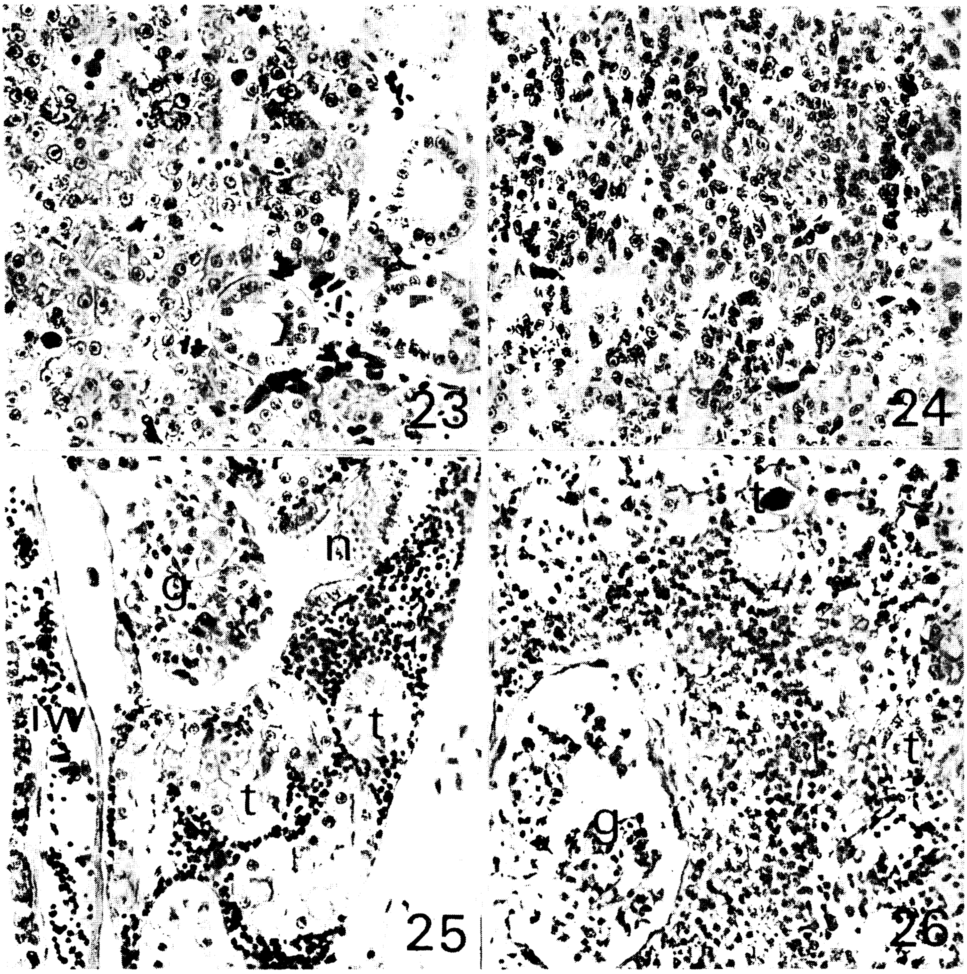


Fig. 23. Liver of 60 mm-long ammocoetes caught in January. Note bile ducts on the right. Dark cells are mainly erythrocytes. ×280.

Fig. 24. Liver of immature adult (male) caught in January. ×280.

Fig. 25. Kidney of 83 mm-long ammocoetes caught in June. Note hematopoietic activity in intertubular tissue. g, glomerulus; iw, intestinal wall; n, neck segment; t, urinary tubule. ×280.

Fig. 26. Kidney of stage 5 lamprey caught in October. Note degeneration of glomerulus (g) and tubules (t). ×280.

The epithelial cells of the intestine were occasionally ciliated, not only in ammocoetes, but also in adults.

The typhlosole is a hematopoietic organ in ammocoetes (Fig. 18) and may be regarded as the primitive spleen. The hematopoietic stem cells aggregated in a dense mass especially at the region distal to the typhlosolar artery. The hematopoietic activity as judged from density of stem cells did not show distinct seasonal changes. For detailed descriptions of the typhlosole, Tanaka et al. (1981) and Fujii (1982) may be referred to.

During metamorphosis, especially after stage 3, the muscle layer of the intestine became disintegrated, the intestinal epithelium was folded, and hematopoietic activity in the typhlosole drastically decreased (Fig. 19). The diameter of the intestine also decreased. The epithelial infolding was still prominent in immature adults caught in November (Fig. 20), but was inconspicuous in adults caught in later seasons (Fig. 21).

