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THE "TAIL" OF ASCAPHUS:

A Historical Résumé and new Histological-Anatomical Details

by

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With 45 Text-figures

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ABSTRACT

The pelvic girdles of the two anuran genera *Ascaphus* and *Leiopelma* of the family *Ascaphidae* are very similar. Attached to them by cartilage (or connective tissue in some *Ascaphus* specimens) is a cartilaginous, in *Leiopelma* somewhat ossified, epipubis. In *Ascaphus*, as in *Xenopus*, the epipubis originates from two Anlages, and its muscles are also paired in the *Ascaphidae*, while in *Xenopus* only one is present, although this also appears to originate from two muscles. The cloaca extends behind the pelvic girdle in both sexes in *Ascaphus*, and it is supported by two rods consisting of strong connective tissue (Faserknochen?). These rods are attached to the ventral surface of the pelvic girdle, in the female closely, in the male by means of tendons. Between the rods and the epipubis a broad tendinous band extends, which is thick in the male; in the latter the mm. compressores cloacae have their origins posteriorly on the rods, while in the female the rods are completely imbedded in these muscles posteriorly. In the female particularly there are transverse muscle fibres which are not striped although probably derived from the mm. compressores cloacae. Behind the pelvic girdle there is cavernous tissue in both layers of the tunica muscularis, and ventrally it covers the mm. compressores cloacae. The circular and longitudinal muscle layers are posteriorly separated by gliding planes. The cloaca is supplied by branches of the a. mesenterica posterior and the aa. pudendae anteriores, and is drained by the vv. pudendae and a small medial v. caudalis. The cloaca is innervated dorsally by the plexus ischio-coccygeus and ventrally by a branch of the n. ischiadicus (the n. pudendus). The cloaca of the male serves as a copulatory organ. There is internal fertilization.

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## INTRODUCTION

This investigation was undertaken at the suggestion of Prof. C. G. S. de Villiers, to whom I am indebted for material, advice and criticism.

The object of the investigation was to provide information on the skeletal elements of the pelvic region, and on the form, blood vessels and nerve supply of the erectile tissue of the cloacal extension. The importance of this region is stressed by de Villiers (1934a, p. 45): "The pelvic, prepelvic and postpelvic regions of *Ascaphus* are of very great interest; when their development will have been studied and their adult anatomy compared with that of *Liopelma*, important results regarding the morphology of the skeletogenous strata may be expected. The development of the phallic organ on the other hand will almost certainly contribute towards the elucidation of the problem of the adaptation of the endgut as an intromittent organ in vertebrates."

## HISTORICAL INTRODUCTION

Stejneger (1899) described "a New Genus and Species of Discoglossid Toad from North America" from a single specimen, naming it *Ascaphus* ("From  $\acute{\alpha}$ , without;  $\sigma\kappa\acute{\alpha}\phi\omicron\varsigma$  spade" — footnote p. 899) *truei*, "in honor of Dr. F. W. True, head curator of the Department of Biology, U.S. National Museum". (footnote, p. 900). "The genotype, evidently a female, was captured at Humptulips, Chehalis County, Washington." (Gauge, 1920, p. 1). Van Denburgh (1912, p. 264) reported the presence of a "tail" in the males and observed: "It is possible that this 'tail' may be a sexual organ." He reported the presence of two thin plates of calcified cartilage at the interior and ventral aspect of the pelvis. Gauge (1920, p. 5) noted that in breeding males "the underside of the 'tail' is greatly congested".

Noble (1922) in dealing with the thigh musculature of the *Anura* made numerous references to conditions in *Ascaphus*, and, when dealing with the caudalipuboischiotibialis muscle which he found only in *Ascaphus*, described the "tail" at some length. The work included figures of the thigh musculature which also show the "tail", photographs of the male *Ascaphus*, and figures of pelvic girdle showing a "calcified public cartilage", "prepubis", and two "post-pubic cartilages".

Noble (1925, p. 16—17), referring to *Ascaphus* as a liopelmid and pointing out similarities in the reproduction of the *Liopelmidae* and the urodeles, said of *Ascaphus*, "In the male a ring of enlarged cloacal glands is formed well inside the orifice of the 'tail'. A cluster of horny spines is found inside the cloaca just posterior to the enlarged glands". He noted that "sections of the urinogenital organs of the breeding female reveal great masses of spermatozoa in the lumen of the oviducts. Sections of the oviducts of the females taken after their eggs have been laid show many of the glands of the posterior part of the oviduct still filled with spermatozoa".

Slater (1931) described the mating of *Ascaphus* but did not add any information as to the structure of the "tail".

Noble and Putnam (1931) described the copulation of *Ascaphus* and observed (p. 99) of the "tail" that "the organ is strengthened by two pairs of vascular pads extending the long axis of the structure under the skin on its ventral surface. These are apparently homologous to the corpora cavernosa of the penis of higher vertebrates". They observe (p. 100) that "The female is provided with a small cloacal appendage and an egg, on being laid, is directed downwards because the cloacal orifice is on the ventral surface of the structure". Noble (1931) illustrated the "tail" flaccid and distended, adding no information regarding structure.

De Villiers (1933) gave a brief description of the pelvic skeleton and the structure of the "tail", noting (p. 693) that "The Nobelian 'cartilages' prove to be true bones", "suspiciously like sesamoid bones (tendon bones)". De Villiers (1934a) described the pelvic skeleton and the microscopic anatomy of the "tail" in greater detail with illustrations of parts of nineteen transverse sections, one of them through the "tail".

#### Taxonomic Status:

Stejneger (1899), Stejneger and Barbour (1917 and 1923), Van Denburgh (1912), Grinnell and Camp (1917), Gaige (1920), Noble (1922), Storer (1925), and Slevin (1928) referred *Ascaphus* to the *Discoglossidae*. Fejérváry (1921) included "(?) *Ascaphus* Stejn." in the Subfamilia *Discoglossinae* of this family in his classification. Following Noble's description of the pelvic skeleton (1922), Fejérváry (1923) instituted the family *Ascaphidae* for *Ascaphus*. Noble (1924) noted characters common to *Ascaphus* and *Liopelma* and created the family *Liopelmidae*, following "present-day custom in using the oldest generic name in forming the family name". (p. 9). He thenceforth consistently adopts the name *Liopelmidae* (Noble 1925, 1926, 1927, 1931). De Villiers (1929, 1933, 1934a, 1934b), Wagner (1934a and 1934b), De Vos (1938a and 1938b) and Pusey (1938 and 1943) use the name *Liopelmidae*, and Piveteau (1937) the gallicized form "Liopelmidés". Turbott (1942) observed in a footnote on page 247 that "Fitzinger's original spelling, although incorrectly transliterated, should be retained, and extended to the family name". He therefore refers to *Liopelmidae*, which term Szarski (1951) adopts. N. G. Stephenson (1951) in a footnote on p. 18 remarked on this and stated that "Furthermore, Noble's familial name was incorrectly formed from the root and should be amended to LEIOPELMATIDAE". E. M. Stephenson (1951 and 1952) uses this term. Van Eeden (1951, p. 43) remarked of the term *Liopelmidae* that "The strict application of the taxonomic rules, however, invalidates this term and gives priority to *Ascaphidae*, the family name instituted by FEJERVARY in 1923". Gordon (1939) used the term *Ascaphidae* without comment. It is the name that will be adopted here. De Villiers (1934b) discussed the history of the taxonomy of *Ascaphus* at some length.

#### MATERIAL AND TECHNIQUE

The material examined consisted of serial transverse sections of three males, two females and six larvae, of which those of one male, one female and the larvae were loaned by Prof. de Villiers, all of them having been sectioned at  $\pm 20\mu$  after bulk-staining in haemalum, and then variously

counterstained. The remaining two males and one female were all fixed in formalin, decalcified for three weeks in 5% nitric acid in 70% alcohol, treated with 5% sodium sulphate solution followed by washing in water, bulk-stained with Grenacher's borax-carmin in 70% alcoholic solution for a week at 35°C, sectioned in paraffin-wax, and counterstained with azan where possible. One male and the female were presented by Mrs. Gaige and were sectioned at  $20\mu$ . The other male, a juvenile presented by Mr. R. Clare, was sectioned at  $15\mu$ .

The greater part of the investigation is based on the series of the male presented by Mrs. Gaige and collected at Mt. Rose, Mason County, Washington. It was possible to use azan counterstain only for the sections through the "tail" in this series, since in the anterior region the borax-carmin did not penetrate completely and it was necessary to destain and then restain on the slides with Delafield's haematoxylin, counterstaining with eosin.

Section drawings were made by means of a micro-projector and used as described by Pusey (1939) to make graphic reconstructions 25x and 50x enlarged, and to make wax models of the "tails" of the three males, the phallosome of the female sectioned, and the pelvic skeleton and the bladder and associated structures of the chief series. The models were all 50x enlarged except the one from the  $15\mu$  sections, which was 66.6x enlarged. For reconstructions of the nerves and blood vessels, section drawings (x25) were made of the least distorted of groups of eight sections through the entire series. For the other structures, and the blood vessels and nerves of the "tail", alternate sections were drawn (x50). Fig 28 was drawn from the wax model by means of a dioptrigraph. Fig. 29 was constructed by reducing the horizontal scale of the section drawings by  $\frac{1}{2}$  and the intervals by  $\sqrt{\frac{3}{2}}$ .

Towards the end of the investigation sagittal sections of the pelvic region of a male presented by Prof. James R. Slater of Tacoma and collected at the Carbon River, Rainier National Park, Pierce County, Washington, were cut at  $20\mu$  and  $10\mu$  and variously stained. A series of an adult male *Liopelma hochstetteri* loaned by Prof. de Villiers was used throughout for comparison.

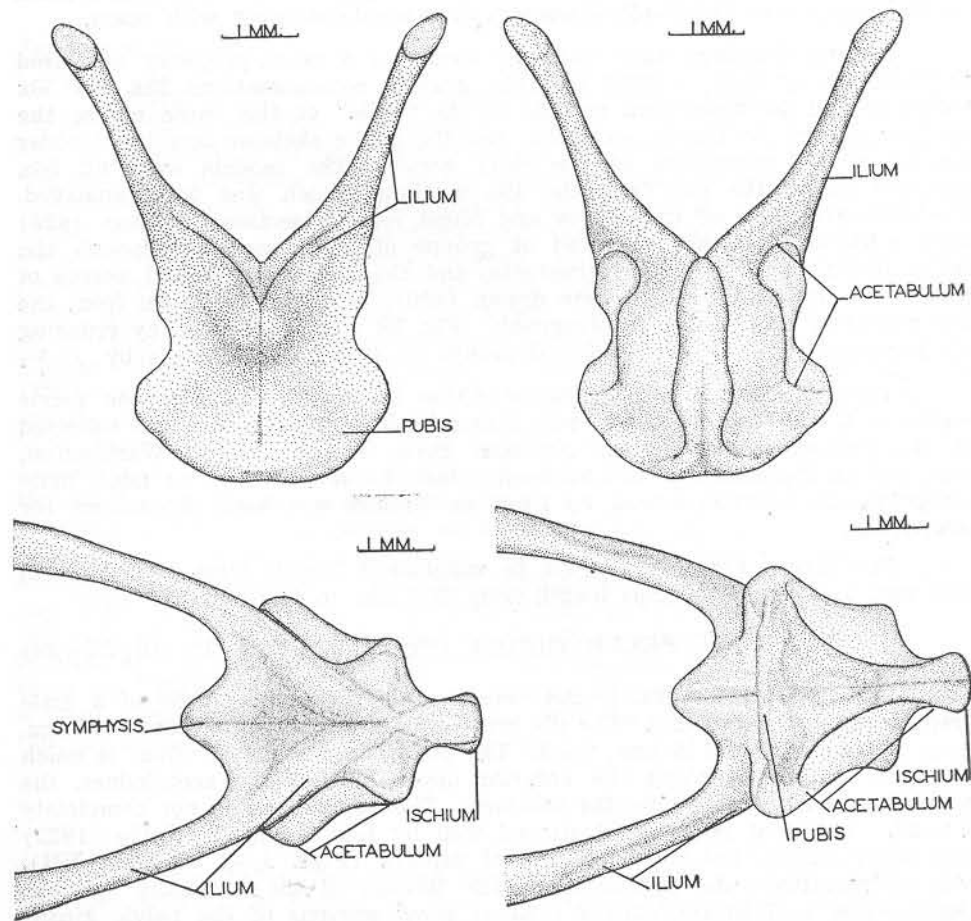
The larvae examined varied in snout-anus length from 18.0 mm. to 20.3 mm., and snout-tail (tip) length from 33.2 mm. to 41.0 mm.

#### PELVIC GIRDLE (figs. 1, 2, 3, 4, 9; 11-16; 37-39)

Van Denburgh (1912, p. 264) observed of the pelvic girdle of a male prepared as a skeleton that "The ilia are very slender. They measure 9.5 mm. long, .7 mm. wide and .5 mm. thick. The posterior end of the ilium is much enlarged, and forms about the anterior upper half of the acetabulum, the remainder being supplied by the ischium. The acetabulum is not completely closed". This last point is illustrated well by figs. 1 and 2. Noble (1922) illustrated lateral, anterior and ventral aspects (Figs. 1-3 of Plate VII), which illustrations also appeared in "The Biology of the Amphibia" (Noble, 1931). Figs. 3-7 in De Villiers (1934a) show sections of the pelvic girdle. Noble (1922) diagrammatically represented the origins of the thigh muscles on the pelvic girdle.

*Comparison with Leiopelma:*

The pelvic girdle of *Leiopelma* (figured by Stephenson, 1952) resembles that of *Ascaphus* even as regards extent of ossification, in which respect the only notable difference is that the antero-ventral ossification centres (pubes) (fig. 15) are replaced by calcified cartilage in *Leiopelma* anteriorly, while posteriorly they are more mediad in *Leiopelma* than in *Ascaphus*. (Stephenson observed that in *Leiopelma* "The pubis remains cartilaginous throughout life". op. cit., p. 609—610.) The ilia of *Leiopelma* have smaller, excentric marrow cavities, are anteriorly more rounded, particularly laterally, than in *Ascaphus* (figs. 11—13, A, B, C), and are posteriorly more rounded dorsally (figs. 14, 15). (Stephenson's fig. 5 of the pelvic girdle does not show antero-ventrally projecting, and laterally perichondrally ossified, tips of the ilia such as



FIGS. 1—4. Anterior, Posterior, Dorsal and Ventral Aspects of the Pelvic Girdle (10 x). Male Adult. Same Specimen as figs. 5—28 and 30—41.

were observed in the specimen examined and occur in *Ascaphus*.) The ventral surface of the pelvic girdle at its broadest point is slightly convex, instead of concave as in *Ascaphus* (fig. 15, level E). The anterior face is more concave, and just posterior to the acetabulum the portion ventral to it is less concave laterally, and the portion dorsal to it nearly rectangular instead of convex as in *Ascaphus* (fig. 16, level F).

EPIPUBIS (figs. 5, 6, 9; 11—14; 37, 38; 45)

*Historical:*

Van Denburgh (1912, p. 264) first observed this skeletal element, reporting that "At the interior and ventral aspect of the pelvis, at the lower margin of the sutures between the ilia and ischia, are two thin plates of calcified cartilage about 1.5 mm. in diameter, which probably represent the pubes". Noble (1922 and 1931) illustrated it together with the pelvic girdle, terming it "prepubis" and showing an anterior region of uncalcified cartilage and a posterior calcified region. Fejérváry (1923) interpreted Noble's illustrations as indicating a division into a cartilaginous part and a bony part, describing it (p. 179) as "consisting of a bony part lying caudad and evidently formed by the fusion of two halves, and bearing a subtriangular process which is cartilaginous and directed forward". He continued: "The designation of this skeletal portion — the bony part of which might, perhaps, prove to be the 'true' pubis — as 'prepubis' seems to be . . . inadmissible, because we are unable to homologize it with the homonyme element occurring in the Reptiles". He suggested provisionally "subpubis", and "cartilago subpubica" for "the cartilaginous portion, which undoubtedly suggests some resemblance to the cartilago epipubica or epipubis of the Urodeles and of *Xenopus*". De Villiers (1934a, p. 26) noted "that the epipubic (or subpubic) plate is exclusively cartilaginous and shows no trace of ossification", and described at length its relations to the linea alba, abdominal veins, its muscles, and to the pelvic girdle. De Vos (1938a, p. 75) figured "Graphical reconstructions of ventral views of the epipubes of *Ascaphus*, *Liopelma* and *Xenopus* respectively, to show the areas of muscular attachments". These figures (Fig. 7, A, B and C) are of dorsal views. In the text the epipubes of these genera are compared with one another and with urodelan epipubes.

*Homology in Anura:*

De Villiers (1934a, p. 26) remarked of the epipubis that "in view of the undoubted affinity of the Amphicoela and Opisthocoela, it is more than likely that the plate in *Ascaphus* is homologous with that of *Xenopus*", and (p. 30) that "In *Xenopus* . . . the epipubis is in mere syndesmotie relation to the pelvic girdle, and develops as chondrifications of the linea alba. It is very probable that the epipubis of *Ascaphus* arises in the same way, and that the synchondrotic continuity of epipubis and girdle is secondary". Examination of *Ascaphus* larva 2 (fig. 45) showed the epipubis, as described for *Xenopus* by De Villiers (1925, p. 133), "originating as paired strips of cartilage developed on the inner margin of the musculus rectus", but these strips of cartilage are not isolated from the pelvic girdle, which at this stage is still a paired structure. It would nevertheless seem that the epipubis of *Ascaphus* and *Xenopus* are homologous.

### Homology in Amphibia:

Noble (1922, p. 27) remarked "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", but, in view of muscle homologies discussed below, "It seems most probable that the prepubis is a recently acquired structure of no phylogenetic significance". Fejérváry (1923, loc. cit.) noted that it "undoubtedly suggests some resemblance to the cartilago epipubica or epipubis of Urodeles and of *Xenopus*". Whipple (1906, p. 270) observed that it "appears" from a "necessarily limited study of larval forms, that the ypsiloid apparatus "arises as an unpaired structure . . . when the girdle itself still exhibits its paired nature", and (p. 294) that "In origin the ypsiloid cartilage is independent of the pelvic girdle. Its stem arises as a chondrification of the linea alba of the somite immediately anterior to the pelvic girdle". Low (1927) illustrated the unpaired, independent origin in a 28 mm. embryo of *Hynobius*. Green (1931) cited the work of Whipple and Low on urodeles, and that of de Villiers (1925) on *Xenopus*, concluding (p. 1281): "From the origins of the two structures it would appear that ypsiloid and prepubis are not homologous". Hoffman (1930) worked on *Cryptobranchus alleghaniensis* and noted (p. 450) that "The ypsiloid apparatus develops in the form of a paired chondrification of the linea alba immediately in front of the girdle. There is never any cartilaginous continuity between the ypsiloid cartilage and the pubic region of the girdle". He concluded: "The ypsiloid cartilage must be considered as homologous to the epipubis of *Xenopus*". The epipubis of *Ascaphus* would thus also be homologous with the ypsiloid apparatus of *Cryptobranchus*. De Villiers (1933, p. 693) noted that "some Urodeles have a prepelvic element developing as a zonal derivative, and therefore not homologous with an epipubis". Whipple (1906), quoted also by Green (1931), commented on this prepelvic element of primitive urodeles noting also that it is not homologous with the ypsiloid. (cf. also Hoffman, 1935).

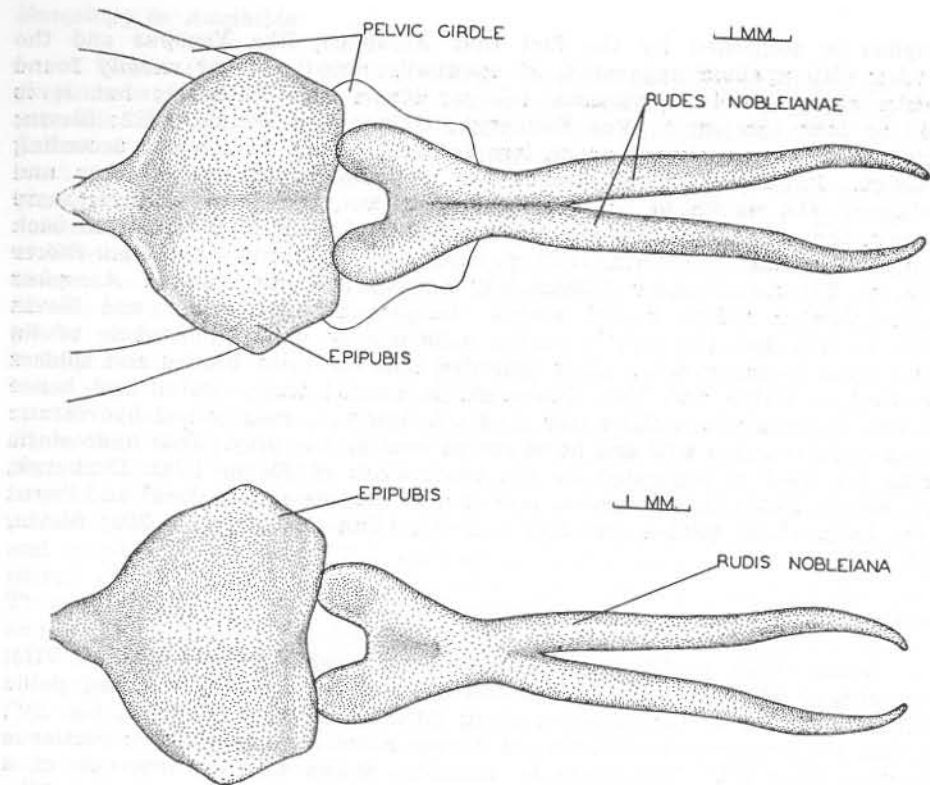
### Function:

Whipple (op. cit.) described the function of the ypsiloid apparatus and Green (1931, p. 1281) stated of the epipubis, "prepubis", of *Xenopus* that "It seems quite clear . . . that it is the functional homologue of the Urodelean ypsiloid" and described its function in *Xenopus*. Noble (1931, p. 240) remarked of the ypsiloid apparatus that "Whipple (1906) has shown that this structure and its muscles serve to control the shape of the inflated lungs which . . . act largely as hydrostatic organs. Contraction of the muscles pulls the cartilage dorsally, forcing the air anteriorly into the lungs and making the head end of the animal more buoyant. It may be noted, however, that *Ascaphus*, which frequents streams and has no need of a hydrostatic organ, has also a cartilaginous plate anterior to the pubis, and hence a prepubis may have been a primitive character of modern Amphibia". De Villiers (1934a, p. 26) reported "that *Leiopelma* also possesses this structure". This observation was confirmed by examination of a series of *Leiopelma hochstetteri* loaned by Prof. de Villiers. The epipubis is thus a feature of the *Ascaphidae*. That it may perform a hydrostatic function in

*Ascaphus* is suggested by the fact that *Ascaphus*, like *Xenopus* and the urodeles with ypsiloid apparatus, is essentially aquatic, being usually found beneath stones in swift streams (Gauge; Noble and Putnam); but it is found on land (Stejneger; Van Denburgh; Gauge; Van Winkle, 1922; Slevin; Noble and Putnam), though much less frequently than in streams according to Gauge. Putnam, however, found few in streams in wet weather and considered "the reason to be that when it is wet, what few of them there are leave the water, and during a dry spell, lack of moisture forces them back again to the water". (Slevin, 1928, p. 82). Of Californian *Amphibia* Storer (1925, p. 23) noted under "Completely aquatic species" only "? *Ascaphus truei*". Gordon (1939, p. 31) stated "tongue not protrusible" and Slevin (1928, p. 78) that the tongue "being attached by nearly the whole of its base, cannot be protruded". This indicates that the prey, beetles and spiders according to Gauge and Van Denburgh, is hunted under water and hence probably in pools where the water does not flow very swiftly and hydrostatic organs could function well and be of use in hunting the prey. That hydrostatic organs are used is suggested by the observation of Slevin (Van Denburgh, 1912; Slevin, 1928) that *Ascaphus* both swam "just as a toad does" and "went to the bottom and settled just like a frog". (Van Denburgh, p. 260; Slevin, p. 82).

### Muscles:

Noble (1922, p. 27) reported that "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)", and that the prepubis "occurs also in *Xenopus* and a portion of the pectineus originates from it". The figure he mentions shows also the insertion of a muscle to which he refers as the rectus abdominis. He observed that "the puboischiofemoralis internus of the salamander, which . . . is homologous to the pectineus, does not insert on the ypsiloid apparatus". Grobbelaar (1923, p. 159) described a muscle situated in a similar position in *Xenopus* to those labelled rectus abdominis by Noble and called it M. epipubicus, noting that "Dieser kurze Muskel entspringt ventral von der Symphyse der Darmbeinflügel, verläuft ventralwärts und setzt sich an der Dorsalfläche\* der knorpligen Epipubica an. Er fehlt bei den übrigen Anuren". (\*Corrected by Dr. C. S. Grobbelaar, University of Stellenbosch, in the copy examined. The original read "Ventralfläche".) He observed of the sartorius muscle that "Er entspringt von der Dorsalfläche der knorpligen Epipubica, und von dort aus erstreckt er sich bis zur Beckensymphyse" (p. 155), but further no muscles are mentioned as attaching to the epipubis. Hoffman (1930, p. 449) reported "In verband met die ypsiloid-apparaat tree daar twee eie spiere op: die musculus ypsiloideus posterior en die musculus ypsiloideus anterior, wat as differenserings van die musculus rectus ontstaan. Dan word daar in sommige gevalle ook nog een van die buikgordelspiere, die musculus puboischiofemoralis internus, aan die ypsiloid-apparaat geheg". (This last answers Noble's chief objection to the homologizing of the epipubis and the ypsiloid quoted above, De Vos, quoted later, also observing this). "By *Xenopus* is daar net een 'ypsiloidspier', die musculus epipubicus, wat in verband met die epipubis optree . . . Verder word die volgende buikgordelspiere ook nog



FIGS. 5 and 6. Ventral and Dorsal Aspects of the Epipubis and Rudis Nobleianae (10 x).

Male Adult. Same Specimen as figs. 1—4, 7—28 and 30—41.

aan die epipubis geheg: die musculus sartorius; musculus pectineus; musculus adductor magnus en musculus adductor longus. Die epipubis van *Xenopus*, wat die spierstelsels betref, mag derhalwe miskien nie as homolog met die ypsiloid-apparaat beskou word nie". As noted above Grobbelaar reported only the m. epipubicus and m. sartorius as attaching to the epipubis of *Xenopus*. Noble (1922), like Hoffman, however, also reported a portion of the m. pectineus as arising from it. De Vos (1938a, p. 76) referring to the muscles of the epipubis of the *Leiopelmidae* observed: "It is a remarkable fact that homologues of these muscles are attached to the ypsiloid apparatus of Urodeles. Differentiated portions of the posterior segments of the m. abdominis rectus become the anterior and posterior ypsiloid muscles (see WHIPPLE 1906 and A. C. HOFFMAN 1935) while the m. pubo-ischio-femoralis internus which is homologized by NOBLE (1922, p. 55) with the m. pectineus of Anura, likewise sometimes inserts on the ypsiloid apparatus. Such similarity is of interest in view of the accepted homology of the epipubis of Anura and the ypsiloid cartilage of Urodeles". Of the m. epipubicus of *Xenopus* she

remarked (p. 77—78): "The development of this muscle, its derivation and ontogenetic relation to the neighbouring muscles merits investigation. In the meantime, however, the comparative anatomical data make it probable that it is, as in *Ascaphus*, *Liopelma* and the Urodeles, a specialized portion of the posterior part of the m. abdominis rectus, which can pull the corpus epipubis in a dorsal direction. This posterior segment of the m. rectus, if such it should prove to be, is not directly and wholly comparable in *Xenopus* and the *Liopelmidae* . . . The m. pectineus, as in *Ascaphus* and *Liopelma*, inserts not only on the pelvic girdle, but also on the dorsal surface of the epipubis. There is however an interesting and perhaps important difference between the relation of the m. pectineus, to (the) posterior segment of the m. abdominis rectus in the *Liopelmidae*, and the relation of the m. pectineus to m. epipubicus in *Xenopus*. Whereas in the *Liopelmidae* the slip of the m. pectineus which inserts on the epipubis has to pass in front of the m. rectus segment to join the main body of the pectineus, in *Xenopus* the m. pectineus passes laterally behind the m. epipubicus. This latter muscle therefore, is not directly comparable with the posterior rectus segment in its relations to the neighbouring muscles. Moreover, it also differs in form, being a rounded median muscle, and not divisible into paired left and right halves. If it should prove to be a specialized portion of the m. abdominis rectus, the specialization has proceeded further in *Xenopus* than in the *Liopelmidae*. Three other pelvic muscles also insert on the epipubis of *Xenopus*, being attached along its lateral edges. These are the m. sartorius, m. adductor magnus, and m. adductor longus (cp. GROBBELAAR op. cit. and HOFFMAN op. cit. 1935). Although the epipubis is therefore presumably homologous within the Amphibia, being an autochthonous chondrification of the linea alba, the genera possessing it have undergone separate specialisation with respect to the muscles which have become attached to it". In *Ascaphus* larva 2 (snout-anus 18.5 mm.; snout-tip of tail 41.0 mm.; male) the pectineus muscles already have origins on the two cartilages destined to form the epipubis; and there are also muscles dorsal to each cartilage which are attached to the pelvic girdle halves posteriorly, and are probably, but not obviously, part of the rectus abdominis. De Villiers (1925) appears to have observed the m. epipubicus in *Xenopus* arising as a single median muscle, independent of and earlier than the epipubis, only secondarily acquiring attachment to it. Ryke, in work on the muscles of *Xenopus* as yet unpublished, makes no mention of there being any signs of the m. epipubicus arising as a paired structure, but notes that "it develops from a mass of myogenic tissue of the pelvic girdle", and "During subsequent stages in *Xenopus* the epipubicus shifts forwards, attaching itself to the antero-dorsal surface of the epipubis". "There is, however, no proof that the muscles of the pelvic girdle do not, at least partly, originate from the m. rectus abdominis. In fact, during the formation of the anlage of the hind limb-bud the m. rectus abd. constantly proliferates cells which migrate in the direction of the former". (Ryke). Grobbelaar (1923) appears to have found no trace of a paired nature of the m. epipubicus in the adult *Xenopus*; neither did De Vos (quoted above). Examination of series of a young male *Xenopus* loaned by Prof. de Villiers, and of larvae, of which two stages just after metamorphosis had begun were particularly used, revealed that there are indications of the m. epipubicus arising as a paired structure which is posteriorly quite close to the m. rectus abdominis, and could easily have

arisen from it. Posteriorly the two halves are more distinct than anteriorly, the fibres curving latero-ventrally, particularly in the younger stage. The interpretation of the situation in *Xenopus* is very much complicated by asymmetry which, associated with the presence of the vena abdominalis on one side, apparently causes inhibition of the muscle of that side, for in the young adult the insertion on the epipubis is practically confined to the opposite side. There is no obvious reason, however, for doubting that the epipubic muscles of *Ascaphus* similarly situated to the epipubic muscle of *Xenopus* are its homologues, and hence it will be provisionally named m. epipubicus here. (See figs. 37, 38, 40, 34; 39, 40).

