a small fraction of the whole muscle makes it seem very probable that this double innervation is a specialized condition having arisen by the fusion of some of the fibres of the iliofemoralis, together with their nerve, to the ilio-tibialis.

The iliofemoralis (that portion of the puboischiofemoralis internus mass arising on the outer face of the ilium or wrapping around it posteriorly) possesses in the several salamanders I have examined only a peroneal or better a peroneal-ischiadic innervation, since the more proximal branch arises from the common peroneal-ischiadic stem. In the reptiles, the iliofemoralis is partly (in some forms wholly) innervated by a crural nerve. The Salientia retain a peroneal innervation similar to the salamanders. There can be no doubt that the iliofemoralis of the Salientia is homologous, at least in part, to the iliofemoralis of the urodeles.

The chief difficulty in attempting to homologize the main nerve branches, or nerve groups, of the salamander with those of the frog lies in the fact that there is no obturator nerve in the latter. The pelvis of the Salientia was recognized long ago as a very specialized structure and DeMan (1873) assumed that the obturator nerve, together with its foramen, was squeezed out of the pelvis by the approximation of the two halves of that structure in evolution from a more salamander-like prototype. Such is probably the correct view, but this loss is not a very great one. In certain plethodontids where there is no compression of the pelvis, the obturator nerve has already begun to dwindle. It does not reach the puboischiotibialis, and the puboischiofemoralis externus is chiefly supplied by the ischiadic. DeMan assumed a migration of obturator fibres around the ilium took place in the change from the salamander to the frog type. But the obturator supply is such an insignificant one in the more specialized urodeles that the assumption of a complete loss without any migration of fibres seems to me to be the most reasonable one.

In previous accounts of the nerve supply to the thigh muscles of salamanders, the same omissions have been made that we find in the accounts of the thigh muscles. It has not been recognized that the nerves which supply the adductor femoris are very distinct from the nerves which supply the pubotibialis and the puboischiofemoralis externus. This I have indicated in a drawing of the nerves, both inter- and intra-muscular, supplying the ventral thigh muscles of *Desmog-*

nathus (Plate XXI, fig. 1). In figure 3 (same plate), I have represented the complete innervation of the pubotibialis of the same species. It is clear that none of the nerves to the pubotibialis receive or send twigs to the adductor femoris. This evidence supports the view expressed above that the adductor femoris is a very distinct muscle, perhaps not at all closely related genetically to the pubotibialis.

The second innervation which has not been clearly defined is that to the iliotibialis. It has been recognized that the anterior part of the "iliotibialis" (DeMan) received a crural supply, but it has not been pointed out that the iliotibialis and the ilio-extensorius, confused together under the name "iliotibialis," have a totally different innervation. I have pointed out that in *Rhyacotriton* a small twig of the nerve to the iliofemoralis extends to the iliotibialis but this condition, which I have suggested above as secondary, does not mar the distinctness of the innervation of the iliotibialis and ilio-extensorius. In Plate XXI, fig. 2, I have represented the complete innervation of the three dorsal muscles, iliotibialis, ilio-extensorius, and iliofibularis, of *Desmognathus*. This innervation I consider typical of the urodeles. The first muscle receives a crural, while the two latter a peroneal innervation. It will appear that the nerves to these two latter muscles are very closely associated, suggesting that the muscles may be more or less related genetically. I have, in Plate XX, fig. 1, indicated the main nerve trunks in *Desmognathus*. A comparison of the figure with that of the main nerves in *Acris* (Plate XX, fig. 2) will make it clear that several of the nerve groups found in the Salientia may also be found in the urodeles. We may consider these apparent homologies under the group headings we have applied to the Salientia.

Group I, Group II, and Group III are certainly represented in the femoral nerves of the urodeles. The obturator nerve has already been discussed. It apparently dropped out in phylogeny. Group II of the Salientia is apparently more closely related to Group I than to Group III. This allows us, so far as relative position is concerned, to homologize Group III, or the nerve to the tensor fasciæ latæ, with the nerves to the iliotibialis of the salamander.

It becomes much more difficult to distinguish any other groups in the urodele innervation, but, judging from position and mutual relations, it would seem that the following homologies might be suggested:

Group IV, Salientia Ischiofemoralis, urodele
Group VII, " Ilio-extensorius, "
Group VIII, " Iliofibularis, "
Group IX, " Iliofemoralis, "
Group X, " Caudalifemoralis (+Caudalipuboischiotibialis), urodele

These homologies become very apparent when the muscles inner-vated by these nerves are considered at the same time.   In fact, the nerves cannot be homologized with any assurance unless the muscles are considered at the same time; nor can the muscles be homologized without the evidence derived from the innervation. Both muscles and nerves are mutually, although neither wholly, dependent on the other for support in determining these homologies.

COMPARISON OF MUSCLES

It has already been mentioned that the thigh muscles of the primi-tive Salientia (such as *Ascaphus*) are not very different from those of the more generalized salamander. This will be clear by comparing the outline figures (Plate XVII, figs. 4 and 5) of the thigh muscles of *Ascaphus* with a figure of the muscles of a salamander such as *Rhyaco-triton* (Plate XVII, figs. 2 and 3). In order to facilitate this comparison, I have indicated salamander names on homologous muscles in *Ascaphus*.

There can be little doubt that the puboischiofemoralis internus of the salamander has broken up in the frog into the pectineus ventrally and the two (primitively three) iliacus muscles dorsally. I have sug-gested these changes in a series of schematic drawings (Plate XXIII). The drawings may be taken as representing ideal cross-sections of the thigh at a point near the acetabulum. It will be noted that the inner-vation permits of no other interpretation, unless it be in regard to the tensor fasciæ latæ. This is primitively a well-developed muscle in the Salientia and I have homologized it directly with the iliotibialis which, as we have seen above, is a very distinct muscle, although one often confused with the ilio-extensorius.

Again referring to our figures and to the diagrams, it will appear that the generalized salientian and urodele have almost exactly the same number of elements on the ventral surface of the thigh and that these are similarly placed. In *Ascaphus*, the so-called ventral head of the ad-ductor magnus (actually a distinct muscles as origin, insertion, and inner-vation show) possesses a tendinous proximal head and overlies the powerful obturator externus precisely as the pubotibialis overlies the adductor femoris in the same relative position in *Rhyacotriton*. The innervation, too, supports the view that the adductor magnus, caput ventrale is homologous to the pubotibialis, the obturator externus to the adductor femoris. In the Salientia, immediately adjacent to the obtura-tor externus, there is a small muscle which the innervation shows to be closely allied to the obturator externus. This, the quadrator femoris,

may have recently split off from the latter. At least, it probably finds its homologue in a small part of the adductor femoris.

A glance at the ventral surface of the thigh of *Ascaphus* and that of any salamander will make another comparison obvious. The puboischiotibialis of the salamander has precisely the same relations as the sartorio-semitendinosus of the primitive Salientia. The origin and insertion, as may be seen from the figures, are the same. The presence of an obturator innervation in some salamanders has already been mentioned as having little significance. In the schematized drawings (Plate XXIII) I have suggested how this obturator innervation probably gradually disappeared.

In *Ascaphus*, but more particularly in the pipids and pelobatids, the adductor magnus, caput dorsale retains its primitive position and independence. It is apparent that this head, actually a distinct muscle, must be homologous to the puboischiofemoralis externus of the salamander. It has the same relative position and, further, its innervation except for the obturator nerve is the same.

There can be little doubt about the homologies of the three remaining ventral (or posterior) muscles. In *Ascaphus*, the two coccygeal muscles mark these off from the dorsal muscles. The origin, innervation, and insertion demonstrate that the coccygeal muscles of *Ascaphus* are homologous to the caudalifemoralis and caudalipuboischiotibialis, respectively, of the salamander. The semimembranosus and gracilis major and minor must be represented in the ischioflexorius of the salamander, for that muscle lies between the extrinsic tail muscles and the puboischiotibialis of the urodeles. The latter muscles are carried over to the frog in such an unmodified form that their homologies are readily recognizable. Further, the innervation supports the view that the semimembranosus and gracilis major and minor are represented in the ischioflexorius of the salamander. In *Ascaphus*, we find the posterior coccygeal muscle (of each side) attaching to the inscriptio tendinea of the semimembranosus exactly as the caudalipuboischiotibialis attaches in part to the ischioflexorius of salamanders.

It will be seen from the diagrams (Plate XXIII) and the figures of the muscle origins in *Rhyacotriton* (Plate XXII, fig. 1) and *Ascaphus* (Plate XXII, fig. 3) that the obturator internus and gemellus of the frog must have become greatly modified to have evolved from the ischiofemoralis of salamanders. Nevertheless, the innervation, as we have seen above, seems to indicate that this is what has taken place, and there is no damaging evidence to be derived from origins, insertions, or relative position of these muscles.

TABLE 1.—THE HOMOLOGIES OF THE THIGH MUSCLES

		PLACENTAL	SPHENODON	SALAMANDER	FROG	REMARKS
Plexus Cruralis — N. Femoralis		Psoas major, Iliacus, Pectineus	Puboischiofemoralis internus	Puboischiofemoralis internus	Dorsal = {Iliacus externus, Iliacus internus} Ventral = Pectineus ⤳ Adductor longus	Adductor longus not differentiated from pectineus in more primitive frogs (and certain higher genera)
		Sartorius	Ambiens	Iliotibialis (+small twig from nerve to iliofemoralis (Peroneus) in *Rhyacotriton*)	Tensor fasciæ latæ	Iliotibialis of salamander often confused with ilio-extensorius. Tensor fasciæ latæ of frog primitively a well-developed muscle, reduced in specialized forms
Plexus Cruralis — N. Obturatorius		Obturator externus / Quadratus femoris (ischiadic only)	Puboischiofemoralis externus (+ischiadic)	Puboischiofemoralis externus (mostly ischiadic)	Adductor magnus, caput dorsale (only ischiadic)	Adductor magnus of the frog composed primitively of two distinct muscles
		Adductor brevis, Adductor longus, Adductor magnus (+ischiadic in Man)	Adductor femoris (Ischiofemoralis of Gadow) (+ischiadic)	Adductor femoris (ischiadic only)	Obturator externus, Quadratus femoris (ischiadic only)	Primitively a long muscle; in the frog similar in form and relations to the Adductor femoris of salamander
Plexus Sacralis — N. Ischiadicus		Gracilis (obturator only)	Puboischiotibialis (obturator only; in lizard ischiadic and obturator)	Puboischiotibialis (+obturator in *Rhyacotriton*)	Semitendinosus ⤳ Sartorius	The Semitendinosus of the most primitive frogs (i.e., *Ascaphus*) has almost identical origin and innervation as the puboischiotibialis of the salamander
		Absent	Pubotibialis (+obturator)	Pubotibialis	Adductor magnus, caput ventrale	
Plexus Sacralis — N. Ischiadicus		Absent Semimembranosus Semitendinosus / Tenuissimus (common nerve with adductor magnus in Man)	Flexortibialis externus / Flexortibialis internus (+obturator)	Ischioflexorius	Semimembranosus, Gracilis major ⤳ Gracilis minor	Gracilis minor of frog a slip of the gracilis major attaching primitively to the skin
		Obturator internus Gemellus superior Gemellus inferior	Ischiotrochantericus	Ischiofemoralis	Gemellus, Obturator internus	These two muscles of frog innervated either by the same or different nerves
		Pyriformis	Coccygeo-femoralis brevis	Caudalifemoralis	Pyriformis	Caudalipuboischiotibialis found among frogs only in *Ascaphus*. Has no relation to "tail"
		Cruro-coccygeus	Coccygeo-femoralis longus	Caudalipuboischio-tibialis	Caudalipuboischiotibialis	
Plexus Sacralis — N. Peroneus	(Femoralis only)	Rectus femoris, Vastus lateralis, Vastus medialis, Vastus intermedius	Iliotibialis (+femoral) / Femorotibialis (femoral only)	Ilio-extensorius / Absent	Cruralis, Glutæus / Absent	In some salamanders (*Desmognathus*, *Tylototriton*, etc.), the anterior part of ilio-extensorius tendinous forming an incipient head homologous to the cruralis
		Tensor fasciæ latæ (femoral only) Glutæus medius " minimus " profundus " ventralis (Femoralis) " maximus	Iliofemoralis (+Femoral)	Iliofemoralis	Iliofemoralis	Name iliofemoralis of salamander restricted to that portion of the puboischiofemoralis internus mass arising on outer surface of ilium. It is innervated by two branches from the peroneal only
N. Peroneus		Biceps	Iliofibularis	Iliofibularis	Iliofibularis	

Little difficulty is experienced in determining the homologies of the dorsal thigh muscles. The origin and insertion, but especially the innervation, show that the iliofibularis and iliofemoralis of the frog are homologous to the muscles of the same name in the salamander. It is also apparent from the innervation that the glutæus and cruralis are simply two heads of a single muscle undoubtedly homologous to the ilio-extensorius of the salamander. I have represented in Plate XXIII the changes which this region probably underwent in changing from the salamander to the frog type.

SUMMARY

The following table gives a summary of the homologies of the thigh muscles of the Salientia and the Caudata, as I see them, together with some supplementary remarks. I have added a list of what appears to be the homologous muscles in a reptile and a mammal. It will be obvious that most of the mammalian names applied to the frog are misnomers, in that the frog muscles are in practically all cases not at all homologous to the mammalian muscles of the same name. I have accepted Gadow (1882) for these reptilian and mammalian homologies, except where these homologies have been corrected by Mr. A. S. Romer, whose unpublished manuscript has been available to me. There is no doubt that the Salientia are specialized creatures, far removed from the main line of mammalian evolution. Still, the Pro-Salientia were probably not unlike the Caudata in regard to their pelvic musculature. The mammalian muscles have been traced with a fair degree of accuracy down to their beginnings in the urodeles. By homologizing these muscles in the urodeles with those in the salientians we have a basis of comparison between mammal and frog. I may add that it is only this extended systematic method which can give a sound basis to the determining of homologies.

OUTLINE OF SALIENTIAN PHYLOGENY

ADAPTATION AND PHYLOGENY

It was recognized long ago by Günther that the dilation of the sacral diapophyses has little adaptive significance. Mivart (1869a) and since then several others have pointed out that arboreal, terrestrial, fossorial, or aquatic forms may possess dilated sacral diapophyses or they may possess cylindrical ones. It surely cannot be said that the dilated sacral diapophyses are adapted to any one type of locomotion. Similarly, it was pointed out by Günther and later by Mivart that the presence or absence of teeth are hardly correlated with the food habits of the species. I have recently examined a great many stomachs of African frogs and have come to the conclusion that toothed forms of large size (*Rana occipitalis*, etc.) may seize vertebrates occasionally or even prey on them nearly exclusively (*Rana ornatissima*), while toothless forms (*Bufo*), regardless of size, never take vertebrate prey. The absence of teeth is a limiting factor; it is not an adaptation to a food habit, for these toothless forms prey upon a great variety of invertebrates, chiefly insects.

It is highly probable that not only the dilation of the sacral diapophyses and the loss of teeth but also the acquisition of bony growths on the mandible, similating teeth, and the fusion of the pectoral girdle in the midline have all taken place, if not regardless, at least independently, of the environment. Highly specialized frogs (*Cerathyla*, *Ceratobatrachus*) exist in regions of maximum abundance of amphibian life. Still, it cannot be said that they are highly adapted to their environment. Many features of these and other specialized genera can have no adaptive significance.

