The occurrence of cartilage canals in shark vertebrae

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Cartilage canals were found in the vertebrae of 16 species of sharks from five families. The canals variously contain blood vessels, lymph-like material, clumps of immature chondrocytes, unidentified amorphous material, or appear empty. Of 10 species examined in the family Carcharhinidae, only the dogfish, *Mustelus canis*, was devoid of canals. No canals were seen in the two batoid fish examined. The presence of canals may depend on the phylogenetic position or the maximum size attained by the species.

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Des canaux ont été trouvés dans les vertèbres cartilagineuses de 16 espèces de requins appartenant à cinq familles différentes. Certains de ces canaux étaient vides tandis que d'autres contenaient des vaisseaux sanguins, des substances ressemblant à des produits lymphatiques, des amas de chondrocytes immatures ou des substances amorphes non identifiées. Parmi les 10 espèces examinées dans la famille Carcharhinidae, *Mustelus canis* était le seul à ne pas présenter de canaux. Les deux espèces de raies examinées en étaient également dépourvues. Il est possible que la présence de canaux vertébraux chez une espèce dépende de la position phylogénique de cette espèce ou de la taille maximum qu'elle puisse atteindre.

Introduction

The endoskeleton of sharks is composed of cartilage (Moss 1977). While studying vertebral rings in sharks for an age and growth study, the first author noticed prominent canals throughout the intermedialia of the vertebral centra from a variety of species. Cartilage is generally thought of as avascular tissue, but vascularized canals passing through cartilage have been reported from a variety of mammals (Levene 1964) and chickens (Lutfi 1970). The function, degree of vascularization, and persistence of the canals are variable (Lutfi 1970).

In elasmobranchs, however, the presence of blood vessels or canals in the vertebrae has been largely overlooked. Ridewood (1921) reported that the actively dividing cartilage at the periphery of the intermedialia of unspecified carcharhinid sharks sometimes contains blood vessels that penetrate from the superficial connective tissue. Ridewood also reported "radial, rod-shaped tracts of uncalcified cartilage in the intermedialia with blood-vesels penetrating into them" in *Sphyrna* spp., and blood vessels in calcified tubes that penetrate the vertebrae from the periphery in *Cetorhinus maximus* and *Squatina* spp. (Ridewood 1921). These accounts, and a figure by Hasse (1882) of a *Hypoprion* sp. vertebra, are the only reports of blood vessels in elasmobranch vertebrae. This study was undertaken to determine the phylogenetic occurrence of cartilage canals and to examine their structure.

Materials and methods

Vertebral sections prepared for a growth study were examined for the presence of canals (Table 1). The vertebrae were decalcified, embedded, cut longitudinally through the center of the lateral intermedialia in 100-μm sections, and stained with hematoxylin. Whole dried vertebrae from seven species were also examined (Table 1). Both caudal and precaudal vertebrae were examined from two species.

The histology of the canals was studied in seven species (Table 1). Trunk vertebrae were cut in 6-μm sections and stained with hematoxylin–eosin.

Results

All of the shark species examined except the smooth dogfish (*Mustelus canis*) have canals in the intermedialia of the centra. No canals were found in the two batoid fish examined (the little skate, *Raja erinacea*, and the pelagic ray, *Dasyatis violacea*). Macroscopic inspection of the dried precaudal centra from seven species of shark revealed the presence of canals (Fig. 1).

The canals in the carcharhinid and sphyrnid species are branching structures found throughout the intermedialia (outside the notochordal sheath). They are especially numerous near the anterior and posterior faces of the centra (Fig. 2). In the shortfin mako (*Isurus oxyrinchus*) they penetrate the calcified lamellae (rays) of the intermedialia from the superficial connective tissue surrounding the vertebral column.