#### Variations and Sex differences:

In the specimen figured, synchondrotic connexion of epipubis and pelvic girdle is very slight, not exceeding  $20\mu$  in thickness, a thin tendinous layer separating the epipubis from a flange (see figs. 4 and 36) of the pelvic girdle ventral to it. The male sectioned longitudinally is essentially similar to this. In Prof. de Villiers's specimen and in the juvenile male the cartilaginous bridges are as thick as the rest of the epipubis. In the juvenile male the bridge is apparently continuous across the entire breadth of the epipubis, there being no clear division posteriorly into two arms connected by ligaments as in the other males.

The epipubis of the females examined are synchondrotically fused with the pelvic girdle and divided posteriorly into two arms. Their form and their muscles are very similar to those of the male. (See figs. 43 and 44).

#### Comparison with *Leiopelma*:

The epipubis of *Leiopelma* in the single series of a male examined, "corresponds in all essentials with that of *Ascaphus*". (De Vos, 1938a, p. 75). "As in *Ascaphus*, the epipubis is synchondrotically fused with the pelvic girdle. There is, however, in this region a slight difference, inasmuch as the epipubis does not bifurcate immediately anterior to its fusion with the pelvic girdle, as it does in *Ascaphus* (cp. Figs. 7A and B)". (op. cit., p. 75—76, which observations were confirmed). This single broad synchondrotic connexion is like that in the juvenile male *Ascaphus*. De Vos (p. 76) observed that "*Leiopelma*, like *Ascaphus* shows a strong calcification of the cartilage, without any sign of ossification. A thin strip of cartilage however, at the junction of epipubis and pelvic girdle, remains uncalcified, constituting a hinge, which allows the anterior free corpus of the epipubis to swing up or down; a similar hinge is present in *Ascaphus*". Immediately anterior to this hinge in the specimen examined, a thin layer of perichondral bone around the epipubis begins and stretches over the greater part of its surface. This accords with what Stephenson (1952, p. 609) observes about the epipubis of *Leiopelma*: "It remains cartilaginous until maturity, but there is considerable evidence to show that in older specimens of *Leiopelma hochstetteri* at least it ultimately ossifies more or less completely. An epipubis in which two centres of ossification are present is shown in Text-figure 4C, while Text-figure 4A illustrates an epipubis which is almost completely ossified except for a posterior strip of cartilage". The epipubis is broader than in *Ascaphus*, covering

the entire breadth of the posterior tip of the rectus muscle ventrally (compare fig. 36). The anterior tip is broad and concave dorsally as compared with the almost circular transverse section in *Ascaphus*. The pectineus muscle has a much larger origin on the epipubis than in *Ascaphus* (fig. 38), and attaches to the entire antero-ventral surface of the pelvic girdle with the exception of two small areas, immediately dorsal to the epipubis, on the lateral edges, where the epipubic muscles have their origins (cp. figs. 39 and 40). The m. epipubici are very much less developed than in *Ascaphus*, making a more acute angle with the epipubis and only near the pelvic girdle curving obliquely dorso-ventrally.

#### Form and Relations:

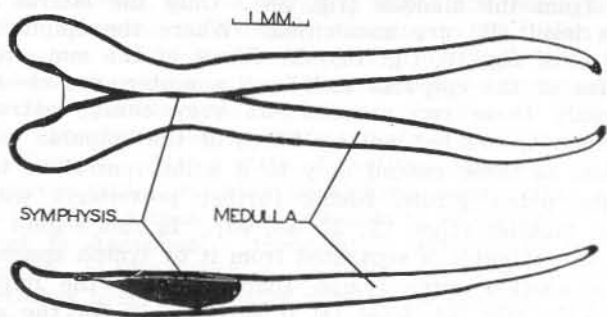
As shown in figs. 5 and 6, the form is that of a very stout Y with the arms directed posteriorly. Medially there is a shallow ridge dorsally and a groove ventrally; laterally there are concavities dorsally and convexities ventrally which are only pronounced in the region of greatest width. Anteriorly the epipubis becomes flat and slopes ventrally, probably (judging from longitudinal sections) more steeply than shown in the reconstruction (fig. 9); posteriorly it slopes ventrally mesiad. Anteriorly, where the epipubis is narrow and uncalcified (level A of fig. 10, see fig. 11), the two halves of the m. abdominis rectus meet immediately dorsal to it and the vena abdominalis lies just above their junction, while ventrally there lies connective tissue in which two lymph canals are excavated. Where the epipubis broadens sharply (just before level B of fig. 10, see fig. 12) the vena abdominalis receives the ramus abdominalis of the vena femoralis of each side, the m. rectus abdominis dorsal to the epipubis gives way to longitudinal fibres of the m. epipubicus, and a tendinous layer (see figs. 10 and 34), bounded ventrally by a lymph space, attaches to the ventral surface of the epipubis (see fig. 36). Posterior to the fork formed by the rami abdominales, the epipubic portion of the m. pectineus of each side has its origin on the epipubis lateral to two mediad venae vesicales from the bladder (fig. 38). Only the lateral edges of the epipubis at this level (B) are uncalcified. Where the epipubis is broadest (just past level C of fig. 10, fig. 13) the fibres of the m. epipubici insert in the concavities of the epipubis and have a postero-dorsal—antero-ventral direction. Dorsally these two muscles are very close, ventrally they are separated by lymph spaces but not by fibres of the epipubic portions of the pectineus muscles, as these extend only to a point ventral to the tip of the symphysis of the pelvic girdle, fusing further posteriorly with the pelvic portions of these muscles (figs. 13; 37, 38, 40). In this region the tendinous layer ventral to the epipubis is separated from it by lymph spaces, and ventral to this layer is another large lymph space. Where the epipubis becomes narrower posteriorly (fig. 14, level D) it serves only for the attachment of the m. epipubici which originate from the symphysis of the pelvic girdle in this region, the rectus abdominis muscle, which attaches to the edges of the epipubis anteriorly, not reaching as far posterior as this. The posterior extremities of the epipubis lie dorsal to a flange of the pelvic girdle which extends almost as far forward as the median notch of the epipubis (cp. figs. 4, 5 and 35).

In the female the relations are very similar, but the tendinous layer ventral to the epipubis is much less developed (fig. 44).

RUDES NOBLEIANAE (figs. 5—9; 10; 15—27; 36; 37; 42—45).

*Historical:*

Noble (1922), discussing the m. pectineus of *Ascaphus* (p. 27), noted: "It is probable that this prepubis, like the two post-pubic cartilages, is an adaptive structure of recent acquisition". Discussing the m. caudalipubischiotibialis he observed (p. 34) of the "tail" of *Ascaphus* 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)", and referred to "the cartilaginous prongs (Plate VII, fig. 3) which very probably represent a specialized portion of the rectus abdominis". He labelled them "post-pub." in Plate VI, fig. 2 and Plate VII, fig. 1 and 3, but did not use the term postpubis in the text. Fájerváry (1923) referred to Noble's Plate VII, observing the structures labelled "post-pub." which he concluded (p. 178) "Mr. NOBLE designates . . . as 'postpubis'", but, "the name 'postpubis' having been applied, by some authors, to what appears to be the true pubis of the *Ornithischia* (Dinosaurians)", and (p. 179) "also for the reason of the cartilaginous prongs not having any more intimate (genetic) relation to the pubis, especially if they would effectively prove to be a 'specialized portion of the rectus abdominis', as assumed by Mr. Noble", he proposed to name "these cartilages, which seem to represent a special acquisition of *Ascaphus*, cartilago abdominalis Nobleiana (comprising a cornu dexter and c. sinister)". Noble and Putnam (1931), observing that the "tail" can be rotated ventrally, that "The forward position of the structure is maintained by two postpubal cartilages found in no other *Salienta*". (p. 99). Noble (1931) included the figures of his work of 1922, adding no new information, and making only one reference in the text (p. 240) to "a pair of rodlike cartilages . . . serving as a support for the copulatory



FIGS. 7 and 8. Frontal Section (Dorsal Aspect) and Sagittal Section (Left Lateral Aspect) of the Rudes Nobleiana. (10 x).

Taken along the lines of greatest horizontal and vertical diameters respectively.

Male Adult. Same Specimen as figs. 1—6, 9—28, 30—41.

apparatus", without naming them. De Villiers (1933, p. 693) remarked: "The Nobelian 'cartilages' prove to be true bones with enormous marrow cavities. Their ontogeny is unknown, but they look suspiciously like sesamoid (tendon bones)". He added, "Presumably the epipubis and the Nobelian 'cartilages' represent chondrifications of the pre- and post-pelvic portions of the linea alba respectively". De Villiers (1934a) reviewed the literature briefly and stated (p. 26) "that in the male microtomized . . . the Nobelian 'cartilages' were not cartilages: in fact they show no trace of ever having been cartilaginous, but are bony". He therefore refers to "Nobelian bones", noting (p. 30) that in the section Fig. 6 "they are underlain by spaces in the general connective

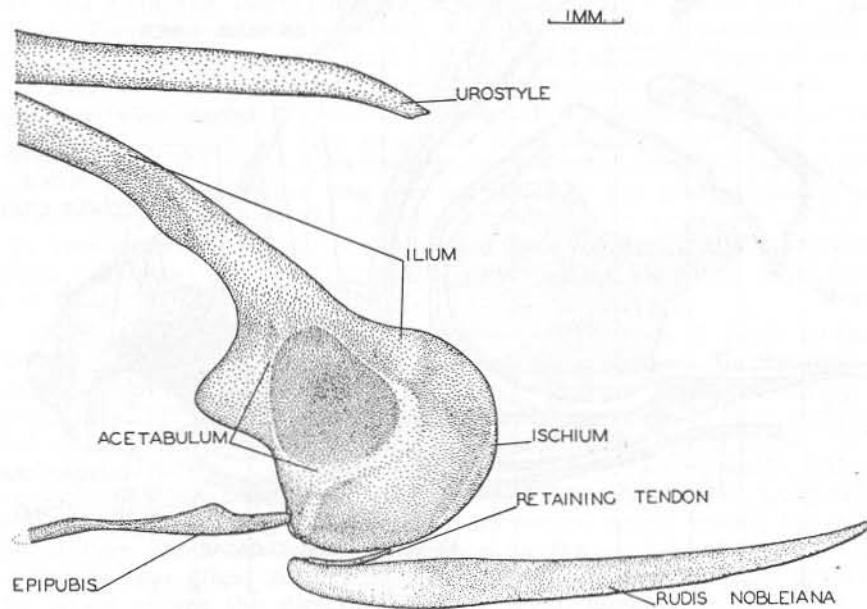


FIG. 9. Left Lateral Aspect of the Skeleton of the Pelvic Region. (10 x). Male Adult. Same Specimen as figs. 1—8, 10—28 and 30—41.

tissue capsule and are almost certainly capable of considerable motion", and, posterior to section Fig. 8, i.e. near the tip of the "tail", "shifting of position by the Nobelian bones, so as to occupy a dorso-lateral position" and each "ending in a short dorsally flexed hook". (p. 36). In the résumé (p. 44) he observed: "The Nobelian bones possibly do not belong to the category of skeletal elements developed in the linea alba; such derivatives go through a cartilaginous phase, whereas the Nobelian bones presumably do not".

*Histology in the Male:*

The term tendon bone apparently does not refer to a single distinct type of bone. Jarecki (1932) expressed doubts as to the autonomy of sesamoid or tendon bones, quoting the findings of other authors, particularly Pfitzner



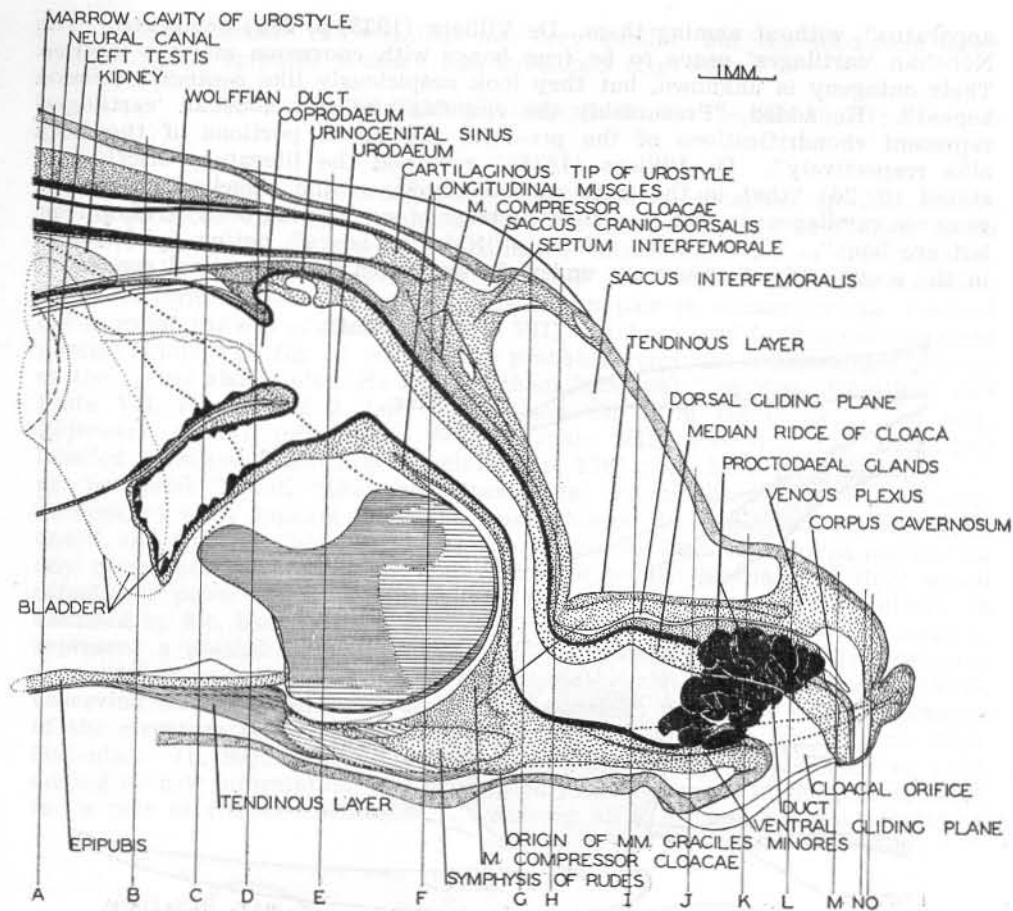


FIG. 10. Stereogram of the Pelvic Region. (10 x).

Lines A—O indicate the levels of the transverse sections figs. 11—27. The rudis Nobleiana and bladder of the left side are indicated by stippled lines, the testis by a broken line; on of the right side the Wolffian duct, kidney and the internal view of the proctodæal glands are shown. The epithelium and stratum proprium of the cloaca along approximately its mid-ventral line and on the right of the median ridge are indicated by a thick line.

Male Adult. Same Specimen as figs. 1—9, 11—28 and 30—41.

(p. 290), and remarked: "Und dennoch scheinen mir die von diesen Autoren vorgebrachten Gesichtspunkte so schwerwiegend, dass ihrer Schlussfolgerung, wonach die Sesambeine zu dem echten, wenn auch rudimentären Skeletteilen gezählt werden müssen, nennenswerte, durch diese Autoren nicht schon widerlegte Bedenken kaum noch entgegenstellt werden dürften". Koch (1926, p. 138) pointed out how little literature there was and also expressed doubts about the homology and autonomy of tendon bones: "Mit Ausnahme der

Arbeit von WEIDENREICH fehlen insbesondere Angaben über den histologischen Aufbau der Sehnenverknöcherungen, so dass es weder genügend bekannt ist, inwieweit die verknöcherten Sehnen mit dem Gewebe der Skelettknochen übereinstimmen, noch auch, ob die bei verschiedenen Tieren beobachteten Sehnenverknöcherungen übereinstimmen". Koch found Haversian systems in the tendon bones of Marsupials, Brioli (1922) and Moodie (1928) in those of Dinosaurs. Moodie remarked (p. 2): "The arrangement of Haversian systems is strikingly regular, and there is no evidence of stellate cells, or bundles of tissue, so characteristic of recent tendons". Haversian systems can only occur in Weidenreich's "Schalenknochen", so that the rods of Noble, if they are bones at all, cannot be tendon bones of the same type as those of Brioli, Moodie, and Koch, for, lacking Haversian systems, as De Villiers (1934a, p. 32) observed, "There seems to be no doubt, that the Nobelian bones belong to the category of WEIDENREICH and VON KÖLLIKER'S 'Faserknochen'". Weidenreich (1923, p. 140) defined Faserknochen as follows: "Der Faserknochen, d.h. der grobfaserige oder geflechtartige Knochen der Autoren, ist sklerosiertes präformiertes Bindegewebe, das weder im Charakter seiner Fasern noch in dem seiner Zellen bei dieser Umformung eine besondere strukturelle Änderung erfährt. Der Schalenknochen dagegen ist in bezug auf seine Grundsubstanz eine Neubildung". Whether the structures in *Ascapus* are bones or not can only be established by testing the untreated rods for the presence of calcium (calcified cartilage not being present), consequently they are here termed rods of Noble or rudis Nobleiana.

De Villiers (1934a) studied the structure of the rods of Noble as far as it was ascertainable from transverse sections of  $20\mu$  thickness. He distinguished an outer layer, termed bone, and a core or medulla. Of the former he observed (p. 31): "Nuclei are almost entirely confined to the peripheral portion of the bone, and are extremely scarce. The bony tissue (in its decalcified state, of course) consists of very fine fibres lacking nuclei although they must be of cellular origin (cp. Krompecher 1931a and 1931b)". Longitudinal sections revealed that the fine fibres by no means lacked nuclei, but rather presented very much the same appearance as the peripheral layer does in transverse section (figs. 26 and 27), there being apparently little difference in the layers except the direction of the fibres, circular in the outer and longitudinal in the inner. It is interesting to note that the tunica albuginea of the penis of mammals shows a similar division into circular and longitudinal fibres, the circular fibres forming an *inner* layer about the corpora cavernosa penis and the longitudinal fibres the *outer* layer. (cp. Maxwell and Bloom, 1940, p. 520). This was confirmed by examination of sections of a 6½ month human foetus and the penis of a child, where it was noticed that the outer layer contains numerous trabeculae continuous with the inner layer. In the longitudinal sections the inner layer of the rudis Nobleiana resembles the connective tissue surrounding the urostyle seen in the same sections, including its staining reactions. De Villiers (1934a, p. 31) noted that, unlike membrane or cartilage bone, the rods "do not take up the haemalum at all, but stain with the plasmal dye", in the case of his sections eosin. With borax-carmin—azan also, it is the counterstain which is taken up, the rods staining with aniline blue. In some of the longitudinal sections stained with azo-carmin—azan there was a tendency for some of the fibres at the

junction of the inner and outer layers to retain the azo-carmine red when the rest had been completely decolorized by differentiation.

De Villiers (op. cit., p. 32) observed of the medulla of the rods: "It consists of a fairly homogenous fibrous connective tissue, whose fibres form an open network, with which the cellular processes are continuous. The nuclei of the cells stain very deeply with the haemalum and are particularly large. Their shape varies from circular through ovoid to pear-shaped and somewhat resemble the nuclei of mast cells of areolar connective tissue . . ." The appearance in longitudinal section is very similar to this, and obviously different to the marrow of the pelvic girdle, femurs and urostyle and to the marrow described by Tretjakoff (1929). In none of the specimens were there blood vessels in the medulla, and not a single erythrocyte was observed.

#### *Histology in the female:*

In the female the rudes Nobleianae are present, but considerably smaller than in the male. Histologically they are similar, but posteriorly the medulla, which is more densely packed posteriorly in both sexes, is very dense and has only a very thin layer of fibres, mostly circular, surrounding it. The posterior extremities are without this tendinous layer, are confluent dorsal to the cloaca in the adult female examined, and are also associated with a median dorsal tendinous structure which attaches anteriorly to the urostyle.

#### *Histology in the larvae:*

In the earliest and oldest stages examined the rods are present and show little change, consisting of a peripheral layer of somewhat flattened cells arranged in a circular direction surrounding a medulla of cells arranged in rings peripherally, which arrangement gradually disappears as the cells become more densely packed towards the middle. The medulla looks not unlike the densest adult medulla. In the older larvae (snout-anus 18.5 and 20.3 mm., with complete fusion of pelvic girdle, and perichondral, but not endochondral ossification of femurs and of ilia), in the region of the pelvic girdle, the peripheral layer on the dorsal side of the rods is more dense, and there are numerous slender eosinophil fibres, nearly all of which lie in a circular direction and are suggestive of the peripheral fibres of the adult rods.

#### *Form and Relations in the Male:*

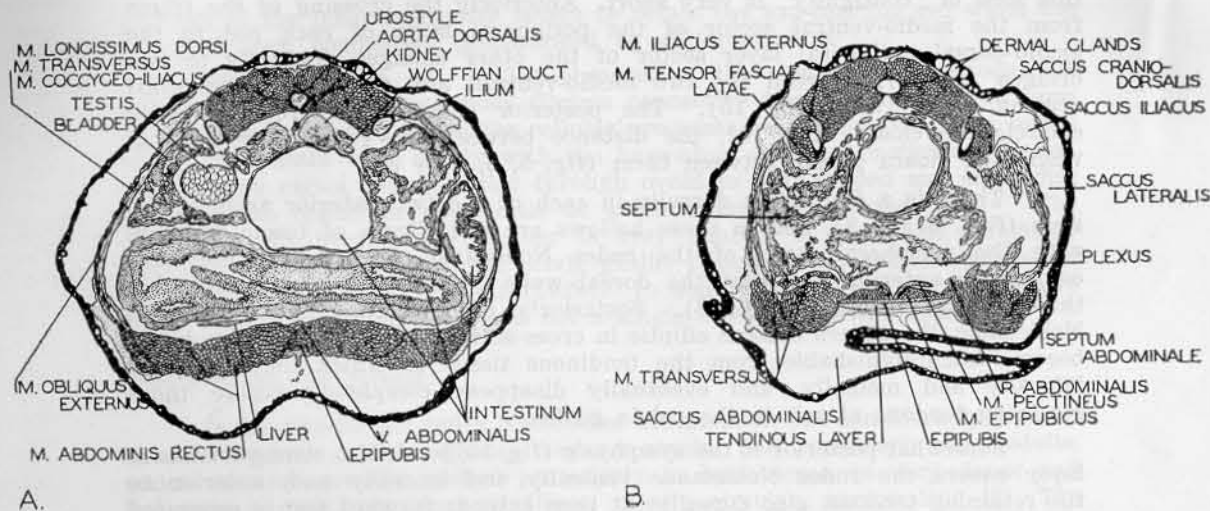
The general form was described and illustrated by Noble (1922) (see above), but he figured the rods as curving ventrally behind, whereas the reconstructions and models made in this investigation, the relations in the females and larvae, and longitudinal sections show them to curve dorsally, as was also observed by De Villiers (quoted above). The rods approach each other near their anterior ends, and "They are joined by stout fibres forming a sort of chiasma between the two bones, in such a way, that the fibres running from the top and the bottom of the left bone are attached to the bottom and the top respectively of the right bone. The contiguity then becomes real continuity, so that the two Nobelian bones are actually fused for some distance". (De Villiers, 1934a, p. 32—33). (See figs. 7, 8, 10, 16). Posteriorly

this zone of "contiguity" is very short. Anteriorly the crossing of the fibres from the medio-ventral sector of the peripheral layer of each rod to the medio-dorsal peripheral layer sector of the other changes gradually to two bridges (fig. 7), between the two medio-ventral, and the two medio-dorsal regions respectively (fig. 15). The posterior ends of two rods partially encircle the cloaca (fig. 10), the distance between the rods being greatest where the cloaca passes between them (fig. 5, 6, 7 or 8).

There is a depression dorsally in each of the two anterior arms of the rods (figs. 6 and 8), and in these hollows are flat slivers of tissue identical with the peripheral layer of the rudes Nobleianae, with which they are continuous anteriorly so that the dorsal walls of the rods are considerably thickened in this region (fig. 8). Posteriorly, on separating from the rudes Nobleianae, the slivers become elliptic in cross-section (fig. 15), then gradually become indistinguishable from the tendinous tissue in which they lie, first laterally and medially, and eventually disappear completely before these retaining tendons attach to the pelvic girdle.

Somewhat posterior to the symphysis (fig. 10, level G) a strong tendinous layer covers the rudes Nobleianae ventrally and laterally and, anterior to the retaining tendons, also dorsally. It then extends forward and is separated from the epipubis by a layer of loose connective tissue which becomes narrower and narrower until the tendinous layer attaches to the epipubis ventrally a short distance posterior to the narrow tip (fig. 36). Anteriorly there is a distinct median cleft in the tendinous layer in addition to several less distinct longitudinal divisions of its tissue. In transverse section it has the appearance of "dense felt-like connective tissue, which upon microscopic inspection might easily be mistaken for the posterior fibres of the m. abdominis rectus. This seems to be exactly what NOBLE has done, for on Fig. 2, plate VI of his work of 1922, a muscle sheet is seen stretching between the Nobelian bones (labelled 'post-pub.') and the last segment of the m. abdominis rectus, (labelled in the penultimate segment 'Rect. abd.')." (De Villiers, 1934a, p. 28). In longitudinal section the tendinous layer is seen to consist of coarse cords extending from the perichondrium of the epipubis anteriorly, to the rudes Nobleianae in the region of the symphysis (figs. 34 and 36). The fibres extend between those of the peripheral layer of the rods posteriorly and lie anteriorly in mere contact with them without attaching to their tissues. Between the fibres lie numerous blood vessels and the appearance is not unlike that of well-vascularized muscle; but striped muscle (and hence rectus abdominis), at least, it definitely is not.