So many cases of muscular adaptation occur in the Mammalia that it would seem, *a priori*, that the specialization of the thigh musculature in the Salientia must have taken place in adaptation to various modes of life. Long-legged, arboreal frogs have narrow, often tendinous muscles. The sartorius of *Leptopelis*, an arboreal ranid, is tendinous distally, similar to that of some of the more arboreal species of *Hyla*. Other modifications of proportion and extent may be correlated with the degree of use to which the limb is subjected. But the degree of differentiation does not seem to be definitely correlated with any particular mode of life. Fossorial and terrestrial pelobatids have the same number of elements in the thigh; arboreal, fossorial, aquatic, and terrestrial bufonids exhibit no differences in the number of elements. We find the

more specialized discoglossids and pelobatids have independently developed an adductor longus, but just how great a part any specific functioning might have played it is impossible to say. Possibly the differentiation of this muscle is correlated with certain springing movements, but on this point we have no information. It would seem that the differentiation of the thigh musculature has progressed from the generalized condition exhibited by the discoglossids to the specialized condition found in the ranids. Aquatic life may be said to have called forth a maximum development of the muscles, but it has not fostered the development of special swimming muscles. Possibly function has played a part in the sinking of the tendon of the semitendinosus through the gracilis mass. We have seen that this took place independently in a number of different genera. Too little is known about the mode of life of these specialized forms to state what part function might have played in the specialization of the semitendinosus. Although function must have played some part in muscular differentiation, this action has been more general than specific. Adaptation has not obscured the main trend of phylogeny. The myology as well as the osteology of the Salientia gives definite evidence as to the natural groups of genera.

In the accompanying chart I have attempted to schematize the phylogeny of the Salientia as I understand it. The four primary categories defined above are made the basis of this phylogeny and a few of the numerous parallelisms occurring in each of these categories are indicated. It is apparent from the above discussion that the vertebral column was originally opisthocœlous and consisted of eight presacral vertebræ. From this condition the vertebral column seems to have evolved the procœlous and finally the diplasiocœlous type, while a fusion of the vertebræ occurred independently of these changes. In the Salientia, teeth were primitively confined to the upper jaw and from this condition forms, on one hand with no teeth on either jaw and on the other with pseudo-teeth (in one instance true teeth) on the lower jaw, were evolved. Other changes which have occurred in more than one series are the dilation of the sacral diapophyses, the fusion of the pectoral girdle in the midline, and the development of intercalary phalanges, the latter being sometimes accompanied by the development, of claw-shaped terminal phalanges. For the sake of clearness, I have listed the more essential changes in the following columns. If this table is compared with the accompanying chart, the orthogenetic and often parallel modifications of the Salientia will be more readily understood.

If the end stages indicated on the chart actually represent the terminations of a series 'of orthogenetic changes, they most certainly do not form the ancestral stock from which other groups possessing more primitive features have been derived. For example, in the diagram I have represented *Scutiger, Ophryophryne,* and *Ælurophryne* as the terminal twigs of the anomocœlous branch and the end of a distinct line of specialization, which specialization, as we have seen above, may be muscular as well as osteological. Nevertheless, Boulenger (1919, p. 470), although he correctly regards these three genera as toothless pelobatids, prefers to believe that they "may be desaribed as lowly forms approaching the Discoglossidæ and leading on one hand to the Cystignathidæ (through *Batrachopsis,* Blgr.), and on the other to the Bufonidæ."

Such speculations might seem to receive some support from the ontogeny of frogs in general, since the tadpole, of course, possesses no true teeth. But we have seen above that in the adult only the specialized Salientia lack teeth. We have been able to trace out, with considerable detail, lines of specialization at the end stages of which the teeth were lost. Further, we have seen that the musculature of the thigh readily distinguishes the "Cystignathidæ" (=Bufonidæ, part) from the Discoglossidæ and Pelobatidæ. There is no evidence to believe that *Scutiger, Ophryophryne* and *Ælurophryne* are transitional genera in either their osteology or their myology.

The Salientia have not undergone innumerable and haphazard changes. Few possibilities of modification have seemed open to them. In nearly every family the same modifications crop out as if these were destined to appear as the family matured. There are, to be sure, certain modifications peculiar to certain families. As the anatomy of the Salientia becomes better known, other diagnostic characters will be brought out. The accompanying chart and table will, I believe, help to determine what characters may be expected to be fundamental.

COMPARISON OF THE PHYLOGENY OF THE SALIENTIA WITH THAT OF THE CAUDATA

The thigh musculature of the frogs and toads has been compared with that of the urodeles. It may be well in closing to glance briefly at the phylogeny of the urodeles, for that apparently has been very different from the phylogeny of the Salientia. In the frogs and toads adaptation seems to have played a small part in the fundamental changes which have taken place, while in the Caudata adaptation seems to have been correlated with morphogenesis to a large extent.
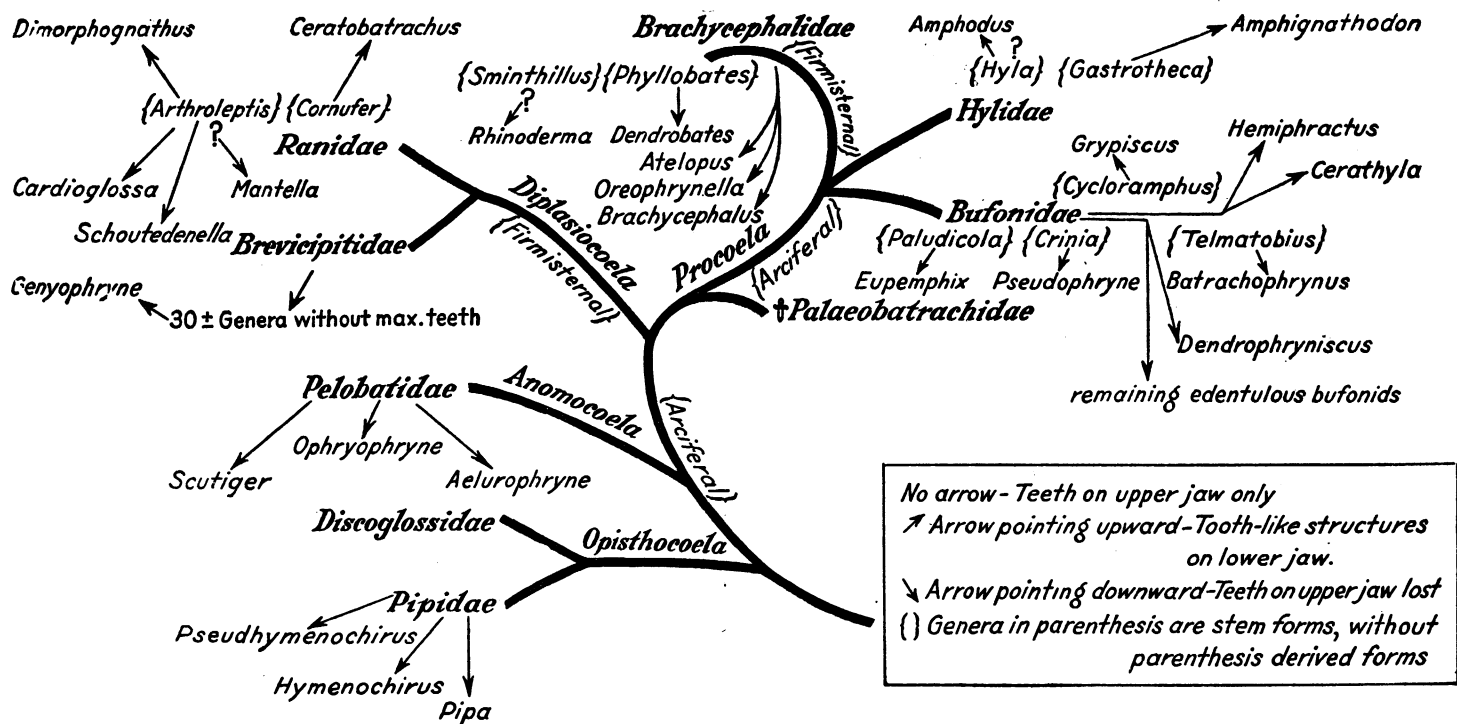
Dimorphognathus   Ceratobatrachus   *Brachycephalidae*   Amphodus   ➚Amphignathodon

{Arthroleptis} {Cornufer}   {Sminthillus}{Phyllobates}   {Hyla} {Gastrotheca}

Cardioglossa   *Ranidae*   Rhinoderma   Dendrobates   *Hylidae*   Grypiscus   Hemiphractus

Mantella   Atelopus   {Cycloramphus}   ➚Cerathyla

Oreophrynella   *Bufonidae*

Schoutedenella *Brevicipitidae*   Brachycephalus   {Paludicola} {Crinia}   {Telmatobius}

Cenyophryne   Eupemphix Pseudophryne   Batrachophrynus

↘30 ± Genera without max. teeth   ✝*Palaeobatrachidae*   Dendrophryniscus

remaining edentulous bufonids

Pelobatidae *Anomocoela*

Ophryophryne

Scutiger   Aelurophryne

Discoglossidae   *Opisthocoela*

Pipidae

Pseudhymenochirus

Hymenochirus

Pipa

No arrow - Teeth on upper jaw only
↗ Arrow pointing upward - Tooth-like structures on lower jaw.
↘ Arrow pointing downward - Teeth on upper jaw lost
{ } Genera in parenthesis are stem forms, without parenthesis derived forms

Genetic Relations of the Salientia
with especial reference to dentition, vertebral column and pectoral girdle

TABLE 2.—PARALLEL MODIFICATIONS OF THE SALIENTIA

	OPISTHOCŒLA	ANOMOCŒLA	PROCŒLA	DIPLASIOCŒLA
DENTITION	Teeth primitively present on the maxillaries and vomers, completely lost in the end stages of specialization	Parallel modifications	Parallel modifications, but in the end stages, pseudo-teeth may develop on the mandible (in one genus true teeth)	Parallels the Procœla (but no true teeth ever present on mandible)
SACRAL VERTEBRA	Diapophyses of sacral vertebra primitively slightly dilated, becoming broadly expanded in specialized genera	Diapophyses typically dilated	Diapophyses primitively cylindrical, becoming greatly expanded in end stages of specialization	Parallels the Procœla
RIBS	Present at some period in the ontogeny	Absent	Absent	Absent
VERTEBRAL COLUMN	Primitively eight presacral vertebræ, reduced to five in end stages of specialization. Opisthocœlous	No reduction of vertebræ (except abnormally). Anomocœlous	Parallels Opisthocœla in fusion of vertebræ in the specialized brachycephalids. Procœlous	No reduction of vertebræ (except abnormally). Diplasiocœlous
PECTORAL GIRDLE	Primitively arciferal, becoming semi-firmisternal in the specialized pipids	Arciferal	Typically arciferal, becoming semi-firmisternal and firmisternal in the brachycephalids	Firmisternal
THIGH MUSCLES	Primitively no adductor longus; no sartorius; semitendinosus broad and superficial; iliacus externus broad or with accessory head; adductor magnus divided distinctly into two parts; obturator externus large; two pairs coccygeal muscles present. In specialized forms, adductor longus present; two heads of adductor magnus partly fused; only one pair of coccygeal muscles	Primitively similar to Opisthocœla but only one pair coccygeal muscles. Parallels Opisthocœla in development of adductor longus and reduction of the semitendinosus. Parallels Procœla in loss of accessory head of iliacus externus in *Pelodytes*	Differs in presence of adductor longus (typically) and sartorius; the deep position and narrow form of semitendinosus, loss of accessory head of iliacus externus; partial fusion of two heads of adductor magnus; reduced condition of obturator externus. Specialized forms possess an accessory head of the adductor magnus and specialized gracilis minor	Same as Procœla but adductor longus always present; also accessory head of adductor magnus. Parallels Procœla in expansion of the gracilis minor
DISTAL TENDONS OF THIGH	Primitively the tendon of the semitendinosus overlaps that of the gracilis major and minor; the tendon of the sartorius not developed. Specialization occurs in the pipids, the tendon of the semitendinosus becoming either partly enclosed within the gracilis (*Pipa*) or coming to underlie it (*Xenopus*) (see Pl. xvi)	The primitive condition of the discoglossids retained in this suborder. Specialization limited to the insertion of the gracilis minor (see *Scaphiopus* Pl. xi)	Typically the tendon of the semitendinosus overlaps that of the gracilis major and minor; the sartorius inserts on the tendon of the semitendinosus (Pl. xiv, fig. 2). Specialization limited to a sinking of the tendon of the semitendinosus into the gracilis mass or nearly completely through it; head of sartorius attaches to knee. Some modification from the typical condition in *Rhinophrynus* (Pl. xvi, fig. 6)	Differs consistently from Procœla in having the tendon of the semitendinosus always deep to that of the gracilis major and minor and never closely bound to it (Pl. xiv, fig. 3). Specialization limited to the development of secondary ligaments

It is now generally recognized that the most aquatic urodeles are not the most primitive, nor the most "larval," the most generalized. Terrestrial salamanders exhibiting the fewest losses of structure are believed to be more or less ancestral to the others. Some of these others are also terrestrial, but many are aquatic. A large number of the aquatic forms have failed to develop all the adult structures. These are recognized today as cases of arrested development, and the larval habitus of the forms is considered a secondary specialization.

The Necturidæ embraces only two genera, *Proteus* and *Necturus*. Both are "larval adults." The family habitus is therefore larval. The distinctive features of the family, the heritage by which its true relations may be determined, is greatly obscured by this habitus. It is only such obscure features as the absence of an ypsiloid apparatus, the presence of lungs, the presence of a distinctive auditory apparatus, and some features of the pelvis and skull which make it apparent that the Necturidæ represent a distinct line of evolution, their immediate ancestors not to be found in any of the existing Caudata.

The Sirenidæ, like the Necturidæ, are of uncertain origin. Their whole structure has been modified for an aquatic and burrowing life. In no family of Salientia except the Pipidæ are all the members highly adapted to one particular mode of life.

Another aquatic family is the Cryptobranchidæ. *Cryptobranchus* is more "larval" than *Megalobatrachus*, but both have a very similar habitus. It is very probable that the immediate ancestors of the Cryptobranchidæ will be found in less aquatic hynobiids. Without considering the structure of either group, it may be said that the more superficial changes which the Cryptobranchidæ have undergone seem to adapt them to an aquatic existence.

The most splendid cases of adaptation occur in the higher Caudata. Wilder and Dunn (1920) have suggested that the Plethodontidæ evolved in a mountain brook habitat, and that the loss of the lungs in this family is correlated with such an origin. Today, plethodontids are found in a variety of habitats but they all retain their heritage of lunglessness.

Recently Reed (1920) has reviewed the morphology of the auditory apparatus in the urodeles. He has found that practically every family is distinguished by a definite type of apparatus which is, as might be expected, highly adapted to the needs of the respective groups. In the Salientia, the auditory apparatus undergoes remarkable changes within a single family. It is, to be sure, more or less adapted to the definite

needs of the animal, but the genera in each family have such a diversity of habits that the auditory apparatus does not possess a distinctive form in any one of the larger groups.

The Caudata do not exhibit numerous parallelisms in their phylogeny, such as we have seen in the Salientia. The Plethodontidæ, for example, have specialized along a line of their own. They have undoubtedly arisen from the more generalized salamandrids and many of their distinctive features may be considered losses. The loss of the pterygoid and ypsiloid apparatus may be taken as an example.

The amphiumids may also have arisen from the salamandrids. Their loss of ypsiloid apparatus and reduction of the limbs seems to be an adaptation to their semi-fossorial and aquatic life. The ambystomids are in many ways more generalized than the salamandrids. They may have given rise to the latter family. It is important to note that each family has a more or less definite habitus characterized in general by adaptations to a particular life. In the Salientia, but few of these restrictions occur. The families are not so circumscribed by particular adaptations. The habitus of the families of Salientia is too varied to be distinctive, while it is otherwise with most Caudata. In the urodeles, adaptations seems to have played a considerable rôle in the morphogenesis of the families; in the Salientia, this rôle seems to have been reduced to a minimum.

Characters which define genera and species of Salientia are of a very different kind from those which define the families. In the first place, they are often highly adaptative. Differences in the extent of webbing between the digits, in the development of metatarsal tubercles, in the position of the digits, and in the ossification of parts of the pectoral girdle seem to have an adaptive significance. Not all of the characters which define the genera are obviously adaptive. Differences in the form and extent of the vomerine teeth, in the exact form of the pupil, in the loss of elements from the pectoral girdle, etc., are either not at all adaptive or only slightly so. In general, it may be said that, in the Salientia, the characters defining the species are more adaptive than those defining the genera, those distinguishing the genera more adaptive than those diagnostic of families, while the few characters we have found to define the suborders are the least correlated with function or habit.

