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Urogenital Morphology of Dipnoans, With Comparisons to Other Fishes and to Amphibians

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ABSTRACT The morphology of the urogenital system of extant dipnoans is compared among the three genera, and to that of other fishes and amphibians. Analysis is based on dissections, sectioned material, and the literature. Urogenital system morphology provides no support for the hypothesis of a sister-group relationship between dipnoans and amphibians, for virtually all shared characters are primitive, and most characters shared with other fishes are also primitive. Urogenital morphology is useful at the familial level of analysis, however, and synapomorphies support the inclusion of *Lepidosiren* and *Protopterus* in the family Lepidosirenidae separate from *Neoceratodus* of the family Ceratodontidae.

Analysis of relationships of the Dipnoi to other fishes and to tetrapods have largely been based on the morphology of hard tissues—the skeleton, tooth plates, and scales. Several studies of other systems are available in the literature, but most are descriptive and few are comparative, at least in considering all three genera of living lungfish. Soft-tissue systems have had limited evaluation in terms of assessing evolution and relationships.

Several current hypotheses of the relationships of the Dipnoi exist. These include the proposal by Romer ('66) that dipnoans are the sister group to actinistians and rhipidistians; that of Miles ('77) classifying dipnoans as the sister group of rhipidistians only; and that of Rosen et al. ('81) in which dipnoans are the sister group of tetrapods, with actinistians the outgroup and rhipidistians (porolepiforms) in an unresolved cladistic position. Within the Recent Dipnoi, *Neoceratodus* (one species: *forsteri*) is placed in the family Ceratodontidae; *Lepidosiren* (one species: *paradoxa*) and *Protopterus* (four species: *amphibius*, *aethiopicus*, *annectens*, and *dolloi*) are placed in the Lepidosirenidae. Soft-tissue morphology, because of the extreme paucity of extinct forms, can offer virtually nothing to our understanding of the relationships of dipnoans to rhipidistians, and little to the association of dipnoans with actinistians (*Latimeria* not necessarily being "representative"). However, soft-tissue morphology can contribute to information about dipnoan-tetrapod relationships (Rosen et al., '81, utilized muscle characters, for example) and to generic and familial relationships.

This survey and review of urogenital morphology of the three genera of extant dipnoans and of the literature is undertaken with the following objectives: 1) to provide information from a direct comparison of representatives of all three extant genera; 2) to see if the urogenital system offers support for any of the current hypotheses of dipnoan relationships; and 3) to determine whether or not the urogenital system offers additional characters for the familial allocation of the genera. Urogenital morphology and physiology have received little consideration in these contexts (see, for example, Thomson, '69; Rosen et al. '81). In this paper I review the morphology of the components of the urogenital system in dipnoans, adding new information where possible, and I compare the morphology of these components among dipnoan species as well as with the urogenital structures of other fishes and amphibians. For each component I discuss the implications of the morphology for assessment of relationships and suggest directions for further research.

MATERIALS AND METHODS

Urogenital organs from five specimens of *Lepidosiren paradoxa* (220–300 mm standard length) from Laguna Oca, Rio Paraguay, Formosa, Argentina, six of *Protopterus aethiopicus* (230–320 mm standard length) from Kusa Beach, Lake Victoria, near Kisumu, Kenya, and four of *Neoceratodus forsteri* (520–560 mm standard length) from the Brisbane River system, Queensland, Australia, were dissected. Specimens had been fixed in 10% formalin and stored in 70% ethanol. Males and females including immature specimens of each species were examined; several mature males and females were in breeding condition, with active spermatogenesis in the former and well-yolked eggs in the latter. Parts of each urogenital structure were excised and prepared for histological examination. Twenty histological preparations of the kidneys, gonads, ducts, and cloacas of each species were made by embedding in paraffin, cutting at 10 μm, and staining with hematoxylin-eosin.

The nomenclatorial format for the morphological comparisons is as follows: The generic epithet only is used in situations in which morphological descriptions are 1) appropriate to all species of a genus, 2) obviously my work on the species listed above, 3) relate to the single species in the genera *Neoceratodus* and *Lepidosiren*, or, 4) if an author did not identify species. If the morphology is species-specific, or if inter-specific variation is questionable or unknown, the *Protopterus* species examined is identified.

DESCRIPTION AND ANALYSIS

The kidney and the gonads

Kidney

Considerable attention has been paid to kidney structure, especially its development, in considering vertebrate relationships. In fact, few vertebrate organs have so extensive a developmental and morphological data base. Those data have been treated in terms of physiological and ecological correlates, and in terms of evolutionary relationships, including the origins of major vertebrate groups. Several decades of pertinent literature on vertebrates in general are summarized by Goodrich ('30) and Fraser ('50), and by Gerard ('54) and Hickman and Trump ('69) for fishes specifically. Fox ('60, '61, '62, '63) made significant contributions to understanding both dipnoan and amphibian kidney development. (He emphasized the similarities between those two groups, but seems not to have considered teleosts; see below.) Torrey ('65) reviewed the morphogenesis of the vertebrate kidney. Jesperson ('69) examined kidney structure of *Neoceratodus* with reference to the testicular network and summarized much of the literature produced during the 1930s on lungfish nephron structure.

Gross morphology. Lungfish kidneys are paired, somewhat lobed, elongate, highly pigmented retroperitoneal structures (Fig. 1). As illustrated by Kerr ('01) and confirmed in my material (Fig. 1B,E), the kidneys of *Lepidosiren* are nearly as long as the testes and are closely bound to the testes, some testicular tissue invading the kidney posteriorly. The kidneys of *Protopterus* (*annectens*; Kerr, '01; *aethiopicus*, this work) are shorter but stouter, lying more posteriorly in the body cavity (Fig. 1A,D). *Neoceratodus* (Fig. 1C,F) also has short, stout, posteriorly situated kidneys, more lobular than those of other genera. Kerr ('01) distinguished the genital or vesicular posterior portion of the kidney from the anterior urinary part, the latter recognizable in part by reduced pigment, especially in *Protopterus*. Jesperson ('69) was not able to distinguish two such regions in *Neoceratodus* grossly or in section, nor can I in my material.

Histology. Several workers have examined nephron structure in both the anterior and "vesicular" parts of the kidney. Hickman and Trump ('69) summarize research on *Protopterus* and *Lepidosiren* and describe the regions of the nephron—a typical corpuscle and glomerulus, a ciliated neck segment, a proximal tubule of two components, a ciliated intermediate segment, a distal segment, and a collecting duct system. Jesperson ('69) added information on *Neoceratodus* and compared its nephron cytology to that of *Lepidosiren* and *Protopterus dolloi* and *P. aethiopicus*. My observations agree with these reports (Fig. 2). The structure of the urinary nephrons approaches uniformity among the three genera. Hickman and Trump ('69) conclude that the cytological features of the nephron of lungfishes are similar in all aspects to those of a number of "typical" freshwater teleosts.

The nephrons in the vesicular portion of the kidney have all of the components described above, including a well-developed glomerulus (as in Kerr's, '01, Figs. 50 and 51 of *Lepidosiren*). Kerr ('01) did not find capsules and glomeruli in *P. annectens*, but I find them in the posterior kidney in the specimens of *P. aethiopicus* I examined (Fig. 1A). They differ little from anterior nephrons but have greater tubular diameters, as Jesperson ('69) noted. Anterior nephric tubules have outer diameters of approximately 0.1 mm (Fig. 2B), while posterior tubules have outer diameters of 0.15–0.3 mm. Capsules are approximately 0.13 mm wide and 0.15–0.2 mm high in both regions of the kidney. The tubule dilation may be due to the recent presence of sperm, for capsule and tubule may be packed with sperm at breeding season (Fig.