The dorsal surfaces of the rudes Nobleianae serve for the attachment of the mm. compressores cloacae, the fibres of which curve from an antero-posterior direction anteriorly to a ventro-dorsal direction posteriorly, extending almost to the posterior tips (figs. 34, 36, 37). Behind the symphysis a wedge of vascular tissue lies medio-ventrally between the rods, gradually extending ventrally and in breadth as the cloaca curves ventrally between the rods (figs. 10 and 17—20), until the cloaca divides it into two posteriorly. The vascular tissue encroaches on the attachments of the mm. compressores cloacae dorsally and laterally (figs. 20—22, levels J—L), until these are confined posteriorly to the dorso-lateral quadrants of the rods. In the same region the vascular tissue extends ventro-mesial and ventro-laterally, on the lateral



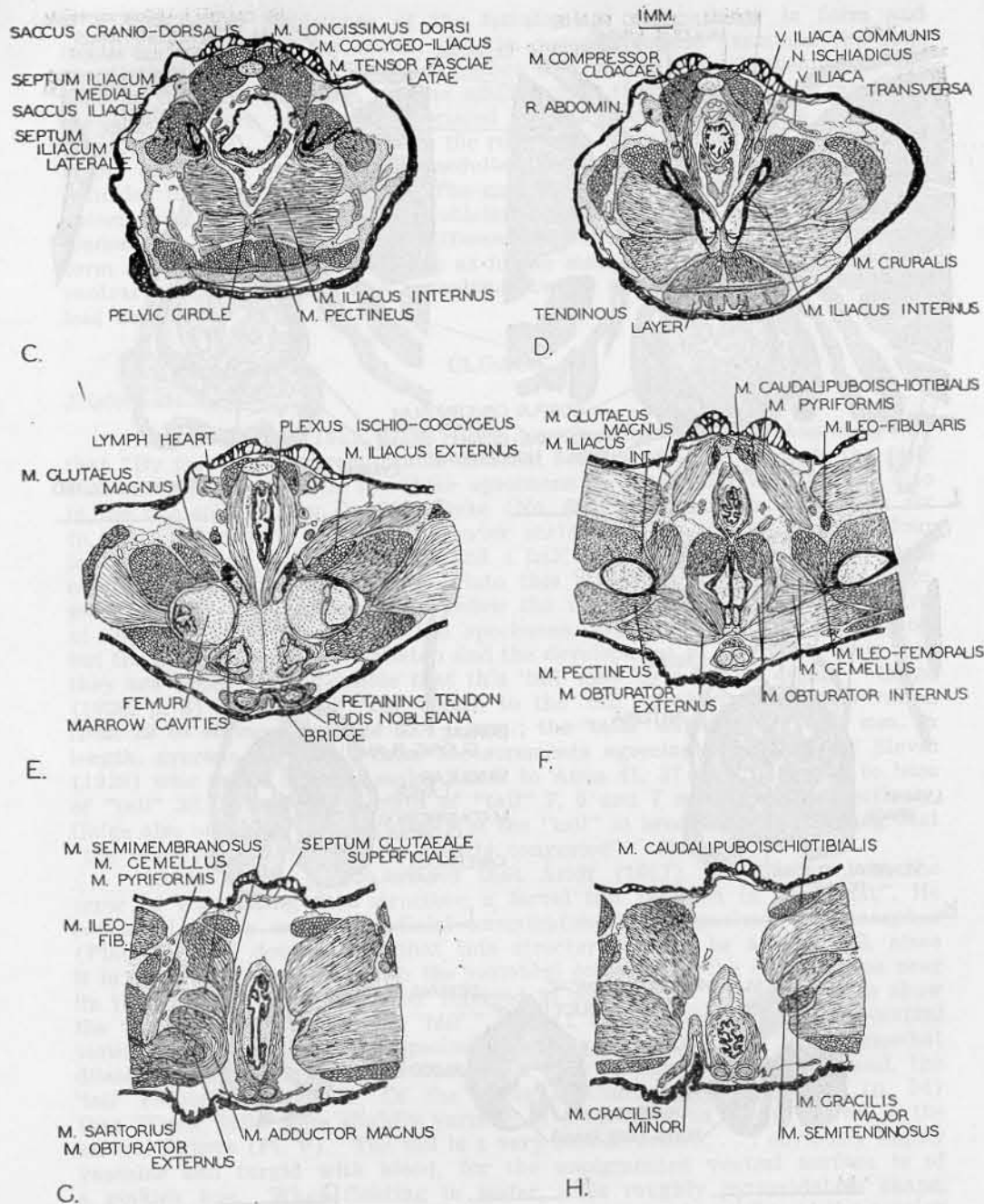
FIGS. 11 and 12. Transverse Sections (Posterior Aspects) at Levels A and B of fig. 10. (5 x).

and medial sides respectively of the rods, until it is continuous ventral to them. (Compare fig. 19 with figs. 20 and 21, and fig. 26 with fig. 27). Lying within the vascular network, between the rudes Nobleianae, there appear to be *unstriated* fibres of the mm. compressores cloacae continuous ventrally and dorsally, around the rods, with the striped fibres. (Between levels I and J).

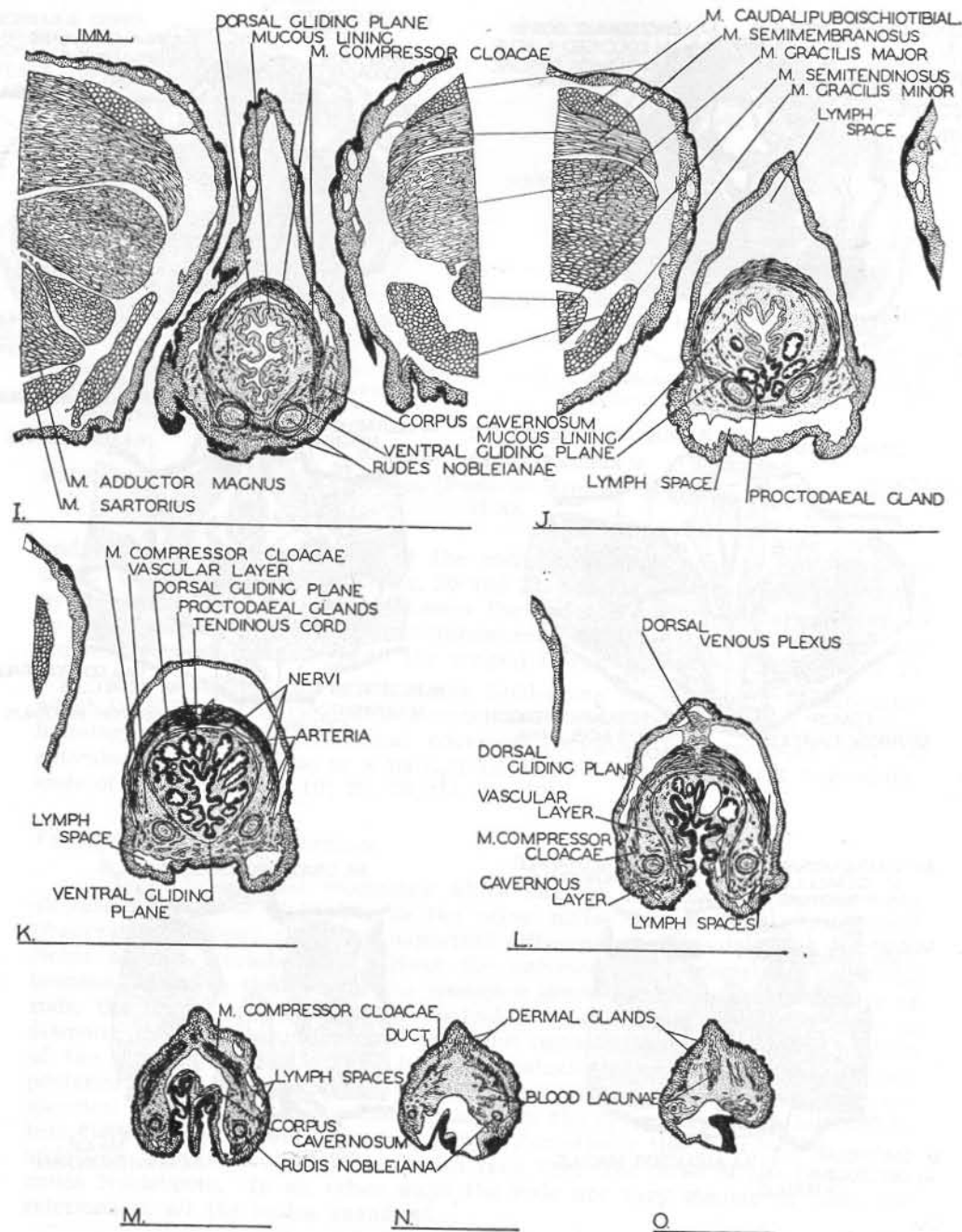
The posterior tips of the rudes Nobleianae extend into a protuberance which De Villiers (1934a, p. 36) described as "a sharp fleshy tubercle, consisting histologically of an ectodermal covering enclosing an excavated core of cuticular tissue", and lie in a pair of canals which are confluent beyond the ends of the rods (figs. 10; 28, 29; 24, 25; 42).

*Variations and Sex differences:*

Apart from other variations which suggest that it is a member of a different species of *Ascapus* to the other males examined (see Additional Observations, below), there are important differences to be noted in the rods of Noble of the juvenile male. Near the anterior ends, where the retaining tendons attach to the rods in the specimen described, there are *two* pairs of rods, the dorsal pair being more medially in position and slightly smaller in diameter than the normal ventral pair, and representing the retaining tendons of the other specimens. They become gradually narrower and less distinct posteriorly until they disappear into retaining tendons. These dorsal rods are identical in structure to the main rods, both the outer layer and the medulla being continuous between the two pairs. Posteriorly the rods end in canals which are confluent and are lined with cells very like those of the tips of the rudes Nobleianae. In all other ways the rods are very similar in form and relations in all the males examined.



FIGS. 13-18. Transverse Sections (Posterior Aspects) at Levels C-H of fig. 10. (5 x).



FIGS. 19—25. Transverse Sections (Posterior Aspects) at Levels I—O of fig. 10. (10 x).

The rudes Nobleianae of the females are very similar in form and relations to those of the males. In the juvenile female examined the rods are distinct posteriorly and lie on either side of the cloacal opening as far back as they are traceable. In the adult female they are confluent dorsal to the cloaca where they are associated with a median tendinous structure. (Figs. 44 and 43). In both females the rods posteriorly are without the external layer, consisting only of the "medulla", and do not lie in canals in the cuticular tissue as in the males. The mm. compressores cloacae do not stretch anteriorly dorsal to the rudes Nobleianae in the female, and the retaining tendons are replaced by a less differentiated sheet of tissue. Otherwise the form and relations of the rods are as in the male, though the tendinous layer ventral to the rods, and the vascular network around them are very much less developed. (Fig. 43).

### CLOACA

#### Historical:

Van Denburgh (1912, p. 261) first described the male *Ascaphus* observing that "By far the most remarkable external feature of these toads is the tail! This is well-developed in the three specimens at hand, and was present also in the one collected by Dr. Van Dyke (No. 6907). It extends back from six to eight millimeters from the posterior surface of the thighs, is about four millimeters wide, and about three and a half deep at its base. The cloaca is continued from its usual position into this structure, and ends in a large, swollen orifice just in front and below the tip of the 'tail'. This structure, at first glance, suggests that the specimens were but recently transformed, but the ossification of the skeleton and the development of the testes show that they are adult. It is possible that this 'tail' may be a sexual organ". Gaige (1920, p. 5) stated that "The length to the 'tail' of thirty-one males varied from 29 to 40 mm., average 35.4+ mm.; the 'tails' were from 3 to 9 mm. in length, average 5.4 mm.", these measurements agreeing with those of Slevin (1928) who found in three males Snout to Anus 41, 37 and 37; Snout to base of "tail" 38, 36 and 34; Length of "tail" 7, 5 and 7 millimeters respectively. Gaige also observed the vascularity of the "tail" in breeding males, noting that "the underside of the 'tail' is greatly congested". (loc. cit.).

Noble (1922, p. 33) stated that Arldt (1917) had "fallen into the error of considering this structure a larval tail retained in the adult". He continued: "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". (p. 33—34). The plate referred to consists of "Photographs to show the variation in shape of the 'tail'", figs. 1 and 2 being dorsal and ventral views of a "Freshly killed specimen floating in water, the 'tail' somewhat dilated", and fig. 3 a ventral view of a "Living specimen playing dead, the 'tail' reduced in width". Of the living specimens Noble reported (p. 34) that "Their 'tails' were slightly variable in proportion, as is well shown in the several figures (Pl. V). The tail is a very soft structure, . . . 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 rectus abdominis seems to form the anterior part of this structure".

Fejérváry (1923) observed that Simroth (1914) had regarded the cloacal extension of *Ascaphus* as a tail. Noble (1925, p. 16—17) stated: "In the male a ring of enlarged cloacal glands is formed well inside the orifice in the 'tail'. A cluster of horny spines is found inside the cloaca just posterior to the enlarged glands". He made further observations on the manner of function of the cloaca which will be quoted in that connexion together with other remarks on function from Noble and Putnam (1931), Slater (1931), and Noble (1931). The latter included illustrations of a male "A. Showing the cloacal appendage of this sex. B. The appendage viewed ventrally. C. The same fully distended, showing the spines which occur within the orifice of the cloaca", the first illustration being a dorsal view of a specimen.

De Villiers (1933, p. 693) noted: "The cloaca is continued into the tail, at the end of which it has a groove-like opening. The cloacal opening has large dermal proctodeal glands. The 'tail' is a mass of spongiöse fibres, the interstices of the network filled with blood. This erectile tissue is distributed into a pair of strands ventral to the cloaca and lateral to the Nobelian bones, and a strand is pierced by the cloaca. The skin is separated from the erectile tissue by large subdermal lymph spaces, but is adherent ventrally and mid-dorsally". De Villiers (1934a) described the muscles and erectile bodies of the cloaca, the blood vessels, nerves and lymph spaces associated with them, and the cloacal glands, illustrating with a section (Fig. 8) through the "tail".

#### *Form and Relations in the Male:*

As far posterior as just behind the urinogenital sinus (fig. 16, level E of fig. 10) the cloaca is very similar in relations to that of *Leiopelma* and *Xenopus* in the same region. Posterior to this level the cloaca slopes ventrally away from the urostyle, between the mm. compressores cloacae, so that the two dorsal ends of these muscles become detached from the urostyle. They meet a layer of connective tissue which separates them in the midline and extends dorsally, as the septum interfemorale, to the urostyle and to a frontal sheet of connective tissue (the septum glutaeale superficiale) behind the urostyle, and become continuous with the cutis further posteriorly. (Figs. 17 and 18, levels G and H of fig. 10). In *Leiopelma* the mm. compressores cloacae attach to either side of a cord of fibrous tissue, which broadens anteriorly and is suspended laterally from the urostyle, and the mm. compressores cloacae extend beyond the urostyle as in *Ascaphus*, but the dorsal suspensory lamina is absent. In *Ascaphus* somewhat anterior to the tip of the urostyle the two mm. compressores cloacae, while still attached ventrally to the pelvic girdle, become continuous ventral to the cloaca and dorsal to the longitudinal muscles attaching further posteriorly to the pelvic girdle (figs. 10 and 16). In *Leiopelma* and *Xenopus* the mm. compressores cloacae do not extend posterior to their pelvic attachments, and the cloaca is connected to the pelvic girdle

by a portion of the septum interfemorale absent in *Ascaphus*. In *Ascaphus* the cloaca is flexed ventrally immediately behind the pelvic girdle, and the dorsal lamina divides into a dorsal and a ventral portion, the posterior edge enclosing a vein draining the post-urostyler connective tissue and joining the v. caudalis (figs. 30 and 31). (Fig. 17, level G of fig. 10). The cloaca, with its outer muscular layer derived from the mm. compressores cloacae, extends almost to the rudus Nobleianae, turns sharply antero-posteriorly with resultant folding of the dorsal side (fig. 10, level H; fig. 18), continues in this direction almost to its end, turns dorso-ventrally between the rudus Nobleianae and opens between two ridges on the ventral side of the "tail". A large lymph space, apparently corresponding to the sacchi interfemorales in *Rana*, separates the cloaca dorsally from the skin in the region where the cloaca lies antero-posteriorly (figs. 17—21, levels G—K of fig. 10), a highly vascular cutis bridge connecting the dorsal skin with the mm. compressores cloacae where the cloaca turns ventrally (fig. 22, level L of fig. 10). At the level of the dorsal fold of the cloaca (level H of fig. 10, fig. 18) the latter is attached to the ventral skin only via a sheet of connective tissue, the septum femorale inferius (indicated in fig. 36), which attaches to the ventral surfaces of the gracilis minor muscles. Where the "tail" separates from the thighs (level I of fig. 10, fig. 19) the skin is closely applied to the cloaca ventrally and ventro-laterally, enclosing numerous lymph spaces. Further posteriorly the ventro-lateral attachment is continuous but much excavated into lymph spaces, while ventrally there are regions of close approximation alternating with large lymph spaces. Two ventro-lateral folds on the "tail" are occupied by large lymph spaces continuing posteriorly on either side of the cloacal orifice and gradually giving way to smaller lymph spaces at the tip of the "tail". Dorso-laterally the skin becomes attached to the mm. compressores cloacae only behind the cloacal opening. (Figs. 20—25, levels J—O of fig. 10).

#### *Muscles and Cavernous Tissue:*

There are three muscle layers associated with the cloaca: an innermost layer of circular unstriated muscle, a thin layer of longitudinal unstriated muscle, and an outermost layer consisting of the paired and striated mm. compressores cloacae. All three layers are apparently partly converted to cavernous tissue posteriorly. That these cavernous bodies have been labelled "corpora cavernosa" does not imply that they are considered to be homologous with the corpora cavernosa penis or corpus cavernosum urethae of man.

#### *Circular muscles:*

The circular muscles encircling the coprodaeum and forming an irregular layer around the bladder continue along the cloaca, and are interrupted only where the Wolffian ducts join the dorsal wall of the coprodaeum (level D of fig. 10, see fig. 14), for the circular muscles do not encircle the Wolffian ducts, and are complete again dorsally behind them (Somewhat behind level E of fig. 10). In the ventral, horizontal, portion of the cloaca (behind level H) the circular muscles alter in form and in relation to surrounding tissues, being separated from these dorsally and ventrally by gliding planes (fig. 10, levels I to L; figs. 19—22). The dorsal gliding plane extends laterally posteriorly,

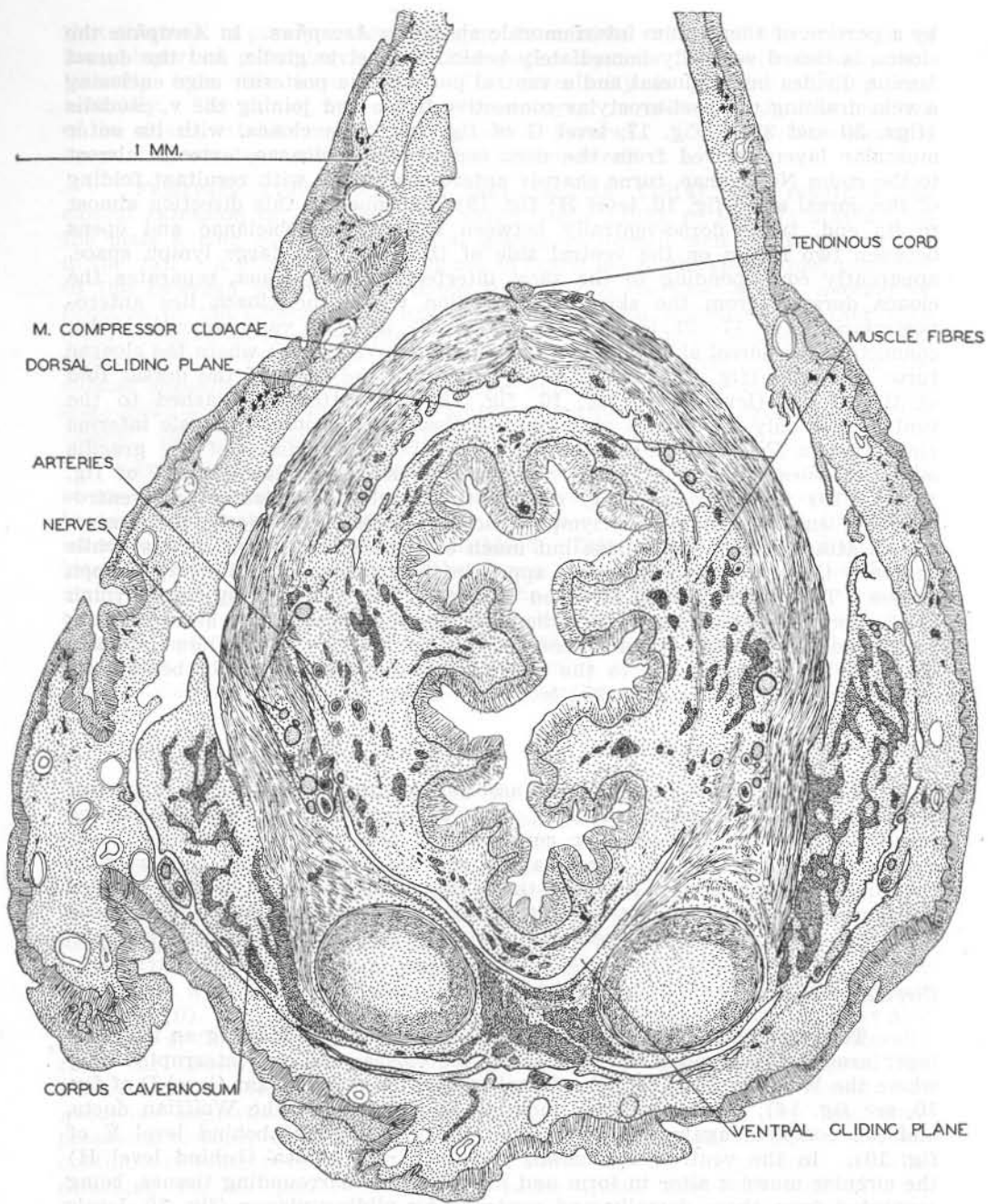


FIG. 26. Transverse Section (Posterior Aspect) through the "Tail" at Level I of fig. 10. (50 x).

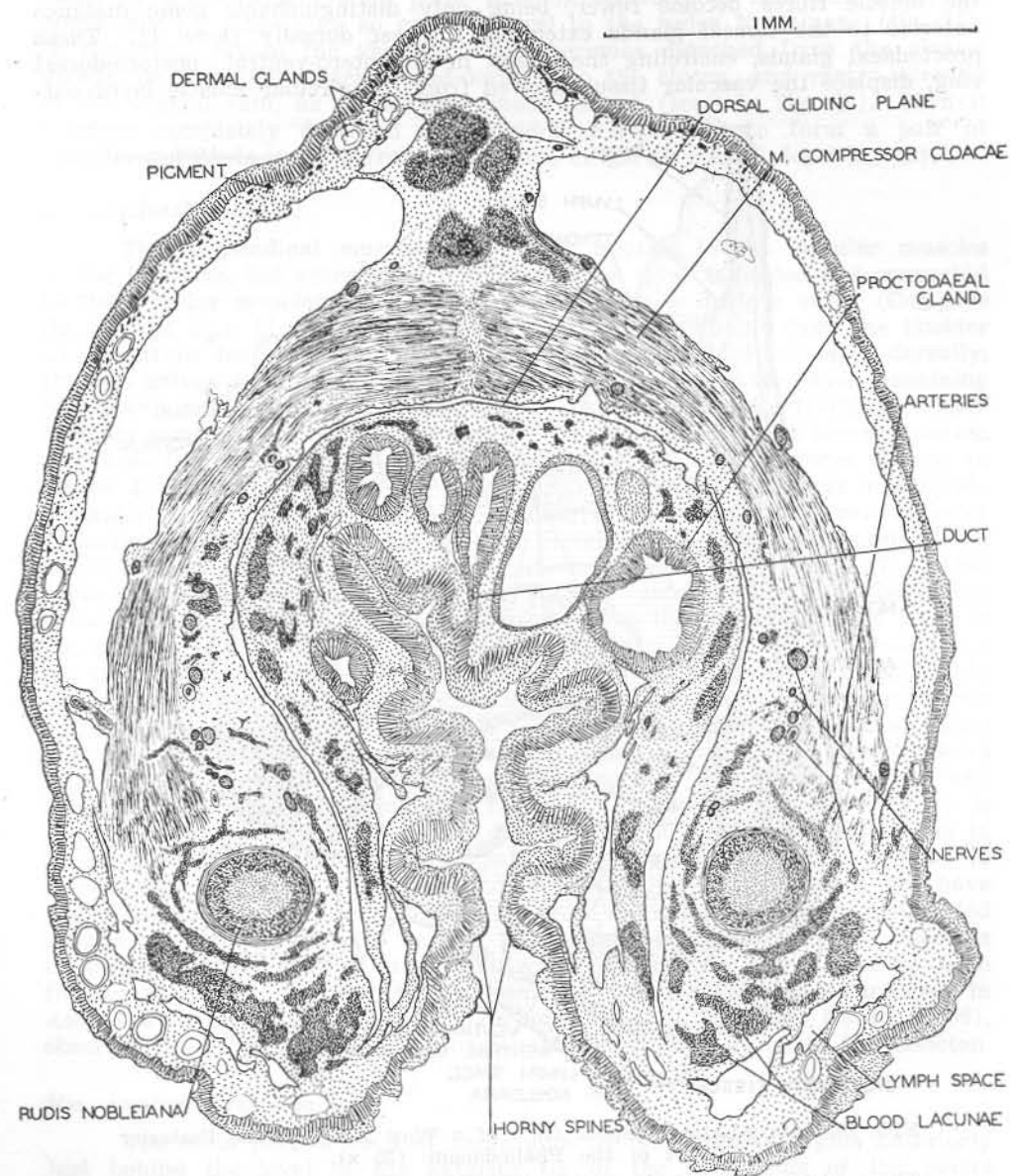


FIG. 27. Transverse Section (Posterior Aspect) through the "Tail" at Level L of fig. 10. (50 x).

(compare figs. 19 and 20) and the ventral one becomes smaller and bridged with connective tissue as it is replaced laterally by the dorsal gliding plane (compare fig. 21). The vascularization of the layer increases posteriorly, while the muscle fibres become fewer, being only distinguishable some distance anterior to the cloacal glands extending furthest dorsally (level I). These proctodaeal glands, encircling the cloaca in an antero-ventral—postero-dorsal ring, displace the vascular tissue derived from the circular muscle layer out-

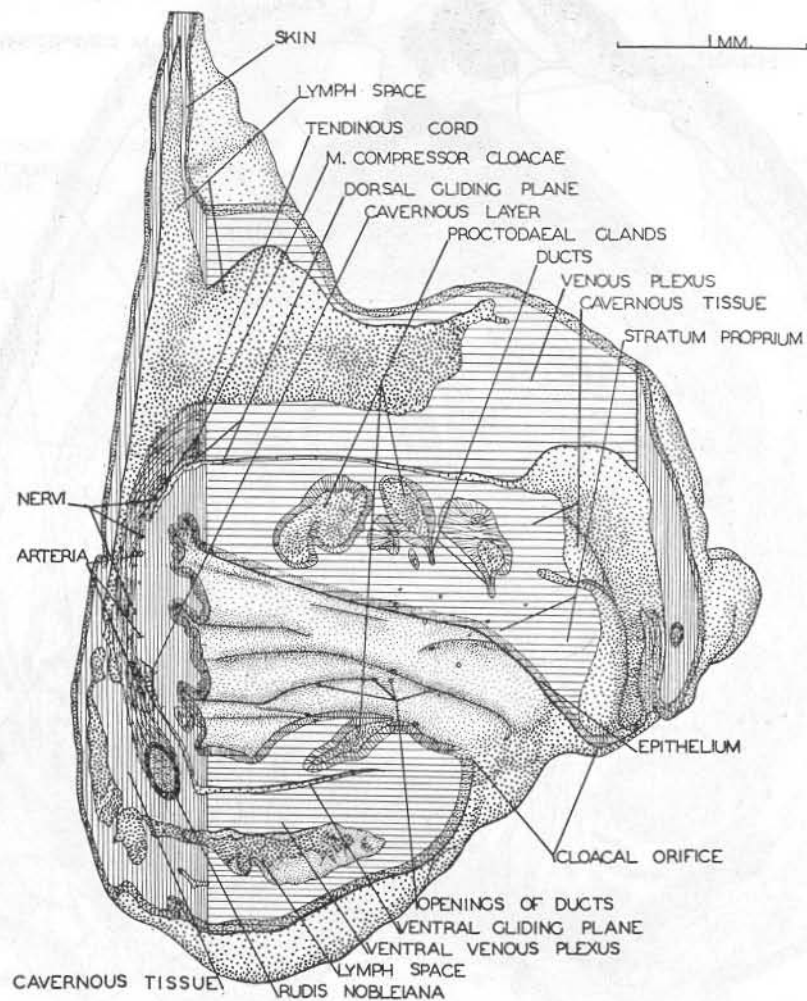


FIG. 28. Antero-Lateral Aspect (30°) of a Wax Model of the Posterior Part of the Phallodaem. (25 x).