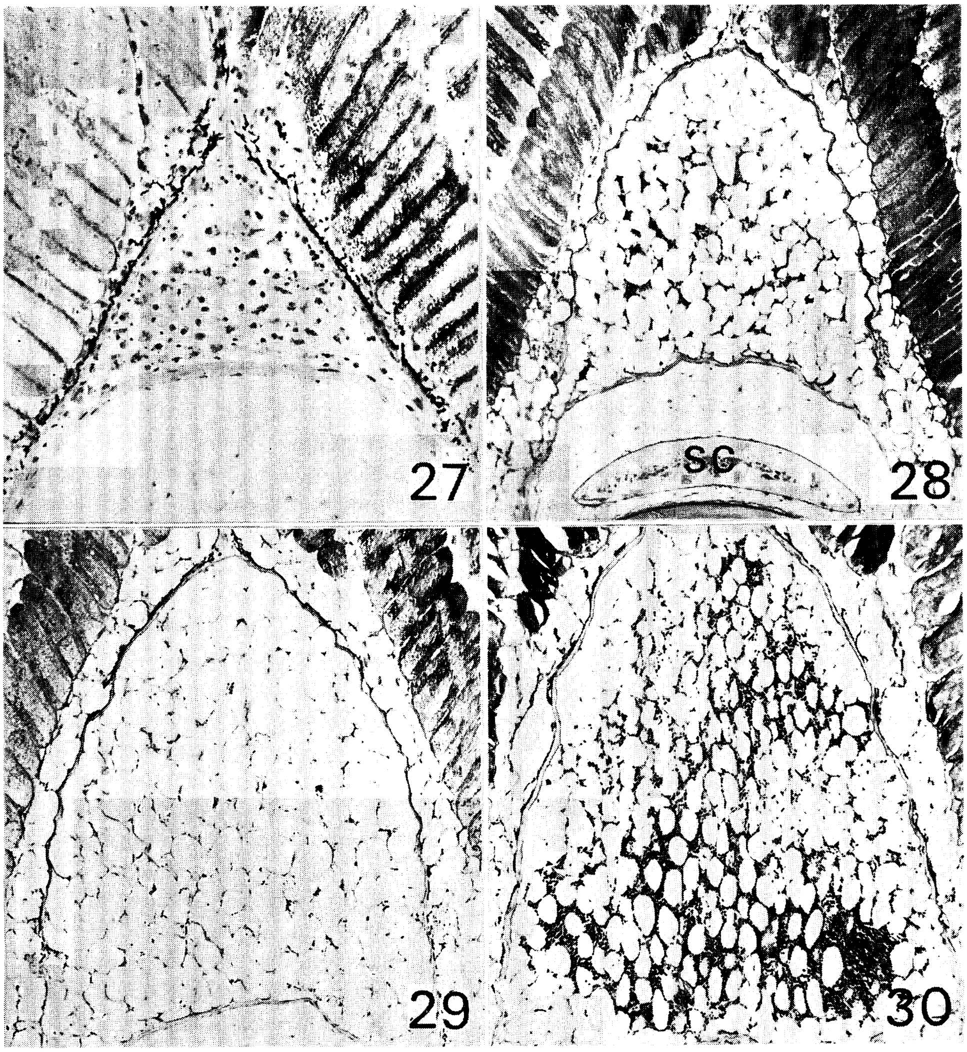


Fig. 27. Fat column of 60 mm-long ammocoetes caught in February. Note "foamy cells" in it. Two sides of the fat column triangle are surrounded by parietal muscles. ×140.

Fig. 28. Fat column of 82 mm-long ammocoetes caught in May. Slight hematopoietic activity is seen among adipose tissue. sc, spinal cord. ×70.

Fig. 29. Fat column of 95 mm-long ammocoetes caught in June. Note the absence of hematopoietic activity. ×70.

Fig. 30. Fat column of immature adult caught in November. Hematopoietic activity is prominent among adipose tissue. ×70.

Although the gut contents of winter ammocoetes mainly consisted of detritus, those of spring and summer ammocoetes contained many diatoms such as *Navicula*, *Gomphonema*, *Cymbella*, and *Cocconeis* (Fig. 22).

Liver. The liver of ammocoetes was a tubular gland (Fig. 23). Smaller bile ducts gradually drained into larger bile ducts and finally into the hepatic duct. The change from tubular gland to the structure typical of adult vertebrates occurred between stages 2 and 3. The hepatic cells of individuals older than stage 4 contained brown granules. Such granules were especially abundant in livers of some male animals. These granules might be related to degradation of bile. Melanophores were occasionally found in some adult livers, but not in others (Fig. 24). The relative length of the liver (liver length × 100/TL) was significantly longer in females (8.0 ± 0.4, $n=9$) than males (4.4 ± 0.4, $n=5$) ($P<0.01$).