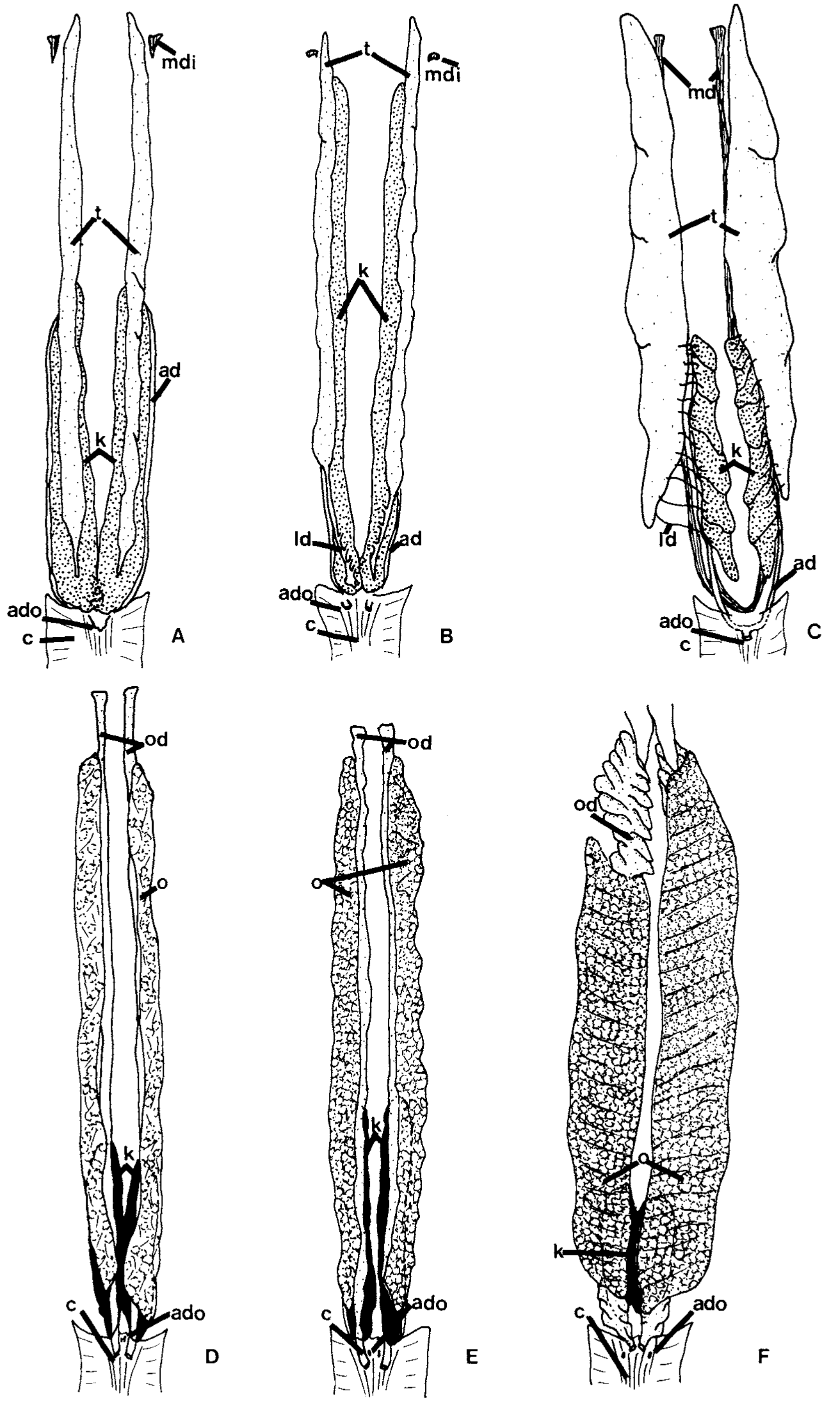


Fig. 1. Urogenital morphology of dipnoans. A) Male *Protopterus aethiopicus* (dissection, and after Kerr, '01). B) Male *Lepidosiren paradoxa* (dissection, and after Kerr, '01). C) Male *Neoceratodus forsteri* (dissection, and after Jesperson, '69). D) Female *Protopterus aethiopicus* (dissection). E) Female *Lepidosiren paradoxa* (dissection). F) Female *Neoceratodus forsteri* (dissection). Ventral view. Abbreviations: ad, archinephric duct; ado, archinephric duct orifice; b, bladder; c, cloaca; k, kidney; ld, lateral duct; md, Müllerian duct; mdi, Müllerian duct infundibulum; o, ovary; od, oviduct; t, testis. Not drawn to scale.

6D). The morphology suggests that the posterior nephrons are capable of urinary function. It is not known specifically whether they are functional at any time, nor is it known whether lungfish urine would inhibit sperm in any way. Smith ('30) found that *P. aethiopicus* urine is very dilute (16.5–18.8 mOsm/l) and contains 5 mEq/l of Na^+ and 3.5 mEq/l of $NH4^+$.

The modification of the kidney for sperm transport is distinctly different in dipnoans when compared with amphibians, which seems not to have been noted previously. In dipnoans the posterior kidney is involved in sperm transport, and the nephrons are essentially unmodified from typical urinary structures. In amphibians the *anterior* mesonephros is utilized for sperm transport if the kidney is used reproductively. In gymnophiones the nephrons are unmodified; in anurans and urodeles the nephrons are altered for sperm transport, usually lacking a capsule and glomerulus (see Wake, '70).

Development. Several workers have drawn attention to the similarity of dipnoan and amphibian pronephric development. In particular, Semon ('01), working on *Neoceratodus*, Kerr ('19) examining *Lepidosiren* and *P. annectens*, Kindahl ('37) and especially Fox, from work on *Neoceratodus* ('60, '61) and numerous urodeles (summarized in '63), indicated marked similarities of pattern. These similarities include: 1) A reduced number of pronephric units is present in larval dipnoans, urodeles, and anurans; 2) the pronephroi in these groups are related positionally to the anteriormost spinal nerves; and 3) the pronephric (archinephric) duct is similarly induced.

The pattern of development is indeed very similar, but the conclusion that ontogenetic similarity suggests an evolutionary relationship between dipnoans and amphibians is faulty. First, the similarity in number of functional nephrostomal units (two in larvae of all three dipnoan genera, two in a number of urodeles, and three in anurans) is a property of *derived* amphibian (and fish) taxa. In fact, the more primitive urodeles have up to five nephrostomial units (Fox, '63). The only gymnophione amphibian examined, *Hypogeophis rostratus*, has nine functional units (Brauer, '02), and the greater number is thought to represent the primitive condition. Many authors note that greater numbers of pronephric units develop in all of these taxa, but that many are eliminated or are nonfunctional. There is slight variation among dipnoans and amphibians in the body segment from which the functional pronephric units are derived (Fox, '63). Very few amphibians of each of the orders have actually been examined, and therefore there is inadequate information to permit generalizations on variation or patterns of change.

Pronephric development of few osteichthyans has been examined, and the available data are crucial to consideration of relationships. Fraser ('27) rigorously analyzed kidney development in the sturgeon *Acipenser* and Maschowzeff ('34–'35) examined *Salmo*, as well as the sturgeon, a frog, and a salamander. Fraser ('27) also carefully compared development among fishes and amphibians. She found that *Acipenser* has six nephrostomic units in the pronephros, derived from somites four through nine. This pattern also occurs in *Salmo*; it has three functional pronephric units which must be assumed to be the primitive actinopterygian condition. It seems logical that the pronephric units arise from the anterior-most body segments as a property of cephalized development. Fraser ('27) summarized her own work and the literature, with the following conclusions:

1. The pronephric chamber is segmented early on in cyclostomes, *Polypterus*, and gymnophione amphibians, but slightly later in chondrosteans (her "ganoids") and dipnoans. The pronephric chamber is recognizable as segmental only in terms of numbers of tubules in anurans and urodeles and is a single, never metameric chamber in teleosts.

2. In gymnophiones the pronephric nephrostomal units remain serial; in cyclostomes, chrondrosteans, *Polypterus*, and dipnoans the walls of the units break down, a limited occurrence in anurans and urodeles.

3. In cyclostomes, *Polypterus*, amphibians, and dipnoans the units open into the coelomic space; in chondrosteans only anterior units are open (the units of dipnoans close developmentally like those of chondrosteans); and the pronephric units of teleosts are closed off from the coelom. Goodrich ('30) also presented a useful summary of pronephric development. *Polypterus* (Kerr, '02) has two functional tubules, *Lepisosteus* three, *Amia* (Jungersten, 1900) three or four. The number varies among teleosts and includes retention of a functional pronephros in adults of some species. Elasmobranchs have three to seven functional units (Goodrich, '30).

It therefore seems apparent that chondrosteans, holostean neopterygians, amphibians, dipnoans, elasmobranchs, and even cyclostomes share a primitive pattern of pronephric development and structure. Reduction in number of pronephric units is a general derived state in *each* lineage. Teleosts show a similar pattern but with a greater diversity of derived states. In addition, mesonephric development shows considerable diversity among cyclostomes, elasmobranchs, primitive osteichthyans, dipnoans, teleosts, and amphibians. Therefore there are no shared derived states that support the hypothesis of a sister-group relationship between amphibians and dipnoans, unless one were to assume that gymnophiones are ancestral to sharks, osteichthyans, and other amphibians, and are a sister group to cyclostomes. The pattern is one of convergence in reduction of numbers of pronephric units in *all* vertebrate lineages. It seems that workers who saw the similarity in the pattern: 1) selected *among* amphibians to find data to support the hypothesis; 2) ignored the work on osteichthyans or chose not to compare them to dipnoans and amphibians; and 3) did not recognize that shared primitive character states and patterns of convergence do not provide evidence of relationship except at the most general level.

Gonads

The testis. The testes of dipnoans also have been described extensively. Günther (1871), Ballantyne ('28), and Jesperson ('69) have examined *Neoceratodus*, and Kerr ('01) has described *Lepidosiren* and *P. annectens.* I have examined material representing all three genera (one of the surprisingly few such examinations) and can largely corroborate earlier descriptions, while putting the patterns of development and of spermatogenesis in a more current context.

Dipnoan testes are elongate structures (Fig. 1A–C), bound to kidney and dorsal body wall by mesenteries, and overlain by fat, especially before the dry season, as Kerr ('01) noted. The testes are stout medially, tapering laterally. In *Protopterus* and *Lepidosiren* the posterior part of the testis is not spermatogenic, but is "vesicular" (Kerr, '01). The vesicular testis invades kidney tissue (Fig. 3C). *Neoceratodus* lacks a vesicular posterior region (Jesperson, '69; confirmed by my dissections). The vesicular region is described by Kerr ('01) as spongy, trabecular, and lacking spermatogenic tubules; this too is confirmed by the present study (Fig. 4B).

During the breeding season the spermatogenic part of the testis is filled with tubules containing mature sperm (Figs. 3A,B; 4A). The tubules are enlarged and have nests of primary spermatogonia peripherally, secondary spermatogonia somewhat more medially, and spermatids in the lumen (Figs. 3A,B; 4A). Tubules open into a longitudinal testis duct that extends posteriorly to a series of lateral ducts, the "vasa efferentia," which carry sperm to the nephrons as described below and illustrated by Jesperson ('69), Kerr ('01), and Goodrich ('30).

The regressed testis has much stromatous tissue. Tubules are reduced and few spermatogonia are stained, although a few mature sperm are still present (Fig. 3C).

Grier et al. ('80) reevaluated testicular morphology in several orders of teleosts and found two different tubular types. Salmoniform, perciform, and cypriniform fishes have spermatogonia distributed the length of the tubule; atheriniform fishes have spermatogonia only in the distal end of the tubule. My observations indicate that all three genera of dipnoans have a spermatogonial distribution identical to the salmoniform, perciform, and cypriniform type. Lungfish therefore share the primitive osteichthyan pattern with many teleosts and are unlike amphibians (reviewed in Wake, '79).

My material did not allow spermatogenesis to be traced. However, spermatogenesis and the fine structure of sperm have been examined by several workers. Agar ('11) described spermatogenesis in *Lepidosiren*, as did Boisson ('61, '63), and Boisson et al. ('67) in *P. annectens.* Jesperson ('71) described the fine structure of the sperm of *Neoceratodus*, and Boisson and Mattei ('65) and Purkerson et al. ('74) described spermatozoa of *P. aethiopicus.* Sperm of *Protopterus* have a long tapering head, a short middle piece, and two flagella each about twice the length of the head. The head piece of *Neoceratodus* is similar to that of *Protopterus*, but sperm of *Neoceratodus* have a single flagellum about three times the length of the head. Agar ('11) did not describe mature sperm of *Lepidosiren.* In my material the head pieces of *Lepidosiren* sperm are similar to those of other dipnoans, but the tail could not be distinguished. Purkerson et al. ('74) note that biflagellate sperm occur normally in diverse species of fishes. This appears to be a convergence, assuming that the monoflagellate state is primitive, and as such allows no evaluation of relationship.