The model consists of the entire tip and the right half of the rest of the "tail".

Male Adult. Same Specimen as figs. 1—27 and 30—41.

wards (figs. 10, 20—22) and reduce its thickness, particularly ventrally and ventro-laterally. Immediately anterior to the cloacal opening the connective tissue of the ventral gliding plane extends ventrally to the skin, while the dorsal gliding plane does so medio-ventral to the rudis Nobleiana (fig. 22). In the same region the vascular layer becomes detached from the cloacal glands, but remains attached mid-dorsally to the cloaca, and ventro-laterally to the ventral skin, as far as the glands extend (level L, fig. 22). Then it becomes completely detached and divides m'd-dorsally to form a pair of vascularized cords isolated from the cloaca. (Figs. 10 and 23, level M; 42).

#### Longitudinal muscles:

The longitudinal muscles are closely applied to the circular muscles of the intestine, but anterior to the bladder the layer is folded and connected to the circular muscles of the coprodaeum by cutis bridges only. (Compare fig. 14 and figs. 11—13). Longitudinal muscles are absent from the bladder and Wolffian ducts; the tissue enclosing the ducts divides the layer dorsally, the two halves attaching to the urostyle behind them and the layer remaining incomplete dorsally as far as the tip of the urostyle. Ventrally the layer becomes complete behind the bladder, but the thickened median ventral portion separates from the rest and passes between the mm. compressores cloacae to attach to the pelvic girdle (figs. 10 and 16), leaving the layer incomplete ventrally for a short distance. The folding of the longitudinal muscle layer is marked in the region of the bladder (level E, fig. 15) and is present but reduced beyond the tip of the urostyle (levels F and G, figs. 16 and 17) by the encircling mm. compressores cloacae. In the ventral portion of the cloaca behind the pelvis (from level H posteriorly) the longitudinal muscle layer is not seen in contact with the circular muscle layer, but is divided from it by the gliding planes and is not easily distinguished. It appears to form a thin vascularized layer on the inner side of the mm. compressores cloacae in this region (figs. 19—24, and 26 and 27). This layer cannot be distinguished posteriorly from the ventral vascularized cords derived from these muscles (fig. 25). The longitudinal muscles of the cloaca of *Leiopelma*, *Xenopus* and *Rana grayi* show similar folds in the same (bladder) region and there is similar division of the layer by the Wolffian ducts and bladder. There is in all of them an attachment to the pelvic girdle, single (as in *Ascaphus*) in *Rana grayi*, paired in *Leiopelma* and *Xenopus*; but *Xenopus* does not have fibres attaching to the urostyle. In *Rana grayi* there are a few fibres distributed around the circular muscles beyond these skeletal attachments, but there is no continuous layer as in *Ascaphus*, while in *Xenopus* and *Leiopelma* such fibres are absent. A few fibres from the cloaca behind the urostyle in *Ascaphus* attach to it near its tip. Lereboullet (1851), quoted by Gaupp (1904), observed the attachments of the longitudinal muscles of *Rana* to the skeleton.

#### Mm. compressores cloacae:

The main part of each of these muscles in *Ascaphus* begins anteriorly just behind the level of the anterior tip of the symphysis of the pelvic girdle, where it is attached to the ventro-lateral surfaces of the urostyle, and connected to the pelvic girdle between the ilia at the level of the anterior edge of the acetabulum. Posteriorly the attachments to urostyle and pelvic

girdle are lost, and the two muscles meet mid-dorsally and mid-ventrally on either side of dorsal and ventral fasciae. In *Rana* Gaupp (1904, p. 362) observed: "So sind also eigentlich drei hinter einander gelegene Portionen von Muskelfasern zu unterscheiden, die Lereboullet auch thatsächlich mit verschiedenen Namen belegt. Marcussen fasst die erste und die zweite zu einem Muskel zusammen, und da seine Nomenclatur schon vielfach angenommen worden ist, so will ich ihr hier folgen; es sind dann an dem vorderen Muskel zwei Portionen zu unterscheiden, von denen nur die hintere in engere Beziehung zur Cloake tritt". The posterior muscle which Marcussen (1848 and 1853) named *m. sphincter ani* and Gaupp (1904) *m. sphincter ani cloacalis*, is not separate from the anterior muscle, which Marcussen and Gaupp named *m. compressor cloacae*, in *Ascaphus* and *Leiopelma*. It appears to be absent in *Leiopelma* and continuous with the *mm. compressores cloacae* in *Ascaphus*. The *m. compressor cloacae* in *Leiopelma* also does not have a separate portion anteriorly situated as in *Rana*. In *Ascaphus* (fig. 40), in much the same way as Gaupp (1904, p. 363) reported of the anterior portion in *Rana*: "Ganz eigenartig verhält sich ein schmales Bündel, das sich vom vorderen Rande des Muskels ablöst. Es gelangt nicht ganz bis zum Steissbein, sondern biegt vorher lateralwärts um, umgreift schlingenartig den *N. ischiadicus* nebst der *A. ischiadica* und der *V. ischiadica*, und strahlt dann in die *Membrana abdominopelvica* aus (Fig. 89)". In *Ascaphus*, however, the *v. ischiadica* lies further dorsally and is not encircled (fig. 14), and a few fibres of the obliquely antero-ventral—postero-dorsally directed lateral portion of the *m. compressor cloacae* curl mediad ventral to the *n. ischiadicus* and are apparently connected to the main portion of the muscle by a membrane on the mesial side of the nerve and artery (fig. 40). This anterior portion of the muscle has no apparent relation to the lymph hearts dorsal to it in either *Ascaphus* or *Rana grayi*, although Gaupp (1904, p. 364) observed of the contraction of this muscle that "Es wäre zu untersuchen, ob dadurch auch eine Wirkung auf das in die Nähe gelegene hintere Lymphherz oder die in dasselbe einmündenden Ostien ausgeübt wird".

Behind the pelvic girdle the *mm. compressores cloacae*, which closely encircle the cloaca, are continuous with each other ventrally and expand ventral to the pelvic girdle as a single muscle which attaches anteriorly to the connective tissue dorsal to the *rudes Nobleianae* (figs. 36, 40; 16, level F of fig. 10). At about the level of the posterior tip of the symphysis of the rods of Noble, the *mm. compressores cloacae* attach ventrally to them (figs. 17 and 18, levels G and H of fig. 10), posterior to this extending ventral to the rods in the form of vascular tissue through which a few unstriped fibres cross from one muscle to the other. (Figs. 19—27). The vascularized cords ventro-lateral craniad (levels I—K), and ventral further caudad (levels L—O), to the *rudes Nobleianae* are apparently also derived from the myogenic tissue from which the *mm. compressores cloacae* arise, while the *rudes Nobleianae* appear to be specialized portions of the same stratum.

Noble (1922, p. 34) noted of the "tail": "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". Noble's outer layer is thus clearly the *mm. compressores cloacae* with its layer of vascular tissue internally, derived apparently from the longitudinal muscles, while the inner layer is that

consisting of unstriated circular muscles. Noble (loc. cit.) considered "that the inner layer represents the sphincter ani cloacalis of other genera" and the outer layer "is apparently a portion of the sphincter ani cloacalis which has become attached ventrally to the ischium and dorsally to the skin" and "seems to be a muscle . . . found very pronounced in *Scaphiopus* and *Rhinophrynus*". This muscle Noble designated the ischio-cutaneous. De Villiers (1934a) identified the outer layer as the *mm. compressores cloacae*, and the name is adopted here in preference to sphincter ani cloacalis (which may be more correct) as the muscle is a cloacal compressor and not an anal sphincter.

#### *Sphincters:*

De Villiers (1934a, p. 40) remarked that "In spite of very careful searching, no sphincters were found at the cloacal opening or at the boundary between coprodaeum and urodaeum, or at the neck of the bladder". The *mm. compressores cloacae* in the region just behind the pelvic girdle closely encircle the cloaca and clearly serve as a sphincter. Just anterior to the boundary between coprodaeum and urodaeum the lumen of the former narrows posteriorly and is further restricted by folding of the epithelium. In this region there is a urodaeal diverticulum (fig. 10, level D; fig. 14), not present in *Leiopelma*, *Rana*, or *Xenopus*, whose floor bounds the coprodaeum dorsally and includes the circular muscle layer of the latter, which layer is very thick at this level. The floor of this short diverticulum, with its muscles, divides posteriorly into two lateral folds which continue in an obliquely ventral direction. The circular muscle layer posteriorly becomes thin and incomplete dorsally, with a thick portion mediad directed dorso-ventrally across each of the lateral folds. Examination of a model of the coprodaeum, urodaeum and bladder shows that it is possible for contraction of the thick circular muscles to reduce the already narrow lumen to such an extent that it is only necessary for the two lateral folds to be more deeply folded and applied to each other by contraction of the dorso-ventral muscles across them (thus extending the dorsal partition) for the lumen to be reduced to negligible proportions. Because the circular muscle layer further posteriorly is continuous ventral to the neck of the bladder, it is possible for that its contraction may result in the obliteration of the already narrow lumen of the bladder by dorso-ventral compression against the wall of the coprodaeum.

#### *Stratum proprium, Epithelium and Proctodaeal Glands:*

As in the coprodaeum, the stratum proprium of the cloaca lies in close contact with the circular muscle layer surrounding it. Posteriorly, where the circular muscle layer is replaced by cavernous tissue, the stratum proprium is closely encircled as far as the posterior edge of the ring of proctodaeal glands. Behind this ring the cavernous layer becomes detached, except for cutis bridges, first laterally and then dorsally. (Compare figs. 19, 20 and 21 with 22 and 23; see figs. 28 and 29). Beyond the cloacal opening the stratum proprium is continuous with the cutis of the skin ventrally.

At the level of the anterior tips of the bladder the coprodaeum is lined with a thin glandular epithelium which posteriorly becomes thicker and



folded (compare figs. 11—13 with fig. 14) as the lumen narrows towards the opening of the bladder. Of the 10—12 folds (fig. 14) several disappear just anterior to the opening of the bladder owing to the smallness of the lumen. The epithelium of the bladder is complexly folded, particularly anteriorly (figs. 11 and 12), giving the bladder the appearance of a highly active gland. There are frontal septa projecting into the two caeca of the bladder from their anterior and posterior walls and greatly increasing the epithelial surface (fig. 12). The septa contain muscle fibres which could considerably reduce the lumen of the bladder by their contraction. Anteriorly each half of the bladder folds around the posterior tip of the testis of that side (figs. 10 and 11). The cloacal epithelium undergoes little change until the region of the proctodaeal glands is reached. Up to this point there are numerous goblet cells, but the epithelium within the ring of proctodaeal glands changes sharply into a cornified epithelium with no goblet cells (figs. 26 and 27, 20 and 10).

Examination of *Ascaphus* larvae 5 and 6 showed that the proctodaeal glands arise as involutions of the epithelium of the cloaca after the pelvic girdle halves have fused and perichondral ossification of femurs and ilia is well under way. These glands were first observed by Noble (1925, p. 16—17), who reported as follows: "In the male a ring of enlarged cloacal glands is formed well inside the orifice of the 'tail'. A cluster of horny spines is found inside the cloaca just posterior to the enlarged glands". De Villiers (1934a, p. 35—36) noted: "Towards the tip of the tail, tubular dermal glands of the proctodaeum make their appearance (Fig. 8), and reach an enormous development. They are unbranched tubular glands consisting of a very high epithelium, whose nuclei are located at the base of the cells, whereas the cytoplasm, directed towards the lumen of the tubule, consists of fine fibrillae; goblet cells are entirely absent. The histology of the glands is in many respects reminiscent of that of the 'Rachendrüse', which also shows the fibrillation of the cytoplasm. The glands are not in open communication with the cloaca, but are each provided with a short narrow ductlet, the epithelium of which is short and lacks any fibrillation noted in the large tubules, which they place in communication with the cloaca". The ducts are directed backwards (fig. 28) and open usually in the grooves of the epithelium. There are 19 openings on the right side of the cloaca of the male represented in fig. 28, and these ducts carry the products of some 30 lobules; there is thus some branching (figs. 10 and 28), mostly in the longitudinal planes and well seen in longitudinal sections.

De Villiers (1934a, p. 36) observed that spines were absent in his specimen and suggested "that the spines described by Noble are bulges made on the cloacal wall by the large dermal glands". As spines were found in the specimen sectioned longitudinally, a careful search was made in the males sectioned transversely and in Prof. de Villiers's specimen (which was also sectioned transversely). The result was that spines were found in all these specimens, and were most distinct in the juvenile male but scarcely discernible in Prof. de Villiers's specimen. These spines consist of paraboloidal projections of the stratum germinativum covered by a stratum corneum — thicker than that of the general epithelium of this region — which is sometimes raised into a ventro-laterally-curved spine. The spines occur in clusters (fig. 42) on the edges of the most ventrally situated ridges of the cloacal epithelium (fig. 27).

They are deeply pigmented in the specimen sectioned longitudinally, somewhat less in the juvenile male, and scarcely at all in the other two males examined. The form is similar to that of stimulatory papillae such as those that have been described by Groenewald in work as yet unpublished on *Cercopithecus*, *Galago* and some human penes, and by Hill (1946) on the penis of *Pan*. Noble (1931) mentions the presence of horny spines in the cloaca of some *Gymnophiona*.

#### *Müllerian ducts in the Males of Ascaphus and Leiopelma:*

De Villiers (1934a, p. 39) observed: "The vestigial Müllerian duct, present in male Gymnophiones and Urodeles, is absent in *Ascaphus*, in spite of Noble actually figuring it in his diagram of the male urinogenital system of the genus ('Biology of the Amphibia', 1931)". In Prof. de Villiers's specimen and in the juvenile male there are no signs of Müllerian ducts; but in the other male very distinct vestigial Müllerian ducts were observed ventro-lateral to the Wolffian ducts and opening behind the urino-genital sinus into a small vesicle in the median dorsal ridge of the cloaca. This vesicle does not open into the cloaca and does not have the distinctive type of epithelium of the Wolffian and Müllerian ducts. Anteriorly the ducts become indistinct and disappear before the Wolffian ducts reach the kidneys, whereas Noble (1931) illustrated them as continuing along the sides of the kidneys. In the single specimen of *Leiopelma* examined there were very distinct Müllerian ducts which were traced from the urinogenital sinus to the caudad tip of the kidneys and a short way beyond.

#### *Lymph spaces associated with the Cloaca:*

De Villiers (1934a) noted that "The 'tail' is separated from the skin by large subcutaneous lymph spaces . . ." and that posteriorly "The subdermal lymph spaces undergo gradual diminution". (p. 36). There are fundamentally two lymph spaces in the "tail", a very large dorsal sac and a smaller ventral one, and these are subdivided posteriorly by bridges between the cloaca and skin. These lymph spaces correspond to the sacci interfemorales of *Rana*, (saccus periproctalis of Jourdain, see Gaupp) being dorsally separated from the saccus cranio-dorsalis by a sheet of connective tissue behind the urostyle and corresponding to the septa glutaealia superficialia of *Rana* (figs. 10, 17 and 18). Gaupp (1899, p. 490) noted of the saccus interfemoralis: "Die proximale Begrenzung des Sackes ist die eigenthümlichste. In der Hauptsache wird sie gebildet durch das Septum interfemorale. Da dieses aber am Ventralumfang des *M. sphincter ani* aufhört und dorsal vom Rectum (gewöhnlich!) keine Fortsetzung erhält, so bildet auch der laterale Umfang des *M. sphincter ani* einen Theil der proximalen Begrenzung des *Saccus interfemoralis*, und dorsal von der Cloake gehen die Sacci beider Seiten in einander über. . . . Hier, am Dorsalumfang des Rumpfes, bildet dann das *Septum glutaeale superficiale*, lateral bis zum *Septum femorale intermedium*, die proximale Begrenzung beider *Sacci interfemorales*. Ventral reicht der *Saccus interfemoralis* proximalwärts bis zum *Septum inguinale superficiale*. Aber auch hier gehen die Interfemoralsäcke beider Seiten in einander über, da das *Septum interfemorale* nicht vollständig ist. Am Dorsalumfang des Schenkels wird der *Saccus interfemoralis* durch das *Septum femorale intermedium* vom

*Saccus suprafemoralis* getrennt, ventral durch das *Septum femorale inferius* vom *Saccus femoralis*". Apart from the absence of that part of the septum interfemorale which attaches to the posterior face of the pelvic girdle in *Rana* the situation is similar in *Ascaphus*. Gaupp (loc. cit.) notes further: „Der *Saccus interfemorale* wird durch ein *Septum intrasacculare* unvollständig in zwei Etagen eine *Pars ventralis* und eine *Pars dorsalis*, getheilt. Dieses *Septum intrasacculare* spannt sich zwischen der Oberfläche des *M. gracilis minor* und der Haut am medialen Umfange des Oberschenkels aus". This septum apparently corresponds to the connective tissue by means of which the mm. compressores cloacae and vascularized cords attach laterally to the skin in the "tail".

De Villiers (1934a, p. 40) describing the cloaca, observed: "There is a layer of circular muscle followed by a layer of longitudinal muscle of varying thickness and characteristically thrown into folds. Longitudinal and circular layers are apparently separated by lymph spaces traversed by strands of connective tissue, containing blood vessels". Posteriorly these lymph spaces are eliminated by the close approximation of the longitudinal and circular muscle layers where the cloaca turns horizontally. The gliding planes are apparently enlargements of these lymph spaces still further posteriorly, since they separate the circular muscle layer from what is apparently the longitudinal layer, represented by a vascular layer on the inner side of the mm. compressores cloaca.

Noble (1931, p. 196—197) observed: "In the primitive *Ascaphus* there may be three pairs of lymph hearts near the coccyx . . .". There are four distinct pairs in the specimen examined, and these lie in the sacci iliaci (fig. 15), with which the lymph space of the "tail" is in communication via narrow canals bounded by the septa glutaealia superficialia dorsally, the septa glutaealia profunda laterally, and the mm. pyriformes and mm. caudalipuboischiotibiales ventrally (figs. 16 and 17). The tissue surrounding the posterior lymph hearts contains a venous plexus.

Some of the larger lymph spaces have been labelled in the sections (figs. 11—25).

#### Blood Vessels of the Cloaca (figs. 30 and 31; 30B and 31B; 26 and 27):

Gaige (1920) was the first to notice in breeding males that "the underside of the 'tail' is greatly congested" (p. 5). Noble (1922, p. 34) observed: "It is obviously highly vascular and turgid with blood, for the unpigmented ventral surface is of a pinkish hue", and Slater (1931) stated: "The color at the base of the tail and the tail itself is reddish brown, indicating a rich blood supply". Noble and Putnam (1931, p. 99) referred to "two pairs of vascular pads extending the long axis of the structure under the skin on its ventral surface". De Villiers (1933 and 1934a) has given the only fairly detailed information on the blood supply and vascular tissue of the "tail". In the latter work, on p. 34, in discussing the vascular strands lateral to the mm. compressores cloacae, he noted: "At certain spots the blood plexus pierces the muscular capsule, and in this way the tissue surrounding the cloaca, and that lining the muscular capsule are very intensely vascularised. . . . The arterial blood unquestionably comes partly from the arteria mesenterica posterior,

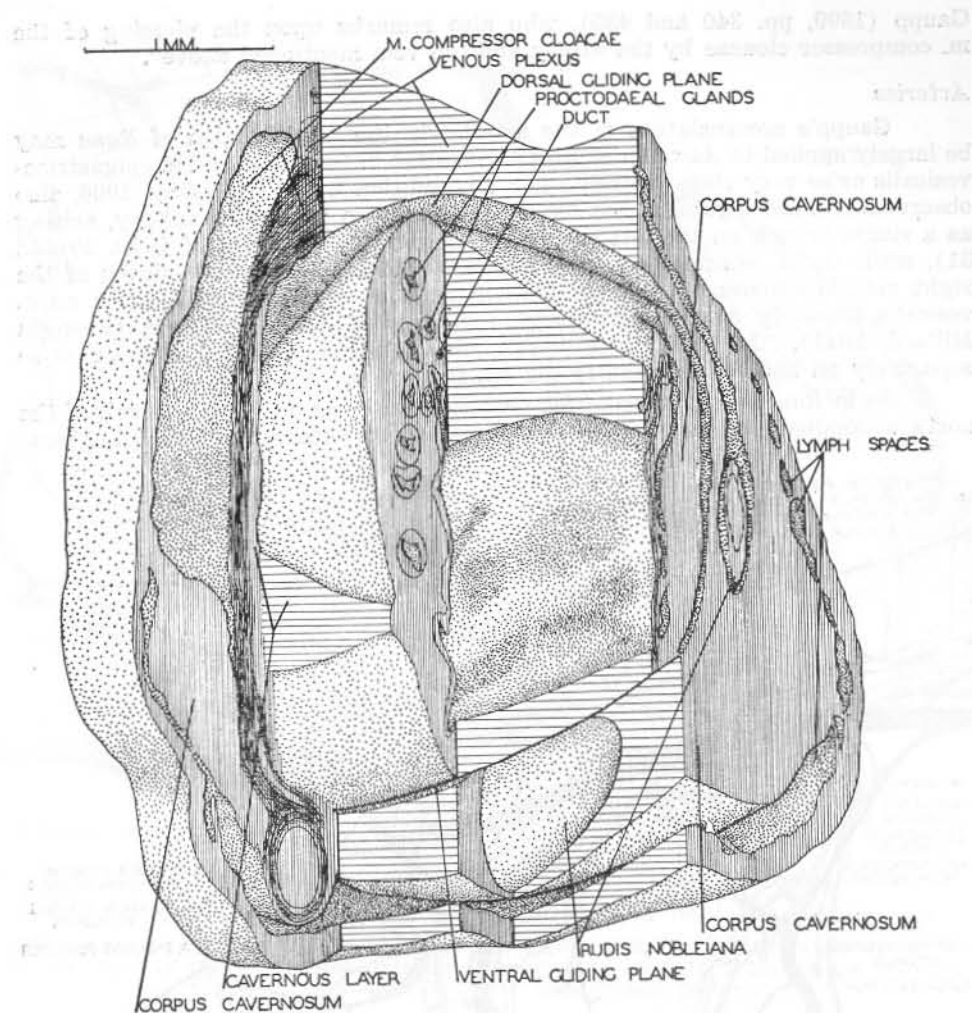


FIG. 29. Postero-Lateral (30°) Stereogram of the Posterior Part of the Phallosome during Erection. (25 x).

which, as in *Rana*, arises from the aorta between the posterior ends of the kidneys, and may be observed in several of the drawings. But the main source of arterial blood is from the ramus haemorrhoidalis posterior of the r. pudendus anterior, which comes from the glutaeal branch of the a. ischiadica. Rostral to the posterior end of the pelvic girdle, a capsule enclosing a vein, an artery and some branchlets of the nervus ischiadicus may be seen lying ventral to the m. pyriformis. The artery is the ramus haemorrhoidalis posterior and the vein is the vena pudenda, a branch of the posterior root of the vena ischiadica. These details are in most respects similar to those described for *Rana* by

Gaupp (1899, pp. 340 and 435), who also remarks upon the piercing of the m. compressor cloacae by the artery and the vein mentioned above".

#### Arteries

Gaupp's nomenclature of the arteries in the pelvic region of *Rana* may be largely applied to *Ascaphus*. In *Ascaphus* the a. femoralis and a. epigastrico-vesicalis arise very close to each other (a condition which Crawshaw, 1906, also observed in a *Rana hexadactyla* female) and tend to lose their identity, arising as a single branch on the left side of the specimen reconstructed (figs. 30 and 31), while the a. vesicalis dorsalis branch of the a. epigastrico-vesicalis of the right side is apparently associated with the a. femoralis. In *Xenopus* an a. vesicalis similarly arises from the a. femoralis of each side near its origin (Millard, 1941). In Prof. de Villiers's specimen the vesicular arteries arise separately on both sides close to the aa. femorales.

As in *Rana*, an a. mesenterica posterior arises as a visceral branch of the aorta abdominalis a short distance anterior to its bifurcation into aa. iliacae

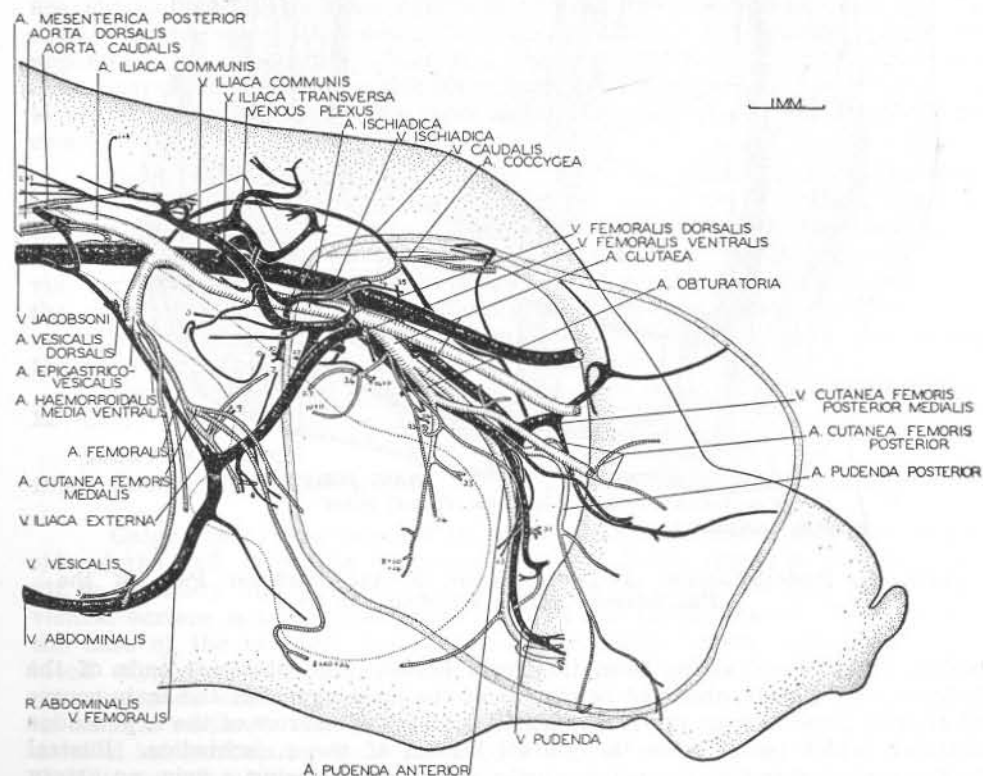


FIG. 30. Left Lateral Aspect of the Blood Vessels of the Pelvic Region. (10 x). O indicates blood vessels of the skin, 1-27 those of the muscles so numbered in the text. Male Adult. Same Specimen as figs. 1-28, 31-41.

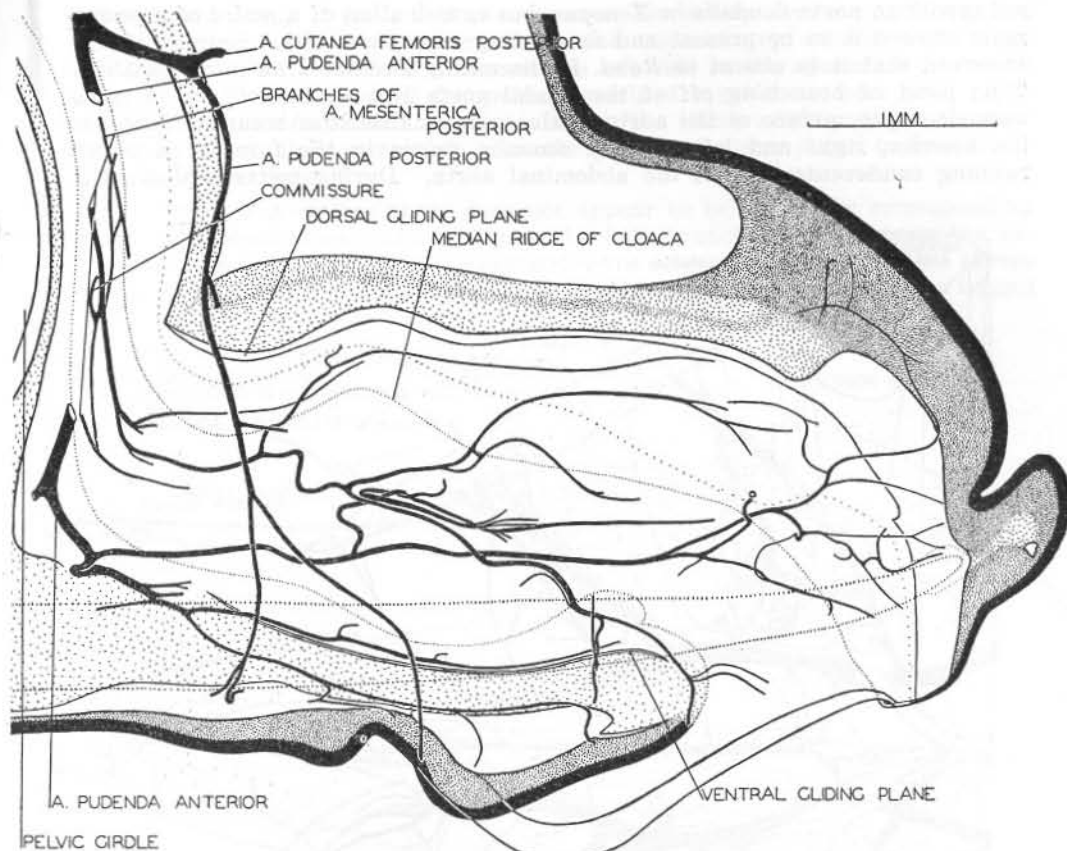


FIG. 30B. Left Lateral Aspect of the Arteries of the "tail". (25 x).