Canals were found in vertebrae from fully mature specimens with large vertebrae. They were also consis-

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TABLE 1. Elasmobranch species examined for cartilage canals

Species with canals	Species without canals
Odontaspidae	Carcharhinidae
Odontaspis taurus (B)	*Mustelus canis* (A)
Lamnidae	Dasyatidae
Cetorhinus maximus (B, C)	*Dasyatus violacea* (A)
Lamna nasus (B)	
Isurus oxyrinchus (A, B, C)	Rajidae
*Carcharodon carcharias** (B)	*Raja erinacea* (A)
Sphyrnidae	
Sphyrna lewini (A)	
S. zygaena (B)	
Carcharhinidae	
Negaprion brevirostris (A, C)	
Prionace glauca (A)	
*Galeocerdo cuvieri** (A, B)	
Carcharhinus isodon (A)	
C. plumbeus (A, C)	
C. obscurus (A)	
C. leucas (A, C)	
C. falciformis (A, C)	
C. limbatus (A, C)	

NOTE: A, 100-μm slide prepared for growth study; B, whole vertebra examined macroscopically; C, 6-μm slide prepared for histological study.
*Both precaudal and caudal vertebrae were examined and found to have canals.

tently found in a series of vertebrae from young-of-the-year *Carcharhinus obscurus* and *C. plumbeus* specimens with vertebrae measuring 7 to 9 mm in diameter. The canals extended to within 1 mm of the central axis. In the *M. canis* specimens, no canals could be found in specimens with vertebrae as large as 12 to 13 mm in diameter.

The canals are histologically similar in all the species. Their maximum diameter ranged from 120 to 200 μm except in the shortfin mako (*I. oxyrinchus*) where canals with diameters up to 350 μm were found. All of the species had red blood cells or endothelial linings in some of the canals except the bull shark, *Carcharhinus leucas*. The lack of apparent vascularization in the bull shark specimen is attributed to poor preservation.

Connective tissue or amorphous material surrounded a central lumen in some canals of all species except the bull shark, *C. leucas*. Immature chondrocytes were evident in the zone immediately adjacent to the canal lumen in all species except the basking shark, *Cetorhinus maximus* (Fig. 3). There was also evidence that previously patent canals had been filled by immature chondrocytes which were confluent with the surrounding mature cartilage. Lymph or lymph-like material was found in the sandbar shark, *C. plumbeus*, and the small blacktip shark, *Carcharhinus limbatus*.