ORIGIN OF THE SALIENTIAN FAUNÆ

GENERAL STATEMENT

If the genetic relationships of the frogs and toads as outlined above have been correctly interpreted, many difficulties of distribution are at once removed. To take but a single example, Hewitt (1911, p. 36) was at a loss to account for the occurrence of "dendrobatids" in Madagascar, tropical Africa, and tropical America. Arldt (1917, p. 134) boldly revives the phantom land bridge which has been thrown so many times across the Atlantic. The real explanation, however, is simple. *Cardioglossa* in Africa has arisen from the *variabilis* group of *Arthroleptis* by a loss of the maxillary teeth, while *Dendrobates*, in tropical America, has arisen directly from *Phyllobates* by a similar modification. *Mantella* in Madagascar has arisen from a Madagascan ranid, very probably *Arthroleptis*, and has no relation to *Dendrobates*, which, as we have seen above, has evolved from the bufonids.

If the recent herpetological literature is critically examined, it will appear that today there is no need for the antarctic continents or mid-Atlantic land bridges which have been revived from time to time to account for the distribution of the Salientia. Perhaps the most recent of these revivals is that of Metcalf (1921a) who has brought some additional evidence derived from a study of the opalinid parasites of the Salientia. There seems to me to be little need for the land bridges Metcalf has revived. Hylids and "leptodactylids" occur in the Ethiopian region. We have merged the "leptodactylids" into the Bufonidæ, while the hylids have almost certainly evolved from this bufonid stock. The pipids now include four genera: *Pipa*, *Xenopus*, *Hymenochirus* and *Pseudhymenochirus*. This explanation of a former wide dispersal and present restriction of range is much simpler than the assumption of a mid-Atlantic land bridge. A land bridge admits a flood of forms. Witness the numerous forms which have certainly migrated in comparatively recent times across the Isthmus of Panama. The fauna of Africa is essentially unlike that of South America. The few resemblances between the two faunæ are not to be accounted for by assuming a land bridge between the continents.

It is well known that the fossil record gives us little aid in determining the past history of the Salientia. We have barely mentioned the fossil evidence in discussing the phylogeny, for this evidence neither supports nor refutes the conclusions reached. None of the fossils may be considered more annectant than forms living today. In fact, the majority

of these forms are referred to living genera. Nor does the fossil record suggest early centers of dispersal, widely removed from present ranges. In determining the origin of the salientian faunæ, we have had to rely on the genetic relations of the groups and their present geographical positions.

Several of the families of Salientia were probably differentiated as early as the Jurassic. The oldest known frog has been referred to the genus *Palæobatrachus* by Vidal. It comes from the Kimmeridge beds of Spain. Of almost equal antiquity are the fragments of a skeleton described as *Eobatrachus agilis*. These were secured in Quarry 9 of the Como Bluff, Wyoming. They have recently been redescribed (Moodie, 1912, 1914) and apparently represent two individuals: "one specimen, a lower end of a left humerus, somewhat smaller than the type; the other or type humerus; the lower end of a tibio-fibula; the entire left (?) femur; the entire right ilium; all, apparently of a single individual excepting the humerus first referred to, which indicated a second frog though possibly of the same species." Moodie was unable to distinguish these bones from similar ones in modern Salientia. In fact, he goes so far as to place *Eobatrachus agilis* in the Bufonidæ, "and possibly even in the genus *Bufo*." This, of course, is merely a guess, as no family characters have yet been distinguished in the elements under discussion. Still, the evidence is sufficient to demonstrate that the families of modern Salientia were at least in part defined as early as the Jurassic. It is no wonder, then, that certain families of modern Salientia exhibit today a discontinuous distribution.

AFRICAN FAUNA

Twenty-nine of the thirty-nine genera of frogs and toads found in Africa are peculiar to that continent. Four of the ten exceptions have their headquarters in Africa, three (*Arthroleptis, Hyperolius,* and *Megalixalus*) of these having extended their range to Madagascar, and the fourth (*Phrynomantis*) having a representative, probably not at all congeneric with it, on two islands of the East Indies. Three other non-indigenous genera (*Rana, Bufo,* and *Discoglossus*) have apparently migrated into Africa in comparatively recent times and by way of the northeast or northwest. Two others (*Nectophryne* and *Pseudophryne*) are representatives of an ancient and highly modified group which may or may not have gained access to Africa from the northeast. The last genus (*Hyla*) represents a complex problem, two races of one species having barely reached Africa on the north, while the only other represen-

tative of the genus, although restricted in range to Abyssinia, seems to have its nearest affinities in certain South American species.

The record of a *Hyla* from Abyssinia has received little or no comment in the literature. Nieden (1911) described it as *H. wachei* and gives Dire Daua as its type locality. Although Nieden pointed out that this species was the first *Hyla* recorded from the Ethiopian region, he did not discuss its relationships. One would imagine from the consideration of the distribution of African reptiles that the species would show close affinities to *Hyla arborea savignyi* of Syria and Palestine. Such is not the case. It has very little in common with any Asiatic *Hyla* and but little more with any Australian or East Indian species. It agrees entirely with the *maxima* group of species from northern South America. In fact, only one point of difference appears in the original description to distinguish *H. wachei* from *H. maxima* as represented by a large series before me from British Guiana and Colombia. Nieden gives the web of the fourth toe of *H. wachei* reaching only to the end of the antepenultimate phalanx, while in *H. maxima* it reaches to the end of the penultimate. It is very possible that the peculiar arrangement of the vomerine teeth, characteristic of the *maxima* group, could have had a parallel evolution in two such widely separated areas as Abyssinia and South America. The species of "*Hylella*" and *Nyctimantis* have very probably evolved independently in the East Indies and South American regions by a parallel modification of the *Hyla* stock. *H. wachei* is known only from the type. If this specimen actually came from Abyssinia, and we have no reason to doubt it, the genus *Hyla* must have existed in Africa for a very long time, since *H. wachei* shows no close affinity to the eastern representatives of the genus.

Perhaps more remarkable from the standpoint of zoögeography than the discovery of a *Hyla* of South American affinities in Abyssinia was the recent find of a "leptodactylid" in South Africa. This genus, *Heleophryne*, is very distinct but it seems to be more closely related to certain Australian-New Guinean genera than to any of the South American. Still, it agrees with *Centrolene* and *Centrolenella* of Ecuador and Colombia in lacking the omosternum and in possessing moderately dilated sacral diapophyses and T-shaped terminal phalanges. *Heleophryne* differs from both *Centrolene* and *Centrolenella* in several features. It lacks the intercalated phalanx and the web between the fingers. It possesses a vertical pupil and well-developed series of vomerine teeth.

Heleophryne is apparently most closely related to the *Limnodynastes-Ranaster* group of genera. The numerous differences which distin-

guish it from these genera seem to me to be of secondary importance. It is possible that the dilation of the sacral diapophyses and reduction of the omosternum have arisen independently in these Australian, African, and South American genera under discussion. In that event, the true relationships of *Heleophryne* have been obscured through convergence.

The Ranidæ and Brevicipitidæ very probably have been in Africa since Eocene times and both may have come in from the north. Madagascar has been a center of differentiation for "dyscophids" but the two genera in Africa suggest that the toothed brevicipitids may have gained access to Madagascar from the nearby continent. No serious difficulties are met with in assuming a center of dispersal for the brevicipitids in southern Asia and a subsequent migration on one hand to the Malay Archipelago, the East Indies, and especially to New Guinea,[1] and, on the other hand, an early migration to Africa at a time when Madagascar, if not connected with Africa, at least was not beyond the reach of the African stock which, upon reaching Madagascar,[2] formed a line of specialization parallelling to a large extent the East Indian series.

The ranids must have reached Africa at an early time. Their center of generic differentiation is the Cameroon-Gaboon area. If the distribution of forest and open country was then very much as it is now, we would expect that the Cameroon mountains might afford just such a region fostering specialization. Forests alone apparently do not contain all the requisites for the maximum possibilities of amphibian life. Compare,[3] for instance, the amphibian fauna of the Organ Mountains with that of the surrounding Brazilian forests, or the peculiar genera of the Ecuadorian montaña with that of the Amazonian forests lying to the east. Geographical evidence has recently been brought forward to support the view that the Congo basin has been inundated for some time. Such a condition would also account for the obvious fact that the forest fauna of the Upper Congo is a derived one, composed of either wide-ranging forest forms or migrants from the Cameroon-Gaboon area. In brief we may assume that the Cameroon-Gaboon area has been a center of differentiation either because of its diverse topography or because it has not suffered the drowning process of the Congo Basin. Both factors may have played a part.

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[1] Van Kampen (1919, p. 54) recognizes 13 genera and 35 species of brevicipitids in New Guinea lacking teeth in the upper jaw.
[2] Boettger (1913) recognized 9 genera of the more primitive brevicipitids possessing the maxillary teeth and 4 genera lacking them.
[3] Baumann (1912).

It should be emphasized that, while the Brevicipitidæ and Ranidæ have almost certainly gained access to Africa from the north, the same may be said for the Bufonidæ. If we assume a similar polar origin for the Pipidæ, Hylidæ, and "Leptodactylidæ," we escape the necessity of building any land bridge. If we assume a single land bridge, one from South Africa to Australia, we have to explain why only such a limited representation of such diverse stocks was able to cross to Africa. The same may be said for a land bridge across the Atlantic.

Hewitt (1911) and many earlier workers have insisted that there is good geological proof of the former existence of these land bridges. With this opinion I cannot agree. Many of the statements made by Hewitt (1911) are contrary to fact. Hewitt's paper is apparently the most comprehensive account of the distribution of African amphibians published in recent years, but his opinions are based on the conclusions of others. If his evidence is re-examined from the different point of view emphasized above, the necessity for much of this bridge building will be eliminated. I agree entirely, however, with his final conclusions (1911, p. 39) as to his land bridge hypothesis:

. . . it must be admitted that the kind of evidence that is required to properly establish these hypotheses is altogether lacking, in the almost complete absence of fossil forms: nor do we possess the whole evidence of comparative anatomy, for our judgements of generic relationships are based upon the more easily ascertained and superficial characters, and the data for a genetic arrangement of the genera are still wanting.

I have attempted in the first part of this paper to indicate the broad features of these genetic relations. We are justified, I believe, in assuming that the entire amphibian fauna of Africa, either directly or indirectly, gained access to Africa from the north.

NEOTROPICAL FAUNA

The continent of South America, probably because of its diverse topography, supports a rich salientian fauna. Only thirty-nine genera of frogs and toads occur in Africa, while in South America there are no less than sixty. The exact number will, of course, vary according to whether or not one recognizes such unnatural assemblages as *Hyella*. In the present instance I have included only natural groups. Fortunately, I have had at one time or another the opportunity of examining the majority—forty-six—of these genera.

Twenty-one of the sixty genera occur also in Central America, but only two of these, aside from the nearly cosmopolitan *Rana, Bufo,* and

Hyla, occur outside the neotropics. These two, *Hypopachus* and *Gastrophryne*, are brevicipitids found today in southern United States. Their distribution suggests the route by which the Brevicipitidæ probably reached South America. The Brevicipitidæ may be the oldest firmisternal family on that continent. At least it includes the most specialized forms. We have suggested above that all toothless brevicipitids arose directly or indirectly from forms possessing maxillary teeth. It is not probable that any of the South American brevicipitids have been recently evolved from toothed forms. It is more probable that they have all arisen from some *Hypopachus*-like ancestor which gained access to South America at comparatively early times. Today, eight genera of brevicipitids are known to occur in South America. They are *Hypopachus, Stereocyclops, Gastrophryne, Ctenophryne, Chiasmocleis, Glossostoma, Dermatonotus* and *Otophryne*.

There is a second firmisternal stock in South America which, unlike the Brevicipitidæ, must have reached the continent at very recent times, certainly since the Panama connection, and very probably by way of the north. This is *Rana*, the sole representative of that typically Ethiopian family, the Ranidæ. Most text books cite several genera of ranids as occurring in South America. But in a recent revision I have shown[1] that *Prostherapis* and *Phyllodromus* should be referred to *Phyllobates*, while *Colostethus* should be deleted from the system. We have seen above that *Phyllobates* is a typical brachycephalid, much more closely related to the bufonids than to the ranids. This leaves *Rana* with one or more, probably two, species to represent the great family of Ranidæ in South America. Several other species of *Rana* occur in Central America. The restricted range of the genus in northern South America is further proof of its having only recently gained a foothold upon that continent.

The third family of firmisternal forms in South America I have defined above as the Brachycephalidæ. Their procœlous vertebral column, their bufonid type of distal tendons in the thigh, and, lastly, their occasionally incomplete firmisternal girdle, all point towards their independent origin from the bufonids. Future work may show that they have had a polyphyletic origin. It seems probable that *Sminthillus* has acquired its semi-firmisternal girdle independently of the other genera. All brachycephalids very probably evolved from the Bufonidæ and from that family alone. In recognizing this fact, I believe we have made a distinct advance, whether or not we divide the Brachycephalidæ

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[1]Barbour and Noble (1920, p. 398).

into subfamilies or into groups of genera having a close affinity. It is not difficult to divide the family into groups of related genera. At the present time, ten genera are referable to the family. I have dissected all except one (*Chilixalus*) of these, but one other (*Oreophrynella*) has been studied only in part. These ten genera are: *Brachycephalus, Atelopus, Rhinoderma, Sminthillus, Geobatrachus, Oreophrynella, Phyllobates, Hyloxalus, Chilixalus* and *Dendrobates*. Four of the ten genera are found in neotropical regions beyond the limits of South America. Three of these may have migrated into Central America since the Panama connection, but one (*Sminthillus*) may have arisen, at least in part, in Cuba. It is very probable that all brachycephalids (except *Sminthillus*, in part) have arisen in South America from bufonid genera existing there.

Under the present system of classification, I recognize nine genera of Hylidæ as occurring in South America. This includes *Amphignathodon*, which we have seen above is merely a specialized *Gastrotheca*. Five of the nine genera occur in Central America, which may boast of two genera of hylids peculiar to it. Still, these two genera are not strikingly different from *Hyla*.

The genus *Hyla* possesses nearly a world-wide distribution, except for a great gap in the Indo-Oriental region. Formerly considerable emphasis was placed on this gap in its present distribution. This, together with the abundance of the genus in the South American and Australian regions, seemed to lend some support to the Gondwana land hypothesis. But today we know of one true *Hyla* from the Ethiopian region and three toothed bufonids. The latter are all referable to the single genus *Heleophryne*. It thus seems most likely that the genus *Hyla* originated in the north and pushed southward into Africa and the Oriental region. Finally, when the genus gained access to Australia, it died out in most of the more northern regions except in Papua and some of the East Indian islands where it is still abundant.

The great bulk of the neotropical salientian fauna is composed of bufonids. We have shown above that there is no real distinction between those genera possessing and those lacking the maxillary teeth. I recognize thirty genera in South America and two additional genera restricted to Central America. Except for one or two stragglers in northern Mexico and Florida, none of these Salientia except *Bufo* extend their range beyond the neotropics. *Bufo* is undoubtedly a hardy migrant from some other region. It probably gained access to South America at the same time that *Rana* did. The majority of the bufonids in South America probably originated there from allied genera. Only eight of

the thirty genera in South America occur north of the Isthmus. Probably the majority of these have pushed their way northward since the Panama connection.

It is surprising that no primitive salientian except *Pipa* occurs in South America. The discoglossids and pelobatids are totally absent. The presence of *Pipa* does not prove a former land connection between South America and Africa. It cannot be too strongly emphasized that the faunæ of these two continents are very unlike. Just how a land bridge would have permitted the entrance into South America of a pipid and none of the numerous ranids (save *Rana*) which must have swarmed in Africa, one cannot explain. *Pipa*, even if greatly specialized to an aquatic existence, shows itself in its structure to be one of the most primitive Salientia. The absence of fossil record prevents us from estimating when *Pipa* may have gained access to South America, but, because of its lowly position among the Salientia, it would seem likely that this may have been in Mesozoic or early Tertiary times. There is no evidence against *Pipa* having reached South America from the north in these early days.