The arteries are represented in black in this figure, whereas the veins are black in fig. 30. Part of the a. pudenda anterior is omitted to show the commissure between it and the branches of the a. mesenterica posterior.

communes and gives off branches anteriorly and posteriorly to the cloaca. The posterior branches come to lie medially to the circular muscle layer in the stratum proprium and continue into the "tail", at the base of which they anastomose with the aa. pudendae anteriores (figs. 31, 30B and 31B). Szarski (1947) reported the absence of the a. mesenterica posterior (caudal mesenteric artery or a. mesenterica caudalis) in *Bombina bombina* and *Bufo bufo*, and its presence in three of six specimens of *Pelobates fuscus*. Dorsal to the aorta abdominalis there is a branch apparently corresponding to the parietal branch designated aorta caudalis (or a. sacralis media) by Szarski, who noted its presence in *Pelobates fuscus*, *Bombina bombina* and *Bufo bufo*. Klinckowström (1894) also describes it in *Pipa americana* where it attains the greatest development among the *Anura* according to Szarski. Millard (1941) does

not report an aorta caudalis in *Xenopus*, but examination of a series of a young male showed it to be present and originating asymmetrically. Szarski (1947) observed that it is absent in *Rana*. In discussing *Pelobates* he says (p. 152): "The point of branching off of the caudal aorta lies on the left, or in some animals, right surface of the aorta." He explains that it is because "both the ilic arteries, right and left, have a common origin in the form of a vessel running caudoventrad from the abdominal aorta. During metamorphosis the

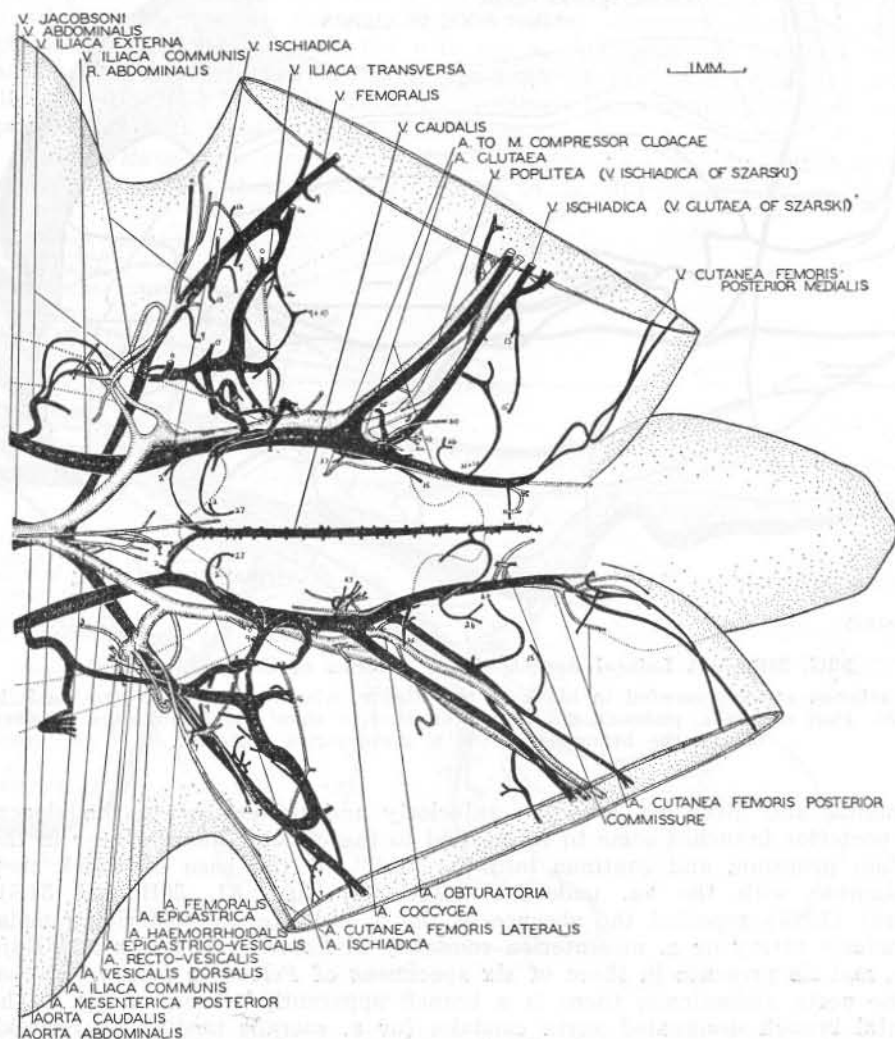


FIG. 31. Dorsal Aspect of the Blood Vessels of the Pelvic Region, (10 x).  
For the interpretation of the numbers see fig. 30.

pelvic arch moves dorsad, and the common ilic artery forms a prolongation of the abdominal aorta, pushing aside the rudimentary caudal aorta". In *Ascaphus* the aorta caudalis arises on the left side in the specimens examined (fig. 31). The specimen of *Leiopelma* examined appears to have both an a. mesenterica posterior and an aorta caudalis, the latter arising medio-ventrally from the left a. iliaca communis. Szarski (1951) was later found to have made similar observations.

Since in *Ascaphus* there does not appear to be an artery corresponding to the a. vesiculae seminalis of *Rana*, the only branches arising from the aa. iliaca communes are the aa. epigastrico-vesicales and aa. femorales. From the a. ischiadica of each side an a. coccygea arises as in *Rana*; then just behind

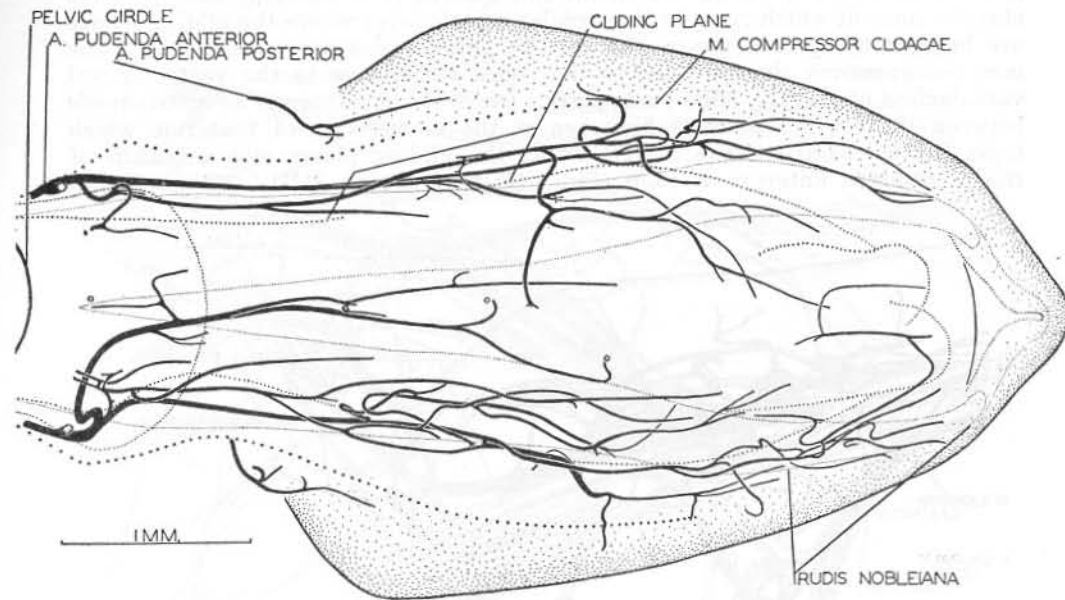


FIG. 31B. Dorsal Aspect of the Arteries of the "tail". (25 x).  
The arteries are represented in black in this figure, whereas the veins are black in fig. 31.

the level of the origins of the m. ileo-femoralis and m. ileo-fibularis the a. glutaea arises and curves medio-ventrally from the a. ischiadica (figs. 30 and 31), beneath the nervus ischiadicus. The first large branch to separate from the a. glutaea is the a. obturatoria, in contrast to *Rana*, in which the latter is terminal. (Gaupp, 1899, fig. 99). A small branch passes medially and anteriorly from the a. glutaea to penetrate and supply the m. compressor cloacae in the region of the lymph hearts. This may correspond to the r. anterior of the a. pudenda anterior of *Rana*, although in the latter it apparently lies superficially on the m. compressor cloacae and supplies the tissues near the lymph hearts. Behind the pelvic girdle the a. pudenda anterior arises ventral to the a. glutaea and stretches along the side of the cloaca. A small branch

arises from the a. pudenda anterior medially on each side of the specimen reconstructed and penetrates the m. compressor cloacae of that side to anastomose with branches of the a. mesenterica posterior (fig. 31, 30B and 31B). Similar conditions obtained in Prof. de Villiers's specimen. The main stem of the a. pudenda anterior lies along the side of the cloaca up to a point near the rudis Nobleiana where it penetrates the m. compressor cloacae and divides into branches passing backwards along the inner surface of this muscle. A small branch is given off anteriorly at the point at which the m. compressor cloacae is penetrated and supplies the m. compressor cloacae ventral to the pelvic girdle. The aa. pudendae anteriores are the chief vessels supplying blood to the cloaca; some of the blood is conveyed through the anastomoses with the branches of the a. mesenterica posterior to the circular muscle layer, but the main route is via the branches on the inner surfaces of the mm. compressores cloacae, some of which cross to the circular muscle layer where the gliding planes are bridged by fibrous tissue (fig. 31B). Others pass outwards through the mm. compressores cloacae close to the rudis Nobeliana to the ventro-lateral vascularized cords (fig. 30B) posteriorly. On both sides there is an anastomosis between the continuations of branches of the a. mesenterica posterior which cross the connective tissue bridge across the gliding plane, and a branch of the a. pudenda anterior of each side. (Figs. 30B and 31B). The branches

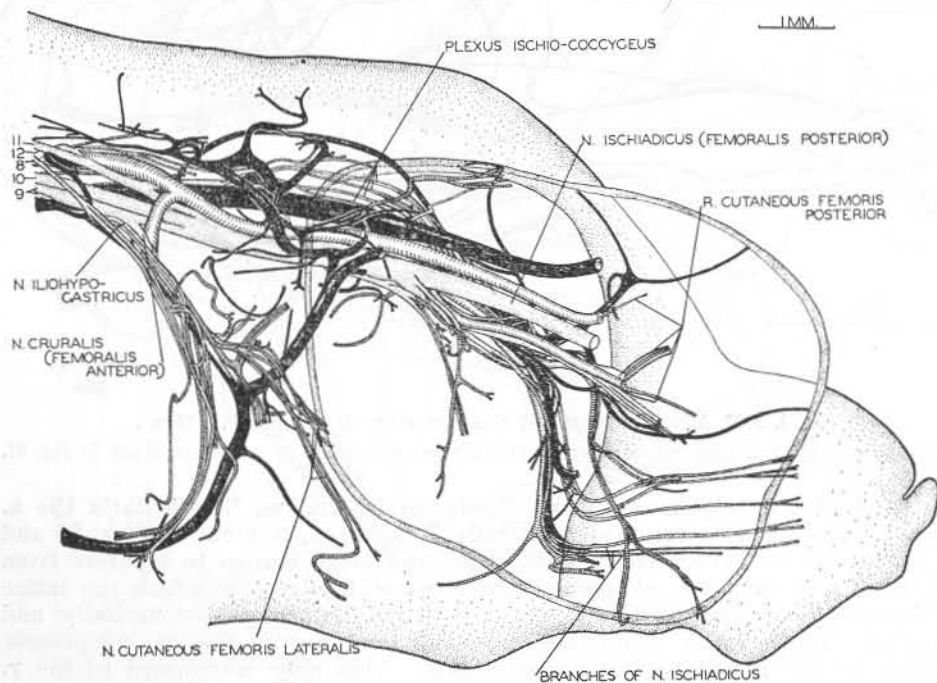


FIG. 32. Left Lateral Aspect of the Nerves of the Pelvic Region. (10 x).  
The spinal nerves are indicated by large numbers.

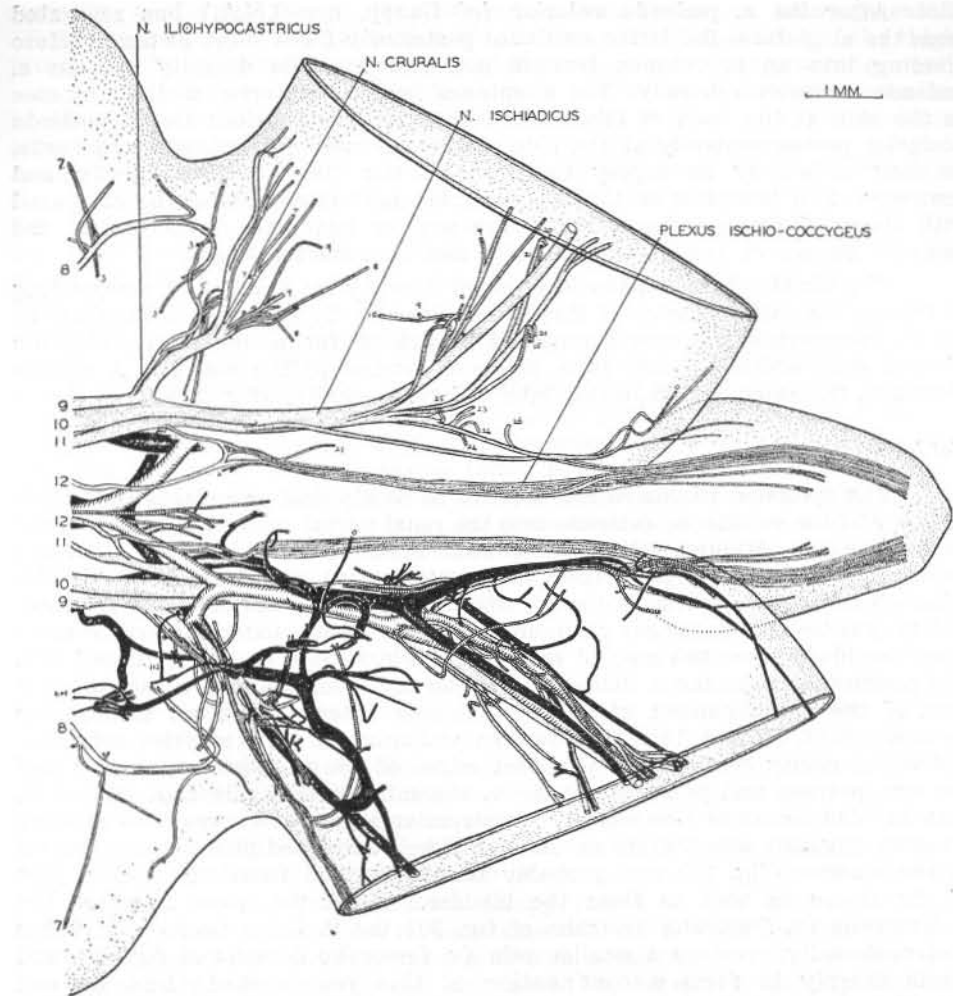


FIG. 33. Dorsal Aspect of the Nerves of the Pelvic Region. (10 x).

The spinal nerves are indicated by large numbers. For the interpretation of the small numbers see fig. 30. The plexus ischio-coccygeus is represented somewhat diagrammatically in view of the superimposition of nerves in the same plane.

of the aa. pudendae anteriores in *Ascaphus* cannot easily be compared with those in *Rana*, as the three primary branches of the a. pudenda anterior in *Ascaphus* correspond to the r. musculares and r. haemorrhoidalis posterior of *Rana*. The branch supplying the portion of the mm. compressores cloacae projecting ventral to the pelvic girdle seems comparable to the r. musculares, but the rest can scarcely be called the r. haemorrhoidalis posterior, as the latter also supplies the posterior part of the bladder in *Rana*, and in *Ascaphus* is separated from it by the pelvic girdle.

After the a. pudenda anterior (of Gaupp, non-B.N.A.) has separated from the a. glutaeta, the latter continues posteriorly for a short distance before dividing into an a. cutanea femoris posterior medialis dorsally and an a. pudenda posterior ventrally. The a. cutanea femoris posterior medialis crosses to the skin at the back of the femur before further division; the a. pudenda posterior passes ventrally at the side of the ventro-lateral vascularized cords, dividing ultimately to supply the skin of the "tail" ventro-laterally and ventrally. The branches of the aa. pudendae posteriores cannot be compared with those of *Rana* and apparently are not, or but little, concerned in the vascular supply of the cloacal muscles and vascularized cords.

The bladder in *Ascaphus* is supplied dorsally by branches corresponding to the aa. vesicales dorsales of *Rana*, and ventrally by branches comparable to the a. haemorrhoidalis media ventralis branch of the a. epigastrico-vesicalis of each side, which together form a plexus ventral to the bladder. A venous plexus in the same region drains into the vv. vesicales. (fig. 12).

#### Veins:

The specimen reconstructed appears to be atypical as regards the points of entry of the vv. iliacae externae into the renal portal system, for these veins, as in *Xenopus* (Millard, 1941), enter what must be called the vv. Jacobsoni anterior to the caudal tips of the kidneys. (Compare figs. 30 and 10). In the other specimens the course of the vv. iliacae externae is less obliquely forward, and they enter the vv. iliacae communes. The vv. iliacae externae receive roots from the bladder, on the mediad surfaces of which they lie (figs. 30 and 31). The junction between the v. iliaca externa and the v. femoralis is on the anterior face of the thigh caudad of the m. obliquus externus and m. transversus (compare figs. 30 and 34). The two rr. abdominales vv. femorales enter the abdominal cavity between the posterior edges of the m. rectus abdominis and the mm. pectinei and join to form the v. abdominalis (compare figs. 30 and 31 with 34) (as occurs in *Leiopelma*). They receive a pair of vv. vesicales at their junction (fig. 30) which drain an extremely well-developed plexus lying ventral to the bladder (fig. 12) and probably receiving blood from the ventral part of the cloaca as well as from the bladder. From the main trunk of the v. femoralis (v. femoralis ventralis of fig. 30) the v. iliaca transversa curves postero-dorsally, receives a smaller vein (v. femoralis dorsalis of fig. 30) and bends sharply to form a continuation of this vein mediad (figs. 30 and 31). In the region of the lymph hearts the main part of the v. iliaca transversa of each side turns anteriorly and receives a number of veins from a plexus round the lymph hearts and from the region lateral to the m. coccygeo-iliacus (see figs. 30 and 34; 31 and 35), then turns sharply caudad and curves mediad to enter the v. iliaca communis, receiving further veins posteriorly. On both sides of the specimen reconstructed there is a bridge across the V-shaped portion of the vv. iliacae transversae (figs. 31 and 30). In *Bufo*, *Bombina* (Szarski, 1947) and *Xenopus* (Millard, 1941) the v. iliaca transversa is not connected with the veins of the thigh as it is in *Rana* (Gaupp), *Pelobates* (Szarski, 1947) and *Ascaphus*. Szarski (op. cit., p. 192) remarked: "The short segment of v. iliaca transversa situated between the posterior lymph hearts and the opening of the veins into the common iliac vein is homologous in all animals, as it is developed from v. caudalis lateralis of the tadpole in the

majority of forms, or, in the fire-bellied toad from v. intersegmentalis (Fedorowicz 1914). The connection of this segment with the veins of the thigh, present in the spade-foot toad and the edible frog, is a secondary arrangement".

Dorsal to the cloaca in the three male specimens of *Ascaphus* examined in transverse section, there is a well-developed median vein which drains anteriorly into the vv. iliacae communes by means of branches lying in association with the Wolffian ducts and better developed on the left side of the specimen reconstructed (figs. 31, 30 and 35). De Villiers (1934a) observed this vein which is illustrated in his Fig. 9C, where it is labelled "vein". This vein is clearly that designated v. caudalis by Szarski (1947), who noted (p. 163) that in *Pelobates* it "arises from the union of branches collecting the blood from m. sphincter ani, on the dorsal side of the cloaca. It runs cranial along the middle line of the body, over the ventral surface of m. coccygeo-sacralis, reaches the caudal margin of the kidneys, bends laterad and joins one of the common iliac veins. In three animals the caudal vein opened into the left common iliac veins and in one to the right". In the same work (p. 165) he observed: "Three salientians described above retain in the adult condition the caudal vein (*P. fuscus* Laur., *B. bombina* L. and *B. bufo* L.), in *R. esculenta* L. only this vessel is absent. It was not however hitherto been described in any adult salientian. In connection with this fact it is worth mentioning that Bhaduri (1938) found the caudal vein in a specimen of *Rana catesbeiana*, but lacking the comparative material was unable to interpret this fact correctly". Examination of a series of a young *Xenopus* male revealed a small median vein between the Wolffian ducts; it enters the caudal tip of the kidney close to the posterior abdominal vein. This vein is presumably a caudal vein, although Millard (1941) does not report its presence. The specimen of *Leiopelma* examined has a v. caudalis much less developed than that of *Ascaphus*. The v. caudalis of the urodeles is very similar to that of *Ascaphus* in its relations to the v. ischiadica and v. Jacobsoni (see Francis, 1934; Millard, 1941). In the females of *Ascaphus* examined there is a vein dorsal to the cloaca which continuous dorsal to the tissue containing the ureters and Müllerian ducts, but it is difficult to decide without making graphic reconstructions whether it is merely one of the oviducal veins or a v. caudalis.

Of the vv. pudendae of *Rana* Gaupp (1899, p. 435) stated: "In den Endabschnitt der V. ischiadica münden eine oder zwei Venen ein, die aus dem M. compressor cloacae kommen und von diesem, sowie von dem M. sphincter ani, Blut aufnehmen. In sie ergiessen sich noch Vv. haemorrhoidales posteriores von der Schleimhaut des hinteren Rectumabschnittes". Of the v. cutanea femoris posterior medialis he states (loc. cit.): "Kommt von der Haut am medial-dorsalen Umfange des Oberschenkels und dringt zwischen M. semimembranosus and M. piriformis in die Tiefe zur V. ischiadica". In *Ascaphus* there is on either side a single vein which can be compared to the v. pudenda of *Rana*. This lies parallel to the a. pudenda anterior and joins a vein from the skin of the back of the femur, comparable with the v. cutanea femoris posterior medialis, at a point near the place where the a. pudenda anterior arises from the a. glutaeta. The roots of the v. pudenda lie close to the branches of the a. pudenda anterior on the medial surface of the m. compressor cloacae but cannot be traced far back. A tributary to the right v. pudenda drains the vascular tissue between the rudes Nobleianae (fig. 31), the rest of the "tail" being drained by sinuses into the vv. pudendae.

Gaupp's nomenclature of the veins of the thigh has been followed, but, as Szarski remarked of *Rana*, "The vein parallel to the artery and nerve *V. ischiadica* is absent. The vein described by Gaupp under this name does not follow the artery and nerve, but returns blood from the dorsal (posterior) muscles of the thigh and accompanies *a. glutaea*. I therefore give it the name *v. glutaea*. *V. femoralis ventralis* is absent. *V. femoralis dorsalis* named more shortly *v. femoralis* is strongly developed". (op. cit., p. 189—190). Since the *a. ischiadica* has a vas comitans in *Ascaphus*, Szarski's nomenclature has been added in fig. 31. Likewise in fig. 30, a *v. femoralis ventralis* and a *v. femoralis dorsalis* are distinguished. In *Ascaphus* it is the more ventral of the femoral veins which is the more strongly developed, whereas in *Pelobates* it is the dorsal; in *Bufo*, *Bombina* and *Rana* the ventral is absent (Szarski). In *Ascaphus*, as in *Pelobates* (Szarski) and *Xenopus* (Millard; Grobbelaar, 1924b) "the main blood-stream from the lower leg flows into the post-axial vein or *V. ischiadica*, and not into the *V. femoralis* as in *Rana*". (Millard, on *Xenopus*; op. cit., p. 432). Grobbelaar (1924a), quoted also by Millard (1941), regards the condition in *Xenopus* as primitive and states that "the femoral vein in *Rana* has only secondarily become the important blood-vessel which it is". Szarski reported both the *v. femoralis* and *v. ischiadica* to be well-developed in *Bombina*, and the condition in *Bufo* to be like that in *Rana*. A vein apparently corresponding to Szarski's *v. pubica* joins the *r. abdominalis v. femoralis* (figs. 30 and 34; 31) in *Ascaphus*.

#### *Sinuses:*

The direction in which the blood flows in the sinuses in the "tail" is difficult to conceive. The dorsal venous plexus (figs. 22 and 23) is continuous caudally with the ventro-lateral vascularized cords (figs. 24 and 25) and these, together with the vascularized cord associated with the circular muscle layer and the vascular tissue on the medial surfaces of the *mm. compressores cloacae*, clearly carry blood cranial. The direction of the blood in the anterior parts of the ventro-lateral vascularized cords is probably backwards, but this is by no means certain.

#### *Nerves of the Cloaca* (figs. 32 and 33; 26 and 27):

E. M. Stephenson (1952) found the sacral plexus of *Leiopeltis* to consist of the 9th—13th spinal nerves. In *Ascaphus* there appear to be only four spinal nerves participating in the sacral plexus and these are presumably the 9th—12th (as labelled in figs. 32 and 33). On the left side the 9th spinal nerve gives off the *n. iliohypogastricus* and the *n. cruralis* before fusing with the 10th, the configuration being like that designated  $\zeta$  by Adolphi (1893 and 1895). On the right side the 9th gives off these nerves at the point at which it meets the 10th spinal nerve, Adolphi's configuration  $\delta$ .

The plexus ischio-coccygeus is derived from the 11th and 12th spinal nerves. On the left side these nerves are first connected by a strand stretching between them, then the branch of the 11th to the plexus ischio-coccygeus is given off, and further caudally the 11th then meets the 10th nerve. On the right side the branch of the 11th to the plexus ischio-coccygeus is given off more cranial, and the connexion between this branch and the 12th is caudad of

this at about the level where the 10th and 11th nerves meet. The plexus ischio-coccygeus supplies the dorsal part of the cloaca in the "tail" region, while the ventral part is supplied by two branches from the *n. ischiadicus* (figs. 32 and 33). Of these one arises dorsally from the 11th where this joins the 10th nerve, stretches along the side of the cloaca in association with an artery and vein supplying and draining the *m. compressor cloacae* in this region, and comes to lie ventral to the *v. pudenda* between this vessel and the *a. pudenda anterior* ventrally. The other branch originates from the *n. ischiadicus* more caudad and lies more laterad, coming to lie dorsal to the *v. pudenda* and giving branches which accompany the *a. cutanea femoris posterior* and *a. pudenda posterior*. It appears to be the *n. pudendus* of Appleton (1928). The nerves of the posterior part of the cloaca lie on the inner surfaces of the *mm. compressores cloacae*. A few branches cross to the ventral part of the median vascularized cord, while other branches penetrate the *mm. compressores cloacae* dorsally near the midline to supply the region of the dorsal venous plexus (fig. 27).

Each spinal nerve appears to arise by fusion of a dorsal and a ventral root within the neural canal. Sympathetic nerves could not be identified with certainty.

The innervation of the thigh muscles was investigated and found to be as in *Rana*, with the exception of the *m. iliacus internus* which is innervated by a branch of the *n. ischiadicus* in addition to a branch of the *n. cruralis*.

#### *Variations and Sex differences:*

The differences between the cloaca of the specimen reconstructed and that of Prof. de Villiers's specimen are largely attributable to a state of partial erection in the latter, but between these specimens (and the specimen sectioned longitudinally) and the juvenile male examined there are important differences, which are probably not attributable to the differences in age. The cloaca in the juvenile male resembles that of the other specimens up to the point where it turns ventrally behind the pelvic girdle. Here its ventral surface is more concave than that of the other specimens, and it curves completely under the pelvic girdle, then turns backwards into the "tail", folding completely double. The posterior margin of the lumen of this fold of the cloaca is a little behind the level of the tip of the urostyle, and cranial the lumen extends as a narrow diverticulum to a point considerably cranial of the caudal margin of the acetabulum. The cloacal glands extend anteriorly beyond the posterior margin of the pelvic girdle (compare fig. 10). There is no question of the differences being entirely attributable to differences in orientation, as can be seen by comparing figs. 10 and 42. Dorsally the skin curves backwards slightly in the region of the septum glutaeale superficiale (see fig. 42). The "tail" is apparently situated considerably more anteriorly and ventrally than in the other specimens.