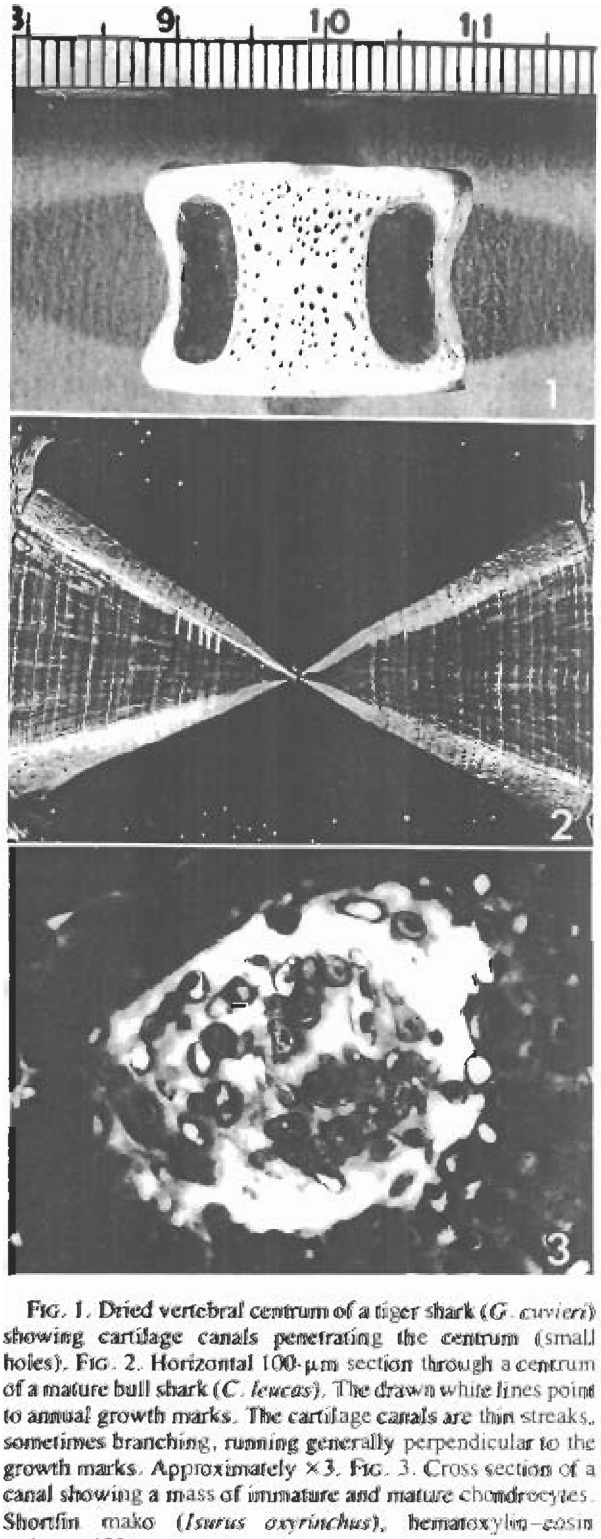

FIG. 1. Dried vertebral centrum of a tiger shark (*G. cuvieri*) showing cartilage canals penetrating the centrum (small holes). FIG. 2. Horizontal 100-μm section through a centrum of a mature bull shark (*C. leucas*). The drawn white lines point to annual growth marks. The cartilage canals are thin streaks, sometimes branching, running generally perpendicular to the growth marks. Approximately ×3. FIG. 3. Cross section of a canal showing a mass of immature and mature chondrocytes. Shortfin mako (*Isurus oxyrinchus*), hematoxylin–eosin stain. × 400.

Discussion

These findings indicate that cartilage canals are present in the vertebrae of a variety of sharks in the families Carcharhinidae, Sphyrnidae, Lamnidae, and Odontaspidae. According to Applegate's (1967) classification, these families represent two of the eight basic shark vertebral morphotypes. These two morphotypes correspond to the two major lines of evolution within the Galeoidea. Ridewood (1921) reported canals in a third morphotype (*Squatina*) but the remaining five types have not been investigated. No canals were found in the centra of the smooth dogfish, *M. canis*, the skate, *R. erinacea*, or the ray, *D. violacea*.

The function of cartilage canals is not clearly understood. In birds and mammals they appear to serve osteogenic and nutritive roles and may provide stem cells for interstitial cartilage growth (see Lutfi 1970). The osteogenic function cannot apply to elasmobranch vertebrae but the nutritive role is probable. The absence of canals in the three smallest species examined (*M. canis*, *R. erinacea*, and *D. violacea*) may be due to the adequacy of diffusion in providing nutrition and removing cellular wastes. However, canals were found in young *C. obscurus* and *C. plumbeus* specimens whose vertebrae were smaller than the largest *M. canis* vertebrae. Alternatively, the presence of canals may depend on the phylogenetic position of a species. Examination of more species will be necessary to resolve this question.

The canals may also serve as part of the mechanism that regulates the levels of calcium in the serum and tissues. Simkiss (1974) suggested that there is a relatively simple equilibrium between the calcium in the vertebrae and the serum. Thus, calcium is added to or removed from the vertebrae, as needed, to help regulate the serum calcium levels. If this is true, then the cartilage canals would provide an effective mechanism for the rapid exchange and transport of calcium between the vertebrae and the serum. Moss (1977), however, has speculated that sharks do not normally utilize their skeletal tissues for calcium regulation.

In higher animals, cartilage canals may persist in adulthood, as in human costal cartilage (Weber 1827, cited in Levene 1964), or they may degenerate and be filled in, as in chicken tibia bones (Lutfi 1970). Two methods of canal occlusion have been described (Watermann 1961; Kajawa 1919). In transient cartilages, occlusion generally occurs by compression by the surrounding tissues. In permanent cartilages, the canals are usually filled by chondrogenesis within the canals.

The shark cartilage canals are persistent structures since they are found throughout the intermedialia in vertebrae from mature individuals. However, the presence of immature cartilage surrounding and even filling some canals suggests destruction by chondrogenesis. No evidence of destruction by compression was noted.

Some minor differences in the histology of the canals in the different species were found. In all species at least some contain blood or blood vessels. In *C. plumbeus* and *C. limbatus* they may also transport lymph. Many of the canals in each species appeared devoid of blood cells, endothelial tissue, and lymph. Unfortunately, the specimens were obtained opportunistically from many sources and were preserved in various ways. Thus, some of the minor differences between species may be due to poor preservation or to interspecific or age-dependent variations in function and morphology.

Vascularized cartilage canals are common in the calcified vertebrae of many large sharks. Further studies on the phylogenetic occurrence and histology of these canals will be required to fully understand their role in cartilage physiology and calcium regulation.

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