AUSTRALIAN-PAPUAN FAUNA

Australia is very poor in Salientia, while New Guinea, although comparatively richer, possesses a fauna not unlike that of northern Queensland, except that one group, the Brevicipitidæ, has undergone a remarkable radiation. The Australian relationship of the Salientia of New Guinea has never been sufficiently emphasized. Nor has the case for a northern origin of the Australian Salientia been satisfactorily argued.

The great bulk of the salientian fauna of Australia is composed of bufonids. Fifteen genera are recognized today. Of these only three are toothless. One toothless genus, *Pseudophryne*, has been directly derived from a toothed form, *Crinia*, occurring in the same region, while the internal structure of the other two edentulous genera is not sufficiently known for us to state from what toothed bufonid they have arisen. Still, it may be safely assumed that their relations are to be sought within the region. The comparatively recent and aggressive genus *Bufo* does not occur in Australia, a condition which is to be expected if the genus, as we have assumed above, is of holarctic origin and has pushed southward only in late Tertiary or recent times.

The fact that numerous toothed bufonids occur in Australia and in South America has for many years lent some support to the Antarctic continent theory. We have already stated above that this recent dis-

covery of toothed bufonids in Africa together with a recognition of the close affinity of toothed and toothless forms removes much of the argument in favor of this view. For years the distribution of the hylids has been used as supplementary evidence in favor of a former South American-Australian land connection. But it should be emphasized that of the hylids, the genus *Hyla* alone occurs in Australia. The genus *Hylella* is untenable, for the presence or absence of vomerine teeth is a character of little significance.

The distribution of the genus *Hyla* is very difficult to explain. We have already remarked on the discovery of a *Hyla* in Abyssinia. The genus is now known from all the major zoölogical regions except for a remarkable hiatus, extending from the Philippines, Borneo, Celebes, Siam, and the Malay Archipelago through India. Several of the Asiatic Hylas encroach upon the border of this region (as in Burma), but these are readily recognizable as ectogenetic forms. Why this Indo-Oriental region should be a closed territory to *Hyla* is not known, but I do not believe there is good reason to assume that it has always been a closed territory, that the genus has never existed in any of this region.

The Hylidæ, and especially *Hyla*, are nothing but arboreal bufonids, some of which have returned again to a terrestrial existence. A close parallel occurs in the Ranidæ. A group of ranid genera are characterized by an intercalary disc between the ultimate and penultimate phalanges of the digits. Not all of these genera are arboreal. But the osteology, especially the pectoral girdle, indicates that the terrestrial have evolved from the arboreal forms. Thus it would seem that the intercalary disc once formed is never absorbed, and that the presence of this disc is indicative of an arboreal ancestry. I have had the occasion of discussing this problem in another connection (Noble, in manuscript). It is interesting to note that all hylids possess this disc, although it occurs also in other families. It is found in certain arboreal bufonids (*Centrolene*) which have retained the T-shaped terminal phalanges.

If we overlook for a moment the great gap in an almost world-wide distribution of the genus *Hyla* and recognize that the genus must have arisen from the toothed bufonids known today from the Ethiopian as well as the neotropical regions, if we admit that the toothless bufonids of this Indo-Oriental region must have arisen from toothed forms probably existing in the same or not far distant regions, then it is not difficult to understand that *Hyla*, too, may have arisen from these or related bufonids. The argument in brief is that in all probability there existed in the Indo-Oriental region toothed bufonids not found there today.

Similarly, there may have been hylids there. At least it is much simpler to account for the present distributions of the genus *Hyla* by assuming a northern origin and later migration southward by three routes, the first leading into South America, the second into Africa, and the third into the East Indies and Australia, than to assume land connections between South America and Australia when we would have still to account for the *Hylas* in Africa and northern Asia.

New Guinea and many of the East Indian islands are rich in species of *Hyla*. A second genus of hylids occurs in New Guinea. This has been considered identical with *Nyctimantis*, a South American genus, but it was recognized by Stejneger (1916) that here was a case of parallel modification and he erected for the New Guinean form a new genus, *Nyctimystes*. There can be no doubt that the single character, the vertical pupil, which distinguishes *Nyctimystes* from *Hyla* was acquired independently in the former and in the South American *Nyctimantis*.

It has been recognized for a long time that northern Queensland possessed much in common with New Guinea. For this reason, it has been called the Torresian or the Papuan district of Australia. The Salientia of this subregion are largely of those genera found in other parts of Australia but in addition there is found here a ranid and four brevicipitids. The ranid, *Rana papua*, occurs also in New Guinea, Ceram, Aru and Tenimber Islands, Batanta, Waigeu, Jobi and d'Entrecastaux Islands. It is therefore a wide-ranging species. New Guinea, according to Van Kampen (1919), possesses about nine species of *Rana*, but the status of certain of these is in doubt. The only other genus of ranids in New Guinea is *Platymantis* which has an extended distribution in the East Indies. It is apparent that the two genera of ranids in New Guinea are of recent arrival, both belonging to wide-ranging groups.

Although New Guinea has not been a center of radiation for the ranids, it has been one of the highest specialization for the brevicipitids. The four species of brevicipitids in Australia are all referable to a single genus, *Austrochaperina*, closely allied to the wide-ranging *Chaperina*. Van Kampen (1919) recognizes thirteen genera and thirty-five species of brevicipitids in New Guinea. All these lack the maxillary teeth and thus in all probability represent the extreme type of specialization. Only three of the thirteen genera of brevicipitids occur beyond New Guinea. It is therefore probable that most of the genera have probably arisen within the region. I have suggested above that the original stock from which the New Guinean brevicipitids arose was formerly widely distributed in southern Asia. This must have been a "dyscophid" stock, pos-

sessing maxillary teeth and exhibiting few losses in the pectoral girdle.
Whether the southern migration through the Malayan Archipelago and
the East Indies occurred before or after the loss of maxillary teeth it is
impossible to say. Probably brevicipitids, both with and without the
maxillary teeth, formed the original brevicipitid fauna of New Guinea.

Van Kampen (1919) records a single genus, *Lechriodus*, of pelobatids
from New Guinea. I have suggested above that this genus is in all
probability a bufonid. I have not had the opportunity of examining a
specimen, but Fry (1915, p. 75) has figured the genus as possessing two
articular condyles for the coccyx.

One other genus of bufonids, *Ranaster*, occurs in New Guinea. This
is represented by only a single species. The two species of bufonids in
New Guinea do not give its salientian fauna very much of an Australian
facies. Nevertheless, the fauna of New Guinea is essentially like that of
Queensland. There are very probably no pelobatids in New Guinea.
There are no ranids except representatives of two wide-ranging genera.
New Guinea shares with Queensland its brevicipitids, hylids, and
bufonids. In the former region, the brevicipitids and hylids have under-
gone a remarkable radiation; in the latter, the bufonids have specialized
along lines of their own. Although the facies of the salentian fauna of
New Guinea is unlike that of Australia, nevertheless, the components of
this fauna find closer affinity with the latter than with the fauna of India
or the Oriental region. Still, it is highly probable that the salientian
fauna of both New Guinea and Australia originated in these more north-
ern regions.

The salientian fauna of Tasmania is merely an extension of that of
Australia. According to English (1910), only seven species occur on the
island and these are referable to the four genera *Limnodynastes*, *Crinia*,
Pseudophryne, and *Hyla*.

Only two indigenous species of Saientia occur in New Zealand[1] but
these are of great interest. They are both referable to the genus *Liopelma*.
This genus has long been known as a discoglossid but recently Boulenger
(1910) without giving any reason has referred it to the "leptodactylids"
or toothed bufonids. It is apparent that some skeletal material was
available to Boulenger, but of this I have no information. It came as a
distinct surprise to me to find McCulloch (1919) describing a second
species of *Liopelma* and referring the genus without comment to the
Discoglossidæ. There is no doubt in my mind that the genus is a dis-

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[1]There are also two introduced species.

coglossid. The pectoral girdle figured by McCulloch (1919, figs. 1 and 2) is unlike that of any bufonid but agrees very well with that of *Ascaphus*. It is unfortunate that McCulloch did not make a complete dissection of *Liopelma hamiltoni* and settle the exact relations of the genus.

Stejneger (1905) would make the "country south-east of the Himalayas as the original center of radiation of the discoglossoid toads." There is much evidence to believe that this is the correct interpretation. It is to be noted that wide areas formerly occupied according to this view by discoglossids are now totally devoid of them. The Discoglossidæ, being the oldest family of Salientia, would be the most apt to show a discontinuous distribution. Following this same reasoning, the pipids would exhibit the next most discontinuous range, while the bufonids and hylids would have a more scattered distribution than the ranids, brevicipitids, or brachycephalids. It will be noted that the facts of distribution given above agree very well with this hypothesis, although some exceptions may be made, as in the case of the Pelobatidæ which, although primitive, exhibit a fairly continuous range. *Hyla* is not a recent genus, even if not a very archaic one. Its distribution would be expected to be more discontinuous than that of *Rana*, *Bufo*, etc. In fact, it is probable that in former times its distribution was more discontinuous than it is today, for the Asiatic *Hylas* seem to be recent arrivals from the west. In passing, a comparison may be made between the distribution of *Hyla* and that of the marsupials. The present ranges do not agree exactly, but in both they are discontinuous. Yet, in the case of the marsupials, the fossil evidence seems to demand a former wide distribution in the holarctic region and a later migration southward into Australia on one hand and South America on the other.

INDO-ORIENTAL FAUNA

Little need be said about the origin of this fauna for it has never been the subject of very much dispute. It is primarily a recent fauna showing closest affinities with that of Africa and Madagascar. It is rich in ranids, brevicipitids, and toothless bufonids, all more or less allied to African genera. The unique feature of this fauna is the abundance of pelobatids. The center of dispersal of the Pelobatidæ cannot be determined until the structure of more genera has been investigated. Still, it is safe to assume that this center was in the Palæarctic region. In fact, there is good reason to believe that the entire salientian fauna of India and southeastern Asia has migrated into the region from more northern realms.

HOLARCTIC FAUNA

Nor is it necessary for us to consider in detail the Salientia of the Palæarctic and Nearctic regions. As is well known, these regions are poor in Salientia. Some of the forms at present found there may have come in from more southern climates. There has been much easterly and westerly migration in the Palæarctic realm. In the Nearctic, the migrations seem to have been chiefly from the north to the south.

SUMMARY

Taxonomy and Phylogeny

(1). The classification of the Salientia in general use is largely artificial. Although this has been recognized, no better classification has been proposed but certain welcome changes in the system have been made.

(2). A review of the osteology of the Salientia with a view to determining characters of phylogenetic significance has shown that the maxillary teeth are lost at the end stages of many different lines of specialization and that their absence has no taxonomic significance. Further, the development of pseudo-teeth (in one case true teeth) on the lower jaw must also be considered an extreme case of specialization and without phylogenetic importance. In former classifications, considerable value was placed on the form of the sacral diapophyses in determining relations, also on the structure of the pectoral girdle and on certain features in the skull. A critical examination of the evidence makes it necessary to reject any of these characters as of primary importance.

(3). The modifications of the vertebral column offer a basis of dividing the Salientia into four primary groups, or suborders. Other features, such as the presence or absence of ribs, support this arrangement. The four suborders may again be divided into families on the basis of the most stable osteological characters at present known.

(4). In eliminating the variable characters, it becomes necessary to delete from the system the families based upon them. The following families have been rejected: Dendrobatidæ, Ceratobatrachidæ, Genyophrynidæ, Hemiphractidæ, Amphignathodontidæ, Dendrophryniscidæ, Leptodactylidæ and Dyscophidæ.

(5). A combination of characters in the vertebral column and thigh musculature distinguishes a group of neotropical genera from the ranids and brevicipitids which they parallel while the structure of their pectoral girdle distinguishes them from their bufonid progenitors. For this group I have erected the name Brachycephalidæ.

(6). The modifications of the thigh musculature exhibited by the families of Salientia, especially the arrangements of the distal tendons of the sartorius, semitendinosus, and gracilis major and minor, agree entirely with the classification proposed and not completely with any other scheme.

(7). This agreement of myological and osteological data makes it appear that the classification proposed is a natural one, while all other schemes are artificial to a greater or less extent.

(8). The phylogeny of the Salientia exhibits a series of orthogenetic and often parallel modifications. Adaptation seems to have been only slightly correlated with the major changes in the evolution of the group. As shown in the chart certain modifications, such as the loss of teeth or the fusion of the pectoral girdle in the midline, have taken place at the end stages of specialization in several different lines. It is not apparent that these and many other modifications of the Salientia are adaptive. This unadaptive phylogeny of the Salientia stands in striking contrast to that of the Caudata, which seems to have been closely correlated with the habits and habitats of the respective families.

(9). The classification proposed removes many difficult problems of distribution which existed under the former schemes. It becomes quite unnecessary to assume hypothetical land bridges to account for the present distribution of the Salientia. All the families of frogs and toads except the Brachycephalidæ seem to have originated in the Holarctic regions, or at least in the northern hemisphere and to have pushed southward into southern regions. Migrations in other directions also occurred, but no family of Salientia except the recently derived Brachycephalidæ had their center of dispersal on a southern continent.

MYOLOGY

(1). A comparison of the thigh musculature and its innervation throughout a large series of genera has shown many modifications even within a family. The adductor longus must be regarded as a mere slip of the pectineus, not differentiated in the more generalized forms. Similarly, the sartorius is only the anterior portion of a primitively broad and superficial muscle, the sartorio-semitendinosus. The gracilis minor may be regarded as a specialized slip of the gracilis major and primitively attaching to the skin.

(2). The most primitive type of thigh musculature is found in the more generalized discoglossids. In addition to the absence of an adductor longus and a sartorius, there is no accessory head to the adductor magnus. The latter muscle consists primitively of two very distinct muscles, which partly fuse in the advanced types. The semitendinosus is represented in the posterior part of a broad muscle which lies superficial on the ventral surface of the thigh. The obturator externus and the tensor fasciæ latæ are well-developed muscles (in general) showing that

their condition in higher types is due to a reduction in size. Other muscles, such as the iliacus externus, have a more generalized form than in higher forms.

(3). *Ascaphus* is remarkable in possessing two pairs of coccygeal muscles attaching to the thigh. The posterior pair is doubtlessly homologous to the caudalipuboischiotibialis of the urodeles. These two pairs of muscles are in no way associated with the "tail" of the male *Ascaphus*, which is purely a copulatory organ formed chiefly by an extension of the cloaca.

(4). In homologizing the thigh musculature of the Salientia with that of the Caudata, little difficulty is experienced when comparing primitive forms. The homologies suggested by the relative position, origin, and insertions of the muscles are fully supported by the innervations. These homologies have been tabulated above.

(5). Few modifications occur in the thigh musculature of the Caudata. These modifications have not been understood by earlier investigators. Two muscles, the adductor femoris and the iliotibialis, have been confused in most accounts with other muscles. The innervation, as well as the relative arrangement, indicates the distinctness of these muscles.

(6). It is inferred that the Pro-Salientia retained a pelvic musculature similar to the Caudata. The muscle areas on the pelvis of *Eryops* suggest this, while the presence of two pairs of coccygeo-femoral muscles in *Ascaphus* and the urodele appearance of the thigh musculature in all primitive Salientia seem to confirm this inference. This may not indicate a closer affinity of Salientia and Caudata than hitherto believed, but it may permit us to assume that the ancestral Caudata, Salientia, and possibly Reptilia possessed a type of pelvic musculature that was essentially alike.