In the females examined the cloaca dorsal to the pelvic girdle is very similar to that of the males in the same region. The longitudinal muscles attach dorsally to the ventro-lateral surfaces of the urostyle and ventrally there is an attachment to the pelvic girdle similar to that in the male. Towards the tip of the urostyle the *mm. compressores cloacae* close around the cloaca

as in the male, but the suspensory lamina is much thicker and more tendinous in nature, while the vein in the posterior margin of the lamina in the male is not found in the female. As in the male there is no septum interfemorale ventrally. The cloaca is directed slightly ventrally, but there is no fold comparable to that in the male (fig. 10), although its position is indicated by the a. pudenda anterior and v. pudenda, which turn sharply ventrally and penetrate the m. compressor cloacae as in the male. An a. pudenda posterior continues more obliquely ventrally, and both pudendal arteries are accompanied by nerves as in the male. The layers of longitudinal and circular muscles are thin, and posteriorly they become vascular, particularly the latter, as in the male. The mm. compressores cloacae, with their inner layer of vascular tissue derived from the longitudinal muscle layer, seem to be free from the circular muscle layer ventrally and dorsally cranial and dorsally and laterally caudad, the gaps formed corresponding to the gliding planes of the male. The mm. compressores cloacae become extremely thick dorsally caudad and contain pigment. At the point at which the rudes Nobleianae fuse with the cloaca they are close together as in the male. The muscular tissue extending between the rudes as they separate caudad is distinctly different from the rest of the mm. compressores cloacae with which it is continuous, and no striations were observed in this region. The ventral edges of this apparently unstriated muscle layer extend into a membrane which attaches to the ventral skin, the septum femorale inferius, while the dorsal edges extend along the inner surfaces of the striated mm. compressores cloacae. Nowhere are there indications of intensive vascularization of the mm. compressores cloacae. Near the cloacal orifice the mucous lining of the cloaca gives way to a cornified epithelium and there are cloacal glands similar to those of the male, though much smaller, and with similar ducts. Since the vascular layer in which they lie is very thin, the glands fit closely between the folds of the epithelium of the cloaca. The cloacal orifice in the female is terminal, and not ventral as described by Noble and Putnam (1931); this fact was confirmed by a wax model of the posterior tip of the cloaca (see fig. 44). On either side of the cloacal orifice there is a fold of skin; the two do not meet ventrally or dorsally.

#### Function:

Van Denburgh (1912, p. 261) observed of the "tail" in *Ascaphus*: "It is possible that this 'tail' may be a sexual organ". Gaige (1920, p. 5) noted that in breeding males "the underside of the 'tail' is greatly congested". Noble (1922, p. 34-35) stated: "One would imagine, of course, that the 'tail' must be an intromittant 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". Noble (1925, p. 17) observed spermia in the oviducts of the females (which fact was confirmed in the present study) and observed: "A cluster of horny spines is found inside the cloaca just posterior to the

enlarged glands. When the 'tail' is turgid with blood the cloaca is slightly everted until the spines are exposed. This mechanism suggests that the tail is pressed against the cloaca of the female in copulation (as the cloaca of certain salamanders). Breeding specimens readily extend their 'tails' forward under the body until in the position to perform such an operation". Slater (1931) observed the mating of *Ascaphus* and noted: "When the male and female met, the male crawled on the female's back and clasped her around her body opposite the sacrum, not posterior to her fore limbs as most other Anura do. Whereupon the female straightened her hind limbs so that they extended posteriorly in the same general line of the body and held them so that they formed a narrow V. The male flexed his sacroiliac joint so that his pelvis made nearly a right angle with his vertebral column. Then by muscular manipulation bent his so-called 'tail' ventrally so that it made nearly a right angle to his pelvic girdle and brought it into position to transfer sperm to the female. This 'tail', when the male is in a natural position, points posteriorly, but with the two flexes mentioned above it comes to point anteriorly. The color at the base of the tail and the tail itself is reddish brown, indicating a rich blood supply". Noble and Putnam (1931, p. 98) remarked: "The very recent observations of Slater (1931) confirm the earlier observations of Noble but the question still remains of whether the cloacal appendage of *Ascaphus* actually serves as intromittent organ. Fortunately our field and laboratory observations have now definitely settled this question". According to their observations copulation is ventral as "The efforts of the male are apparently directed toward throwing the female on her back. In this position she falls into a state of tonic immobility, permitting the male to readily secure a body grip". They note (p. 99): "When the vascular system of the male *Ascaphus* is injected with a suitable medium the appendage can be greatly dilated, exposing the spines within the cloacal orifice. During copulation the appendage has never this form but remains narrow with a point formed by the tip and not by the spines of the orifice. Since the male with his appendage thrust within the cloaca of the female remains passive, the spines cannot serve as stimulating organs. It is possible that they assist the male in maintaining his position in much the same manner as the spines on the hemipenis of a snake function". Noble (1931) illustrated the normal appendage and the turgid appendage with exposed spines, and remarked (p. 283): "In *Ascaphus*, one of the most primitive frogs, the cloaca is extended into a highly vascular tube which may be bent forward by the contraction of the *rectus abdominis*". De Villiers (1934a) referred to this statement, and observed (p. 40): "The lowering of the insertible tip of the phallic organ is rendered possible by contraction of the m. compressor cloacae (cp. NOBLE, 1931, p. 283)".

The rudes Nobleianae, if they are not bones, would appear to function in a manner similar to the chorda dorsalis, i.e. by turgescence. The cells of the medulla of the rudes of the adults are very much larger than those of the larvae, particularly where the peripheral layer of the rods is thick, and it would seem that the cells of the medulla become turgid and thus maintain the form of the rudes Nobleianae by swelling against the resistance of the strong connective tissue of the outer layer.

The movement between vertebral column and pelvic girdle described by Slater could be brought about by contraction of the rectus abdominus muscle and antagonized by the mm. coccygeo-iliaci and the mm. compressores cloacae



dorsal to the pelvic girdle. The rotation of the rudes Nobleianae ventrally cannot be brought about by contraction of the m. rectus abdominis as implied by Noble (1931). It would seem that De Villiers (1934a) is correct in thinking that it is the portion of the m. compressor cloacae ventral to the pelvic girdle which moves the rudes Nobleianae since this is the only muscle inserting on them. Since the tendinous layer ventral to the rods attaches caudad of the insertions of the m. compressor cloacae dorsal to them, the tendinous layer can act as the fulcrum about which the rods rotate in the manner of a lever of the first order. The movement will be restricted by the retaining tendons and must be less than 90°. As regards the position of the female in copulation, the orifice of the cloaca being terminal and not on the ventral surface of a distinct tail (Noble to the contrary), copulation can probably be equally easy dorsally (as described by Slater) or ventrally (as described by Noble and Putnam). The form of the "tail" during copulation is presumably that which is assumed in the turgid condition, otherwise the function of the vascular tissue is difficult to explain. A wax model made of Prof. de Villiers's specimen showed that the cloacal orifice becomes terminal in the turgid appendage, sloping only slightly ventrally, while the fleshy tip becomes a fleshy protuberance dorsal to the orifice (as observed by De Villiers, 1934a). This movement of the orifice can also be seen in Noble's illustrations (1931). That the "tail" is in this condition during copulation is suggested by Noble and Putnam's references to the rôle in copulation of the horny spines, which are apparently only everted in the fully erect appendage. (Even in Prof. de Villiers's specimen the slight thickenings of the epithelium which represent the spines are still just within the orifice). Since the tip of the flaccid appendage has no canal or groove which could conduct spermia, its insertion into the female cloaca could scarcely be considered copulation. Since the turgid "tail" cannot be inserted into the cloaca (wax models on the same scale were compared) it must be assumed until further information can be obtained that the "tail" is merely applied to the cloacal orifice of the female.

The regulation of the blood supply to the "tail" in *Ascaphus* may be brought about in any of a number of different ways. Deysach (1939) distinguishes three possibilities: arterial regulation where the arterial supply is increased, venous regulation where the flow of blood in the main veins is decreased and "sluice valve" regulation where side branches of main veins are made to carry less blood. De Villiers (1934a) observed that the anterior slip of the m. compressor cloacae encircles the a. ischiadica, but not the v. ischiadica as well (as in *Rana*), and (p. 41) remarked on the possibility "that the muscle plays an important role in connection with the blood supply of the cloacal wall and consequent distension of the cavernous tissues". The a. ischiadica is certainly very much compressed by this muscle in the specimen reconstructed, and De Villiers illustrated its compression in his specimen in Fig. 9A. Hirsch (1931, p. 61) noted (for *Homo*) that "Cadiat in 1877 showed that the perineal muscles (m. ischio and bulbo cavernosi and m. transversus perinei) were incapable of exerting any constricting action on the penile arteries or veins because these vessels coursed through protected canals and did not pass through any site where the muscles could compress them". In *Ascaphus* the a. pudenda anterior and its commissure with the branches of the a. mesenterica posterior pass through the m. compressor cloacae and compression

by this muscle is a distinct possibility. Relaxation of the muscle would thus increase the flow of blood. Compression of the v. pudenda is equally possible since the a. pudenda anterior and the v. pudenda are vasa comitantia, and if both are compressed the vein is likely to be the more obstructed in view of the thinner muscle layer. This is particularly true in view of the sinus-like nature of the veins in the m. compressor cloacae.

Kiss (1921) reported funnel-like structures in the veins of the human penis (Trichtervenen) and attributed retarding function to them. Bargmann (1934) considered that they are of questionable significance and Deysach (1939) could not demonstrate them. Ercolani (1869) observed (to quote Hirsch, 1931, p. 61—62) that "the intima of the penile arteries was folded and projected into the lumen. This infolding he believed permitted great dilatation of the artery during sexual stimulation but decreased the lumen of the vessel during flaccidity and limited the inflow of blood". Ebner (1900), Ebert (1904) and Kiss (1921) concurred; Hirsch (1931) considered the folds to be pathological and Bargmann (1934) criticized his conclusions. Deysach (1939) could find no intimal thickenings in the arteries of the penis of any of the mammals studied, but reported a type of venous valve, which he termed sluice valves, at the entrances of side branches of the venae profundae into these veins in the animals which he examined and which lacked an os penis. In *Ascaphus* no intimal thickenings (Polsterarterien) were observed, although virtually every arteriole in the "tail" was examined throughout its traceable length. In view of the sinus-like drainage of the "tail" venous valves could not be detected and would be difficult to detect if present. It was observed that the arterioles gave way to lacunae which could be traced for some distance by virtue of the arterial nature of their walls, although they had sinus-like forms. The work of Conti (1952) on the mechanism of erection in the human penis arrived too late for detailed consideration. It is clear from the figures that "Polsterarterien" or similar structures are considered by Conti to be of importance. Although no reference is made to Deysach, structure similar to his "sluice valves" are also shown.

#### Homology:

Rauther (1909) investigated the copulatory organs of *Clinus* and Eggert (1931) the genital systems of the *Gobiiformes* and *Blenniiformes*, and both reported and illustrated copulatory organs consisting of projecting vascularized urino-genital papillae, Eggert also noting vascularization in the female. These copulatory organs are dorsal to the rectum and hence are not homologous with the copulatory organs of reptiles, birds or mammals, which are situated ventral to the cloaca or rectum.

Von Bedriaga (1878, p. 122) reported an investigation which he said "liess mich unter Anderem vermuthen, dass ein ausgeprägtes Begattungsorgan beim marmorirten Triton nachweisbar sei, dass ferner ein wirklicher Begattungsact, d.h. eine innere Befruchtung stattfindet, und das Anschliessen der Geschlechtstheile beider Geschlechter mittelst der warzigen, an den Wülsten der Cloake vertheilten Gebilde bei den Schwanzlurchen geschehe". He noted further (p. 122—123): "Inzwischen war die innere Befruchtung von anderen Forschern, z.B. von Wiedersheim für die ovipare Salamandrina perspicillata, sowie auch andererseits die Beihülfe der erwähnten warzigen Gebilde an die

Lippen der Cloake (brosses copultrices) bei dem Begattungsacte nachgewiesen worden". Blanchard (1881) observed that several authors had reported cloacal papillae in various urodeles and (p. 10) concluded: "On peut donc dès à présent annoncer que la papille cloacale se rencontre chez un très-grand nombre de Batraciens urodèles, sinon chez tous, et il suffira de la rechercher avec soin pour s'assurer de sa présence. La plupart des observateurs, partant de ce fait que certains Salamandres sont vivipares et que, par conséquent, la fécondation est interne, ont considéré la papille cloacale comme une sorte de pénis". He referred to Von Bedriaga's observations but cited (p. 11) observations of Gasco (1880) which indicated that the first spermatophore of Triton had been seen to be deposited without copulation and that further "Sorpesa, sedotta dallo spettacolo sessuale maschile, la femmina, che sin qui è stata immobile, si muove, s'avanza e vuol toccare e vuol fiutare la beante cloaca, che le sta dinanzi, il maschio a sua volta procede a piccoli tratti e solleticato dal muso della compagna compie ben presto una seconda ed anche una terza emissione seminale". Blanchard commented (p. 12): "Cette belle observation de Gasco démontre donc à la fois l'absence d'accouplement chez les Tritons et la manière dont se fait la fécondation chez ces animaux. Elle nous enseigne encore quel est le rôle probable de la papille cloacale, qui serait, non point un pénis, mais un organe particulièrement sensible et que la femelle viendrait frotter de son museau pour inviter le mâle à une nouvelle émission spermatique". Von Bedriaga (1881) referred to the observations of Gasco and Blanchard and concluded that his previous observations must have been of courtship, noting that Nauck confirmed the absence of copulation. Nauck observed: "Die Schwänze beider waren im Halbkreise gebogen und berührten sich mit den Spitzen, so dass das Paar die Gestalt eines S darbot. Während die so verbundenen Schwänze lebhaft hin und her vibrirten, sah man die Kloake des Weibchens deutliche Schluckbewegungen machen. Durch die Vibration gelangte der männliche Samen an die Kloake des Weibchens und wurde von dieser abgenommen. Die Tritonen legt also nicht, wie viele Amphibien, unbefruchtete Eier . . ." (Quoted by von Bedriaga, op. cit., p. 157). Subsequent articles of von Bedriaga (1882 and 1893) describe spermatophores being passed between the closely approximated cloacas of males and females of *Megapterna*, *Euproctus* and *Molge* but the rôle of the cloacal papillae is not elaborated. Kammerer (1907) reported the passing of the spermatophore directly from the male to the female of *Salamandra* in a similar manner on land, the spermatophores simply being deposited on the bottom when fertilization occurred in the water. Dunn (1923, p. 26) observed that the females of the *Cryptobranchoidea* have no spermathecae, the male cloaca of these forms is devoid of papillae, and all the observations of their breeding indicate external fertilization. He concluded: "It is therefore extremely probable that the primitive method of external fertilization characterizes the *Cryptobranchoidea*, and that the more specialized method of internal fertilization by means of cloacal papillae, spermatophores, and spermathecae, characterizes the *Salamandroidea*". Nakamura (1927b, p. 524) noted: "La papille cloacale des Tritons . . . représente la première apparition dans le phylum des Vertébrés du tubercule génital. Elle a sa situation et sa structure, avec un élément de tissu érectible vasculaire très simplifié qui contribue à déterminer l'œdème caractéristique de la période des amours". He also stated (1927a, p. 353): "Par sa structure, la papille cloacale des Tritons est bien l'équivalent d'un pénis,

c'est-à-dire du tubercule génital des Vertébrés supérieurs". Noble (1927, p. 35) observed: "Within the genus *Ambystoma* further observation may show that there is some variation in the courtship. For example, the spermatophores of *A. jeffersonianum* are unknown and both Allen and Bishop have noted the males embracing the females". As regards descriptions of the cloacal papillae of the urodeles, Francis (1934, p. xvii) observed: "The celebrated Monro secundus, in his inaugural dissertation (1755), gives us an admirable description of the male genitalia of 'Salamandra'. . . . Monro's paper is the most careful account of the male genitalia and renal organs with their ducts, the cloacal glands (which he notes are not developed in the female), lung and fat body of a Urodele so far published, but the subject was undoubtedly Triton and not Salamander". Descriptions by Spengel (1876), Nakamura (1927b), Abbayes (1932 and 1934), Smith (1927), Beaumont (1933) and Francis (1934) enable a reasonably good idea to be formed of the cloaca, Smith and Francis giving information on the blood supply in *Triturus* and *Salamandra* respectively. Francis (1934, p. 286) described in *Salamandra* "a small ridge-like projection from the antero-ventral wall of the cloacal chamber which may be called the *cloacal papilla* (it has sometimes been called the *penis*, but this is a misnomer)" and noted also (p. 287) that "there is a slight median ridge passing along the dorsal wall of the cloaca, which apparently corresponds with the structure labelled *penis* in Heidenhain's figures of Triton, but it is very much less developed in *Salamandra*". It is not at all clear what the function of the cloacal papilla is, how the erectile tissue is distributed, supplied with and drained of blood, and what the relations of the erectile tissue to the muscles of the cloaca and the pelvic skeleton are. Until this information is available a comparison with *Ascaphus* is extremely difficult.

Copulation occurs in the *Gymnophiona*, Müller referring in 1836 to an observation of Nitzsch on *Coecilia*: "bei welcher aus dem After ein penisartiges Organ herausgehangen, welches Prof. Nitzsch für einen wirklichen Penis hielt, obgleich er dasselbe nicht näher untersucht hat". (p. 172). Spengel (1876), Wiedersheim (1879) and Tonutti (1931, 1932, 1933 and 1934) have described the cloaca of the *Gymnophiona*, Tonutti (1932 and 1934) attempting to derive the copulatory organs of higher vertebrates from the condition in this group, equating the retractor and propulsor muscles of the *Gymnophiona* with the corpora cavernosa urethrae and corpora cavernosa penis respectively. Comparison of the condition in the *Gymnophiona* with that in *Ascaphus* and the *Amniota* is made difficult by the absence of the pelvic girdle and limbs with their associated muscles, blood vessels and nerves in the *Gymnophiona*. It is also difficult to explain how the propulsors came to be attached to the pelvic girdle to form the crura penis, while the cloacal and caudal regions of the *Gymnophiona* are apparently very specialized by the limbless means of progression, the blood system being particularly affected (von Schnurbein, 1935). The fate of the circular muscle layer internal to the retractor muscles is also difficult to imagine, while Tonutti's derivation compares the condition in the *Gymnophiona* with that of the penis of higher vertebrates rather than the clitoris which, when the development of the male phallus is considered (e.g. Broman, 1946), would appear to be more primitive.

Gadow (1888), Boas (1891) and Fleischmann (1902a and 1902b) discussed the interrelation of the copulatory organs of *Amniota*; Unterhössel (1902) and Wöpke (1931) added information on lizards and snakes and *Lacerta*; Hellmuth

(1902) and Gerecke (1932) on tortoises and crocodiles and *Testudo*; Pomayer (1902) and Grimpe (1930) on birds and the ostrich respectively. V. d. Broek (1910a) studied marsupials and (1910b) discussed the relation of these copulatory organs with other mammals and lower vertebrates. Tonutti (1932) emphasized the differences between two types of copulatory organs encountered in reptiles, one type in the crocodiles, tortoises and birds, the other in snakes and lizards. The existence of these two types strengthens Tonutti's argument that a form from which both can be derived must be sought among the *Amphibia*: "Die Kloake der männlichen Gymnophionen, die wir in ihrer temporären Eigenschaft als Kopulationsorgan zu dienen, als 'Prophallus' bezeichnen, bietet den Schlüssel für das Verständnis einer Zusammenhörigkeit und gemeinsamen Abkunft von Enddarm und Kopulationsorgan der Amnioten". (op. cit., 1932, p. 101). He quoted Fleischmann's (1906) conclusion: "Heute erkläre ich es mit voller Bestimmtheit für unmöglich, die verschiedenen Spezialfälle der Kopulationsorgane bei Reptilien, Vögeln und Säugern als Stufen einer von niederen Formen zu höherer Vervollkommnung fortschreiten den Entwicklung zu deuten".

While the copulatory organ of *Ascaphus* does not provide a solution to the problem of the evolution of the copulatory organs of vertebrates, it does suggest lines of investigation which may lead to such a solution. In *Ascaphus* the ventral vascularized cords are apparently derived from the ventral portion of the mm. compressores cloacae and apparently contain unstriated fibres of this muscle, unstriated fibres appearing also to be present in this region in the female and possibly in the mm. compressores cloacae of *Xenopus* where they attach to the pelvic girdle. Since the mm. compressores cloacae attach to the ischia, these vascularized cords are suggestive of the corpora cavernosa penis (and clitoridis) with their attachments to the pelvic girdle via the crura penis (and clitoridis). The relation between the mm. compressores cloacae and the m. sphincter ani externus and m. bulbocavernosus deserves investigation, since it may be possible to derive the corpora cavernosa penis (and clitoridis) from the ventral portion of the m. bulbocavernosus, which in turn is closely related to the m. sphincter ani. The vascularized cord derived from the circular muscle layer is suggestive of the corpus cavernosum urethrae, and it is interesting to note that it is posteriorly bifid. A study of the origin and development of the visceral muscles of the cloaca, and the mm. compressores cloacae, of *Ascaphus*, *Xenopus* and other *Anura*, and a comparison with the development of the hind-gut of higher vertebrates may help to elucidate the problem of the phylogeny of copulatory organs. A study of the blood vessels and nerves of the cloacal papilla of *Triturus* and other urodeles is another line of investigation which would provide interesting data for comparison with *Ascaphus* and higher vertebrates.

#### MUSCLES OF THE PELVIC REGION

The muscles of the pelvic region have been reconstructed and identified as accurately as was possible from sections. Where necessary the conditions in the other specimens available were investigated, and the portions of the legs cut off were compared with the reconstructions of the stumps, particularly fig. 34. The only problem quite insoluble from sections was whether a m. quadratus femoris is present. Noble (1922) found it to be present, but no

distinct division between it and the m. gemellus could be found in the sections. Bigalke (1926) did not describe a m. quadratus femoris in *Bufo* and (p. 341) observed: "Nussbaum zieht es vor, den M. obturator externus und den M. quadratus femoris von *Gaupp*, wie *de Man*, als einen einheitlichen Muskel zu bezeichnen, und nennt ihn den M. adductor brev's". (Nussbaum 1896 and 1898; de Man 1874). He noted further: "Ebenso gelingt eine Trennung zweier Köpfe des M. adductor brevis nicht bei *Bombinator igneus*. Nach *Grobbelaar* ist auch bei *Xenopus laevis*, Daud. der M. obturator externus (*Gaupp*) mit dem M. quadratus femoris (*Gaupp*) verwachsen, so dass eine Trennung nicht möglich ist". (Grobbelaar, 1924a).

The muscles are numbered below, and these numbers used in figs. 30—33 to indicate innervations and blood vessels supplying and draining the corresponding muscles. The illustrations cited for each muscle are grouped those which illustrate the form and position of the muscle, those which show its origin, and those which show sections of it.

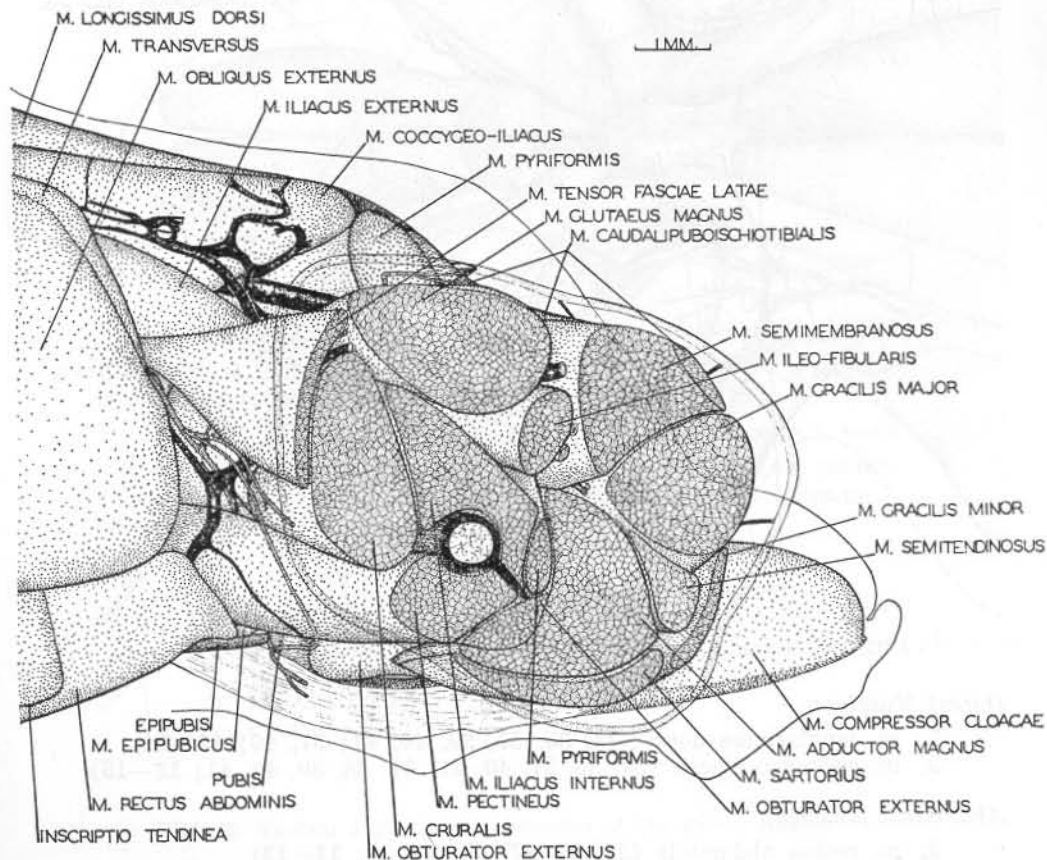


FIG. 34. Left Lateral Aspect of the Muscles of the Pelvic Region. (10 x). Male Adult. Same Specimen as figs. 1—28, 30—33 and 35—41.

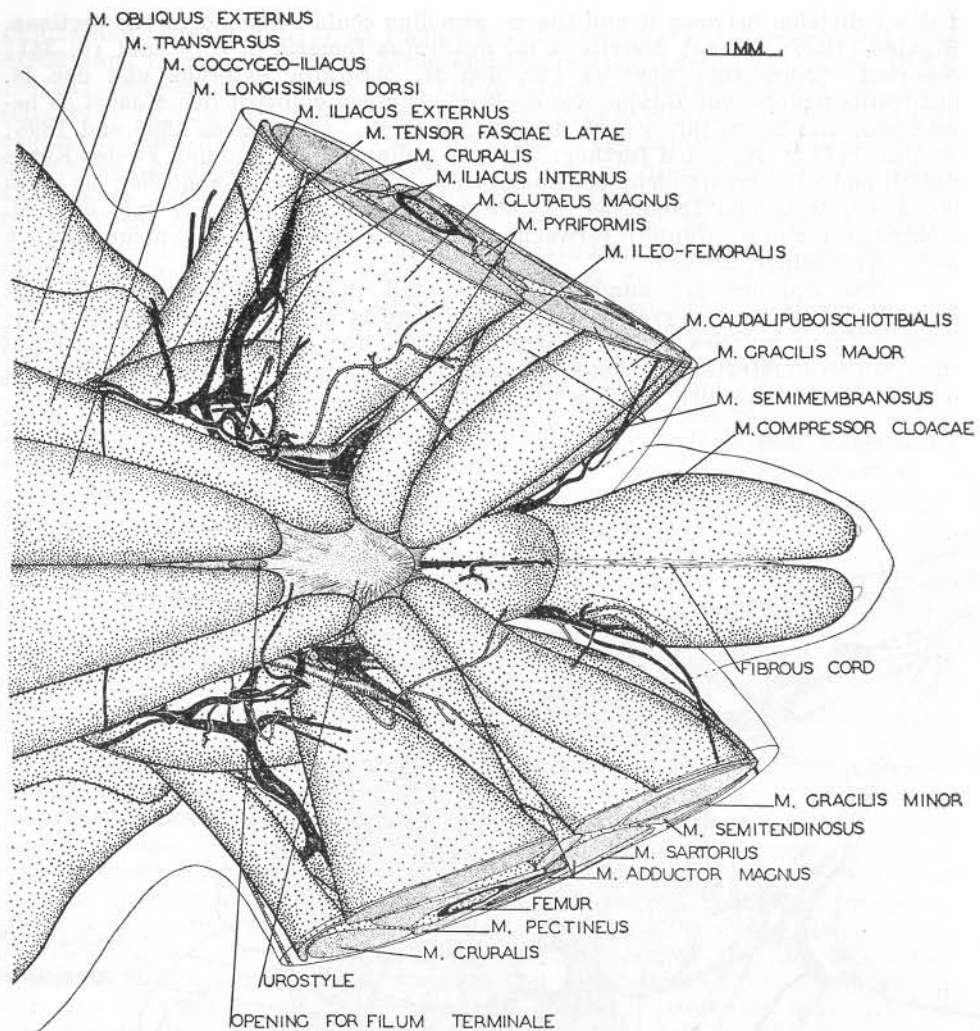


FIG. 35. Dorsal Aspect of the Muscles of the Pelvic Region. (10 x).