The ovary. Very little attention has been paid to the morphology of the female urogen-

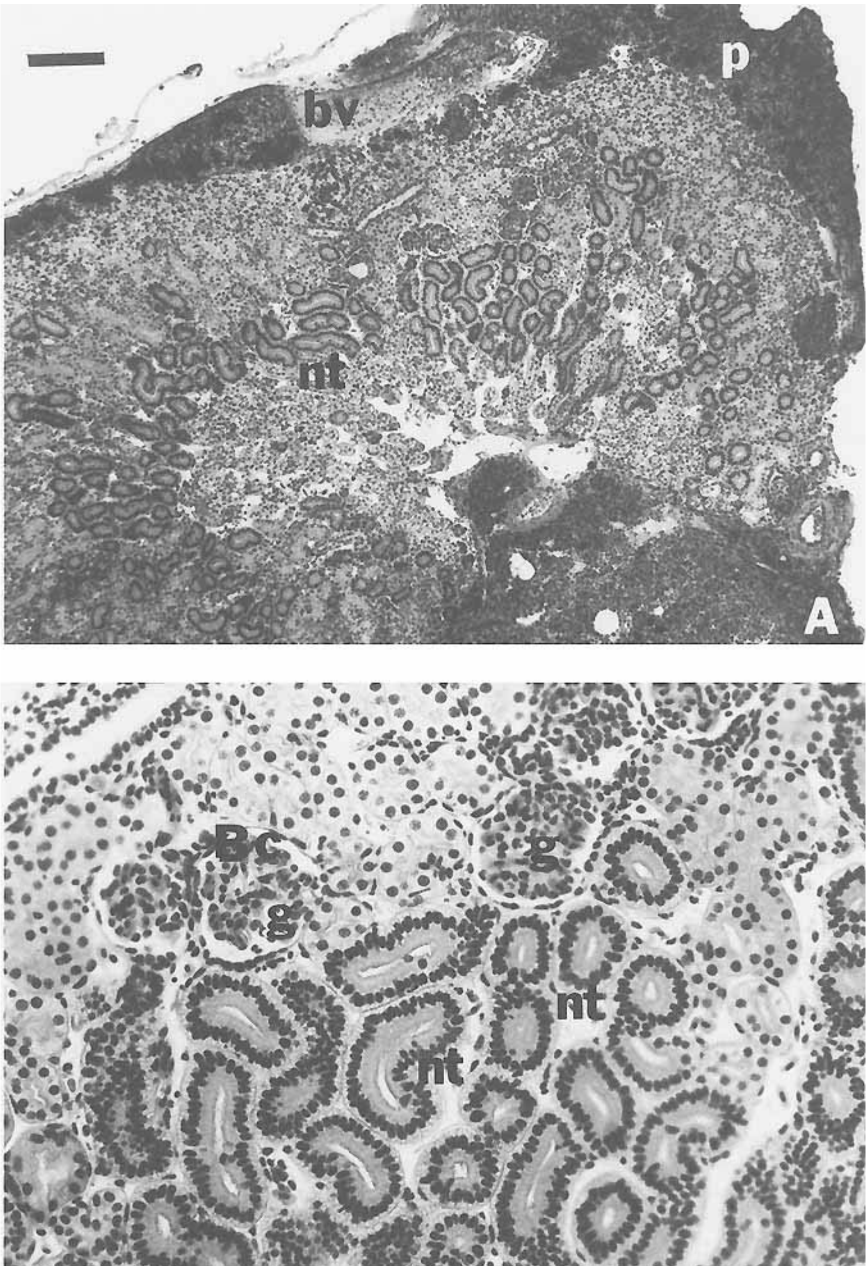
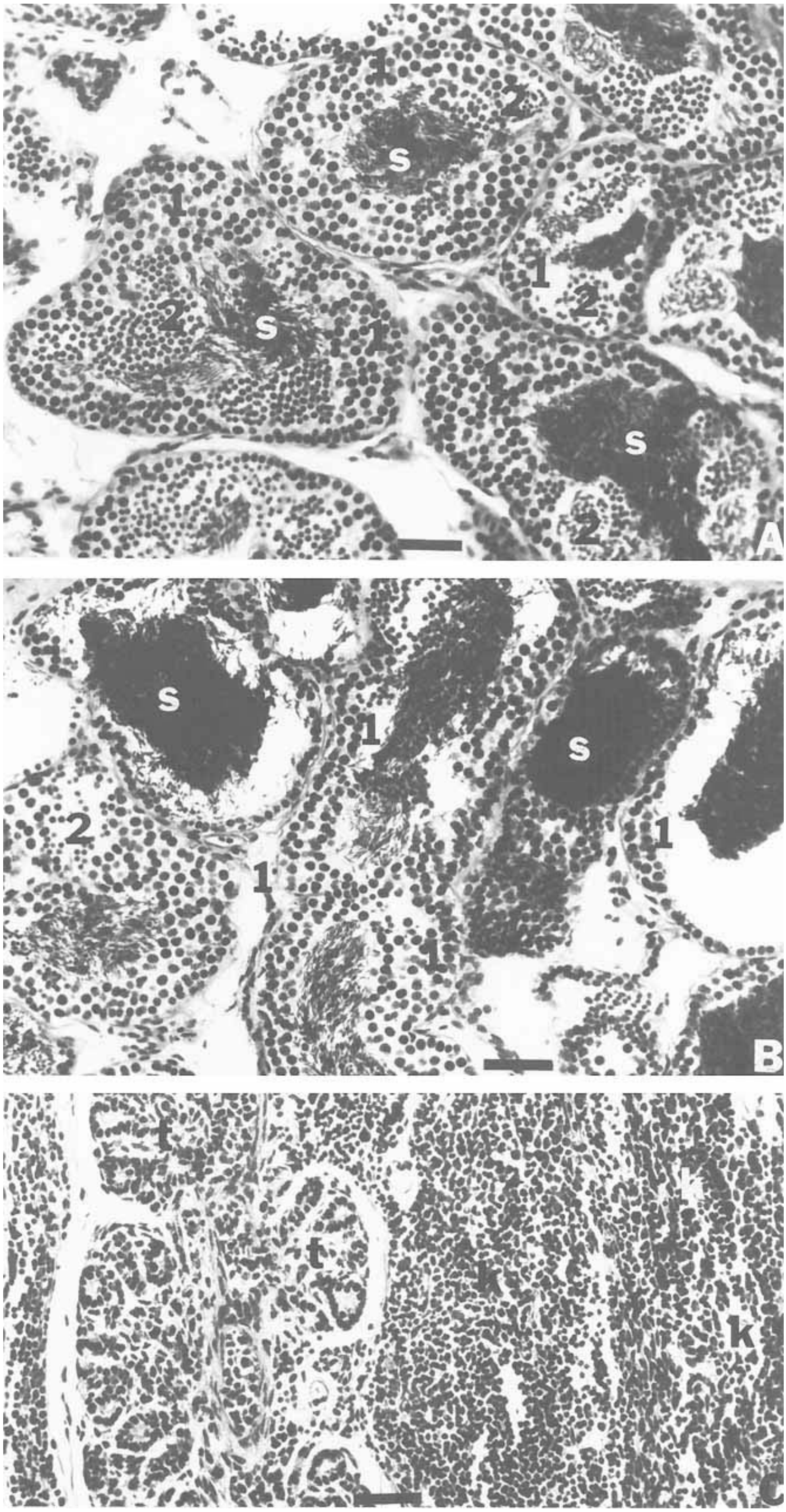


Fig. 2. Kidney structure in *Protopterus aethiopicus.* A) Posterior "vesicular" part of the kidney. Note the pigmented periphery, the orientation of tubules, and the large diameter of the nephric tubules. B) Anterior region of the kidney, illustrating large Bowman's capsules and glomeruli and the tubules of the "urinary" part of the kidney. Abbreviations: Bc, Bowman's capsule; bv, blood vessel; g, glomerulus; nt, nephric tubule; p, pigmented region. Scale bar in A, 0.4 mm; in B, 50 μm.