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EXPLANATIONS OF ABBREVIATIONS IN PLATES I–XXIII

Add. fem. = Adductor femoris
Add. long. = Adductor longus
Add. mag. = Adductor magnus
(cap. ventr.) = ventral head
(cap. dors.) = dorsal head
(cap. acc.) = accessory head
Ang. = Angular
Art. = Articular
Bind. lig. = Binding ligament
Cart. Meck. = Meckel's cartilage
Caud. fem. = Caudalifemoralis
C.p.i.t. = Caudalipuboischiotibialis
Caud. pubo. isch. tib. = Caudalipubo-
    ischiotibialis
Cocc. = Coccyx
Cocc. il. = Coccygeo-iliacus
Compr. cloac. = Compressor cloacæ
Crur. = Cruralis
Dent. = Dentary
Fem. fib. = Femorofibularis
Gem. = Gemellus
Glut. = Glutæus
Grac. maj. = Gracilis major
Grac. min. = Gracilis minor
Il. ex. = Iliacus externus
Il. ext. = Ilio-externsorius
Il. fem. = Iliofemoralis
Il. fib. = Iliofibularis
Il. tib. = Iliotibialis
Il. int. = Iliacus internus
Isch. cut. = Ischiocutaneus
Isch. fem. = Ischiofemoralis
Isch. flex. = Ischioflexorius
Lat. dors. = Latissimus dorsi
N. fem. = Femoralis nerve
N. iliohyp. = Iliohypogastric nerve
N. isch. = Ischiadic nerve
N. obt. = Obturator nerve
N. peron. = Peroneus nerve
Obl. ext. = Obliquus externus
Obl. int. = Obliquus internus
Obt. ext. = Obturator externus

Obt. int. = Obturator internus
Os il. = Ilium
Pect. = Pectineus
Peron. = Peroneus
P.i.f.e. = Puboischiofemoralis externus
P.i.f.i. = Puboischiofemoralis internus
P.i.t. = Puboischiotibialis
Plant. long. = Plantaris longus
P. mentalis. = Pars mentalis
post-pub. = Postpubis
pre-pub. = Prepubis
pubo. isch. = Puboischium
P.t. = Pubotibialis
Pub. isch. fem. ext. = Puboischiofemoralis
    externus
Pub. isch. fem. int. = Puboischiofemoralis
    internus.
Pub. isch. tib. = Puboischiotibialis
Pub. tib. = Pubotibialis
Pul. = Pulmonary muscle
Pyrif. = Pyriformis
Quad. fem. = Quadratus femoris
R. cut. fem. lat. = Ramus cutaneus fe-
    moris lateralis
Rect. abd. = Rectus abdominis
Sac. = Sacrum
Sart. = Sartorius
Sart.-semitend. = Sartorio-semitendino-
    sus
(cap. semitend.) = Semitendinosus head
    of sartorio-semitendinosus
Sec. lig. = Secondary ligament
Semimbr. = Semimembranosus
Semitend. = Semitendinosus
Sph. an. cl. = Sphincter ani cloacalis
Tend. grac. = Tendon of the gracilis
    major and minor
Tend. sart. = Tendon of the sartorius
Tend. semitend. = Tendon of the semi-
    tendinosus
Tens. fasc. lat. = Tensor fasciæ latæ
Tib. ant. long. = Tibialis anticus longus

Mandibular "teeth" of various Salientia. Tooth-like protuberances are found on the lower jaw of various specialized genera. Only in *Amphignathodon* (Figs. 5 and 6) are these true teeth, in all other genera they are mere processes of the bony elements composing the lower jaw and to be compared with excess bony growths on other parts of the skull.

Fig. 1. *Cerathyla johnsoni* Noble, medial aspect of mandible, A. M. N. H. No. 1343.

Fig. 2. Same, outer aspect.

Fig. 3. *Dimorphognathus africanus* (Hallowell), medial aspect of mandible, A. M. N. H. No. 11294.

Fig. 4. Same, outer aspect.

Fig. 5. *Amphignathodon güntheri* Boulenger, medial aspect of mandible, collection of University of Michigan.

Fig. 6. Same, outer aspect.

Fig. 7. *Ceratobatrachus guentheri* Boulenger, medial aspect of mandible, A. M. N. H. No. 5335.

Fig. 8. Same, outer aspect.
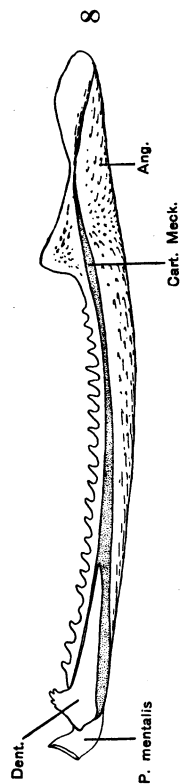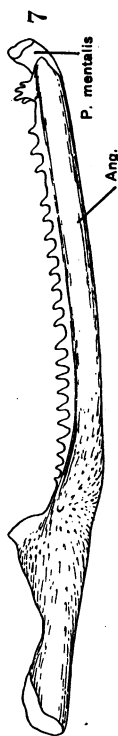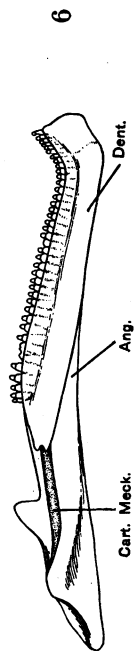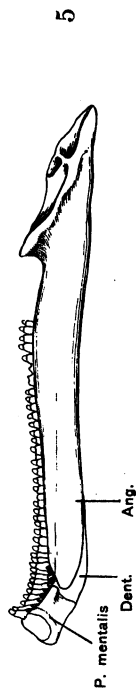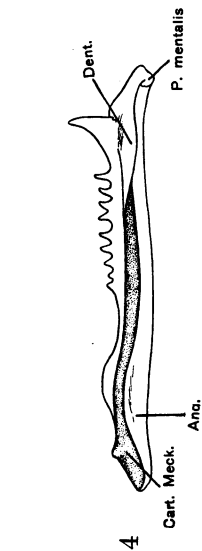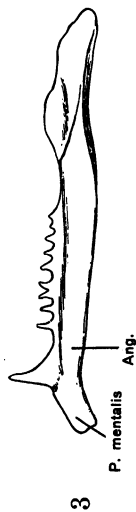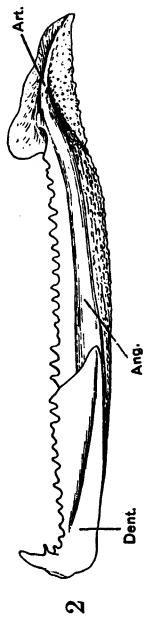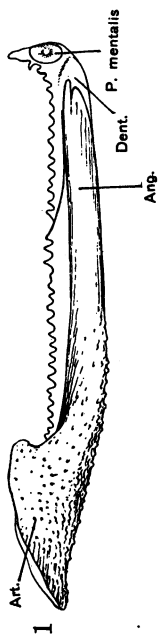
Dendrobates typographus Keferstein.   Vertebral column as seen from lower (Fig. 1) and upper (Fig. 2) surfaces.   Vertebral column of an immature specimen (Fig. 3) showing early fusion of vertebræ.
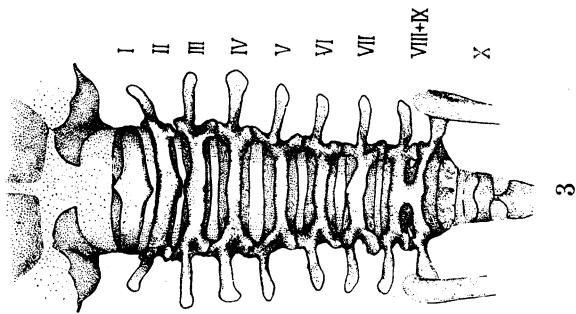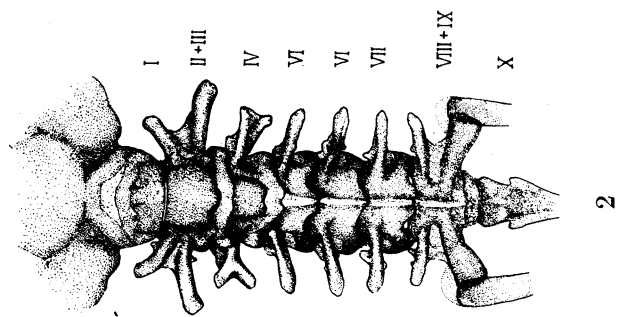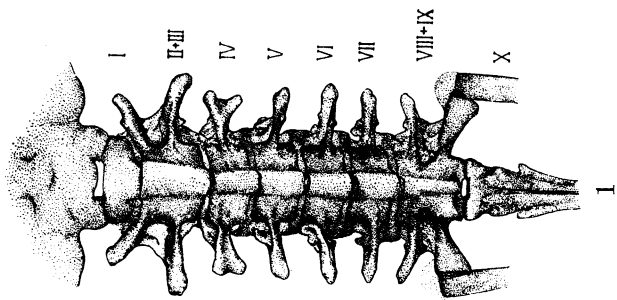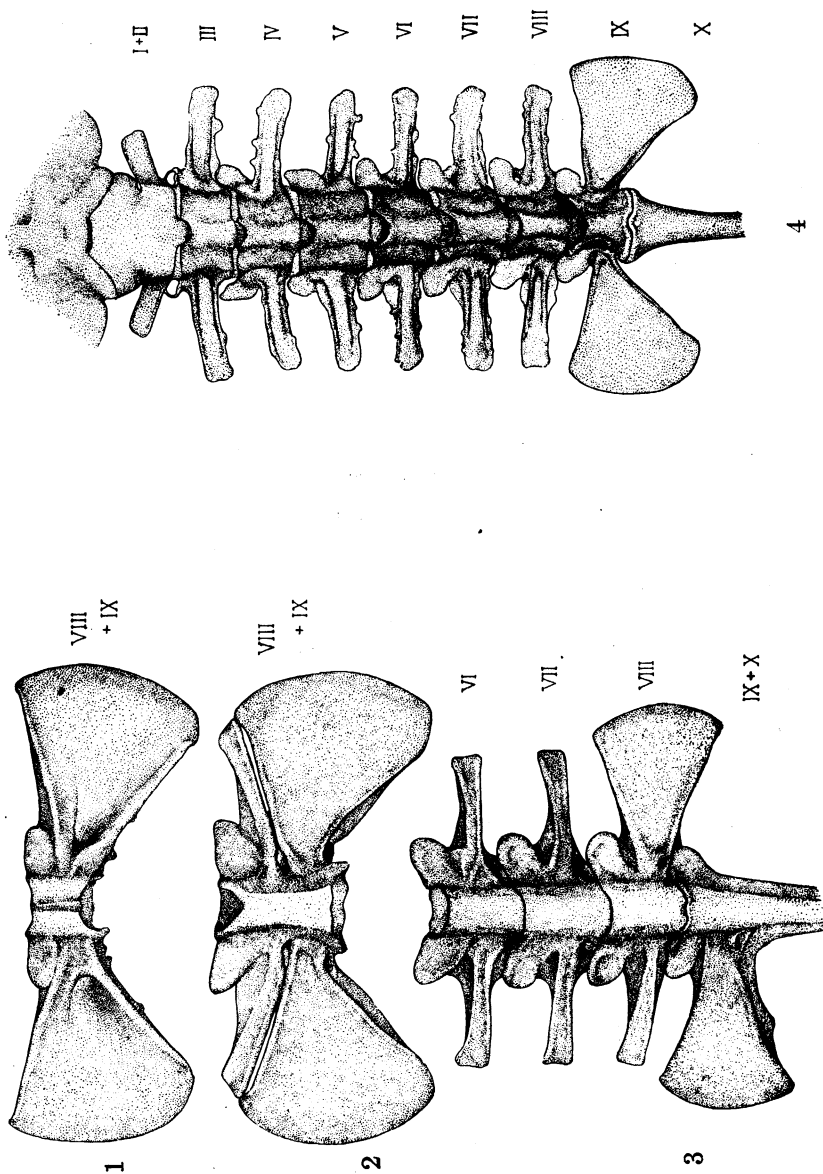
Pectoral girdles as seen from dorsal (medial) side. The series illustrates the change from the arciferal to the firmisternal type.

Fig. 1. *Eleutherodactylus bransfordii* (Cope).

Fig. 2. *Sminthillus peruvianus* Noble.

Fig. 3. *Sminthillus limbatus* (Cope).

Fig. 4. *Rhinoderma darwinii* Duméril and Bibron.
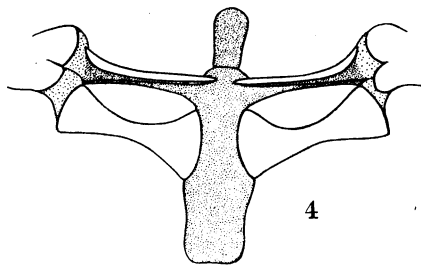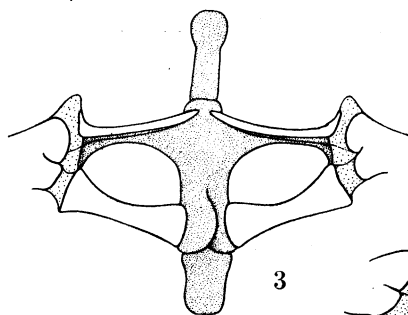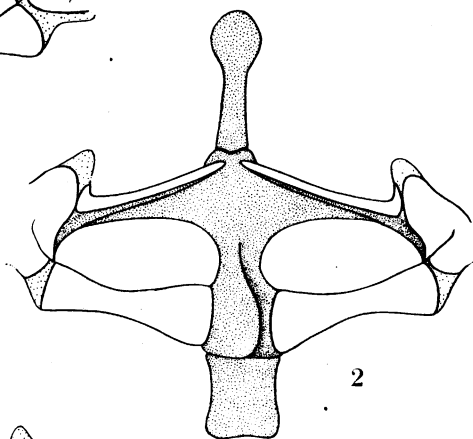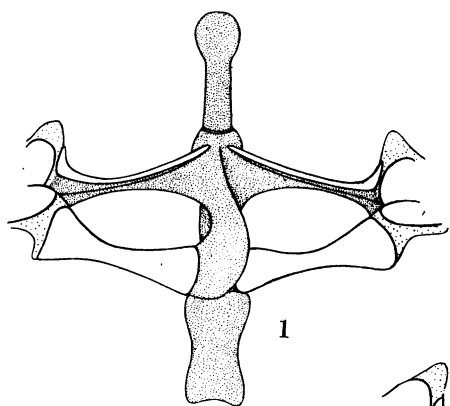
1

2

3

1

Crur.
Glut.
Tens. fasc. lat.
ll. int.
ll. ext.
Cocc. il.
Semimbr.
Pyrif.
"tail"
Semimbr.
Grac. maj.
Grac. min.
Caud. pubo. isch. tib.
Plant. long.
Peron.
ll. fib.

2

Rect. abd.
Pect.
Crur.
Sart.-semitend.
Add. mag. (cap. ventr.)
Tib. ant. long.
Grac. maj.
Grac. min.
"tail"
post-pub.

3

Add. mag. (cap. ventr.)
Add. mag. (cap. dors.)
Grac. maj.
Semitend.
Semimbr.
ll. fib.
Pyrif.
Glut.
Semimbr.
Gem.
Sart.-semitend.
"tail"
Grac. min.
Grac. maj.

4

Add. mag. (cap. ventr.)
Add. mag. (cap. dors.)
Grac. maj.
Obt. ext.
Semimbr.
Semimbr.
ll. fib
Glut.
Sart.-semitend
Pyrif.
Pect.
Add. mag. (cap. ventr.)
Quad. fem.
Gem.
Add. mag. (cap. dors.)
Sart.-semitend.
"tail"
Grac. min.
Grac. maj.
Semimbr.