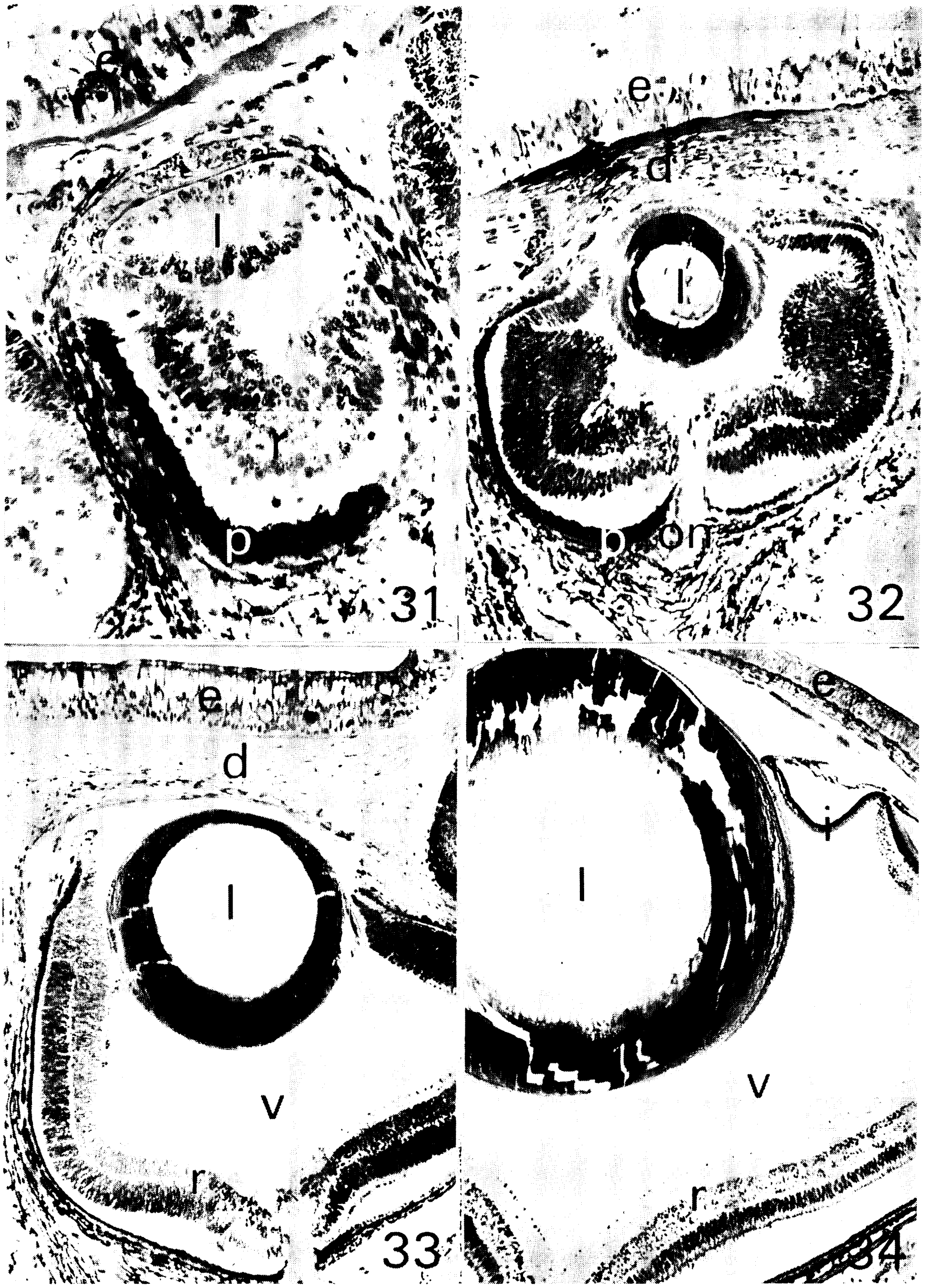
Kidney. The kidney was a bilateral structure. It was located lateral to the gonad, and each renal lobe flanked the intestine. In each renal lobe, the dorsal part was occupied by adipose tissue, and the ventral part by urinary tubules. The ureter (mesonephric duct or opisthonephric duct) occupied the ventral tip of the lobe, and the glomerulus occupied the ventro-medial aspect (Fig. 25). The adipose tissue became larger as the ammocoetes grew. The intertubular space was occupied by hematopoietic tissue in ammocoetes. The density of hematopoietic stem cells was variable, apparently without relation to the season or the size of ammocoetes. As an exception, some small ammocoetes caught in January contained only a few stem cells in the kidney.