Fig. 3. Testis morphology of *Protopterus aethiopicus.* A) Spermatogenic tubules in transverse section. B) Tubules in longitudinal section. Note primary spermatogonia peripherally the length of the tubule, secondary spermatogonia somewhat more medially, and spermatids projecting into the lumen of the tubule. C) Vesicular part of the testis. Note absence of spermatozoa and invasion of testicular tubules into kidney tissue. Abbreviations: k, kidney; s, spermatids; t, spermatogenic tubule; 1, primary spermatogonia; 2, secondary spermatogonia. Scale bar, 50 μm.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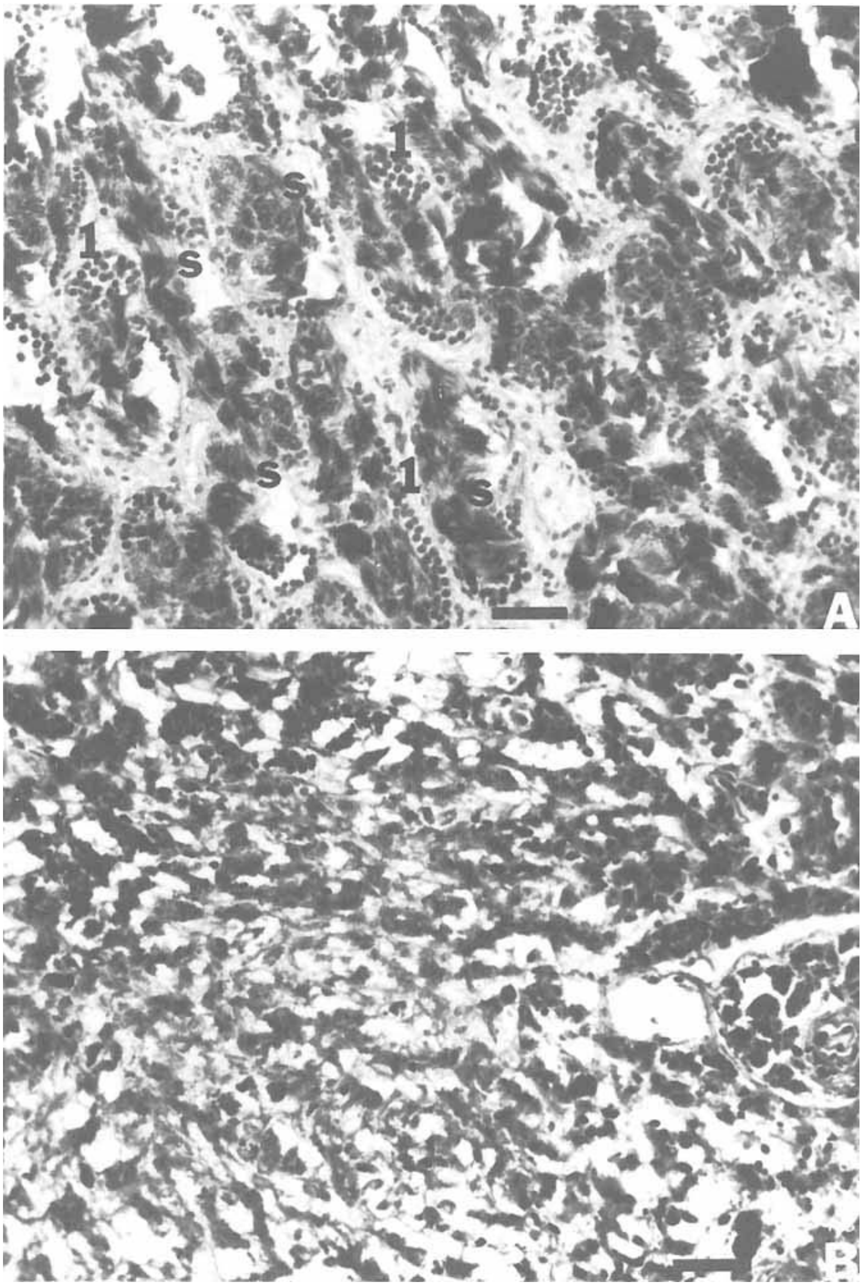


Fig. 4. Testis morphology of *Neoceratodus forsteri* and *Lepidosiren paradoxa*. A) Spermatogenesis in *Neoceratodus*. Tubules are elongate and lined with primary spermatogonia. Spermatids in the lumen are in small, sworled masses in contrast to the large amorphous mass of *Protopterus*. The tubules of *Neoceratodus* are smaller in diameter than those of *Protopterus*; both are large adult specimens. B) The vesicular region of the testis of *Lepidosiren*. It is "spongy" and virtually atubular. Abbreviations: s, spermatids; 1, primary spermatogonia; 2, secondary spermatogonia. Scale bar, 50 μm.

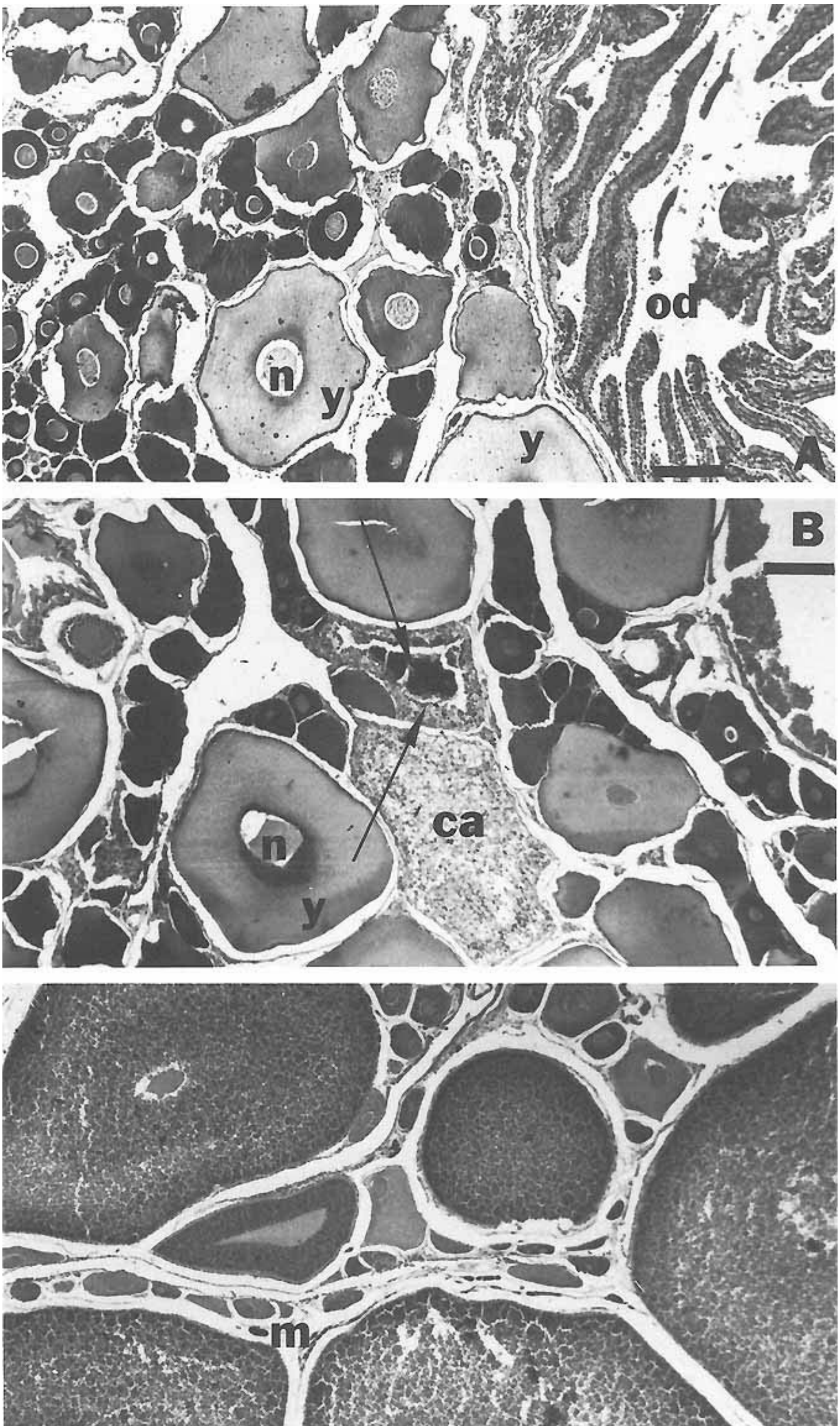
ital systems, perhaps because it presents a "typical vertebrate" pattern. Only the early descriptive work of Owen (1841), Ayers (1885), and Parker (1892) on *P. annectens*, and Günther (1871) on *Neoceratodus* contain substantive information, most of which has simply been restated by others. By dissecting adult females of each of the living genera and examining the female urogenital structures histologically, I corroborate their descriptions, 100 years later.

The ovaries are large, elongate structures that extend from near the heart to the posterior end of the kidneys (Fig. 1D–F). They are paired, and held to the dorsal body wall by a stout mesovarium. The ovaries are also tightly bound to the oviducts by a mesentery, as illustrated by Goodrich ('30).

Approximately 5,000 large mature oocytes ("ova") may be present in each ovary (extrapolated from my count of $46/cm^3$ of a mature *Neoceratodus* ovary 350-mm long, 40-mm wide most of its length, and 8 mm deep; the female was 560 mm standard length). Greenwood ('58; this volume) found more than 5,000 larvae in one *P. aethiopicus* nest and more than 2,000 in another and noted that the latter was an incomplete sample. Communal nesting is not likely. Ovaries of the females of the three genera that I examined all contained oocytes of three sizes and maturation (state of vitellogenesis) classes (Fig. 5). None appeared recently spent of mature ova. I have been unable to find data on size of mature ova. Ovarian oocytes of the largest size class in a large *Neoceratodus* are 3.0 mm in diameter (Fig. 5C). This probably represents full development, for Kemp ('81) illustrates a fertilized ovum beginning second cleavage at 3 mm diameter, which should reflect the size of eggs just laid and before any embryonic growth would have occurred. Kerr (1900) noted that the laid egg of *Lepidosiren* is very large (6.5–7.0 mm diameter) and surrounded by a capsule that is thick and jelly-like before fertilization but "thin and horny" after. The mature egg is unpigmented. Division is similar to that of large yolky eggs in diverse fish and amphibians (Kemp, '81; '82; this volume). Egg structure and vitellogenesis were described 100 years ago by Beddard (1886a,b). His description of ovum maturation in all three genera is basically accurate, though the terminology must be updated. His "germinal vesicle" is the unfertilized nucleus; the "vesicular dots" are nucleoli; plate 29 in Beddard (1886a) suggests the true vesicle, or enlarged, diplotene nucleus but does not label it. My histological examination of the ovaries of each of the three genera confirms Beddard's basic description, including staining characteristics of oocytes. In vitellogenic oocytes the yolk stains differently medially and peripherally. The nucleoli at that stage are adjacent to the nuclear envelope, and are numerous. Beddard (1886a) did not comment on the pigmentation of the ovary. Melanocytes are present in ovaries of all three genera; they are few and largely peripheral in *Protopterus* and *Lepidosiren*, whereas they are very numerous and distributed throughout the ovarian stroma as well as densely in the periphery of the ovary in *Neoceratodus* (see Fig. 4).

Beddard (1886a,b) paid much attention to what he called "multinuclear bodies" or "multinuclear ova" in the ovaries of the three genera. He described these as multicellular structures that coalesced, modified the follicular layer, and acquired yolk. At maturity, they were fully yolked and the equivalent of ova that had undergone the standard pattern of vitellogenesis. He constructed a sequence of development based on stages observed in his sections but of course could not trace a particular oocyte through development. I interpret his multicellular bodies rather differently. I consider that they are simply atretic follicles and that Beddard (1886a,b) construed their place in the sequence of development backward. I suggest that the bodies observed to have some yolk, multicellular invasion of the center of the follicle, and a modified follicle wall are early in atresia; those that lack yolk and have a fully cellular center and virtually no follicle wall are late in atresia and are being resorbed. I note numerous red blood cells in the cellular mesh of such bodies, which suggests capillary invasion during resorption (Fig. 5B), but Beddard made no mention of the presence of blood cells.

