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COMPARATIVE STUDISE OF THE SPLEEN IN SUBMAMMALIAN VERTEBRATES*

I. TOPOGRAPHICAL ANATOMY AND RELATIVE WEIGHT OF THE SPLEEN

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In a previous phylogenetical survey of the hemocytopoietic tissues in submammalian vertebrates, it has been demonstrated that true lymphoid tissue comes into appearance for the first time in the spleen as early as at the evolutional level of elasmobranchs, and that spleen is an important seat of lymphocytopoiesis throughout the vertebrate series, with the exception of cyclostomes (*Osogoe*, 1953 and *Kanesada*, 1956). This is in sharp contrast to the opinion of *Jordan* (1938) and others, who claim that in lower vertebrates the spleen is the chief site of production of erythrocytes and thrombocytes. It is true that in urodeles the spleen does participate in erythropoiesis. In other animals, however, it scarcely shows such activity.

In order to enlarge and refine our knowledge concerning the role of the spleen in hemocytopoiesis in lower vertebrates, the author has made an extensive comparative survey of this organ in submammalian vertebrates, in which special attention was directed to the fundamental structural elements of the spleen, the so-called "periarterial lymphoid sheath" in particular. This report, the first of a series of observations made along this line, will deal with the shape, position and relative weight of the spleen.

MATERIAL AND METHODS

In the present study twenty species representing the following different classes and orders or suborders of the vertebrates were examined. The majority of the animals were collected for study during the period from April to August. Every species obtained is indigenous to Japan.

I. Cyclostomata

1. *Entosphenus japonicus*
2. *Lempetra planeri*

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* A preliminary report covering certain phases of this series of studies was read by *Osogoe* at the autum meeting of the Japan Hematological Society in Tokyo, October 1953 (Symposium on Hematology, **7**: 1-35, 1954).

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3. *Ammocetes branchialis* (the larval stage of Lampetra)

II. Pisces
   A. Elasmobranchii (cartilaginous fishes)
      1. *Mustelus manazo* (a kind of shark)
      2. *Dasybatus akajei* (sting ray)
   B. Teleostei
      1. *Carassius auratus* (crusian carp)
      2. *Lateolabrax japonicus* (perch)
      3. *Mugil cephalus* (gray mullet)
      4. *Parasilurus asotus* (catfish)
      5. *Odontobutis obscurus*

III. Amphibia
   A. Urodela
      1. *Megalobatrachus japonicus* (giant salamander)
      2. *Triturus pyrrhogaster* (newt)
   B. Anura
      1. *Bufo vulgaris japonicus* (toad)
      2. *Rana nigromaculata* (frog)
      3. *Rana catesbiana* (bullfrog)

IV. Reptilia
   A. Chelonia
      1. *Clemmys japonica* (tortoise)
      2. *Geoclemys reevesii* (tortoise)
   B. Lacertilia
      Eumeces lasticutatus (lizard)
   C. Ophidia
      Elaphe quadrivirgata (snake)

V. Aves
   A. Galliformes
      Gallus domesticus (domestic fowl)
   B. Passeriformes
      Passer montanus saturatus (sparrow)

The spleen was weighed immediately after it had been removed.

OBSERVATIONS AND DISCUSSION

Comparative anatomy

The shape and position of the spleen in submammalian vertebrates are subject to considerable variations even within the same orders or suborders. The findings on individual species examined, from Pisces to Reptilia, are summarized in Table 1.

Table 1. Shape and position of the spleen in fishes, amphibians and reptiles.

Class	Order or suborder	Species	Shape and position of the spleen
Pisces	Elasmobranchii	*Mustelus manazo*	Elongated and multi-lobulated; extending from the caudal part of the stomach to the cranial part of the midgut
	//	*Dasybatus akajei*	Bean-shaped; lying in relation to the caudal part of the stomach
	Teleostei	*Carassius auratus*	Elongated and multi-lobulated; extending from the caudal part of the stomach to the middle of the midgut
	//	*Mugil cephalus*	Spherical; lying at the transition of the stomach into the midgut
	//	*Farasilurus asotus*	Discoidal; lying in relation to the caudal part of the midgut
	//	*Odontobutis obscurus*	Bean-shaped; lying in relation to the caudal part of the midgut
Amphibia	Urodela	*Triturus pyrrhogaster*	Tongue-shaped; lying in relation to the caudal part of the stomach
	//	*Megalobatrachus japonicus*	Tongue-shaped; lying in relation to the caudal part of the stomach
	Anura	*Eufo vulgaris japonicus*	Spherical; lying in relation to the caudal part of the midgut
	//	*Rana nigromaculata*	Bean-shaped; lying in relation to the middle part of the midgut
	//	*Rana catesbiana*	Bean-shaped; lying in relating to the caudal part of midgut
Reptilia	Chelonia	*Clemmys japonica*	Spherical; lying at the transition of the midgut into the hindgut
	Lacertilia	*Eumeces latiscutatus*	Spherical; lying in relation to the cranial part of the midgut
	Ophidia	*Elaphe quadrivirgata*	Spherical; lying at the transition of the stomach to the midgut