Pelvis of *Ascaphus truei* Stejneger (male).
Fig. 1. Lateral aspect.
Fig. 2. Anterior aspect, showing muscle areas.
Fig. 3. Ventral aspect.
Cartilage even stipple, semi-calcified irregular stipple, calcified or bony struc-
tures in outline.
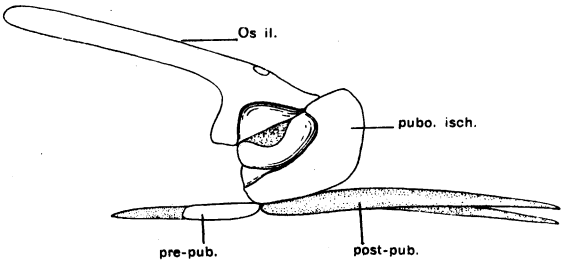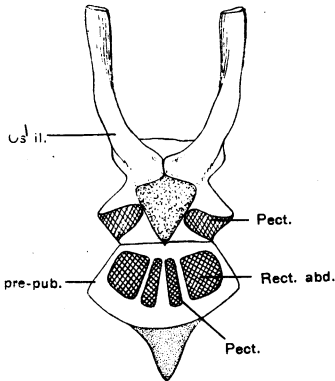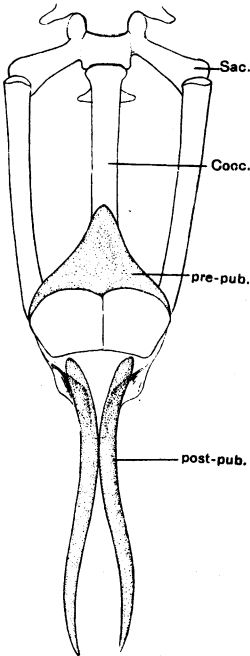
PLATE IX

Thigh Muscles of *Hymenochirus boettgeri* (Tornier).
Fig. 1.   Dorsal aspect, superficial muscles.
Fig. 2. . Ventral aspect, superficial muscles.
Fig. 3.   Ventral view of the thigh, the more superficial muscles cut and turned
aside
Fig. 4.   Posterior aspect of the thigh, showing the deep muscles.
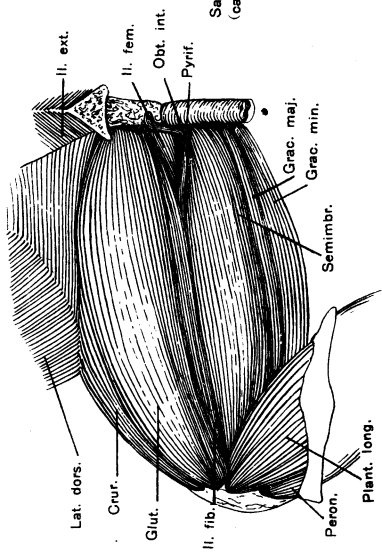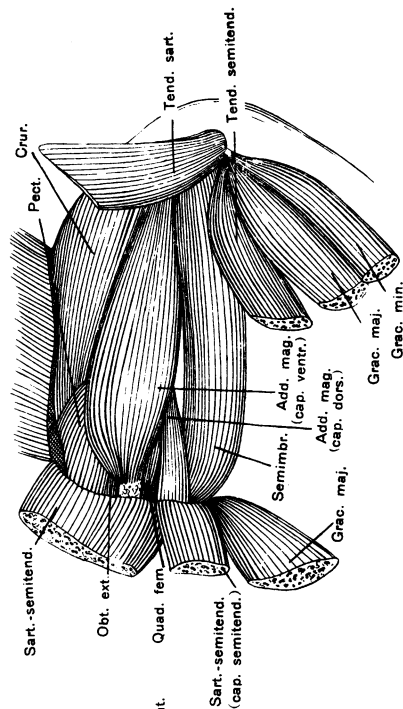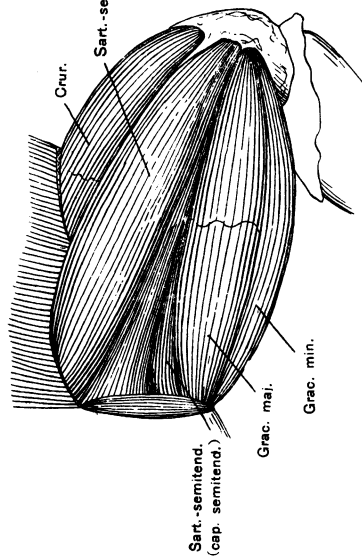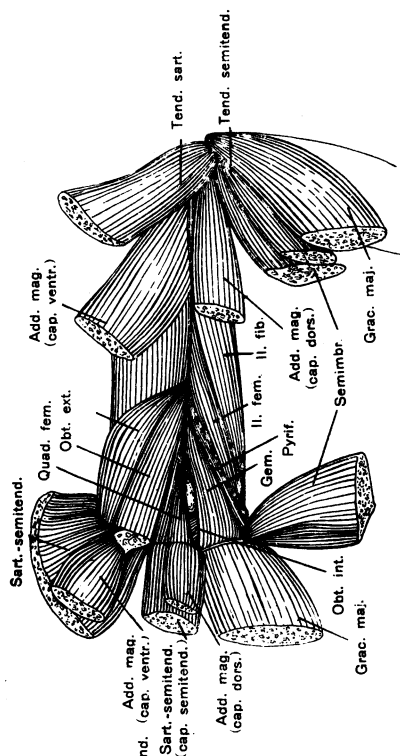
Ventral thigh musculature of the pelobatids. Series illustrating the differentia-
tion of the adductor longus as a slip of the pectineus; also, showing the specialization
of the sartorio-semitendinosus.

Fig. 1. *Megalophrys hasseltii* (Tschudi).
Fig. 2. *Megalophrys montana* Kuhl.
Fig. 3. *Pelobates fuscus* (Laurenti).
Fig. 4. *Pelodytes punctatus* (Daudin).
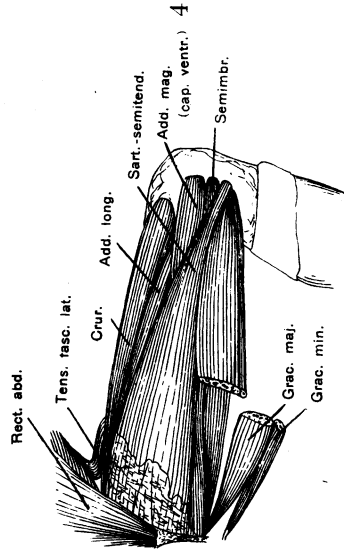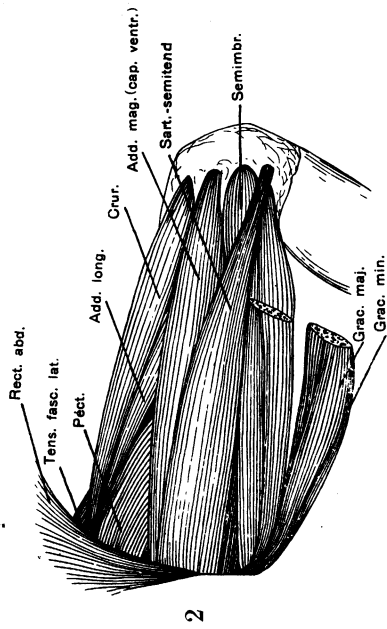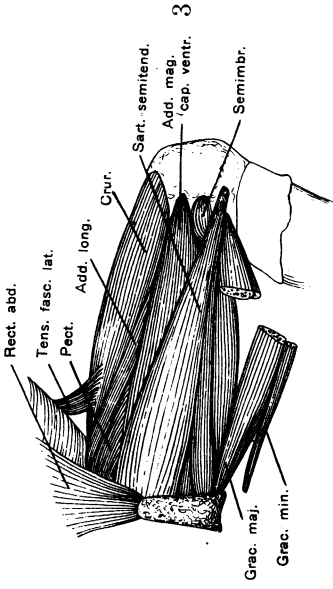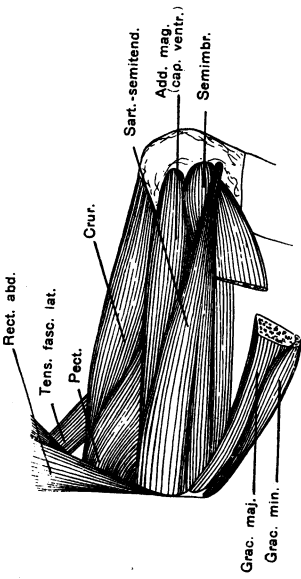
Superficial musculature of *Rhinophrynus dorsalis* Duméril and Bibron.
Fig. 1.   Dorsal aspect.
Fig. 2.   Ventral aspect.
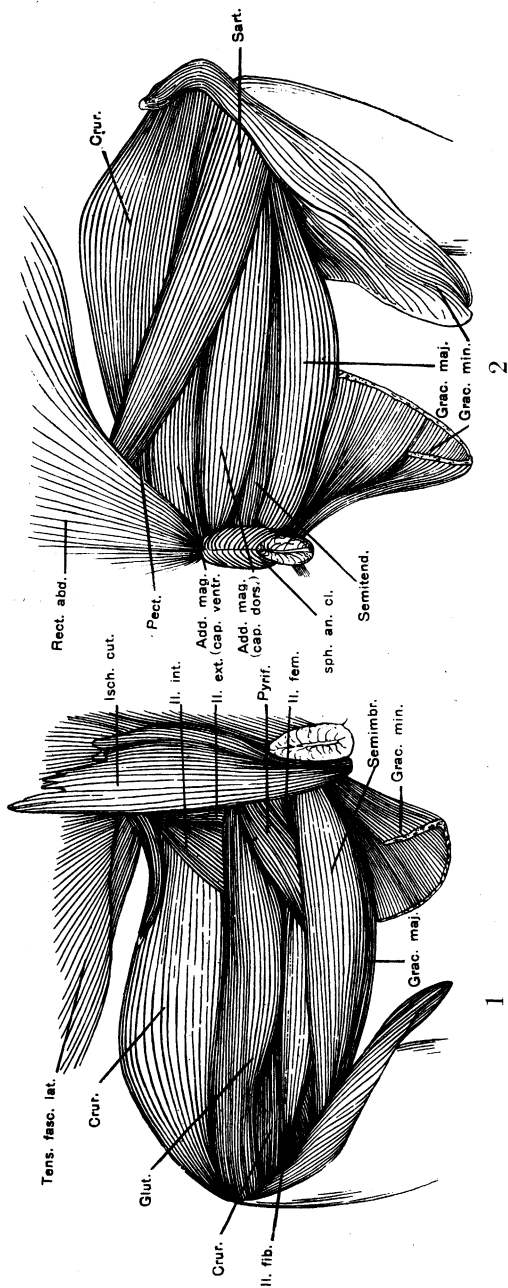
PLATE XIV

Distal tendons of the thigh.

Fig. 1. *Bombina maxima* (Boulenger), exhibiting the primitive type of complex, from which the more advanced types have evolved.

Fig. 2. *Leptodactylus pentadactylus* (Laurenti), illustrating the typical bufonid type.

Fig. 3. *Rana clamitans* Latreille, an example of the ranid type of complex.

Fig. 4. *Atelopus ignescens* (Cornalia), although firmisternal, exhibiting the bufonid plan of complex. Compare with Fig. 2.
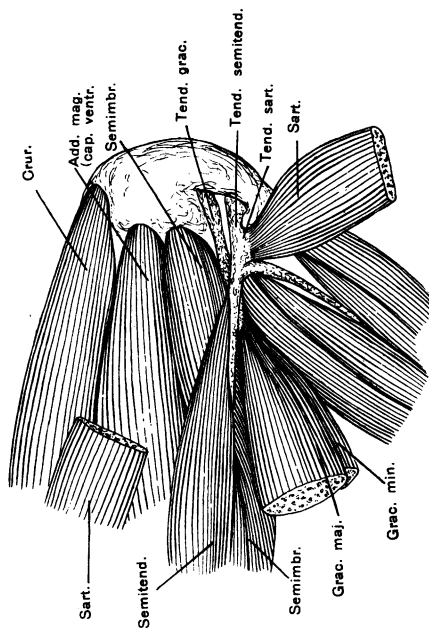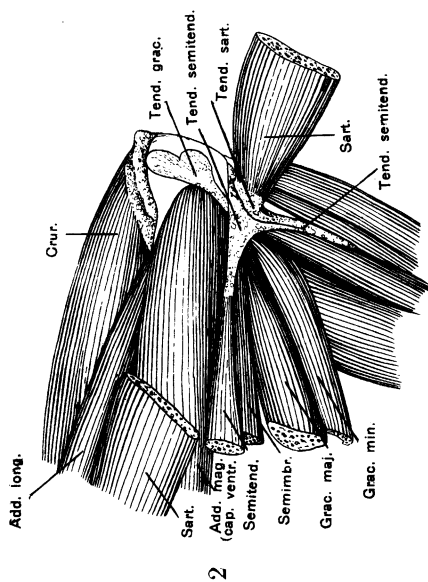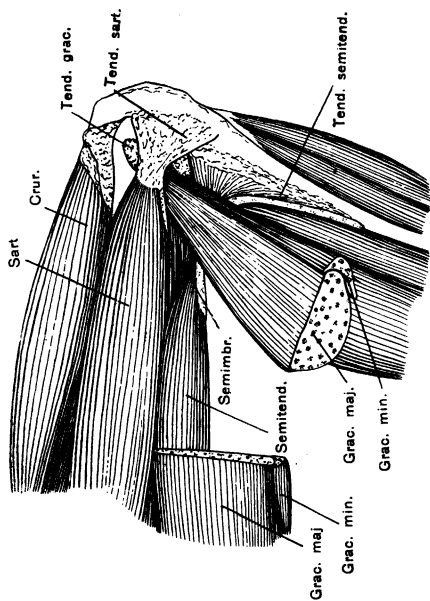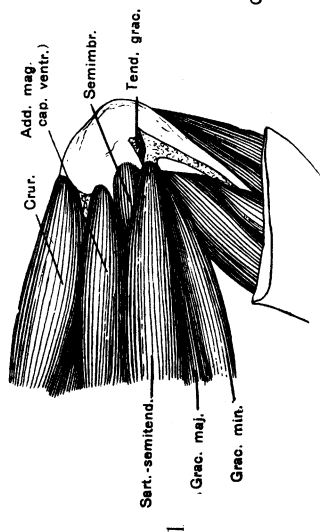
Specialization of the distal tendons of the thigh as exhibited by the Procœla.

Fig. 1. *Pleurodema bibronii* Tschudi, retaining the typical bufonid plan of complex.

Fig. 2. *Pleurodema cinerea* Cope, intermediate stage in the sinking of the distal tendon of semitendinosus through the gracilis major.

Fig. 3. *Pleurodema brachyops* (Cope), final stage of specialization exhibited by the genus.

Fig. 4. *Limnodynastes ornatus* (Gray), intermediate stage in the sinking of the tendon of the semitendinosus through the gracilis mass.

Fig. 5. *Pseudophryne australis* (Gray), extreme stage of specialization found in the Procœla. Compare with Fig. 6 and with tendon complex in *Rana* (Pl. XIV, fig. 3).

Fig. 6. *Hyloxalus granuliventris* (Boulenger), extreme stage of specialization; the brachycephalids and bufonids have independently evolved this modification of the bufonid plan of complex.
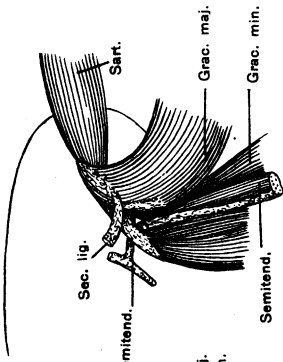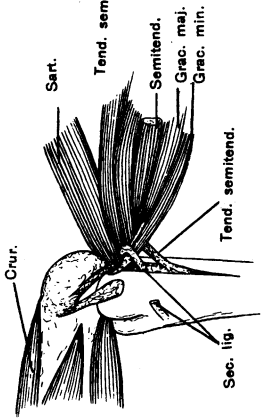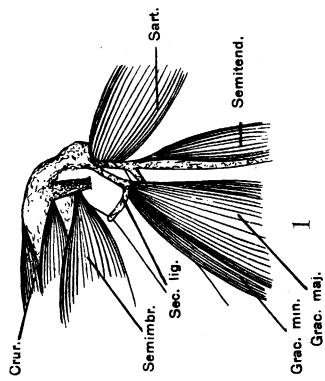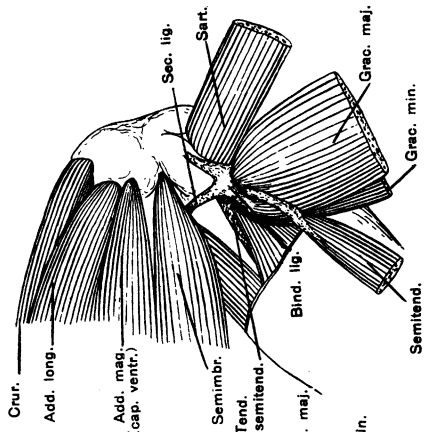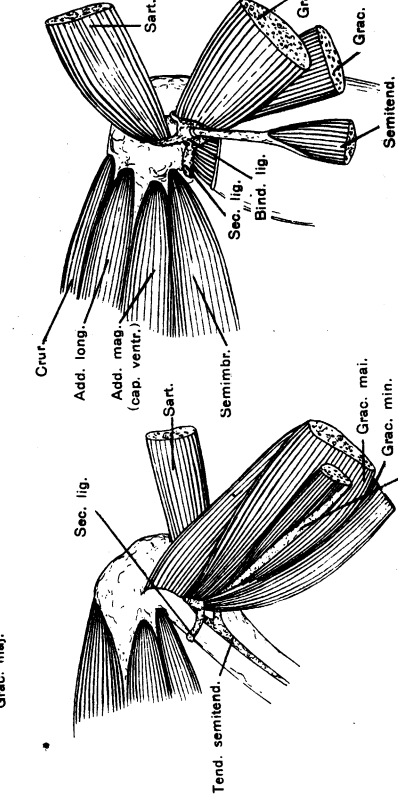
Crur.