Ovarian structure and pattern of ovum development in dipnoans shed no light on dipnoan relationships. The pattern is a primitive one, shared with most osteichthyans and many amphibians, particularly frogs. Grodzinski's ('72) work on yolk structure in *Neoceratodus* indicates closest similarity to that of *Latimeria*. The yolk spheres are structurally the same, though much smaller in *Neoceratodus*. There is also some resemblance to elasmobranch yolk granules, particularly in boundary organization, but less similarity to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those of chondrosteans and holosteans which lack the peripheral organization of the yolk spheres.

The urogenital ducts and the cloaca

The urinary ducts

In development and function, the archinephric (mesonephric, Wolffian) ducts of female dipnoans are typical of female vertebrates in general, except teleosts. The archinephric duct transports urine from the adult mesonephric kidney to the cloaca. The ducts in all three genera are separate, rather than fused, as they enter the cloaca, according to Ayer's (1885) and Parker's (1892) figures and my observations (Fig. 1D–F).

Much more attention has been paid to the ducts of males, for the archinephric duct transports both urine and sperm. The lengthy literature is summarized by Jesperson ('69), and his own work on *Neoceratodus* sheds considerable light on the male system. In all three genera of lungfish, the archinephric duct drains the elongate kidney (Fig. 1A–C). In *Neoceratodus* 11–13 "vasa efferentia" (lateral ducts) connect the longitudinal testis duct to nephrons over the entire length of the kidney. The testis does not have discrete sperm-producing and vesicular components. Thus the archinephric duct evacuates urine, and also sperm during the breeding season, from the entire extent of the kidney. Sperm packing the nephrons and the archinephric duct are shown in Figure 6A,C,D. *Lepidosiren* has sperm transported from a tubular longitudinal testis duct extending through the vesicular part of the testis, where 5–6 lateral ducts lead to nephrons of the posterior part of the kidney (Fig. 1; Kerr, '01, '02). *Protopterus* had a reduced "testicular net" in which a single lateral duct extends from the longitudinal testis duct to several posterior nephrons (Fig. 1; Parker, 1892; Kerr, '01, '02).

The dipnoan situation differs significantly from that in amphibians. In gymnophiones the archinephric duct transports both sperm and urine and lateral ducts conduct sperm from the longitudinal testis duct to the mesonephrons, which lead to collecting ducts and then to the archinephric duct (Wake, '68, '70). The gymnophione testis is essentially unmodified for sperm transport. In urodeles the anterior part of the kidney is reduced, and in anurans it is reduced or lost; in dipnoans, as noted, the posterior part of the kidney is modified. The trend is for the archinephric duct to bear sperm from reduced anterior mesonephric tubules (received by lateral ducts from the longitudinal testis duct) and to bear a limited quantity of urine from the medial part of the kidney. A further trend in urodeles, and especially in anurans, is for the development *de novo* of a variable (by taxa) number of accessory ducts that evacuate urine to the cloaca from the posterior or urinary part of the kidney. Such accessory ducts do not occur in dipnoans. Jesperson ('69) notes that in *Polypterus* the testis duct opens into the distal part of the archinephric duct. He commented that *Lepisosteus* and *Acipenser* resemble *Neoceratodus*, with several lateral ducts leading from the short testes to the kidney. *Amia* (Jungersen, 1900) has numerous vasa efferentia that conduct sperm from the testis duct to a longitudinal kidney canal, then to the nephrons, and finally to the archinephric duct and the cloaca. Jesperson ('69) concluded that *Neoceratodus*, at least, showed a primitive osteichthyan pattern similar to that of primitive actinopterigians. Clearly, sperm transport in dipnoans differs significantly from that of amphibians, probably due to the constraint of the pattern of mesonephric reduction as noted above.

The oviducts

The oviducts are Müllerian duct derivatives that extend from near the heart to their entrance in to the cloaca dorsal to the urinary caecum. The full sequence of development has not yet been traced for any dipnoan, though Semon ('01) described several stages. Members of all three genera that I examined have slightly dilated infundibula (Fig. 1D–F). In all genera examined, adult females with yolky ovarian ova have ducts that are highly convoluted, hyperemic, and lined with a multi-layered secretory epithelium (Fig. 7B,C). The regressed duct of a specimen with very few large ova has a luminal epithelium without secretory cells and a much reduced diameter.

The primitive vertebrate state has the embryonic Müllerian ducts becoming the adult oviducts. Among osteichthyans, this pattern is retained by dipnoans, actinistians, chondrosteans, and some holostean neopterygi-

Fig. 5. Dipnoan ovaries. A) *Protopterus aethiopicus*. Ovary closely adheres to oviduct. Note stages of ovum development. Nuclei have numerous peripheral nucleoli. B) *Lepidosiren paradoxa*. Note ova in two different stages of atresia. The upper one (arrows) still contains some yolk; the lower is multicellular and the follicle is nearly disintegrated. C) *Neoceratodus forsteri*. Note large, yolky, (postvitellogenic) ova, a second class of vitellogenic ova, and a third class of slightly-yolked ova. Abbreviations: ca, corpus atretecum; m, melanocyte; n, nucleus; od, oviduct; y, yolk. Scale bar, 50 μm.

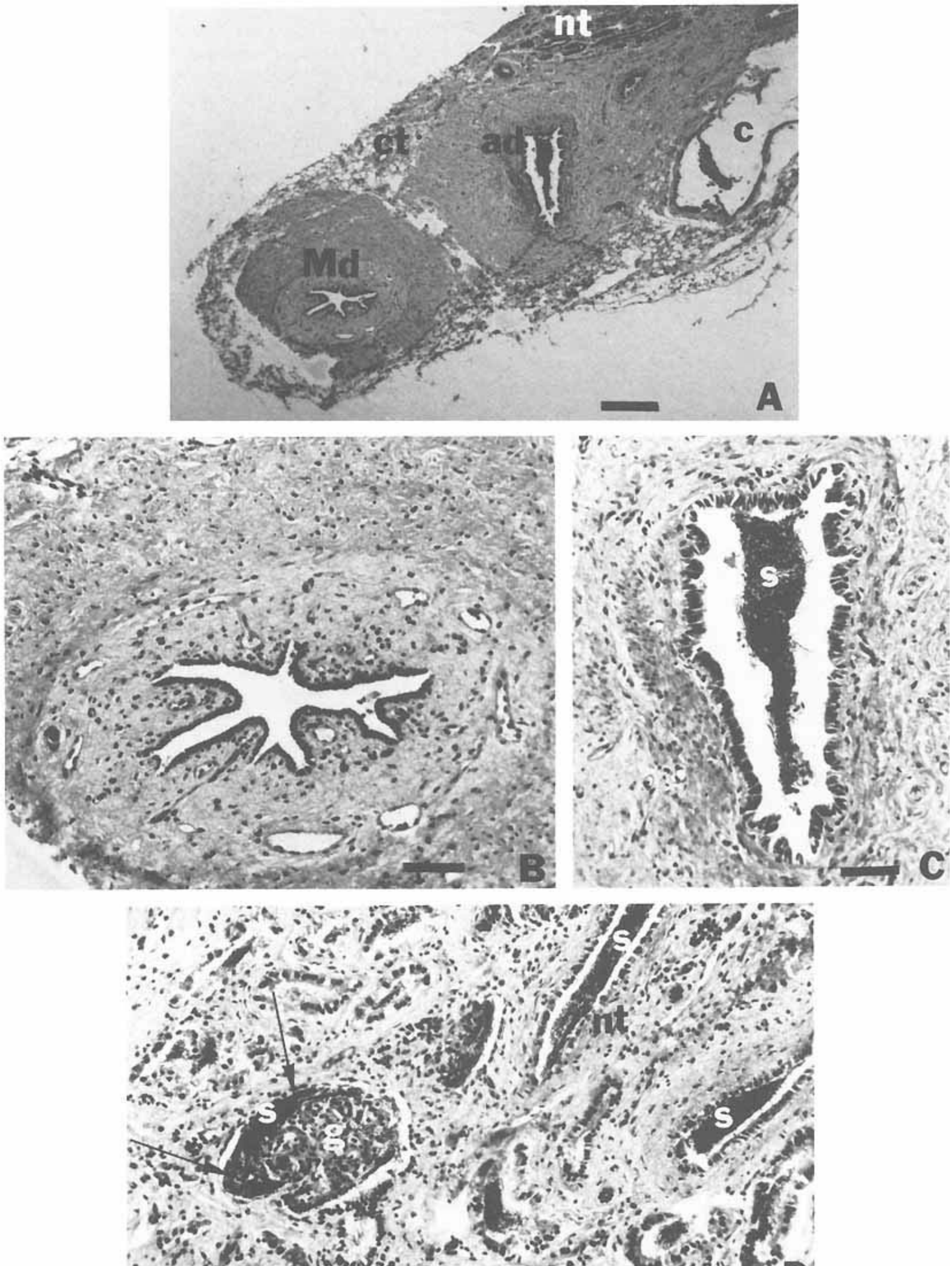


Fig. 6. Cloaca, archinephric duct, Müllerian duct, and posterior kidney of a male *Neoceratodus forsteri.* A) Transverse section of periphery of cloaca with ducts bound to cloaca by connective tissue. Section taken just above juncture of ducts with cloaca. B) Müllerian duct. Epithelium of lumen is not secretory. C) Archinephric duct. Note mass of sperm in lumen. D) Posterior kidney. Note glomerulus and tubules packed with sperm (arrows). Abbreviations; ad, archinephric duct; c, cloaca; ct, connective tissue; g, glomerulus; md, Müllerian duct; nt, nephric tubule; s and arrow, sperm. Scale bar in A, 0.4 mm; in B,C,D, 50 μm.

ans. The condition in which most neopterygians do not develop Müllerian ducts (their "oviducts" are therefore not homologous to those of other vertebrates) is a derived state (see Wake, '85). The presence of oviducts of dipnoans therefore gives no positive support to hypotheses of relationship using presence of Müllerian duct derivatives as a character. The abdominal pores of *Protopterus* opening by a single aperture was likened by Goodrich ('30) to the condition in "primitive osteichthyans," but this conclusion seems very tenuous.