In cyclostomes, the mesenchymal tissue of the spiral fold of the intestine may be regarded as being an ancestral form of the splenic tissue. In the ammocetes (larval) stage of Lampetra, the spiral fold of the intestine is almost completely filled with hemopoietic tissue, which represents the chief site of blood-formation. In the adult stage, however, the spiral fold become shrunk to a large extent, or is substituted entirely by adipose tissue, as described previously (*Kanesada*, 1956). *Entosphenus* also lacks splenic tissue in its adult stage.

As described in a preceding paper by *Kanesada* (1956), the hemopoietic tissue in the spiral fold of the larval lamprey is composed of agranular and granular cells densely packed in the meshes of the reticular stroma. A longitudinal artery runs through the axis of this tissue. This artery gives off numerous radial capillaries which connect with capilliform venous sinusoids. These sinusoids are enveloped by blood-forming tissue. Thus, the fundamental structure of the spiral fold closely resembles that of mammalian spleen. For this reason, it is considered that spiral fold of the larval lamprey constitutes an initial step in the evolution of spleen.

At the higher evolutional levels, beging with Pisces, the spleen is present within the dorsal mesentery in the form of an independent, circumscribed organ outside of the intestinal tract. Among elasmobranchs, *Mustelus manazo* has a long, multilobulated spleen, extending from the caudal part of the stomach to the cranial part of the midgut. In contrast, the spleen of *Dasybatus akajei* is bean-shaped and lies in relation to the caudal part of the stomach. It is important to emphasize here that the spleen of elasmobranchs, irrespective of its shape and position, is very well developed, particularly with respect to lymphoid tissue, and its fundamental structure closely resembles that of the mammalian spleen, as will be mentioned later.

A very long spleen extending from the caudal part of the stomach to the middle of the midgut was seen in *Carassius auratus*, while in other teleost fishes examined the spleen was found to be either spherical, discoidal, or bean-shaped and located within the dorsal mesentery in relation to the caudal part of the midgut.

In amphibians, a sharp contrast is to be seen between the urodeles and anurans with respect to the shape and position of the spleen. Namely, in the urodeles the spleen is tongue-shaped and located cranially near the stomach; whereas in the anurans this organ is spherical or bean-shaped and lies caudally in relation to the caudal part of the midgut.

Among reptiles, a similar difference in the topography of the spleen was also seen between the tortoise and snake. Namely, the spleen of the tortoise (*Clemmys japonica*) lies in relation to the caudal part of the midgut, whilst the spleen of the snake (*Elaphe quadrivirgata*) is situated cranially near the stomach. In the lizard (*Eumeces latiscutatus*) the position of the spleen resembles that of the snake, though situated somewhat more caudally.

In the next higher evolutional levels, from Aves to Mammalia, the spleen lies in the dorsal mesogastrium as a tongue-shaped or bean-shaped organ and there is little variation in the position of this organ.

The above-mentioned variations in the topography of spleen among different groups of the vertebrates are generally in accord with the observations of *Klaatsch* (1891–92).* This author found the ancestral form of the amphibian spleen in sirens (*Sirens lacertina*), which have a very long spleen extending along the entire length of the gut, and assumed that the entire dorsal mesentery has the phylogenetical capacity of forming splenic tissue. On the basis of this assumption, the cranial position of the urodelan spleen lying near the stomach may be explained by reduction of the developmental potency at the caudal portion of the mesen-

* Cited from *Klemperer* (1938).

tery. Similarly the caudal position of the anuran spleen, which lies at the transition of the small intestine into the hindgut, may be interpreted as being due to an arrest of development at the cranial portion of the mesentery. The same explanation is also applicable to the reptiles, among which a distinct difference in the position of the spleen is seen between the tortoise and snake. Of particular interest in this connection is the observation of *Klaatsch* that, among reptiles, the ancestral forms of the Rhynchocephalia has a long spleen extending from the stomach to the hindgut. The existence of a long spleen in a cartilaginous fish, *Alopias vulpes* has been reported by *Hemmeter* (1926) and is confirmed in *Mustelus manazo* in the present study. This may be regarded as being the ancestral form for the fishes.

As outlined above, it seems justified to assume that, from the phylogenetical viewpoint, the entire dorsal mesentery retains a developmental potentiality of forming splenic tissue, and this accounts for variations in the topography of the spleen in different classes and orders or suborders of the vertebrates.