*Dorsal Muscles:*

1. m. longissimus dorsi (34, 35, 37, 39, 40, 41; 37, 40; 11-14)
2. m. coccygeo-iliacus (34, 35, 37, 40, 41; 37, 38, 39, 40, 41; 11-15)

*Abdominal Muscles:*

3. m. rectus abdominis (34, 36, 37, 38; 37, 38; 11-13)
4. m. obliquus externus (34, 35, 36; 11-12)
5. m. transversus (34, 35, 37; 37, 38; 11-13)

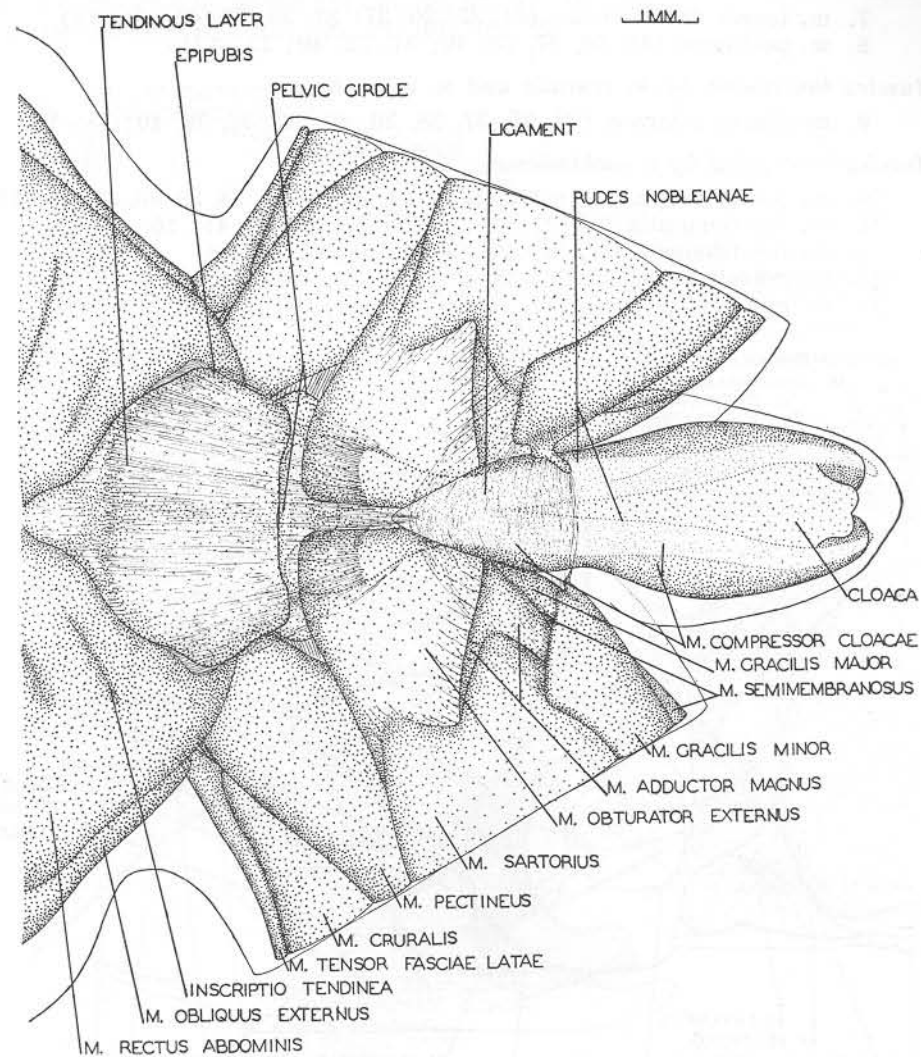


FIG. 36. Ventral Aspect of the Muscles of the Pelvic Region. (10 x).

*Epipubic Muscles:*

6. m. epipubic (34, 37, 38, 40; 39, 40; 12—14)

*Muscles innervated by n. cruralis:*

7. m. tensor fasciae latae (34, 35, 36, 37; 37, 38, 39, 40; 12—15)  
8. m. pectineus (34, 36, 37, 38, 40; 37, 39, 40; 12—17)

*Muscles innervated by n. cruralis and n. ischiadicus:*

9. m. iliacus internus (34, 35, 37, 38, 39, 40; 37, 38, 39, 40; 13—17)

*Muscles innervated by n. ischiadicus:*

10. m. iliacus externus (34, 35, 37, 38, 39, 40, 41; 37, 38, 39, 40, 41; 12—15)  
11. m. ileo-femoralis (35, 37, 38, 39, 41; 37, 38, 39, 41; 16)  
12. m. ileo-fibularis (34, 37, 38, 39, 41; 38, 41 16—18)  
13. m. cruralis (34, 35, 36, 38, 39, 40; 37; 14—15)  
14. m. gluteus magnus (34, 35, 37, 40, 41; 37, 38, 41; 15—18)

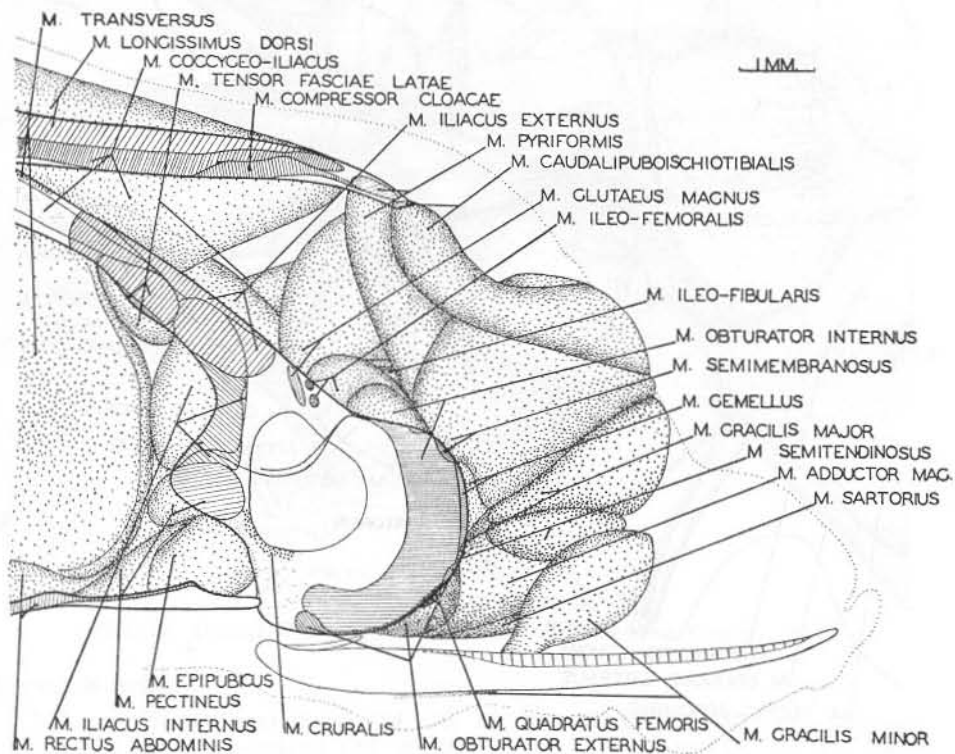


FIG. 37. Left Lateral Aspect of the Pelvic Girdle and Urostyle (Diagrammatic to show Origins of Muscles) and Internal Aspect of the Muscles of the Right Side. (10 x). The areas of attachment of the muscles are indicated by shading with parallel lines. Where these areas are on the medial side of the ilia they have been indicated by faintly dotted parallel lines shading in areas enclosed by solid lines.

15. m. semimembranosus (34, 35, 36, 37, 38, 39, 41; 37, 38, 41; 16—20)  
16. m. semitendinosus (34, 37, 39; 37; 18—20)  
17. m. gracilis major (34, 35, 36, 37, 38, 39; 37; 18—21)  
18. m. gracilis minor (34, 35, 36, 37; 37; 18—20)  
19. m. sartorius (34, 36, 37, 40; 16—19)

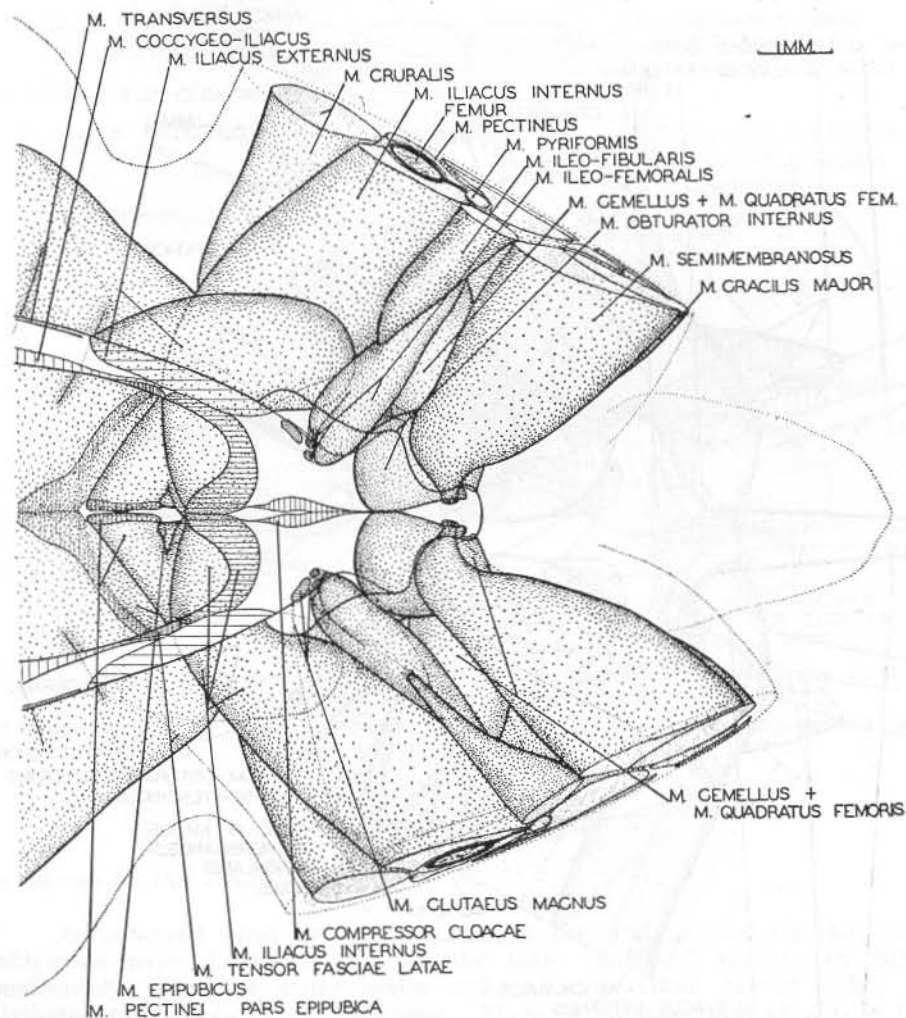


FIG. 38. Dorsal Aspect of the Pelvic Girdle and Epipubis (Diagrammatic to show Origins of Muscles) and the Deep Dorsal Muscles.

On the right side the m. tensor fasciae latae, m. gluteus magnus, m. pyriformis (dorsal portion), m. caudalipuboischiotibialis, m. transversus, m. obliquus externus and on the left side also the m. iliacus externus have been removed. The gut including the mm. compressores cloacae is not shown.

20. m. obturator externus (34, 36, 37, 40, 41; 37, 39, 41; 16—17)
21. m. adductor magnus (34, 35, 36, 37; 17—19)
22. m. quadratus femoris (39; 16) if this muscle is distinct from 23.
23. m. gemellus (37, 38, 39, 41; 37, 40; 16)
24. m. obturator internus (37, 38, 39, 41; 37, 39, 41; 16)
25. m. pyramiformis (34, 35, 37, 39, 41; 37, 39, 41; 16—17)

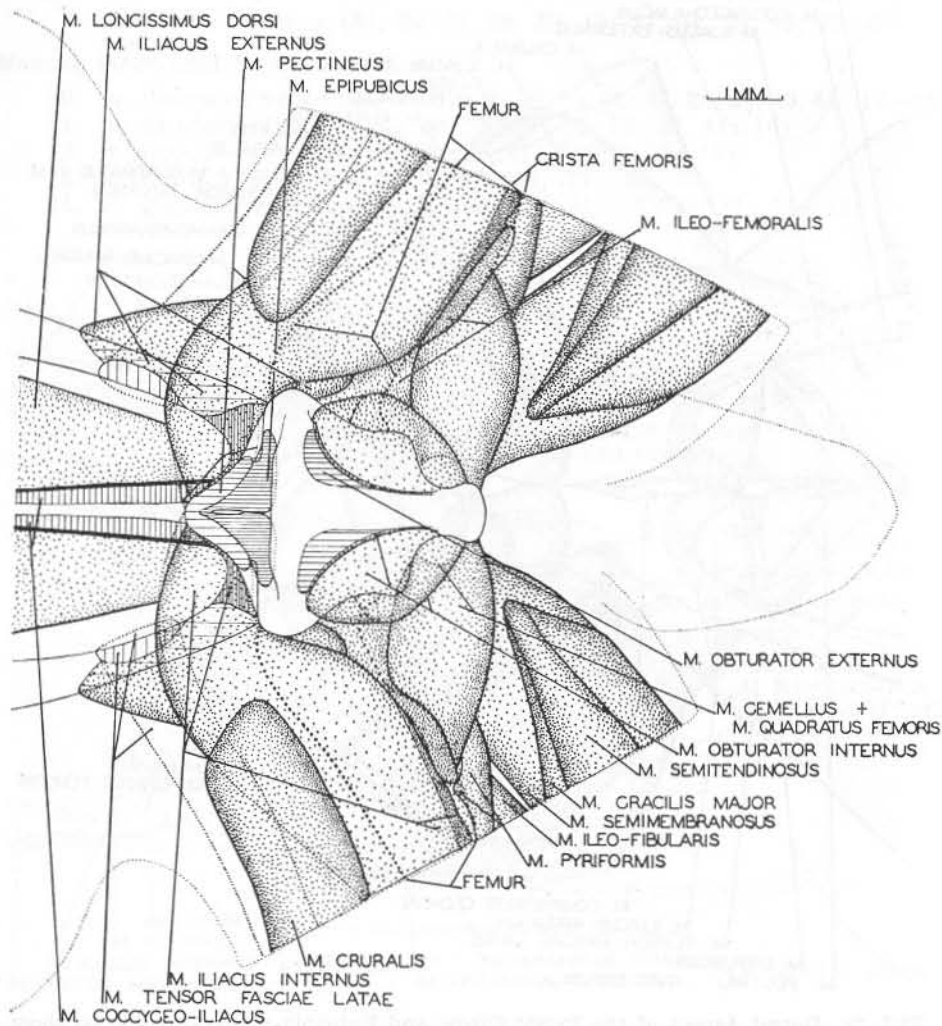


FIG. 39. Ventral Aspect of the Pelvic Girdle and Urostyle (Diagrammatic to show Origins of Muscles) and the Deep Ventral Muscles. (10 x).

On either side the m. gracilis minor, m. adductor magnus, m. obturator externus, m. sartorius, m. pectineus, m. tensor fasciae latae, m. rectus abdominis, m. obliquus externus, m. transversus and m. coccygeo-iliacus have been removed.

26. m. caudal-puboischiotibialis (34, 35, 37, 41; 37, 41; 16—20)
27. m. compressor cloacae (34, 40; 38; 13—27)

As Noble (1922 has observed, there does not appear to be an adductor longus muscle, a condition which, according to him, *Ascapus* shares with the discoglossids and pipids.

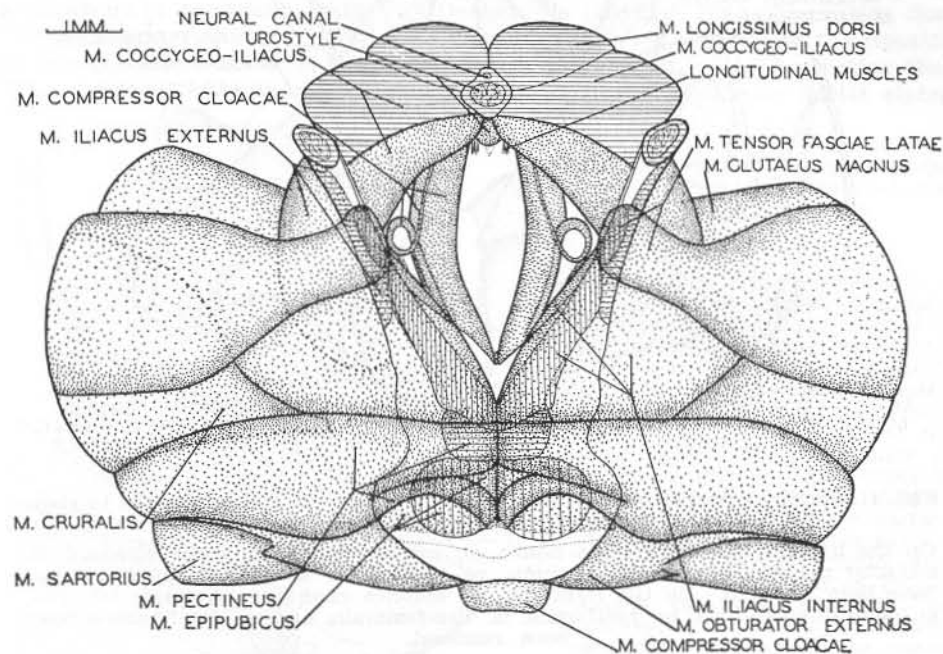


FIG. 40. Anterior Aspect of the Pelvic Girdle and Epipubis (Diagrammatic to show Origins of Muscles) and Associated Muscles. (10 x).

On either side the m. rectus abdominis, m. obliquus externus and m. transversus have been removed.

#### ADDITIONAL OBSERVATIONS

##### *Variations in the Juvenile Male:*

As observed when the pelvic girdle, cloaca, and particularly the rudens Nobleiana were discussed, the juvenile male examined appears to differ considerably from the other males and the differences cannot easily be attributed to the age of the specimen. There is no indication of a true tail and the specimen is therefore post-metamorphic; but the marrow cavities of the ilia, urostyle and femurs have not been completely formed, as there is still considerable cartilage towards the extremities which would later have been replaced by bone trabeculae and marrow. It would seem necessary to examine all specimens of *Ascapus* encountered for evidence of specific variations in the mating behaviour.

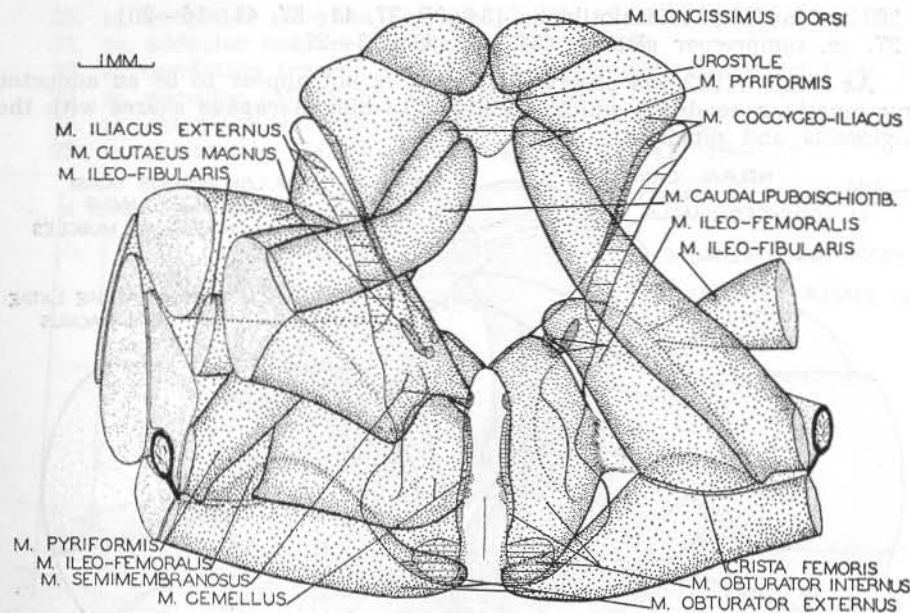


FIG. 41. Posterior Aspect of the Pelvic Girdle and Urostyle (Diagrammatic to show Origins of Muscles) and Associated Muscles. (10 x).

On the left side the m. gracilis minor, m. gracilis major, m. semitendinosus, m. adductor magnus, m. rectus abdominis, m. transversus and m. obliquus externus have been removed. On the right side all muscles except m. obturator internus, m. obturator externus, m. pyriformis, m. ileo-femoralis and m. ileo-fibularis have been removed.

#### Parasites and Symbionts:

All three adult males examined contained parasites (provisionally identified as *Acanthocephala*) in the bladders and urodaeum. In the juvenile male where the glandular epithelium of the bladder is undeveloped, there was an encapsulated parasite in the wall of the bladder but none free in the lumen. In the females no such parasites were observed. These observations suggest that the glandular epithelium of the adult males produces some secretion favouring the existence of these parasites, while the lesser development of the epithelium in the juvenile specimen and the females suggests some connexion with reproduction.

In the female sectioned the coprodaeum contained numerous bodies which were identified as *Protozoa* (*Ciliophora*). In the juvenile male a pair of structures each about .25 mm. in diameter was observed in the skin ventral and anterior to the pelvic girdle. Two pairs of similar structures were observed in the connective tissue behind the tip of the urostyle, these however having thicker capsules than the ventral pair. The tissue of these thicker capsules closely resembles that of the outer layers of the rudes *Nobleiana* but has a markedly greater affinity for borax-carmin and aniline blue. Within

the capsules are bodies which are highly differentiated and must provisionally be considered to be parasites.

#### Contents of the Alimentary Canal:

The sections examined indicate that the food consists largely of Arthropods in accordance with Van Denburgh's (1912, p. 264) observation that "The alimentary canal . . . contained a small bright red spider and the remains of two beetles of different species", and Gage's (1920, p. 4) observation that "The stomach contents consist almost entirely of unidentifiable beetle elytra

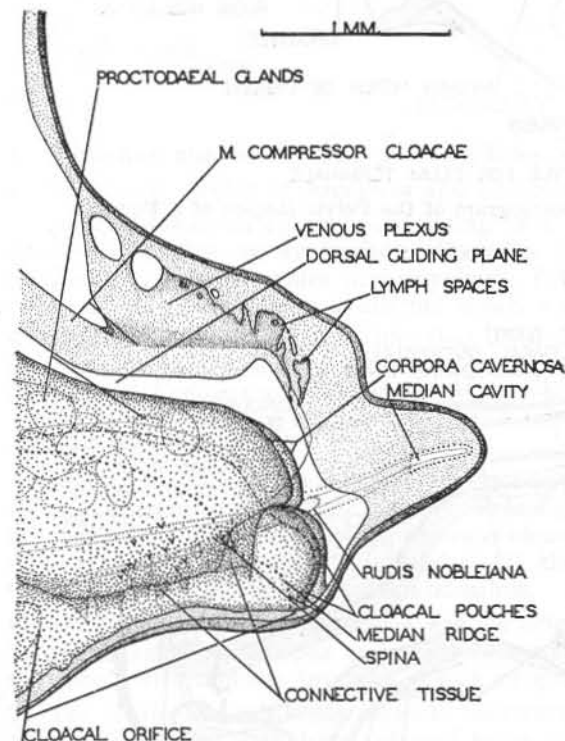


FIG. 42. Left Lateral Aspect of the Posterior Part of the Proctodaeum of a Juvenile Male. (25 x).

The posterior tip is represented in median section with heavy stipples representing the median portion of the cavities in which the rudes *Nobleiana* lie; further anteriorly the left side has been removed along lines through the most ventral and dorsal extents of the lymph spaces and the midline of the dorsal gliding plane, exposing the proctodaeum. A fine stippled line represents the inner surface of the epithelium (i.e. the surface in contact with the stratum proprium) where it is hidden by the corpora cavernosa anteriorly; an interrupted line shows the furthest extent dorsally of the lumen of the cloaca, a heavy stippled line the median ridge of the dorsal wall. The positions of the spinae of the left side on the inside of the cloacal wall are indicated by v's, those of the right side by very light dotted v's. The posterior limit of the m. compressor cloacae, the proctodaeal glands, and the left ruds *Nobleiana* are represented by stippled lines.

and spider fragments". De Villiers (1934b, p. 7) observed: "Very prominent in sections of the tip of the snout are the glandulae intermaxillares, to which Noble (1931, p. 201) ascribes the function of secreting a sticky secretion for making the tongue adhesive. . . . If the usually accepted theory of the function of these glands is correct, *Ascaphus* must be an active insect hunter". But Slevin (1928, p. 78) noted that the tongue "being attached by nearly the whole of its base, cannot be protruded", and Gordon (1939, p. 31) that the tongue is "not protrusible". It would seem that a sticky secretion for making the tongue adhesive could not function if the tongue is not protrusible.

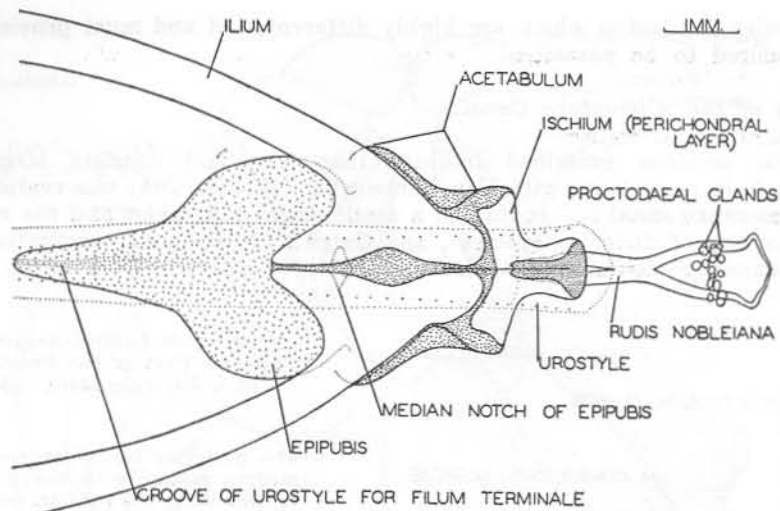


FIG. 43. Dorsal Aspect of a Stereogram of the Pelvic Region of a Female.

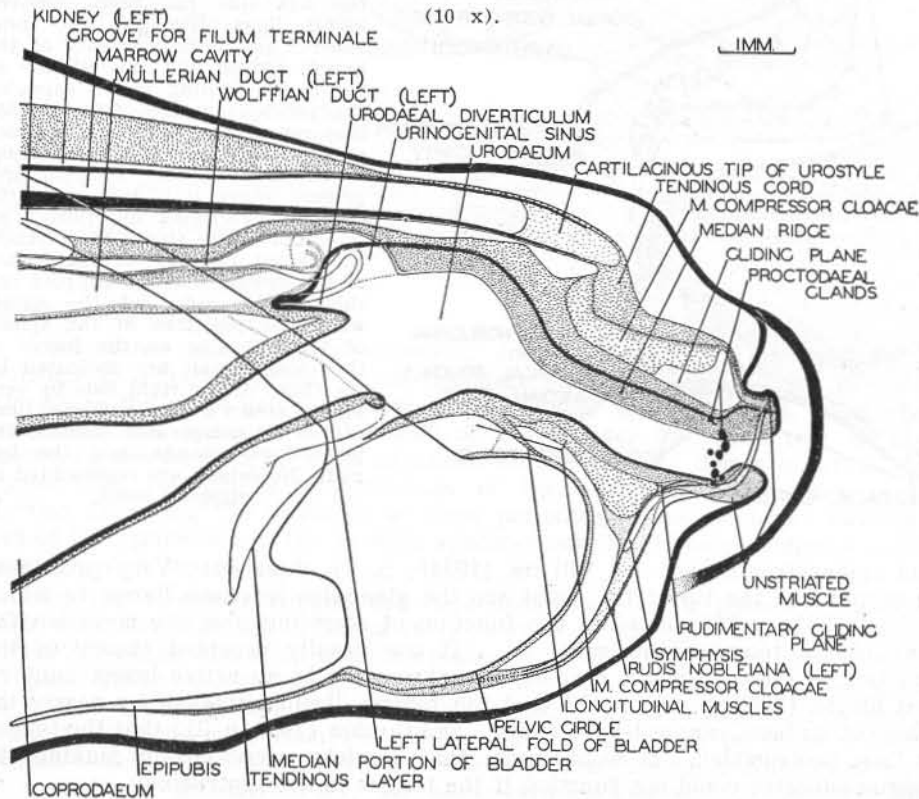


FIG. 44. Left Lateral Aspect of a Stereogram of the Pelvic Region of a Female (10 x).