The male Müllerian ducts

Males of all three genera of lungfish retain Müllerian ducts, at least to some extent. Those of *Neoceratodus* extend from the anterior end of the testis to the cloaca, where they fuse. They do not open to the cloaca (Jesperson, '69), as confirmed in my dissections (Fig. 1C) but *contra* Gunther (1871). Jesperson's ('69) Figure 4 shows the duct with a dilated infundibulum; I did not find such a dilation. The ducts are thin, non-functional, connective tissue strips.

In *Protopterus*, adult males retain vestiges of the infundibulum at the anterior end of the kidney, and a few millimeters of each duct posteriorly. The ducts unite in the wall of the cloaca. My dissection of *P. aethiopicus* revealed a condition similar to that described by Kerr ('01) for *P. annectens*, but the ducts do not reach the urogenital papilla in my specimen (Fig. 1A). The ducts are even more reduced in males of *Lepidosiren* (Fig. 1B). Only the anterior infundibula are present (the funnels of Kerr, '01). Kerr ('01) reported that additional vestiges of the ducts were present in a second-year male.

In amphibians, if Müllerian ducts are retained at all by males, they are represented only by connective tissue strips of varying lengths beside the kidneys or, as in gymnophiones, by connective tissue strips anteriorly followed by several millimeters of glandular tissue posteriorly. The lumen of the glandular portion opens into the cloaca. Wake ('81) suggested that this secretory activity in the male Müllerian duct of amphibians is correlated with internal fertilization and terrestriality. I find no indication of secretory cells in the posterior ducts of *Neoceratodus* (Fig. 5B) and *P. aethiopicus*. The retention of anterior components and the lack of effective association with the cloaca by lungfish is distinctly different from the situation in amphibians that retain the ducts.

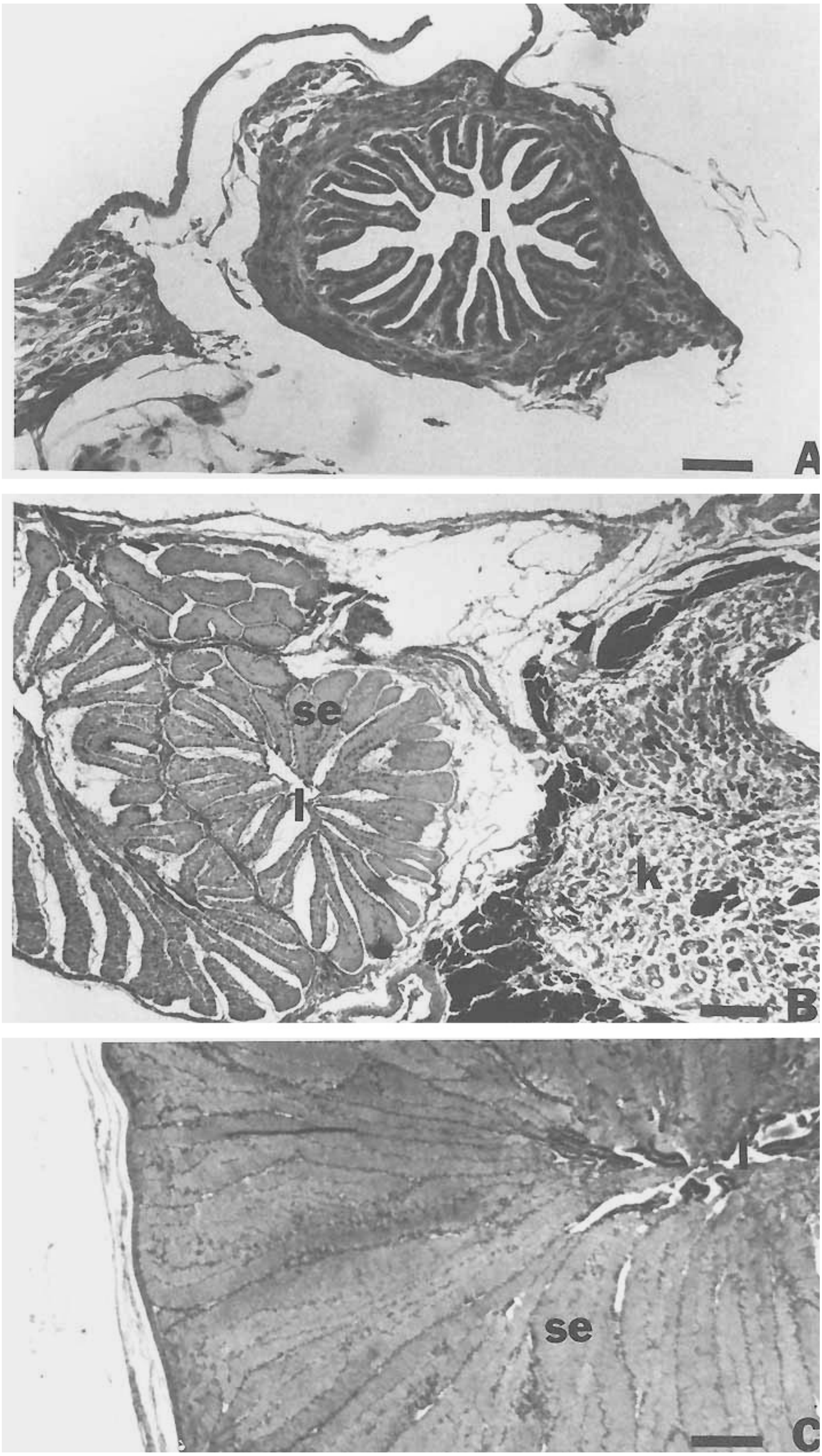
Abdominal pores

Despite the reports of a single abdominal pore in *Lepidosiren* (Owen, 1841) and paired pores in *Neoceratodus* (Gunther, 1871), it seems reasonable that the large numbers of mature ova of all genera are borne to the cloaca via the convoluted, glandular oviducts and extruded via the vent. The pores are located at the vent opening just beyond the cloaca (but may be variable according to Owen, 1841), and the oviducts open into the cloaca anteriorly. Bles (1898) noted that *Lepidosiren* lacks pores, in contradiction to Owen's 1841 report. The abdominal pores are therefore likely not associated with ovum transport as Goodrich ('30) also stated. Bles (1898) argued that the abdominal pores are excretory, alluding to data on kidney-gonad development that are unclear to me. They may be vestigial, or involved in other fluid flow, as Goodrich ('30) suggested.

The cloaca

All three genera of dipnoans retain a simple cloaca (Fig. 1) with the urinary ducts opening by a single aperture (Jesperson, '69, *Neoceratodus*; Kerr, '01, *Lepidosiren* and *P. annectens*). All three genera have a urinary caecum or bladder. Kerr ('01) considered the caecum to be an anteriorly projecting dilation of the fused urinary ducts, or the urogenital sinus. The amphibian bladder is an outpocketing of the cloaca. In males the archinephric (testis) ducts open separately on the dorsal wall of the cloacal caecum at its juncture with the cloaca proper (Fig. 1A–C). Kerr ('01) noted that each aperture is marked by a prominent papilla during the breeding season in *P. annectens* and *Lepidosiren*. I observed slight prominences at the openings in spermatogenic specimens of *Lepidosiren*, *P. aethiopicus*, and *Neoceratodus*, but I do not know if these were in breeding condition. Goodrich ('30) illustrates genital and urinary papillae in a female *P. annectens*. My dissections of females of all three genera of dipnoans revealed slight rings of tissue at these apertures but not pronounced papillae. The rectal portion of the intestine is dilated and narrows slightly at its juncture with the cloaca. The vent opens to the left of the tail fin in the specimens I examined.

Lagios and McCosker ('77) report the presence of a cloacal gland in *P. aethiopicus* and *P. dolloi*, and its absence in *Neoceratodus* and *Lepidosiren*. The gland is dorsal and posterior to the urinary caecum and opens into the cloaca at the juncture of the caecum with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the cloaca. Lagios and McCosker ('77) suggest that the gland may be cation-secreting, functionally similar to the rectal glands of elasmobranchs, holocephalans, and *Latimeria*, though the anatomical relationship differs from that of the latter groups. The sizes of Lagios and McCosker's ('77) specimens were not indicated; I cannot determine whether they looked for age or sex differences in the morphology of the gland.

Presence of a cloaca is of course the primitive vertebrate pattern, and all bony fish that lack a cloaca are derived.

The "adrenal"

Several workers have cited the "amphibian characteristics" of the interrenal or adrenocortical homolog tissue of dipnoans (Chester Jones and Mosley, '80; Janssens et al., '65; Call and Janssens, '75). Such tissue has been identified in *Protopterus* (Gerard, '54; Janssens et al., '65) (species not listed) and in *Neoceratodus* (Call and Janssens, '75) based on morphology and histochemistry. Cord-like cell groups located on the postcardinal veins and their tributaries between renal and perirenal tissue converted progesterone to corticosterone when tested *in vitro*, and tested positively for cholesterol (Call and Janssens, '75). No chromaffin tissue was found in either genus (Call and Janssens, '75). The position and histochemical characteristics of the interrenal tissue in *Protopterus* and *Neoceratodus* were considered to be very similar to those of interrenal tissue in adult *Pleurodeles* (Certain, '61), a urodele, and the larvae of certain frogs (Chester Jones and Mosley, '80).