In some teleost fishes, e.g., *Crassius auratus*, pancreatic tissue fragments are constantly present, incorporated witin the spleen. In his comprehensive review on the spleen, a similar finding is emphasized by *Klemperer* (1938), who maintains a close phylogenetical relationship between the spleen and pancreas.

Relative weight of the spleen

The relative weight of the spleen is quite variable among the different species of vertebrates. The results of examinations on various vertebrate animals with respect to the ratio of splenic weight to body weight are summarized in Table 2. According to *Gray* (1854), this ratio is greatest in mammals, averaging 1:277 = 0.361%, and decreases in the following order: reptiles (snake), 1:1150 = 0.087%; amphibians, 1:1476 = 0.068%; fishes, 1:2121 = 0.047%; and brids, 1:2838 = 0.035%. Our figures are generally higher that those of *Gray*. It was found that the relative splenic weight was as high as $2.966 \pm 0.1855\%$ in *Mustellus manazo* but much lower in other submammalian vertebrates, varying within a wide range between 0.049% and 0.495%. Relatively higher values (greater than 0.100%) were obtained for *Mugil cephalus* (teleost fish), *Megalobatrachus japonicus* (giant salamander), *Triturus pyrrhogaster* (newt), *Geoclemys reevesii* (tortoise), *Gallus domesticus* (domestic fowl) and *Passer montanus saturatus* (sparrow). In contrast, the corresponding figures were much lower (less than 0.100%) in *Latelobrax japonicus* (perch), *Rana nigromaculata* (frog), *Rana catesbiana* (bullforg), and *Elaphe quadrivirgata* (snake). In this connection, it is of interest to note that the relative weight of the rabbit spleen (average 0.0537%) approaches the low extreme and the corresponding figure for the human spleen (average 0.29% or 0.31%) lies near

* Cited from *Klemperer* (1938).

Table 2. Relative weight of the spleen (expressed as percentage of body weight) in various vertebrate animals.

Class	Order or suborder	Species	No. of animals	Spleen : body weight ratio (%)		
				Minimum	Maximum	Mean ± S. E.
Pisces	Elasmobranchii	*Mustelus manazo*	9	2.647	4.000	2.966±0.1855
	Teleostei	*Lateolabrax japcnicus*	8	0.050	0.135	0.089±0.0094
	〃	*Mugil cephalus*	15	0.117	0.344	0.214±0.0161
Amphibia	Urodela	*Megalobatrachus japonicus*	6	0.116	0.277	0.173±0.0254
	〃	*Triturus pyrrhogaster*	15	0.161	0.833	0.495±0.0561
	Anura	*Rana nigromaculata*	34	0.020	0.133	0.071±0.0045
	〃	*Rana catesbiana*	11	0.020	0.146	0.047±0.0113
Reptilia	Chlonia	*Geoclemys reevesii*	7	0.095	0.216	0.139±0.0116
	Ophidia	*Elaphe quadrivirgata*	5	0.023	0.106	0.049±0.0149
Aves	Galliformes	*Gallus domesticus*	5	0.083	0.150	0.120±0.0118
	Passeriformes	*Passer montanus saturatus*	10	0.051	0·481	0.155±0.0509
Mammalia	Rodentia	*Oryctolagus cuniculus* var. *domesticus** ♂	35	—	—	0.0537±0.0027
		♀	30	—	—	0.0935±0.0063
	Primates	*Homo sapiens*** (Japanese) ♂	676	—	—	0.29
		♀	356	—	—	0.31

* Cited from *Latimer* and *Sawan* (1957).
** Calculafed from the data of *Harada* (1956).

the high extreme noted above.

The relatively high splenic weight in some species of Pisces, Urodela and Aves deserves special attention, since it seems to be in close relation to the degree of development of the lymphoid tissue and other structural elements.

SUMMARY

A comparative survey was made of the spleen of submammalian vertebrates, from Cyclostomata to Aves, with respect to the topographical anatomy and relative weight of the organ. There are considerable variations in the topography of the spleen in various submammalian vertebrates. However, an elongated spleen extending the entire length of the gut is regarded as the ancestral form, and the variations in the shape and position of this organ among different groups are explained on the basis of an assumption that the entire dorsal mesentery retains phylogenetically a developmental potentiality of forming splenic tissue, but an arrest of development either at the caudal or at the cranial portion of the mesentery usually takes place.

The relative weight of the spleen, expressed as percentage of body weight, is

also quite variable. An exceedingly high value was obtained for the spleen of *Mustelus manazo* (a kind of shark) as great as $2.966 \pm 0.1855\%$, but the corresponding values were much lower in other submammalian vertebrates, varying within a wide range between 0.049% and 0.495%. The presence of a relatively heavy spleen was noticed in some species of Pisces, Urodela and Aves.

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