Semimbr.

Sec. lig.

Sart.

Semitend.

Grac. min.
Grac. maj.

1

Crur.

Sart.

Sec. lig.

Tend. semitend.

Semitend.
Grac. maj.
Grac. min.

2

Crur.

Sec. lig.

Tend. semitend.

Sart.

Grac. maj.
Grac. min.

Semitend.

3

Sec. lig.

Crur.

Add. long.

Add. mag.
(cap. ventr.)

Sart.

Semimbr.

Tend. semitend.

Grac. mai.
Grac. min.
Semitend.

4

Crur.

Add. long.

Add. mag.
(cap. ventr.)

Sart.

Semimbr.

Sec. lig.
Bind. lig.

Grac. maj.
Grac. min.
Semitend.

5

Crur.

Add. long.

Add. mag.
(cap. ventr.)

Sec. lig.
Sart.

Semimbr.

Tend.
semitend.

Grac. maj.

Bind. lig.

Semitend.

Grac. maj.
Grac. min.

6

Add. mag.
(cap. dors.)

Add. mag.
(cap. ventr.)

Crur.

Sart.

Sec. lig.

Grac. maj.

Grac. min.

Semimbr.

Plant. long.

Semitend.

3

Crur.

Blnd. lig.

Sec. lig.

Sart.

Grac. maj.

Grac. min.

Semitend.

Semimbr.

Tend. semitend.

Sec. lig.

2

Grac min.

Grac. maj.

Crur.

Sart.

Tend. semitend.

Semitend.

Grac. min.

Semitend.

Sart.

6

Crur.

Add. mag.
(cap. ventr.)

Sec. lig.

Sart.

Grac. maj.

Semitend.

Semimbr.

Tend. semitend.

Grac. min.

Grac. maj.

5

Crur.

Add. mag.
(cap. ventr.)

Sec. lig.

Sart.

Grac. maj.

Grac. min.

Semitend.

Tend. semitend.

1

Sec. lig.

Sar

Semitend.

Grac. maj.

Grac. min.

Tend. semitend.
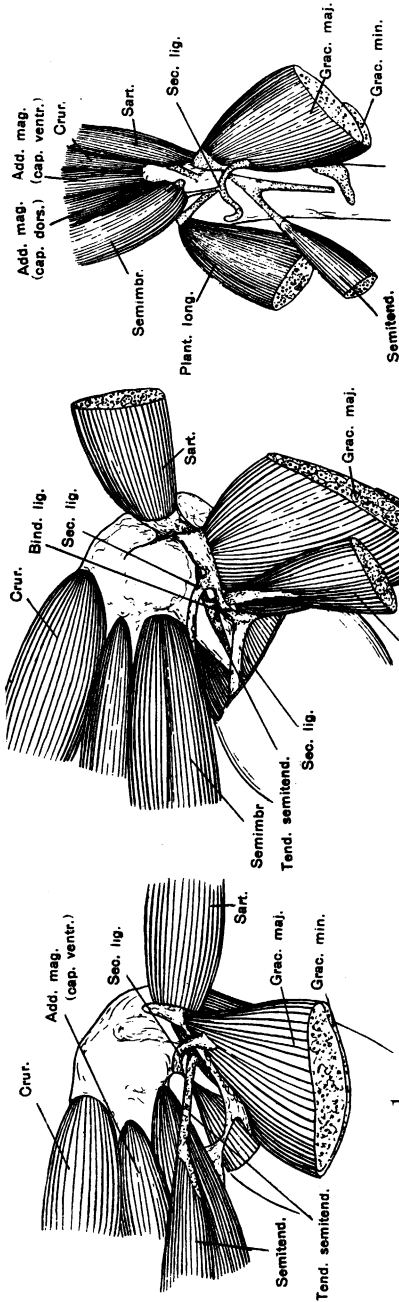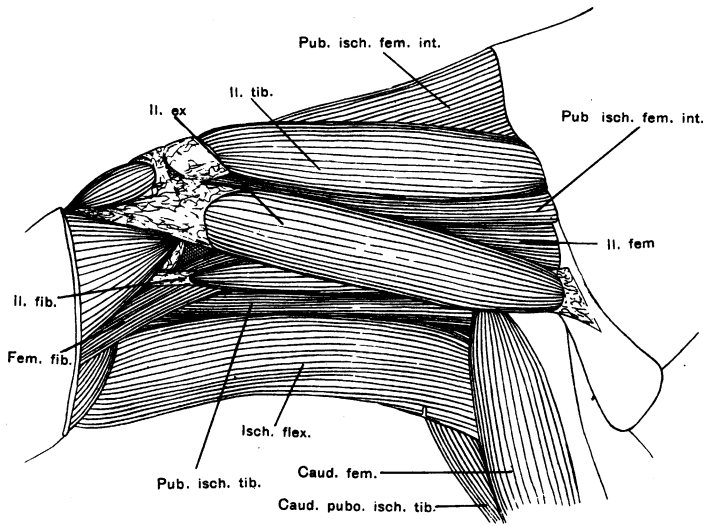
4
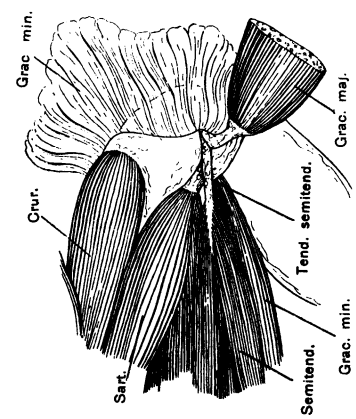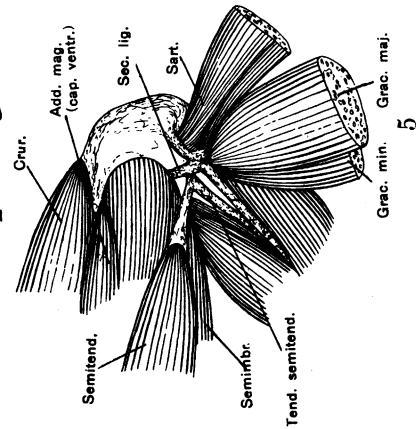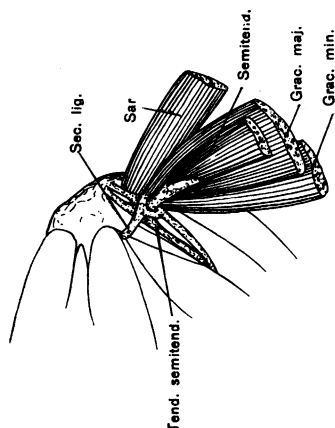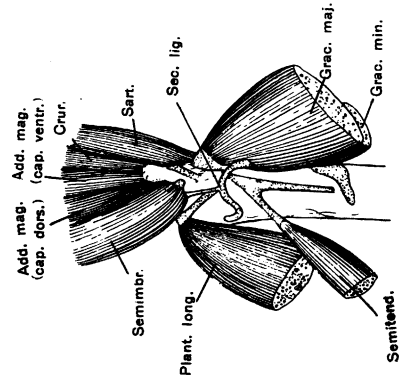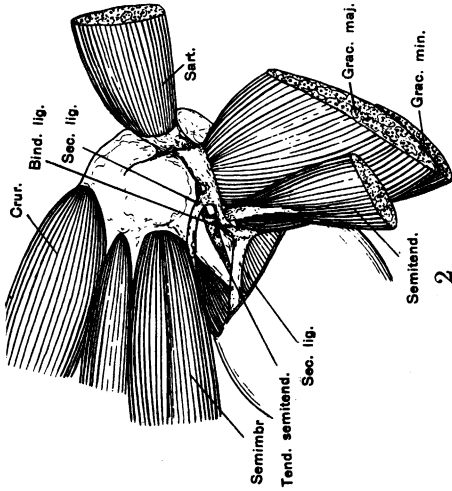
Thigh muscles of urodeles compared with those of *Ascaphus*.
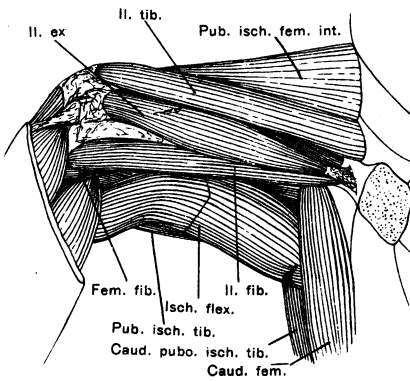
Fig. 1.   *Cryptobranchus alleganiensis* (Daudin).

Figs. 2 and 3.   Dorsal and ventral aspect of the thigh of *Rhyacotriton olympicus* (Gaige).

Figs. 4 and 5.   Outline drawings of the dorsal and ventral surface of the thigh of *Ascaphus*.   The homologies of the muscles are indicated in brackets.   Compare with the table of homologies, Table 1, and with the detailed figures of the thigh of *Ascaphus* (Pl. VI).
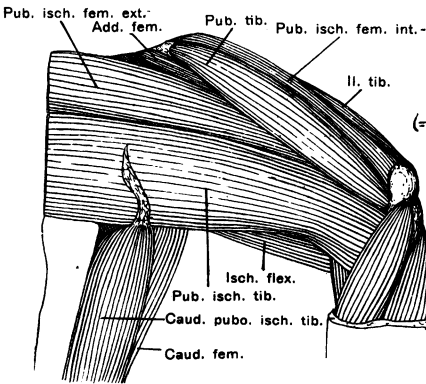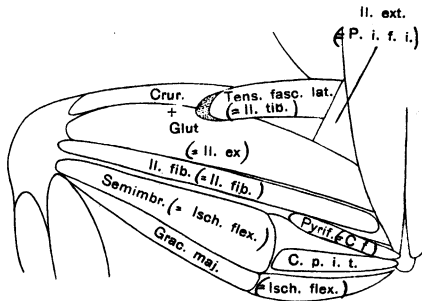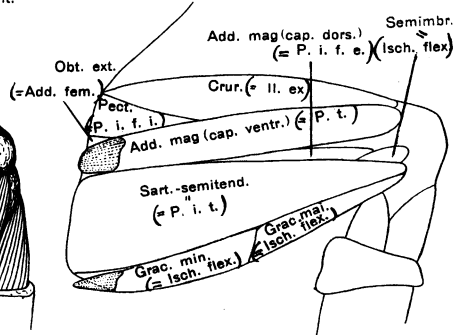
Pub. isch. fem. int.

Il. tib.

Il. ex

Pub isch. fem. int.

Il. fem

1

Il. fib.

Fem. fib.

Isch. flex.

Pub. isch. tib.   Caud. fem.

Caud. pubo. isch. tib.

Il. ext.

(P. i. f. i.)

Il. tib.

Il. ex   Pub. isch. fem. int.

Crur.   Tens. fasc. lat.
  +   (= Il. tib.)
Glut

2   (= Il. ex)   **4**

Il. fib. (= Il. fib.)

Semimbr. (= Isch. flex.)

Grac. maj.   Pyrif. (= C. I.)

C. p. i. t.

Fem. fib.   Il. fib.   (= Isch. flex.)

Isch. flex.

Pub. isch. tib.

Caud. pubo. isch. tib.

Caud. fem.

Pub. isch. fem. ext.

Add. fem.   Pub. tib.   Pub. isch. fem. int.-

Il. tib.   Obt. ext.   Add. mag (cap. dors.)   Semimbr.

(= Add. fem.)   (= P. i. f. e.)(Isch. flex)

(P. i. f. i.)   Crur. (= Il. ex)

Pect.

Add. mag (cap. ventr.) (= P. t.)

3   Sart. -semitend.   **5**

(= P. i. t.)   Grac. maj.

Isch. flex.   Isch. flex.

Pub. isch. tib.

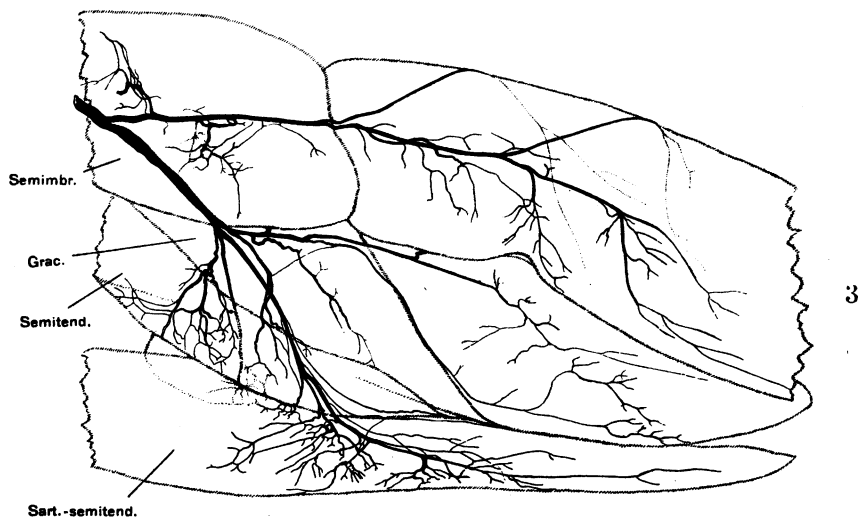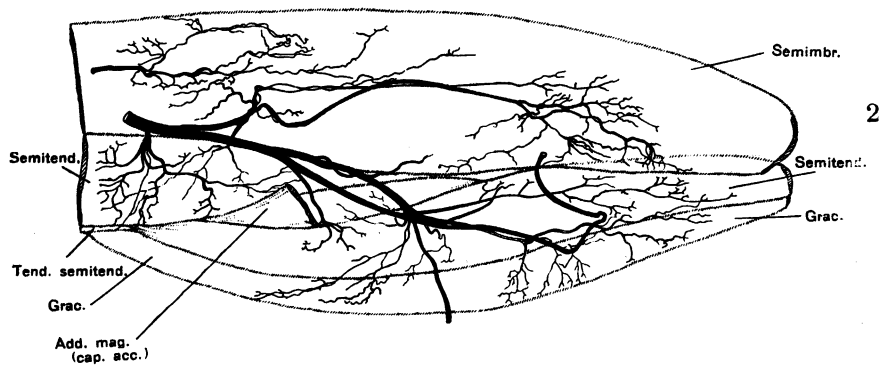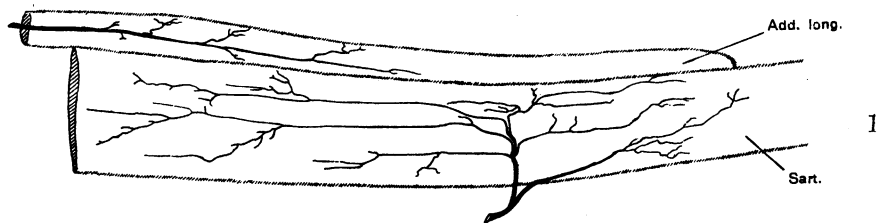Caud. pubo. isch. tib.   Grac. min.
(= Isch. flex.)