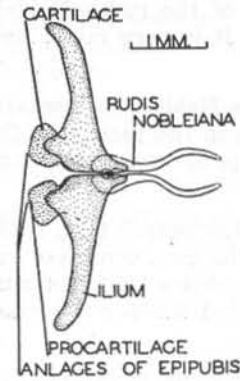


FIG. 45. Dorsal Aspect of the Pelvic Girdle and Epipubis of a Larva. (10 x).

### SUMMARY

- 1 *Ascaphus* shares the family *Ascaphidae* with *Leiopelma*.
- 2 The pelvic girdles of *Ascaphus* and *Leiopelma* are very similar.
- 3 *Ascaphus* has an epipubis consisting of a plate of calcified cartilage fused synchondrotically or syndesmotically with the pelvic girdle. There is no ossification such as occurs in *Leiopelma*. Posteriorly the epipubis is medially notched; in one specimen a distinct notch was not observed.
- 4 The epipubis of *Ascaphus*, like that of *Xenopus*, develops as paired chondrifications in the linea alba and is therefore presumably homologous with the epipubis of *Xenopus* and some urodeles but not with the processus praepubicus (zonal) of the pelvic girdle of other urodeles.
- 5 The epipubis can be lifted by contraction of a pair of muscles inserted on its dorsal surface and originating on the pelvic girdle, such movement presumably having a hydrostatic effect. These muscles presumably correspond to the m. epipubicus of *Xenopus*, which shows evidence of arising as a paired structure, and the ypsiloid muscles of urodeles, all these muscles probably arising as differentiations of the m. rectus abdominis.
- 6 A portion of the m. pectineus has its origin on either side of the epipubis in *Ascaphus* as in *Xenopus* and *Leiopelma* and like its urodelan homologue, the m. pubo'schiofemorales internus, which originates on the ypsiloid cartilage.
- 7 The cloaca in both sexes extends backwards behind the pelvic girdle and is supported by two rods, here referred to as rudes Nobleianae, fused anteriorly, which are neither cartilaginous (as reported by Noble) nor, in the absence of evidence of calcification, obviously bone (as reported by De Villiers).
- 8 The rudes Nobleianae consist of two layers of fibrous tissue, a circular outer and a longitudinal inner, enclosing a medulla totally unlike marrow and unvascularized.
- 9 The posterior tips of the rudes Nobleianae curve dorsally around the cloaca, approaching in the males and meeting in the females.
- 10 Anteriorly in the male the rods are attached to the pelvic girdle by means of caudad-directed tendons anteriorly contiguous with the outer layer of the rudes Nobleianae.



11 A dense tendinous sheet surrounds the anterior part of the rudes Nobleianae and stretches to the ventral surface of the epipubis. It is very much less developed in the female than the male.

12 The mm. compressores cloacae originate on the rudes Nobleianae dorsally and appear to extend between the rods as unstriped fibres in the male. In the female the rudes Nobleianae are imbedded in the mm. compressores cloacae and between the rods there is unstriped muscle.

13 The cloaca in the male beyond the pelvic girdle turns downwards then backwards with resultant folding of the capsule consisting of the mm. compressores cloacae then turns to open ventrally. In the female the cloaca with its mm. compressores cloacae capsule slopes slightly ventrally behind the pelvic girdle, but opens terminally.

14 The circular muscle layer of the cloaca, which in the male is interrupted only where the Wolffian ducts enter the urodaeum, is vascularized in the "tail" region of the male and the corresponding region of the female, and is separated from the surrounding tissues by ventral and dorsal gliding planes much less developed in the female than in the male.

15 The longitudinal muscle layer forms two cords which attach dorsally to the urostyle and ventrally a single cord attaching to the pelvic girdle. Further posteriorly it is much reduced, apparently forming a vascularized layer on the inner surface of the mm. compressores cloacae in the "tail" region.

16 The anterior slip of the mm. compressores cloacae in *Ascaphus* does not encircle the v. ischiadica (as in *Rana*) but only the a. ischiadica and n. ischiadicus.

17 The mm. compressores cloacae reach from the urostyle to the pelvic girdle on either side of the cloaca. Beyond the urostyle and pelvic girdle the two muscles attach on either side of a septum dorsally, and ventrally attach to the rudes Nobleianae. The two muscles extend anteriorly and fuse ventral to the pelvic girdle, the fibres being antero-posterior in direction and attaching to the dorsal surface of the rudes Nobleianae.

18 At the junction of the coprodaeum and urodaeum the circular muscle layer is markedly thicker and can act as a coprodaeal sphincter, the lumen being reduced dorsally by the floor of the urinogenital sinus.

19 The mm. compressores cloacae immediately behind the pelvic girdle act as a cloacal sphincter.

20 The epithelium of the bifid bladder is highly glandular in the male, less so in the female, its area being increased by folding.

21 There are proctodaeal glands immediately anterior to the cloacal orifice in both sexes but they are much more developed in the male.

22 Within the ring of proctodaeal glands the cloacal epithelium changes from a mucous lining to a cornified integument which, just within the orifice in the male, is raised into horny spines.

23 Vestigial Müllerian ducts were observed in only one male *Ascaphus*, in which they were not nearly as well developed as figured by Noble (1931). In the single specimen of a male *Leiopelma* examined they were observed to be well-developed.

24 The cloaca is supplied by branches of the a. mesenterica posterior and the aa. pudendae anteriores which anastomose in the "tail" region.

25 An aorta caudalis is present in *Ascaphus*, *Leiopelma* and *Xenopus*.

26 The cloaca is drained by a v. pudenda on either side, and more anteriorly, by a median v. caudalis.

27 The sacral plexus of *Ascaphus* is made up of four pairs of spinal nerves, apparently the 9th—12th.

28 The cloaca is innervated by the plexus ischio-coccygeus dorsally and a branch of the n. ischiadicus (the n. pudendus) ventrally.

29 The thigh muscles are innervated much as in *Rana*, except that the m. iliacus internus is innervated by a branch of the n. ischiadicus in addition to a branch of the n. cruralis.

30 Copulation could be ventral or dorsal.

31 Vento-laterally in the "tail" there are vascularized cords which appear to be derived from the mm. compressores cloacae. When they, as well as the vascularised tissue derived from the circular muscle layer, are turgid, the cloacal orifice comes to lie at the tip of the "tail" and the horny spines are exposed.

32 The turgid "tail" can only be applied to the cloacal orifice of the female and not inserted into it.

33 The rudes Nobleianae may maintain their form by virtue of turgidity of the cells of the medulla. They are probably moved by contraction of the mm. compressores cloacae.

34 "Trichtervenen" and "Polsterarterien" were not observed in association with the cloaca. Regulation of the blood supply of the cloaca may be a function of the mm. compressores cloacae.

35 The erectile tissue and cloaca of *Ascaphus* cannot be interpreted in the light of present knowledge of the copulatory organs of *Pisces*, *Urodela* and *Gymnophiona*, nor can conditions in *Ascaphus* be interpreted as a "phylogenetic link".

36 The median vascularized cord derived from the circular muscle layer may be comparable with the corpus cavernosum urethrae, and the paired vascularized cords with the corpora cavernosa penis or clitoridis, of *Amniota*.

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## BIBLIOGRAPHY

- Abbeyes, H. des 1932. Quelques détails anatomiques sur l'appareil uro-génital mâle des Tritons. C. R. Soc. Biol. Paris, 111 : 684
- Abbeyes, H. des 1934. Contribution a l'étude des voies urogénitales mâles des Tritons (Batraciens Urodèles). Thèses, Paris. 2e Thèse.
- Adolphi, H. 1893. Über Variationen der Spinalnerven und der Wirbelsäule anurer Amphibien. I. (*Bufo variabilis* Pall.) Morph. Jb., 19 : 313.
- Adolphi, H. 1895. Über Variationen der Spinalnerven und der Wirbelsäule anurer Amphibien II. (*Pelobates fuscus* Wagl. und *Rana esculenta* L.). Morph. Jb., 22 : 449.
- Appleton, A. B. 1928. The Muscles and Nerves of the Post-axial Region of the Tetrapod Thigh. J. Anat. Lond., 62 : 364 and 401.
- Arltdt, Th. 1917. Die Ausbreitung der Lurche. Arch. Naturgesch., 82A : 94. Quoted by Noble (1922).
- Bargmann, W. 1934. Über die Polsterarterien und Trichtervernen des Penis. Z. Zellforsch., 20, 5 Heft : 803.
- Beaumont, J. de 1933. La différenciation sexuelle dans l'appareil uro-génital des Tritons et son déterminisme. Roux Arch. Entw. Mech. Organ., 129, 1 Heft : 120.
- Bedriaga, J. von 1878. Vorläufige Bemerkung über das Begattungsorgan der Tritonen. Arch. Naturgesch., ? : 122.
- Bedriaga, J. von 1881. Prof. Nauck's Mittheilung über die Fortplanzung der Tritonen. Zool. Anz., 4 : 157.
- Bedriaga, J. von 1882. Über die Begattung bei einigen geschwänzten Amphibien. Zool. Anz., 5 : 265.
- Bedriaga, J. von 1893. Über die Begattung bei einigen geschwänzten Amphibien. Zool. Anz., 16 : 102.
- Bhaduri, J. L. 1938. An abnormal renal-portal vein in an American bullfrog *Rana catesbeiana*. Anat. Anz., 86 : 65.
- Bigalke, R. 1926. Zur Myologie der Erdkröte (*Bufo vulgaris*, Laurenti). Z. ges. Anat., I. Abt., 82 : 286; Inaugural-Dissertation, Berlin
- Blanchard, R. 1881. Sur les glandes cloacale et pelvienne et sur la papille cloacale des Batraciens Urodèles. Zool. Anz., 4 : 9 and 34.
- Boas, J. E. V. 1891. Zur Morphologie der Begattungsorgane der amnioten Wirbeltiere. Morph. Jb., 17 : 271.
- Broek, A. J. P. v. d. 1910a. Untersuchungen über den Bau der männlichen Geschlechtsorgane der Beuteltiere. Morph. Jb., 41 : 347
- Broek, A. J. P. v. d. 1910b. Entwicklung und Bau des Urogenital-Apparates der Beutler und dessen Verhältnis zu diesen Organen anderer Säuger und niederer Wirbeltiere. Morph. Jb., 41 : 437.
- Broili, F. 1922. Über den feineren Bau der „Verknöcherten Sehnen“ (= verknöcherten Muskeln) von Trachodon. Anat. Anz., 55 : 465.
- Broman, I. 1946. Beiträge zur Kenntnis der Embryonalentwicklung der äusseren Geschlechtsorgane beim Menschen. Acta Univ. Lund., N. F. Avd. 2. Bd. 42. Nr. 12; K. fysiogr. Sällsk. Lund. Förh., N. F. Bd. 57. Nr. 12.
- Cadiat, M. 1877. Étude sur les Muscles du Perinée. J. Anat. Paris, ? : 39. Quoted by Hirsch.
- Camp, C. L. 1917. Another Record of *Ascaphus truei* Stejneger. Copeia, No. 40 : 13. Quoted by Storer.
- Conti, G. 1952. L'érection du pénis humain et ses bases morphologico-vasculaires. Acta anat., 14 : 217.
- Crawshay, L. R. 1906. On Variations in the Arterial System of certain Species of the Anura. Proc. zool. Soc. Lond., 1008.
- de Man, J. G. Myologie comparée de l'extrémité postérieure chez les Amphibies. Niederländ Arch. zool., 2 : 53. Quoted by Bigalke.
- de Villiers, C. G. S. 1925. On the Development of the "Epipubis" of *Xenopus*. Ann. Transv. Mus., 11, part 2 : 129.
- de Villiers, C. G. S. 1929. The Comparative Anatomy of the Breast-Shoulder Apparatus of the three Aglossal Anuran Genera: *Xenopus*, *Pipa* and *Hymenochirus*. Ann. Transv. Mus., 8, part 1 : 37.
- de Villiers, C. G. S. 1933. The "Tail" of the Male American Toad, *Ascaphus*. Nature, Lond., 131 : 692.
- de Villiers, C. G. S. 1934a. On the Morphology of the Epipubis, the Nobelian Bones and the Phallic Organ of *Ascaphus Truei* Stejneger. Anat. Anz., 78 : 23.
- de Villiers, C. G. S. 1934b. Studies of the Cranial Anatomy of *Ascaphus truei* Stejneger, the American "Liopelmid". Bull. Mus. comp. Zool. Harv., 77, No. 1 : 1.
- de Vos, C. M. 1938a. The zonal and sternal skeleton of the Liopelmidae (Anura). Anat. Anz., 87 : 54.
- de Vos, C. M. 1938b. The inscriptional ribs of *Liopelma* and their bearing upon the problem of abdominal ribs in Vertebrata. Anat. Anz., 87 : 82.
- Deysach, L. 1939. The comparative morphology of the erectile tissue of the penis with especial emphasis on the probable mechanism of erection. Amer. J. Anat., 64, no. 1 : 111.
- Dunn, E. R. 1923. The Breeding Habits of Salamanders and Their Bearing on Phylogeny. Copeia, No. 115 : 25.
- Eberth, C. J. 1904. Die männlichen Geschlechtsorgane, Bardeleben; Handbuch d. Anat. d. Mensch. Bd. 7, Th. 2, Abth. 2, Fischer, Jena, 1904. Quoted by Hirsch.
- Ebner, V. von 1900. Über klappenartige Vorrichtungen in den Arterien der Schwellkörper. Verh. anat. Ges. Pavia, 1900; Kölliker's Handbuch d. Gewebelehre. Quoted by Hirsch.
- Eggert, B. 1931. Die Geschlechtsorgane der Gobiiformes und Blenniiformes. Z. wiss. Zool., 139 : 249.
- Ercolani, J. B. 1869. Des Tissus et des Organes Erectiles. J. Anat. Paris. Quoted by Hirsch.
- Fejérváry, G. J. de 1921. Kritische Bemerkungen zur Osteologie und Systematen der Anuren. Arch. Naturgesch., 87A : 25.
- Fejérváry, G. J. de 1923. *Ascaphidae*, a New Family of Tailless Batrachians. Ann. hist.-nat. Mus. hung., 20 : 178.
- Fleischmann, A. 1902a. Morphologische Studien über Kloake und Phallus der Amnioten. Einleitung. Morph. Jb., 30 : 539.
- Fleischmann, A. 1902b. Morphologische Studien über Kloake und Phallus der Amnioten. IV. Die Säugethiere. V. Die Stilik des Urodäum und Phallus bei den Amnioten. Morph. Jb., 30 : 653 and 666.
- Fleischmann, A. 1906. Das allgemeine Resultat meiner Phallusstudien. S.B. phys.-med. Soz. Erlangen, 38 : 358.

Francis, E. T. B. 1934. The Anatomy of the Salamander. Oxford, Clarendon Press, 1934.

Gadow, H. 1887. Remarks on the cloaca and copulatory organs of Amniota. Philos. Trans., 178B : 5.

Gaige, H. T. 1920. Observations Upon the Habits of *Ascaphus truei*, Stejn. Occ. Pap. Mus. Zool. Univ. Mich., No. 84 : 1.

Gaupp, E. 1896. A. Ecker's und P. Wiedersheim's Anatomie des Frosches, T. 1. Vieweg & Sohn, Braunschweig.

Gaupp, E. 1899. A. Ecker's und P. Wiedersheim's Anatomie des Frosches, T. 2. Vieweg & Sohn, Braunschweig.

Gaupp, E. 1904. A. Ecker's und P. Wiedersheim's Anatomie des Frosches, T. 3. Vieweg & Sohn, Braunschweig.

Gerecke, H. 1932. Das Kopulationsorgan von *Testudo graeca* L. Jena. Z. Naturw., 66 : 119.

Gordon, K. 1939. The Amphibia and Reptilia of Oregon. Oregon State Monographs, Studies in Zoology No. 1.

Green, T. L. 1931. On the Pelvis of the Anura: a Study in Adaption and Recapitulation. Proc. zool. Soc. Lond., 1259.

Grimpe, G. 1930. Über den Penis von *Struthio camelus* L. Zool. Gart., 2 : 184.

Grinnell, J. and Camp, C. L. 1917. A Distributional List of the Amphibians and Reptiles of California. Univ. Calif. Publ. Zool., 17, No. 10 : 127.

Grobbelaar, C. S. 1923. Beiträge zu einer anatomischen Monographie von "Xenopus laevis" (Daud.). Inaugural-Dissertation, Berlin; 1924a Z. ges. Anat., 72 : 131.

Grobbelaar, C. S. 1924b. On the Venous and Arterial Systems of the "Platanna" (*Xenopus laevis*, Daud.). S. Afr. J. Sci., 21 : 392.

Groenewald, A. A. v. J. Die Prikkelorgaantjies van *Galago moholi* met vergeelykende aantekeninge oor die prikkelorgaantjies van *Cercopithecus lalandii*, *Papio ursinus* en *Homo sapiens*. Thesis awaiting publication.

Grönberg, G. and Klinckowström, A. v. 1894. Zur Anatomie der *Pipa americana*. III. Gefäßsystem und subcutane Lymphsäcke. Zool. Jb., 7 : 894. Quoted by Millard.

Hellmuth, K. 1902. Morphologische Studien über Kloake und Phallus der Amnioten. II. Die Schildkröten und Krokodile. Morph. Jb., 30 : 582.

Hill, W. C. O. 1946. Notes on the Male External Genitalia of the Chimpanzee. Proc. zool. Soc. Lond., 116, part 1 : 129.

Hirsch, E. W. 1931. The So-called Arterial Valves in the Penile Arteries. A Critical Survey. J. Urol., 25, No. 1 : 61.

Hoffman, A. C. 1930. Opsomming van Nuwe Navorsinge oor die Opbou en Ontogenese van die Zonaalskelet by Amphibia, Vernaamlik van *Cryptobranchus alleghaniensis*, *Necturus maculatus*, *Heleophryne* en *Xenopus laevis*. S. Afr. J. Sci., 27 : 446.

Hoffman, A. C. 1935. Oor die Non-homologie van die Medio-ventrale Presonale Skeletelemente by die Amfibië, Anura en Urodela. Soöl. Nav. nas. Mus. Bloemfontein, Deel I, p. 3.

Jarecki, G. 1932. Anatomisch-Physiologisches über die Kniescheibe. Anat. Anz., 74 : 289.

Jourdain, S. 1881—1882. Recherches sur le système lymphatique de la *Rana temporaria* L. Rev. Sci. nat., 3e série, T. I, Nr. 2, 1881; Nr. 4, 1882. Quoted by Gaupp (1899).

Kammerer, P. 1907. Über den Copulationsakt der Erdmolche (*Salamandra Laur.*). Zool. Anz., 32 : 33.

Kiss, F. 1921. Anatomisch-histologische Untersuchungen über die Erektion. Z. ges. Anat., 61 : 455.

Klinckowström, see Grönberg.

Koch, W. 1926. Über verknöcherte Sehnen bei *Macropus*. Anat. Anz., 62 : 138. Lereboullet, 1851. Quoted by Gaupp (1904).

Low, J. W. 1927. Contributions to the Development of the Pelvic Girdle: II. — The Pelvic Girdle in the Batrachian *Hynobius nebulosus* s. *Ellipso-glossa nebulosa* Dum. et Bibr. Proc. zool. Soc. Lond., part 2, 865.

Maximow, A. A. and Bloom, W. 1940. A Textbook of Histology, W. B. Saunders Company, Philadelphia and London, 3rd Ed.

Millard, N. 1941. The Vascular Anatomy of *Xenopus laevis* (Daudin). Trans. roy. Soc. S. Afr., 28, part 5 : 387.

Moodie, R. L. 1928. The Histological Nature of Ossified Tendons Found in Dinosaurs. Amer. Mus. Novit., No. 311.

Müller, J. 1836. Über zwei verschiedene Typen in dem Bau der erektilen männlichen Geschlechtsorgane bei den straussartigen Vögeln und über die Entwicklungsformen dieser Organe unter den Wirbelthieren überhaupt. Abh. Akad. Wissen. Berlin, 137.

Nakamura, T. 1927a. Étude anatomo-comparative, embryologique et embryomécannique de la papille cloacale des Tritons. Bull. biol., 61 : 333.

Nakamura, T. 1927b. Étude de la papille cloacale des Tritons. Contribution à l'étude de la différenciation des sexes. C.R. Soc. Biol. Paris, 96 : 524.

Noble, G. K. 1922. The Phylogeny of the Salientia I. The Osteology and the Thigh Musculature; Their Bearing on Classification and Phylogeny. Bull. Amer. Mus. nat. Hist., 46 : 1.

Noble, G. K. 1924. A New Spadefoot Toad from the Oligocene of Mongolia with a Summary of the Evolution of the Pelobatidae. Amer. Mus. Novit., No. 13.

Noble, G. K. 1925. An Outline of the Relation of Ontogeny to Phylogeny Within the Amphibia I. Amer. Mus. Novit., No. 165.

Noble, G. K. 1926. An Analysis of the Remarkable Cases of Distribution Among the Amphibia with Descriptions of New Genera. Amer. Mus. Novit., No. 212.

Noble, G. K. 1927. The Value of Life History Data in the Study of the Evolution of the Amphibia. Ann. N.Y. Acad. Sci., 30 : 31.

Noble, G. K. and Putman, P. G. 1931. Observations on the Life History of *Ascaphus truei* Stejneger. Copeia, No. 3 : 97.

Noble, G. K. 1931. The Biology of the Amphibia. New York, McGraw Hill Co.

Nussbaum, M. 1898. Nerv und Muskel. II. Der Oberschenkel einiger anuren Batrachier. Arch. mikr. Anat., 52 : 367. Quoted by Bigalke.

Piveteau, J. 1937. Paléontologie de Madagascar XXIII. — Un Amphibien du Trias Inférieur. Essai sur L'origine et L'évolution des Amphibiens Anoures. Ann. Paléont., 26, Fascicules III et IV.

Pomayer, C. 1902. Morphologische Studien über Kloake und Phallus der Amnioten. III. Die Vögel. Morph. Jb., 30 : 614.

- Pusey, H. K. 1938. Structural Changes in the Anuran Mandibular Arch during Metamorphosis, with reference to *Rana temporaria*. Quart. J. micr. Sci., 80, part IV : 479.
- Pusey, H. K. 1939. Methods of Reconstruction from Microscopic Sections. J. R. micr. Soc., 59 : 232.
- Pusey, H. K. 1943. On the head of the Liopelmid frog, *Ascaphus truei*. I. The Chondrocranium, Jaws, Arches, and Muscles of a partly-grown Larva. Quart. J. micr. Sci., 84 : 105.
- Rauther, M. 1909. Zoologische und antropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika. Bd. 3. VII. Das Kopulationsorgan von *Clinus*. Denkschr. med.-naturw. Ges. Jena, 15 : 467.
- Ryke, P. A. J. The Ontogenetic Development of the Somatic Musculature of the Trunk of the Aglossal Anuran *Xenopus laevis* (Daudin). Thesis in the Press.
- Simroth, H. 1914. Die Pendulationstheorie. 2 Aufl., Berlin. p. 593. Quoted by Fejérváry (1923).
- Slater, J. R. 1931. The Mating of *Ascaphus truei* Stejneger. Copeia, No. 2 : 62.
- Slevin, J. R. 1928. The Amphibians of Western North America. Occ. Pap. Calif. Acad. Sci., 14 : 1.
- Smith, G. M. 1927. The Detailed Anatomy of *Triturus torosus*. Proc. roy Soc. Can., Series III, 21 : 451.
- Spengel, J. 1876. Das Urogenitalsystem der Amphibien. I Theil. Der anatomische Bau des Urinogenitalsystems. Zool.-zootom. Inst. Univ. Würzburg, 3, Heft 1 : 1.
- Stejneger, L. 1899. Description of a New Genus and Species of Discoglossid Toad from North America. Proc. U.S. nat Mus., 21 : 899.
- Stejneger, L. and Barbour, T. 1917 and 1923. A Check List of North American Amphibians and Reptiles. Cambridge, Harvard University Press. 1st Ed. 1917, 2nd Ed. 1923.
- Stephenson, E. M. 1951. The Anatomy of the Head of the New Zealand Frog, *Leiopelma*. Trans. zool. Soc. Lond., 27, part 2 : 225.
- Stephenson, E. M. 1952. The Vertebral Column and Appendicular Skeleton of *Leiopelma hochstetteri* Fitzinger. Trans. roy Soc. N.Z., 79, parts 3 and 4 : 601.
- Stephenson, N. G. 1951. Observations on the Development of the Amphicoelous Frogs, *Leiopelma* and *Ascaphus*. J. Linn. Soc. (Zool.), 42 : 18. (No. 283).
- Storer, T. I. 1925. A Synopsis of the Amphibia of California. Univ. Calif. Publ. Zool., 27 : 1.
- Szarski, H. 1947. On the blood-vascular system of the *Salientia*. Bull. Acad. polonaise. Sci. Lett., Série B, p. 145.
- Szarski, H. 1951. Remarks on the Blood-vascular System of the Frog *Leiopelma hochstetteri* Fitzinger. Trans. roy. Soc. N.Z., 79, part 1 : 140.
- Tonutti, E. 1931. Beitrag zur Kenntnis der Gymnophionen XV. Das Genitalsystem. Morph. Jb., 68 : 151.
- Tonutti, E. 1932. Vergleichend-morphologische Studie über die Phylogenie des Enddarmes und des Kopulationsorganes der männlichen Amnioten, ausgehend von den Gymnophionen. Morph. Jb., 70 : 101.

- Tonutti, E. 1933. Beitrag zur Kenntnis der Gymnophionen XIX. Untersuchungen der Kopulationsorgane bei weiteren Gymnophionenarten. Morph. Jb., 72 : 155.
- Tonutti, E. 1934. Einheitliche Ableitung der Wirbeltierkopulationsorgane. Ergänzungsh. Anat. Anz., 78 : 148.
- Tretjakoff, D. 1929. Das Knochenmark des Frosches. Anat. Anz., 67 : 66.
- Turbott, E. G. 1942. The Distribution of the Genus *Leiopelma* in New Zealand, with a Description of a New Species. Trans. roy. Soc. N.Z., 71, part 4 : 247.
- Unterhössel, P. 1902. Morphologische Studien über Kloake und Phallus der Amnioten. I. Die Eidechsen und Schlangen. Morph. Jb., 30 : 541.
- van Denburgh, J. 1912. Notes on *Ascaphus*, the Discoglossoid Toad of North America. Proc. Calif. Acad. Sci., 3 : 259.
- van Eeden, J. A. 1951. The Development of the Chondrocranium of *Ascaphus truei* Stejneger with Special Reference to the Relations of the Palatoquadrate to the Neurocranium. Acta zool. Stockh., 32 : 41.
- van Winkle, K. 1922. Extension of the Range of *Ascaphus truei* Stejneger. Copeia, No. 102 : 4. Quoted by Storer.
- von Schnurbein, A. F. 1935. Der Bewegungsapparat von *Hypogeophis*. Beitrag zur Kenntnis der Gymnophionen XXIII. Morph. Jb., 75 : 315.
- Wagner, D. S. 1934a. *Leiopelma* Studies Nr. 1. The structure of the inner ear in relation to the reduction of the middle ear in the Liopelmidae (Noble). Anat. Anz., 79 : 20.
- Wagner, D. S. 1934b. *Leiopelma* Studies Nr. 2 On the cranial characters of *Leiopelma hochstetteri*. Anat. Anz., 79 : 65.
- Weidenreich, F. 1923. Über den Begriff "Knochen" und die Beziehungen des Knochengewebes zu Bindegewebe und Knorpel. Ergänzungsh. Anat. Anz., 57 : 138.
- Whipple, I. L. 1906. The Ypsiloid Apparatus of Urodeles. Biol. Bull. Woods Holl. 10, No. 6 : 255.
- Wiedersheim, R. 1879. Anatomie der Gymnophionen. Jena.
- Wopke, K. 1931. Die Kloake und die Begattungsorgane der männliche Zauneidechse (*Lacerta agilis* L.). Jena Z. Naturw., 65 : 275.