An examination of the position and cellular characteristics suggests that the similarity of dipnoan and amphibian interrenals is a tenuous one. The interrenal of *Latimeria* has a large number of corpuscles in the walls and along the extent of the postcardinals and their tributaries in the kidney (Lagios and Stasko-Concannon, quoted in Chester Jones and Mosley, '80). *Acipenser* has a similar interrenal distribution along the cardinals and their tributaries beside and within the kidney (Youson and Butler, '76a); corpuscles are found throughout the kidney, but primarily in the reduced anterior two-thirds of the kidney. Corpuscles lie in the anterior two-thirds of the kidney of the brachiopterygian *Polypterus* (Youson and Butler, '85). A similar situation obtains in *Polyodon* (Lagios and Stasko-Concannon, quoted in Chester Jones and Mosley, '80) and in the neopterygian "holostean" *Amia* (Youson and Butler, '76b). In the neopterygian *Lepisosteus*, corpuscles are in the anterior half of the kidney (Bhattacharyya et al., '81). As Youson and Butler ('85) point out, the distribution of adrenocortical corpuscles offers little to support (or negate) current hypotheses of the taxonomic status of the "primitive" osteichthyans. Among teleosts, interrenal tissue is confined to the head kidney, so far as is known, which is largely lymphoid and hemopoietic tissue. I found no information about the interrenal tissue of teleosts that: 1) lack a head kidney (*sensu* Nandi, '62); or 2) retain a functional pronephros throughout life, as do some teleosts (*Zoarces*, for example). When one examines the data on interrenal tissue for amphibians, one quickly realizes that there is no common amphibian pattern, despite assertions in the literature. Dittus ('36) considered the gymnophione condition primitive for amphibians. The interrenal tissue starts anterior to the kidney and is associated with the aorta. Masses of interrenal tissue extend posteriorly in the entire extent of the kidney associated with post-cardinal and renal vessels. Tissue may also lie medial to the kidneys or embedded in the medial kidney tissue, especially ventrally (see also Gabe, '71). Urodele interrenal tissue shows considerable variation, from association with blood vessels only in *Siren*, to being embedded in the kidney along the renal vessels in *Amphiuma*, and embedded and concentrated anteriorly in *Necturus* (Hartman and Brownell, '49) and several other diverse species (Hanke, '78). Anurans usually have interrenal tissue concentrated as a longitudinal mass on the ventral side of each kidney associated with branches of the renal vein.

The literature is contradictory with regard to dipnoans. Chester Jones and Mosley ('80:422) state that "the adrenocortical homologue consists of small cells closely associated with the post-cardinal veins and their

Fig. 7. Dipnoan oviducts. A) Regressed duct in *Protopterus aethiopicus*. The ovary of the specimen lacked large yolky ova; thus I infer that it is post-breeding. B) *Lepidosiren paradoxa* oviduct bound to posterior part of the kidney. The epithelium of the lumen is proliferated and secretory. C) *Neoceratodus forsteri* oviduct in a hyperemic, secretory state. The ovary contained large ova; thus I infer that ovulation is imminent, and the oviduct ready to transport ova. Little appears to be known of endocrine regulation of breeding in dipnoans. Abbreviations: k, kidney; l, lumen of oviduct; se, secretory epithelium. Note that all three specimens are photographed to the same scale. Bar, 50 μm.

tributaries where these vessels pass through the kidneys." Balment et al. ('80:529) claim that "jawed fish, teleosts and elasmobranchs" share a common association with the cardinal vein and pronephric-mesonephric units, but they state that dipnoans have an amphibian-type interrenal associated with kidney tissue. Hanke ('78) defines the amphibian characteristic as a "close association [of interrenal tissue] with kidney cells, separated from the tubules only by a basement membrane and a thin layer of connective tissue." The "amphibian characteristic" does *not* obtain for many amphibians and appears to be a derived state among some urodeles and most frogs. This is probably a convergence within amphibians, since some frogs show a more primitive condition. It appears then that urodeles and anurans (and gymnophiones) followed independent evolutionary courses to their particular states, although it should be noted that information is available only for primitive gymnophiones (Dittus, '36). The interrenal morphology of *Protopterus* (see Janssens et al., '65) approaches the "amphibian characteristic" less closely than does *Neoceratodus* (see Call and Janssens, '75) and is clearly associated with postcardinal and renal veins. Dipnoan interrenals, while resembling those of *selected* amphibians, also resemble to some degree those of chondrosteans and *Latimeria*. Chester Jones ('57) suggested teleost and crossopterygian affinities before he emphasized the "amphibian" features.

I concur with Lagios and Stasko-Concannon (in Chester Jones and Mosley, '80) that the diffuse distribution of interrenal tissue along the cardinal veins and their branches is a primitive condition in vertebrates. A number of lineages often have modified that pattern in different ways, apparently independently. There are no shared derived characters of the interrenals that ally dipnoans with amphibians as a group, or with urodeles in particular. There are, however, some convergences among derived genera in several fish and amphibian lineages.

CONCLUSIONS

It is apparent that analysis of the comparative biology and evolution of the dipnoan urogenital system is incomplete for several reasons: 1) lack of direct comparison of members of all three genera; 2) lack of information for many primitive osteichthyans and for an effective representation of the diversity of teleosts; 3) lack of any attempt to compare dipnoans with other fish taxa for which information is available; and 4) an almost dogmatic assumption that amphibian morphology provides information crucial to understanding dipnoan biology. Some very general but similar aspects of dipnoan and amphibian biology suggest that bases for similarity should be explored, but that exploration has rarely been done on an appropriate scale. Further, comparisons with amphibians have usually been made with highly selected species, not considering whether the species were primitive and representative of the entire amphibian grade, or exhibiting states derived for particular lineages and therefore indicative of convergence if "shared" by dipnoans and one or more amphibian species. As indicated above, analysis of urogenital morphology almost invariably indicates one of three conclusions: 1) Dipnoans share a primitive vertebrate pattern with fishes and with amphibians; 2) dipnoans share general features with many osteichthyans, and various teleostean lineages are derived; and 3) the derived features shared by dipnoans and *some* amphibian species are not those of the order, let alone the class, and often not even the family of amphibians being compared. Therefore, convergence, not relationship, must be inferred. In general, the data do not support hypotheses of dipnoans being the sister group of tetrapods. Urogenital system morphology is more similar to that of actinistians, chondrosteans, and primitive teleosts, but there are few shared derived characters of the urogenital system to ally even these groups (Fraser, '27, lists some). This is not to say definitively that dipnoans are not the sister group of tetrapods, but that support for that hypothesis (and most others) must come from other systems.

Urogenital morphology does, however, provide support for the familial allocation of dipnoans, in agreement with osteology (Marshall, this volume), myology (Bemis, this volume), and numerous other features (Goodrich, '30). *Lepidosiren* and *Protopterus* have four synapomorphies; *Protopterus* and *Neoceratodus* each have an autapomorphy (see Fig. 8). These data support the inclusion of *Lepidosiren* and *Protopterus* in a family separate from *Neoceratodus*. Even these data are incomplete. For example, *Neoceratodus* has uniflagellate sperm and *Protopterus* biflagellate, as noted above. However, there is no comparable information about the sperm of *Lepidosiren*; thus the difference between *Lepidosiren* and *Neoceratodus* is not a useful character.

Examples of paucity of complete information for most aspects of urogenital morphology have been indicated in several instances above. Therefore my first goal, that of providing a direct comparison of all three genera of dipnoans, is not yet completely fulfilled. First, more basic data on structure and development of the urogenital system of dipnoans, non-teleostean osteichthyans, various teleosts, and a greater diversity of amphibians of all three orders are needed. These should be provided systematically, using modern technology. Second, an objective cross-comparison of *many* taxa must be undertaken. Third, hypotheses of relationship must be structured rigorously, and alternative hypotheses also considered. Identification of character states should be done according to current methods, with assessment of polarities and analysis of grades and clades, not by comparisons of just randomly (or worse, subjectively) chosen species. With these three criteria met, analysis of the urogenital system should provide insight into the functional biology of the system and its pattern of diversification, thereby giving clues to the evolutionary relationships of dipnoans to other vertebrates.

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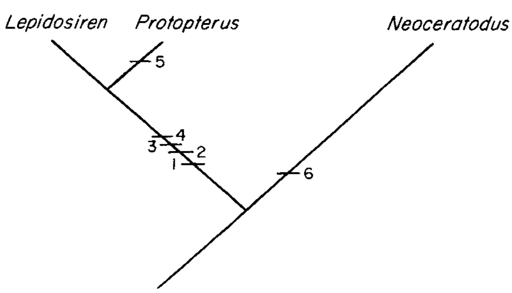

Fig. 8. Cladogram of dipnoan interrelationships based on urogenital morphology. Many symplesiomorphies ally the two groups of genera. Synapomorphies of *Protopterus* and *Lepidosiren* are: kidney divided into urinary and "vesicular" regions (1); testis divided into spermatogenic and vesicular regions (2); reduced number of "vasa efferentia" (3); reduced male Müllerian duct (4). The *Protopterus* autapomorphy (5) is the presence of the cloacal gland, that of *Neoceratodus* (6) is the invasive pigmentation of the ovary.

LITERATURE CITED

Agar, W.E. (1911) The spermatogenesis of *Lepidosiren paradoxa*. Q. J. Microsc. Sci. *57*:1–44.

Ayers, H. (1885) Beiträge zur Anatomie und Physiologie der Dipnoer. Z. Naturwiss. Jena *18*:479–527.

Ballantyne, F.M. (1928) Note on the male genito-urinary organs of *Ceratodus forsteri*. Proc. Zool. Soc. Lond. *1928*:697–698.

Balment, R.J., I.W. Henderson, and I. Chester Jones (1980) The adrenal cortex and its homologues in vertebrates; evolutionary comparisons. In I. Chester Jones and I.W. Henderson (eds): General, Comparative and Clinical Endocrinology of the Adrenal Cortex. London: Academic Press, pp. 525–562.

Beddard, F.E. (1886a) Observations on the ovarian ovum of *Lepidosiren* (*Protopterus*). Proc. Zool. Soc. Lond. *1886*:272–292.

Beddard, F.E. (1886b) Observations on the development and structure of the ovum in the Dipnoi. Proc. Zool. Soc. Lond. *1886*:502–527.

Bhattacharyya, T. K., D. G. Butler, and J. H. Youson (1981) Distribution and structure of the adrenocortical homolog in the garpike. Am. J. Anat. *160*:231–246.

Bles, E. J. (1898) The correlated distribution of abdominal pores and nephrostomes in fishes. J. Anat. Physiol. *32*:484–512.

Boisson, D. (1961) La spermatogénèse de *Protopterus annectens* (Dipneuste) du Sénégal. Ann. Fac. Sci. univ. Dakar *6*:133–144.