Caud. fem.

PLATE XVIII

Detailed innervation of certain superficial muscles in the Salientia as shown by cleared acetic-osmic preparation.

Fig. 1.   Adductor longus and sartorius in *Acris gryllus* (Le Conte) viewed from ventral (outer) aspect.   It will be noted that the innervation of these two muscles is entirely distinct.

Fig. 2.   Semimembranosus, semitendinosus, and gracilis major and minor of *Acris gryllus* (Le Conte); viewed from femoral side.

Fig. 3.   Same in *Ascaphus truei* Stejneger.   In this form the sartorius forms part of the semitendinosus.   Thus this figure should be compared with both Figs. 1 and 2.

Add. long.

Sart.

1

Semimbr.

2

Semitend.

Semitend.

Grac.

Tend. semitend.

Grac.

Add. mag.
(cap. acc.)

Semimbr.

Grac.

Semitend.

3

Sart.-semitend.

Detailed innervation of certain thigh muscles in *Acris gryllus* (Le Conte), as shown by cleared acetic-osmic preparations.
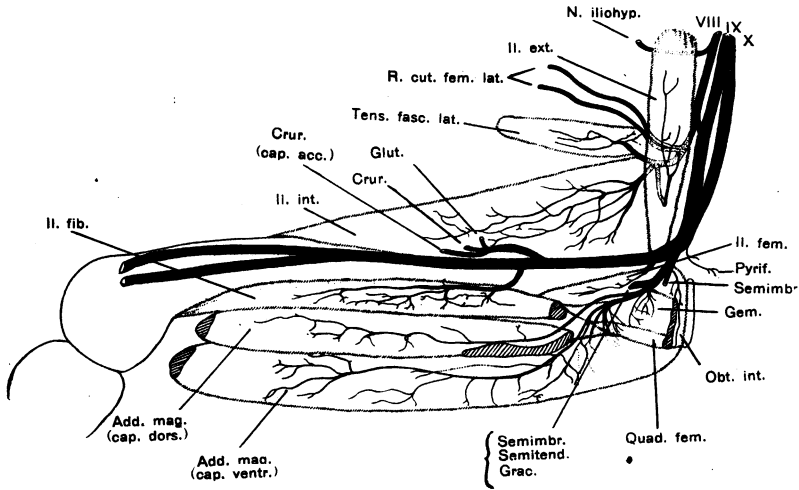
Fig. 1.   Glutæus and cruralis, femoral aspect.

Fig. 2.   Deep muscles of the thigh together with their innervation, dorsal view. Most of the muscles have been cut near their attachments in order to bring the nerves into the same plane.
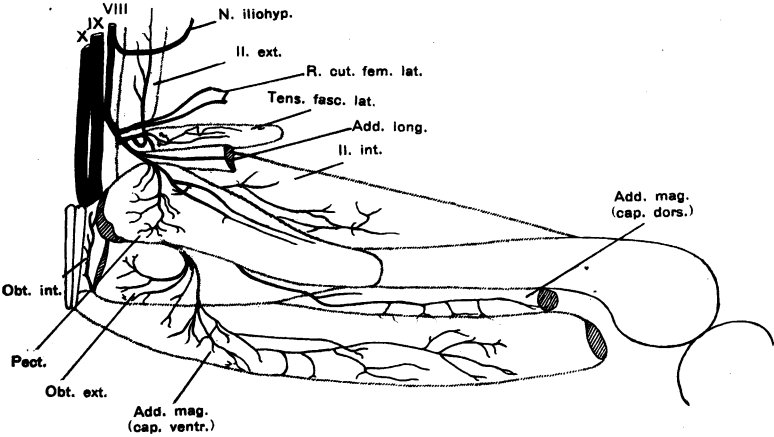
Fig. 3.   Ventral aspect of the thigh, showing the deep muscles and their innervations.

1

2

3
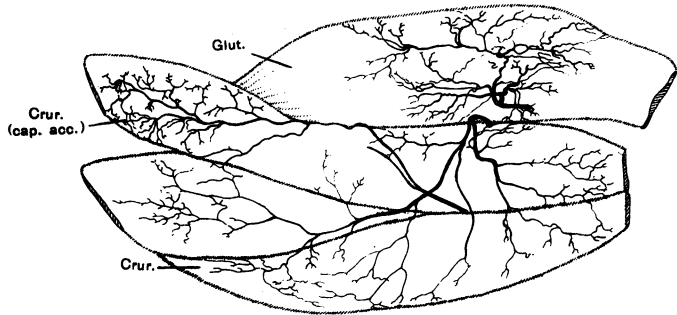
Comparison of the main nerve trunks in a urodele and frog.
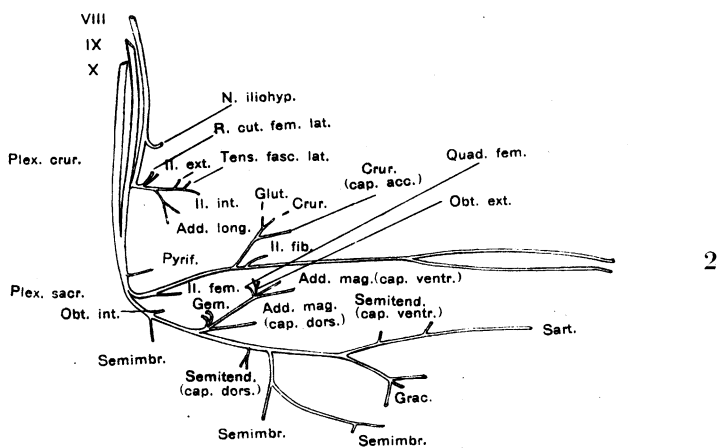Fig. 1. *Desmognathus fuscus* (Rafinesque).
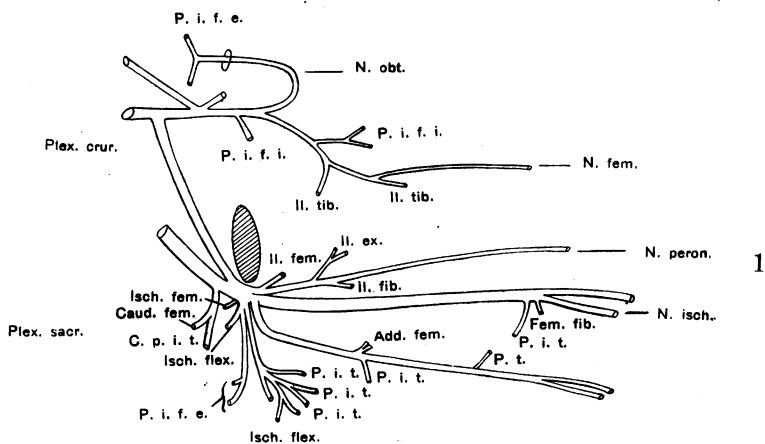Fig. 2. *Acris gryllus* (Le Conte).

P. i. f. e.

N. obt.

P. i. f. i.

Plex. crur.
P. i. f. i.

N. fem.

Il. tib.   Il. tib.

Il. ex.
Il. fem.   N. peron.   **1**
Il. fib.

Isch. fem.
Caud. fem.   Fem. fib.   N. isch.
Plex. sacr.
C. p. i. t.   Add. fem.   P. i. t.
Isch. flex.   P. t.
P. i. t. P. i. t.
P. i. t.
P. i. f. e.   P. i. t.

Isch. flex.

VIII
IX
X

N. iliohyp.

R. cut. fem. lat.

Plex. crur.
Il. ext.   Tens. fasc. lat.   Quad. fem.
Crur.
(cap. acc.)
Il. int.   Glut.
Crur.   Obt. ext.
Add. long.
Il. fib   **2**
Pyrif.
Il. fem.   Add. mag.(cap. ventr.)
Plex. sacr.
Gem.   Add. mag.   Semitend.
Obt. int.   (cap. dors.) (cap. ventr.)
Sart.
Semimbr.
Semitend.
(cap. dors.)   Grac.

Semimbr.   Semimbr.

Pub. isch. fem. int.

Pub. isch. fem. ext.

Add. fem.

Pub. tib.

1

Pub. isch. tib.

Isch. flex.

Pub. isch. tib.

Caud. fem.

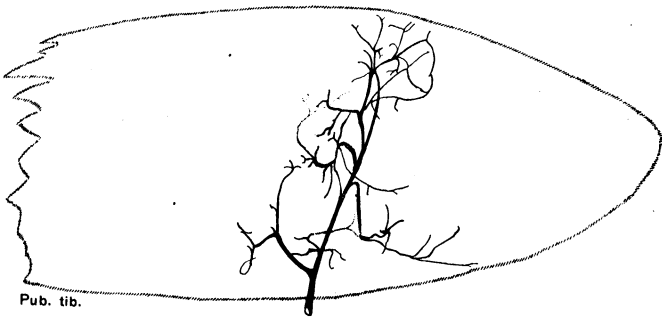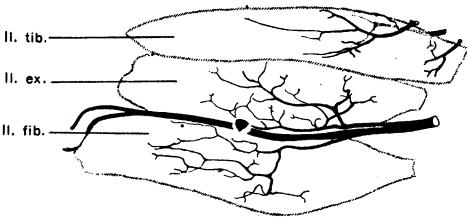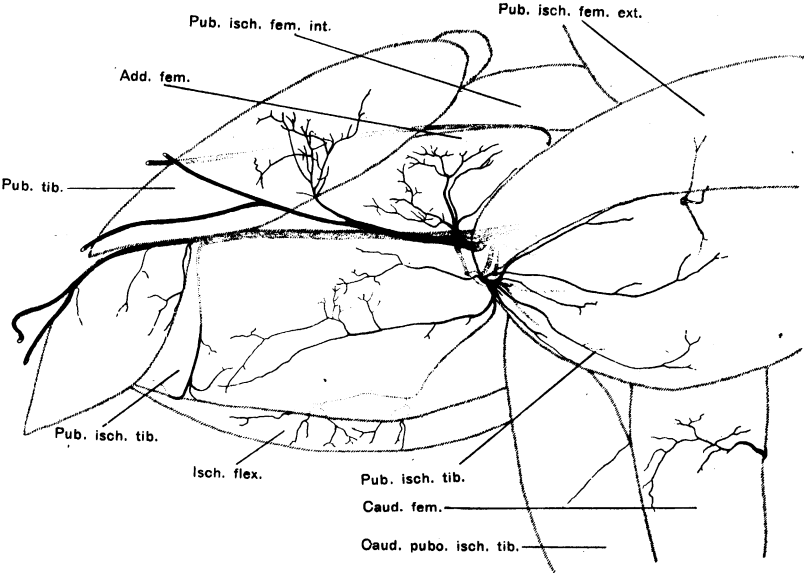Caud. pubo. isch. tib.

II. tib.

II. ex.

II. fib.

2

Pub. tib.

3

Pelvis with its muscle areas in a urodele and a frog, with inferred areas in *Eryops*.

Oblique hatch muscle areas on outer aspect of pelvis.

Even stipple muscle areas on inner aspect of pelvis.

Irregular stipple cartilage.

Outline bone.

Fig. 1.　*Rhyacotriton olympicus* (Gaige).

Fig. 2.　*Eryops macrocephalus* Cope.
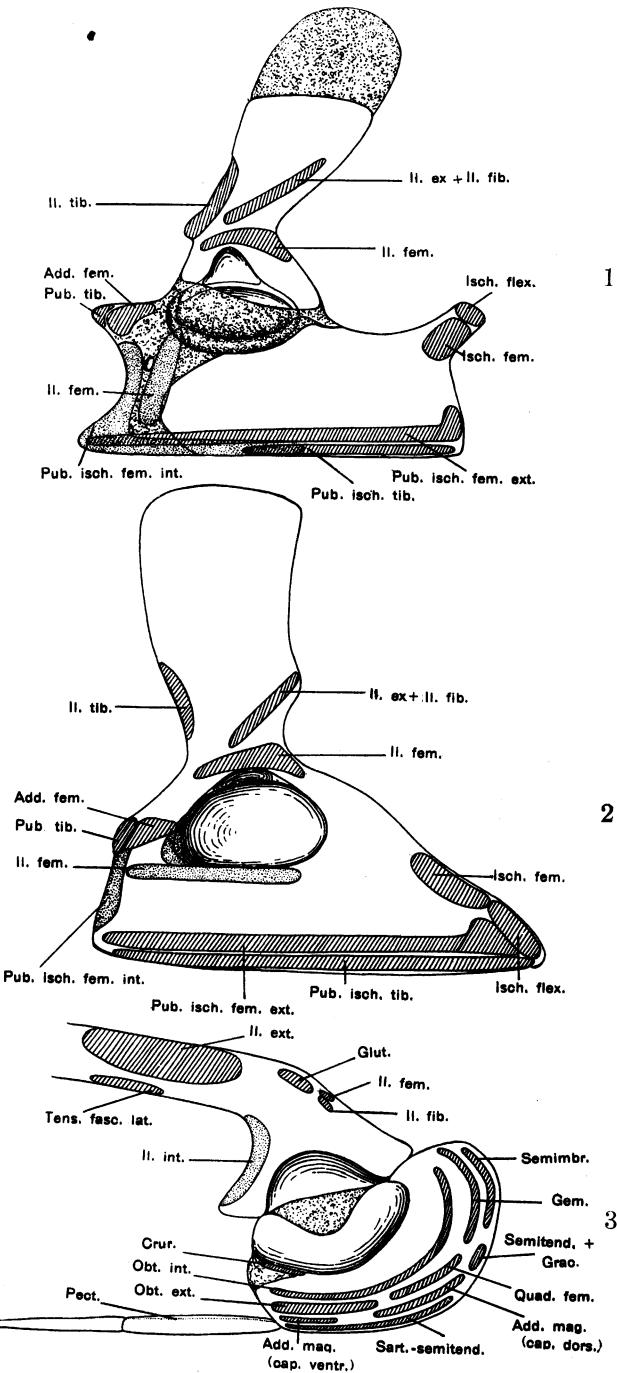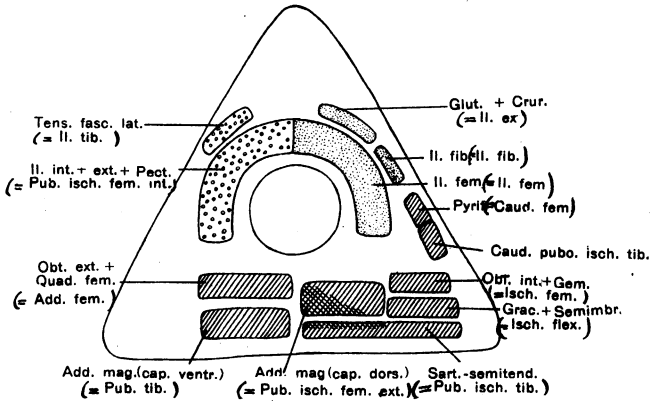
Fig. 3.　*Ascaphus truei* Stejneger, female.

Fig. 1

Il. tib.
Il. ex + Il. fib.
Il. fem.
Add. fem.
Pub. tib.
Isch. flex.
Isch. fem.
Il. fem.
Pub. isch. fem. int.
Pub. isch. fem. ext.
Pub. isch. tib.

Fig. 2

Il. tib.
Il. ex + Il. fib.
Il. fem.
Add. fem.
Pub. tib.
Il. fem.
Isch. fem.
Pub. isch. fem. int.
Pub. isch. fem. ext.
Pub. isch. tib.
Isch. flex.

Fig. 3

Il. ext.
Glut.
Il. fem.
Il. fib.
Tens. fasc. lat.
Il. int.
Semimbr.
Gem.
Crur.
Semitend. +
Obt. int.
Grac.
Pect.
Obt. ext.
Quad. fem.
Add. mag.
(cap. dors.)
Add. mag.
(cap. ventr.)
Sart.-semitend.

1

2

3