Degeneration of the larval kidney at the midtrunk region started about stage 2 or 3 of metamorphosis, although incipient degeneration was noticed even in some large ammocoetes. In stage 4 and 5 individuals, degenerative processes were evident (Fig. 26). The number of tubules decreased, the tubular epithelium became flat, brown granules appeared in the cytoplasm of tubule cells, some tubules were surrounded by a prominent thick basement membrane, and urine cast was found in the tubule lumen. The glomeruli also degenerated, showing abnormally dilated Bowman's capsules. Although the larval kidney degenerated, intertubular space was occupied by hematopoietic stem cells even in adults caught in February.

Fat column. In some ammocoetes smaller than 60 mm in TL, the fat column consisted of "foamy cells" enmeshed in a fibrous network (Fig. 27). These cells were characterized by a round nucleus and abundant cytoplasm of densely flocculent appearance. They might be immature adipose cells. In the other small ammocoetes and larger ammocoetes, the fat column consisted mainly of adipose tissue (Figs. 28, 29). Hematopoietic stem cells were rare, but were found in small numbers in some ammocoetes caught in late spring and summer (Fig. 28). After stage 3 of metamorphosis, abundant stem cells were observed in the fat column (Fig. 30).

Eye. Although the eye was not visible externally, it was formed subcutaneously in all ammocoetes studied. In the 36 mm-long ammocoetes, the pigment layer of the retina (stratum pigmenti retinae) was already distinct on the dorsal side (Fig. 31). A thin epithelium directly covered the outer surface of the lens. The lens lumen was indistinct. The vitreous body was very small. From 45 mm- to 64 mm-long ammocoetes, no fundamental changes occurred, although photoreceptor processes (rods and cones) became distinct. In 70 mm-long ammocoetes, stratification of the retina into inner and outer granular layers proceeded further. In 82 mm-long ammocoetes, the vitreous body became larger. In 98 mm-long ammocoetes, the epithelium covering the lens (corneal endothelium) became very flat. In 119 mm-long ammocoetes, the outer (distal) zone of the lens was occupied by cells arranged in a monolayer. At this stage, crystalline structure was first observed in the lens (Fig. 32). The retina could be subdivided topographically into three regions: perilenticular, intermediate and central regions. The photoreceptive processes were found only in the central region close to the optic nerve. The inner plexiform layer was prominent in the central region. However, the boundary of these three regions was not distinct. The clearly tripartite retina shown in Fig. 32 may be partly due to artifact. In 125 mm-long ammocoetes, the anterior chamber space was evident. In 146 mm-long ammocoetes, the inner plexiform layer was prominent also in the intermediate region of the retina. In 138, 146 and 152 mm-long ammocoetes, photoreceptive processes were seen in the intermediate region in addition to the central region, although they were poorly differentiated in the former. In 179 mm-long ammocoetes, the corneal endothelium became indistinct (Fig. 33).

At stage 2 of metamorphosis, the pigments were distributed all over the entire pigment layer of the retina, although the amount was much smaller in the ventral side of the eyeball. In the retina proper, the inner plexiform layer was well developed. The anterior chamber became larger. At stage 3, the dermis (corneal stroma) was thinner and looser (about 40 μm as compared with about 60 μm at stage 2 and about 100 μm in large ammocoetes). The epidermis (corneal



Figs. 31–34. Eyes. Left side is dorsal. The space between retina proper (r) and pigment layer of retina (p) is artifact. Note a gradual decrease of magnification from Fig. 31 to 34. e, epidermis; d, dermis; i, iris; l, lens; on, optic nerve; v, vitreous body.

Fig. 31. 36 mm-long ammocoetes caught in August. ×370.

Fig. 32. 119 mm-long ammocoetes caught in January. ×140.

Fig. 33. 179 mm-long ammocoetes caught in May. ×95.

Fig. 34. Immature adult caught in November. ×70.

epithelium) also became gradually thinner (about 50 μm as compared with about 75 μm at stage 2 and about 100 μm in large ammocoetes). In metamorphosing individuals, photoreceptive processes were developed all around the retina, but those located peripherally (perilentic region) were short. In adults, the thickness of the corneal epithelium was about 50 μm, and that of the corneal stroma was about 20 μm. The corneal stroma was dense again in adults. In adults, the corneal epithelium contained very few specialized epidermal cells such as thread cells and granular cells (Fig. 34), which were abundant in the epidermis of the other regions.