Boisson, C. (1963) La spermiogénèse de *Protopterus annectens* (Dipneuste) du Sénégal étudiée au microscope optique et quelques détails au microscope électronique. Ann. Fac. Sci. Univ. Dakar *10*:43–72.

Boisson, C., and X. Mattei (1965) A propos de l'acrosome des spermatozoïdes du Dipneuste *Protopterus annectens* Owen. C. R. Soc. Biol. Paris *159*:2247–2249.

Boisson, C., C. Mattei, and X. Mattei (1967) Troisième note sur la spermiogénèse de *Protopterus annectens* (Dipneuste) de Sénégal. Bull. Inst. Fondam. Afr. Noire Ser. A. Sci. Nat. *29*:1097–1121.

Brauer, A. (1902) Beitrag zur Kenntnis der Entwicklung and Anatomie der Gymnophionen. III. Entwicklung der Excretionsorgane. Zool. Jl. Anat. *3*:1–176.

Call, R. N., and P. A. Janssens (1975) Histochemical studies of the adrenocortical homologue in the kidney of the Australian lungfish, *Neoceratodus forsteri*. Cell Tissue Res. *156*:533–538.

Certain, P. (1961) Organogénèse des formations interrénales chez le bactracien urodèle *Pleurodeles waltlii*. Mich. Bull. Biol. France-Belgique *95*:134–148.

Chester Jones, I. (1957) The Adrenal Cortex. London: Cambridge University Press.

Chester Jones, I., and W. Mosley (1980) The interrenal gland in Pisces. In I. Chester Jones and I. W. Henderson (eds): General, Comparative and Clinical Endocrinology of the Adrenal Cortex. New York: Academic Press, pp. 395–472.

Dittus, P. (1936) Interrenalsystem und chromaffine Zellen im Lebenslauf von *Ichthyophis glutinosus*. Z. Wiss. Zool. *147*:459–512.

Fox, H. (1960) Early pronephric growth in *Neoceratodus* larvae. Proc. Zool. Soc. Lond. *134*:659–663.

Fox, H. (1961) The segmentation of components in the hind region of the head of *Neoceratodus* and their relation to the pronephric tubules. Acta Anat. *47*:156–163.

Fox, H. (1962) A study of the evolution of the amphibian and dipnoan pronephros by an analysis of its relationship with anterior spinal nerves. Proc. Zool. Soc. Lond. *138*:225–256.

Fox, H. (1963) The amphibian pronephros. Q. Rev. Biol. *38*:1–25.

Fraser, E. A. (1927) Observations on the development of the pronephros of sturgeon, *Acipenser rubicundus*. Q. J. Microsc. Sci. *71*:75–112.

Fraser, E. A. (1950) The development of the vertebrate excretory system. Biol. Rev. *25*:159–187.

Gabe, M. (1971) Données histologiques sur la glande surrénale d'*Ichthyophis glutinosus*. Arch. Biol. (Liège) *82*:1–23.

Gerard, P. (1954) Organes uro-génitaux. In P. P. Grasse (ed): Traité de Zoologie. Vol. 12. Paris: Masson Publ., pp. 974–1043.

Goodrich, E. S. (1930) Studies on the Structure and Development of Vertebrates. (Republished by Dover Publications, Inc., New York, 1958)

Greenwood, P. H. (1958) Reproduction in the East African lung-fish *Protopterus aethiopicus* Heckel. Proc. Zool. Soc. Lond. *130*:547–567.

Grier, H. J., J. R. Linton, Q. F. Leatherland, and V. L. de Vlaming (1980) Structural evidence for two different testicular types in teleost fishes. Am. J. Anat. *159*:331–345.

Grodzinski, Z. (1972) The yolk of *Neoceratodus forsteri* Krefft (Dipnoi-Pisces). Acta Biol. Cracov. Ser. Zool. *15*:193–199.

Günther, A. (1871) Description of *Ceratodus*, a genus of ganoid fishes, recently discovered in rivers of Queensland, Australia. Trans. R. Soc. Lond. *161*:511–571.

Hanke, W. (1978) The adrenal cortex of Amphibia. In I. Chester Jones and I. W. Henderson (eds): General, Comparative and Clinical Endrocrinology of the Adrenal Cortex. Vol. 2. London: Academic Press, pp. 419–495.

Hartman, F. A., and K. A. Brownell (1949) The Adrenal Gland. Philadelphia: Lea and Febiger.

Hickman, C.P., Jr., and B. F. Trump (1969) The Kidney. In W. S. Hoar, and D. J. Randall (eds): Fish Physiology. Vol. 1. New York: Academic Press, pp. 91–239.

Janssens, P. A., G. P. Vinson, I. Chester Jones, and W. Mosely (1965) Amphibian characteristics of the adrenal cortex of the African lungfish (*Protopterus* sp.). J. Endocrinol. *32*:373–382.

Jesperson, A. (1969) On the male urogenital organs of *Neoceratodus forsteri*. Biol. Skr. Dan. Vidensk. Selsk. *16*:1–11.

Jesperson, A. (1971) Fine structure of the spermatozoon of the Australian lungfish *Neoceratodus forsteri* (Krefft). J. Ultrastruct. Res. *37*:178–185.

Jungersen, H. F. E. (1900) Ueber die Urogenital-organe von *Polypterus* and *Amia*. Zool. Anz. *23*:328–334.

Kemp, A. (1981) Rearing of embryos and larvae of the Australian lungfish, *Neoceratodus forsteri*, under laboratory conditions. Copeia *1981*:776–784.

Kemp, A. (1982) The embryological development of the Queensland lungfish, *Neoceratodus forsteri* (Krefft). Mem. Qd. Mus. *20*:553–597.

Kerr, J. G. (1900) The external features in the development of *Lepidosiren paradoxa*. Trans. R. Soc. Lond. *192*:299–330.

Kerr, J. G. (1901) On the male genito-urinary organs of the *Lepidosiren* and *Protopterus*. Proc. Zool. Soc. Lond. *1901*:484–498.

Kerr, J. G. (1902) The genito-urinary organs of dipnoan fishes. Proc. Cambridge Philos. Soc. *11*:329–333.

Kerr, J.G. (1919) Textbook of Embryology. Vol. II. Vertebrata. London: MacMillan and Co.

Kindahl, M. (1937) Zur Entwicklung der Exkretionsorgane von Dipnoern und Amphibien. Acta. Zool. (Stockh.) *19*:1–190.

Lagios, M.D., and J.E. McCosker (1977) A cloacal excretory gland in the lungfish *Protopterus*. Copeia *1977*:176–178.

Maschkowzeff, A. (1934–1935) Zur Phylogenie der Geschlechtsdrüsen und der Geschlechts-ausführgange bei den Vertebrata auf Grund von Forschungen betreffend die Entwicklung des Mesonephros und der Geschlechtsorgane bei den Acipenseridae, Salmoniden und Amphibien. Zool. Jb. Anat. *59*:1–68, 201–276.

Miles, R.S. (1977) Dipnoan (lungfish) skulls and the relationships of the group: A study based on new species from the Devonian of Australia. Zool. J. Linn. Soc. *61*:1–328.

Nandi, J. (1962) The structure of the interrenal gland in teleost fishes. Univ. Calif. Publ. Zool. *65*:129–212.

Owen, R. (1841) Description of the *Lepidosiren annectens*. Trans. Linn. Soc. Lond. *18*:327–361.

Parker, W.N. (1892) On the anatomy and physiology of *Protopterus annectens*. Trans. R. Irish Acad. *30*:109–216.

Purkerson, M.L., J.U.M. Jarvis, S.A. Luse, and E.W. Dempsey (1974) Analysis coupled with scanning and electron microscopic observations of spermatozoa of the African lungfish, *Protopterus aethiopicus*. J. Zool. (Lond.) *172*:1–12.

Romer, A.S. (1966) Vertebrate Paleontology. Chicago: University of Chicago Press.

Rosen, D.E., P.L. Forey, B.G. Gardiner, and C. Patterson (1981) Lungfishes, tetrapods, paleontology, and plesiomorphy. Bull. Am. Mus. Nat. Hist. *167*:159–276.

Semon, R. (1901) Zur Entwicklungsgeschichte des Urogenitalsystems der Dipnoer. Zool. Anz. *24*:131–135.

Smith, H.W. (1930) Metabolism of the lungfish, *Protopterus aethiopicus*. J. Biol. Chem. *88*:97–130.

Thomson, K.S. (1969) The biology of the lobe-finned fishes. Biol. Rev. (Cambridge) *44*:91–154.

Torrey, T.W. (1965) Morphogenesis of the vertebrate kidney. In R.L. DeHaan and R. Ursprung (eds): Organogenesis. New York: Holt, Rinehart and Winston, pp. 559–579.

Wake, M.H. (1968) Evolutionary morphology of the caecilian urogenital system. Part I. The gonads and fat bodies. J. Morphol. *126*:291–332.

Wake, M.H. (1970) Evolutionary morphology of the caecilian urogenital system. Part II. The kidneys and the urogenital ducts. Acta Anat. *75*:321–358.

Wake, M.H. (1979) The comparative anatomy of the urogenital system. In M.H. Wake (ed): Hyman's Comparative Vertebrate Anatomy. 3rd Ed. Chicago: University of Chicago Press, pp. 555–614.

Wake, M.H. (1981) Structure and function of the male Müllerian gland in caecilians (Amphibia: Gymnophiona), with comments on its evolutionary significance. J. Herpet. *15*:17–22.

Wake, M.H. (1985) Oviduct structure and function in non-mammalian vertebrates. In H.-R. Duncker and G. Fleischer (eds): Functional Morphology of Vertebrates. Fortschr., Zool., *30*:427–435.

Youson, J.H., and D.G. Butler (1976a) The adrenocortical homolog in the Lake Sturgeon, *Acipenser fulvescens*. Rafinesque. Am. J. Anat. *145*:207–224.

Youson, J.H., and D.G. Butler (1976b) Fine structure of the adrenocortical homolog and the corpuscles of Stannius of *Amia calva* L. Acta Zool. (Stockh.) *57*:217–230.

Youson, J.H., and D.G. Butler (1985) Distribution and structure of the adrenocortical homolog in *Polypterus palmas* Ayres. Acta Zool. (Stockh.) *66*:131–143.