Discussion

The observation that in all ammocoetes the gonad is first an ovary-like structure is in accordance with the situation in the European brook lamprey, *Lampetra planeri* (Hardisty, 1965, 1971, 1979). The testis appeared to originate from undifferentiated germ cells surviving among a large number of growing oocytes (large cells in meiotic prophase) which ultimately degenerate. This is also a finding made in *L. planeri* (Hardisty, 1979). In *L. reissneri*, female ammocoetes larger than 120 mm in TL possessed a definite ovary, but male ammocoetes of comparable sizes possessed a very small testis. The observation that the ovary differentiates earlier than the testis was also made in the parasitic *L. japonica* (Fukayama and Takahashi, 1982). The development both of the testis and the ovary was very rapid during metamorphosis. This is easily understood, because the brook lamprey spawns only a few months after the completion of metamorphosis.

The histological organization of the ammocoetes intestine is unique among vertebrates. It lacks a distinct lamina propria mucosae. Moreover, the inner muscular layer is composed of longitudinal fibers, and the outer layer of circular fibers. The orientation of muscle fibers is just the opposite to the situation in the muscular layer of other vertebrate intestines. However, it may be possible to assign the inner longitudinal muscles to lamina muscularis mucosae. In any case, the intestinal wall does not possess only lamina propria mucosae, but also tela submucosa. Nutrients absorbed might be delivered to capillaries located among muscle fibers. The degeneration of the intestine in metamorphosing and adult animals is obviously related to the cessation of feeding.

In *L. reissneri*, the adult liver of males and females was different both in size and in the amount of brown granules present. Since the liver is generally considered to be a site of vitellogenesis in lower vertebrates, and estrogen stimulation on liver vitellogenesis has been demonstrated in *L. fluviatilis* (Pickering, 1976), the larger liver in female lampreys may be related to active vitellogenesis. Sexual difference of the liver was noted also in spawning sea lamprey (Kott, 1970).

The main hematopoietic organs of the lamprey are typhlosole, kidney, and fat column. In ammocoetes of *L. reissneri*, the main hematopoietic sites were the typhlosole and the intertubular tissue of the kidney. In metamorphosing and adult animals, the fat column was the main site. The typhlosolar contribution was very small in metamorphosing animals, and negligible in adults, as judged from density of stem cells. These schemes are concordant with the observations made in *P. marinus* (George and Beamish, 1974), and *L. planeri* and *L. fluviatilis* (Percy and Potter, 1977). In *L. reissneri*, however, the larval fat column was not always necessarily nonhematopoietic. In some ammocoetes caught in late spring and summer, a weak hematopoietic activity was apparent in the fat column. Another discrepancy is a renal contribution to hematopoiesis in adults. In *L. planeri*, the kidney does not contribute to adult hematopoiesis (Percy and Potter, 1977). In *L. reissneri*, however, a renal contribution as judged from density of stem cells was apparent, at least in those adults caught in December and February.

The observation that retinal differentiation started around the optic nerve was also made in *P. marinus* (Dickson and Graves, 1981). The retina was rather well differentiated in large ammocoetes in which the eye was not yet externally visible. However, the biological significance of the larval eye may be negligible, since the ammocoetes is totally a burrowing animal. Hardisty (1979) considered that the larval stage is a secondary introduction to the lamprey life cycle. If so, the eye once formed might be somehow arrested in its further development until the onset of metamorphosis.

Acknowledgments

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スナヤツメの成長に伴う内部諸器官の組織学的変化

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スナヤツメの成長過程において，生殖腺，口腔，鰓，食道，唾液腺，腸，肝，腎，脂肪柱（原始骨髄），および眼にみられる組織学的変化を調べた．全長 7～9 cm の個体の生殖腺は，一様に若い卵母細胞で占められていた．その後，雌では卵母細胞がそのまま成長を続けたが，雄では卵母細胞が退化し，少数の残存未分化生殖細胞から精巣が分化した．性は全長 12 cm 以上の個体では，容易に決定できた．歯の分化は，変態の第 5 期で始まった．成体型の食道と唾液腺も第 5 期で形成された．一方，成体型の肝は第 3 期で形成された．腸と腎は変態期の間に退化した．幼生の造血巣は，腸管内縦隆起（原始脾臓）と腎の細尿管の間隙にみられたが，成体の造血巣は脂肪柱であった．幼生の眼は外部からでは見えないが，網膜はすでに分化していた．

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